

# Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna

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## Summary

**1** The relative roles of climate and management for driving changes in woody cover in savannas over the past century are the subject of active debate. Perspectives arising from short-term, small-scale, local experiments are rarely tested over larger scales and longer time frames.

**2** Regression analysis and aerial photography were used to assess the relative importance of land-use history (fire and grazing), rainfall and initial woody cover (woody cover at the beginning of a sample period relative to the range of woody cover expressed within a land type) in accounting for rates of change in overstorey and understorey cover between the 1940s and 1990s in central Queensland, Australia. Analyses included 279 site-period combinations representing five semi-arid eucalypt savanna land-types within a 125 755 km<sup>2</sup> region.

**3** Fire and grazing variables provided no explanatory power. In general, relative rainfall (rainfall for a given period standardized against mean annual rainfall) was positively related and initial woody cover negatively related to rates of change in both the overstorey and the understorey. The interaction between rainfall and initial woody cover was significant, reflecting the fact that increases in cover coincided with low initial cover when rainfall is higher than average, whereas decreases in cover typically occurred with high initial cover, regardless of rainfall.

**4** On average, overstorey and understorey cover increased over the second half of the 20th century. This pattern is consistent with the first half of the 20th century having more intense droughts and being drier overall than the relatively wet second half.

**5** The findings highlight the primary importance of interactions between rainfall fluctuations and density dependence as determinants of large-scale, long-term woody plant cover dynamics in savannas subject to large rainfall excess and deficit over multi-year time-scales.

*Key-words:* density dependence, drought, eucalypt savanna, fire, grazing, rainfall variability, structural change, woody dynamics

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## Introduction

Climate change has been cited as the impetus for directional shifts between grass and woody plant domination, but evidence in support of this contention is mixed. Neilson (1986) hypothesized that the grasslands present at the time of Anglo-European settlement of south-western North America had developed during the cooler, moister conditions of the ‘little ice age’ and

were in the process of shifting towards domination by xerophytic woody plants as conditions became warmer and drier in the 18th and 19th centuries. Numerous examples of vegetation change in areas with no known alterations in disturbance regimes (Hastings & Turner 1965) are consistent with a climatic interpretation. In South American savannas, tree densities have been increasing throughout a matrix of land-use histories ranging from heavily disturbed by fire and grazing to ungrazed and rarely burnt, suggesting climate rather than disturbance may be driving increases in woody life-forms (Silva *et al.* 2001).

On the other hand, there have been no clear trends in climate variables that coincide with increases in woody cover over the past 100–150 years at various locations in the North American south-west (e.g. Bahre 1991; Conley *et al.* 1992). Furthermore, climate operates over relatively large areas and cannot be invoked as an explanation for local vegetation changes such as fence-line contrasts (see examples in Archer 1994). This is not to say that climate has not been important as short-term fluctuations in climate do influence the rates and dynamics of woody plant spread and contraction (e.g. Brown *et al.* 1997; Allen & Breshears 1998). For example, in southern Texas, USA, woody cover decreased significantly between 1941 and 1960 in response to the drought of the 1950s, then increased dramatically during the post-drought decades, resulting in a substantial net increase in woody cover between 1941 and 1983 (Archer *et al.* 1988). The effects of multiple year rainfall deficits have also been observed in Australian eucalypt savannas (Fensham & Holman 1999). *Eucalyptus* tree death was similar across landscapes where livestock grazing intensities ranged from absent to heavy (Fensham 1998), suggesting the strong influence of rainfall on woody plant community dynamics. Precipitation may therefore influence woody plant community development in an epicyclic fashion, promoting recruitment under some circumstances (e.g. Watson *et al.* 1997) and widespread mortality of adult plants under others (e.g. Allen & Breshears 1998).

Grazing can foster woody plant proliferation both directly (by reducing competition from perennial grasses and spreading seeds of woody plants; Knoop & Walker 1985; Brown & Archer 1987, 1999; Harrington 1991) and indirectly (by reducing fuel loads and hence fire frequency and/or intensity; Savage & Swetnam 1990; Archer 1995; Roques *et al.* 2001). Alternatively, preferential utilization of woody plants by browsers may suppress their growth and reduce their cover, facilitating grass production and subsequent fire (e.g. Dublin *et al.* 1990; Weltzin *et al.* 1997). In the absence of climatic constraints, fire, browsing and grazing could interact in various ways through time to promote or retard woody plant expansion. For example, in north-western New South Wales, Australia, the widespread phenomenon of shrub encroachment in *Eucalyptus* semi-arid savanna is hypothesized to occur in waves during wet periods when soil moisture is sufficient for shrub seedlings to establish in the matrix of grass competitors (Hodgkinson 1991; Noble 1997). These same wet periods also produce high fuel loads and conditions conducive to fire in subsequent dry periods. Noble (1997) proposes that prior to Anglo-European settlement, natural or Aboriginal ignitions would have initiated extensive, hot fires that would have thinned these waves of shrub regeneration and maintained a savanna structure. With the advent of pastoral management, heavy utilization of grasses by domestic stock reduced fine fuel loads, effectively

removing the major impediment to woody plant recruitment imposed by fire (Harrington 1991). Indeed, in the absence of fire, forest species may colonize dryland savannas (Fensham & Butler 2004), suggesting that climate *per se* is not a limiting factor in their distribution.

