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Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia

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Abstract. Variation in structural and compositional attributes of tropical savannas are described in relation to variation in annual rainfall and soil texture along a sub-continental-scale gradient of rainfall in the wet–dry tropics of the Northern Territory, Australia. Rainfall varies along the gradient from over 1500 mm p.a. in the Darwin region (*c.* 12° S) to less than 500 mm in the Tennant Creek region (*c.* 18° S). Soils are patchy, and sands, loams and clays may occur in all major districts within the region. We utilized a large data set (1657 quadrats × 291 woody species; with numerous measured and derived sample variables) covering an area of 0.5 million km^2. Correlations between floristic composition of woody species and environmental variables were assessed using DCA ordination and vector fitting of environmental variables. Vectors of annual rainfall and soil texture were highly correlated with variation in species composition. Multiple regression analyses incorporating linear and quadratic components of mean annual rainfall and topsoil clay content were performed on three structural attributes (tree height, tree cover, tree basal area) and two compositional attributes (woody species richness, deciduous tree species richness). Tree height declined with decreasing rainfall; cover, basal area, woody species richness and deciduous species richness all declined with decreasing rainfall and increasing soil clay content. Regression models accounted for between 17% and 45% of the variation in the data sets. Variation in other factors such as soil depth, landscape position and recent land-use practices (for which there were no data on an individual quadrat basis) are likely to have contributed to the large residual variation in the data set.

Key words. Gradient analysis, rainfall, regression models, savanna, soil texture.

INTRODUCTION

Savannas are one of the world's most extensive biomes. They are generally defined as a discontinuous tree stratum overlying a continuous grassy ground layer, occurring in regions subject to a wet–dry tropical climate—summer rainfall and an annual winter dry season (Mott *et al.*, 1985; Walker & Menaut, 1988; Haynes, Ridpath & Williams, 1993). In Australia, this is approximately north-west and east of the northern 500 mm rainfall isohyet—northwest Western Australia, the northern half of the Northern Territory and north Queensland (Mott *et al.*, 1985), representing about 20% of the continent. The savannas of northern Australia are forests and woodlands (*sensu* Specht, 1981) and are the matrix within which other tropical ecosystems occur, such as rainforests (Russel-Smith, 1992) and floodplains (Whitehead, Wilson & Bowman, 1990).

In most of the world's tropical savannas population density is high. In Australia, by contrast, tropical savannas support a very low population—less than 5% of the total—and few areas have been cleared for agriculture (Ridpath, 1985; Anon, 1993). Partly as a result of this, the savannas of northern Australia are relatively intact ecologically (Woinarski & Braithwaite, 1990). Australia is thus the only country in the world with vast areas of savanna which are in a relatively unmodified condition. Their sustainable use will require a predictive understanding of their structure, function and resilience in the face of climatic and landscape variability, and disturbance.

The biotic and abiotic factors which determine the functioning of tropical savanna ecosystems at the landscape scale are not well-understood. Savannas occur under a wide range of moisture conditions, from humid to arid, and soil conditions, from light to heavy textured soils. Globally, therefore, it is hypothesized that the composition, structure and dynamics of savannas depend primarily upon the extent of the limitation and degree of variation in plant available moisture (PAM) and available nutrients (AN); secondary

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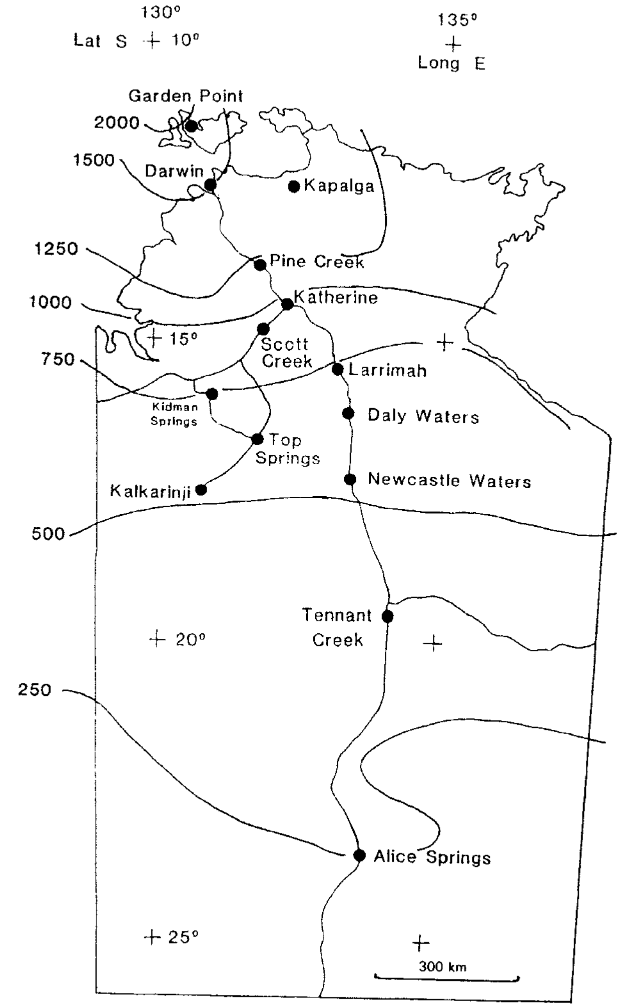

FIG. 1. Annual rainfall (mm) isohyet map of the Northern Territory.

determinants of savanna function are fire and herbivory (Goldstein, Medina & Werner, 1988; Skarpe, 1992). Savanna attributes which are important globally include the abundance and structure of the tree stratum, the composition of the tree stratum in terms of deciduous and evergreen elements, the standing crop and productivity of the grasses, the relative abundance of annual grasses and perennial grasses, and the fauna, both vertebrate and invertebrate. There have been no attempts, as far as we know, to assess the importance of variation in PAM and AN in relation to these key savanna attributes across sub-continental- and continental-scale gradients of soil and moisture. In this paper, we present a set of such analyses for the savannas of the Northern Territory.

