Ecological Applications, 17(3), 2007, pp. 815–827

RELEVANCE OF RANGELAND DEGRADATION IN SEMIARID NORTHEASTERN SOUTH AFRICA TO THE NONEQUILIBRIUM THEORY

Konrad J. Wessels,[1,2,4] Stephen D. Prince,[1] Mark Carroll,[1] and Johan Malherbe[3]

[1]*Department of Geography, University of Maryland, 2181 LeFrak Hall, College Park, Maryland 20742 USA*
[2]*Remote Sensing Research Unit, Meraka Institute, CSIR, P.O. Box 395, Pretoria, 0001 South Africa*
[3]*Agricultural Research Council, Institute for Soil, Climate and Water, Pretoria, South Africa*

Abstract. According to the nonequilibrium theory, livestock grazing has a limited effect on long-term vegetation productivity of semiarid rangelands, which is largely determined by rainfall. The communal lands in northeastern South Africa contain extensive degraded areas which have been mapped by the National Land Cover (NLC) program. Much evidence suggests that long-term heavy grazing is the cause of this degradation. In order to test for the prevalence of nonequilibrium dynamics, we determined the relative effects of rainfall- and grazing-induced degradation on vegetation productivity. The vegetation production in the NLC degraded areas was estimated using growth-season sums of the Normalized Difference Vegetation Index (ΣNDVI), calculated using data from both the Advanced Very High Resolution Radiometer (AVHRR) (1985–2003) and Moderate-resolution Imaging Spectroradiometer (MODIS) (2000–2005). On average, rainfall and degradation accounted for 38% and 20% of the AVHRR ΣNDVI variance and 50% and 33% of the MODIS ΣNDVI variance, respectively. Thus, degradation had a significant influence on long-term vegetation productivity, and therefore the rangelands did not behave according to the nonequilibrium model, in which grazing is predicted to have a negligible long-term impact.

Key words: AVHRR; communal land; grazing; land degradation; MODIS; NDVI; nonequilibrium; rainfall; rangeland; South Africa.

Introduction

Before the 1970s, rangeland ecology was largely based on the equilibrium theory in which ecosystems are thought to be regulated internally through negative feedback mechanisms, such as density dependent plant–animal interactions, which lead to stability (Briske et al. 2003). Vegetation was accordingly believed to respond to disturbances in a predictable and directional manner, always inclined toward a single, predisturbance climax state (Westoby et al. 1989). As such, the vegetation community and range condition of a site at a particular time was viewed as a point along a linear trajectory of successional stages, from a heavily grazed, highly disturbed pioneer community in poor condition to a lightly grazed, undisturbed climax community. The equilibrium theory emphasized the role of grazing and rangeland management in determining community composition and also suggested that overgrazing could lead to rangelands becoming degraded. Degradation is defined here as a permanent, irreversible decline in the rate at which vegetation produces forage for a given input of rainfall (Abel and Behnke 1996). More recently, aspects of equilibrium theory have been questioned, particularly because the theory fails to account for more complex vegetation dynamics in highly variable environments (Westoby et al. 1989, Behnke and Scoones 1993). As a result, the competing theory of nonequilibrium has gained acceptance.

According to nonequilibrium theory, the productivity of arid and semiarid vegetation is controlled primarily by the characteristically highly variable rainfall. Consequently, proponents of nonequilibrium theory have suggested that the productivity of semiarid regions is very rarely affected by grazing and rangeland management (Behnke and Scoones 1993, Ellis 1994, Scoones 1994). It is argued that plant production is largely determined by unpredictable rainfall events and is unaffected by animal population density because intermittent animal die-offs during the droughts keep animal densities below those expected in an equilibrium state (Illius and O'Connor 1999). As a result of the variable climate, these systems are inherently dynamic: they do not reach long-term equilibria, and they are less predictable than equilibrium systems. Under these conditions, livestock are not expected to have a long-term effect on vegetation productivity, and the risk of rangeland degradation is limited (Scoones 1994).

The opposing theories of rangeland processes can have far reaching ecological, managerial, and sociopolitical implications, and therefore a heated debate has been conducted between their proponents (Illius and O'Connor 1999, Sullivan and Rohde 2002). During the

Manuscript received 27 June 2006; revised 12 October 2006; accepted 16 October 2006. Corresponding Editor: J. Belnap.

[4] Present address: Remote Sensing Research Unit, Meraka Institute, CSIR, P.O. Box 395, Pretoria, 0001 South Africa. E-mail: kwessels@csir.co.za

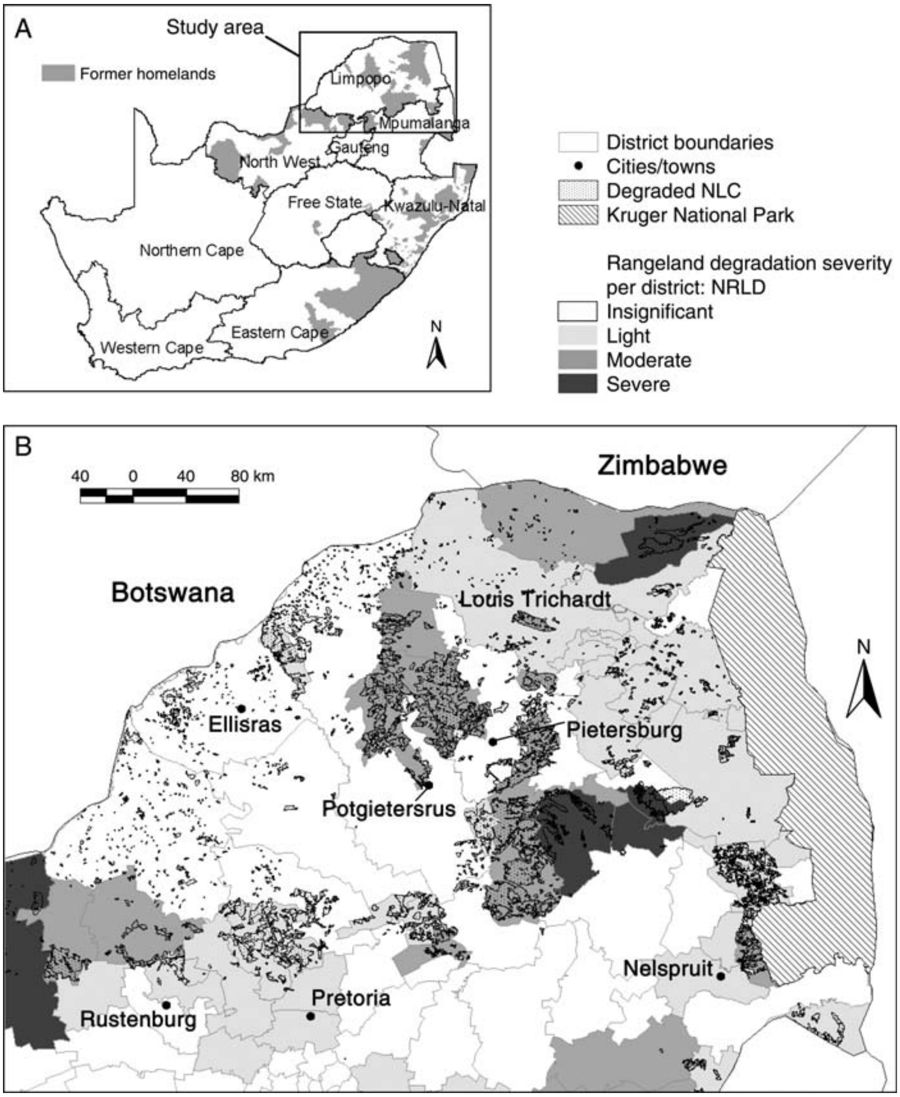

FIG. 1. (A) Provinces of South Africa with location of study area and former homelands. (B) Study area indicating severity of rangeland degradation per district according to National Review of Land Degradation, NRLD (after Hoffman et al. 1999), overlaid by degraded areas mapped by the National Land Cover, NLC (Fairbanks et al. 2000).

