Journal of Vegetation Science 18: 71-80, 2007
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Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture

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Abstract

Questions: For eucalypt savanna in northeast Australia subject to multi-year rainfall deficits this paper asks whether (1) dominant tree species (Ironbarks, Boxes) are more drought susceptible than the sub-dominant Bloodwoods; (2) whether soil moisture is beyond wilting point in surface soil layers but available at depth; (3) soil conditions (moisture availability and texture) are related to tree death during drought; (4) the root systems of the Boxes and Ironbarks are shallower than the Bloodwoods; and the survivors of drought within species have deeper root systems than those that died.

Location: Central Queensland, Australia.

Methods: Patterns of tree death between eucalypt species were compared from field data collected after drought. Soil conditions during drought were described and compared with patterns of tree death for the Ironbark *Eucalyptus melanophloia*. The basal area and orientation of coarse roots were measured on upturned trees after broad-scale tree clearing, and compared between species, and between live and dead trees with tree size as a covariate.

Results: Drought-induced tree death was higher for dominant Ironbark-Box than for sub-dominant Bloodwoods. During a moderate to severe drought in 2004, 41% of 100 cm deep subsoils had soil matric potential less than –5600 kPa. The drought hardy Bloodwoods had a greater root basal area and particularly so for vertical roots compared to the drought sensitive Ironbark-Box. Within species there was no significant difference in root basal area characteristics between trees that were recently killed by drought and those that remained relatively healthy. Surface soil moisture availability was lower where tree densities were high, and tree death increased as surface soil moisture became less available. Tree death was also greater as the clay content of sub-soils increased.

Discussion: The study suggests species with roots confined to upper soil layers will suffer severe water stress. The results strongly indicate that root architecture, and the way it facilitates water use during drought, is important for the relative dominance of the tree species. Patchiness in drought-induced tree death seems to be at least partially a product of heterogeneity in sub-soil conditions and competition for soil moisture.

Keywords: Australia; Dieback; Drought; Eucalypt woodland; Niche separation; Root architecture; Savanna; Soil.

Nomenclature: Because of the complex nomenclature of the taxa to be treated here vernacular names as elucidated in Table 1 will be used (see also Henderson 2002).

Introduction

Drought has the capacity to cause widespread tree-death in semi-arid environments (e.g. Allen & Breshears 1998; Villalba & Veblen 1998; Lloret et al. 2004). It has been suggested that this effect may be a critical factor determining the dynamics of woody vegetation structure in Australian savanna (Fensham & Holman 1999; Fensham et al. 2005) and major shifts in species composition in the pinyon-juniper woodlands of the USA (Mueller et al. 2005). In the Australian example, the widespread death of savanna trees seems to be largely independent of management. Fensham (1998) recorded no difference in the magnitude of drought-induced tree death between areas that have never been grazed by cattle and nearby areas encompassing moderate to heavy utilisation. Within the same ungrazed areas, 85% of woodland basal area was represented by savanna trees that had recently died in coincidence with the intense drought between 1992-1997 on a permanent monitoring plot (Fensham et al. 2003). Fensham & Holman (1999) record that the substantial patchiness in tree death was not related to bare ground, a key variable for the degradation indices employed by MacGregor & O'Connor (2002) to demonstrate that land degradation exacerbated tree death during drought in an African study.

In Australian savanna both Sharp & Bowman (2004) and Fensham & Holman (1999) document variations in drought-induced tree death between *Eucalyptus* and the closely related *Corymbia*. Rice et al. (2004) have demonstrated that the field xylem pressure potentials are substantially more negative in the Ironbark *Eucalyptus crebra* than the Bloodwood *Corymbia erythrophloia*. During the extreme of the drought period, the lowest mid-day pressure potentials for Ironbark were measured at about –5600 kPa and for Bloodwood at –3000 kPa. These authors suggest that the drought susceptibility of the two species may reflect their relative rooting depth with the Bloodwood having a requirement for deeper roots. Growth strategies may influence the dominance hierarchy of related genera in semi-arid savanna as has been indicated for sub-generic dominance hierarchies

Table 1. Vernacular names of eucalypt tree species referred to in this paper and their taxnomic relations.

Current species name	Species name (Brooker 2000)	Subgeneric classification (Brooker 2000)	Common name used in this paper
Eucalyptus crebra F. Muell.	*Eucalyptus crebra*	Subgenus *Symphyomyrtus* Section *Adnataria*, Series: *Siderophloiae*	Ironbark
Eucalyptus melanophloia F. Muell.	*Eucalyptus melanophloia*	Subgenus *Symphyomyrtus* Section *Adnataria*, Series: *Siderophloiae*	Ironbark
Eucalyptus populnea F. Muell.	*Eucalyptus populnea*	Subgenus *Symphyomyrtus* Section *Adnataria*, Series *Buxeales*	Box
Corymbia clarksoniana (D.J. Carr & S.M. Carr) K.D. Hill & L.A.S. Johnson	*Eucalyptus clarksoniana*	Subgenus *Corymbia*, Section *Rufaria*	Bloodwood
Corymbia dallachiana (Benth.) K.D. Hill & L.A.S. Johnson	*Eucalyptus tessellaris*	Subgenus *Blakella* Section *Extensae*	Bloodwood
Corymbia erythrophloia (Blakely) K.D.Hill & L.A.S. Johnson	*Eucalyptus erythrophloia*	Subgenus *Corymbia* Section *Septentrionale*	Bloodwood

within *Eucalyptus* elsewhere in Australia (Noble 1989). In southern Australia the dominant *Monocalyptus* subgenus appears to adopt a more profligate physiological strategy (e.g. less stomatal control) than the sub-dominant *Symphyomyrtus*.