In the northern half of the Northern Territory, there is a pronounced rainfall gradient from the humid, coastal regions of the Darwin region, where annual rainfall generally exceeds 1500 mm, to the semi-arid region of Katherine/Daly waters, to the arid interior of the Tennant Creek region, where annual rainfall is less than 500 mm (Fig. 1; Anon, 1975). There is substantial variation in soil texture along this moisture gradient, although the variation is not systematic along the gradient (Isbell, 1983). At the broadest, sub-continental scale, the savannas of the NT tend to be moist/dystrophic or arid/eutrophic, like many of the world's savannas (e.g. Huntley, 1982). Sands, loams and clays may occur in each of the humid, semi-arid and arid rainfall zones. The savanna vegetation consists of a discontinuous woody overstorey, usually of *Eucalyptus*, but sometimes *Acacia*, and an understorey of annual and/or perennial grasses. Thus, the biophysical gradients of the wet–dry tropical, northern half of the Northern Territory are ideally situated to test hypotheses concerning the interaction between rainfall and soil type as determinants of savanna form and function.

Studies of continental-scale biophysical gradients in moisture, temperature and landuse have been proposed as a means of assessing the potential responses of the world's ecosystems to global environmental change (Anon, 1994). Numerous transects through such gradients have been established, or are proposed, which cover the major biomes of the world. In the savanna regions, several transects have been established—e.g. in the Côte d'Ivoire region of West Africa, in the Kalahari region of southern Africa and the Northern Territory (the North Australian Tropical Transect, NATT). Recently, there have been ecological studies along such gradients, e.g. Egan & Williams (1996), Matheson & Ringrose (1994) in the NT; Specht & Specht (1989a,b) across Australia; Schulze *et al.* (1991) in Namibia, O'Brien (1993) across southern Africa and Ruess & Seagle (1994) in the Serengeti.

The aim of this paper is to assess the extent to which variation in a set of compositional and structural attributes of savannas along the sub-continental-scale biophysical gradient of the Northern Territory can be accounted for by variation in two broad-scale surrogates for PAM and AN—mean annual rainfall and soil texture. In this preliminary analysis, we ask—to what extent can functional attributes of savannas be predicted on the basis of the two simplest landscape attributes—annual rainfall and soil texture—across a substantial region of savanna? We concentrate on the woody component of the savannas; subsequent studies will examine attributes of the ground stratum.

METHODS

The data set

The study was based on a large species × quadrat data set, used recently in the production of the vegetation map of the Northern Territory (Wilson *et al.*, 1990). The full data set consists of approximately 2000 quadrats (each 20 m × 20 m) defined by the cover-abundance measures of some 2000 species, and numerous measured and derived sample variables. We have restricted our analyses to approximately half the data set—those quadrats which lie north of 18° S within the NT. This is because, within this region, annual rainfall is predictably summer-dominant from year to year, rain occurs in all years, and the vegetation is predominantly tropical savanna. Within this region, sixty-six different vegetation types, mostly savannas, were mapped by Wilson

TABLE 1. Structural, compositional and environmental variables for each 20 × 20 m quadrat, either recorded by Wilson *et al.* (1990), or subsequently derived, which are of relevance to the present study.

Structural variables	Compositional variables	Environmental variables
Tree:	Tree species	Annual rainfall
Height	Tree species richness	Soil clay (%)
Basal area	Deciduous tree richness	Rock cover
Cover		Slope
		Gravel (%)
		Aspect
		Bare ground
		Latitude/Longitude
		Rainfall coolest quarter
		Rainfall warmest quarter
		Coefficient of variation, annual rainfall

et al. (1990) at a scale of 1:1,000,000. The vast majority of the savannas were dominated by eucalypts, but for our analyses several non-eucalypt savanna types, such as *Acacia* forests, *Melaleuca* forests and treeless grasslands, were included. Non-savanna units such as tidal/littoral complexes and rainforests (closed forests) were excluded from the analyses. We have restricted our analyses to the woody component of the flora as the presence/absence and abundance data of the herb layer were not considered to be sufficiently robust, given that some sampling occurred during the dry season when the herbaceous layer was potentially desiccated and/or burnt. The data are stored on the DECODA data base (Minchin, 1990), and housed at the Wildlife Research Section of the Parks and Wildlife Commission of the Northern Territory.

