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Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation

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Abstract During the extreme 1992–1997 El Niño drought event, widespread stem mortality, or tree “dieback”, of both mature and juvenile eucalypts occurred within the tropical savannas of northeast Australia. Most of the dieback occurred in individuals of the ironbark species complex (*Eucalyptus crebra* – *E. xanthoclada*) while individuals of the bloodwood species *Corymbia erythrophloia*, exhibited significantly less stem mortality. Indicative of greater water stress, predawn and midday xylem water potentials of ironbark adults and saplings were significantly more negative than predawn values of bloodwoods. The very negative xylem water potentials in ironbarks suggest that stem mortality in both adult and juvenile ironbarks results from drought-induced embolism and that ironbarks perhaps have a shallower and less extensive root system than bloodwoods. Although predawn and midday water potentials for ironbark adults and saplings were similar, a census of mature and juvenile ironbark trees indicated that mortality was higher in adult trees. Cavitation vulnerability curves indicated that ironbark saplings may be better buffered against cavitation than adult trees. If they possess smaller root systems, saplings are more likely than adults to experience low xylem water potentials, even in non-drought years. Xylem conduits produced in adult trees during periods of normal

rainfall, although perhaps more efficient in water conduction, may be more vulnerable to cavitation during infrequent severe droughts.

Keywords Xylem cavitation · Drought stress · *Eucalyptus* · Hydraulic conductance · Water relations

Introduction

Forest dieback is a recurring phenomenon that has been reported from a variety of woodland and forest communities in many parts of the world (Mueller-Dombois 1986; Auclair 1993; Tafangenyasha 1997; Nepstad et al. 1999). Dieback is characterized by rapid defoliation and progressive stem mortality in overstory trees and has been attributed to a wide range of potential causes (Landsberg and Wylie 1983; Pook and Forrester 1984; Mueller-Dombois 1990). In Australia, tree or eucalypt dieback occurs in a number of woodland and savanna habitats throughout the continent (Old et al. 1981; Kirkpatrick and Marks 1985). Although dieback events in the late nineteenth and early twentieth century were primarily in southern locations on the continent, diebacks occurring within Australia in the last 50 years are now more widespread (Kile 1981). Using scientific records and historical accounts, the occurrence of dieback has been related to the severe droughts Australia has experienced periodically during the last 150 years (Fensham and Holman 1999). These El Niño drought events have had a significant effect on Australian savanna structure and composition (Newell 1998; Weste et al. 2002) as well as the fauna associated with these habitats (Newell 1997; Ford et al. 2001). Some researchers have questioned the primary role of drought as the factor initiating dieback (Podger 1981; Landsberg 1985). However, the most widely accepted view is that drought stress causes dieback directly by inducing cavitation (Auclair 1993) and also renders the tree more susceptible to insect attack (Lowman and Heatwole 1992) and pathogens (Old et al. 1990).

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Australian eucalypt species differ significantly in susceptibility to dieback on both regional and local scales (Old et al. 1981; Martin et al. 2001). Interspecific differences in dieback are well documented; however there has been less study of the ecophysiological mechanisms underlying these differences (Auclair 1993; McFarlane and Adams 1998; Fensham and Holman 1999; Burgess et al. 2001).

During the El Niño event from 1992 to 1997, northeast Australia experienced a severe drought; analyses of regional patterns of soil moisture deficit indicated that the drought in northern Queensland was the most severe on record (Fensham and Holman 1999). This period of drought in northern Queensland was accompanied by widespread tree dieback in a variety of savanna woodlands and a survey conducted by Fensham and Holman (1999) at the end of the drought demonstrated strong differences in rates of dieback among tree species. In part these interspecific differences were explained by variation in geology and soil characteristics that presumably influences water availability. However, the factors responsible for interspecific differences in dieback within a site were less clear and the authors noted that further study is needed to determine how variation in drought tolerance may affect local patterns of dieback.

During the middle of the drought in November 1995, our initial observations of tree dieback at two field stations located in northern Queensland revealed a large amount of stem mortality in adults and saplings of the dominant overstory tree species. Our preliminary survey also suggested that there were interspecific differences in dieback at both sites. In particular, ironbark eucalypts at both sites appeared much more susceptible to dieback than bloodwood eucalypts.

To better understand the causes underlying these apparent differences in dieback, we conducted a study that combined field surveys of stem mortality with ecophysiological measurements of drought stress and cavitation resistance. In particular we were interested in: (1) documenting whether there were differences in stem mortality among species and among age classes within a species, and (2) exploring the possibility that these differences were related to differences in drought stress or drought tolerance, or both.