While drought-induced tree death seems to be a normal part of ecosystem function in semi-arid Australia, the patchiness in its occurrence is unexplained. Both Fensham & Holman (1999) and Sharp & Bowman (2004) postulate that variability of soil conditions and drought-relieving rainfall events may be important factors. These ideas can be tested by comparing patterns of drought-induced death with empirical data on soil moisture availability and soil conditions.

For a particular species it is also possible that drought susceptibility of individual trees may be related to the development of deep rooting. Resolution of the role of rooting depth within and between species as a mechanism for surviving drought requires information on root architecture and soil moisture availability during drought. The current study elucidates the role of drought susceptibility as a mechanism for structuring Ironbark-Box-Bloodwood savanna in semi-arid Queensland. It includes a description of (1) species abundances and corresponding levels of drought-related tree death; (2) the magnitude of a recent drought in relation to soil moisture data; (3) the root architecture of Ironbark, Box and two Bloodwood species. Specifically it aims to address the following five hypotheses:

1. The dominant Ironbark-Boxes are more drought susceptible than the sub-dominant Bloodwoods.
2. Soil moisture is beyond wilting point in surface soil layers but is available at depth.
3. Soil moisture conditions during drought are related to tree death.
4. The root systems of Ironbark-Box are shallower than Bloodwood.
5. Within a species the survivors of drought will have deeper root systems than those that died.

Methods

Relative dominance and tree death susceptibility

The study is focused on Ironbark (*E. melanophloia*)-Box (*Eucalyptus populnea*) savanna. The closely related Bloodwoods (*Corymbia clarksoniana* and *C. dallachiana*) are common as sub-dominants in this savanna throughout central and southern Queensland with related species extending into north Queensland. There is no data on seasonal leaf fall for these eucalypt species. However, the Box and Ironbark would be classified as evergreen and the Bloodwoods as brevideciduous using the scheme of R.J. Williams et al. (1997). The Ironbark-Box savanna woodlands covered about 13 M ha of Queensland prior to large areas being extensively cleared to improve pasture production for cattle (Wilson et al. 2002).

To describe relative abundance and the susceptibility of the dominant Ironbark-Box and sub-dominant Bloodwood species to drought during the 1990s (Fig. 1), data from central Queensland were compiled. Data were collected during October 1998 and June 1999 from 46

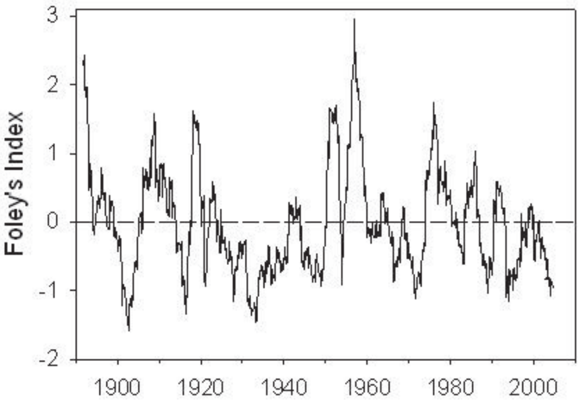

Fig. 1. Rainfall Index through time at the soil moisture study site in central Queensland (23°28' S 146°21' E). Negative values represent rainfall deficit over the preceding 3-year period.

sites (see Hannah et al. in press) where the combined total basal area of the four target species Ironbark (*Eucalyptus melanophloia*), Box (*E. populnea*) and Bloodwoods (*Corymbia clarksoniana* and *C. dallachiana*) is greater than any other single tree species. At each site between 12 and 30 Bitterlich sweeps (trees counted from a central point according to their intersection with a specified angle in circular plots with variable radii, Grosenbaugh 1952) were taken at least 50 m apart. The counts from the sweeps were assigned to species and categorised as live (includes trees from healthy crowns to some major branches dead) or dead (recently dead trees as identified by bark still firm on trunk or almost dead, as evidenced by weak epicormic growth). Fensham et al. (2003) have demonstrated that debilitated savanna Ironbarks with only epicormic growth do not generally recover. From these data-sets the basal area of the target species were summarised using live and dead trees in combination.

This data-set was collected after a period of drought in the early 1990s. For central Queensland the rainfall deficit during the 1990s drought coincided with about a once in 30-year event (Fensham et al. 2005). To establish the relative drought sensitivity of Ironbark, Box (*Eucalyptus populnea*) and the two Bloodwoods, data from sites with paired combinations of any of the four target species were compiled. The level of tree death at each site was calculated for each species as: basal area dead/dead and live basal area. Comparisons of tree death were performed for all species pairs using Wilcoxon's paired sample test.