For each quadrat, a series of additional variables—latitude, longitude, slope, rock cover, gravel content and surface soil texture—were recorded at the time of survey by Wilson *et al.* (1990). For each woody species, quantitative attributes such as cover, basal area, and qualitative attributes (life form, deciduousness) were also determined. In addition to these variables, we estimated mean annual rainfall from latitude and longitude, using an Australia-wide climatic predictive package BIOCLIM (Busby, 1990). Clay content of the topsoil was calculated as the mid-point percentage of clay in each of six standard texture classes of the topsoil (McDonald & Isbell, 1984), which were assessed during the field survey. A summary of the major sample and species variables—both measured and derived—utilized in this study is given in Table 1.

Data analysis

We used a variety of numerical techniques—direct gradient analysis, indirect gradient analysis (ordination) and multiple regression—to assess the extent to which variation in structural and compositional attributes of the woody species could be accounted for by variation in rainfall and soil texture.

(1) Direct gradient analysis

A direct gradient analysis was undertaken on the dominant savanna units (as defined by Wilson *et al.*, 1990) within the northern NT. Forty savanna units were chosen, and for each the mean estimated annual rainfall and the mean surface soil clay content was calculated. The number of quadrats within each of the forty units varied, but was always greater than ten. The position of the unit was then plotted in two dimensions, defined by mean rainfall and mean clay content of the constituent quadrats.

(2) Indirect gradient analysis

An indirect gradient analysis (ordination) was carried out on the individual quadrats of the 40 savanna units, using detrended correspondence analysis (DCA; Hill & Gauch, 1980), on the basis of floristic presence–absence of the woody species. Species which occurred in less than 5% of samples were excluded. The final data set was a matrix of 1657 samples × 291 species. For data display, the ordinations have been restricted to two dimensions, as addition of third and subsequent axes did not add to the interpretation of the pattern. Vector fitting (Kantvilas & Minchin, 1989) was undertaken on the two dimensional DCA ordination to determine vectors of maximum correlation for various environmental variables listed in Table 1. The mean score on each of DCA axes 1 and 2 was calculated for each savanna vegetation community (as defined by Wilson *et al.*, 1990) from the individual axis scores of the constituent quadrats in each group.

(3) Multiple regression analyses of structural and compositional attributes in relation to rainfall and soil texture

The relationship between annual rainfall, soil texture and a suite of univariate savanna attributes (both structural and compositional) was tested using least squares multiple regression models, with rainfall and soil clay content as the predictor variables. Preliminary principal components analysis, using the environmental variables in Table 1 indicated that rainfall and clay were independent, because rainfall had a high loading on PCA1, and a low loading on PCA2, whilst clay content had high/low loadings on PCA2 and PCA1 respectively. Three structural attributes were analysed: maximum tree height, average tree canopy cover and total tree basal area. The two compositional attributes were total woody species richness and deciduous tree species richness. Quadrats were excluded from the analyses if structural data such as height and cover were missing or if soil data were missing. This reduced the data set to 940 quadrats. Canopy cover and tree basal area data were log-transformed, to normalise frequency distributions. Linear and quadratic functions of both rainfall and soil texture were fitted initially as the full model. Interactions were also tested, but most low-order interactions and all higher order interactions between these terms were nonsignificant, with virtually no improvement in the R^2 of the equations. Statistical analyses were performed using SYSTAT (Wilkinson, 1988). Response surfaces were generated from the regression equations using SYGRAPH (e.g. Shipley *et al.*, 1991), appropriately back-transformed for those variables which had been log-transformed.

RESULTS

Direct gradient analysis

The direct gradient analysis is given in Fig. 2a and b, respectively for the community types (see Table 2 for details) and structural types (*sensu* Specht, 1981). Within the environmental space defined by rainfall and clay, there is considerable separation of the floristic units, (as defined by Wilson *et al.*, 1990). The distribution of soils is patchy, with a greater range of textural classes apparent in the low rainfall sectors of the gradient than at the high rainfall end. The predominant soils in the wetter end of the gradient are loams and sands associated with extensive, highly laterized bedrocks. Clay soils are more extensive in the drier sectors of the gradient, and are primarily associated with extensive Early Palaeozoic basalt formations in the Victoria River District, and Lower Palaeozoic carbonates in the Barkley Tableland region.

At the wet end of the gradient, the vegetation is characterized by open forests or woodlands of *Eucalyptus miniata* and *E. tetrodonta*, on sand-loam soils (e.g. Units 3–9; nomenclatural authorities are given in Wilson *et al.*, 1990). Forests and woodlands dominated by these two species are widely distributed over the NT, with respect to latitude and rainfall, but are restricted to lighter soils. The heavier soils in the wetter regions are associated with the floodplains of the major river systems, and are characterized by *Melaleuca* forests and various grasslands and sedgelands. As rainfall decreases there is a trend from taller vegetation (forests and woodlands) in high rainfall situations, to low, sparse vegetation (low open-woodlands and grasslands); a similar trend is evident as clay content increases. Where rainfall is low and clay content high, the vegetation is essentially grassland with scattered trees, the most common of which are *Eucalyptus microtheca* and *Terminalia arostrata*.