Materials and methods

Two field stations in north Queensland, Australia were used for stem mortality surveys and water relations studies. Both the Hillgrove Station site (19°40'S, 145°45'E) and the Cardigan Station site (20°11'S, 146°43'E) are characterized by a sub-humid climate; precipitation is highly seasonal with most rainfall (approx. 80%) occurring from December to April. The Hillgrove site receives an average rainfall of 535 mm. Although long term rainfall records for Cardigan are not available, annual rainfall at nearby Ravenswood (20°06'S, 146°53'E) averages 684 mm (McIvor and Gardener 1991). During the period of our study, northern Queensland was undergoing the most severe drought ever recorded (Fensham and Holman 1999); the average annual precipitation from 1992 to 1996 was 42% and 40% below the long-term average at Hillgrove and Cardigan, respec-

tively. The soil at the Hillgrove site is a clay loam (Ustic Paleagid) derived from basalt parent material and is slightly more fertile than the soil at the Cardigan site (McIvor and Gardener 1995). Soil at the Cardigan site is a sandy clay loam (Typic Rhodustalf) derived from granodiorite parent material. Tree density within the open woodland at Hillgrove is 64 trees per hectare. Using tree distribution data and nomenclature from Henderson (1997), the overstory is dominated by red-barked bloodwood, *Corymbia erythrophloia* and a species complex of two closely related narrow leaf ironbark species *Eucalyptus crebra* and *E. xanthoclada* (hereafter referred to as the *E. crebra* complex). An understory of warm season, perennial grasses consists primarily of *Heteropogon contortus*, *Chrysopogon fallax*, and *Bothriochloa ewartiana* (McIvor et al. 1991). *C. erythrophloia* and the *E. crebra* complex are also the dominant overstory species at Cardigan with a tree density of 127 trees per hectare. Understory composition is similar to that at Hillgrove with perennial grasses that include *H. contortus*, *C. fallax*, *B. ewartiana*, and *Sehima nervosum* (McIvor and Gardener 1991).

To quantify patterns of stem mortality, a series of four 100 m belt transects were established at 200 m intervals from an initial random point located within relatively continuous woodland stands at each site. Within each 20 m wide belt transect, the number of saplings and adults exhibiting total stem dieback (i.e. no stems with leaves) were recorded; trees with partial stem dieback were noted but included in the totals. Saplings were defined as plants with a stem diameter between 1 and 5 cm at a height of 1 m and adults were defined as plants with a diameter greater than 5 cm at a height of 1 m. Seedlings (i.e. plants less than 1 cm stem diameter at 1 m height) were rare at both sites and were not recorded. At Cardigan the total number of bloodwood plants counted was 320 adults and 536 saplings and the number of ironbark plants counted was 382 adults and 608 saplings. At Hillgrove the number of bloodwood plants counted was 85 adults and 156 saplings while for ironbark the totals were 305 adults and 472 saplings.

During the initial survey of stem dieback, eight adult trees and eight saplings of the ironbark and bloodwood species at each site were selected in a stratified random procedure and tagged. For each of the tagged plants, stem xylem pressure was measured in November 1995 and September 1996 using a Scholander pressure chamber (PMS Instruments, Corvallis, Ore., USA). Replicate shoot tips from each of the tagged plants were measured at predawn (0200–0500 hours) and at midday (1200–1400 hours). Shoots were placed in plastic bags and measured within 5 min of collection to minimize water loss (Turner 1987). Because of some mortality, the number of plants measured in 1996 was slightly less than in 1995. Following a series of rainstorms in March 1997, predawn and midday measurements were made on surviving tagged plants at the Hillgrove site to examine patterns of xylem pressure at the end of the drought.

Native embolism and vulnerability measurements were taken in September 1996 for ironbark and bloodwood plants at both sites on a random subset of at least five tagged trees and saplings used in xylem pressure measurements. At Hillgrove the sample size for ironbark was increased to seven adults and saplings. Stem material, estimated at no more than 2 years old, was collected in early morning and transported to the laboratory in plastic bags containing moist paper towels to minimize water loss. From each branch, stem segments approximately 20 cm long and 0.5 cm in diameter were cut underwater with a razor blade to prevent the introduction of additional embolisms. Stem length and diameter were measured. To measure native embolism (i.e. xylem embolism associated with in situ cavitation), stems were fitted to tubing attached to a hydraulic head of 0.003 MPa. Using a filtered (0.22 µm) 0.5% sodium hypochlorite perfusion solution that retards microbial growth (Matzner et al. 2001), this hydraulic head induced flow through the stem segment. Stem exudate was collected and weighed to determine an initial flow rate (k_{hi}). The initial flow rate was used to calculate native embolism (see below).

To construct vulnerability curves for the collected stem samples, the air-injection procedure was used (Salleo et al. 1992; Sperry and Saliendra 1994). After measurement of the initial flow rate (k_{hi}), stems were then flushed for 15 min at 0.1 MPa to refill any

