



ELSEVIER

Journal of Arid Environments 60 (2005) 509–530

www.elsevier.com/locate/jnlabr/yjare

Journal of
Arid
Environments

Micro-patch and community scale spatial distribution of herbaceous cover in a grazed eucalypt woodland

B.K. Northup^{a,c,*}, C.D. Dias^{b,*}, J.R. Brown^{a,e}, W.C. Skelly^{c,d}

^a*Davies Laboratory, CSIRO Tropical Agriculture, PMB, Aitkenvale QLD 4814, Australia*

^b*Tropical Environment Studies and Geography, James Cook University, Townsville QLD 4810, Australia*

^c*USDA-ARS Grazinglands Research Laboratory, 7202 West Cheyenne, El Reno, OK 73036, USA*

^d*USDA-NRCS Jornada Experimental Range, P.O. Box 3003, Las Cruces, NM 88003-8003, USA*

^e*Ministry of Health, Safety & Regulation Branch, 133 Molesworth Street, P.O. Box 5013, Wellington, New Zealand*

Received 26 February 2004; accepted 24 May 2004

Available online 5 August 2004

Abstract

This study described changes in spatial distribution of herbaceous cover in experimental paddocks in a eucalypt woodland of northern Australia after 5 years of different grazing pressures and drought. Herbaceous cover was irregularly distributed, with high cover zones in distinct bands across slopes on paddocks in stable and degrading condition, and irregular patches in a degraded paddock. Size and density of these zones declined with paddock condition, as native perennial tussock grasses were lost and replaced by an exotic stoloniferous grass. Describing disturbance responses of herbaceous cover in this community requires sampling at multiple spatial scales.

Crown Copyright © 2004 Published by Elsevier Ltd. All rights reserved.

Keywords: Geostatistics; Grazing impacts; Landscape ecology; Spatial dynamics

*Corresponding author. USDA_ARS, Grazingland Research Laboratory, 7207W. Cheyenne Street, El Reno, OK 73036, USA.

E-mail address: bnorthup@grl.ars.usda.gov (B.K. Northup).

*Deceased.

1. Introduction

Spatial heterogeneity in the distribution of ecological characteristics is derived from sets of hierarchically organized factors (Meisel and Turner, 1998). These factors range from broad-scale characteristics (climate, geomorphology) at regional levels, through distribution patterns of organisms at intermediate scales, to biotic interactions at localized (individual plant) scales. Interactions among such multi-scale factors are thought to create distinct distribution patterns of organisms and soil resources within arid and semi-arid landscapes (Lavorel et al., 1993; Schlesinger et al., 1996). High levels of heterogeneity in the distribution of vegetal and soil characteristics have been noted in northern Australia (Ludwig and Tongway, 1995; Ash et al., 1999; Northup et al., 2003). In this area the entire range of variability of some attributes occurs at scales $< 100 \text{ m}^2$, and often at sub-metre scales in proximity to plants (Tongway and Ludwig, 1997, pp. 13–22; Jackson and Ash, 1998; Northup et al., 1999a). Disturbance related to grazing or climate can affect the organization of plants and soil characteristics in arid ecosystems across multiple scales (Behnke et al., 1993; Derner et al., 1997; Northup et al., 1999a), and the function of Australian landscapes (Ludwig et al., 1994; Tongway and Ludwig, 1997). Much of the land area in northern Australia has undergone some level of degradation (Tothill and Gillies, 1992). This damage appears related to a lack of understanding by producers on how spatial and temporal variability in rainfall and community responses affects landscape productivity (Brown and Ash, 1996). As such, the spatial pattern of plant communities and their disturbance responses must be quantified to help define management effects on landscape function (Turner, 1990; Weins et al., 1993; Tongway and Ludwig, 1997).

Landscapes in north Australia have fine-grained scales of organization that are critical to the conservation of limited resources, and ultimately productivity at larger scales (Tongway and Ludwig, 1994, 1997; Ludwig and Tongway, 1995). This fine-grained distribution of characteristics, and inherent variability found in distributions, means disturbance responses may be more accurately determined with high-resolution, spatially referenced data (Ash et al., 1999; Northup et al., 2003). However, assessments of land condition in the dry tropics regularly focus on coarser scales to match those at which management decisions are generally made (Friedel, 1990; Behnke et al., 1993). This can result in a limited understanding of landscape function in north Australia (Tongway and Ludwig, 1997), and assessments may not identify the early stages of change in condition (Northup et al., 2003).

Spatial analysis techniques like semivariogram, fractal, or spectral analyses can address questions about the organization of landscapes at different scales (Webster, 1985; Plotnick et al., 1993; Vasiliev, 1996, pp. 17–30). These tools have not received widespread use in some areas of ecological research due to their relative novelty, computational complexity, and use as descriptive analyses (Turner and Gardner, 1991; Meisel and Turner, 1998). However, they could help define variability in spatial patterns of soil and vegetal characteristics, temporal responses to disturbance, and outline potential impacts on landscape function. We undertook a

study to examine the spatial dynamics of herbaceous vegetation in a set of managed north Australian landscapes. The objectives were to compare spatial patterns in the distribution of herbaceous plants at different scales, and how management and climate influenced distribution patterns.

2. Materials and methods

2.1. Study site

Three sets of experimental paddocks ($n = 2$ per set) at the CSIRO ‘Cardigan’ research site near Charters Towers, Queensland ($20^{\circ}11'S$, $146^{\circ}43'E$) were included in the experiment. They were part of a larger study on grazing management of tropical woodlands during 1993–1998. Applied grazing regimes consisted of two use levels of current years herbage by yearling cattle, with or without wet season grazing deferments (Table 1). In the decade prior to application of grazing, the paddocks were ungrazed and in similar condition at the start of grazing in 1993. Condition of the paddocks in 1997 were described as stable, degrading and degraded based on herbaceous basal area, ground cover (litter and herbaceous plants) and standing crop, as noted by studies in similar plant communities (McIvor et al., 1995; Ash and McIvor, 1998).

The plant community was dry eucalypt woodland with an overstorey dominated by *Corymbia erythrophloia* (Blakely) K.D. Hill & L.A.S. Johnson and *Eucalyptus drepanophylla* F. Muell. ex Benth. trees (McIvor and Gardener, 1991). Composition of the herbaceous understorey depended on grazing history. The understorey of

Table 1
Grazing management of experimental paddocks on a dry eucalypt woodland, Queensland, Australia, during 1993 through 1997, and 1997 standing crop (± 1 S.D.)

Community type ^a	Utilization level (%) ^b	Stocking rate (ha/AU) ^c	Grazing deferment ^d	State ^e	Paddock size (ha)	Standing crop (kg/ha) ^f
Stable	25	5.0	Yes	I	1.3	1412(998)
Degrading	75	1.7	Yes	I	1.4	425(640)
Degraded	75	1.7	No	II	1.7	85(168)

^aAll paddocks were in similar condition ($1250 [\pm 250]$ kg/ha standing crop; $1.6 [\pm 0.5]\%$ basal area) prior to the initiation of grazing in 1993.