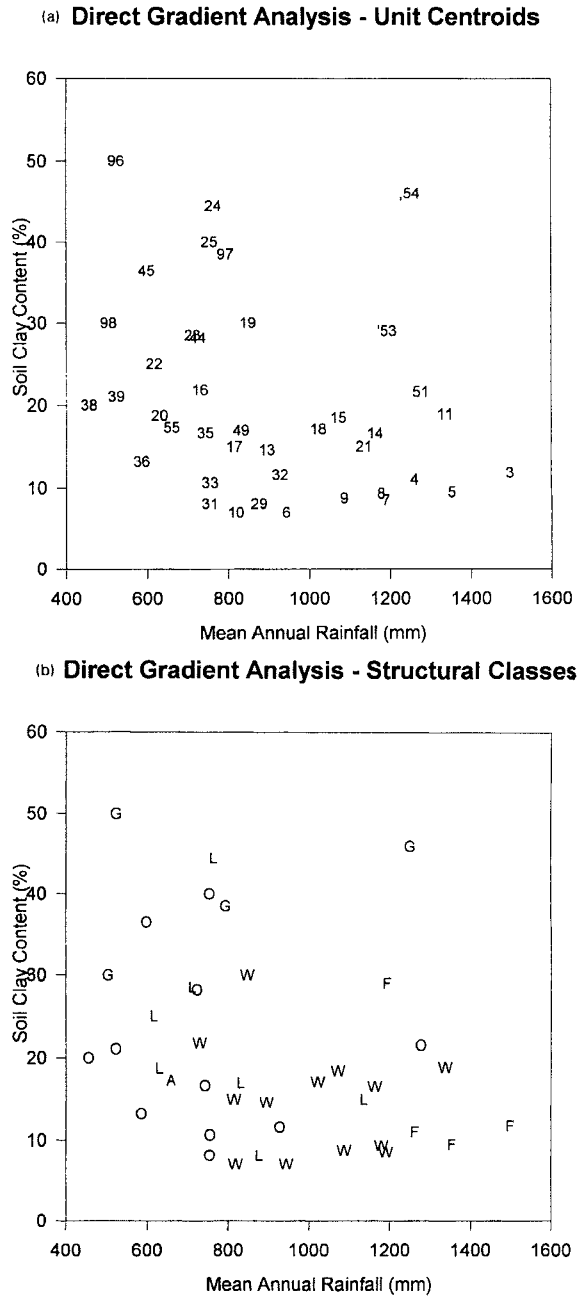

FIG. 2. Direct ordination of community types as defined by Wilson *et al.* (1990). (a) Ordination of Unit numbers (are those of Wilson *et al.*, 1991; see Table 2). (b) Ordination of structural classes (after Specht, 1981). Forest (F), woodland (W), open-woodland (O), low open-woodland (L), *Acacia shirleyi*—lancewood—woodland (A), grassland (G).

DCA Ordination and vector fitting

The DCA ordination of the data (Fig. 3a,b) showed considerable separation of savanna vegetation types on the basis of floristic composition along DCA axes 1 and 2, which together accounted for 50% of the variation in the data. The floristic gradient from left to right along Axis 1 of the DCA corresponds to gradients in vegetation structure (open-forests to low open- woodlands and grasslands) and moisture (moist to dry). The open-forests and woodlands dominated by *Eucalyptus miniata* and *E. tetrodonta* (groups 3–13) are clustered, indicating relatively little floristic variation, despite wide latitudinal distribution (Fig. 2a,b). Units associated with heavier, clay soils in drier situations (Units 44, 45 96–8) are also relatively tightly clustered. Unit 55—open forest dominated by *Acacia shirleyi* (lancewood)—is a clear floristic outlier. The vectors of maximum and significant correlation to the ordination axes

TABLE 2. Summary data for the forty savanna vegetation units defined by Wilson *et al.* (1990) which were used in the present study. Structural formations after Specht (1981). Generic abbreviations: C., *Callitris*; D., *Dichanthium*; E., *Eucalyptus*; Ex., *Exoecaria*; L., *Lysiphyllum*; M., *Melaleuca*; T., *Terminalia*.

Unit no.	Dominant species	Structural formation
3	*E. miniata/tetrodonta/nesophila*	Open-forest
4	*E. miniata/tetrodonta*	Open-forest
5	*E. miniata, C. intratropica*	Open-forest
6,7	*E. tetrodonta, C. intratropica*	Woodland
8	*E. tetrodonta/miniata/ferruginea*	Woodland
9	*E. tetrodonta/miniata/bleeseri*	Woodland
10	*E. tetrodonta*	Woodland
11	*E. miniata*	Woodland
13	*E. miniata/tetrodonta/dichromophloia*	Woodland
14	*E. tetrodonta/tectifica*	Woodland
15	*E. tectifica/latifolia*	Woodland
16	*E. tectifica/terminalis*	Woodland
17	*E. dichromophloia/tetrodonta*	Woodland
18	*E. papuana/polycarpa*	Woodland
19	*E. terminalis/patellaris*	Woodland
20	*E. dichromophloia*	Low woodland
21	*E. tintinans*	Low woodland
22	*E. terminalis/chlorophylla*	Low woodland
23	*E. pruinosa*	Low woodland
24	*E. microtheca, Exoecaria parvifolia*	Low woodland
25	*E. microtheca*	Low open-woodland
29	*E. phoenecea*	Low woodland
31	*E. dichromophloia/tetrodonta*	Low open-woodland
32	*E. dichromophloia/miniata*	Low open-woodland
33	*E. dichromophloia*	Low open-woodland
35	*E. leucophloia*	Low open-woodland
36	*E. leucophloia*	Low open-woodland
38	*E. brevifolia*	Low open-woodland
39	*E. pruinosa, L. cunninghamii*	Low open-woodland
44	*T. arostrata*	Low open-woodland
45	*L. cunninghamii, E. pruinosa*	Low open-woodland
49	*Melaleuca citrolens*	Low woodland
51	*M. viridiflora, E.* spp.	Low open-woodland
53	*Melaleuca* spp.	Open-forest
54	Mixed grasses & sedges	Grassland
55	*Acacia shirleyi*	Open-forest
96	*Astrebla pectinata*	Grassland
97	*Astrebla*	Grassland
98	*Chrysopogon fallax, D. fecundum*	Grassland