1980s, equilibrium rangeland management became increasingly unpopular, since it was associated with government intervention to reduce livestock numbers and futile attempts to stabilize variable rangelands (Abel and Blaikie 1989, Abel and Behnke 1996). The nonequilibrium theory suggested that livestock numbers can be allowed to increase without threatening degradation and generally professed mobility and opportunism in response to climate variability (Vetter 2005). The nonequilibrium theory has influenced policy to the extent that the relevance of stocking rates to rangeland management was completely dismissed in some regions (Vetter 2005). Critics argue that the nonequilibrium theory overemphasizes abiotic drivers of vegetation change and shifts the responsibility of rangeland management from humans to the vagaries of the climate, and thus may decrease the incentive to practice adaptive management (Watson et al. 1996, Briske et al. 2003). Central to this debate is the relative importance of biotic and abiotic factors in driving primary and secondary production and the consequences of this regarding the potential for grazing-induced degradation.

Assessing the competing theories requires a study area with highly contrasting rangeland management regimes. Such a situation exists in South Africa (SA), a country where divergent grazing systems have been created by extraordinary political circumstances. In South Africa, native reserves or communal areas (formerly called "homelands") were established under the Natives Land Acts of 1913 and 1936, and during the apartheid era, indigenous African people were involuntarily resettled and confined to these areas (Christopher 1994; Fig. 1A).

A detailed survey of 453 agricultural resource experts compiled in the National Review of Land Degradation (NRLD) found that the communal areas are widely believed to be degraded (Hoffman et al. 1999, Hoffman and Todd 2000). These communal homelands are characterized by high human and livestock populations, overgrazing, soil erosion, and the loss of more palatable grazing species (Hoffman et al. 1999, Hoffman and Todd 2000). Animal stocking rates are more than twice that of the neighboring commercial farms (Shackleton 1993). Consequently, there is a general consensus that this perceived degradation is the result of overgrazing (Hoffman and Ashwell 2001, Pollard et al. 2003, Scholes and Biggs 2004). Proponents of the nonequilibrium theory have questioned the existence of grazing-induced degradation in the communal lands of southern Africa (Abel and Blaikie 1989, Abel and Behnke 1996). In recognition of this long-standing, controversial debate, the present study attempted to objectively quantify the productivity of suspected degraded rangelands in communal areas.

Evaluating the competing theories furthermore requires a suitable measure of rangeland condition. The most readily interpretable measure of rangeland condition is the quantity and quality of forage production (Walker et al. 2002). At the local scale, the most reliable indication of forage quality is plant species composition (Fynn and O'Connor 2000). However, such data sets (e.g., Parsons et al. 1997) are rare and typically restricted to a few small study sites which provide no information on the regional distribution of degradation. At the regional scale, primary production and desertification have been monitored in semiarid areas using vegetation indices derived from coarse-resolution remote-sensing data. Remote-sensing base monitoring is cost-effective, repeatable, and spatially explicit (Prince et al. 1998, Diouf and Lambin 2001, Prince 2004, Anyamba and Tucker 2005). Although degradation that causes species changes in arid areas is often associated with a reduction in vegetation cover that is detectable with remote sensing (Pickup et al. 1994, Wessels et al. 2001), this is not always the case (Parsons et al. 1997, Diouf and Lambin, 2001). Therefore, some aspects of degradation, such as a loss of palatable grass species and forage quality, cannot be monitored with coarse-resolution satellite data. Vegetation surveys will therefore always remain an essential part of regional rangeland monitoring programs.

One remotely derived vegetation index that has been used widely in land degradation studies is the Normalized Difference Vegetation Index (NDVI). NDVI has a strong linear relationship with the fraction of photosynthetically active radiation (PAR) absorbed by the plant (f_{PAR}), which sets the upper limit for primary production (Prince 1991). The 10-daily maximum NDVIs, summed over the length of a growing season, provide a reliable estimate of total primary production. In Kruger National Park (SA), located inside the current study area (Fig. 1B), the growth season sum of 10-daily maximum NDVI (ΣNDVI) based on Advanced Very High Resolution Radiometer (AVHRR) data has proven to be strongly correlated with interannual changes in herbaceous vegetation production (1989–2003) (Wessels et al. 2006). Since land degradation reduces production, and thus f_{PAR}, remotely sensed NDVI data provide a reliable measure of degradation (Prince et al. 1998, Diouf and Lambin 2001, Prince 2004, Wessels et al. 2004, Anyamba and Tucker 2005). In the current study, vegetation production was estimated with ΣNDVI from AVHRR and the new Moderate-resolution Imaging Spectroradiometer (MODIS) data (Huete et al. 2002).

Although satellite remote sensing has previously been used to qualitatively map SA's degraded rangelands, further work is needed to characterize the vegetation production of these degraded areas and thereby evaluate the nonequilibrium theory. Preliminary information on rangeland degradation is available from SA's National Land Cover map (NLC). The NLC map was derived from Landsat TM satellite images (1995–1996) and includes degraded land cover classes defined, for photo-interpretation purposes, as areas with higher surface reflectance and lower vegetation cover than surrounding similar vegetation (Fairbanks et al. 2000). During field validation, the degradation was recognized by the prevalence of sparse, herbaceous vegetation cover accompanied by sheet and gully erosion. NLC degraded areas were thus subjectively mapped based on the interpretation of structural surface properties observed by satellite and in the field. The NLC mapped large, contiguous degraded areas, which were mostly confined to the communal lands, although small degraded patches were also mapped in commercial areas (Fig. 1B). The NRLD reported that agricultural resources experts judged the communal areas as degraded (Hoffman et al. 1999), while the NLC independently mapped the distribution of degradation, which largely occurred within these communal lands. Since the reduction in vegetation production in the NLC degraded areas has not yet been measured, it may be referred to as "perceived degradation." To characterize this perceived degradation, the current study quantified the vegetation production of the NLC degraded areas using multi-year AVHRR and MODIS NDVI data.

The proximity of NLC degraded and nondegraded areas allows the quantification of the relative impacts of the perceived grazing-induced degradation and of rainfall. Specifically, it allows the comparison of adjacent degraded (Fig. 1B) and nondegraded areas, which were equivalent in all other respects (e.g., soils, local climate, and topography; Wessels et al. 2004). Since northeastern SA experiences rainfall with an interannual coefficient of variation (rainfallCV) greater or equal to 33% (Schulze 1997) it is expected to be a nonequilibrium environment (Ellis 1994). Therefore, if these rangelands behaved strictly according to the

Table 1. Results of analyses of AVHRR ΣNDVI for nondegraded (n) and degraded areas (d) of land capability units 1–13.

LCU	Mean ΣNDVI†		Percentage difference (PD)			Rainfall		Correlation PD vs. rainfall	R^2 ΣNDVI vs. rainfall	
	n	d	Mean 1985–1986 to 2002–2003†	SD	Mean 2000–2001 to 2002–2003	Mean annual (mm)†	CV†		n	d
1	74.5	72	3.0	3.4	2.5	780	25.5	0.20 ns	0.31*	0.37*
2	54.8	47.9	12.7	2.7	14	455	32.8	−0.26 ns	0.69*	0.66*
3	55	52.4	4.7	2.4	3.8	472	32.5	0.18 ns	0.60*	0.59*
4	71.4	66.9	6.2	2.9	6.2	718	28.4	0.24 ns	0.59*	0.68*
5	79.8	68.2	14.6	3.0	16.9	718	26.4	−0.49*	0.33*	0.43*
6	59.6	53.2	10.9	4.5	14.8	529	30.6	−0.19 ns	0.16 ns	0.16 ns
7	59.3	54.9	7.4	3.0	11.4	554	29.7	0.14 ns	0.47*	0.45*
8	62.2	60.5	3.0	2.3	1.1	594	29.2	0.07 ns	0.245 ns	0.215 ns
9	71.4	63	11.8	2.7	12.7	535	26.8	0.08 ns	0.060 ns	0.040 ns
10	66.7	53.3	20.1	2.9	21.6	663	29.5	−0.38 ns	0.289*	0.420*
11	52.4	51.6	1.4	3.6	1.0	491	31.3	−0.12 ns	0.570*	0.520*
12	66.7	57.4	14	2.5	15.5	612	28.6	−0.18 ns	0.039 ns	0.119 ns
13	64.3	60.9	3.4	1.7	6.8	643	28.1	−0.47 ns	0.241 ns	0.333*

Note: Percentage difference (PD) = [(nondegraded ΣNDVI − degraded ΣNDVI)/degraded ΣNDVI] × 100.
† Measurement period is 1985–1986 to 2002–2003.
*$P < 0.05$; ns = not significant ($P > 0.05$).

nonequilibrium model (Briske et al. 2003), the vegetation productivity could be expected to be dominated by rainfall, while the perceived degradation in the NLC degraded areas should have a very limited impact on long-term vegetation productivity (Ellis and Swift 1988, Walker et al. 2002).