Drought, tree death and soil conditions

All of the subsequent field sampling was conducted at three separate locations within 30 km of each other in central Queensland. All sites have similar rainfall histories and are situated on the mid to lower slopes of gently undulating plateaux formed from Quaternary sand deposits equivalent to the Wollola Land System, described as having 'moderately deep to deep soils' (Turner 1978). Sites were only included if they were either grey-brown or yellow deep chromosols (Australian Soil Classification: Isbell 1996). Soil sampling at all sites indicated that the non-sodic sandy clay loam or clay loam subsoils extended to at least 150 cm. The soils are deep and well drained and provide no apparent impediment to rooting depth except during extremely dry conditions when the soils are hardsetting (Mullins et al. 1990). Vegetation is mostly dominated by either Ironbark (*Eucalyptus melanophloia*) but can also be dominated by Box (*E. populnea*) with Bloodwoods (*Corymbia clarksoniana* and *C. dallachiana*) as sub-dominants.

Soil moisture was determined during a period of intense rainfall deficit in October 2004 at location 23°28' S, 146°21' E. 'Sites were selected along 7 km of track to represent a range of tree densities and levels of drought-induced tree death.

Twenty-two soil profiles were sampled at 7.5 cm, 30 cm, 50 cm and 100 cm depth and samples stored in airtight plastic bags. To determine gravimetric moisture content these were weighed and re-weighed following drying at 105 °C for 48 h. Soil texture was determined for each of the samples using the guide in McDonald et al. (1990) and assigned to loamy sand, sandy loam, sandy clay loam and clay loam.

Twelve samples representing the range of soil textures were employed to derive soil moisture- matric potential relationships at –100 kPa, -300 kPa, -500 kPa and –1500 kPa using the method of McIntyre (1974) and equipment supplied by the Soil Moisture Equipment Co. of California.

After assigning the average fitted curve for each of the soil texture grades, the gravimetric moistures for all sites and depths were converted to matric potential. Median and ranges were generated to demonstrate matric potential values in relation to soil depth during the drought period. The matric potential data is examined in relation to indicative thresholds for Ironbark and Box of –5600 and –3000 kPa respectively, derived from extreme measures of xylem pressure potential during an intense drought period (Rice et al. 2004). These values are substantially more negative than other measures of xylem pressure potential from trees elsewhere in the Australian tropics (Eamus et al. 2000).

Data on woodland structure were collected from circular plots around each of the 22 soil holes. Trees greater than 2 m tall and less than 10 cm diameter (at 1.2 m high) were identified and their diameter measured in a 10 m radius plot centred on the soil hole, and the same data recorded for trees greater than 10 cm diameter within 15 m radius circular plots. Trees were assigned as live or dead (see above). Total and dead, basal area and stem density were standardised to unit area. Total and the proportion of dead stem density and basal area were compared with soil matric potential, and soil texture grades using Spearman's Rank Correlation Coefficient.

To describe the relative intensity of rainfall deficit for the soil moisture sites, monthly rainfall values were obtained from modelled climate (SILO: Jeffrey et al. 2001). This comprehensive climate surface is interpolated from actual long-term climate stations, the nearest of which is Alpha ca. 35 km to the southeast. There are 13 other stations with records beginning at least from 1890 within 100 km. The density of actual rainfall stations that inform the index increases with time. A 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 standardised variations in annual rainfall were then calculated for a 3-y period prior to and including each month (i.e. 3-y drought index for November 1970 is the running total from December 1967- November 1970) (Foley 1957).

Rooting characteristics

Recently cleared paddocks of eucalypt savanna that included patchy tree death following the 2001-2003 drought were identified. Clearing occurred by a process that involves two large bulldozers dragging a large ship chain that uproots and overturns woody vegetation. The trees are left lying on the ground with their coarse (greater than 1 cm diameter) root systems partially intact and exposed, although deep roots are snapped below ground. This study utilises measurements of roots 45 cm from the tree bole to represent the depth of root penetration. Thus a primary assumption of this study is that vertical root and horizontal root area measured close to the bole of the tree is a meaningful surrogate of surface and deep root biomass respectively. We tested this assumption by randomly selecting ten Ironbark (*Eucalyptus melanophloia*) trees in a 100 m × 40 m area at location 23º29' S, 146º24' E. The root systems were excavated to expose the main vertical tap-root and the horizontal roots. Measurements were made of the diameter of all the roots and the direction of their branches at a distance of 45 cm and 100 cm from the bole (Fig. 2) to test the assumptions; the majority of the area of horizontal coarse roots near the bole of a tree remain near the surface, the majority of the area of vertical coarse roots near the bole of a tree penetrate into subsoil layers deeper than 100 cm.

Another cleared area (23°20' S, 146°10' E) was traversed during October 2003 and every tree encountered was assessed, with the exception of those where the root systems were sufficiently damaged to preclude accurate assessment. For every sampled tree the following was determined (see Fig. 3):

- species identity;
- trunk girth (cm at 1.3 m from the base);
- live, dead (see above);
- diameter (cm) of horizontal roots (horizontally orientated, 0-60 cm depth) in the upper hemisphere of the upturned root bole at 45 cm distance from trunk centre;
- diameter (cm) of all vertical roots (vertically orientated) at 45 cm from ground level.