There is also evidence suggesting woody plant dynamics in savannas are density dependent (e.g. Smith & Goodman 1986; Martens *et al.* 1997; Hoffmann 2002). In Australian monsoonal eucalypt savannas, woody plant recruitment is enhanced when overstorey competition is reduced (Fensham & Bowman 1992), and tree dieback for some species is positively related to stand basal area in semi-arid savanna (Fensham & Holman 1999). Penridge & Walker (1986) observed enhanced growth of *Eucalyptus populnea* when the competitive influence of neighbouring trees was diminished by artificially reducing tree density. This study examines density-dependent effects on structural change of woody plant communities in the context of landform, climate and disturbance variability.

Studies quantifying rates and patterns of regional changes in woody cover in savanna have been carried out in North America (e.g. Archer *et al.* 2001; Asner *et al.* 2003), South America (e.g. Silva *et al.* 2001), Australia (e.g. Burrows *et al.* 2002; Fensham *et al.* 2003b) and Africa (e.g. Hudak & Wessman 1998; Roques *et al.* 2001). Assessing the relative importance of the agents causing change is challenging, but is required to improve models seeking to predict woody plant dynamics under various land management and environmental conditions (e.g. Neilson 1995; Daly *et al.* 2000).

Australian tropical savannas have been subject to a variety of climate and land management histories. In this study changes in overstorey and understorey woody plant cover determined from sequential aerial photography of central Queensland (Fensham *et al.* 2003b), site-specific information on grazing and fire history (Fensham & Fairfax 2003a), and rainfall data, are married to identify the most important drivers of woody vegetation cover change. Regression analysis was employed to test the following hypotheses in relation to one- to four-decadal changes in woody cover: (i) change rates in overstorey are primarily related to variations in rainfall; (ii) change rates in understorey are primarily related to variations in grazing pressure, fire frequency and fire season; and (iii) change rates of both overstorey and understorey woody cover are density dependent. The influence of rainfall on the woody dynamics of the region was then assessed at a broader scale by interpreting the average cover trend for the second half of the 20th century in the context of rainfall patterns prior to and during that period.

## Methods

### STUDY AREA

The study area comprises 125 755 km<sup>2</sup> in central Queensland and is more fully described in Fensham &

**Table 1** Description of land types and sample sizes. Structural nomenclature follows Specht (1970)

Land type	Vegetation, landform, soil description	Total		With fire history*	
		Sites	Site-periods	Site	Site-periods
Acacia-on-clay	<i>Acacia harpophylla</i> with <i>E. cambageana</i> open forest on clay sheets and shales	31	44	9	9
Eucalypt-on-clay	<i>Eucalyptus orgadophila</i> open woodland on level or gently undulating clay soils derived from basalt or shales	15	30	7	9
Eucalypt-on-sand	<i>Eucalyptus crebra</i> and <i>E. melanophloia</i> open woodland on level sand sheets derived from sandstone	33	65	19	25
Eucalypt-on-hills	<i>Eucalyptus crebra</i> and <i>Corymbia citriodora</i> woodland and open forest on hills	31	68	15	26
Eucalypt-on-duplex	<i>Eucalyptus populnea</i> and <i>E. melanophloia</i> woodland on level or gently undulating texture contrast soils formed on clay sheets or shales	44	72	20	28

\*Based on Fensham & Fairfax (2003a).

Fairfax (2003a). Climate of the region is mesothermal subhumid to semi-arid (Thorntwaite 1948), with a rainfall peak in the summer and annual average totals ranging from 500 mm in the west to 850 mm in the east. Major land-types in the region are summarized in Table 1. Cattle grazing has been the dominant land use in the study area throughout the 20th century, although sheep were relatively common prior to about 1970 (Lloyd 1984). Extensive clearance for pasture and crops has been undertaken in the acacia-on-clay, and to a lesser extent in the eucalypt-on-clay and eucalypt-on-duplex land types. Conservation reserves presently cover about 3% of the area.

The average fire frequency in central Queensland has shown a slight downward trend, with values of 1.2 fires decade<sup>-1</sup> in the 1950s, and 0.9–1.0 decade<sup>-1</sup> in the 1960s, 70s, 80s and 90s (Fensham & Fairfax 2003a). The second half of the 20th century also coincides with increased densities of drought resistant *Bos indicus* cattle breeds (Gardener *et al.* 1990; Fensham & Fairfax 2003a).

