

Temporal and spatial patterns in drought-related tree dieback in Australian savanna

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Summary

1. Determining the relative importance of anthropogenic and non-anthropogenic influences on structure is essential for informed management of savannas and for carbon accounting under greenhouse obligations.

2. The magnitude of drought and dieback was examined using the rainfall records for Queensland and historical records of dieback. Tree dieback was examined in *Eucalyptus* savanna in north Queensland by random sampling after a recent drought.

3. Analysis of rainfall records revealed that particularly severe droughts occurred three times this century in inland Queensland, while more local droughts of similar intensity had been less frequent elsewhere. A review of historical records confirmed extensive tree death following past droughts.

4. Approximately 29% of trees were dead or nearly dead over a sampled area of about 55 000 square kilometres. Dieback was greatest on alkaline igneous rocks, intermediate on metamorphics, sedimentary rocks and acid igneous rocks, and lowest on alluvia.

5. Of the widespread dominants, the *Eucalyptus crebra*–*E. xanthoclada* species complex was highly susceptible to dieback, *E. brownii* and *E. melanophloia*–*E. whitei* moderately affected, and *Corymbia clarksoniana* and *Melaleuca nervosa* less severely affected. Preferential death of large over small size classes was significant for only *E. crebra*–*E. xanthoclada*.

6. The 1990s drought was especially intense in the vicinity of the North Queensland study area. However, within the study area there were only weak correlations between dieback and rainfall deficits as derived from modelled data. A classification of seasonal rainfall revealed no evidence of localized aberrant rainfall events, such as might result from heavy localized storms, within the study area during the drought. Thus the substantial patchiness in dieback within the study area was only poorly related to local rainfall patterns. Significant correlations of the dieback of some taxonomic groups with predrought basal area suggested that the competitive influence of trees may be a partial cause of the patchiness of dieback.

7. The magnitude of drought should be included in functional models predicting tree–grass ratios and must be accounted for if the magnitude and cause of structural trends in *Eucalyptus* and other evergreen savanna vegetation are to be deciphered.

Key-words: Australia, *Eucalyptus*, tree death.

Journal of Applied Ecology (1999) **36**, 1035–1050

Introduction

Structural change in savannas has consequences for management because of its effects on herbage quan-

tity (Heitschmidt, Schultz & Scifres 1986; Burrows *et al.* 1990) and composition (Pieper 1990; Lunt 1997) and nutrient dynamics (Kellman 1979; Weltzin & Coughenour 1990). There is also new found relevance for structural change because of the latest predictions of global climate change in response to anthropogenically increased atmospheric

carbon concentrations. Carbon accounting is set to become an international obligation under treaties that seek to curtail carbon emissions (IPCC 1997). For countries with a large surface area, such as Australia, relatively minor changes in woody vegetation stocks provide a major proportion of the national carbon budget. Accurate accounting of vegetation change and a full understanding of climatic vs. anthropogenic influences on vegetation carbon stocks will become imperative for such countries.

The classical models of savanna function suggest that soil moisture is a primary determinant of tree densities, but that grazing and/or fire can maintain levels below their climatic equilibrium (Belsky 1990). All of these models recognize that soil moisture relations, as determined by total rainfall, seasonal allocation of rainfall or competition by herbaceous strata, are critical for determining the development of woody vegetation stocks. Given the emphasis on water for existing models of savanna function, it is surprising that long-term fluctuations in rainfall, particularly prolonged drought, have not been incorporated more thoroughly (Walker & Noy-Meir 1982; Goldstein *et al.* 1988). The limitations imposed by extreme climatic events may be just as important as average totals or seasonal distribution for determining savanna composition and structure. Where drought has been included in tree-grass savanna function models there has been no reference to real data (Jeltsch *et al.* 1996). The effect of extreme drought on tree cover has barely been studied in tropical savanna (Viljoen 1995). Opportunities to do so are rare because by their nature droughts occur at irregular intervals. Furthermore, many tropical savannas may be immune from extended droughts because of the reliability of monsoon rain.

The propensity for Australia to suffer the effects of El Niño Southern Oscillation-driven droughts is notorious. Clearly there is an urgent need to document the impact of such droughts on Australian vegetation. Previous studies have used drought-induced dieback to assess the moisture tolerance of tree species (Ashton, Bond & Morris 1975; Kirkpatrick & Marks 1985) at individual sites. There have been no studies that have examined patterns of tree dieback over a large area, although Landsberg & Wylie (1983) synthesized data from a range of studies to develop a model of dieback in rural eucalypts, of which drought is only one interacting component. Their model has most relevance to temperate environments where agriculture and pastoralism are relatively intense and incorporates factors such as improved pasture, excessive clearing and fertilization. In rangelands these processes have little application and Fensham (1998) has demonstrated that dieback rates are comparable with or without cattle grazing. The only primary component

of the Landsberg & Wylie model that can be held accountable for dieback is water stress as a result of drought. However, their model proposes an interaction where foliar nitrogen increases as a result of water stress that leads to relatively higher rates of phytophagy. Phytophagy during drought for the evergreen tropical savanna dominants *Eucalyptus* and *Corymbia* (nomenclature follows Henderson 1997) may actually increase their likelihood of survival by reducing water loss through transpiration. These genera are replete with epicormic buds that allow rapid recovery after leaf loss providing there is adequate soil moisture.

This study analyses drought both spatially and temporally across Queensland, and collates evidence of previous dieback events as a consequence of drought. We document the effects of a severe drought during the 1990s to provide quantification of the proportion of dieback across a large area of tropical savanna. We then address the hypothesis that dieback is primarily a consequence of drought by relating death to rainfall patterns at different spatial scales. Patterns of dieback will also be related to other features of the physical environment. We seek to relate patterns of dieback between species and size classes to examine the regeneration potential of tree stocks. The relevance of drought-related dieback to the dynamics of the savanna system is discussed.

Materials and methods

QUEENSLAND RAINFALL

For the purposes of this study Queensland has been divided into eight regions on the basis of broad patterns of total rainfall and seasonality of rainfall (Fig. 1). Mean annual rainfall varies from less than 200 mm in the west and south-west regions to more than 4000 mm in the wet tropics (Clewett *et al.* 1994). The coastal areas of the central coast and south-east regions are relatively wet compared with the coastal parts of the north and central regions. Coefficients of variation range from over 120% in the gulf and far north regions to less than 30% in the south and south-east regions.

DROUGHT INDEX

AUSRAIN (Clewett *et al.* 1994) provides rainfall records for 348 stations dating from before 1898, and for 333 stations dating between 1898 and 1925. Foley's drought index ($D_{m,y}$) (Foley 1957; Maher 1973), a rainfall deficit standardized by the mean annual rainfall (A) of a site, was calculated for each month at every site, where the rainfall in month m of year y was $a_{m,y}$ and we defined:

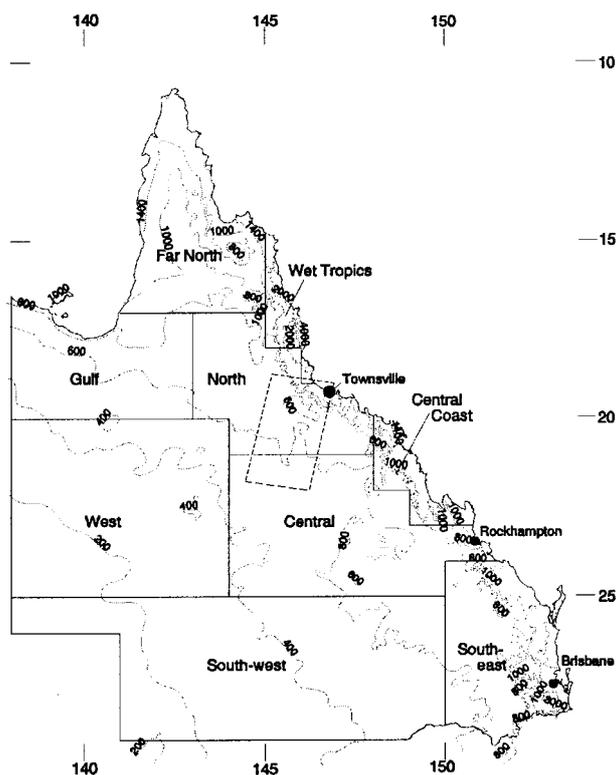


Fig. 1. Locality map showing mean annual rainfall isohyets for Queensland and the regions used in this study (see Fig. 3 and Table 1). The area outlined with a dashed line is that given in Fig. 2.

$$d_{m,y} = \sum_{i=m-12+1}^m \frac{a_{i,y} - A}{A}$$

where $a_{-m,y} = a_{12-m,y-1}$ for $m = 0, \dots, 11$.