are also shown in Fig. 3a. Vectors with the highest correlation with the variation in floristic composition were mean annual rainfall ($r=0.77$, $P<0.001$) and soil clay content ($r=0.58$, $P<0.001$). Associated vectors with a significant correlation were gravel content ($r=0.26$; $P<0.01$) surface rock cover ($r=0.26$, $P<0.01$) and slope ($r=0.17$, $P<0.01$).

Multiple regression analyses of structural and compositional attributes in relation to rainfall and clay content

Response surfaces of the structural and compositional attributes as a function of annual rainfall and clay content are given in Figs 4–8. Regression equations relating structural variables to annual rainfall and soil clay content are summarized in Table 3. Incorporation of other rainfall characteristics—such as the co-efficient of variation of annual rainfall, and rainfall in the coolest/warmest quarters—as predictors in the regression models generally resulted in lower r^2 values than those given by the annual rainfall•soil models presented in Table 3. The models which variously incorporated linear and quadratic components of annual rainfall and clay were all highly significant ($P<0.001$) and accounted for 17–45% of the variation in the respective response variables. The amount of variation explained by the models was higher for the structural attributes than for the compositional attributes. All variables generally decreased with decreasing rainfall and increasing clay content, but the forms of the responses were in general non-linear.

Tree height showed a significant, positive response to the quadratic component of rainfall (Fig. 4; Table 3). Equations for tree cover (log transformed) included the linear component of rainfall (positive), and both linear (positive) and quadratic (negative) components of clay (Fig. 5; Table

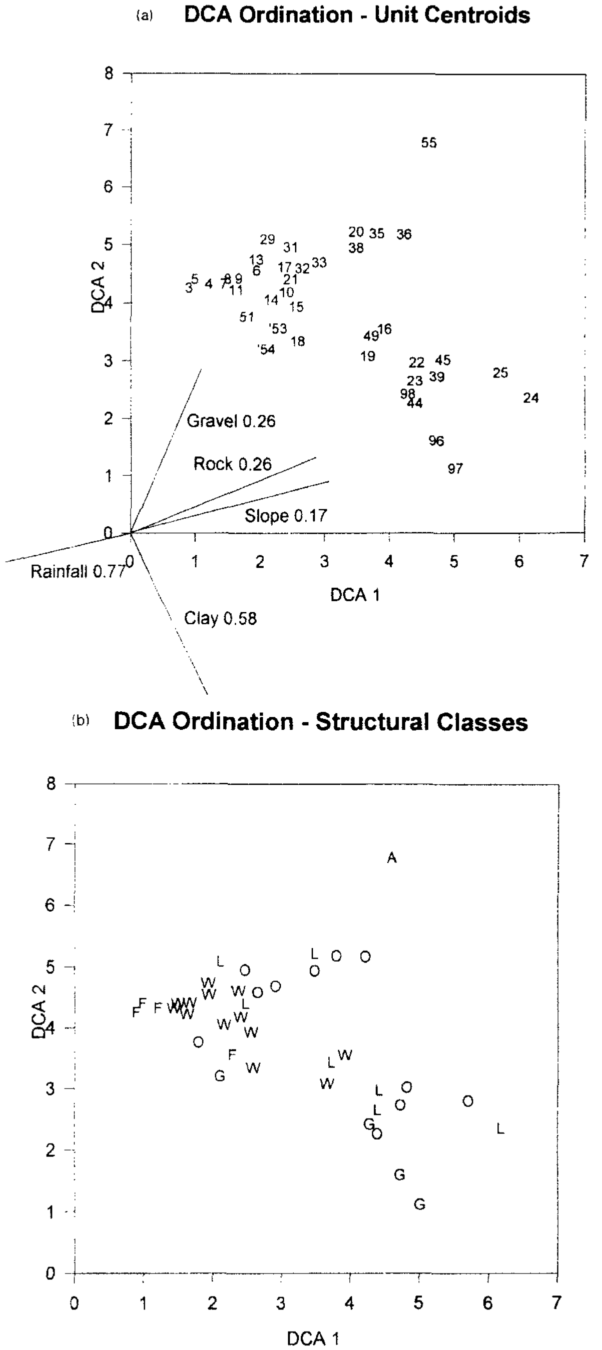

FIG. 3. DCA ordination of Units, as defined by Wilson *et al.* (1990). (a) Ordination of Unit numbers. Fitted vectors, and the associated *r*-values, relating annual rainfall (Rainfall), clay content of topsoil (Clay), Slope, % rock cover of quadrat (Rock) and % gravel content of soil (Gravel) are indicated. (b) Ordination of structural types. Symbols as in Fig. 2.

