Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia

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Abstract: Most trees in the eucalypt savannas of Australia have hollow cores, or pipes, caused by termite activity, yet little is known about their effect on tree growth or survival. Five hundred and forty-one trees with known growth and survival histories were cored to determine pipe diameters in wooded savanna of Kakadu National Park, north Australia. Generalized linear modelling and multi-model inference was used to analyse frequency and degree of piping relative to initial tree diameter at breast height (dbh), eco-taxonomic group or species of eucalypt. Growth (dbh increment) and survival (4 y) were analysed relative to initial tree size, pipe ratio (pipe diameter:dbh) and eco-taxonomic group. The frequency of piping was strongly dependent on dbh, increasing with size of tree, and was highest in eucalypts. Growth and survival of eucalypts increased with tree diameter and decreased with pipe ratio. For example, from modelled data, 10-cm-diameter trees without pipes grew $0.14 \, \text{cm} \, \text{y}^{-1}$ with 85% survival vs. 10-cm trees with pipe ratios of 0.60 which had near-zero growth and only 46% survival. Comparing 40-cm-diameter trees without pipes to those having pipe ratios of 0.80, growth was 0.22 vs. $0.05 \, \text{cm} \, \text{y}^{-1}$, with little difference in survival, 97–99%, respectively. Contrary to the suggestion that tree hollows are an adaptive trait whereby trees benefit by the release of nutrients, in the north Australian eucalypt savannas the net effect of termite piping on individual tree growth and survival was negative.

Key Words: Australia, *Coptotermes acinaciformis*, demography, *Eucalyptus*, nutrient cycling, savanna, termites, tree growth, tree hollows, tree survival

INTRODUCTION

It has been postulated that tree-piping termites in natural systems may benefit trees in nutrient-poor habitats (such as the Australian savannas), because the termites and associated fungi decompose heartwood and return nutrients to circulation, and also various hollow-dwelling animals import nutrients from elsewhere (Andersen & Braithwaite 1996, Apolinário & Martius 2004, Janzen 1976, Jones 1990). Indeed, in a broad-scale survey within Kakadu National Park in northern Australia, the frequency of trees with hollows was negatively correlated with total soil phosphorus and total soil nitrogen (Braithwaite 1985). The degree to which any individual tree might benefit from tree piping, however, is unknown. To the authors' knowledge, there is no published study describing the relationship between tree-piping termites and the growth and mortality of individual trees.

Tropical north-central Australia is an ideal location to examine such a relationship. By far, the majority of trees in the eucalypt savannas of this region have hollow cores, or pipes, attributable to termite activity (Fox & Clark 1972). An early survey of 1700 trees in open eucalypt forests near Darwin reported that 84% of eucalypt trees were piped, at an average of half their diameter (Fox & Clark 1972). Another survey east of Katherine, Northern Territory reported that 89% of 295 trees were hollow (Forner 2006), and an extensive survey within the northern sectors of Kakadu National Park reported that 66–79% of the three most common tree species in the northern sectors were piped (Braithwaite 1985).

On the negative side, tree-piping termites have been mentioned as a contributing factor in the death of the largest trees following fires in eucalypt savannas near Darwin (Lonsdale & Braithwaite 1991, Williams *et al.* 1999), or a major cyclone (Stocker 1976). They have been implicated as a major cause of death of large mangrove

trees in Malaysia (Putz & Chan 1986) as well as the smallest eucalypt trees on Melville Island off the coast near Darwin (Fensham 1992). Termites have been long recognized as responsible agents of defects in and damage to potential timber enterprises in the region (Cameron 1985, Fox & Clark 1972, Lacey 1979). Further, tree-piping termites in northern Australia remain the scourge of horticulturalists and farmers growing other tree crops (e.g. mangoes, avocados, bananas, rambutan), as they are known to kill even healthy and well-watered trees (Andersen *et al.* 2005).

In a protected area of eucalypt savanna in Kakadu National Park, we examined natural-grown trees of known diameters for incidence of termites and diameter of hollow (pipe), and related these to tree growth rates (diameter increment) and mortality. The results show strong size-dependent and species-dependent relationships, and in the short term and on an individual tree basis, effects contrary to those predicted for a 'fertilization' role for termites.

METHODS

Study area and study plots

The study was conducted in the monsoonal tropics of northern Australia, in a eucalypt savanna 200 km east of Darwin, Northern Territory, in Kakadu National Park (KNP), a World Heritage site (Press *et al.* 1995), specifically at the Kapalga Research Station (12° 34′S, 132° 22′E). Rainfall is highly seasonal, with 96% of its annual average total of 1485 mm occurring during the months of November–April (Bureau of Meteorology, http://www.bom.gov.au/). The geomorphology, soils, climate, and vegetation of Kakadu National Park are detailed in Press *et al.* (1995) and Finlayson & von Oertzen (1996), and those of Kapalga in Andersen *et al.* (2003).