#### OVERSTOREY AND UNDERSTOREY COVER

The 205 randomly generated sites used by Fensham *et al.* (2003b) were employed for cover change analysis. Aerial photography (1 : 25 000 to 1 : 40 000) for these sites spans a period from 1945 to 1999, with an average elapsed time between consecutive photo dates of 17 years (range = 8–41 years). To avoid confounding effects of clearing or recovery from clearing, site-period combinations were included in the analysis only if there was no evidence of clearing in any of the photos. Sites affected by tree killing (ringbarking and tree poisoning) within 25 years of photo dates (determined from landholder questionnaires described below, or as evident from the aerial photograph as tree death bounded by

the straight edges of fence lines) were also excluded from the analyses. Only the five land types represented by  $\geq 15$  sites were included (Table 1).

Percentage tree and understorey cover for each site-time combination was determined from aerial photography within a 25-ha area using the point-intercept technique described by Fensham *et al.* (2002). Overstorey and understorey woody cover was predicted from tree and shrub cover as measured from the aerial photography using models provided by Fensham *et al.* (2002) with one minor modification. Photo-scale was incorporated in all models regardless of statistical significance because numerous exploratory analyses on a range of calibration data sets indicated a consistent effect (Fensham *et al.* 2002; Fensham & Fairfax 2003b). The upper canopy of most land types was sufficiently open that this method was able to distinguish between overstorey cover (woody plants > 5 m height) and understorey cover (woody plants < 5 m height). The exceptions are acacia-on-clay, where the shrub layer is obscured by the tree layer, and the eucalypt-on-clay, where understorey cover is very low. These land types were thus excluded from the analysis of understorey cover change.

#### RESPONSE VARIABLES

Cover change was determined using the woody cover assessments from the aerial photography for 279 site-periods (period between consecutive aerial photographs for any given site) from 154 sites (Table 1). The response variables are the rate of overstorey cover change and the rate of understorey cover change (% y<sup>-1</sup>), determined as the change in percentage cover over a site-period divided by the duration of that site-period.

## PREDICTIVE VARIABLES

An index based on woody cover (relative initial overstorey cover and relative initial understorey cover) is used to describe relative woody stocks. Woody cover is an easily measured surrogate of leaf area, which is directly related to the functional variables of plant productivity and water uptake. Although there are no studies of density dependence in savannas that disentangle the effects of woody plant density *per se* and other measures of tree structure such as basal area or tree cover, numerous studies have demonstrated statistically significant relationships between these variables (e.g. Roques *et al.* 2001; Fensham *et al.* 2002). In interpreting trends in cover, the term 'density dependence' is used in a general sense to describe relative woody stocks rather than in the strict sense of describing the density of individual plants regardless of size.

The relative initial overstorey cover and relative initial understorey cover at the start of each period were calculated by first determining a nominal low level of cover for understorey and overstorey for each land type within the region. To determine whether this nominal low level of cover might vary as a function of rainfall across the study area, minimum values of both overstorey and understorey cover for each site over all of the sampling dates were compared against the mean annual rainfall (m.a.r.) for that site using Spearman's rank correlation coefficient. These comparisons were not significant ( $R = -0.112$  to  $0.089$ ,  $P > 0.05$ ), with the exception of overstorey cover and m.a.r. in the eucalypt-on-hills land type ( $0.01 < P < 0.05$ ), and even there, m.a.r. accounted for only 12% of the total variance. The nominal low level of cover can therefore be considered independent of m.a.r. and its value was designated as the 10th percentile of the woody cover levels for a particular land type. The relative initial overstorey cover at the beginning of each site-period combination was thus determined as the overstorey cover at the beginning of a site-period divided by the 10th percentile for the overstorey cover values. Relative initial understorey cover was determined in the same way, although the 10th percentile in the eucalypt-on-hills land type was set at one, as its actual value was zero.

Relative rainfall was calculated for each site-period combination using monthly rainfall data interpolated with smoothing functions developed from actual rainfall stations (Jeffrey *et al.* 2001) using SILO software algorithms (<http://www.nrm.qld.gov.au/silo>). The median distance from the sites to a station with at least 5 years of data.decade<sup>-1</sup> declined from 18.1 km in the 1950s to 14.5 km in the 1990s, with the maximum distance declining from 59.3 km in the 1950s to 37.3 km in the 1990s. The accuracy of modelled data is enhanced because average rainfall isohyets are widely spaced across the region. Relative rainfall was represented as the annual average for the accumulated rainfall commencing 2 years before the start of a site-period until 2 years before the end of a site-period, divided by the

average long-term annual rainfall (modelled data from 1890 to 2002). The 2-year lag was based on field studies suggesting this best represents the delay in woody plant growth response to rainfall input (Fensham *et al.* 2003a). Extreme rainfall events for each site-period were represented as the accumulated rainfall during the wettest (extreme wet) and driest (extreme dry) 3 years within the period, incorporating the 2-year time lag, divided by the long-term 3-year average rainfall.