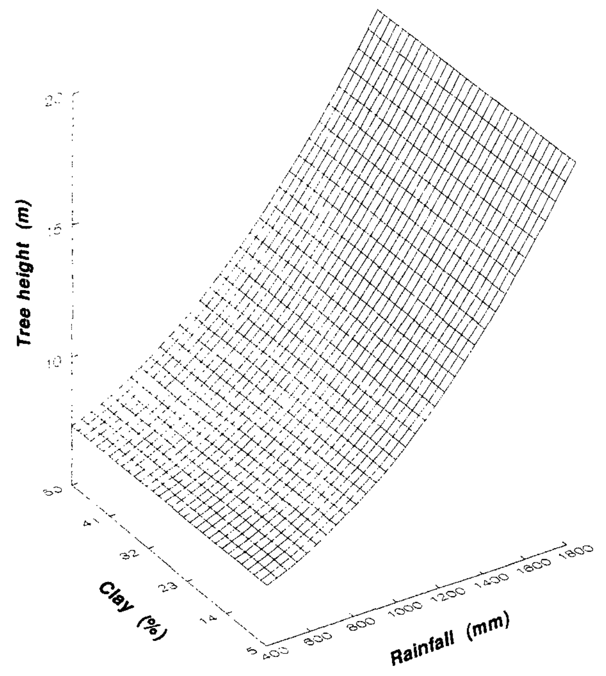

FIG. 4. Response surface of tree height (m) as a function of annual rainfall (mm) and clay content (%) of the soil. See Table 3 for regression equations, for Figs 4–8.

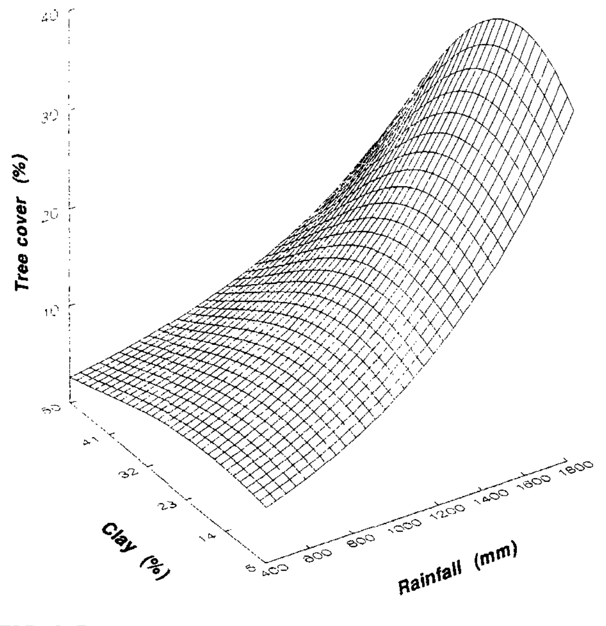

FIG. 5. Response surface of tree canopy cover (%) as a function of annual rainfall (mm) and clay content (%) of the soil.

3): those for basal area (log transformed) included the linear component of rainfall (positive), and the quadratic component of clay (negative: Fig. 6; Table 3). With respect to the compositional variables, woody species richness varied with the linear and quadratic components of rainfall, and the quadratic component of clay. Deciduous tree richness had the most complex response surface, varying with both linear and quadratic components of both rainfall and clay (Figs 7–8; Table 3). The response surface of deciduous tree richness was more complex than those of the other response variables, due to the significant (albeit small) negative coefficient associated with the quadratic component of rainfall. This indicates that deciduous tree richness declines with increasing rainfall above about 1800 mm p.a. The relationship between deciduous tree

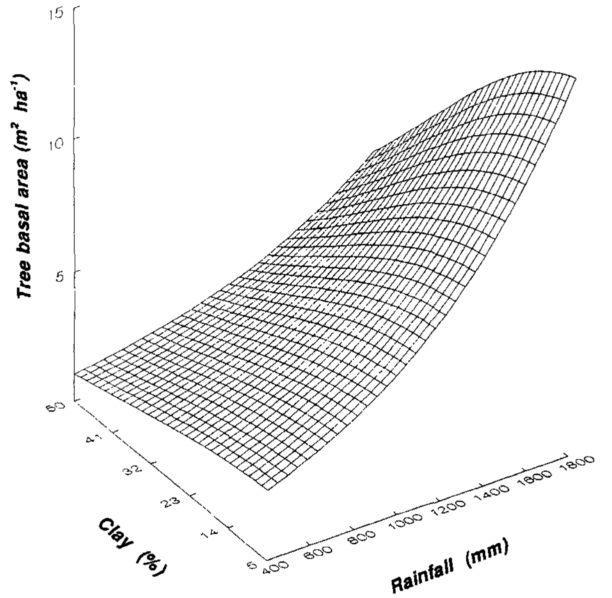

FIG. 6. Response surface of tree basal area ($m^2\,ha^{-1}$) as a function of annual rainfall (mm) and clay content (%) of the soil.