^bTarget utilization level of current years herbage by cattle.

^cWet season (December–April) stocking rate; AU represents one, 454 kg cow plus 136 kg of calf, or the equivalent amount of other grazing animals.

^dApplication of early wet season deferment from grazing.

^eCurrent condition of paddocks within a conceptual state and transition model for a north Australian woodland (Ash et al., 1994).

^fHerbaceous standing crop in 1997, as determined by BOTANAL procedures applied to 200, 0.5 m^2 quadrats per paddock prior to grazing (Tothill et al., 1992).

ungrazed and lightly grazed areas was dominated by the native tussock grasses *Bothriochloa ewartiana* (Domin.) C.E. Hubb., *Chrysopogon fallax* S.T. Blake, and *Themeda triandra* Forrskul. Paddocks receiving heavy grazing were dominated by mixtures of surviving *B. ewartiana*, *Bothriochloa pertusa* (L.) A. Camus (an exotic stoloniferous perennial), *Aristida* spp., annual grasses, and forbs. Soils are Haplic Eutrophic Red Chromosols (oxic Paleustalfs and Haplustalfs), and of moderate fertility (0.05% total N, 0.75% organic C) for north Australia (Ahern et al., 1994; Soil Survey Staff, 1994; Isbell, 1996). The climate is sub-humid, tropical, with an average (1984–1997) annual rainfall of 527 mm, with 80% received in November–April, and 1807 mm measured evaporation.

2.2. Data collection

Data were collected in August 1997 at community (1.3–1.7 ha paddocks) and micro-patch (3.0 × 4.2 m) scales, on one paddock receiving each treatment, to define distributions of projected herbaceous cover (Fig. 1). At the paddock scale, digital images ($n = 215$) were collected and processed by a system comprised of: a gantry frame mounted to a quadbike and supporting a digital camera to image 3.2 × 4.2 m plots; an electronic theodolite (total station) to record bearings (± 3 s. arc over 2.5 km) and distance to plot locations and elevations (± 5 mm per 1000 m); and readily available software to process images (Dias, 1997; Northup et al., 1999b). After collection, location data were transferred to computer, and plot positions rectified. Images were transferred to computer, and processed with image enhancement software to differentiate projected canopy cover of herbaceous plants from bare ground and surface litter (Northup et al., 1999b). These enhancements created images with cover and non-cover components represented by contrasting colours, and resulted in distinct pixel groupings in binary images (Dias, 1997). Percent of pixels in both classes were determined for each image.

At the micro-patch scale, cover was estimated on 3.0 × 4.2 m micro-patches by BOTANAL procedures (Tothill et al., 1992), an extensively used double-sampling technique based on dry-weight rank procedures to estimate vegetal characteristics. On each paddock, one micro-patch was located by randomly generated x , y coordinates, which served as the bottom left corner of the plots; the remainder of the micro-patches were located with long axes oriented parallel to the slope. Herbaceous cover was estimated within 0.3 × 0.3 m grids ($n = 140$), and an additional set ($n = 162$) of 0.1 × 0.1 m cells nested within 18 (nine, 0.1 × 0.1 m cells per larger grid) of the larger grids (Fig. 1); 16 were organized in a uniform pattern and two were randomly located.

Species dominance of herbaceous vegetation and basal area (percent of soil surface occupied by living tillers) of grasses was determined by BOTANAL procedures on 100, 0.5 m⁻² quadrates along two permanent transects per paddock ($n = 2$) receiving treatments in 1993 and 1997. BOTANAL (Tothill et al., 1992) is a double-sampling technique, including training in visual estimation and standardization procedures, used to assay herbaceous characteristics.

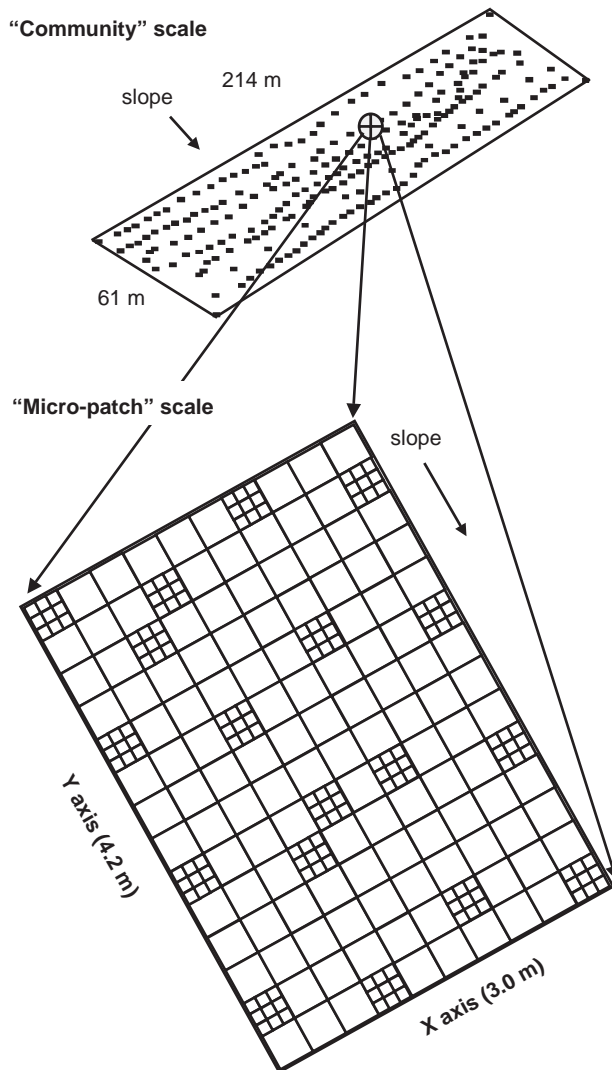


Fig. 1. Illustration of data collection points within paddocks and micro-patches. Examples represent locations of sample points on the stable paddock; \oplus indicates location of the intensively sampled micro-patch.

2.3. Data analysis

Changes in species dominance and basal area were tested by analyses of variance, with grazing treatment and year as the main effects, and transect means as replicates. Contrasts of significant differences ($p < 0.10$) were conducted with Fisher's protected least significant difference (Steel and Torrie, 1980).

Projected aerial cover at each scale (3.2×4.2 m at paddock scale; 0.3×0.3 m and 0.1×0.1 m grids at micro-patch scale) was rectified by equations describing relationships between field estimates and hand-measured cover (Northup et al., 1999b). Rectified cover of each plot was integrated with its spatial location, and distribution functions of cover at each scale were examined by exploratory analyses. The arcsin \sqrt{y} transformation was applied to all data prior to analyses (Steel and Torrie, 1980). Semivariance techniques were used to describe spatial distribution of cover by standardizing semivariograms by their sill variance (Rossi et al., 1992; Mathsoft Inc., 1996). The nugget (unexplained semivariance), sill (total semivariance), range (area of spatial auto-correlation), directional trends (anisotropy) and level of anisotropy in the distribution of cover were determined (Appendix A). Semivariogram models that most accurately defined distributions of cover across the sample areas for each data set were described.