embolized vessels and the maximum flow rate (k_{hf}) was measured. After conductivity was measured on the flushed stems (i.e. k_{hf}), stem segments were sealed in a double-ended pressure sleeve. Forcing air into the xylem vessels as pressure was increased within the sleeve induced xylem cavitation. The amount of cavitation was estimated by measuring hydraulic conductivity in stem segments exposed to pressures of 0.0, 0.5, 1.5, 4.0 and 8.0 MPa. Because xylem in ironbarks and bloodwoods is diffuse porous (Penfold 1961) and stem material represented 2 years of growth, we used hydraulic conductivity at 0.5 MPa as a measure of maximum conductivity. In stems older than 1 year, degraded xylem elements may refill rapidly with flushing thus artificially increasing maximum conductivity rates. In turn, because they cavitate rapidly, these aged xylem elements may give a false indication of high vulnerability (J.S. Sperry, personal communication). For this reason conductivity was expressed as a percentage of the conductance measured at 0.5 MPa. Setting maximum conductance at 0.5 MPa is also justified by the fact that our field measurements of xylem pressure potentials were rarely less negative than -0.5 MPa even during the wet season (K. Rice and W. Byer, unpublished data). Use of the conductivity measured at 0.5 MPa as a maximum did not change the overall shape of the vulnerability curves but it did increase the pressures resulting in 50% conductivity loss by 0.5–0.7 MPa. As a measure of native embolism, conductivity for k_{hi} was expressed as a percentage

of the conductance measured at 0.5 MPa. To check on the consistency of these vulnerability curves with field observations, values of native embolism and their associated midday xylem pressures were compared to rates of conductivity predicted by the vulnerability curves.

Nominal logistic regression (JMP Statistical Program, SAS, Cary, N.C.) was used to analyze both the main and interactive effects of site (Hillgrove vs Cardigan), species (ironbark vs bloodwood) and age class (adult vs sapling) on frequency of stem mortality. Main and interactive effects of site, species and age class on predawn xylem pressure were examined separately for the November 1995 and September 1996 samples as a three-way factorial ANOVA using the general linear model procedure (SAS, Cary, N.C.). Because predawn xylem pressure was highly correlated with midday xylem pressure for all data sets ($P < 0.001$; Pearson's $r > 0.90$), statistical analyses were conducted only on predawn data. A two-way factorial analysis of predawn measurements taken at the Hillgrove site in March 1997 examined species and age class effects only. To reduce heterogeneity of variance among treatments, predawn xylem pressure data were transformed to natural logarithms. Effects of site, species and age class on cavitation vulnerability were analyzed using repeated-measures ANOVA within the SAS general linear model procedure. The within-subject effect was the level of applied pressure while successive hydraulic conductance measurements on