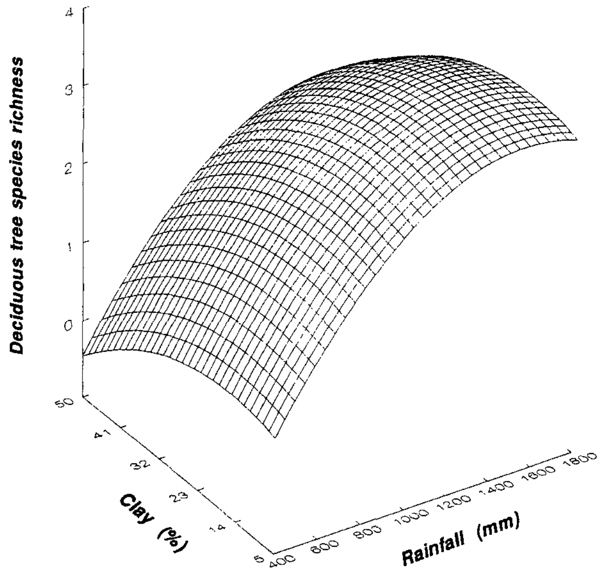

FIG. 8. Response surface of deciduous tree species richness (Number of deciduous trees per 20 × 20 m plot) as a function of annual rainfall (mm) and clay content (%) of the soil.

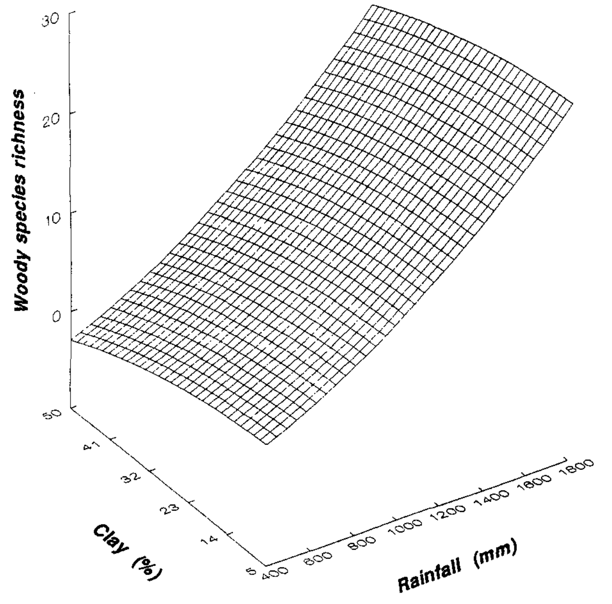

FIG. 7. Response surface of woody species richness (Number of woody species per 20 × 20 m plot) as a function of annual rainfall (mm) and clay content (%) of the soil.

richness, rainfall and clay had the lowest r^2 (0.17), indicating that the quadratic models were not a good predictor of the response variable. Models fitting higher order polynomial functions to these data, however, did not increase the amount of variation explained by the predictor variables.

DISCUSSION

The key compositional and structural attributes of the savannas of the wet–dry tropics of the Northern Territory were strongly related to variation in mean annual rainfall and the clay content of the topsoil. This was clear in each of the three types of analysis which were undertaken—direct gradient analysis, DCA ordination and multiple regression modelling. In the direct gradient analysis, there was clear separation of the floristic groups defined previously by Wilson *et al.* (1990) along axes defined by rainfall and clay content. In the DCA ordination, the strongest correlations with the floristic gradients of the ordination were those of rainfall and soil clay content. Finally, in the regression analysis, models incorporating various linear and quadratic terms of rainfall and clay content were all highly significant, accounting for between 17% and 45% of the variation in the dependent variables.

Tree performance, as measured by height, cover and basal area, and woody species diversity, decreased with decreasing rainfall and, for the latter two variables, increasing clay content. At present we cannot elucidate the underlying mechanisms for these phenomena. More precise estimates of PAM (especially) and AN will be required ultimately to model such patterns. In addition, at the wet end of the gradient, the role of soil texture as a determinant of tree performance may be confounded with that of surface and sub-surface hydrology. Clay soils are associated with the flood plains of the major rivers, and are waterlogged for the duration of the wet season and well into the dry season (Whitehead *et al.*, 1990).

Our results concur with other predictive studies along continental-scale climatic gradients in North America, Europe and Australia. With respect to tree performance, Specht & Specht (1989b) have indicated that, along moisture gradients across Australia, Foliage Projective Cover (FPC; %) is positively correlated with the evaporative coefficient of the atmosphere (an index of site moisture availability). With respect to soil, Fensham & Kirkpatrick (1992)

TABLE 3. Summary of regression models used to predict response variables from linear and quadratic components of mean annual rainfall (RAIN; $RAIN^2$) and topsoil clay content (CLAY; $CLAY^2$). Response variables are tree height (HEIGHT); tree cover (COVER, log transformed); tree basal area (AREA, log transformed); woody species richness (WOODYRICH) and deciduous tree species richness (DECRICH). (SE); standard error of the coefficient. NS; non significant component of the final model (P>0.05). For all models, the significance of the regression is P<0.0001.