The objectives of this study were to (1) compare the long-term vegetation productivity of NLC degraded and nondegraded areas and (2) quantify the relative impacts of rainfall and the perceived degradation caused by intensive grazing on vegetation productivity, in order to gauge the prevalence of nonequilibrium dynamics. Hereafter, the mapped NLC degraded areas will be referred to only as degraded areas, while the perceived grazing-induced degradation will be referred to simply as degradation.

Methods

Study area

This study focused on northeastern SA, which includes the entire Limpopo Province and parts of the Mpumalanga and North West Provinces (~200 000 km^2; Fig. 1A). Land use in this region includes commercial and subsistence cultivation, exotic forestry plantations, national parks (e.g., Kruger National Park), private game reserves, commercial cattle ranching, and communal grazing. The natural vegetation varies from indigenous forest to open grasslands, but primarily comprises savanna woodlands and thickets. The region includes extensive degraded rangelands in the former homelands, now communal lands (Hoffman and Ashwell 2001); however, not all the communal lands are degraded (Fig. 1B). This study was only concerned with areas covered by natural vegetation that are used for grazing wild and domestic animals. The mean annual precipitation in all 13 land-capability units (defined in the next section) examined in this study was 578 mm (Table 1).

Land capability units

In order to isolate the impact of degradation from spatial variation in soils, topography, and climate, the study area was stratified using land capability units (LCUs). Land capability is a widely used concept in agricultural development, and it refers to the suitability of the land for a specific use, e.g., rangeland or rain-fed cultivation (Klingebiel and Montgomery 1961). The very detailed land-type map of SA (MacVicar et al. 1977) was essentially reclassified into LCUs based on its comprehensive database of the following properties: (1) terrain: slope length and gradient; (2) soil: depth, texture, erodibility, internal drainage, mechanical limitations; and (3) climate: moisture availability, length of moist and temperate seasons (MacVicar et al. 1977, Schoeman et al. 2002, Wessels et al. 2004). The LCUs do not consider current vegetation cover, land use or land condition, making it possible to distinguish natural physical variations from human influences. The LCUs were developed by the Agricultural Research Council-Institute for Soil, Climate and Water (ARC-ISCW) and are routinely used by the South African National Department of Agriculture for resource conservation and land-use planning. The LCUs were sufficiently internally homogenous to allow the comparison of NLC degraded and nondegraded areas within them. Only LCUs containing large degraded areas were included in this analysis (Fig. 2).

AVHRR data

Daily AVHRR High Resolution Picture Transmission (HRPT, 1.1-km^2 resolution) data were processed by the ARC-ISCW. Data from 1985 to 2003 were calibrated to correct for sensor degradation and satellite changes (Rao and Chen 1996). Ten-day maximum value NDVI composites were generated. A statistical filter was applied through time to interpolate cloud-flagged or atmospherically affected pixels, which were identified

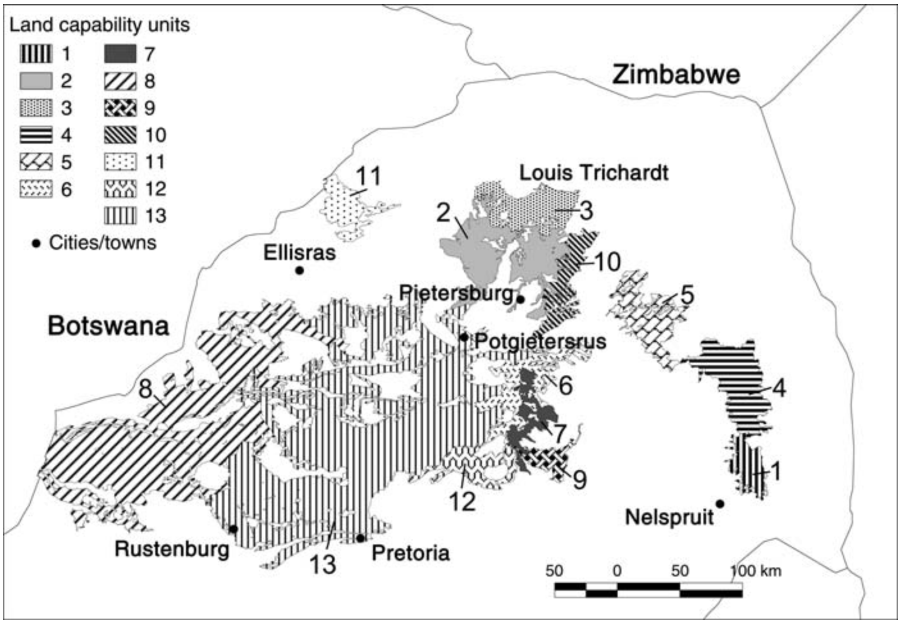

FIG. 2. Selected land capability units (LCU) containing degraded areas in northeastern South Africa.

whenever a relative decrease in the signal of 5% or more was followed within four weeks by an equivalent increase (Lo Seen Chong et al. 1993). The 10-day composites were summed over the entire growing season, October to April (AVHRR ΣNDVI, $N = 16$, 1985–1986 to 2002–2003). Due to the failure of the NOAA13 satellite, data for 1994 were unavailable. For further details on the AVHRR data processing see Wessels et al. (2006).

MODIS data

The standard 8-day MODIS surface reflectance product (MOD09A1) is generated from the daily, 500-m resolution, atmospherically corrected surface reflectance data (MOD09_L2G; Vermote et al. 2002). Four 8-day surface reflectance data sets were combined to produce 32-day composites (Hansen et al. 2003) (*available online*).[5] NDVI was calculated for each 32-day period and summed from Julian day 290 of year t to 129 of year $t + 1$ to give growth season sum NDVI (MODIS ΣNDVI, $N = 5$, 2000–2001 to 2004–2005). The AVHRR data have the advantage of a long-term data record (the early 1980s to the present), while the more recent (2000 to present) MODIS data have greater spectral and spatial resolution, among other technical improvements (Huete et al. 2002).

Rainfall data

Within the study area, rainfall was recorded in a network of 200–350 weather stations managed by the South African Weather Service and ARC-ISCW (Monnik 2001). For each station the long-term mean rainfall was calculated (1965 to present) for every 10-day period of the year, e.g., mean rainfall at station X between 10 and 20 January (1965 to present) might be 50 mm (10-day climatological mean rainfall). For every specific 10-day period in the record (e.g., 10–20 January 1999), the percentage deviation from the 10-day climatological mean rainfall was calculated for each station. For example, if station X received 25 mm during 10–20 January 1999, the percentage deviation would be -50%.

Surfaces were created from the 10-day climatological mean rainfall of all the stations by using multiple linear regression models with independent variable layers such as altitude, distance from ocean, local variation in elevation, latitude, longitude (Malherbe 2001). Surfaces were also produced for the percentage deviations by interpolating (inverse-distance weighted) the data of all the stations for a specific period. Finally, rainfall surfaces for all the specific 10-day periods in the record (e.g., 10–20 January 1999) were produced by multiplying the percentage deviation layers by the 10-day climatological mean rainfall layers (Malherbe 2001). The total growth-season sum rainfall (October to April; hereafter referred to as only as rainfall) was then calculated.

Comparison of NLC degraded and nondegraded areas

For each growth season, the mean ΣNDVI pixel value was calculated for the NLC degraded and nondegraded parts of every LCU. The NLC degraded and non-degraded areas of the same LCU (hereafter referred to as paired areas) were compared in order to quantify the impact of the perceived degradation on vegetation productivity.