Aerial cover, its location, and developed models (Appendix A) were used to interpolate the distribution of cover, corrected for anisotropy, at fine scales (1.0 m grid for paddock, 0.05 m for micro-patch) by regional kriging (Mathsoft Inc., 1996) and develop cover maps. At the community scale, micro-topographic features were interpolated from elevation data (ArcView, 1996). Finished interpolation maps of cover, elevation and micro-topography were integrated into community-scale (e.g. paddock) maps.

3. Results

3.1. Rainfall and paddock conditions

Rainfall during 1992–1997 was below the most-recent 14-year average for both annual and wet season periods, and ranged from 45% (1993) to 97% (1997) of the long-term average (Table 2). Species dominance and basal area of perennial tussocks within the paddocks were similar in 1993, and predominantly comprised of *B. ewartiana* and *C. fallax* mixtures (Table 3). In 1997, the degrading and degraded paddocks had significantly less area dominated by this complex, and the degraded paddock was dominated by *B. pertusa* and bare ground. Mean herbaceous cover was lower and variability higher on the degrading (c.v. = 41%) and degraded paddocks (c.v. = 60%), compared to the stable (c.v. = 25%) unit (Table 4). The highest and lowest ranges were noted on the degrading and degraded paddocks, respectively. Lower means were noted at the micro-patch scale, and ranges were smaller and lower on the degrading and degraded micro-patches. Variability in herbaceous cover was greatest on the degrading micro-patch (c.v. = 111% versus 61% and 67%). Observations at both scales had non-normal distributions in all three paddocks.

3.2. Semivariogram analyses

Semivariance of herbaceous cover was irregularly distributed at the paddock scale. Different ranges of spatially auto-correlated and unexplained semivariance (nugget),

Table 2

Rainfall and evaporation records of a dry eucalypt woodland, Queensland, Australia, during 1992 through 1997. Values in parentheses are ± 1 S.D

Years	Annual rainfall (mm)	Wet season rainfall (mm) ^a	Annual evaporation (mm)
1992	523	317	1881
1993	237	163	2003
1994	368	316	2030
1995	514	323	1847
1996	510	302	1765
1997	448	362	1571
Avg. (1984–1997)	527(164)	432(172)	1801(225)

^aWet season rainfall recorded from November of preceding year through May of current year.

Table 3

Species or bare patch dominance (% of quadrats), and basal area (% of soil surface) of perennial grasses, in a dry eucalypt woodland during 5 years of grazing. Values within species groups with the same letter were not significantly different ($P > 0.10$)

Paddocks	Dominance (%) ^a							
	<i>Boew/Chfa</i>		<i>Bope/Aris</i>		<i>Bare patch</i>		<i>Basal area</i>	
	1993	1997	1993	1997	1993	1997	1993	1997
Stable	83 a	78 a	0 b	2 b	0 b	2 b	1.6 a	1.8 a
Degrading	85 a	35 b	1 b	5 b	1 b	8 b	1.8 a	0.6 b
Degraded	81 a	12 c	3 b	62 a	3 b	19 a	1.6 a	0.1 c

^aCodes for species are: *Aris* = *Aristida* spp.; *Boew* = *B. ewartiana*; *Bope* = *B. pertusa*; *Chfa* = *C. fallax*; bare patch represents quadrats without rooted plants.

and best-fit models, were noted in minimum and maximum directions of anisotropy (Appendix A) in each paddock (Table 5). On the stable paddock (Fig. 2A), range of the direction of maximum anisotropy (135°) in spatial auto-correlation among neighbouring observations was 1.6 times the range of minimum (45°) anisotropy and omnidirectional analyses. The range for the direction of minimum anisotropy in auto-correlation (150°) on the degrading paddock (Fig. 2B) was similar to the omnidirectional semivariogram, while the range of maximum anisotropy (60°) was 1.5 times longer than the omnidirectional. A similar relationship was noted in the semivariograms of the degraded paddock (Fig. 2C). Unexplained semivariance (nugget) mostly became larger with level of accumulated grazing pressure. Nugget effects in the minimum anisotropy analyses were larger than for maximum anisotropy on the stable and degrading paddocks.

Semivariograms from minimum anisotropy analyses displayed “hole” effects (decrease in semivariance at the sill with increasing distance between observations) across portions of the ranges the stable and degrading paddocks over the 30–60 m

Table 4

Descriptive statistics of projected herbaceous cover (%) at two scales in experimental paddocks of dry eucalypt woodland under different grazing regimes

Paddocks	Community			Micro-patch		
	Stable	Degrading	Degraded	Stable	Degrading	Degraded
Sample no.	215	215	219	304	304	304
\bar{x}	60	41	30	38	18	9
S.D.	15	19	18	23	12	10
Minimum	14	6	0	0	0	0
Maximum	98	97	75	100	86	56
Skewness ^a	-0.53	0.32	0.44	1.66	3.04	3.76
Kurtosis ^b	0.42	-0.22	-0.41	2.31	12.26	17.52
K-S Normality ^c	0.09*	0.06*	0.08*	0.22*	0.29*	0.41*

^aFisher’s g1 test measuring symmetry about the mean. Positive values indicate a right-hand skew, negative values a left-hand skew.

^bFisher’s g2 test measuring flatness of the distribution, compared to kurtosis of a normal distribution (value of 0). Distributions with short tails have negative kurtosis.

^cKolmogorov-Smirnov normality test; alpha test value for normality = 0.05; * indicates a distribution significantly different from normal.

Table 5

Analyses of standardized semivariograms describing spatial auto-correlation of herbaceous cover of dry eucalypt woodland in different condition

Paddocks	Angle (deg) ^a	Nugget variance ($\gamma(h)$) ^b	Sill variance ($\gamma(h)$) ^c	Range (m) ^d	Best-fit models ^e
Omni-directional ^f					
Stable	—	0.19	0.84	28.0	Spherical
Degrading	—	0.39	0.69	22.9	Spherical
Degraded	—	0.50	0.53	18.5	Exponential
Minimum					
Stable	135	0.48	0.70	30.0	Spherical
Degrading	150	0.40	0.69	21.7	Spherical
Degraded	45	0.50	0.54	13.9	Spherical
Maximum					
Stable	45	0.17	0.91	48.0	Exponential
Degrading	60	0.23	0.86	32.0	Exponential
Degraded	135	0.47	0.62	31.0	Exponential

^aDirections across communities where variogram analyses were conducted by comparing neighbouring pairs of cover values.

^bPortion of total variance left unexplained by the analyses by application of best-fit models.

^cVariance explained by the analysis using the best-fit models.

^dDistance across which high cover values are spatially auto-correlated.

^eTheoretical models that best described distribution of cover values.

^fComparisons among neighbouring observations in all directions across communities; minimum and maximum anisotropies represent directions with lowest and highest anomalies in distribution of semivariance, respectively.