Response variable	Constant	Rain	$Rain^2$	Clay	$Clay^2$	R^2	n
log HEIGHT	6.699	NS	0.000004	NS	NS	0.45	940
(SE)	(1.38)		(<0.000001)				
log COVER	1.124	0.0013	NS	0.0268	−0.0008	0.35	940
(SE)	(0.10)	(0.0001)		(0.006)	(0.0001)		
log AREA	0.519	0.0012	NS	NS	−0.00037	0.35	940
(SE)	(0.08)	(0.0007)			(0.00004)		
WOODYRICH	−0.718	0.0060	0.000005	NS	−0.00217	0.30	940
(SE)	(0.15)	(0.0010)	(0.000001)		(0.0001)		
DEC RICH	−1.778	0.0062	−0.000002	0.0296	−0.00093	0.17	940
(SE)	(0.50)	(0.0010)	(<0.000001)	(0.010)	(0.0002)		

demonstrated an inverse relationship between canopy cover and soil clay content for savannas in the Darwin region, as did Bowman, Wilson & Hooper (1988) for a site in the Kakadu Region.

Decreasing tree richness with decreasing productivity appears to be a general phenomenon along broad-scale climatic/productivity gradients (McArthur, 1969). Annual Net Primary Productivity is a powerful predictor of tree species richness in North America, Europe, Africa and Asia (Currie & Paquin, 1987; Adams & Woodward, 1989; O'Brien, 1993). Specht & Specht (1989a) showed that tree species richness across Australia decreased from the tropics, through the sub-tropics to the temperate zone, as the evaporative coefficient of the atmosphere (itself proportional to productivity) increased. With respect to soil texture, Bowman, Woinarski & Menkhorst (1993) reported a general decrease in tree richness with increasing clay content for sites in Kakadu National Park, in the north of the NT.

Deciduous trees are common within the savannas of the wet–dry tropics (Sarmiento & Monasterio, 1983). In the Northern Territory the proportion of deciduous tree species within the regional floras decreases with increasing latitude (Egan & Williams, 1996). In the present study, thee was a general decline in the richness of deciduous woody species with decreasing rainfall, although the response surface indicated a slight decline at the highest rainfall levels. With respect to soil texture, deciduous richness was at a maximum on soils of intermediate (loam) texture. These results are consistent with cost–benefit models of foliage retention. The tissue water relations of the leaves of deciduous species indicate that they are less tolerant of drought than are evergreen species (Sobrado, 1986). Leaf construction costs and maintenance costs per unit area also appear to be greatest in leaves with the greatest life-span (Sobrado, 1991). Thus, as water availability decreases, it may be more economical to retain foliage throughout the year than to shed and replace leaves seasonally (Orians & Solbrig, 1977; Chabot & Hicks, 1982). Similarly, at low soil-nutrient levels, such as on shallow sandy soils of the sandstone country of the northeastern NT, deciduous species are relatively uncommon (Wilson *et al.*, 1990). The decline in deciduous tree richness as predicted from our model at high rainfall is consistent with the trend towards relatively low number of deciduous trees in the wettest of the tropical rainforests in coastal, NE Queensland compared with rainforests on drier sites (Webb, Tracey & Williams, 1984).

Despite the significant association between the above savanna attributes and rainfall and clay, the degree of predictability between given attributes and these particular predictor variables was only moderate. There are several reasons for this. First, as indicated above, measurements of PAM for the NT require further refinement. A single index of PAM is likely to require a temporal component of soil moisture, e.g. the length of time during which growth is possible (Knoop & Walker, 1985; Scholes & Walker, 1993) and an atmospheric moisture component (e.g. vapour pressure deficit or evapotranspiration; Specht & Specht, 1989a). Secondly, clay content of the soil and the moisture holding capacity of the soil are clearly related—as clay content increases the amount of available water generally decreases. Thirdly, we have no data on soil depth at the sample sites. Soil depth, as influenced by topographic position and via its influence on soil drainage and water holding capacity, can be an important determinant of savanna form and function both in Australia (Bowman & Minchin, 1987; Fensham & Kirkpatrick, 1992) and elsewhere in the world (Medina & Silva, 1990; Scholes & Walker, 1993). Fourthly, the scale of the sample units—400 m^2—was small in relation to potential heterogeneity of plant community structure at the landscape scale, and there was no account taken of the position of the sample units in relation to small–medium scale variations in topography and microtopography. Such variation will afffect the distribution of run-off and run-on zones, and thence influence ecosystem structure and composition (e.g. southern African savannas; Scholes, 1990; and semi-arid temperate woodlands in south eastern Australia; Tongway & Ludwig, 1990).

Finally, there is considerable variation in land management practice, both current and in the recent past, which is likely to have affected the abundance of trees. For example, the top half of the NT is burned extensively annually or biennially (Graetz, Fisher & Wilson, 1992) and there may be considerable inter-annual variation in fire intensity. The pan-tropical, deciduous tree element in the flora appears to be particularly vulnerable to intense fire (Williams, 1995). Thus, at the scale of less than 0.1 ha, there may be considerable patchiness within a given region with respect to the abundance of particular tree species, which would increase the amount of residual variation in any predictive models.

This study is, to our knowledge, the first numerical analysis of the relationship between attributes of savannas which incorporates both rainfall and soil variables across a wide climatic gradient at a sub-continental scale. There were limitations in the present study, but the concept of the PAM/AN plane as a predictive tool in savanna ecology is supported by this preliminary, empirical study. Future work will primarily need to refine the measures of PAM and AN, by incorporating atmospheric and soil depth variables.

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