Fire history and grazing pressure for the sites in Table 1 were derived from land-holder questionnaires (Fensham & Fairfax 2003a). Verification of the responses to some of the data provided in these questionnaires using independent sources suggested no instances of deliberate or inadvertent misinformation. The land use data base developed from these questionnaires also contains information on distance to artificial or natural water points through time at each site. The inverse relationship between grazing effects on vegetation and distance to watering points (pionsphere effect) has been well documented (see Pickup & Chewings 1994; James *et al.* 1999) and was used here as a surrogate to assess spatial variation in grazing intensity. Mean distance to water varied from 3.6 km in the 1950s to 1.8 km in the 1990s (Fensham & Fairfax 2003a). Grazing effects are also contingent on stocking rates, but those measures were not generally available. In addition to cattle, there is an abundance of native macropods (most commonly the grey kangaroo, *Macropus giganteus*, and common wallaroo, *Macropus robustus*) whose numbers have been enhanced by increased access to water in the pastoral landscape (James *et al.* 1999). Their activities are superimposed over the managed cattle herds and are also highly correlated with distance to water (James *et al.* 1999).

Responses from the land-holder questionnaires (Fensham & Fairfax 2003a) also enabled estimation of the number of fires.decade<sup>-1</sup> for 97 site-period combinations at 70 sites (Table 1). Fire frequency was determined for each period as 0 (no fires), 1 ( $> 0$  but  $\leq 1.10$  decade<sup>-1</sup>), 2 ( $> 1.10$  decade<sup>-1</sup> but  $\leq 2.10$  decade<sup>-1</sup>), and 3 ( $> 2.10$  decade<sup>-1</sup>). Fire intensity, also assessed from the land-holder surveys, was rated as 0 (no fire), 1 (cool, tree crowns not scorched), or 2 (hot, tree crowns scorched). Multiple fires were scored as the average of these values for each period. About 98% of fires reported in questionnaires occurred in either spring or summer (September to March). The variable fire season was thus represented as 0 (spring) or 1 (summer); data from sites experiencing autumn (one site-period) or both spring and summer fires in a given period (four site-periods) were excluded from analyses.

## MODELLING WOODY COVER CHANGE

Forward stepwise linear models (S-PLUS 6) were used to explore the influence of the covariates relative initial understorey cover, relative initial overstorey cover, relative rainfall, extreme wet and extreme dry, distance to water, fire frequency and fire intensity on

the response variables overstorey cover change and understorey cover change. Variables approximated a normal distribution and did not require transformation, except for relative initial understorey cover, which was transformed using  $\ln(x + 1)$ . Response variables were examined for collinearity. Fire frequency and fire intensity were collinear but only because of tied zero values. Variables that were highly collinear (relative rainfall, extreme dry and extreme wet) were added to the models in alternate order to examine their relative influences separately. Parsimonious models were sought by giving priority to simple models that encompassed maximal variance. Fire season had many missing values; hence its effect on cover change was examined independently from all other variables using one-way ANOVA. Land type (using the categories in Table 1) was added to an initial exploratory model as an interactive variable. The factorization of land type was determined following the applications of Scheffé's multiple range test (Scheffé 1953) to a preliminary model developed using the stepwise procedure. Final models were developed following re-application of the stepwise linear regression procedure to the land type groups defined as significantly distinct by the preliminary model. Model building included two-way interactions of all combinations of terms. Models were manipulated after examination of diagnostics to ensure parsimony and that standard linear model assumptions were satisfied (normal distributions, heterogeneous residuals, outliers not unduly influencing linearity).

The fire-history variables had lower degrees of freedom than the other variables because of incomplete data from the questionnaires. To determine whether significant effects may have been an artefact of more power resulting from higher sample numbers, data were re-analysed using a balanced data set that included only sites for which there were fire-history variables.

The integrative, holistic approach used here is limited by the timing and temporal frequency of aerial photos and the errors associated with the measurement and assessment of both response and predictor variables (Fensham & Fairfax 2003a; Fensham *et al.* 2003b), with errors tending to bias results towards null responses. Unexplained variance resides in the inherent distortions in aerial photo images, the inaccuracies of modelled rainfall data, the potential for inaccurate land-use histories derived from people's memories and the coarse approximation of grazing intensity provided by the distance to water surrogate. Despite these limitations, our approach provides a rare opportunity to assess the *relative importance* of management and climate variables that may be impossible to ascertain with experimental field studies.

#### REGIONAL RAINFALL HISTORY AND COVER TRENDS

A drought index designed to identify sustained dry and wet periods was prepared for long-term climate

stations broadly representative of the study region (Clermont, 22°50' S, 147°38' E; Duaringa, 23°43' S, 149°40' E; Rolleston, 24°28' S, 148°37' E; Jericho, 23°36' S, 146°07' E; Emerald, 23°34' S, 148°11' E) using data from Clewett *et al.* (1994). The drought index, computed as actual annual rainfall less mean annual rainfall (m.a.r.) divided by the m.a.r., was calculated for every year. Running totals of these standardized variations in annual rainfall were then calculated for 3-year and 6-year periods prior to and including each year (i.e. 6-year drought index for 1970 is the running total from 1965 to 1970) (Foley 1957). Comparison of these drought indices between the five climate stations revealed broadly similar trends throughout the period of record so only the data from the centrally located Emerald station are presented here.