We continued sampling live and dead trees until at least 10 in each category were recorded in each of three size-class categories (0-10 cm girth, 11-20 cm girth, >20 cm girth) for each of the two dominant tree species Ironbark and Box. During this sampling effort all individuals of the less common Bloodwoods (*C. dallachiana* and *C. clarksoniana*) were also assessed.

For analyses and subsequent presentation horizontal root area (cm^2) was determined as double that calculated from the girths measured for the upper hemisphere (Fig. 3). One-way ANCOVA was employed to compare horizontal root area, vertical root area and total root area between Ironbark, Box and the Bloodwoods with tree diameter as the covariate. Linear variables were transformed using $\log_e$ and zero values of horizontal and vertical root area were excluded because they generally constituted outliers and would require a separate model to decipher. In the same way, two-way ANCOVA with species (Ironbark and Box, the only species representing recently dead trees) and tree death (live, dead) as factors was employed to compare root area characteristics. The range of the covariate over which group means were significantly different at 0.05 was tested using the Wilcox modification of the Johnson-Neyman procedure (Quinn & Keough 2002, p. 351).

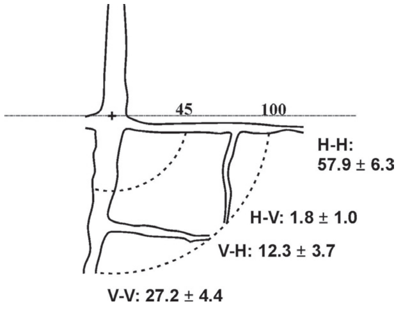

Fig. 2. Proportion (and SE) of root area at 100 cm from root bole relative to the area at 45 cm from the root bole. Root area proportions are presented in four categories: Horizontal-horizontal (H-H), Horizontal-vertical (H-V), Vertical-vertical (V-V), Vertical-horizontal (V-H). By way of example the H-H category represents the proportion of horizontal root area at 100 cm that originates from horizontal roots at 45 cm relative to the horizontal root area at 45 cm.

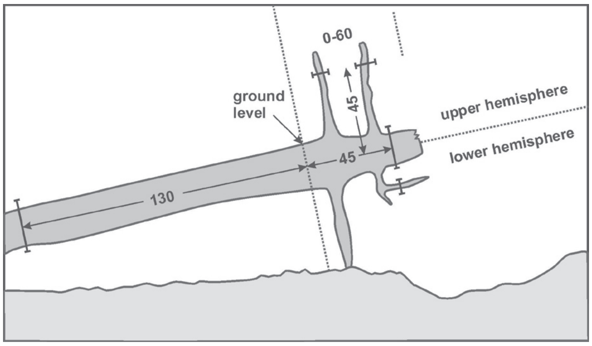

Fig. 3. Measurements (cm) made of upturned root boles. A, stem diameter; B, shallow horizontal root; C, deep horizontal roots; D, E, vertical root; F, G, unmeasured.

Results

Relative dominance and tree death susceptibility

On average Box (*Eucalyptus melanophloia*) constitutes 63% of the basal area in the savanna dominated by this species in central Queensland. Box (*E. populnea*) constitutes 62% of the basal area in savanna dominated by that species (Table 2). The two Bloodwoods *Corymbia clarksoniana* and *C. dallachiana* are sub-dominant species, both averaging 4% of the basal area in both Ironbark and Box dominated woodland (Table 2).

The results of the paired comparisons of tree death between the target species after the 1990s drought were statistically significant with the exception of the two Bloodwood species (Table 3). The results clearly suggest that the Bloodwoods (*Corymbia clarksoniana* and *C. dallachiana*) are the least susceptible followed by Ironbark (*E. melanophloia*) and Box (*E. populnea*).

Drought, tree death and soil conditions

The three-year drought index from the soil-sampling site suggests that the droughts of the 1990s and 2000s that were the subject of this study were of similar magnitude (Fig. 1). The magnitude of the rainfall deficit represented by these droughts is comparable to the 1970s but not as severe as the droughts in the 1930s and 1900s (Fig. 1).

The matric potential curves for the 12 soils were divided into four discrete groups representing the four textural grades with average function parameters described in Table 4. The goodness of fit for the sandy clay loam and sandy loam group is poor because they are represented by multiple samples with substantially different moisture characteristic curves that could not be separated by soil texture grading. The goodness of fit for the loamy sand and clay loam is higher, although the single soil samples for these texture classes may poorly represent variations in the broader sample to which these models were applied.