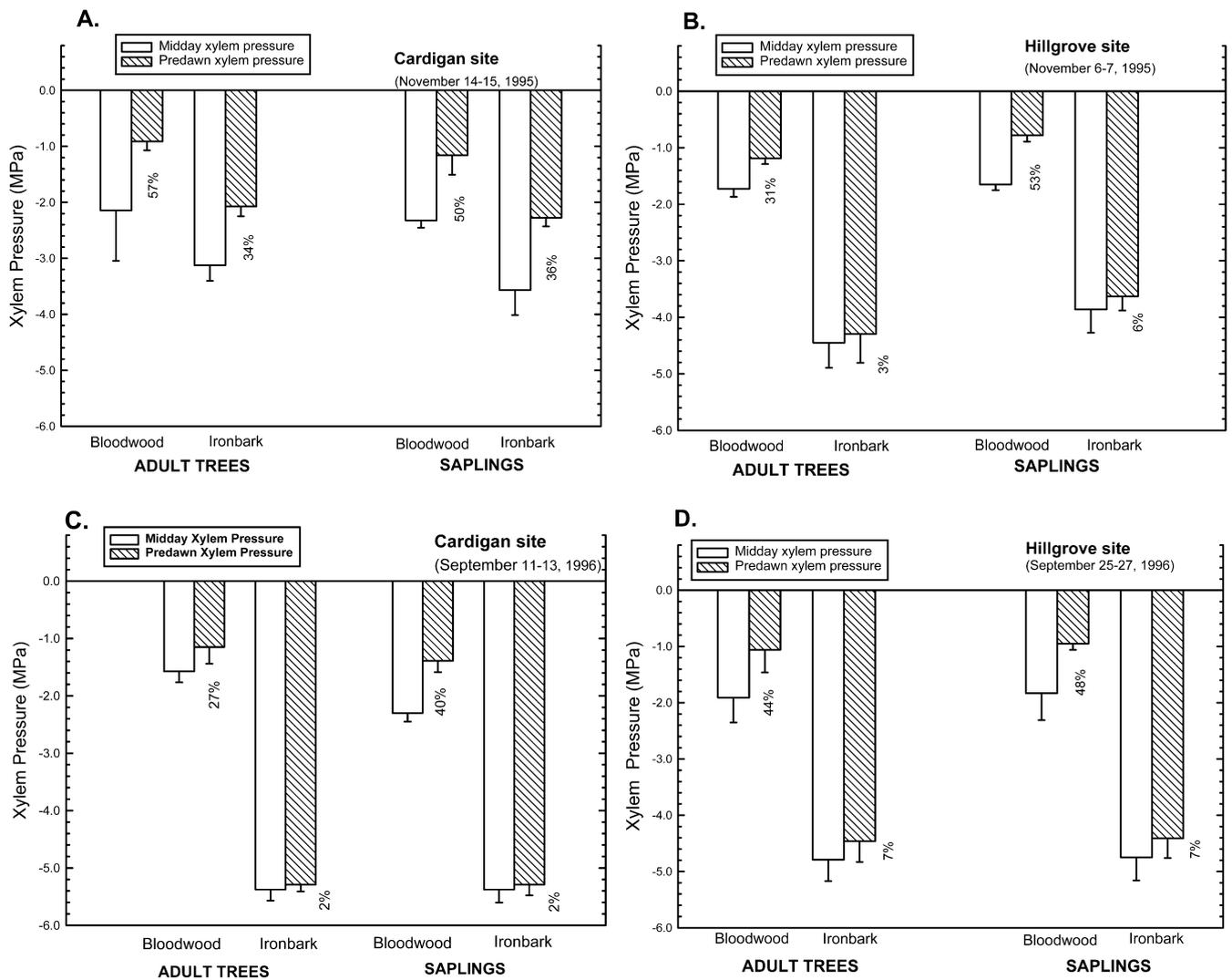


Fig. 1 Variation in average predawn and midday xylem pressures between saplings and adults of bloodwoods and ironbarks at **A** Cardigan and **B** Hillgrove in 1995 and **C** Cardigan and **D** Hillgrove

in 1996. Error bars represent ± 1 SE. Diurnal recovery is represented by the percent change between midday and predawn xylem pressures

single stems represented the repeated factor. Interactive effects of site, species and age class on vulnerability curves were tested by the within-subject by between-subject interaction terms. Hydraulic conductivity data conformed to assumptions of parametric analysis and so were not transformed. Vulnerability curves were created by fitting second order polynomial regressions to the data.

Results

Stem mortality

Stem mortality was significantly higher in ironbark than in bloodwood (Wald $\chi^2=145.31$, $P < 0.0001$); the size of this difference in stem mortality between species was significantly dependent on site (Wald $\chi^2=7.76$, $P = 0.0054$). At Cardigan there was 4.3% stem mortality in bloodwood (*C. erythrophloia*) and 45.2% incidence of stem mortality in ironbark (*E. crebra* complex). At Hillgrove, bloodwood stem mortality was again low (4.1%) while stem mortality in ironbark at this site was 21.5%. This reduction in ironbark stem mortality at Hillgrove might reflect site differences, differences between populations in the ironbark species complex, or both. A significant species by age class interaction in the analysis (Wald $\chi^2=9.31$, $P = 0.0023$) indicates that differences in stem mortality between adult trees and saplings varied between bloodwood and ironbark. In bloodwood there was very little difference in incidence of stem mortality between adults (3.2%) and saplings (4.9%). In contrast, stem mortality was higher in ironbark adults (46.1%) than in saplings (27.5%). A lack of a three-way interaction between site, species and age class ($P = 0.82$) indicates that greater stem mortality in adult ironbarks was found at both sites.

Xylem pressure (November 1995)

Analysis of predawn xylem pressure measurements taken in 1995 indicate that there were strong differences between bloodwood and ironbark ($F = 216.74$, $P < 0.0001$) and that these differences were dependent on site ($F = 19.33$, $P = 0.0002$; Fig. 1A, B). Averaged across adults and saplings, ironbarks at Cardigan had much more negative predawn xylem pressures (mean ± 1 SE $= -2.17 \pm 0.07$ MPa) than bloodwoods (-1.03 ± 0.10 MPa). This difference was even more pronounced at Hillgrove where the average predawn xylem pressure for ironbark was -3.92 ± 0.26 MPa compared to -1.01 ± 0.14 MPa for bloodwood. As noted previously for stem mortality, significant differences in ironbark xylem pressures between Cardigan and Hillgrove may reflect site differences, differences between ironbark populations, or both. A significant site by age class interaction ($F = 8.37$, $P = 0.0080$) indicates that for both bloodwoods and ironbarks, adult predawn xylem pressure at Cardigan was slightly less negative (-1.48 ± 0.22 MPa) than predawn values for saplings (-1.72 ± 0.23 MPa). In contrast, at Hillgrove the opposite was true; Hillgrove saplings exhibited less negative average predawn pres-

ures (-2.56 ± 0.54 MPa) than Hillgrove adults (-2.74 ± 0.64 MPa).

Xylem pressure (September 1996)

Unlike the results for 1995, there were no significant interactive effects between site and species or site and age class on predawn xylem pressure (Fig. 1C, D). There were significant site differences in predawn pressure ($F = 7.74$, $P = 0.010$) such that the Cardigan site, with an average predawn pressure of -3.41 ± 0.53 MPa, appeared to be more water-limited than the Hillgrove site (-2.94 ± 0.45 MPa). There was also a very strong species effect ($F = 318.6$, $P < 0.0001$) in that predawn xylem pressures of the ironbark species complex (averaged across sites and age class) were more negative (-4.89 ± 0.17 MPa) than those measured for bloodwood (-1.23 ± 0.13 MPa).

Xylem pressure (Hillgrove, March 1997)

Taken after a series of storms that signaled the end of the drought, analysis of xylem pressure measurements at Hillgrove indicated a strong interactive effect of species and age class ($F = 7.12$, $P = 0.017$; Fig. 2). Predawn values were high and similar for bloodwood adults (-0.51 ± 0.07 MPa) and saplings (-0.64 ± 0.08 MPa) while predawn pressures in ironbark saplings (-2.58 ± 0.20 MPa) were much more negative than those measured for ironbark adults (-1.04 ± 0.08 MPa).