Foley's Index ($D_{m,y}$) was then calculated as:

$$D_{m,y} = \sum_{z=y-x+1}^{z=y} d_{m,z}$$

where x was the chosen deficit periods, 3, 4, 5 and 6 years.

The minimum $D_{m,y}$ for each year-one degree grid cell combination was then determined for those climate stations with records prior to 1898. This simplified a large data set consisting of values for every month within a given year and every climate station within a given grid cell. Of the 170 one-degree grid cells that intersected Queensland, 128 were represented by at least one climate station prior to 1898 in AUSRAIN. The far north region (refer to Fig. 1 for the regional delineation of Queensland) had the poorest representation, with 14 out of 22 grid cells represented, and the south-east and central region had the best representation, with all 20 and 23 grid cells represented, respectively.

$D_{min}(x)$ for $x = 3$ -, 4-, 5- and 6-year periods for each climate station for the entire period of record were prepared as a climate surface using ArcInfo

Triangulation software (CREATETIN) and interpolated to a regular grid using ArcInfo (TINLATTICE). D_{min} for 3-, 4-, 5- and 6-year periods for the 1990s were also prepared as climate surfaces.

HISTORICAL RECORDS OF DROUGHT-RELATED DIEBACK

Historical drought records were sought. Aside from general references, *The Queenslander* (a now defunct state-wide newspaper with a strong rural basis) was searched for the periods when intense and widespread droughts had been revealed by this analysis, namely editions between July 1901–December 1902; January–December 1929 and January–June 1935.

NORTH QUEENSLAND DIEBACK STUDY AREA

Two contiguous LANDSAT TM scenes covering 55700 km² in north Queensland were chosen as the study area (Fig. 2). This area was chosen because of the following features: it is known to contain areas with severe dieback; it is also known to contain large areas without dieback; it spans a considerable rainfall gradient; it has a variety of geological types; and it has a variety of vegetation types.

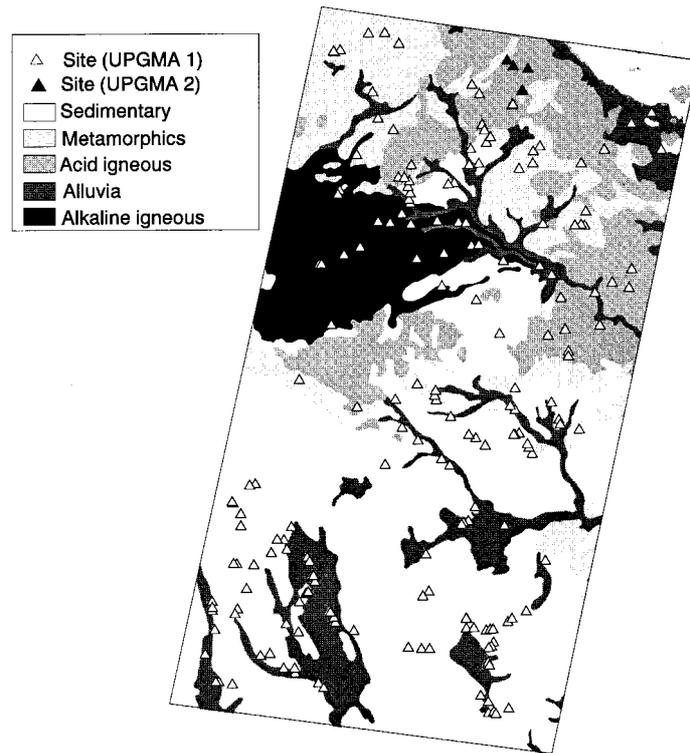


Fig. 2. Geology of the north Queensland study area (derived from Geological Survey of Queensland 1975), location of the sites, and classification of the seasonal rainfall distribution shown according to UPGMA group (see Fig. 6).

Mean annual rainfall declines in a gradient from north-east to south-west. In the north-east, Paluma on the Seaview Range (1000 m altitude) has an orographically enhanced mean annual rainfall of 2662 mm; the coastal lowlands typified by Townsville, in contrast, have a mean annual rainfall of 1136 mm, where 88% falls in the wettest 6 months between November and April. Charters Towers, close to the geographical centre of the study area, has a mean annual rainfall of 648 mm, with 82% of the rainfall between November and April; Uanda, in the south-west of the study area, has a mean annual rainfall of 483 mm, with 78% falling between November and April. The broad surface geology of the study area is presented in Fig. 2. Tertiary sedimentary rocks (chiefly lateritized sandstone) dominate the southern part of the study area, with small areas scattered through the north; large areas of Tertiary basalt occur in the north-west, Palaeozoic granite related rocks and meta-sediments in the north-east, and Quaternary alluvium lines the current large water-courses. Other geologies are localized and occupy minor areas. The vegetation over most of the study area is *Eucalyptus* woodland, although there are minor areas of *Acacia argyrodendron* and *A. cambagei* open forest and *Dichanthium sericeum* grassland on the relatively minor areas of clay-plains. The open forest on these

soils has largely been cleared. Relatively high rainfall has allowed the development of rainforest and tall open *Eucalyptus* forest on the ranges in the far north-east. The major woodland dominants include a complex of the closely related species *Eucalyptus melanophloia* and *E. whitei* (*E. melanophloia*–*E. whitei*), which dominates the higher ground in the southern part of the study area, with *E. brownii* on the lower slopes and flats. A complex of the closely related species *E. crebra* and *E. xanthoclada* (*E. crebra*–*E. xanthoclada*) is a widespread dominant across a range of geologies throughout the north of the study area, with *E. persistens* often occupying the upslope position and *E. brownii* dominating the lower slopes. Cattle grazing is the dominant land-use throughout the study area and cattle numbers have increased dramatically since the 1960s, with the introduction of tropical breeds, artificial waters and feeding supplements. Improved pastures have been developed on only a tiny proportion of the study area. Fire frequency has declined since the 1970s, but most areas would be burnt at a frequency greater than once a decade.

DIEBACK SAMPLING

A random sampling method was designed and implemented with a Geographic Information System

and remotely sensed data. In order to increase sampling efficiency random points were deliberately constrained to within 200 m of roads. To ensure that sampling was not biased by their proximity to roads, a remotely sensed data cover change analysis was used. LANDSAT TM scenes from the area dating from 1995 and 1991 were compared and stratified into categories representing increasing, static or decreasing patterns of cover change between these dates (Paudyal, Kuhnell & Danaher 1997). The cover change analysis had a pixel size of 30×30 m. The sample consisted of 203 sites that were stratified according to the same proportion as the area of the change analysis categories over the whole area. Six of the 203 sites were recently cleared by bulldozer and two sites were treeless grassland. The following sampling description and analysis is based on the remaining 195 sites (Fig. 2).

Sampling was conducted during July and September 1997 after a period of average rainfall ended the 1990s drought. The sampling vehicle stopped at the closest point on the road to the random point and a site was located 100 steps from the roadside in the direction of the random point and a quadrat orientated perpendicular to the road. The exact location of the random points may have been associated with road disturbance, and the actual roads did not necessarily coincide with their gazetted position. Thus our sampled sites were proximal to, but not necessarily positioned at, the randomly generated points. Each quadrat was 100×20 m and the following information was collected.

The identity and d.b.h. of all trees greater than 2 m tall, to the nearest cm, were determined. Each tree was allocated to the following dieback categories: (i) healthy crown; (ii) minor branches dead; (iii) major branches dead; (iv) tree nearly dead, i.e. bark peeling away from the trunk to ground level and live growth restricted to minor branches or basal epicormic growth; (v) tree dead, i.e. bark peeling away from the trunk to ground level and no live shoots. Long standing dead trees without bark were not included within category (v).

Woody sprouts (Fensham & Bowman 1992) (< 2 m tall) were counted and identified in a 100×2 m quadrat down the centre of the larger quadrat.