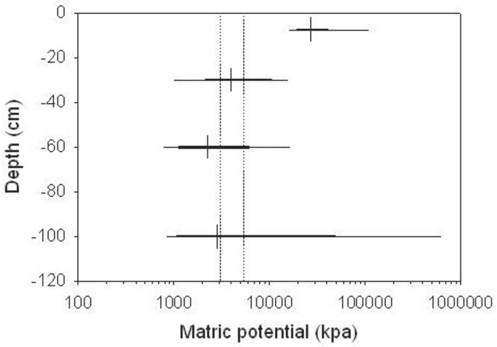

Fig. 4. Absolute median (cross hair), 25-75 percentile (thick line) and 10-90 percentile (thin line) matric potential values in relation to soil depth for the 22 soils sampled. The logarithmic scale cannot be prepared from negative values so negative matric potential values are presented as positive. The indicative critical moisture stress values of -5600 kPa for Ironbark and –3000 kPa for Bloodwood are indicated by dotted lines.

The matric potential functions were applied to the soil moistures obtained at the culmination of a recent drought in September 2004 (Fig. 4). Median matric potential values increase from –27 000 at 7.5 cm to –4000 at 30 cm and show signs of stabilising between –2200 and –2800 kPa between 60 cm and 100 cm. The range of values increases with depth and is considerable at 100 cm. The highly negative values of matric potential at 100 cm occur with clay loam soils, where the matric

Table 2. Basal area ($m^2.ha^{-1}$) for the four target species within savanna dominated by either Ironbark (*Eucalyptus melanophloia*) or Box (*E. populnea*). Standard errors are in brackets.

	Ironbark (*Eucalyptus melanophloia*)	Box (*E. populnea*)	Bloodwood (*Corymbia clarksoniana*)	Bloodwood (*C. dallachiana*)	Other species
Ironbark dominant (*n* = 15)	6.46 (0.75)	1.25 (0.28)	0.39 (0.10)	0.41 (0.08)	1.78 (0.52)
Box dominant (*n* = 31)	0.92 (0.26)	5.66 (0.48)	0.41 (0.11)	0.38 (0.08)	1.82 (0.23)

Table 3. Results of Wilcoxon's test for paired comparisons of tree deaths for Ironbark (*Eucalyptus melanophloia*), Box (*E. populnea*) and Bloodwood (*Corymbia clarksoniana* and *C. dallachiana*) pairs. For significant comparisons ($P < 0.05$) the species with less tree death is indicated in bold. *N* for test is lower than *N* because the Wilcoxon test ignores comparisons of zero difference.

Comparison	N	N for test	Wilcoxon statistic	*P*-value	Estimated difference between medians of proportion basal area dead
Corymbia clarksoniana vs. *C. dallachiana*	14	5	161.5	0.059	–0.0333
C. clarksoniana vs. *Eucalyptus populnea*	15	14	97.0	0.006	0.1358
C. clarksoniana vs. *E. melanophloia*	28	25	251.0	0.018	0.0480
C. dallachiana vs. *E. populnea*	18	17	153.0	0.000	0.1640
C. dallachiana vs. *E. melanophloia*	25	20	210.0	0.000	0.0862
E. populnea vs. ***E. melanophloia***	26	25	79.0	0.026	–0.0709

Table 4. Derived parameters and goodness of fit for the soil moisture characteristic model $\ln|M| = a + b \ln G$, where M is matric potential (kPa) and G is gravimetric soil moisture (%) for the four soil texture grades used in this study. N is represented by the number of samples multiplied by the four pressure potential values used to derive soil moisture-matric potential relationships.

Soil texture class	*a*	*B*	RSE (df)	R^2	*N*
Loamy sand	11.652 ± 1.962	–5.697 ± 1.941	0.598 (2)	0.812	4 (1 × 4)
Sandy loam	9.957 ± 1.323	–2.836 ± 0.928	0.807 (14)	0.400	16 (4 × 4)
Sandy clay loam	12.103 ± 2.062	–2.944 ± 0.985	0.858 (22)	0.289	24 (6 × 4)
Clay loam	33.437 ± 9.827	–11.430 ± 4.086	0.622 (2)	0.797	4 (1 × 4)

Table 5. Correlations between Ironbark (*Eucalyptus melanophloia*) population characteristics and drought-induced mortality characteristics, and soil conditions during drought at a range of soil depths. NS $P>0.05$, * $0.01<P<0.05$, ** $0.001<P<0.01$.

	Total stem density	Proportion dead stems	Total basal area	Proportion dead basal area
Matric potential 7.5 cm	–0.439*	–0.416*	NS	NS
Matric potential 30 cm	NS	–0.564**	NS	–0.501*
Matric potential 60 cm	NS	NS	NS	–0.454*
Matric potential 100 cm	NS	NS	NS	NS
Soil texture 7.5 cm	NS	NS	NS	NS
Soil texture 30 cm	NS	NS	NS	NS
Soil texture 60 cm	NS	0.410*	NS	0.440*
Soil texture 100 cm	NS	NS	NS	NS

potential functions predict that low soil moisture is tightly bound in those moderately fine-textured soils. The proportion of measured soils with matric potential less than –5600 kPa (the indicative threshold of water stress for Ironbark, Rice et al. 2004) is 100% at 7.5 cm, 36% at 30 cm, 27% at 60 cm and 41% at 100 cm. The proportion of measured soils with matric potential less than -3000 kPa (the indicative threshold of water stress for Bloodwood) is 100% at 7.5 cm, 64% at 30 cm, 41% at 60 cm and 41% at 100 cm.