In sum, during the dry season in 1995 and 1996 neither bloodwood adults nor saplings appeared to be significantly water limited at either site. In contrast, both predawn and midday xylem pressures measured in the ironbark saplings and adult trees suggested extreme water-limitation and exposure to significant drought stress. At the end of the

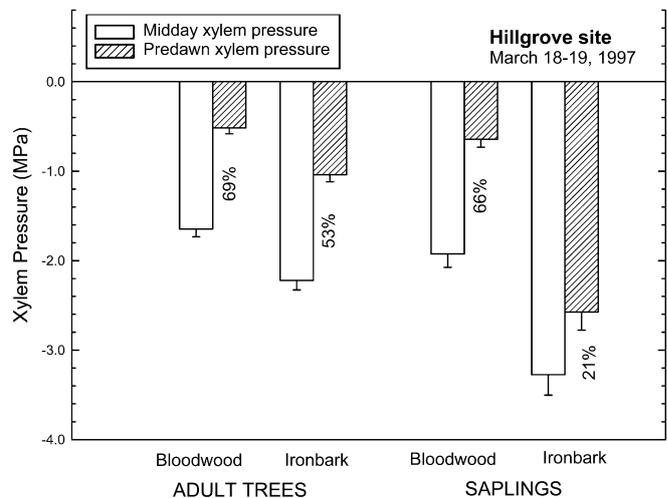


Fig. 2 Variation in average predawn and midday xylem pressures between saplings and adults of bloodwoods and ironbarks at the Hillgrove site at the end of the drought in 1997. Error bars represent ± 1 SE. Diurnal recovery is represented by the percent change between midday and predawn xylem pressures

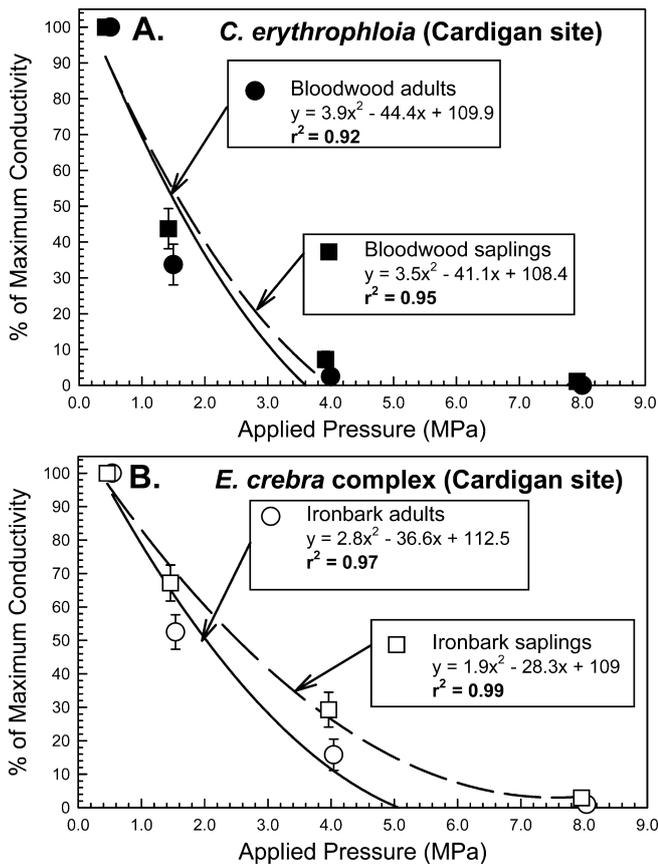


Fig. 3 The relationship between stem hydraulic conductance (expressed as a percentage of maximum conductance) and applied pressure (MPa) for adult and saplings of **A** *E. erythrophloia* and **B** *E. crebra* complex at the Cardigan field site. Curves were fitted using a second-order polynomial and each point represents the average (\pm SE) of at least five individuals