Average regional trends in percentage overstorey and understorey cover for land types combined were developed using the method described by Fensham *et al.* (2003b), who present trends for total above-ground biomass.

## Results

### PREDICTING RATES OF OVERSTOREY COVER CHANGE

Preliminary model building revealed significant differences between the overstorey cover change response of eucalypt-on-hills and eucalypt-on-clay sites, as well as the remaining land types (acacia-on-clay, eucalypt-on-sand and eucalypt-on-duplex). The last three land types showed similar changes and data were therefore pooled (combined land type category).

None of the covariate terms were significant in explaining changes in overstorey cover in the eucalypt-on-clay land type, although there were insufficient data on fire season ( $n < 3$  for both spring and summer burns) to allow for its inclusion in the analysis. Fire season, even for the land types with sufficient data, had no significant effect. Fire frequency, fire intensity and distance to water did not emerge as significant predictors of overstorey cover change in any land type. For the combined land type, change was negatively related to relative initial overstorey cover and positively related to relative rainfall and relative initial understorey cover (Table 2). Inclusion of extreme wet and extreme dry variables with relative rainfall did not significantly increase explained variance. Relative initial overstorey cover was the only significant term in the eucalypt-on-hills land type and this was a negative association (Table 3).

A balanced analysis was conducted to assess the importance of the covariates in regression models built from a data set where all variables had equal sample size. Relationships emerging from the balanced analyses were, for the most part, consistent with the unbalanced analyses, although relative initial understorey cover dropped out as a significant term for the combined land

**Table 2** ANOVA results for the covariates of linear models predicting rates of overstorey cover change in the combined land type category (acacia-on-clay, eucalypt-on-sand, eucalypt-on-duplex) for the unbalanced (full data) and balanced (sites with missing values of covariates excluded) data sets. The model for the unbalanced set is of the form overstorey cover change =  $\beta_0 + \beta_1$ relative initial overstorey cover +  $\beta_2$ relative rainfall +  $\beta_3[\log_e(\text{relative initial understorey cover} + 1)]$ , and for the balanced data set overstorey cover change =  $\beta_0t + \beta_1$ relative initial overstorey cover.  $P(t)$  is the significance of coefficients in the full model and  $P(f)$  is the sequential significance of adding coefficients starting with the null model (intercept only)

Term	Coefficient (SE)	$P(t)$	d.f.	SS	$P(f)$
Overstorey cover change (% $y^{-1}$ )					
Unbalanced analysis ( $R^2 = 0.230$ )					
Intercept	-1.073 (0.484)	0.0278			
Relative initial overstorey cover	-0.397 (0.065)	0.0000	1	8.29	0.0000
Relative rainfall	1.527 (0.424)	0.0004	1	2.27	0.0015
Relative initial understorey cover	0.240 (0.116)	0.0396	1	0.93	0.0396
Residuals			177	38.46	
Balanced analysis ( $R^2 = 0.307$ )					
Intercept	-1.323 (0.773)	0.0923			
Relative initial overstorey cover	-0.336 (0.094)	0.0007	1	4.09	0.0001
Relative rainfall	1.840 (0.688)	0.0096	1	1.54	0.0096
Residuals			59	12.75	

**Table 3** ANOVA results for the covariates for linear model predicting rates of overstorey cover change (%  $\text{year}^{-1}$ ) in the eucalypt-on-hills land type for unbalanced (full data) and balanced (sites with missing values of covariates excluded) data sets. The models for both data sets were of the form overstorey cover change =  $\beta_0t + \beta_1$ relative initial overstorey cover.  $P(t)$  is the significance of coefficients within the full model and  $P(f)$  is the sequential significance of adding coefficients starting with the null model (intercept only)

Term	Coefficient (SE)	$P(t)$	d.f.	SS	$P(f)$
Overstorey cover change (% $y^{-1}$ )					
Unbalanced analysis ( $R^2 = 0.199$ )					
Intercept	1.455 (0.346)	0.0001			
Relative initial overstorey cover	-0.843 (0.208)	0.0001	1	10.73	0.0001
Residuals			66	43.13	
Balanced analysis ( $R^2 = 0.314$ )					
Intercept	2.092 (0.642)	0.0033			
Relative initial overstorey cover	-1.164 (0.351)	0.0029	1	6.75	0.0029
Residuals			24	14.77	

type (Table 2). The models accounted for 23% (unbalanced) and 31% (balanced) of the variance for the combined land type (Table 2), and 20% (unbalanced) and 31% (balanced) for eucalypt-on-hills (Table 3).