---

[5] ⟨www.glcf.umiacs.umd.edu⟩

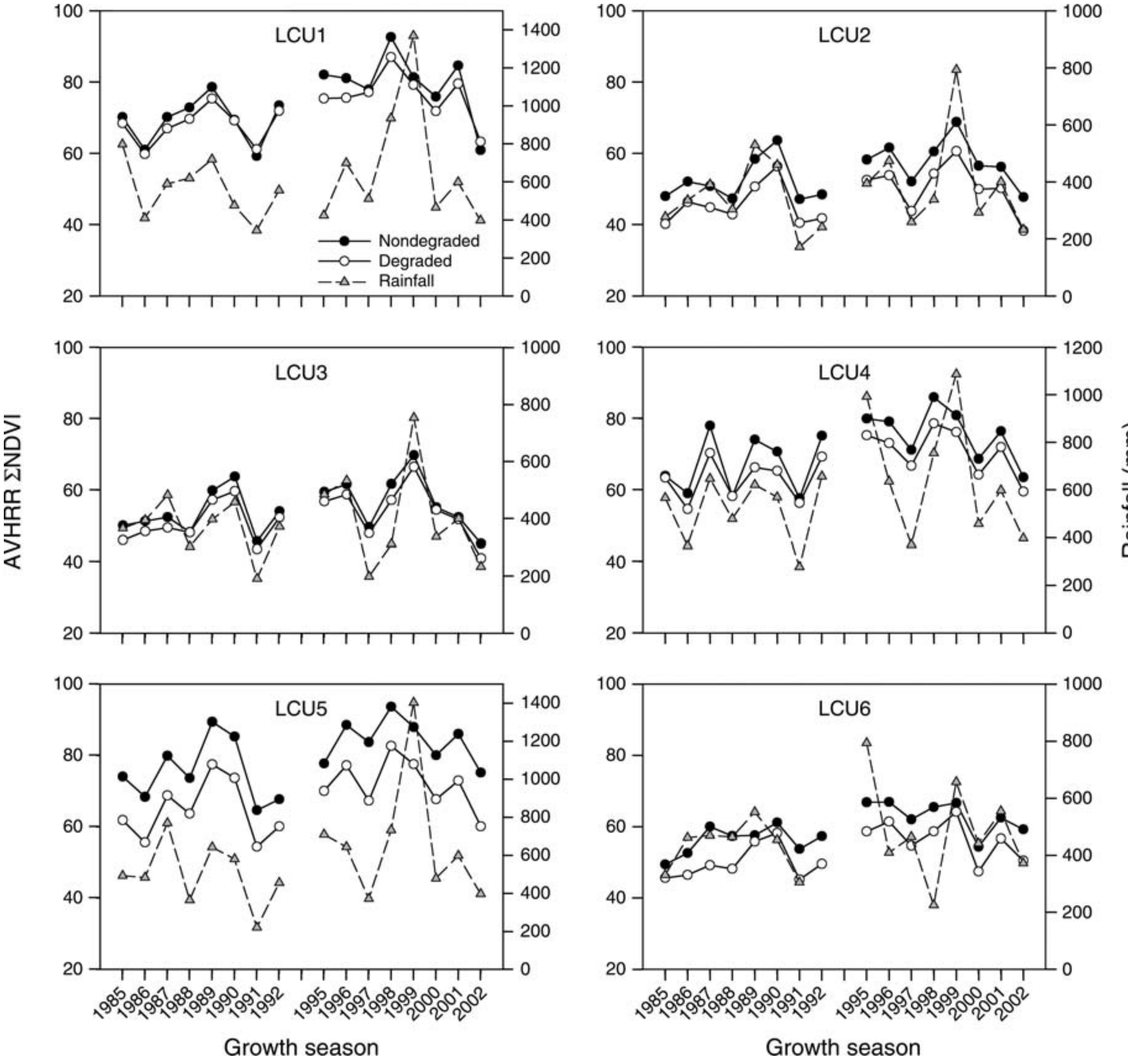

FIG. 3. AVHRR ΣNDVI of degraded and nondegraded areas and rainfall (mm) of land capability units (LCU) per growth season. Each year represents a growing season that begins in the year shown. The Normalized Difference Vegetation Index (ΣNDVI) was calculated using data from the Advanced Very High Resolution Radiometer (AVHRR; 1985–2003).

The percentage difference (PD) in ΣNDVI of paired areas of LCUs 1–13 was calculated as

$$\mathrm{PD} = \frac{\text{nondegraded }\Sigma\mathrm{NDVI} - \text{degraded }\Sigma\mathrm{NDVI}}{\text{nondegraded }\Sigma\mathrm{NDVI}} \times 100.$$

Multiple regression analysis

For each LCU, multiple regression analysis was carried out to quantify the relative influence of rainfall and degradation (independent variables) on ΣNDVI (dependent variable), through time (AVHRR $N = 16$, MODIS $N = 5$). Rainfall was included as the first independent variable in the models, after which a binary categorical variable (degraded or nondegraded) was added to test how much of the remaining variance in ΣNDVI was accounted for by the differences between the paired areas of each LCU. The percentages of the total variance (sums of squares) accounted for by the overall model and each of the independent variables were determined. A ratio of the variances respectively accounted for by degradation vs. rainfall (degradation : rainfall) was calculated to indicate their relative contributions to ΣNDVI variance.

RESULTS

AVHRR ΣNDVI

For all LCUs, the AVHRR ΣNDVI of degraded areas was lower than that of nondegraded areas (Fig. 3). The mean annual percentage difference (PD) values per LCU indicate that the AVHRR ΣNDVI of degraded areas were between 1.4% and 20.1% lower than the non-

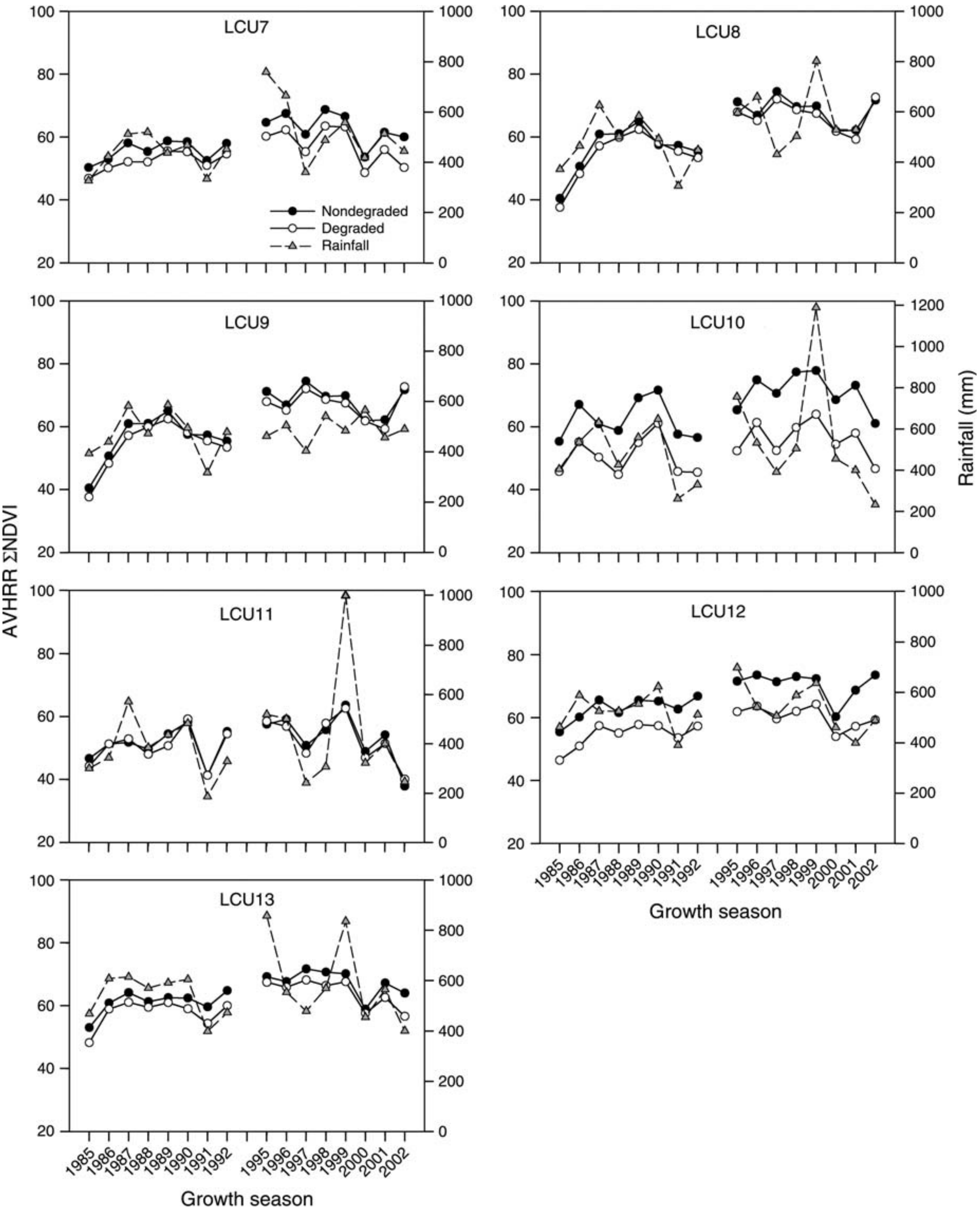

FIG. 3. Continued.

degraded areas (Table 1). LCUs numbered 5, 10, and 12 had the highest mean PD values of 14.6%, 20.1%, and 14.0%, respectively. LCUs 1, 8, and 11 had the lowest mean PD values of 3%, 3%, and 1.4%, respectively (Fig. 2). The mean PD of all the LCUs was 8.70%, indicating the mean reduction in ΣNDVI caused by degradation. The standard deviation of the PD was small (1.7% for LCU13 to 4.5% for LCU6; Table 1), and the PD was also generally not correlated with rainfall, indicating a relatively consistent difference between degraded and

TABLE 2. Multiple regression analyses relating AVHRR ΣNDVI to independent variables rainfall and degradation for each land capability unit (LCU) over 16 growth seasons.