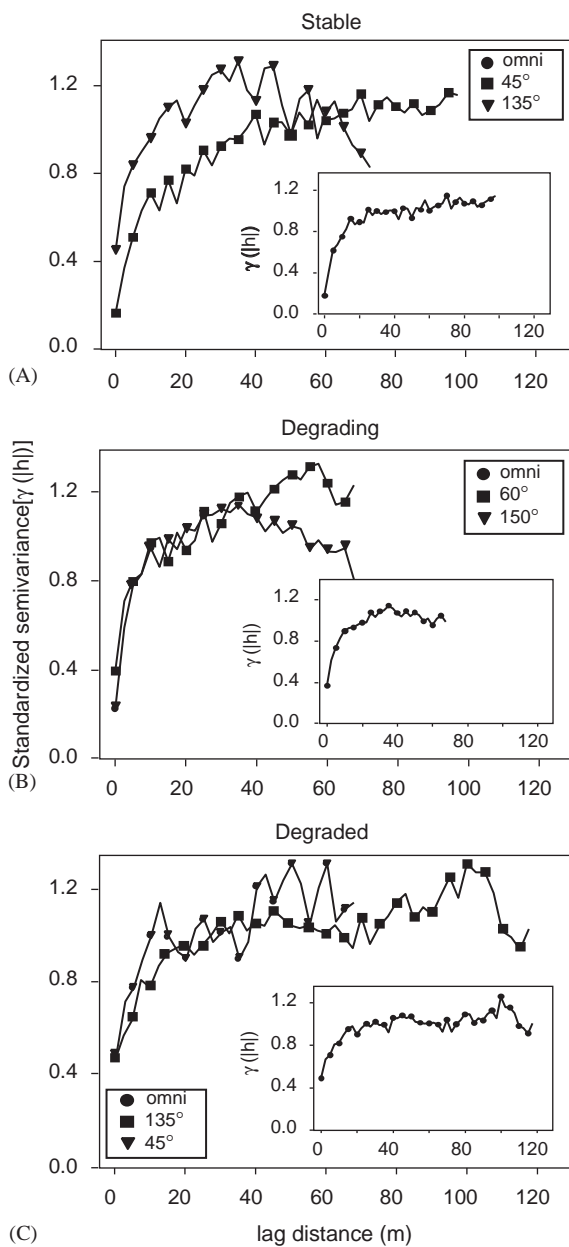


Fig. 2. Community-scale semivariograms of omni-directional (insets), minimum (triangles), and maximum (squares) directions of anisotropy for (A) stable, (B) degrading, and (C) degraded dry eucalypt woodland paddocks.

sections of the ranges (Fig. 2). Also, pronounced cyclic oscillations (5–15 m intervals) of variable amplitude (5–20% of sills) around the sills were noted on all three paddocks. Omnidirectional semivariograms following correction for anisotropy had longer ranges on the stable paddock (28.0 m) than the degrading (22.9 m) or degraded (18.5 m) units (Table 5).

Anisotropy was recorded on the micro-patches, but the effects were more diverse than at the paddock scale (Table 6). The greatest and least amounts of anisotropy were noted in the degrading and degraded micro-patches, respectively. Ranges of spatial autocorrelation were <0.85 m for directional and omnidirectional analyses on all micro-patches. The smallest ranges were noted for the degrading micro-patch (<0.2 m), compared to the other micro-patches (0.7 and 0.84 m). However, the differences in ranges of the directional analyses were similar to, or greater than at the paddock scale; maximum anisotropy was 1.6, 1.5, and 2.2 times that of minimum anisotropy on the stable, degrading, and degraded patches, respectively. Total semivariance (sills) defined in the stable (Fig. 3A) and degraded (Fig. 3C) micro-patches was more consistent than for the degrading (Fig. 3B) micro-patch. Nugget semivariance was lowest on the degraded micro-patch (<10% of sill) and highest on the degrading patch, which was the reverse of noted values at the paddock scale. Oscillations (0.2–0.5 m) around the sill were noted for all micro-patches, and a

Table 6

Analyses of standardized semivariograms describing spatial autocorrelation of herbaceous cover within 12.6 m² micro-patches of dry eucalypt woodland in different condition

Community	Angle (deg) ^a	Nugget variance ($\gamma(h)$) ^b	Sill variance ($\gamma(h)$) ^c	Range (m) ^d	Best-fit models ^e
Omnidirectional ^f					
Stable	—	0.28	0.74	0.49	Gaussian
Degrading	—	0.44	0.57	0.12	Exponential
Degraded	—	0.06	0.98	0.79	Gaussian
Minimum					
Stable	0	0.32	0.68	0.43	Gaussian
Degrading	0	0.62	0.40	0.09	Exponential
Degraded	135	0.12	1.00	0.75	Gaussian
Maximum					
Stable	90	0.32	0.75	0.66	Gaussian
Degrading	90	0.65	0.39	0.17	Exponential
Degraded	45	0.10	1.00	0.84	Gaussian

^aDirections across communities where variogram analyses were conducted by comparing neighbouring pairs of cover values.

^bPortion of total variance left unexplained by the analyses by application of best-fit models.

^cVariance explained by the analysis using the best-fit models.

^dDistance across which high cover values are spatially auto-correlated.

^eTheoretical models that best described distributions of cover values.

^fComparisons among neighbouring observations in all directions across micro-patches; minimum and maximum anisotropies represent directions with lowest and highest anomalies in distribution of semivariance, respectively.

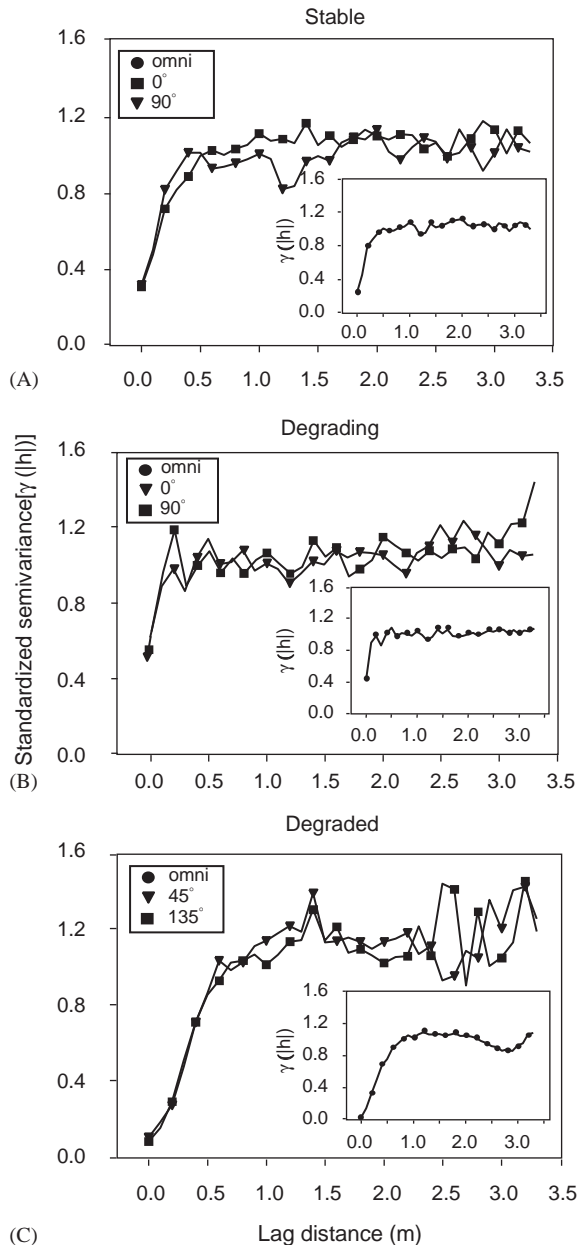


Fig. 3. Micro-patch scale semivariograms of omni-directional (insets), minimum (triangles), and maximum (squares) directions of anisotropy for (A) stable, (B) degrading, and (C) degraded dry eucalypt woodland.