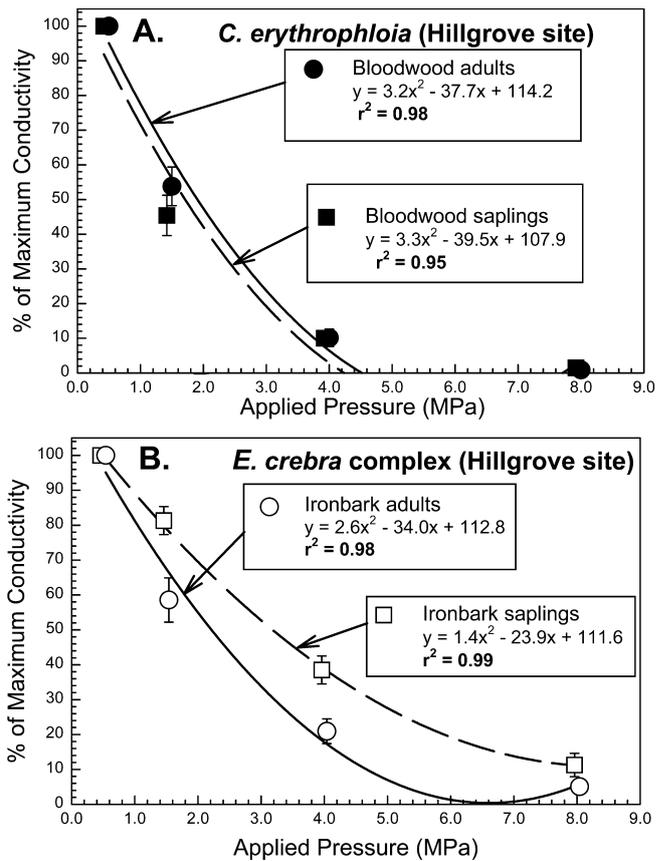


Fig. 4 The relationship between stem hydraulic conductance (expressed as a percentage of maximum conductance) and applied pressure (MPa) for adult and saplings of **A** *E. erythrophloia* and **B** *E. crebra* complex at the Hillgrove field site. Curves were fitted using a second-order polynomial and each point represents the average (\pm SE) of at least five individuals

drought, measurements at Hillgrove in March 1997 indicate that, with significant precipitation, xylem pressures in both adult and sapling ironbarks became less negative. However, adult ironbarks at Hillgrove appear to recover more rapidly than saplings and their xylem pressures approached those measured for bloodwood adults and saplings.

Cavitation vulnerability

Repeated measures analysis of vulnerability curves for plant material collected in September 1996 from both Cardigan (Fig. 3) and Hillgrove (Fig. 4) indicated that

bloodwoods were potentially more vulnerable to cavitation than ironbarks ($F=31.07$, $P<0.0001$) and that vulnerability was similar for sapling and adult bloodwoods. In contrast, a significant age class difference in vulnerability was apparent for ironbarks ($F=9.18$, $P=0.0045$); saplings appeared to be more resistant to cavitation than adults.

Native embolism in stems collected in September 1996 was expressed as the percent loss of conductivity relative to maximum conductivity at 0.5 MPa (Table 1). Although losses of conductivity were less severe than predicted by the vulnerability curves, there was a strong correlation ($r=0.97$; $P<0.001$) between predicted and measured values.

Table 1 Native embolism of stems collected in September 1996. Embolism is expressed as percent loss of conductivity (mean \pm SE) relative to maximum stem conductivity at 0.5 MPa

| | Bloodwood (<i>C. erythrophloia</i>) | Ironbark (<i>E. crebra</i> – <i>E. xanthoclada</i>) |
|----------------|---------------------------------------|---|
| Cardigan site | | |
| Adult plants | 37.6% \pm 6.4 | 76.7% \pm 5.4 |
| Saplings | 60.1% \pm 8.2 | 68.8% \pm 7.5 |
| Hillgrove site | | |
| Adult plants | 40.8% \pm 3.5 | 69.8% \pm 6.9 |
| Saplings | 34.6% \pm 7.6 | 47.6% \pm 8.9 |

Discussion

Patterns of stem mortality

From our survey of stem mortality at both sites, it is clear that there were strong differences among tree species in susceptibility to dieback. In particular, the ironbark populations at both sites exhibited much higher rates of dieback than bloodwood populations. This differential susceptibility among eucalypts to dieback has been observed before in Queensland as well as other locations in Australia (Old et al. 1981). Similar to our findings, previous studies in woodlands in Queensland have identified the ironbarks such as *E. crebra* as species that are likely to exhibit dieback (Wylie and Bevege 1981). A large-scale survey of dieback in the same area of Queensland as our study indicated that individuals in the *E. crebra* ironbark species complex were especially susceptible to dieback during the 1990s drought while *C. erythrophloia* populations exhibited little stem mortality (Fensham and Holman 1999). In comparisons among species that occur in different habitats, site differences in geology, soil depth and soil type have often been suggested as factors causing interspecific differences in dieback (Pook et al. 1967; Fensham and Holman 1999). Although Fensham and Holman (1999) identified some differences between canopy and sub-canopy species, there is a poorer understanding of the causes of species differences in dieback within a single site (Landsberg and Wylie 1983). Suggestions that species may differ in their rooting depth, tolerance of water stress, or susceptibility to cavitation have remained somewhat speculative in the absence of direct measurements of plant xylem pressures and cavitation resistance (Auclair 1993). Perhaps because it is rarely measured, age class differences in dieback similar to what we found for the ironbarks has been rarely reported. Pook and Forrester (1984) found that dieback was generally greater in younger age classes and they attributed it to higher water stress caused by smaller root systems in saplings and seedlings. Fensham and Holman (1999) found that of 21 common overstory species examined for age class differences in dieback, only in the *E. crebra* complex was dieback higher in adult trees; for the other species there was no significant difference among age classes. They offered no direct explanation for this age class difference in populations of the *E. crebra* complex and they argued that local patterns of dieback are probably a complex interaction of local rainfall, soil characteristics and competition. Although their results corroborate our findings for lower sapling dieback in ironbarks, the fact that they found it rarely in their species survey suggests that this pattern may be the exception rather than the rule.