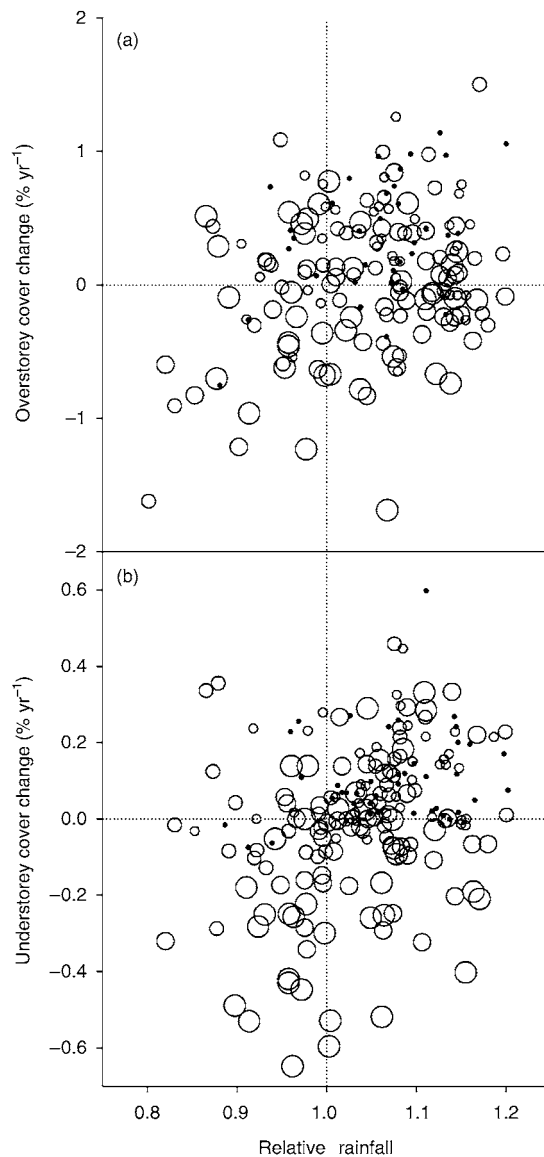
A graphical representation of significant variables for the combined land type illustrates that rates of overstorey cover change are usually positive when relative rainfall is higher than average, also positive when relative initial overstorey cover is low, and negative when relative initial overstorey cover is high, regardless of relative rainfall (Fig. 1a).

#### PREDICTING RATES OF UNDERSTOREY COVER CHANGE

Preliminary modelling revealed no significant differences in rates of understorey cover change between the land types for which the understorey could be reliably detected (eucalypt-on-hills, eucalypt-on-sand and

eucalypt-on-duplex, hereafter combined as eucalypt on non-clay). The final model included relative initial understorey cover, relative rainfall and their interaction. The relationships emerging from balanced analyses were consistent with unbalanced analyses and explained 48% (unbalanced analysis) to 61% (balanced analysis) of the variance (Table 4).

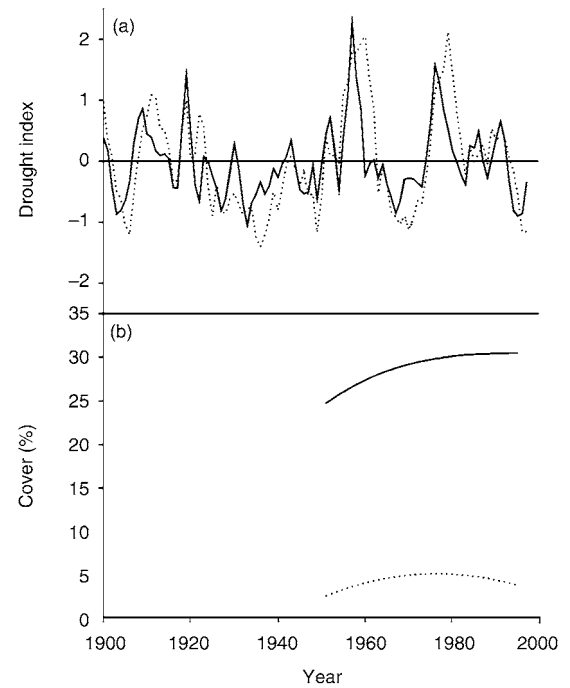
Fire season had no significant effect ( $P = 0.513$ , spring burns = 11, summer burns = 32), nor did fire intensity, fire frequency and distance to water contribute significantly to the understorey cover change model. The strong interactive effect of relative initial understorey cover and relative rainfall reflects the fact that site-periods with lower relative initial understorey cover were much more likely to undergo positive understorey cover change during periods of high relative rainfall and those with higher values to show negative change during periods of low relative rainfall (Fig. 1b).



**Fig. 1** Relative rainfall for individual site-period combination vs. (a) rate of overstorey cover change for the combined land type and (b) rate of understorey cover change rate for the eucalypt-on-non-clay land type. Samples were ordered by their relative initial overstorey cover for (a), and by relative initial understorey cover for (b). The ordered sequence of these values was divided into five segments containing equal numbers of samples. The segments are depicted by circles of increasing size representing low to high relative initial cover. Relative rainfall is average in comparison with long-term data at a value of one.