Ironbark (*Eucalyptus melanophloia*) represented 80% of stems and 91% of basal area in the plots around the soil moisture sampling holes. For this dominant species, soil matric potential at 30 cm depth was negatively related to the proportion of dead stems and the proportion of dead basal area (Table 5). The proportion of dead stems was also negatively correlated with matric potential at 7.5 cm and the proportion of dead basal area with soil matric potential at 60 cm depth (Table 5). There was also a negative relationship between total stem densities and soil matric potential at 30 cm depth. The positive relationships between the proportion of dead stems and the proportion of dead basal area and soil texture at 60 cm depth indicates that these factors increase as subsoils become more heavily textured (Table 5). There were no relationships between stem densities or tree death for soil characteristics at 100 cm depth.

Table 6. Results of Analysis of Covariance of root characteristics between four species (Ironbark *Eucalyptus melanophloia,* Box *E. populnea* and Bloodwoods *Corymbia clarksoniana* and *C. dallachiana* as treatments with tree diameter as a covariate (see Fig. 5).

Source of variation	*df*	MS	*F*	*P*
Horizontal root area				
Species	3	2.303	6.92	0.000
Stem diameter (covariate)	1	273.479	822.03	0.000
Residual	201	0.333		
Vertical root area				
Species	3	6.739	17.13	0.000
Stem diameter (covariate)	1	88.900	226.03	0.000
Residual	191	0.393		
Total root area				
Species	3	2.293	13.29	0.000
Stem diameter (covariate)	1	194.890	1129.24	0.000
Residual	205	0.173		

Table 7. Results of Analysis of Covariance of root characteristics using live and dead trees, and species *Eucalyptus melanophloia* and *E. populnea* as treatments, with tree diameter as a covariate.

Source of variation	Df	MS	*F*	*P*
Horizontal root area				
Tree death	1	0.839	2.59	0.109
Species	1	1.567	4.85	0.029
Tree death × Species	1	0.141	0.43	0.511
Stem diameter (covariate)	1	229.419	793.00	0.000
Residual	161	0.323		
Vertical root area				
Tree death	1	0.229	0.56	0.455
Species	1	0.127	0.31	0.577
Tree death × Species	1	0.028	0.07	0.792
Stem diameter (covariate)	1	73.090	190.03	0.000
Residual	151	0.407		
Total root area				
Tree death	1	0.822	4.85	0.029
Species	1	0.186	1.09	0.297
Tree death × Species	1	0.023	0.14	0.713
Stem diameter (covariate)	1	177.739	1048.56	0.000
Residual	165	0.170		

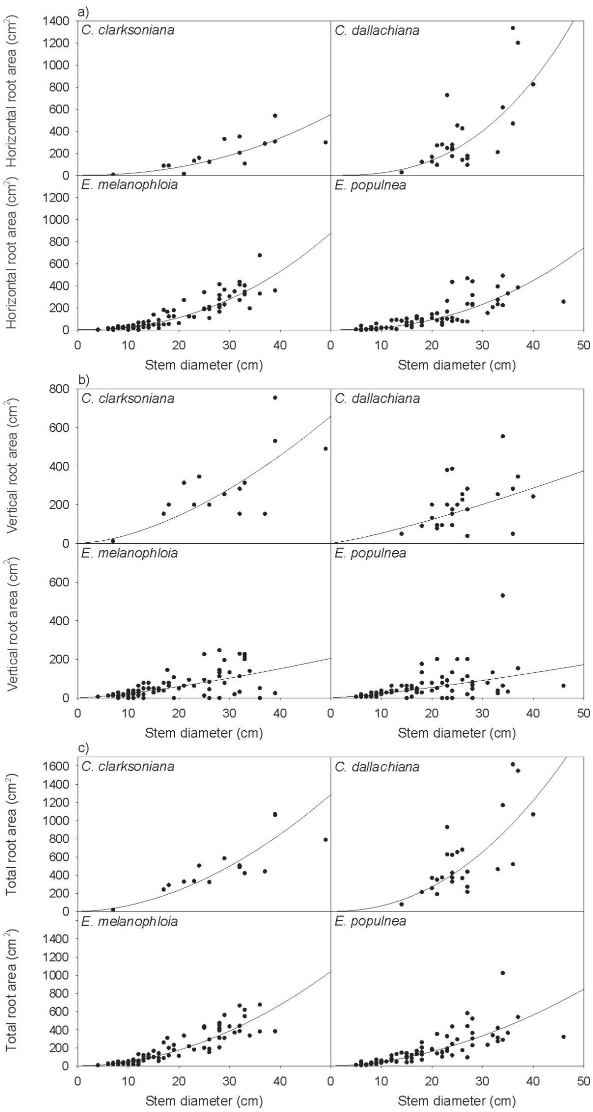

Fig. 5. Relationship between stem diameter and root area characteristics according to tree species *Eucalyptus melanophloia, E. populnea*, *Corymbia clarksoniana* and *C. dallachiana*; **a.** Horizontal root area; **b.** Vertical root area; **c.** Total root area. Regression lines are fitted after excluding trees with zero values for root area characteristics. Curve-shape determined by the log-transformation prior to the ANCOVA (Table 5).