Xylem pressure and stem mortality

It has been noted repeatedly that in situ measurements of water relations of trees undergoing dieback could help to

determine the importance of drought-induced cavitation relative to other potential causative factors such as insect herbivores and pathogens (Old et al. 1981; Auclair 1993). Our measurements of both predawn and midday xylem pressures provide substantial evidence that differences in stem mortality between bloodwood and ironbark species are related to pronounced species differences in water relations. The ironbarks experienced negative midday xylem pressures that would seem likely to initiate significant amounts of stem cavitation. Water stress in ironbarks was especially pronounced in September 1996 when both midday and predawn xylem pressures at Hillgrove and Cardigan were consistently more negative than -4.0 MPa and -5.0 MPa, respectively. Relative differences between predawn and midday xylem pressure potentials provide additional evidence for greater water stress in ironbarks; small relative differences between predawn and midday values in ironbarks suggest low rates of diurnal recovery. Significant cavitation resulting from these very low xylem pressures is supported by our measures of native embolism that indicate substantial losses of conductivity in both adult and sapling ironbarks.

The pronounced differences between bloodwoods and ironbarks in predawn xylem pressures suggest greater soil water availability for bloodwoods. Use of predawn xylem potential as an index of soil water potential is based on the assumption that during the night the plant comes into equilibrium with the “wettest” soil water potential available to a plant’s root system (Ritchie and Hinckley 1975; Richter 1997). Although there is current controversy as to the whether the assumption of predawn equilibrium is always justified (Sellin 1999; Donovan et al. 2001), nighttime transpiration has not been reported for these species so the use of these measurements to characterize general differences in soil moisture availability seems valid. It seems unlikely that localized habitat differences in soil moisture are responsible for higher predawn xylem pressures in bloodwood because we conducted our measurements in stands that were mixtures of bloodwood and ironbark individuals. A more likely explanation for higher moisture availability in bloodwood is a difference in rooting structure, in particular, rooting depth. Although we did not excavate root systems of either species, field observations of exposed roots systems along streams and road cuts suggested that the root systems in bloodwoods are characterized by a deep tap-root structure while the root system in ironbarks are dominated by a series of shallower, lateral roots. These observations coupled with our xylem pressure measurements suggest that during severe droughts the bloodwood tap root system allows access to water deep in the soil profile and thus reduces water stress and embolism.

Given the prevailing assumption that drought stress and resulting cavitation are primary factors underlying dieback (Auclair 1993), measurements of the water status of trees undergoing dieback have been surprisingly few. By comparing predawn and midday xylem pressures, Landsberg and Wylie (1983) found trees undergoing dieback had different diurnal patterns of soil water deficit development.

Although there were no differences in predawn xylem pressures, trees expressing dieback exhibited more negative midday water potentials than healthy trees. Interestingly, a later study by Landsberg (1985), where she measured predawn xylem pressure alone, did not demonstrate a relationship between xylem pressure and probability of stem mortality during a severe drought in 1983. She suggested that previous droughts may have induced changes in root-shoot allocation that buffered trees against effects of the 1983 drought. To monitor the water status of woodland eucalypts during a 1965 drought in New South Wales, Pook (1981) measured the water content of foliage as an index of leaf water potential. Although not analyzed statistically, for two species (*E. rossii* and *E. macrorhyncha*) there was a trend of lower leaf water potential in trees undergoing dieback. Unfortunately, leaf water potential data for *E. polyanthemos*, a species that did not experience significant dieback, were not collected so an interspecific comparison relating susceptibility to dieback and water status was not possible.

By the end of the drought in 1997, xylem pressures in adult ironbarks had recovered from their extremely negative values of 1996 and were comparable to those measured in bloodwood sapling and adults. This rapid recovery underscores the hydraulic resilience of these species and the potential importance of recovery from embolism as an adaptation to drought stress (Tyree and Sperry 1989). Xylem pressures in ironbark saplings were also much higher than measured in 1996 but they were still significantly lower than in ironbark adults. A shallower and less extensive root system in the ironbark saplings may be responsible for these persistently lower xylem pressures. By measuring xylem pressures at the end of the drought we hoped to characterize the water status of the plants under more normal climatic conditions. Our measurements after the 1990s drought suggest that greater water stress relative to adults may be the normal and more modal condition for ironbark saplings. This suggestion that drought is a more chronic condition for juveniles is similar to what has been found previously for other woody species in dry habitats (Griffin 1973; Pook and Forrester 1984; Sperry and Saliendra 1994).