The proportion of bare ground was assessed in $10 \times 0.5 \times 0.5$ m quadrats spaced at 10-m intervals along the long axis through the centre of the quadrat. This measure was selected to provide a coarse measure of recent grazing intensity. The assumption that perennial grass cover declines with utilization rate, given constant soil fertility and rainfall, is central to management models for Australian savanna (McKeon *et al.* 1990) and is verified by empirical evidence

from the study area (Scanlan, Pressland & Myles 1996).

The geology within the quadrats was determined.

Landscape position was assigned according to the categories (a) ridge top; (b) mid-slope (slope > 3%); (c) flat plain (slope = 3%); (d) undulating plain ($0\% < \text{slope} < 3\%$); (e) floodplain (flood-prone); (f) gully (non-flooded).

Percentage rock cover was estimated.

The dieback categories dead (v) and nearly dead (iv) were amalgamated and presented as a proportion of the total basal area for all subsequent analysis of dieback. It was probably justified to include the nearly dead category because data from a permanent monitoring site near the study area suggested that 55% of 10.3 m^2 basal area (1.3 m high) comprising 210 individual trees, which were categorized by our dieback category as (iii) and (iv) in 1996, were dead (v) in 1998 (R. J. Fensham, unpublished data). However, for *E. similis* category (iv) includes individuals where above-ground parts were totally dead but new basal shoots were emerging.

$D_{min}(x)$ during the 1990s for the sampled sites was calculated from rainfall data modelled using mathematical surfaces fitted to real meteorological data and altitude. In this case a was derived from data generated by Data Drill (Queensland Centre for Climate Applications 1998) and A was obtained from BIOCLIM. Data Drill is derived from 130 climate stations within 100 km of the study area. BIOCLIM (McMahon *et al.* 1995) provides values for mean annual rainfall.

STATISTICAL ANALYSES

Simulated actual dry season (May–October) and wet season (November–April) rainfall data were divided by mean values for these periods, respectively. The 13 biennial moisture ratio values between the wet season 1990/1991 and wet season 1996/1997 were classified for each site using the UPGMA classificatory program using the default values within PATN (Belbin 1988). Differences in dieback proportion were examined between the classificatory groups at the 2-, 3-, 4-, 5- and 6-group level using ANOVA. Dieback proportion was always arcsin transformed.

Subsequent analyses were performed on the 187 sites that were revealed by the UPGMA analysis to have had substantially lower than average rainfall for the 1990s drought period (see the Results). The effects of geology on dieback were analysed using one-way ANOVA. Dieback proportion according to the taxonomic categories *Eucalyptus*, *Corymbia*, *Acacia*, other species and total were compared with environmental variables using Spearman's rank correlation coefficient. Taxonomic groups missing from a site were included as a missing value rather than a zero. This analysis was repeated after stratifying the

data into five geology categories: alluvia, alkaline igneous rocks, metamorphics, acid igneous rocks and sedimentary rocks.

Susceptibility to dieback was tested between co-occurring species pairs that were recorded together at more than eight sites, using the Mann–Whitney *U*-test. The effect of size class on the propensity for dieback was tested between stems less than 11 cm and those greater than 10 cm for individual species, where size class–species combinations occurred in a minimum of five sites. Size class histograms for the four most frequent overstorey tree species were prepared. Woody sprout densities were also tested against environmental variables using Spearman's rank correlation coefficient.

Results

RELATIVE DROUGHT INTENSITY

Analysis of historical rainfall records revealed that Foley's drought index for 3-, 4-, 5- and 6-year periods had broadly similar patterns. Only the 3- and 6-year periods are presented. The most intense standardized rainfall deficits occurred in the south-west, west and central regions during the droughts between 1923 and 1935 and 1897–1902 (Fig. 3). Other droughts in the central coast region in the early 1920s and in the south-west and west regions during the 1960s were of intermediate severity. The 1990s drought was most severe in north Queensland relative to other areas, with only relatively localized

areas having undergone similar deficits (Fig. 4). The 1990s drought was the worst drought on record for north Queensland (Fig. 3).

The far north region has a strongly monsoonal climate, the wet tropics has a high total rainfall, and south-east Queensland has a moderate-high total rainfall with a relatively even seasonal distribution. These areas have been relatively immune from the standardized rainfall deficits that have intermittently affected the other regions of Queensland over the period of rainfall record (Fig. 5).

HISTORICAL RECORDS OF DROUGHT-RELATED TREE DIEBACK

Historical records referred clearly to widespread and broad-scale tree dieback as a result of drought (Table 1). The records of Gregory (1884) from the 1850s predate most rainfall records in Queensland but have been attributed to drought by Hunt (1914), and Gregory (1884) ascribed 'the character of the vegetation indicated excessive droughts'. Reports of drought-related dieback towards the end of the late 1890s/early 1900s drought were particularly abundant, although this could be attributed at least partly to the relatively detailed nature of reports in the broadsheet media of that time. All of the major historical droughts identified in Fig. 3 were represented by reports of tree dieback, with the exception of the central coast region drought ending about 1924 and the 1960s drought.

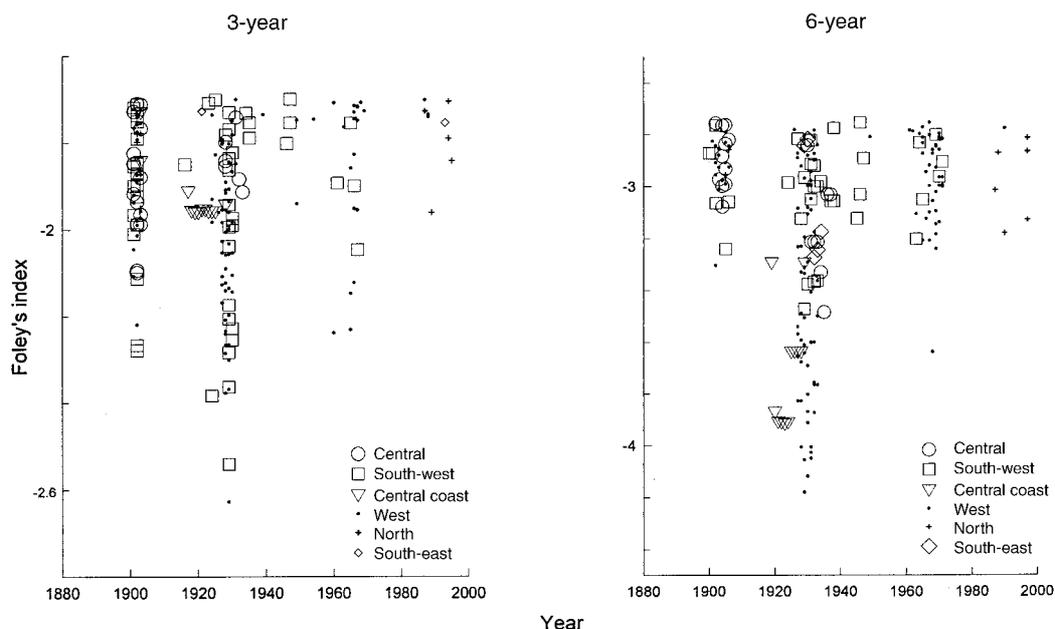


Fig. 3. Minimum Foley's index (D_{min}) for each one-degree grid cell for all years of record in Queensland. Only the 200 lowest grid cell-year combinations are included for the 3- and 6-year standardized rainfall deficit. The points are plotted against the end of the drought deficit period. Grid cells were assigned to a region (Fig. 1).