	Rain			Degradation			Rain + Degradation		
LCU	SS (%)	*F*	*P*	SS (%)	*F*	*P*	SS (%)	*F*	*P*
1	36.1	16.9	<0.001	2.3	1.1	0.3 ns	38.4	9.05	<0.001
2	57.7	84.9	<0.001	22.6	33.1	<0.001	80.1	33.1	<0.001
3	66.1	63.3	<0.001	3.6	3.4	0.07 ns	69.7	29.7	<0.001
4	59.4	52.5	<0.001	7.9	6.9	0.01	67.2	29.7	<0.001
5	33.0	28.1	<0.001	32.9	27.9	<0.001	65.9	28.0	<0.001
6	47.4	49.7	<0.001	24.9	26.1	<0.001	72.3	37.9	<0.001
7	35.5	35.5	<0.001	11.6	11.6	<0.001	61.0	23.5	<0.001
8	15.6	5.4	<0.001	1.0	0.36	0.55 ns	16.6	2.8	0.07 ns
9	20.9	14.9	0.005	38.8	27.8	<0.001	59.6	21.4	<0.001
10	19.7	18.6	<0.001	49.6	46.9	<0.001	69.3	32.8	<0.001
11	60.5	44.8	<0.001	0.4	0.26	0.61 ns	60.9	22.5	<0.001
12	15.2	11.6	<0.001	46.6	35.4	<0.001	61.8	23.5	<0.001
13	31.2	15.3	<0.001	9.9	4.8	0.03	41.1	10.1	<0.001

Notes: Percentage of the total sums of squares was calculated after successively adding the variables to models; ns = not significant ($P > 0.05$).

nondegraded areas in all years, despite large variations in rainfall (Fig. 3).

Multiple regression models, AVHRR ΣNDVI

With the exception of LCU8, the overall model (rainfall + degradation) for the individual LCUs were all highly significant ($P < 0.001$), explaining 38–80% of the variance with a mean of 62% (Table 2). The percentage of the total variance accounted for by rainfall varied between 15% and 66% with a mean of 38% ($P < 0.001$; Table 2) and was negatively correlated with the mean rainfall of the LCUs ($r = -0.51$, $P < 0.001$) and positively correlated with the rainfallCV ($r = 0.58$, $P < 0.001$; Fig. 4). The percentage of the total variance accounted for by degradation varied from 0.4% (LCU 11) to 50% (LCU 10) with a mean of 19.4% ($P < 0.001$; Table 2) and was not correlated with mean rainfall across LCUs ($r = 0.17$). Degradation did not account for a statistically significant portion (<4%) of the NDVI variance of LCUs 1, 3, 8, and 11.

The ratio of variance accounted for by degradation and rainfall varied greatly between the LCUs (Table 2). This degradation : rain ratio was small for LCUs 1, 3, 8, and 11, indicating that rainfall had a large influence and degradation a small influence on NDVI. Where this ratio was near or above 1 (LCUs 5, 9, 10, 12), degradation had a larger influence on NDVI than rainfall. For LCUs 10 and 12, this ratio was 2.5 and 3.0, respectively, and degradation accounted for 49.6% and 46.6% of the NDVI variance, respectively (Table 2).

MODIS ΣNDVI

The MODIS ΣNDVI of the nondegraded areas of the LCUs was consistently higher than that of degraded areas (Fig. 5, Table 3). The MODIS-PD ranged from 8.2% to 22.1%, with an overall mean annual PD of 13.8%, which is nearly double that of the AVHRR-PD (Table 1). The mean annual PD for each LCU calculated using AVHRR ΣNDVI data was 10–70% lower than the PD calculated using the MODIS data (mean across all LCUs = 42%, Tables 1 and 3). The standard deviation of the PD was small (Table 3), indicating a relatively consistent difference between degraded and nondegraded areas through time.

Multiple regression models, MODIS ΣNDVI

The overall model (rainfall + degradation) of the individual LCUs were all highly significant ($P < 0.001$), explaining 62–99% of the variance, with a mean of 81% (Table 4). The percentage of the total variance accounted for by rainfall varied between 3.4% (LCU 12) and 82% (LCU 1), with a mean of 49% (Table 4) and was not correlated with the mean rainfall or rainfallCV of the LCUs ($r < 0.09$). With the exception of LCU 12, rainfall accounted for a significant percentage of MODIS ΣNDVI ($P < 0.001$). The percentage of the

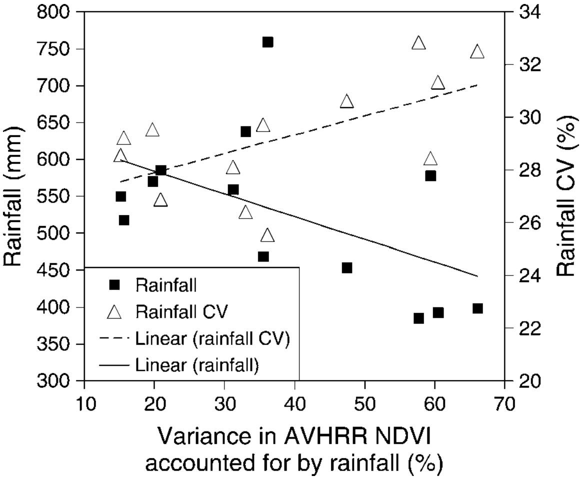

FIG. 4. Percentage of AVHRR ΣNDVI variance explained by rainfall plotted against rainfall and the coefficient of variance of rainfall (rainfallCV) for 13 land capability units.