Cavitation resistance and stem mortality

Analyses of vulnerability curves in bloodwoods and ironbarks clearly indicate that lower stem mortality in bloodwoods is not the result of greater resistance to cavitation. Bloodwood adults and saplings were significantly more vulnerable to cavitation than ironbark adults and saplings. Averaged for adults and saplings, the 50% loss in conductance points for bloodwoods at Cardigan and Hillgrove were -1.6 MPa and -1.8 MPa respectively; the corresponding values for ironbarks were significantly lower at -2.3 MPa and 2.7 MPa, respectively. Taken together, the vulnerability curves, xylem pressure data, relatively low rates of native embolism, and field observations on rooting depth suggest a drought avoidance

strategy in bloodwood that reduces incidence of dieback in both saplings and adults. In contrast, ironbarks appear to employ a drought tolerance strategy with higher resistance to cavitation and an apparent ability for rapid recovery from embolism. Similar results were found in a study on the relationship between cavitation resistance and rooting depth in Great Basin desert shrubs (Sperry and Hacke 2002). Deep-rooted phreatophytic species experienced less water stress and were more vulnerable to cavitation while drought deciduous species had shallower root systems and exhibited greater resistance to cavitation.

The importance of variation in cavitation resistance in preventing dieback during the drought is especially apparent in the comparison of stem mortality between age classes in ironbark. Lower rates of stem mortality in ironbark saplings were not due to reduced water stress because adult and sapling ironbarks experienced similarly negative predawn and midday xylem pressures. Rather, significantly higher resistance in ironbark saplings to cavitation may be the difference between age classes that reduces dieback during severe drought. The higher rate of native embolism that we measured in adult ironbarks relative to saplings provides field evidence of the potential adaptive importance of increased resistance to cavitation. Although adult and sapling ironbark xylem pressures did not differ significantly during the drought, sapling predawn and midday xylem pressures were more negative than in adults after the drought ended in 1997. This would suggest that root systems in saplings are shallower and that under non-drought conditions saplings experience lower soil water availability than adults. Higher vulnerability to drought stress in juvenile plants is often assumed, but there is little evidence available to determine whether the increased resistance to cavitation we observed in ironbark saplings is a general response. Greater cavitation resistance in seedlings was found in *Betula occidentalis* (Sperry and Saliendra 1994). No differences were detected in native xylem pressures between *Betula* adults and juveniles but the authors suggested that increased vulnerability to drought might select for greater cavitation resistance in shallow-rooted juveniles. A study on intraspecific variation in cavitation resistance in live oak (*Quercus wislizenii*) found slight differences in resistance between saplings and adults (Matzner et al. 2001). Although oak sapling xylem pressures were not measured in this study, the authors noted that juveniles of the congener *Q. douglasii* experience lower predawn xylem values than adults and suggested that such differences may also occur in *Q. wislizenii*.

Higher rates of stem mortality in ironbark adults than in saplings was unexpected because we assumed that the larger root system in adults would reduce water stress and thus rates of cavitation and embolism. If reduced stem mortality in ironbark saplings results from higher resistance to cavitation, this difference in embolism among ironbark age classes may be an example of the presumed trade-off between efficiency of conductance and resistance to cavitation (Tyree and Sperry 1989; Tyree et al. 1994; Sperry 1995). A potential example of this trade-off was

provided by a study of intraspecific variation in stem death and cavitation resistance in *Populus trichocarpa* (Sparks and Black 1999). Populations from more mesic sites exhibited poor stomatal control, low resistance to cavitation, and higher rates of stem mortality. The authors argued that this apparently maladaptive condition might be explained by a trade-off between cavitation resistance and maximizing plant conductance. Although data on stomatal behavior is currently not available for ironbarks, it is possible that tighter stomatal control in ironbark saplings may be another mechanism (in addition to changes in cavitation resistance) that reduces stem mortality in saplings relative to adults. Additional evidence for this trade-off comes from a recent comparative study that examined conduit wall strength and cavitation resistance across a wide range of conifer and angiosperm species (Hacke et al. 2001). Wood density and conduit wall reinforcement were found to be positively related to cavitation resistance. Reductions in conductivity and growth rate accompany increases in wood density (Enquist et al. 1999) and thus indicate a cost to cavitation resistance.

Under normal climatic conditions in these dry woodland habitats, ironbark saplings might be expected to produce xylem more resistant to cavitation because their presumably smaller and shallower root system exposes them to frequent periods of reduced soil water availability. Several studies have shown that environmentally induced changes in cavitation resistance can occur. Particularly relevant to our study are the results from Alder et al. (1996) who reported an increase in root cavitation resistance in *Acer grandidentatum* individuals at the drier end of a soil moisture gradient. Other studies have demonstrated that environmental variation in light levels (Cochard et al. 1999) and nutrient availability (Harvey and van den Driessche 1997) can also induce changes in cavitation resistance.

In contrast to saplings, because their more extensive root system reduces water stress, adult ironbarks would be expected to produce xylem that is more efficient at conduction and less resistant to cavitation. If severe droughts occur with a low enough frequency, this may be a viable strategy because in most years adults will not experience xylem pressures negative enough to initiate significant cavitation. However, in extreme drought years when both adults and saplings experience similarly negative xylem pressures, this strategy may result in the adults being more vulnerable than juveniles to cavitation. In a sense, the typically more water-limited environment of juveniles may induce a conservative cavitation resistance strategy that “pre-adapts” saplings for survival during extreme drought. These results suggest that a better understanding of tradeoffs in xylem conduction efficiency and cavitation resistance might benefit from more detailed comparisons of adult and juvenile water relations.

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