“hole” effect (~ 2.5 m) was present on the degraded micro-patch, but not on the other micro-patches.

3.3. Interpolated herbaceous cover

Interpolated cover (1.0 m grid) produced “banded” patterns on the stable (Fig. 4A) and degrading (Fig. 4B) paddocks, with high cover bands separated by low cover areas. Low cover areas dominated much of the degrading paddock. High cover bands did not exist on the degraded paddock (Fig. 4C), but were present as smaller patches of variable (8–25 m) diameter. Band and patch orientation was defined by direction of anisotropy (Fig. 4, inset arrows). Maximum anisotropy (heavy arrows) in the stable and degrading paddocks was oriented parallel to high cover bands (across slope), while minimum anisotropy (light arrows) was oriented perpendicular to the bands. High cover patches on the degraded paddock were not oriented with respect to slope. Modelled micro-topography generated numerous first and second-order streamlets on the stable and degrading paddocks, and a smaller set on the degraded area (Fig. 4, lower halves). Streamlets on the stable and degrading paddocks appeared to originate in low cover areas and feed through high cover zones, but not on the degraded paddock. Interpolation errors were higher on degrading ($\bar{x} = 13\%$) and degraded ($\bar{x} = 14\%$) paddocks (stable paddock; $\bar{x} = 11\%$), and greatest in lightly sampled areas or along paddock boundaries.

Interpolated cover (0.05 m grid) on the micro-patches was also heterogeneously distributed. Small, localized zones of high cover with relatively regular distributions were noted on the stable (Fig. 5A) and degrading (Fig. 5B) micro-patches, and large areas with low herbaceous cover were present. High cover zones on the degraded (Fig. 5C) micro-patch were isolated in small areas, and surrounded by large areas with little or no cover. Mean interpolation errors were 13%, 15% and 11%, respectively, for the stable, degrading and degraded micro-patches; errors were highest along patch boundaries.

4. Discussion

Herbaceous cover of the paddocks exhibited radical differences in condition in response to grazing regimes and low rainfall. These combined factors caused a divergence in condition to where the paddocks were representative of: (a) conservatively grazed and productive landscapes (stable); (b) areas heavily grazed on a seasonal basis and losing condition (degrading); and (c) sites grazed continuously and heavily with little remaining herbaceous vegetation (degraded). As basal area and cover of the dominant tussock grasses were retained on the stable paddock, cumulative grazing pressures were the dominant factors affecting condition of the degrading and degraded areas (Tothill and Gillies, 1992). The below normal rainfall that occurred during the study likely exacerbated the effects of these grazing pressures. Alternatively, the lack of change by the plant community in the stable paddock in response to conservative grazing pressure indicates the integrity of

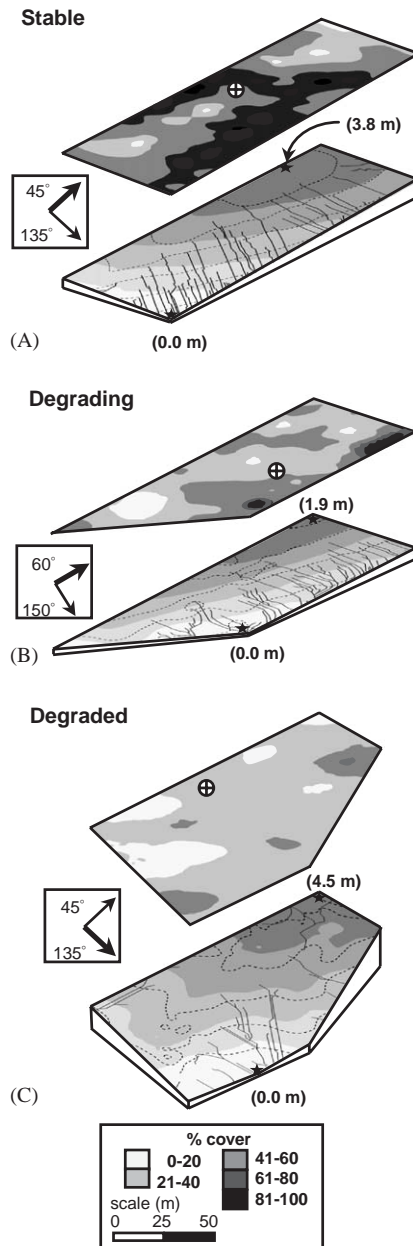


Fig. 4. Interpolated herbaceous cover (top sections) and elevation (bottom sections), with modelled micro-topographic features, of (A) stable, (B) degrading, and (C) degraded dry eucalypt woodland paddocks. Inset boxes represent directions of maximum (heavy arrows) and minimum (light arrows) anisotropy in distribution of herbaceous cover; \oplus were locations of intensively sampled micro-patches.

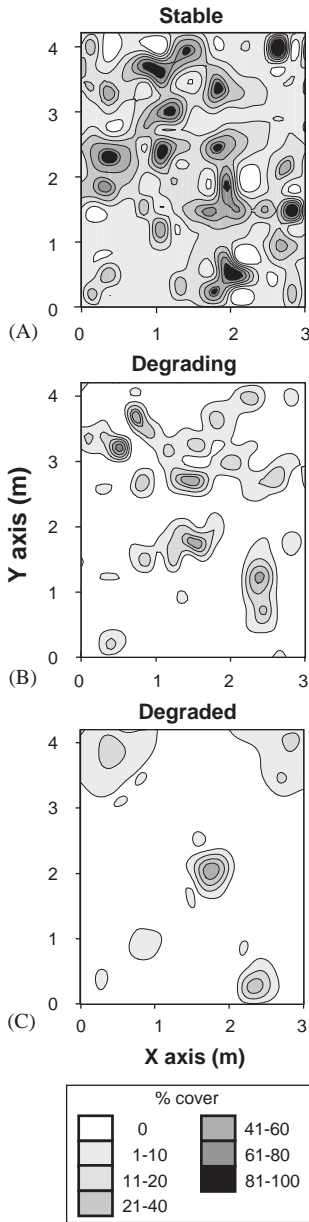


Fig. 5. Interpolated herbaceous cover of 12.6m^{-2} micro-patches in (A) stable, (B) degrading, and (C) degraded dry eucalypt woodland.

grazed plant communities is sustainable with proper grazing management, even in drought conditions. The differences in condition noted here are examples of the potential responses of this Australian plant community to disturbance as defined by

a conceptual state and transition model (Ash et al., 1994), ranging from State I (dominated by native tussock grass) to State II (dominated by weedy grasses and forbs) condition. The grazing pressures applied to the paddocks that lost condition were not entirely experimental contrivances. Some producers in northern Australia have applied similar stocking rates in the short-term, often with dire consequences (Tothill and Gillies, 1992; Brown and Ash, 1996).