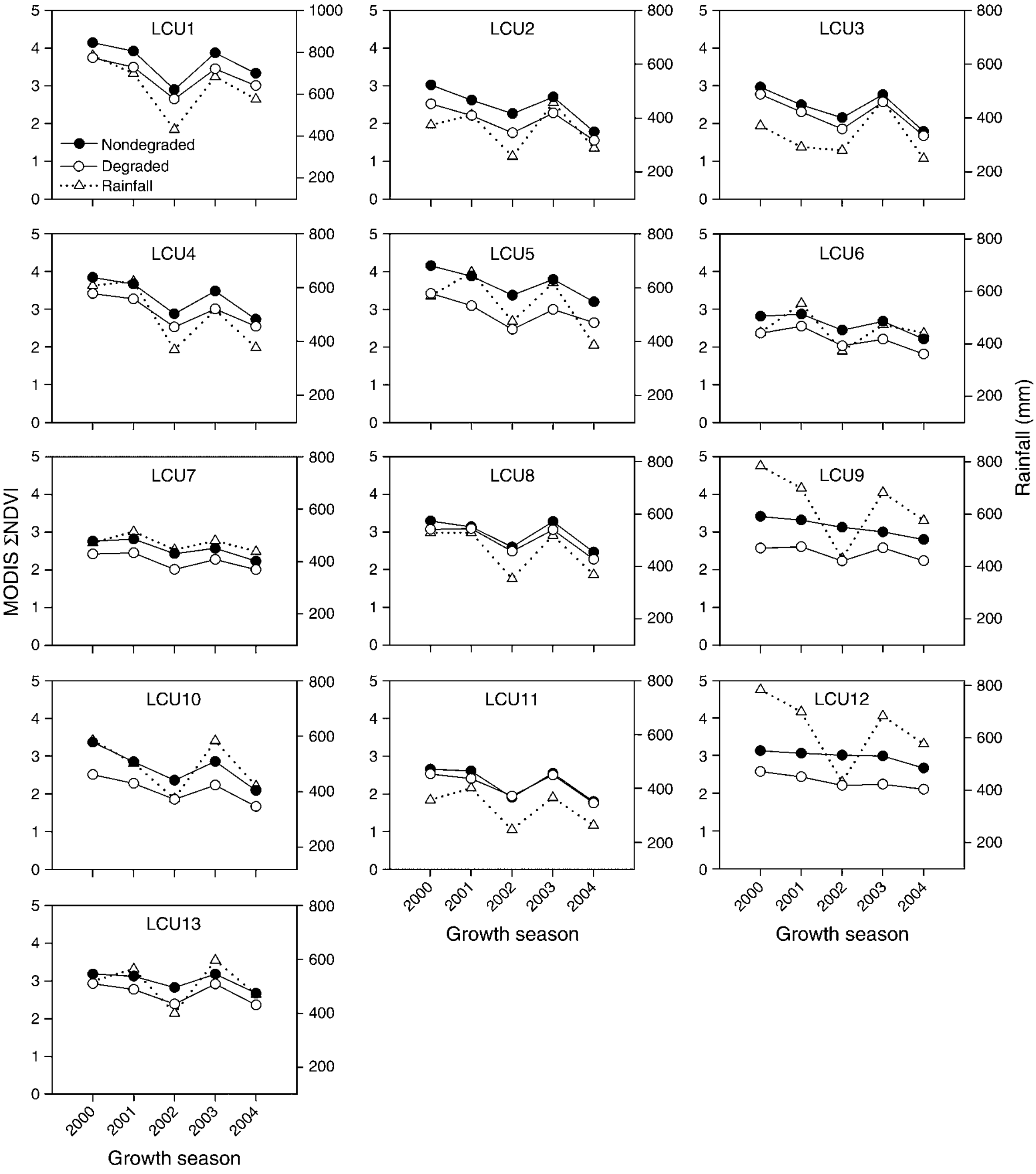

FIG. 5. MODIS ΣNDVI of degraded and nondegraded areas and rainfall (mm) of land capability units (LCU) per growth season. Each year represents a growing season that begins in the year shown. The Normalized Difference Vegetation Index (ΣNDVI) was calculated using data from the Moderate-resolution Imaging Spectroradiometer (MODIS).

total variance accounted for by degradation varied from 1.2% (LCU 11) to 75% (LCU 9) with a mean of 32.8% (Table 4) and was not correlated with mean rainfall across LCUs ($r = 0.17$). With the exception of LCU 3 and 11, degradation accounted for a statistically significant percentage of MODIS ΣNDVI variance ($P < 0.001$), although LCUs 2 and 8 were only marginally significant.

This degradation : rain ratio was small for LCUs 1, 3, 8, and 11, indicating that rainfall had a large influence and degradation a small influence on NDVI (Table 4). Where this ratio was above 1 (LCUs 5, 6, 9, 12), degradation had a larger influence on NDVI than rainfall. For LCUs 9 and 12, this ratio was 4.0 and 23.0, respectively, and degradation accounted for 81% and 80% of the NDVI variance, respectively (Table 4).

TABLE 3. Results of analyses of MODIS ΣNDVI for nondegraded (n) and degraded areas (d) of land capability units.

	Mean ΣNDVI†		Percentage difference (PD)			Rainfall			R^2 ΣNDVI vs. rainfall	
LCU	n	d	Mean†	SD	Mean 2000-2001 to 2002-2003	Mean annual† (mm)	CV†	Correlation PD vs. rainfall	n	d
1	3.6	3.2	9.9	1.03	9.6	780	25.5	0.68 ns	0.98*	0.98*
2	2.4	2.06	16.6	3.6	18.2	455	32.8	−0.4 ns	0.46*	0.6*
3	2.4	2.2	8.2	3.2	9.2	472	32.5	−0.3 ns	0.62*	0.63*
4	3.3	2.9	10.9	2.5	11.4	718	28.4	0.3 ns	0.94*	0.97*
5	3.6	2.9	20.5	3.8	21.5	718	26.4	0.007 ns	0.67*	0.46*
6	2.6	2.2	15.9	2.7	14.7	529	30.6	−0.7*	0.36 ns	0.48*
7	2.6	2.2	12.7	2.6	14.1	554	29.7	−0.07 ns	0.75*	0.78*
8	2.9	2.8	16	2.4	4.3	594	29.2	0.06 ns	0.93*	0.93*
9	3.1	2.4	21.7	5.3	24.8	535	26.8	0.1 ns	0.98*	0.5*
10	2.7	2.1	21.8	2.2	22.4	663	29.5	0.59 ns	0.73*	0.74*
11	2.3	2.2	20.5	3.5	3.5	491	31.3	0.67 ns	0.89*	0.79*
12	2.9	2.3	22.1	3.6	21.5	612	28.6	−0.3 ns	0.12 ns	0.21 ns
13	3.0	2.7	10.9	3.0	11.6	643	28.1	−0.8*	0.59*	0.69*

Note: Percentage difference (PD) = [(nondegraded ΣNDVI – degraded ΣNDVI)/ nondegraded ΣNDVI] × 100.
† Measurement period is 2000–2001 to 2004–2005.
$^*P < 0.05$; ns = not significant ($P > 0.05$).

DISCUSSION

This study clearly demonstrates that growth season ΣNDVI, and thus productivity, was influenced by both rainfall and the grazing-induced degradation. On average, rainfall and degradation respectively accounted for 38% and 20% of the AVHRR ΣNDVI variance and 50% and 33% of the MODIS ΣNDVI variance. The relative contribution of rainfall and degradation to ΣNDVI variance varied considerably between LCUs (Tables 2 and 4), but analysis (*unpublished data*) found no relationship between these relative contributions and the biophysical properties of the LCUs. In the AVHRR ΣNDVI, the influence of rainfall was greater for LCUs with lower mean rainfall and higher rainfallCV (Fig. 4), thus lending support to the notion that productivity in drier, more variable environments is more related to rainfall (Behnke and Scoones 1993, Ellis 1994, Scoones 1994). The difference between the productivity of the nondegraded and degraded was not correlated with the rainfall of the LCUs and was most likely determined by the intensity of the degradation, which may vary along a continuum, from light to severe (Tongway and Hindley 2000). For LCUs 9, 10, and 12, however, degradation had a larger influence on AVHRR ΣNDVI than rainfall (Table 2). In the MODIS ΣNDVI data, degradation had a larger influence relative to rainfall when compared to the AVHRR ΣNDVI, e.g., LCUs 5, 6, 9, 10, and 12 (Tables 2 and 4; Fig. 5). However, this could be the coincidental result of comparing two different time periods of different lengths for the respective sensors, rather than differences in sensor properties or changes in land degradation.

The vast majority of the LCUs (9 out of 13) experienced a significant influence of degradation on productivity and therefore the perceived degradation mapped by the NLC appears to be a reality. The degradation had a long-term impact on vegetation productivity despite substantial interannual variation

TABLE 4. Multiple regression analyses relating MODIS ΣNDVI to independent variables rainfall and degradation, per land capability unit (LCU) over five growth seasons ($N = 5$).

	Rain			Degradation			Rain + Degradation		
LCU	SS (%)	*F*	*P*	SS (%)	*F*	*P*	SS (%)	*F*	*P*
1	82.8	356.2	<0.001	15.6	66.9	<0.001	98.3	211.6	<0.001
2	41.0	7.6	0.02	21.7	6.1	0.05	62.6	5.8	0.03
3	59.8	11.9	0.01	5.2	1.0	0.34 ns	64.9	6.49	0.34 ns
4	78.5	129.7	<0.001	17.3	28.6	0.01	95.7	79.1	<0.001
5	25.4	8.98	0.02	54.9	19.4	0.003	80.2	14.2	0.003
6	25.3	5.1	0.05	40.3	8.1	0.02	65.5	6.6	0.02
7	46.6	22.8	<0.001	39.3	19.3	0.003	85.7	21.1	0.001
8	88.8	99.0	<0.001	4.9	5.5	0.05	93.7	52.2	<0.001
9	18.5	20.2	0.002	75.1	81.7	<0.001	93.5	50.9	<0.001
10	44.4	17.7	0.003	38.1	15.3	0.005	82.5	16.5	<0.001
11	83.4	38.0	<0.001	1.2	0.5	0.4 ns	84.6	19.3	<0.001
12	3.4	1.4	0.27 ns	80.0	33.8	<0.001	83.4	17.6	<0.001
13	43.2	12.7	0.009	33.0	9.7	0.016	76.2	11.2	0.006

Notes: Percentage of the total sums of squares was calculated after successively adding the variables to models; ns = not significant ($P > 0.05$).

in rainfall, as observed in field studies (Kelly and Walker 1977, Milchunas and Lauenroth 1993, Snyman 1999). Because degradation accounted for ~60% as much ΣNDVI variance as rainfall, the results challenge the claim that the risk of grazing-induced degradation in nonequilibrium environments is limited (Ellis and Swift 1988, Abel and Blaikie 1989, Scoones 1994, Briske et al. 2003). These findings also agree with those of field studies in similar environments in Kwa-Zulu Natal, South Africa (Fynn and O'Connor 2000) and Texas, USA (Fuhlendorf et al. 2001), thus suggesting a density-dependent coupling between herbivores and vegetation more in accordance with the equilibrium theory (Illius and O'Connor 1999). The rainfall variability may not maintain these rangelands in a perpetual nonequilibrium state, but rather superimpose fluctuations on an otherwise directional response of vegetation to intensive grazing (Wiens 1984, Fuhlendorf et al. 2001).