Rooting characteristics

The ten excavated trees ranged in size from 22 cm to 95 cm diameter at 1.3 m. Nearly all horizontal coarse roots measured at 45 cm from the tree bole remain near the surface in a horizontal trajectory, although their area diminishes by 42% at 100 cm distance (Fig. 2). Vertical root area diminishes by 60.5% between 45 cm and 100 cm depth, with three quarters of roots maintaining a vertical trajectory and one quarter branching in a horizontal direction (Fig. 2).

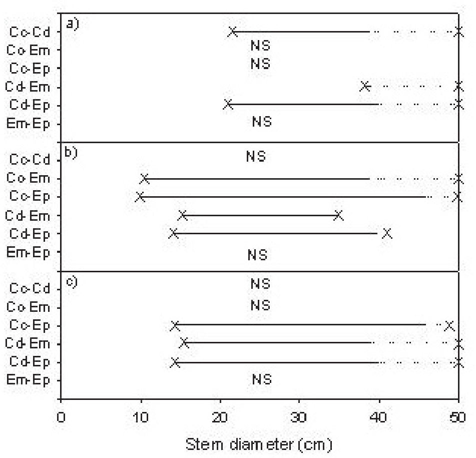

Fig. 6. Range of the covariate (stem diameter) sizes where ANCOVA results were different according to 95% confidence limits between species pairs using the Wilcox test for (**a**) horizontal root area, (**b**) vertical root area, and (**c**) total root area. Solid line: range of differences where they are within the bounds of covariate sizes for both species being compared; dotted line: significant differences beyond the range for one or more of the species compared. Cc = *Corymbia clarksoniana,* Cd = *C. dallachiana,* Em = *Eucalyptus melanophloia,* Ep = *E. populnea*. NS = not significant throughout entire range.

There were significant differences in root area characteristics between species (Table 6). *Corymbia dallachiana* had a large horizontal root basal area compared to the other species at large stem diameters (Figs. 5 and 6). Differences between species were highly significant for vertical root basal area with species pairs significantly different for at least some stem sizes between *Eucalyptus melanophloia-E. populnea* vs. *C. clarksoniana-C. dallachiana* but not within these groups (i.e. *w*ere not significantly different) (Figs. 5 and 6). Differences for total root area were significantly greater for *C. clarksoniana*) than *E. populnea*, and for *C. dallachiana* relative to both *E. melanophloia* and *E. populnea* (Figs. 5 and 6)

The two-way ANCOVA including only the two common tree species suggests a weakly significant difference in horizontal root area between Ironbark and Box (Table 7), although this weak effect was not evident in the overall ANCOVA and was not detectable for any stem sizes using the Wilcox test (Fig. 6). There were no differences in vertical root area between live and dead trees and species or the interaction of these factors. There was a weakly significant difference in total root area between live and dead trees (Table 7). The Wilcox test suggests that this difference applies to stem sizes < 15 cm DBH although this effect appears to have resulted from differing intercept terms for log regression models for live (–0.2) and dead trees (–2.2) and almost certainly does not reflect ecological reality.

Discussion

The Box and Ironbark eucalypts dominate large areas of savanna in sub-coastal and inland Queensland with Bloodwoods typically occurring as sub-dominant species. The results from the surveys of tree death in the eucalypt savanna of central Queensland clarify the drought susceptibility of the major tree species with the Bloodwood *C. dallachiana* being more drought resistant than another Bloodwood *C. clarksoniana,* and both these species being more drought resistant than Ironbark *E. melanophloia* and Box *E. populnea*. These findings support the hypothesis that Bloodwoods (*Corymbia* spp.) are less susceptible to drought than co-occurring Ironbark and Box (*Eucalyptus,* subgenus *Symphyomyrtus*).

The Bloodwoods appear to have a more substantial investment in deep root systems relative to Ironbark and Box. This is consistent with the physiological sensitivity of the species to drought and their survivorship in the field. Rice et al. (2004) found that 50% loss in conductance occurred at substantially less pressure for Bloodwood (*C. erythrophloia*) than Ironbark (*E. xanthoclada*). In the field both predawn and midday xylem pressures were substantially more negative and embolism more prevalent in the Ironbarks than the Bloodwoods. These results were consistent with the successful avoidance of xylem pressure deficit by the deep rooting Bloodwoods. The capacity of the Bloodwoods to avoid cavitation is probably also facilitated by their partial deciduousness. Despite a greater physiological tolerance of low xylem pressure, the evergreen habit and shallow root systems of Box and Ironbark means they are prone to extreme low midday xylem pressure, sufficient to initiate cavitation and death.