Projected herbaceous cover was irregularly distributed at multiple scales within the three paddocks. At the larger scale, it was organized in asymmetric bands of high and low cover (as noted in semivariograms) with the long axes oriented cross-slope on the stable (1000–3000 m²) and degrading (600–1750 m²) paddocks. Within these bands, higher cover patches (15–185 m² groups of tussocks) were present, as noted in the oscillations along the sills of the semivariograms, and comprised of still smaller high production areas (0.03–0.39 m² individual tussocks), as noted in the micro-patch analyses. This complex distribution pattern is representative of the organization of herbaceous vegetation in north Australian landscapes (Tongway and Ludwig, 1990; Ludwig and Tongway, 1995), and at the community level of other arid ecosystems (White, 1971; Austin, 1981). The high cover bands we noted are thought to play key roles in the function of north Australian landscapes. They can operate as sinks where water and nutrients in storm runoff, generated in low cover (source) areas, interacts with biological components (plants) of the system and are incorporated into soil pools (Tongway and Ludwig, 1990, 1994; Northup et al., 1999a). Changes in this form of organization can reduce interactions between grass tussocks and runoff, and limit inputs into soil pools (Tongway and Ludwig, 1997).

In contrast to the stable and degrading paddocks, the degraded unit did not display the banded distribution pattern of native tussocks. Instead, “high” cover areas were largely comprised of patches of the exotic stoloniferous grass *B. pertusa*, organized as diffuse, low-cover mats of variable size. As a result, much of the degraded paddock had 20–40% cover and patches were not organized in relation to topography. At the micro-patch scale, only a few diffuse patches of *B. pertusa* and two *Aristida* tussocks (centre and lower right quadrants) were present in an area that was predominately bare ground. These patterns represented a shift in spatial distribution of plants that could result in changes in landscape function (Ludwig et al., 1994; Tongway and Ludwig, 1997). Theoretically, cover on the degraded paddock should have been restricted to smaller areas than were recorded (i.e. become patchier), since few native tussocks remained. However, the formation of low cover mats by *B. pertusa* appeared to ameliorate some of the impacts of heavy grazing. Vegetal conditions of this paddock may be in the initial stages of change to an alternate state, with the community dominated by an exotic grass of low productivity (Ash et al., 1994). Additional studies are required to address these questions.

‘Hole’ effects noted in semivariograms helped describe how high cover areas within the paddocks were organized. They represented situations in which semivariance in cover at some distance from the ranges (area across which semivariance among neighbouring observations were auto-correlated) was more similar to the ranges than the intervening spaces. This effect indicated the presence of shifts in cover from high (range) through low cover zones (sill) and back through

high cover areas (hole). This effect highlights how cover was distributed within the stable and degrading paddocks and the degraded micro-patch; dense bands or patches of cover concentrated in certain areas and surrounded by low cover zones. The heavily grazed paddocks had less high cover area (shorter ranges), and neighbouring low cover zones were considerably larger. Such results indicate that longer bare fetches with fewer areas containing high plant numbers were present. Such a change in distribution patterns means fewer interactions between plants and storm runoff may occur on degraded areas (Tongway and Ludwig, 1997).

Differences in distribution of herbaceous cover at the two scales, and how it was affected by grazing pressure, were also partially explained by the best-fit models used in analyses. Paddock-scale models (exponential and spherical) showed that spatial autocorrelation in semivariance among neighbouring observations changed abruptly, indicating transitions from high to low-cover zones across relatively 'short' distances. This further described the basic nature of cover distribution within this region—small, dense (e.g. high cover) patches of vegetation situated in areas of low cover and rapid transitions between the extremes (Ash et al., 1999). The high cover (and transition) areas, as per the semivariograms, were also reduced in size with increasing grazing pressure. Best-fit models at the micro-patch scale indicated that grazing effects on distribution patterns differed from the paddock scale. On the stable and degraded micro-patches (Gaussian models), autocorrelation changed more gradually (shifts from high to low cover were more continuous), but still changed abruptly (exponential) across smaller areas on the degrading micro-patch. This response indicates that size of 'high' cover zones on the micro-patches were first reduced as degradation increased (with loss of native tussocks), then enlarged as *B. pertusa* became prevalent in the degraded unit (Northup et al., 2003).

Unexplained semivariance (nugget) was noted at both scales, indicating some information could not be defined. Some of this effect apparently occurred at scales below those sampled (Hoosbeek, 1998), and may be related to interactions between sampling scale and grain size. Cover values from the sampled plots were homogenized means for different-sized areas. As such, information was lost due to "coarseness" of the plot sizes used in comparison to the grain size of cover (Turner and Gardner, 1991). Further, increasingly larger nugget effects were noted under the heavier grazing pressures. This effect apparently represented a management-induced reduction in grain size of cover, relative to plot sizes. Under the heavier grazing pressures, cover was more widely dispersed (reduced plant or patch numbers and sizes), and diffuse (lesser amounts where recorded). A logical extension of our analyses would be to combine sampling at micro-patch and paddock scales to broaden the scope of analyses (Kotlier and Wiens, 1990; Hoosbeek, 1998). However, cross-scale analyses have limited value for defining nugget effects, as coarse-scale information tends to mask fine-scale effects (Meisel and Turner, 1998). Capturing such information requires fine-grain measurements on large numbers of samples, evenly distributed within experimental units (Hoosbeek, 1998).

Our results indicate herbaceous cover in this part of north Australia has spatially and temporally variable distribution patterns that are best described by analysing data collected at multiple scales. They were similar to the findings of Lavorel et al.

(1993), who concluded landscape patterns were scale-dependent, and best understood within hierarchically organized scales. Inferences from this study are constrained as only one replicate per scale, per paddock condition, were included in analyses. This limits the scope of statements about the distribution of herbaceous cover and disturbance responses to a narrow region of the Australian dry tropics. However, they do provide examples of the variability that exists in grazed eucalypt woodlands. Results also identify an important component for future research; focus on the smaller scales of organization for an improved understanding of landscape function. One potentially fruitful area would be spatial and temporal dynamics in plant and soil responses at micro-patch or plant scales (Schlesinger et al., 1996; Northup et al., 1999a). Further, fractal analyses applied to data from multiple micro-patches could help further describe patch dynamics of herbaceous cover and bare ground in response to paddock management (Plotnick et al., 1993).