While, in the current study, the nonequilibrium model overstates the influence of rainfall variability and underestimates grazing as a driver of ecosystem dynamics, equilibrium and nonequilibrium dynamics are not necessarily mutually exclusive, but rather represent two ends of a continuum: from environments with high rainfall and low variability to those with low rainfall and high variability (Wiens 1984). Depending on spatial and temporal scales, most systems exhibit both equilibrium and nonequilibrium characteristics, particularly in semiarid regions (Illius and O'Connor 1999). The state-and-transition model (Westoby et al. 1989, Briske et al. 2003), which accommodates both equilibrium and nonequilibrium dynamics, may be more appropriate for describing the behavior of the rangelands under investigation. The state-and-transition model envisages vegetation dynamics as a set of discrete "states" and a set of equally discrete "transitions" between the states. Transition phases may be a single natural event (e.g., fire or drought) or long-term change in management practices (e.g., grazing management). Continuous and reversible vegetation dynamics prevail within the stable states, while discontinuous, nonreversible dynamics occur when thresholds are crossed and one stable state replaces another (Briske et al. 2005).

It therefore appears that intensive overgrazing in parts of the communal lands may have caused a transition to a different stable state with a lower primary productivity. The existence of a degraded ecological state in these communal lands is supported by reports of increases in unpalatable plant species (Kelly and Walker 1977, O'Connor 1995, O'Connor et al. 2003) and severe soil erosion (Hoffman et al. 1999, Wessels et al. 2001). Within the degraded ecological state, it was found that rainfall caused the same range of variation in productivity that was found in the nondegraded parts of each LCU, suggesting that the altered state may be stable (Westoby et al. 1989, Prince 2002). The difference in the productivity of degraded and nondegraded areas in the same LCU was relatively constant during the study period and did not diminish following good rainfall (Figs. 3 and 5), suggesting that the degraded areas may have experienced an irreversible reduction in productivity (Dube and Pickup 2001). Whether or not these degraded states constitute irreversible change within a managerial time frame, however, can only be determined by removing the grazing pressure for many years (Illius and O'Connor 1999, Prince 2002).

The MODIS data showed much larger differences between the ΣNDVI's of degraded and nondegraded areas than the AVHRR data. The mean percentage difference (PD) calculated from the AVHRR data was 40% lower during the overlapping period (2000–2001 to 2002–2003) (Tables 1 and 3). AVHRR NDVI has a lower sensitivity to vegetation differences than MODIS NDVI due to the smaller dynamic range and considerably broader red and near-infrared bandwidths of the AVHRR sensor (Huete et al. 2002, Ferreira et al. 2003). In addition, the lower resolution of the AVHRR data (1 km vs. 500 m MODIS), causes spatial aggregation that may mask degradation taking place at a finer scale, where the redistribution of soil, organic matter, and propagules may lower productivity at run-off sites and enhance it at receiving sites (Pickup et al. 1998, Walker et al. 2002). The relative variability of estimates of vegetation production is furthermore highly dependent on the spatial scale, and the variability decreases exponentially as the size of field plots or remote sensing pixels increase (Oba et al. 2003, Golluscio et al. 2005). The magnitude of the grazing impacts observed using remote sensing data is, therefore, both scale-dependent and sensor specific.

CONCLUSIONS

This study demonstrated that the grazing-induced degradation caused a substantial reduction in long-term vegetation productivity, despite a strong short-term influence of interannual variation in rainfall. The results challenge the application of nonequilibrium theory which proposes a limited risk of grazing-induced degradation in semiarid environments. Although the degradation observed in the communal lands was a consequence of the oppressive apartheid system rather than the outcome of traditional communal pasturalism, it is clear that high stocking rates have led to degradation. Although there is no doubt that equilibrium vs. nonequilibrium debate will continue, the sustainable management of SA's rangelands will have to address the issue of stocking rates, especially during this period of land restitution and redistribution.

ACKNOWLEDGMENTS

Philip Frost and Dawie Van Zyl of ARC-ISCW processed the AVHRR data. This work was partially funded by NASA Earth Systems Sciences Fellowship O2-0000-0130, SA Department of Agriculture (Land Use and Soil Management Directorate), and SA Department of Science and Technology (LEAD project funding). Simon Trigg gave valuable comments on the manuscript.

LITERATURE CITED

Abel, N., and R. Behnke. 1996. Revisited: the overstocking controversy in semiarid Africa. World Animal Review 87:4–27.

Abel, N. O. J., and P. M. Blaikie. 1989. Land degradation, stocking rates and conservation policies in the communal rangelands of Botswana and Zimbabwe. Land Degradation and Rehabilitation 1:101–123.

Anyamba, A., and C. J. Tucker. 2005. Analysis of Sahelian vegetation dynamics using NOAA-AVHRR NDVI data from 1981–2003. Journal of Arid Environments 63:596–614.

Behnke, R. H., and I. Scoones. 1993. Rethinking range ecology: implications for rangeland management in Africa. Pages 1–30 *in* R. H. Behnke, I. Scoones, and C. Kerven, editors. Range ecology at disequilibrium. Overseas Development Institute, London, UK.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology 40:601–614.

Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2005. State-and transition models, thresholds and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology and Management 58:1–10.

Christopher, A. 1994. The atlas of apartheid. Witwatersrand University Press, Johannesburg, South Africa.

Diouf, A., and E. Lambin. 2001. Monitoring land-cover changes in semiarid regions: remote sensing data and field observations in the Ferlo, Senegal. Journal of Arid Environments 48:129–148.

Dube, O., and G. Pickup. 2001. Effects of rainfall variability and communal and semi-commercial grazing on land cover in southern African rangelands. Climate Research 17:195–208.

Ellis, J. E. 1994. Climate variability and complex ecosystems dynamics: implications for pastoral development. Pages 37–46 *in* I. Scoones, editor. Living with uncertainty. Intermediate Technology Publications, London, UK.

Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. Journal of Range Management 41:450–459.

Fairbanks, D. H. K., M. W. Thompson, D. E. Vink, T. S. Newby, H. M. Van den Berg, and D. A. Everard. 2000. The South African land-cover characteristics database: a synopsis of the landscape. South African Journal of Science 96:69–82.

Ferreira, L. G., H. Yoshioka, A. Huete, and E. E. Sano. 2003. Seasonal landscape and spectral vegetation index dynamics in the Brazilian Cerrado: an analysis within the Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA). Remote Sensing of Environment 87:534–550.

Fuhlendorf, S. D., D. D. Briske, and F. E. Smeins. 2001. Herbaceous vegetation change in variable rangeland environments: the relative contributions of grazing and climate variability. Applied Vegetation Science 4:177–188.

Fynn, R. W. S., and T. G. O'Connor. 2000. Effect of stocking rate and rainfall on rangeland dynamics and cattle performance in semiarid savanna, South Africa. Journal of Applied Ecology 37:491–507.

Golluscio, R. A., J. A. Perez, J. M. Paruelo, and C. M. Ghersa. 2005. Spatial heterogeneity at different grain sizes in grazed versus ungrazed sites of the Patagonian steppe. Ecoscience 12:103–109.