The relatively shallow-rooting of the Ironbarks and Boxes is a high-risk strategy in the climate of semi-arid Queensland. Our data indicate that where multi-year rainfall deficit is moderate to high, such as in September 2004 (Fig. 1), soil matric potentials suggest moisture is effectively unavailable within 30 cm of the surface for all species (Fig. 4). Tree death of the Ironbark *Eucalyptus melanophloia* was related to low moisture availability at depths down to 60 cm. Even at 100 cm over 40% of sites were more negative than –5600 kPa, the indicative moisture stress indicator for Ironbark in these semi-arid environments (Rice et al. 2004). In this study soil coring was limited to 100 cm and the deep soil moisture conditions during conditions of high water stress remains uncertain. For these soils, moisture is available at depths greater than 50 cm (and often less) during the driest times of the year in non-drought periods (Williams & Coventry 1979; J. Williams et al. 1997). It seems likely that the Bloodwood trees in these savanna have deep roots in soil layers more favourable than those presented in Fig. 3, given the relatively low tolerance of Bloodwood to moisture stress demonstrated by minimum xylem pressure potential values of –3000 kPa (Rice et al. 2004).

There are only minor variations in the allometric relationships between tree diameter and above ground biomass for woodland *Eucalyptus* and *Corymbia* (Williams et al. 2005). Thus tree diameter can be used for comparisons of above ground biomass between these genera. The current study suggests that Box and Ironbark (*Eucalyptus*) allocate substantial biomass to above-ground parts at the expense of an expansive root system relative to Bloodwoods (*Corymbia*) (Fig. 5). Given the dominance of Box-Ironbark in large areas of Australian tropical savanna, it could be hypothesised that these species have high growth rates and are capable of rapid regeneration when soil moisture in the upper soil horizon is not limiting compared to the sub-dominant Bloodwoods. However, species with root systems that are insufficient to extract soil moisture reserves during the infrequent periods when available soil moisture is beyond the rooting zone are exposed to population crash during drought. This is evidenced by the widespread death of Box-Ironbark eucalypts during recent drought (Fensham and Holman 1999). Conversely the generous allocation of biomass to the root systems of the Bloodwoods confers a competitive disadvantage with the Boxes and Ironbarks during times of relative abundance of soil moisture but allows for survival during dry times.

Variations between coexisting species in their allocations to root development have been described in desert ecosystems (Carrick 2003). The differences in the root architecture between Australian savanna trees may at least partly represent niche differentiation developed to avoid competition. The literature on niche separation in relation to eucalypts has focused on the ecological and physiological traits that may account for the hierarchy of the dominant eucalypt subgenera *Monocalyptus* and sub-dominant *Symphyomyrtus* that commonly co-occur in temperate forest (see Noble 1989, Landsberg & Cork 1997). Here we describe a hierarchy with dominant *Symphyomyrtus* (Ironbark-Box) and sub-dominant *Corymbia* (Bloodwood) for semi-arid eucalypt savanna and stress the role of rooting depth and architecture as a potential niche separation mechanism. Growth strategies and drought sensitivity probably results in shifting dominance through time between Ironbark-Box and Bloodwood.

Root architecture was poorly related to the drought-related tree death within species. Thus healthy and dead Ironbark and Box expressed a similar range of root architecture characteristics. Patchiness of tree death may be related to sub-soil structure. Lloret et al. (2004) recorded much higher rates of drought-induced mortality of holm-oak (*Quercus ilex*) after drought on geological substrates with exfoliation planes that allowed root penetration than those where the basement rock had a massive structure. In the eucalypt woodlands of this study rooting is not limited by rock, but may be affected by soil properties at greater than 60 cm depth. The range of matric potential values described here for 100 cm depth (Fig. 4) strongly suggest that in many areas available soil moisture may be effectively unavailable at these depths particularly in fine-textured sub-soils. Patchiness in sub-soil conditions is likely to be an important factor determining the patchiness in drought related tree death that could not be related to rainfall patterns by Fensham & Holman (1999). The demonstration that tree death for Ironbark increases where sub-soils around 60 cm depth are clay rich is supporting evidence.

The patchiness of tree death also means that the relative dominance of Box-Ironbark and Bloodwood will be configured through space as well as time. However, because the environmental gradients are shallow in central Queensland it is not expected to result in substantial movement of ecotones such as those inferred for pinyon pine-juniper woodlands across elevation gradients in the southwestern USA (Allen & Breshears 1998; Mueller et al. 2005).

There is evidence from this study that competitive effects may also be influencing the patchiness of tree death. Increasing total stem density was related to decreases in soil moisture availability suggesting that the Ironbark eucalyptus can have local effects on surface soil moisture. Low surface soil moisture availability was in turn related to increased tree death. There is some evidence of density dependence mediated by soil moisture availability. However a better understanding of tree death patchiness continues to confound our understanding of mechanisms causing these major mortality events. The role of competition between tree species and between size classes within the dominant eucalypt species that comprise Australian tropical savannas requires more detailed study.

Acknowledgements. This project was partially supported by funding from Land & Water Australia. Butch Howard is thanked for allowing access to his property. Thanks to Caroline Donnelly, Ian Hoch, Hyunki Kim, John McCabe, Jenny Silcock and Shin Sungmin for assistance with field-work. Kirsten Verburg and Peter O'Reagain are thanked for gracious and enlightening offers of modelling and data to assist with understanding soil moisture patterns. Don Butler and the reviewers provided insightful comment on the manuscript.

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Received 30 January 2006;
Accepted 4 September 2006;
Co-ordinating Editor: N. Kenkel.