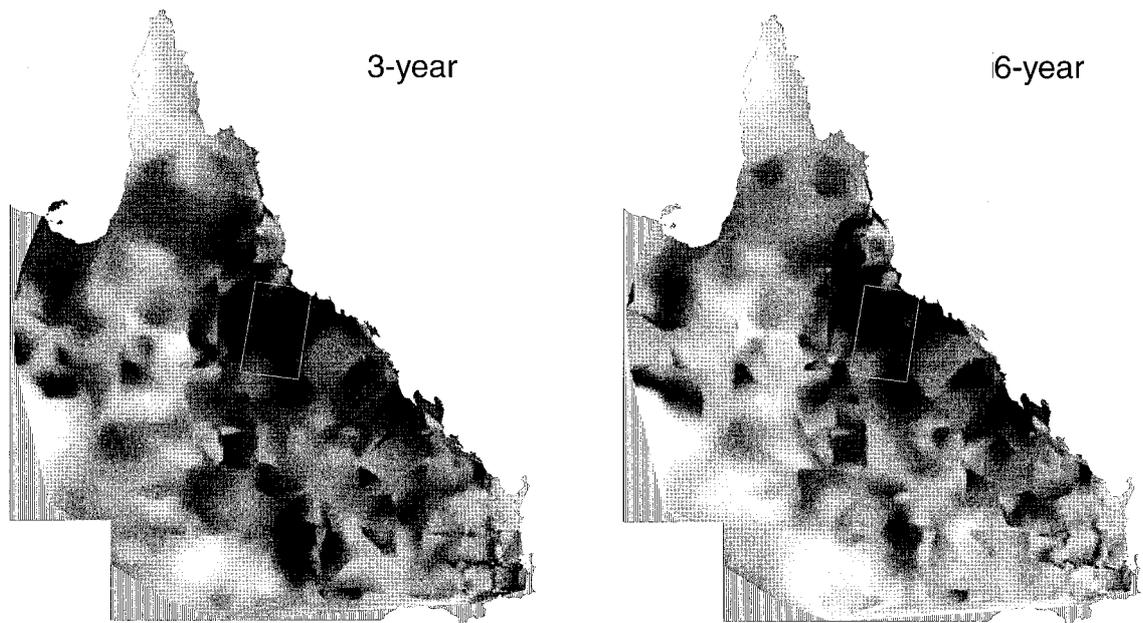


Fig. 4. The severity of the 1990s drought across Queensland for 3- and 6-year standardized rainfall deficit. Shades are derived from the minimum Foley's index value (D_{min}) for all climate stations during the 1990s and vary from less severe drought (white) to more severe drought (black). $D_{min}(3)$ varies from 0.413 to -1.912, and $D_{min}(6)$ from 1.921 to -3.128. The striped pattern indicates those areas where there was no data for the interpolation; the north Queensland study area is indicated.

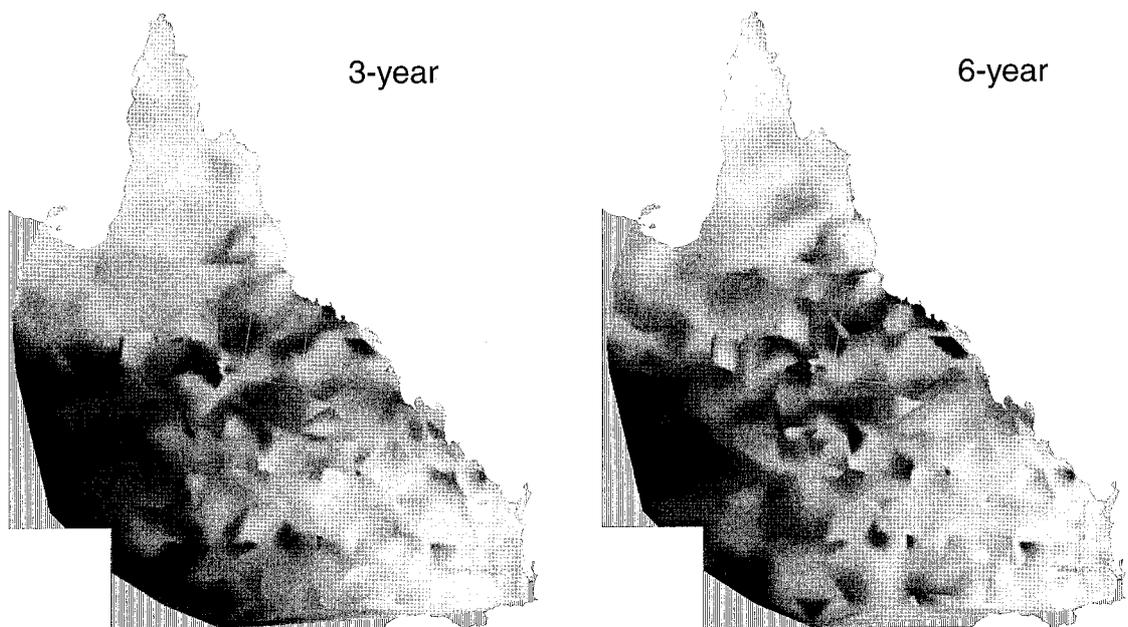


Fig. 5. The worst drought for the period of record in Queensland for 3- and 6-year standardized rainfall deficit. Shades are derived from the minimum Foley's index value (D_{min}) for all climate stations during the 1990s and vary from less severe drought (white) to more severe drought (black). $D_{min}(3)$ varies from -0.774 to -2.628, and $D_{min}(6)$ from -0.881 to -4.180. The striped pattern indicates those areas where there was no data for the interpolation; the north Queensland study area is indicated.

Table 1. Selected historical references to drought-related tree dieback in Queensland. Other references to drought-related tree dieback for the following drought periods and regions are in: 1858, Gregory (1884), p. 204 (south-west); 1890, letter from W. Marsh reported in Hunt (1914), p. 63 (south-west); 1902, Hunt (1914), p. 66 (central), p. 67 (south-east), p. 68 (south-east), *The Queenslander* 31 May 1902, p. 1222 (central), *The Queenslander* 2 August 1902, p. 266 (central), *The Queenslander* 20 September 1902, p. 659 (south-west), *The Queenslander* 26 September 1902, p. 664 (south-east), *The Queenslander* 11 October 1902, p. 839 (south-west)

Source	References	Region (see Fig. 1)	Date
Gregory (1884), p. 191	On the plain we observed that more than half the box ¹ trees had died within the last three years, and that they had not been killed by bush fires, as the old timber which lay on the ground was not scorched	Central	November 1856
Gregory (1884), p. 203	The back country was covered with scrubs of dead acacia ²	Central	April 1858
Letter from G.T. Macmicking reported in Hunt (1914), p. 62	Pine ³ saplings and larger pines died in thousands wherever they were thickly surrounded by their fellows. 'Oak' (balar) ⁴ showed by their withered fringes that a very few months more dry heat would make their growth a thing of the past... hundreds, thousands of the central trees appeared to be, and many were, completely lifeless. The forest gum ⁵ trees died where the underground water-drifts dried away, or lingered on in nearly lifeless misery. The low wattle ⁶ growing on sand ridges shed its seeds and died entirely... The myrtle ⁷ , or 'wait-a-while' ⁸ , and the low brigalow ⁹ ... died in many cases above ground, and so saved their roots for future propagation. Box ¹ and coolibah ¹⁰ trees shed their leaves, and the small limbs and twigs dried and drooped off. Round-leaved iron-bark ¹¹ trees drooped and withered: currajongs ¹² , too, lost their fresh greenness, and many rotted and fell. The sandal wood ¹³ scrubs shed dead twigs and leaves, but their vitality was little impaired. Bendee ¹⁴ , or mulga ¹⁵ , willow ¹⁶ , ironwood ¹⁷ , beefwood ¹⁸ , myall ¹⁹ , yanana ²⁰ , and many other hard polishing woods alone withstood the terrible water famine, and to these trees the graziers owe the salvation of their remaining flocks and herds.	South-west	August 1890
'The drought in Queensland', <i>The Queenslander</i> , 21 September 1901, p. 571	The scrub including the great stand-by mulga ¹⁵ is dying or being eaten out.	West, central or south-west	September 1901
'The drought', <i>The Queenslander</i> , 24 May 1902, p. 1168	On the hills beyond Crow's Nest many ironbark ²¹ trees are dying, while on the ranges facing the Goomburra Valley gum trees ⁵ are perishing in countless numbers, and their dead leaves cause the hills to appear quite a brownish red in the far distance. Such an experience has never before come under the notice of residents who have been over 40 years on the Downs. Ever since the black soil downs of the far West have been occupied the question as to what cause brought about the large areas of dead timber to be seen in the mulga ¹⁵ , gydia ² , and boree ²² scrubs of the interior has been a matter of controversy amongst bushmen. Some attributed it to the action of fire, others to a cold snap, possibly accompanied by snow; again others to a plague of caterpillars, which ate all the leaves and so destroyed the trees: but seeing that timber is now dying in all districts of western Queensland, it would seem not unreasonable to conclude that drought was the cause of thousands of square miles of country in the 'Never Never' being denuded of scrub.	South-east	May 1902
		West, central or south-west	May 1902

Table 1. (continued)