Hansen, M. C., R. S. DeFries, J. R. G. Townshend, M. Carroll, C. Dimiceli, and R. A. Sohlberg. 2003. Global percent tree cover at a spatial resolution of 500 meters: first results of the MODIS vegetation continuous fields algorithm. Earth Interactions 7:1–15.

Hoffman, M. T., and A. Ashwell. 2001. Nature divided: land degradation in South Africa. Cape Town University Press, Cape Town, South Africa.

Hoffman, M. T., and S. Todd. 2000. National review of land degradation in South Africa: the influence of biophysical and socio-economic factors. Journal of Southern African Studies 26:743–758.

Hoffman, M. T., S. Todd, Z. Ntoshona, and S. Turner. 1999. Land degradation in South Africa. National Botanical Institute, Cape Town, South Africa.

Huete, A., K. Didan, T. Miura, E. P. Rodrigues, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83:195–213.

Illius, A. W., and T. G. O'Connor. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. Ecological Applications 9:798–813.

Kelly, R. D., and B. H. Walker. 1977. The effects of different forms of land use on the ecology of the semiarid region in south-eastern Rhodesia. Journal of Ecology 62:553–576.

Klingebiel, A. A., and P. H. Montgomery. 1961. Land capability classification. Agriculture handbook No. 210. USDA, Washington D.C., USA.

Lo Seen Chong, D., E. Mougin, and J. P. Gastellu-Etchegorry. 1993. Relating the Global Vegetation Index to net primary productivity and actual evapotranspiration over Africa. International Journal of Remote Sensing 14:1517–1546.

MacVicar, C. N., J. M. de Villiers, R. F. Loxton, E. Verster, J. J. N. Lambrechts, F. R. Merryweather, J. Le Roux, T. H. Van Rooyen, and H. J. Harmse. 1977. Soil classification. A binomial system for South Africa. Science Bulletin 390. Agricultural Research Council-Institute for Soil, Climate and Water. Pretoria, South Africa.

Malherbe, J. 2001. Integration of radar rainfall estimates, point station data and long-term interpolated rainfall surfaces to estimate rainfall for the Umlindi monitoring system. South African Society for Atmospheric Sciences Conference, Cape Town, South Africa.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Monnik, K. 2001. Agrometeorological database management strategies and tools in South Africa. Page 194 *in* Software for agroclimatic data management: Proceedings of an Expert Group Meeting. Report WAOB-2001-2. USDA, Washington, D.C., USA.

Oba, G., R. B. Weladji, W. J. Lusigi, and N. C. Stenseth. 2003. Scale-dependent effects of grazing on rangeland degradation in Northern Kenya: a test of equilibrium and nonequilibrium hypotheses. Land Degradation and Develoment 14:83–94.

O'Connor, T. G. 1995. Transformation of a savanna grassland by drought and grazing. African Journal of Range and Forage Science 12:53–60.

O'Connor, T., C. Morris, and D. Marriott. 2003. Change in land use and botanical composition of KwaZulu-Natal's grasslands over the past fifty years: Acocks' sites revisited. South African Journal of Botany 69:105–115.

Parsons, D. A. B., C. M. Shackleton, and R. J. Scholes. 1997. Changes in herbaceous layer condition under contrasting land use systems in the semiarid lowveld, South Africa. Journal of Arid Environments 37:319–329.

Pickup, G., G. N. Bastin, and V. Chewings. 1994. Remote-sensing based condition assessment for nonequilibrium rangelands under large-scale commercial grazing. Ecological Applications 4:497–517.

Pickup, G., G. N. Bastin, and V. H. Chewings. 1998. Identifying trends in land degradation in nonequilibrium rangelands. Journal of Applied Ecology 35:365–377.

Pollard, S., C. M. Shackleton, and J. Curruthers. 2003. Beyond the fences: people and the lowveld landscape. Pages 422–446 *in* J. Du Toit, H. Biggs, and K. H. Rogers, editors. The Kruger experience: ecology and management of savanna heterogeneity. Island Press, London, UK.

Prince, S. D. 1991. A model of regional primary production for use with coarse-resolution satellite data. International Journal of Remote Sensing 12:1313–1330.

Prince, S. D. 2002. Spatial and temporal scales of measurement of desertification. Pages 23–40 *in* J. F. Reynolds and M. Stafford-Smith, editors. Global desertification: do humans create deserts? Dahlem University Press, Berlin, Germany.

Prince, S. D. 2004. Mapping desertification in Southern Africa. Pages 163–184 *in* G. Gutman, A. Janetos, C. O. Justice, Emilio F. Moran, J. F. Mustard, R. R. Rindfuss, D. Skole, and B. L. Turner II, editors. Land change science: observing, monitoring, and understanding trajectories of change on the earth's surface. Kluwer, Dordrecht, The Netherlands.

Prince, S. D., E. Brown de Colstoun, and L. Kravitz. 1998. Evidence from rain use efficiencies does not support extensive Sahelian desertification. Global Change Biology 4:359–374.

Rao, C. R. N., and J. Chen. 1996. Post-launch calibration of the visible and near-infrared channels of the Advanced Very High Resolution Radiometer on the NOAA-14 spacecraft. International Journal of Remote Sensing 17:2743–2747.

Schoeman, J. L., M. van der Walt, K. A. Monnik, A. Thackrah, J. Malherbe, and R. E. L. Roux. 2002. Development and application of a land capability classification system for South Africa. Unpublished ARC-ISCW report GW/A/2000/57. Agricultural Research Council-Institute for Soil, Climate and Water, Pretoria, South Africa.

Scholes, R. J., and R. Biggs. 2004. Ecosystem services in Southern Africa: a regional assessment. A contribution to the Millennium Ecosystem Assessment. CSIR, Pretoria, South Africa.

Scoones, I. 1994. New directions in pastoral development in Africa. Pages 1–36 *in* I. Scoones, editor. Living with uncertainty. Intermediate Technology Publications, London, UK.

Shackleton, C. M. 1993. Are the communal grazing lands in need of saving? Development South Africa 10:65–78.

Snyman, H. A. 1999. Short-term effects of soil water, defoliation and rangeland condition on productivity of a semiarid rangeland in South Africa. Journal of Arid Environments 43:47–62.

Sullivan, S., and R. F. Rohde. 2002. On nonequilibrium in arid and semiarid grazing systems. Journal of Biogeography 29:1–26.

Tongway, D., and N. Hindley. 2000. Assessing and monitoring desertification with soil indicators. Pages 89–98 *in* O. Arnalds and S. Archer, editors. Rangeland desertification. Kluwer, Dordrecht, The Netherlands.

Vermote, E. F., N. Z. El Saleous, and C. O. Justice. 2002. Atmospheric correction of MODIS data in the visible to middle infrared: first results. Remote Sensing of Environment 83:97–111.

Vetter, S. 2005. Rangelands at equilibrium and nonequilibrium: recent developments in the debate. Journal of Arid Environments 62:321–341.

Walker, B. H., N. Abel, D. M. Stafford Smith, and J. L. Langridge. 2002. A frame work for the determinants of degradation in arid ecosystems. Pages 75–94 *in* J. F. Reynolds and D. M. Stafford Smith, editors. Global desertification: do humans create deserts? Dahlem University Press, Berlin. Germany.

Watson, I. W., D. G. Burnside, and A. M. Holm. 1996. Event-driven or continuous; which is the better model for managers? Rangeland Journal 18:351369.

Wessels, K. J., S. D. Prince, P. E. Frost, and D. van Zyl. 2004. Assessing the effects of human-induced land degradation in the former homelands of northern South Africa with a 1 km AVHRR NDVI time-series. Remote Sensing of Environment 91:47–67.

Wessels, K. J., S. D. Prince, N. Zambatis, S. MacFadyen, P. E. Frost, and D. VanZyl. 2006. Relationship between herbaceous biomass and 1-km^2 Advanced Very High Resolution Radiometer (AVHRR) NDVI in Kruger National Park, South Africa. International Journal of Remote Sensing 27: 951–973.

Wessels, K. J., H. M. van den Berg, J. P. A. van der Merwe, H. J. Smith, A. van Zyl, and L. Twyman. 2001. Mapping and monitoring the conservation status of the natural resources of Mpumalanga province by means of remote sensing and GIS technology. Report Number GW/A/2001/9. ARC-Institute for Soil, Climate and Water, Pretoria, South Africa.

Westoby, M., B. H. Walker, and I. Noy-Meir. 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. Pages 145–153 *in* D. R. Strong, D. Simberloff, L. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and evidence. Harper and Row, New York, New York, USA.