#### RAINFALL HISTORY AND COVER TRENDS

The 45 years leading up to the study period (1906–50) were generally drier than the 45 years represented by the aerial photos used in this study (1951–95) (Fig. 2a), with droughts more frequent and periods of rainfall excess (positive drought index) less common. This comparison underestimates deficits in the former period, as the running totals do not fully reflect the intense drought in the early years of the 20th century (Fig. 2a).



**Fig. 2** (a) Drought index values for 3-year (solid line) and 6-year (dotted line) periods at Emerald (635 mm mean annual rainfall). Negative numbers represent rainfall deficit and positive numbers rainfall excess. (b) Average overstorey cover (solid line) and understorey cover (dotted line) for all land types combined over the study region between 1951 and 1995. The derivation of the average woody cover trends is fully described in Fensham *et al.* (2003b), including representation of the range of trends at individual size.

The pronounced average increase in overstorey and understorey cover during the period between 1951 and 1965 (Fig. 2b) coincides with a period of rainfall excess (Fig. 2a). The intense droughts of the first half of the 20th century precede the relatively low woody plant cover evident in 1951. Average cover has steadied, or declined, during the period 1965–95 (Fig. 2b) and this is consistent with rainfall conditions fluctuating around the long-term average (Fig. 2a).

#### Discussion

Rainfall emerged as a significant explanatory variable, with a positive effect, in all of the linear models derived to account for rates of overstorey cover change, with the exception of the eucalypt-on-hills land type, where the calibration models used to predict woody cover from aerial cover had particularly low power (Fensham *et al.* 2002). The impact of rainfall on vegetation structure interacted with relative initial overstorey cover in a way that suggests density-dependent regulation. Sites with high relative initial overstorey cover were unlikely to show positive overstorey cover change rate even under favourable rainfall conditions and sites with low cover were relatively immune from cover loss (= canopy or plant dieback) in the advent of drought (Fig. 1a). A weak but significant positive relationship between

**Table 4** ANOVA results for the covariates for linear model predicting rates of understorey cover change (% year<sup>-1</sup>) in eucalypt-on-non-clay land type (combined eucalypt-on-hills, eucalypt-on-sand and eucalypt-on-duplex land types) for the unbalanced (full analysis) and balanced (sites with missing values of covariates excluded) data sets. The models for both data sets were of the form understorey cover change =  $\beta_0 t + \beta_1 [\log_e(\text{relative initial understorey cover} + 1)] + \beta_2 \text{relative rainfall} + \beta_3 [\log_e(\text{relative initial understorey cover} + 1) * \text{relative rainfall}]$ .  $P(t)$  is the significance of coefficients within the full model and  $P(f)$  is the sequential significance of adding coefficients starting with the null model (intercept only)

Term	Coefficient (SE)	$P(t)$	d.f.	SS	$P(f)$
Understorey cover change (% y <sup>-1</sup> )					
Unbalanced analysis ( $R^2 = 0.479$ )					
Intercept	2.629 (0.444)	0.0000			
Relative initial understorey cover	-3.046 (0.345)	0.0000	1	4.26	0.0000
Relative rainfall	-2.294 (0.427)	0.0000	1	0.86	0.0000
Relative initial understorey cover × relative rainfall	2.744 (0.338)	0.0000	1	2.84	0.0000
Residuals			201	8.66	
Balanced analysis ( $R^2 = 0.614$ )					
Intercept	3.933 (0.734)	0.0000			
Relative initial understorey cover	-4.438 (0.563)	0.0000	1	4.019	0.0000
Relative rainfall	-3.605 (0.716)	0.0006	1	0.66	0.0019
Relative initial understorey cover × relative rainfall	4.156 (0.568)	0.0000	1	3.40	0.0000
Residuals			80	5.08	

relative initial understorey cover and overstorey cover change rate also emerged from the analyses (Table 2). This probably represents young trees (scored as shrubs) at the start of a period contributing to increased overstorey cover by the end of the period. This proposition is based on data from field surveys (unpublished data from Fensham *et al.* 2002), which indicate that 40–44% of the understorey layer in eucalypt-on-sand, eucalypt-on-duplex and eucalypt-on-hills study sites was comprised of tree species in small size classes.

Understorey cover change models explained about twice as much variance as the overstorey cover models (compare Tables 2, 3 and 4). Changes were again positively related to relative rainfall via a strong interactive effect of relative initial understorey cover. Positive understorey change rate are most likely with rainfall excess and low understorey cover, while negative understorey cover change rates were typically associated with high understorey cover across a range of relative rainfall values (Fig. 1b).

A thorough examination of the data yielded no relationship between any of the management history variables and either overstorey or understorey cover change rates in any land type. Thus, our hypothesis that the understorey reflects differences in grazing and fire intensity and/or fire frequency was not supported by this correlative, large-scale, long-term study.

Although livestock grazing is commonly presumed to promote woody plant encroachment, evidence in support of this contention is mixed and largely from small-scale, short-term studies (Archer 1995; Van Auken 2000). *Eucalyptus* and its allies are not animal dispersed and other woody species in these Queensland savannas are not widely dispersed by cattle. Thus, dispersal of woody plant seeds by livestock, important for hard-seeded legumes in some savanna systems (e.g.