Source	Reference	Region (see Fig. 1)	Date
'The south-western districts', <i>The Queenslander</i> , 9 May 1903, p. 45	One effect of the drought is that the settlers have been saved considerable trouble ringbarking, as large pine ³ forests have completely perished. This has given the growth of grass a great impetus...	South-west	May 1903
Barker (1934)	The timber on miles and miles of forest and scrub land died, and one could ride all day without seeing a tree with a green leaf.	Central	1901–02
'The mulga is disappearing', <i>The Queenslander</i> , 27 June 1935, p. 19	In parts of the west former aged mulga ¹⁵ forests have died out in more or less natural fashion. In cases possibly dry seasons have accelerated the decay, yet on these portions a thick, vigorous undergrowth sprang into life from the roots of the former trees.	West, central or south-west	June 1935
Agricola (1935), p. 7	Along the Bulloo River and other watercourses box ¹ and coolibah ¹⁰ timber 18in. diameter is now dying. This has never been heard of before in the Adavale district.	South-west	1935
Foley (1957), p. 116	... there was 'appalling devastation' on the lower Thomson and lower Barcoo with miles of dead gidyea ² scrub along the channel country	South-west	February 1939
Foley (1957), p. 22	... native trees including mulga ¹⁵ were dead or dying in parts of the south-west, notably in Warrego on the Paroo and Bulloo	South-west	October 1946

¹*Eucalyptus populnea*, ²*Acacia cambagei*, ³*Callitris glaucophylla*, ⁴*Casuarina cristata*, ⁵*Eucalyptus* spp., ⁶*Acacia* spp., ⁷*Canthium* spp., ⁸*Capparis lasiantha*, ⁹*Acacia harpophylla*, ¹⁰*Eucalyptus coolabah*, ¹¹*Eucalyptus melanophloia*, ¹²*Brachychiton populnea*, ¹³*Santalum lanceolatum*, ¹⁴*Acacia catenulata*, ¹⁵*Acacia aneura*, ¹⁶*Acacia salicina*, ¹⁷*Acacia excelsa*, ¹⁸*Grevillea striata*, ¹⁹*Acacia pendula*, ²⁰*Acacia omalophylla*, ²¹*Eucalyptus crebra*, ²²*Acacia tephрина*.

Records spanned a range of environments, including the major wooded formations of inland Queensland and the forested environments of sub-coastal south-east Queensland. No records were located for rainforest or the eucalypt woodlands of the wet tropics, gulf and far north regions.

NORTH QUEENSLAND TREE DIEBACK SURVEY

The two-group level of the UPGMA classificatory hierarchy divided sites with rainfall values throughout the drought that were high, relative to average values, from those where values were low (Fig. 6). Despite differences in the amount of these relative rainfall values between the two classificatory groups, the seasonal pattern was broadly similar (Fig. 6). This suggests that localized storms did not yield sufficient rain or occur with sufficient consistency to affect seasonal rainfall significantly at any site. The large group 1 (187 sites) with relatively low rainfall had significantly greater dieback than the small group 2 (eight sites) with relatively high rainfall during the drought [$F = 4.98$; $P = 0.037$; d.f.(error) 1(191); mean = 0.303 vs. mean = 0.090]. Inspection of the three-group level of the UPGMA hierarchy

suggested that the further subdivision formed relatively low, moderate and high rainfall groups. However, there was no significant difference in the dieback between the groups forming the three-group level of the hierarchy [$F = 2.20$; $P = 0.113$; d.f.(error) 2(190)] or subsequent groups at lower levels of the hierarchy. Group 2 sites all occupied a limited portion of the study area in the high rainfall portion of the study area (Fig. 2). These sites were excluded from subsequent analyses.

The combination of the dieback categories nearly dead (iv) and dead (v) represented 29.2% of the total basal area from the 187 UPGMA group 1 sites. Dieback exhibited substantial patchiness across the study area within all of the five major geological types (Table 2). Mean values of dieback per site were greatest on alkaline igneous rocks (53%), intermediate on metamorphics (36%), sedimentary rocks (30%) and acid igneous rocks (28%), and lowest on alluvia (16%) (Table 3). There was no significant effect of landscape position on dieback [$F = 0.65$, $P = 0.658$; d.f.(error) 5(189)].

There were significant negative relationships between the dieback of other species and the Foley's drought indices on Tertiary sedimentary rocks [e.g. for $D_{(min)}$: $R = -0.375$, $P < 0.02$; $n = 73$], and these

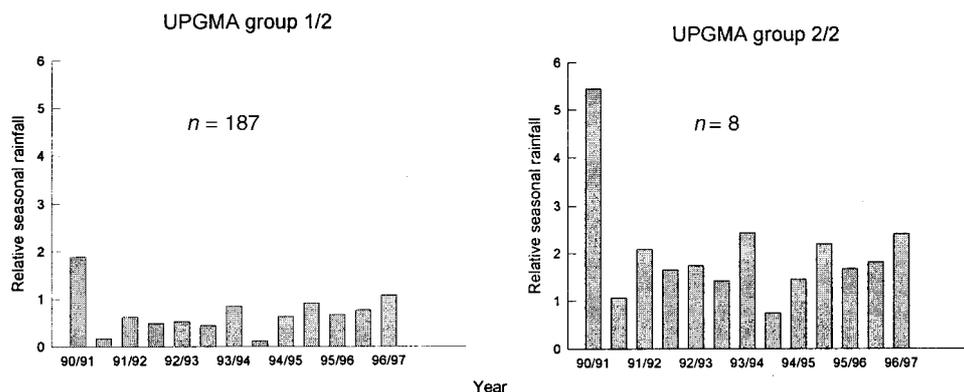


Fig. 6. Mean values of wet and dry season rainfall during the 1990s drought relative to the average rainfall for each season for the two-group UPGMA classification.

Table 2. The proportion of sites in each dieback proportion category and number of sites (in parentheses) for the five geology classes. The proportion of sites was calculated within each geology class rather than for the total data set

Dieback proportion category	Alluvia	Alkaline igneous rocks	Metamorphics	Acid igneous rocks	Sedimentary rocks
0	18.4(7)	16.7(3)	(0)	15.0(3)	6.7(6)
0-0.1	21.1(8)	11.1(2)	23.3(7)	20.0(4)	13.48(12)
0.1-0.2	26.3(10)	(0)	13.3(4)	5.0(1)	21.4(19)
0.2-0.4	15.8(6)	5.6(1)	26.7(8)	15.0(3)	27.0(24)
0.4-0.6	10.5(4)	11.1(2)	20.0(6)	5.0(1)	18.0(16)
0.6-1	(0)	55.6(10)	16.7(5)	15.0(3)	13.5(12)
Total	100.0(37)	100.0(18)	100.0(30)	100.0(15)	100.0(89)

relationships were not significant on other substrates. These differences were evident in the combined analysis, presented in Table 4. There were no significant relationships between total dieback and rock cover and only a weakly negative correlation between the proportion of dieback for other species and bare ground (Table 4). There were significantly positive relationships between dieback and basal area within *Corymbia*, *Acacia* and the other species group, although these relationships were not significant for *Eucalyptus* or total species (Table 4).