5. Conclusions

Grazing pressures applied to the heavily grazed paddocks changed intact and productive sites to less productive conditions within 5 years. The speed of this degradation emphasizes the susceptibility of north Australian grasslands to heavy grazing. Alternatively, patch structure and paddock productivity were sustained under conservative grazing. These results underscore the importance of balancing grazing pressure against ecological and climatic constraints to ensure long-term sustainable use of tropical tallgrass paddocks (Friedel, 1990; Hodgkinson, 1992, pp. 77–94). Herbaceous cover within this non-equilibrium area was heterogeneously distributed in space, as were temporal responses to disturbance. As such, the distribution of cover in north Australian plant communities should be examined by spatial analyses at different scales of organization. Such an approach would help produce an improved understanding of landscape structure and disturbance responses in managed landscapes.

Geostatistical techniques, particularly variogram analyses, could be helpful in defining the state of managed areas, or as warnings of potential approaching thresholds in land condition (Ash et al., 1994). The best use of variogram analyses in such applications would be in identifying changes in patch structure and size with the information found in range and nugget values, or hole effects. Reductions in range or hole effects would indicate reduction in size or loss of tussock patches, while increased nugget values would indicate potential reductions in grain of information; all would indicate changes in patch structure. Using variography in this fashion would not identify actual threshold values, but would indicate approaching changes in landscape organization and function.

Acknowledgments

Data were collected within studies of the Meat and Livestock Australia (MLA) funded project NAP3.205. The authors wish to express their appreciation to Mr. and

Mrs. C. Ferguson, Cardigan Station, Dalrymple Shire, Queensland, for the use of their land.

Appendix A

A.1. Variogram analysis

Semivariogram analyses include exploratory techniques that can define the spatial distribution of a characteristic within an area and its scale(s) of distribution. It uses one of a suite of theoretical models that best define how semivariance [$\gamma(h)$] is distributed within the space of the sampled area (Goovaerts, 1999). It examines the contribution of the average variance in a characteristic between pairs of points, separated by a specific distance, to the total sample variance (Isaaks and Srivastava, 1989). Values for adjacent observations are compared first, followed by every other observation, then every third observation, etc., across distances (between compared pairs) from the nearest (adjacent) observations to approximately 2/3 the size of the area encompassed by the data set (Meisel and Turner, 1998). Semivariance is defined mathematically as

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{n(h)} (X_i - Y_j)^2,$$

where h is the lag distance between observations; $\gamma(h)$ the semivariance at distance h ; $N(h)$ the number of pairs separated by h ; X_i the value of characteristic at the start of observed pair; and Y_j the value of characteristic at the end of observed pair (Goovaerts, 1999).

When semivariance is plotted against distance the variogram generally increases from a theoretical y intercept of zero, with no unexplained semivariance (nugget), and levels off at maximum (sill) semivariance. The distance across which semi-variance increases (range) represents the number of lags (e.g. area or distance) across which observed values for neighbouring observations are spatially auto-correlated (Fig. A1). Distances beyond this range represent pairs of observations that are not auto-correlated (Isaaks and Srivastava, 1989). The shape of the semivariance trace, based on the range, nugget, and sill can be defined by theoretical models that best describe the data, and can take any of a number of shapes (Fig. A1). These models describe how semi-variance is distributed in space around data points within a sampled area. In linear models, the variogram does not contain a maximum semivariance, but produces an ever-increasing distance in which observations are auto-correlated. Alternatively, cases where semivariance approximates a flat line at the sill are described as pure nugget effect, and spatial auto-correlation among observations could not be detected at the scale of sampling. Nugget values > 0 can also represent semivariance, that exists at scales finer than the sampling regime and cannot be defined, or instances of sampling error (Schlesinger et al., 1996).

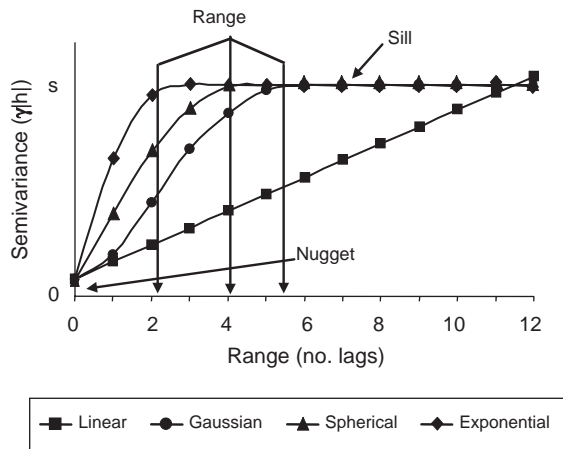


Fig. A1. Semivariograms showing organization of nugget, sill, and ranges of theoretical models commonly used in geostatistical analyses. Linear models have a continually increasing range across the sample area, and no sill.

A.2. Anisotropy

Anisotropy indicates irregularities in the distribution of a characteristic among neighbouring pairs of observations (Goovaerts, 1999). It represents a directional trend that results in a non-normal distribution (in space) of semivariance among observed values that must be identified and corrected (Mathsoft Inc., 1996). Directional variograms are calculated (along major cardinal directions across the sampled area) to test the shape of distribution of auto-correlation among pairs of observations, \pm an angle (22.5°) of tolerance along the directional axes. Minimum anisotropy represents directions across communities with lowest anomalies in semivariance, while maximum anisotropy represents directions with highest anomalies. Anisotropy is noted as differences in the range, nugget and sill between the directions tested. Directional variograms can also be compared to omni-directional variograms to examine anisotropy. Omni-directional variograms include all possible pairs of observations within the sampled space, \pm an angle of tolerance, across all directions. The greater the level of anisotropy noted, the larger the differences in ranges, nuggets and sills among variograms. Discontinuities in distribution may be related to biotic or abiotic phenomena within a sampled area (Rossi et al., 1992).

A.3. Kriging

Kriging is an unbiased method of developing estimates for a characteristic with minimum variance (Isaaks and Srivastava, 1989). Interpolation procedures are applied, using a model that best fits the semivariogram describing spatial auto-correlation among observations. Two assumptions are required for valid kriged

estimates: (1) data distributions are stationary (e.g. variance is due to separation distances between neighbouring observations); and (2) there is no anisotropy, or trends have been mathematically corrected. The assumption of stationary data is required if inferences are to be made for portions of a study plot not directly sampled (Yost et al., 1982).