Brown & Archer 1987), probably has little influence on woody cover dynamics in the land types examined in this study. Support for the notion that grazing of grasses is required for woody seedlings to establish is also mixed. Some studies indicate that the herbaceous layer may inhibit seedling development (Harrington 1991; Van Auken 2000), while others have found no such effect or even that lack of grazing promotes woody seedling establishment (Archer 1995; O'Connor 1995; Jurena & Archer 2003). Indeed, increases in shrub and tree cover have been attributed to relief from grazing (Lenzi-grillini *et al.* 1996; Jeltsch *et al.* 1997). While there is evidence of livestock retarding the regeneration of woody elements through browsing in some African (e.g. Tafangenyasha 1997) and Australian (Scanlan *et al.* 1996; Tiver & Andrew 1997) savannas, other studies have detected no such influence (Hanan *et al.* 1991; Oba *et al.* 2000). The varied (positive, neutral or negative) effects of grazing and browsing on tree–grass interactions and woody plant dynamics may explain why herbivory did not emerge as a significant variable in our regional landscape-scale analyses.

The importance of drought and the minimal effect of fire on woody plant dynamics are consistent with data from a field-monitoring site in semi-arid *Eucalyptus* savanna in north Queensland, where a recent drought caused the death of 85% of the overstorey (Fensham *et al.* 2003a). A long fire-free period (at least half a century) has resulted in only limited understorey development despite a vast pool of vertebrate-dispersed, drought-resistant, fire-sensitive species in the immediate vicinity (Fensham & Butler 2004). In savanna that is regularly burnt, fire-adapted tree species may suffer little mortality except in the smallest and largest size-classes (Williams *et al.* 1999) and may quickly re-establish canopy area via stem, lignotuber or root sprouts.



Mortality may be offset by enhanced growth rates among surviving plants (Penridge & Walker 1986), which possibly accounts for the lack of significant differences in *Eucalyptus* stem basal area on stands subject to long fire-free periods and stands burned annually in the monsoonal savannas of northern Australia (Russell-Smith *et al.* 2003). Such results help explain why fire-history variables did not emerge as strong determinants of decadal-scale changes in woody cover.

The evidence presented suggests a significant portion of the dynamism in the woody layer of semi-arid eucalypt savanna over 8- to 41-year time-scales can be attributed to density-dependent mediation of responses to rainfall excess and deficit. This finding is also consistent with interpreting changes at the regional scale over a century-scale timeframe. The most protracted and intense droughts on record occurred during the first half of the 20th century in central Queensland (Fig. 2a). Our results would predict that these droughts would have resulted in substantial declines in woody cover (Fig. 1), creating a relatively open woodland structure. This prediction made from a large-scale remote sensing perspective is bolstered by field studies documenting a 29% reduction in woodland basal during a recent intense drought in north Queensland (Fensham & Holman 1999). During the second half of the 20th century the coincidence of favourable rainfall conditions and open-structured woodlands would be particularly conducive to woodland development. Woody plant proliferation was thus most rapid during the period 1951–65, tapering off from 1965 to 1995 with the onset of density-dependent interactions and rainfall fluctuating around the long-term average (Fig. 2). It appears that the droughts of the early to mid-1900s created conditions conducive to rapid woody plant expansion in the post-drought period.

Aerial photographs are a useful tool for quantifying patterns of woody cover change over time across large areas and provide perspectives not possible from ground-based studies. However, there are information constraints inherent in photograph interpretation. In addition to those already discussed, it is difficult to ascertain the relative importance of recruitment vs. growth of existing plants, and of plant mortality vs. canopy dieback. Lacking such information, the woody plant cover dynamics observed in this study cannot be directly related to plant population processes or species interactions. Field-based studies are required to augment our understanding of savanna dynamics, but some of the critical processes are difficult to quantify because of their episodic nature. For example, eucalypt recruitment in semi-arid Australian savanna is a rare event (R. J. Fensham & R. J. Fairfax, personal observations) and almost nothing is known about the environmental control of recruitment and post-establishment survival.

The results of this study affirm the importance of multiyear variations in rainfall for both overstorey and understorey woody cover dynamics. Density-

dependence effects (as inferred from canopy cover) also yielded strong signals at the scale of this study. Our data suggest that the interaction of these two factors constitutes the major determinant of woody plant community dynamics in the savannas of the Australian tropics, where multiyear droughts are relatively frequent. Our failure to detect fire and grazing effects strongly suggests these are secondary influences. Existing models seeking to represent the long-term dynamics of savanna have tended to focus on disturbance phenomena and tree–grass interactions (e.g. Jeltsch *et al.* 1996; Hoffmann 1999; House *et al.* 2003). Whilst the primacy of climate and density-dependence effects may not apply to all savanna environments, their effects on woody dynamics should be given greater consideration across a range of global settings.

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