The second most abundant taxon in terms of basal area was *E. crebra*-*E. xanthoclada*, having 44.6% dieback (Table 5). Other abundant species, *E. melanophloia*-*E. whitei*, *E. brownii* and *E. persistens*, had moderate dieback rates between 25.5% and 28.2% (Table 5). The fifth most dominant species, *Corymbia clarksoniana*, had a relatively low dieback rate of 23.8% (Table 5). The dieback of understorey species ranged from 0% for *Atalaya hemiglauca* to 31% for *Maytenus cunninghamii* (Table 5). *Eucalyptus similis* had a high proportion of dieback,

Table 3. The mean proportion of dieback [dieback category (iv) and (v) basal area/total basal area] and standard error according to geological type and results from one-way ANOVA following arcsin transformation. Means not significantly different according to Tukey's test are annotated with the same letter. $F = 6.54$, $P < 0.001$, d.f.(error) 4(190)

	Mean	Standard error	<i>n</i>
Alkaline igneous rocks	0.527 ^B	0.084	18
Metamorphics	0.359 ^{BC}	0.053	30
Sedimentary rocks	0.306 ^C	0.026	89
Acid igneous rocks	0.275 ^{AC}	0.080	15
Alluvia	0.160 ^A	0.027	35

Table 4. Spearman's rank correlation coefficients for dieback according to precipitation, Foley's index (*Dmin*), rockiness, bare ground, the abundance of broad taxonomic groups and a variety of other values. In plots where taxonomic groups were absent as adult plants, missing values were assigned rather than zeros. *n* is indicated in parentheses

	<i>Eucalyptus</i> dieback	<i>Corymbia</i> dieback	<i>Acacia</i> dieback	Other species dieback	Total dieback
Mean annual precipitation	NS(170)	NS(108)	NS(84)	NS(138)	NS(187)
<i>Dmin</i> (3)	NS(170)	NS(108)	NS(84)	-0.17*(138)	NS(187)
<i>Dmin</i> (4)	NS(170)	NS(108)	NS(84)	-0.17*(138)	NS(187)
<i>Dmin</i> (5)	NS(170)	NS(108)	NS(84)	NS(138)	NS(187)
<i>Dmin</i> (6)	NS(170)	NS(108)	NS(84)	NS(138)	NS(187)
Rockiness	NS(170)	NS(108)	NS(84)	NS(138)	NS(187)
Bare ground	NS(170)	NS(108)	NS(84)	-0.19*(138)	NS(187)
<i>Eucalyptus</i> basal area	NS(170)	NS(108)	NS(84)	NS(138)	NS(178)
<i>Corymbia</i> basal area	-0.22*(107)	0.27**(108)	NS(84)	NS(138)	NS(116)
<i>Acacia</i> basal area	NS(170)	NS(51)	0.34*** (84)	-0.17*(138)	NS(91)
Other species basal area	-0.39*** (134)	NS(88)	NS(75)	0.33*** (138)	-0.18*(148)
Total basal area	NS(170)	NS(108)	NS(84)	NS(138)	NS(187)

*** $P < 0.001$, ** $0.001 < P < 0.01$, * $0.01 < P < 0.05$, NS not significant.

Table 5. Number of sites (*n*) where species occur and mean basal area ($\text{m}^2 \text{ha}^{-1}$) per site according to dieback category (see text). The mean values for particular taxa are for those sites where that taxa was present. Percentage dieback according to category (iv) and (v) and category (v) only are included

	<i>n</i>	Dieback category					Total	Dieback (%)	
		(i)	(ii)	(iii)	(iv)	(v)		Category (iv) and (v)	Category (v) only
Common overstorey species									
<i>Acacia argyrodendron</i>	5	2.94	0.23	0.05	0.00	0.43	3.65	11.75	11.75
<i>A. cambagei</i>	4	1.78	0.68	0.06	0.00	0.09	2.61	3.58	3.58
<i>A. excelsa</i>	15	0.09	0.00	0.00	0.01	0.06	0.17	44.78	37.21
<i>Allocasuarina/Casuarina</i> spp.	1	2.07	0.00	0.00	0.05	1.91	3.98	47.88	47.88
<i>Corymbia clarksoniana</i>	38	0.81	0.04	0.00	0.01	0.25	1.12	23.80	22.60
<i>C. dallachiana</i>	62	0.27	0.03	0.05	0.00	0.04	0.39	10.83	9.77
<i>C. erythrophloia</i>	34	0.30	0.13	0.02	0.00	0.03	0.49	6.93	6.64
<i>Corymbia</i> spp.	22	0.36	0.02	0.01	0.04	0.21	0.63	38.84	32.69
<i>Eucalyptus brownii</i>	42	1.48	0.38	0.52	0.16	0.77	3.32	28.22	23.27
<i>E. camaldulensis</i>	9	1.69	0.00	0.00	0.08	0.47	2.25	24.60	20.96
<i>E. crebra-E. xanthoclada</i>	70	0.89	0.31	0.38	0.08	1.19	2.84	44.59	41.76
<i>E. melanophloia-E. whitei</i>	71	1.44	0.45	0.41	0.08	0.71	3.09	25.63	22.95
<i>E. persistens</i>	15	1.57	0.62	0.44	0.17	0.73	3.52	25.49	20.59
<i>E. platyphylla</i>	3	0.85	0.00	0.43	0.00	0.00	1.28	0.00	0.00
<i>E. similis</i>	10	0.71	0.20	0.34	0.47	0.49	2.20	43.50	22.30
<i>Eucalyptus</i> spp.	23	0.73	0.02	0.05	0.03	0.31	1.14	29.74	27.23
<i>Lysiphyllum carronii</i>	13	0.22	0.00	0.00	0.00	0.01	0.23	2.46	2.46
<i>Melaleuca nervosa</i>	17	0.68	0.01	0.02	0.00	0.15	0.87	17.96	17.44
Common understorey species									
<i>Acacia coriacea</i>	48	0.22	0.00	0.00	0.00	0.06	0.29	20.46	19.44
<i>Atalaya hemiglauca</i>	22	0.06	0.00	0.00	0.00	0.00	0.06	0.00	0.00
<i>Bursaria incana</i>	22	0.08	0.00	0.00	0.00	0.01	0.10	13.07	13.07
<i>Eremophila mitchellii</i>	35	0.17	0.01	0.02	0.00	0.06	0.26	25.16	23.66
<i>Maytenus cunninghamii</i>	25	0.02	0.00	0.00	0.00	0.01	0.02	30.97	30.97
<i>Petalostigma banksii</i>	15	0.19	0.01	0.01	0.00	0.09	0.29	30.25	29.17
<i>P. pubescens</i>	19	0.29	0.02	0.01	0.00	0.12	0.43	26.86	26.86
<i>Terminalia aridicola</i>	16	0.17	0.03	0.02	0.00	0.04	0.26	15.23	14.46
<i>Acacia</i> spp.	29	0.33	0.00	0.01	0.04	0.22	0.60	42.63	36.61
Other species									
Rainforest spp.	78	0.41	0.00	0.04	0.01	0.11	0.57	20.80	19.04
Grand total	2	0.14	0.00	0.00	0.00	0.00	0.14	0.00	0.00
Grand total	187	2.48	0.50	0.53	0.16	1.29	4.97	29.18	25.88