References

- Ahern, C.R., Shields, P.G., Enderlin, N.G., Baker, D.E., 1994. Soil fertility of central and northeast Queensland grazing lands. Queensland Department of Primary Industries Information Series, Number Q194065, Brisbane, Australia, 88pp.
- ArcView, 1996. ArcView Spatial Analyst. Environmental Systems Research Institute, Inc., Redlands, WA, 147pp.
- Ash, A.G., McIvor, J.G., 1998. How season of grazing and herbivore selectivity influence monsoon tall-grass communities of northern Australia. *Journal of Vegetation Science* 9, 123–132.
- Ash, A.J., Bellamy, J.A., Stockwell, T.G.H., 1994. State and transition models for rangelands. 4. Applications of state and transition models to rangelands in northern Australia. *Tropical Grasslands* 28, 223–228.
- Ash, A.J., Corfield, J.P., Brown, J.R., 1999. Patterns and processes in loss and recovery of perennial grasses in grazed woodlands of semi-arid tropical Australia. In: Eldridge, D., Freudenberger, D. (Eds.), *Proceedings of the 6th International Rangeland Congress*, Townsville, Australia, pp. 229–230.
- Austin, M.P., 1981. Permanent quadrats: an interface for theory and practice. *Vegetation* 46, 1–10.
- Behnke, R.H., Scoones, I., Kerven, C., 1993. *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas*. Overseas Development Institute, London 260pp.
- Brown, J.R., Ash, A.J., 1996. Pastures for prosperity. 4. Managing resources: moving from sustainable yield to sustainability in tropical rangelands. *Tropical Grasslands* 30, 47–57.
- Derner, J.D., Briske, D.D., Boutton, T.W., 1997. Does grazing mediate soil carbon and nitrogen accumulation beneath C₄ perennial grasses along an environmental gradient?. *Plant and Soil* 191, 147–156.
- Dias, C.D., 1997. Quantifying land degradation in semi-arid environments using FIST (Fine-Scale Image Sampling Technique). Honours Thesis, James Cook University, Townsville, Australia, 85pp.
- Friedel, M.H., 1990. Some key concepts for monitoring Australia's arid and semi-arid rangelands. *Rangelands Journal* 12, 21–24.
- Goovaerts, P., 1999. Geostatistics in soil science: state-of-the-art and perspectives. *Geoderma* 89, 1–45.
- Hodgkinson, K.C., 1992. Elements of grazing strategies for perennial grass management in rangelands. In: Chapman, E.G. (Ed.), *Desertified Grasslands: Their Biology and Management*. Academic Press, London 360pp.
- Hoosbeek, M.R., 1998. Incorporating scale into spatio-temporal variability: applications to soil quality and yield data. *Geoderma* 85, 113–131.
- Isaaks, E.H., Srivastava, R.M., 1989. *An Introduction to Applied Geostatistics*. University Press, Oxford, UK 592pp.
- Isbell, R.F., 1996. . The Australian Soil Classification: Australian Soil and Land Survey Handbook Series, vol. 4. CSIRO Publishing, Collingwood, Australia 143pp.
- Jackson, J., Ash, A.J., 1998. Tree-grass relationships in open eucalypt woodlands of northeastern Australia: influence of trees on pasture productivity, forage quality and species distribution. *Agroforestry Systems* 40, 159–176.
- Kotler, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59, 253–260.
- Lavorel, S., Gardner, R.H., O'Neill, R.V., 1993. Analysis of patterns in hierarchically structured landscapes. *Oikos* 67, 521–528.

- Ludwig, J.A., Tongway, D.J., 1995. Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecology* 10, 51–63.
- Ludwig, J.A., Tongway, D.J., Marsden, S.G., 1994. A flow-filter model for simulating the conservation of limited resources in spatially heterogeneous semi-arid landscapes. *Pacific Conservation Biology* 1, 209–213.
- Mathsoft Inc., 1996. *S+ SpatialStats User's Manual*, Version 1.0. Mathsoft Incorporated, Seattle, WA, 357pp.
- McIvor, J.G., Gardener, C.J., 1991. A description of the ECOSSAT experimental site at cardigan near charters towers, North Queensland. CSIRO Tropical Agronomy Technical Memorandum Number 68, Brisbane, Australia.
- McIvor, J.G., Williams, J., Gardener, C.J., 1995. Pasture management influences runoff and soil loss in the semi-arid tropics. *Australian Journal of Experimental Agriculture* 35, 705–715.
- Meisel, J.E., Turner, M.G., 1998. Scale detection in real and artificial landscapes using semivariance analysis. *Landscape Ecology* 13, 347–362.
- Northup, B.K., Brown, J.R., Holt, J.A., 1999a. Grazing impacts on the spatial distribution of soil microbial biomass around tussock grasses in a tropical grassland. *Applied Soil Ecology* 13, 259–270.
- Northup, B.K., Brown, J.R., Dias, C.D., Skelly, W.C., Radford, B., 1999b. A technique for near-ground remote sensing of herbaceous vegetation in tropical woodlands. *Rangelands Journal* 21, 229–243.
- Northup, B.K., Brown, J.R., Ash, A.J., 2003. Using variability to identify potential state and transition stages of tropical tallgrass sites in northeast Australia. *Proceedings of the 7th International Rangeland Congress*, Durban, South Africa, pp. 2045–2047.
- Plotnick, R.E., Gardner, R.H., O'Neill, R.V., 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology* 8, 201–211.
- Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological Monographs* 62, 277–314.
- Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77, 364–374.
- Soil Survey Staff, 1994. *Keys to Soil Taxonomy*, sixth ed. Pocahontas Press, USDA Soil Conservation Service, Blacksburg, VA, 524pp.
- Steel, R.G.D., Torrie, J.H., 1980. *Principles and Procedures of Statistics: A Biometrical Approach*, 2nd ed. McGraw-Hill Book Company, New York 633pp.
- Tongway, D.J., Ludwig, J.A., 1990. Vegetation and soil patterning in semi-arid mulga lands of Eastern Australia. *Australian Journal of Ecology* 15, 23–34.
- Tongway, D.J., Ludwig, J.A., 1994. Small-scale resource heterogeneity in semi-arid landscapes. *Pacific Conservation Biology* 1, 201–208.
- Tongway, D.J., Ludwig, J.A., 1997. The conservation of water and nutrients within landscapes. In: Ludwig, J., Tongway, D., Freudenberger, D., Noble, J., Hodgkinson, J. (Eds.), *Landscape Ecology, Function and Management: Principles from Australia's Rangelands*. CSIRO Publishing, Collingwood, Australia 158pp.
- Tothill, J.S., Gillies, C., 1992. The pasture lands of northern Australia. Their condition, productivity, and sustainability. *Tropical Grassland Society Occasional Publication*, Number 5.
- Tothill, J.C., Hargreaves, J.N.G., Jones, R.M., McDonald, C.K., 1992. BOTANAL—A Comprehensive Sampling and Computing Procedure for Estimating Pasture Yield and Composition. 1. Field Sampling. CSIRO Tropical Agronomy Technical Memorandum Number 78, Brisbane, Australia.
- Turner, M.G., 1990. Spatial and temporal analysis of landscape patterns. *Landscape Ecology* 4, 21–30.
- Turner, M.G., Gardner, R.H., 1991. *Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity*. Springer, New York 563pp.
- Vasiliev, I.R., 1996. Visualization of spatial dependence: an elementary view of spatial autocorrelation. In: Arlinghaus, S.L. (Ed.), *Practical Handbook of Spatial Statistics*. CRC Press, Boca Raton, FL 307pp.
- Webster, R., 1985. Quantitative spatial analysis of soil in the field. *Advances in Soil Science* 3, 1–70.

- Weins, J.A., Stenseth, N.C., vanHorne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. *Oikos* 66, 369–380.
- White, L.P., 1971. Vegetation stripes on sheet wash surfaces. *Journal of Ecology* 59, 615–622.
- Yost, R.S., Uehara, G., Fox, R.L., 1982. Geostatistical analysis of soil chemical properties of large land areas. II. Kriging. *Soil Science Society of America Journal* 46, 1033–1037.