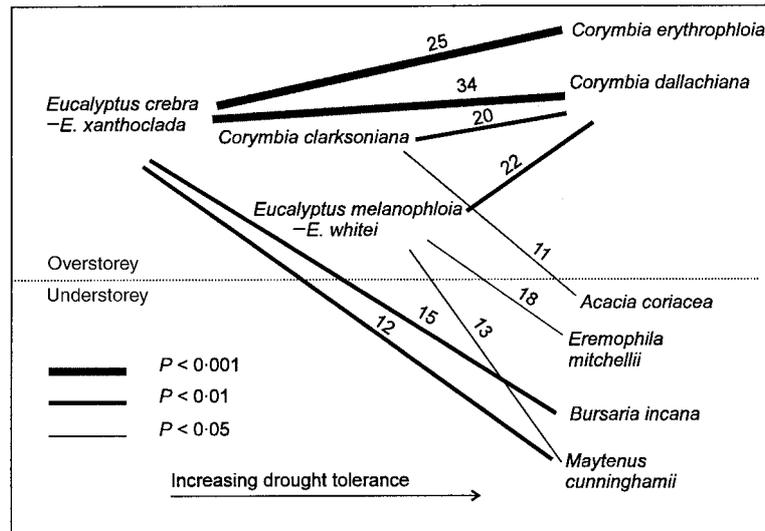


Fig. 7. Significant differences ($P < 0.05$) in the proportion of dieback [dieback categories (iv) and (v) basal area/total basal area] between species that co-occurred in more than seven sites. n is indicated on the line and in parentheses after non-significant differences, and species are ordered such that significant differences reflect increasing drought tolerance. Understorey and overstorey species are separated. Non-significant differences ($P > 0.05$): *Acacia coriacea* vs. *Eremophila mitchellii* (12), *Acacia coriacea* vs. *Eucalyptus melanophloia*–*Eucalyptus whitei* (34), *Acacia coriacea* vs. *Maytenus cunninghamii* (8), *A. excelsa* vs. *Eucalyptus brownii* (8), *Bursaria incana* vs. *Corymbia dallachiana* (8), *C. dallachiana* vs. *C. erythrophloia* (16), *C. dallachiana* vs. *Eremophila mitchellii* (8), *C. dallachiana* vs. *Eucalyptus brownii* (14), *C. clarksoniana* vs. *Eucalyptus crebra*–*Eucalyptus xanthoclada* (19), *C. clarksoniana* vs. *Eucalyptus melanophloia*–*Eucalyptus whitei* (13), *C. dallachiana* vs. *Maytenus cunninghamii* (11), *C. clarksoniana* vs. *Melaleuca nervosa* (11), *Eremophila mitchellii* vs. *Eucalyptus brownii* (15), *Eremophila mitchellii* vs. *Lysiphyllum carronii* (9), *Eucalyptus brownii* vs. *Eucalyptus crebra*–*Eucalyptus xanthoclada* (8), *Eucalyptus brownii* vs. *Eucalyptus melanophloia*–*Eucalyptus whitei* (18), *Eucalyptus crebra*–*Eucalyptus xanthoclada* vs. *Eucalyptus melanophloia*–*Eucalyptus whitei* (8), *Eucalyptus crebra*–*Eucalyptus xanthoclada* vs. *Eucalyptus melanophloia*–*Eucalyptus whitei* (9), *Eucalyptus crebra*–*Eucalyptus xanthoclada* vs. *Petalostigma pubescens* (9), *Eucalyptus melanophloia*–*Eucalyptus whitei* vs. *Terminalia aridicola* (9). Computation impossible because of identical values: *Eucalyptus brownii* vs. *Atalaya hemiglauca* (14), *Atalaya hemiglauca* vs. *C. dallachiana* (8), *Atalaya hemiglauca* vs. *Eremophila mitchellii* (10).

although a large portion of this was represented by the category nearly dead (iv) rather than dead (v) (Table 5). Differences in dieback between species that co-occurred are identified in Fig. 7. The data suggested that the dominant overstorey species *E. crebra*–*E. xanthoclada* were more drought prone than the subdominant overstorey species *C. clarksoniana*, which was more drought prone than the subdominant overstorey species *C. dallachiana* and *C. erythrophloia*. The understorey species *Acacia coriacea*, *Atalaya hemiglauca*, *Bursaria incana*, *Eremophila mitchellii* and *Maytenus cunninghamii* were generally more drought tolerant than the overstorey species (Fig. 7 and Table 5).

Eucalyptus crebra–*E. xanthoclada* was the only species [$F = 6.84$; $P = 0.01$, d.f.(error) 1(113); mean proportion death < 11 cm d.b.h. = 0.26; > 11 cm d.b.h. = 0.45] out of 21 common species that were tested where large stems showed a greater propensity for dieback than small stems.

Woody sprout densities were positively correlated with Foley's drought indices (Table 6). There were no significant relationships between the proportion of total dieback and woody sprout densities

(Table 6). Figure 8 presents the stand structure of the four most frequent overstorey species and indicates that woody sprout densities (individuals < 2 mH) for *C. clarksoniana* and *E. crebra*–*E. xanthoclada* were greater than the adult plants remaining after the dieback event, while for *E. melanophloia*–*E. whitei*, and particularly *E. brownii*, woody sprout densities were lower than adult plants.

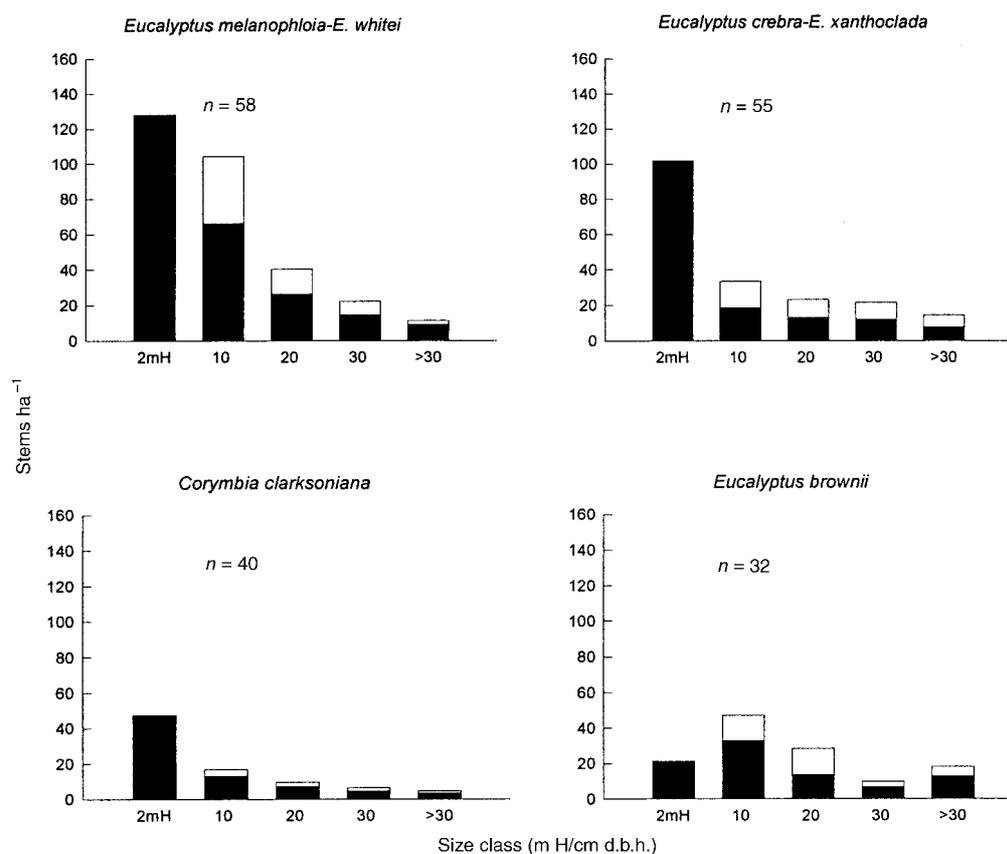
Discussion

The analysis undertaken for this study has spatially and temporally located intense droughts in Queensland during the period of rainfall record. In terms of the standardized rainfall deficit used here, the droughts at the turn of the 20th century, early 1930s and mid-1960s in the south-west, west and central regions were the worst on record. Localized droughts, such as those affecting the central coast region in the early 1920s and the north region in the early 1990s, have been the most intense on record for those particular areas. A more generalized analysis using amalgamated rainfall data from stations

Table 6. Spearman's rank correlation coefficients for woody sprout densities according to precipitation, Foley's index (*Dmin*), rockiness, bare ground, the abundance of broad taxonomic groups and a variety of other values. In plots where taxonomic groups were absent as adult plants, missing values were assigned rather than zeros. *n* is indicated in parentheses

	Eucalyptus	Corymbia	Acacia	Other species	Total
Annual precipitation	NS(170)	NS(112)	NS(98)	NS(163)	-0.15*(190)
<i>Dmin</i> (3)	NS(170)	0.19*(112)	NS(98)	NS(163)	NS(190)
<i>Dmin</i> (4)	NS(170)	0.22*(112)	NS(98)	NS(163)	NS(190)
<i>Dmin</i> (5)	NS(170)	0.20*(112)	NS(98)	NS(163)	NS(190)
<i>Dmin</i> (6)	NS(170)	0.22*(112)	NS(98)	NS(163)	NS(190)
Rockiness	NS(170)	NS(112)	NS(98)	NS(163)	NS(190)
Bare ground	NS(170)	NS(112)	NS(98)	NS(163)	NS(190)
<i>Eucalyptus</i> basal area	0.20**(170)	NS(112)	-0.25*(97)	NS(156)	NS(178)
<i>Corymbia</i> basal area	NS(107)	0.24*(112)	NS(60)	NS(97)	NS(108)
<i>Acacia</i> basal area	NS(83)	0.28*(52)	0.37***(84)	-0.31**(84)	NS(190)
Other species basal area	-0.26**(140)	NS(89)	NS(89)	0.28***(140)	0.20*(140)
Total basal area	NS(170)	NS(112)	NS(98)	0.18*(163)	0.24**(189)
<i>Eucalyptus</i> dieback	NS(170)	NS(110)	-0.26*(97)	NS(156)	NS(170)
<i>Corymbia</i> dieback	NS(107)	NS(108)	NS(60)	NS(108)	0.20*(108)
<i>Acacia</i> dieback	0.31**(83)	NS(52)	0.29**(84)	-0.24*(84)	NS(84)
Other species dieback	NS(134)	NS(89)	NS(89)	NS(138)	NS(138)
Total dieback	NS(170)	NS(112)	NS(98)	NS(163)	NS(190)

*** $P < 0.001$, ** $0.001 < P < 0.01$, * $0.01 < P < 0.05$, NS not significant.

**Fig. 8.** Size class histograms for selected tree species calculated by pooling the data from those sites where the species had a frequency of greater than four. The black portion of the bar represents the mean frequency of the live plants [dieback categories (i)–(iii)] and the white portion the dead [categories (iv)–(v)]. Stem size classes are mutually exclusive and indicated by the maximum value for each class where the smallest size class is height (H) and the others are diameter (cm) at breast height. Dead plants in the 0–2 mH group were not assessed.

across Queensland concluded that the 1990s drought was not abnormal compared with other periods (Lough 1997).

Fluorescent bands in massive sea corals are affected by deposition from floodwaters and provide a surrogate history of summer rainfall extending back to the early 17th century (Isdale *et al.* 1998). This record suggests that the early part of the 19th century was characterized by periods with rainfall at least as low as the droughts during the 20th century. The earlier part of the record indicates fluctuating climatic circumstances including high rainfall periods, the magnitude of which has not occurred since. This record suggests that the droughts that have been recorded within the rainfall record are relatively normal within the last half of the recent millennia.

Historical accounts of tree dieback are provided for semi-arid, arid and subtropical environments in vegetation dominated by the overwhelmingly dominant tree genera in Australia, *Eucalyptus* and *Acacia*. There is good evidence that areas with reliable winter rainfall or a strongly monsoonal wet season are less prone to severe rainfall deficits. However, it is also likely that the biota are poorly adapted to relatively low rainfall deficits in areas with these reliable rainfall features. Evidence of such sensitivity is provided by the historical records of tree death in the south-east region, which has been relatively immune from extreme rainfall deficits during the period of record.

The historical records of the media and other sources clearly demonstrate widespread and substantial tree death as a result of drought. However, historical sources are inadequate for providing quantification of drought-related tree dieback or for providing detail of dieback in relation to local rainfall or other environmental features. Such quantified information was provided in this study from the documentation of a recent severe drought in tropical Australian savanna.

The standardized rainfall deficit represented by Foley's index was most negative during the 1990s in north Queensland relative to other areas. A temporal (Fig. 3) and spatial (Fig. 4) view of this index is entirely compatible with the extensive and substantial dieback in the study area being a product of the exceptional 1990s drought. Accurate modelling of dieback in relation to drought intensity could be advanced with spatial analysis of remote-sensed satellite data both within and beyond the study area examined here.

Tree dieback resulting from the 1990s drought was substantial across a large area of savanna woodland in north Queensland, but was not uniform. There was considerable variation between rock types, and within each broad geological category the extent of dieback was extremely patchy.

There was little evidence that the patchiness in dieback was a direct effect of patchy rainfall because there was a general absence of correlations between dieback and modelled rainfall deficits and the classification did not reveal any evidence of local but substantial storms. The competitive effects of the standing crop of trees may influence the patchiness of dieback. There were significant relationships between dieback and the predrought basal area for some taxonomic groups, although not for total stocks and total dieback across the study area. It is probable that dieback results from complex interactions between tree stocks, soil substrate characteristics and local rainfall deficits.

Fensham (1998) compared tree dieback in north Queensland between grazed and ungrazed woodland. His study demonstrated that dieback was on average about 27% in the ungrazed woodland. However, subsequent monitoring of one of the ungrazed treatment sites suggested that dieback had increased since the original study from 26% to 69%, as moribund trees had subsequently died (R. J. Fensham, unpublished data). Clearly, even in the absence of soil compaction or disturbance by ungulates, substantial tree dieback can occur. In the current study dieback as a result of the 1991–96 drought was unrelated to bare ground. While bare ground is an imperfect surrogate for grazing intensity, neither study has been able to provide any evidence that dieback is exacerbated by the activities of cattle.

The average seedling and sapling density data presented in Fig. 8 would seem to indicate that the recovery of predrought structure is imminent. However, several factors may delay the recovery of tree stocks in drought-affected savanna woodland. The < 10 cm d.b.h. stem densities are lower than the range for that size class recorded during average seasons from six independent monitoring sites within the study area (Scanlan, Pressland & Myles 1996). This suggests that drought-induced dieback of seedlings and saplings may have occurred. Furthermore, not all woody sprouts represent regenerating stock because Fensham & Bowman (1992) provide some evidence that a proportion of the woody sprout pool may be moribund. Germination events are rare in other tropical eucalypt savanna (Lacey 1974; Fensham 1992) and are likely to be further limited after the current drought due to the death of mature trees. There is also some evidence from Australian savanna that grazing increases the mortality of regenerating eucalypts (*Eucalyptus* and *Corymbia* combined) (Scanlan, Pressland & Myles 1996). Nothing is known of the regeneration ecology of the species included in this study in relation to fire.

A model of tree–grass dynamics in savanna predicts that loss of mature trees in dry times would be moderate because of their access to subsurface

moisture (Jeltsch *et al.* 1996). However, this study suggests that the model may underestimate either the magnitude of subsurface moisture deficits during extreme drought or the sensitivity of savanna tree species. There is documentation of substantial drought-related tree dieback in Africa (Scholes 1985; Viljoen 1995; Tafangenyasha 1997) as well as Australia. Viljoen's (1995) study suggests substantial death for some species at some sites (i.e. 78% for *Dichrostachys cinerea*, 72% for *Strychnos madagascariensis* and 93% of *Acacia tortilis*) in Kruger National Park, South Africa. It is likely that obligate evergreen savanna species such as most *Eucalyptus* are less able to withstand the vicissitudes of drought than species that can minimize transpiration by the prolonged maintenance of a deciduous or semi-deciduous habit.

There is irrefutable evidence of forest or scrub encroachment across a range of continents (Van Vegten 1983; Mariotti & Peterschmitt 1994; Boutton *et al.* 1998). The evidence from Australia is unequivocal for rainforest expansion (Harrington & Sanderson 1994) and the invasion of grassland in some situations (Fensham & Fairfax 1996; Crowley & Garnett 1998) and is largely attributed to a reduced fire frequency or, more particularly, a decline in high intensity fires. However, the current study suggests that in at least some Australian savannas, tree stocks are inherently unstable regardless of the influence of fire or grazing. Presumably dieback events are matched by structural recovery during average or relatively mesic times. In this sense dieback in savanna may provide a mechanism for intermittent reversal of the putative trend for increasing wood in savanna environments.

Some tree species were more prone to drought death than others. The general trends established by this study indicate that understorey shrubs are relatively drought tolerant and that the genus *Corymbia* is relatively drought tolerant compared with *Eucalyptus*. Tree species in *Corymbia* are often subdominant to *Eucalyptus* in tropical eucalypt woodlands in the study area, but the results suggest that their relative dominance fluctuates. Within populations, dieback was largely independent of stem size, with the single exception of *E. crebra*–*E. xanthoclada* for which large stems were relatively susceptible. The differential drought tolerance of overstorey and understorey trees highlights the probability that they respond differently to the influence of climate and management in *Eucalyptus* savanna. Specifically we hypothesize that changes in understorey structure are primarily determined by management influences such as fire and that overstorey *Eucalyptus* are primarily controlled by climate. However, the relative importance of climate, atmospheric and management influences on the various components of *Eucalyptus* savanna requires substantially more

research. It is essential to disentangle and quantify non-anthropogenic and anthropogenic effects (IPCC 1997) if stocks and fluxes in savanna vegetation are to be incorporated reliably in carbon budgeting for greenhouse gas obligations. Furthermore these issues have great relevance for the sustainable management of tropical savannas for animal production and the maintenance of biodiversity.

Acknowledgements

This project was partly funded by the Tropical Savannas Cooperative Research Centre. Sel Counter, Tim Danaher and Cheryl Kuhnell are thanked for providing the vegetation cover change analysis. Keith Moodie is thanked for generating the rainfall data from Data Drill. Robbie Price is thanked for the programming that generated the Foley's index values. Arnon Accad is thanked for generating the climate surfaces represented by Figs 4 and 5. David DeWit provided the mathematical notation. Dave Bowman, Gabriel Crowley, Russell Fairfax, Stephen Garnett and the referees are thanked for their comments on the manuscript.

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Received 21 December 1998; revision received 17 July 1999