The most extensive savanna vegetation type (open forest) in the region occurs on well-drained soils, and is dominated by two tall (16–25 m) evergreen eucalypts, *Eucalyptus tetrodonta* and/or *E. miniata*. Both species range across northern Australia from the Kimberly to the Atherton Tablelands (Wilson *et al.* 1996), often as co-dominants making up the canopy. At the edge of floodplains and waterways, the dominant eucalypt is *Corymbia bella*. The mid-canopy consists almost entirely of deciduous broad-leaved woody species such as *Terminalia ferdinandiana*, *Buchanania obovata* and *Planchonia careya*. Various arborescent monocots are found scattered in the mid-storey eucalypt woodlands or as co-dominants in the canopy adjacent to wetlands.

This study took advantage of the permanently marked plots and trees set up in a study of the effect of buffalo and fire on tree growth and mortality and reported in Werner (2005). In that study, six permanent research sites were established in tall savanna woodland in Kapalga in September 1982; each consisting of ten 30 × 30-m plots, for a total area of 0.9 ha. Two of the research sites were in upland open forest dominated by *E. tetrodonta*, two sites were dominated by *E. miniata* and two dominated by *C. bella* (the ridge, slope and flat described in Werner 2005). All trees > 1.4 m height in the plots were permanently marked and monitored for incremental growth and survival, annually, for 8 y (detail in Werner 2005). The individual trees used in this study are the same ones used in the Werner (2005) study.

Field sampling of trees and calculations of growth, survival and pipe ratio

Diameters of all trees were measured over bark to the nearest 0.05 cm, at breast height (1.4 m), annually in October at the end of the dry season to help reduce error in estimating incremental changes in diameter; in general, in any given year, savanna trees exhibit maximum diameters toward the end of the wet season and minimum diameters at the end of the dry season, due both to phenology of growth and wet-season swelling of bark (Prior *et al.* 2004, Werner 2005). Methods used follow Werner (2005). For the current study, we averaged growth increments for two intervals, 1984–1985 and 1985–1986, representing the years just prior and after termite sampling in 1985, and coincidentally, wet seasons that were wetter and drier than average, 1685 mm vs. 1162 mm precipitation, respectively (Bureau of Meteorology, Jabiru Township; Werner 2005). Trees did not experience fire during this period. Tree mortality for all trees alive in October 1985 was determined from the Werner (2005) data set for the 4-y period 1985–1989; during this time, some trees experienced fire. During the course of this study, the area did not suffer high winds such as that due to cyclones.

In April 1985, each marked tree was bored with a tree-coring tool to detect and measure the diameter of any hollow areas at breast height (1.4 m) and at ground level. Boring was continued until a hollow (pipe) was encountered or until the corer had penetrated the entire solid stem. Where a pipe was found, the corer was pushed through until it encountered the solid wood on the opposite side of the hollow, and then pipe diameter was measured to the nearest centimetre.

All trees were also examined for external evidence of termites including mounds at the base of a tree, burls (sizes and height above ground) made in response to the presence of termites, and most commonly, breaches in the bark of a tree where an internal nest has extended through the sapwood to the surface, and serving as external openings for the release of alates.

The proportion of tree stem occupied by the hollow, termed the pipe ratio, was calculated as the diameter of

Table 1. Study species listed by eco-taxonomic group, family, and number of living trees cored to determine pipe diameter, and for which 2-y growth and 4-y survival are known. Also number of trees with hollows and average cross-section of stem removed by piping. Nomenclature is according to Northern Territory Herbarium (2006; www.nt.gov.au/nreta/wildlife/plants/checklist.html).

Eco-taxonomic group and species	Family	Total number of trees cored	Number of trees with hollows	Average cross-sectional area piped (%)
Eucalypts				
Corymbia bella K. D. Hill & L. A. S. Johnson		72	19	2.7
C. bleeseri (Blakely) K. D. Hill & L. A. S. Johnson		16	5	1.0
C. polycarpa (F. Muell.) K. D. Hill & L. A. S. Johnson	All Myrtaceae,	10	6	2.9
C. porrecta (T. S. Blake) K. D. Hill & L. A. S. Johnson	subfamily	77	61	8.9
Eucalyptus miniata Cunn. ex Schauer	Leptospermoideae	102	99	12.4
E. tectifica F. Muell.		35	17	3.0
E. tetrodonta F. Muell		165	135	8.0
E. sp.		1	1	0
Total Eucalypts		478	343	7.6
Pantropical genera				
Buchanania obovata Engl.	Anacardiaceae	7	1	0
Erythrophleum chlorostachys (F. Muell.) Baillon	Caesalpiniaceae	18	11	1.9
Ficus opposita Miq.	Moraceae	2	0	0
Gardenia megasperma F. Muell.	Rubiaceae	3	0	0
Planchonia careya (F. Muell.) Knuth	Lecythidaceae	11	2	1.1
Syzygium eucalyptoides spp. *bleeseri* (O. Schwarz) B. Hyland	Myrtaceae	1	0	0
Syzygium suborbiculare (Benth) T. G. Hartley & L. M. Perry	Myrtaceae	6	2	2.0
Terminalia carpentariae C. T. White	Combretaceae	3	1	0.1
Terminalia ferdinandiana Exell	Combretaceae	13	0	0
Total Pantropics		63	17	1.0
Grand total		541	360	6.8

the hollow divided by the diameter of the tree at breast height. All statistical analyses were calculated using the data on pipes and tree diameters at breast height (1.4 m).

Termites

By far, the most common tree-piping termite species in undisturbed savanna woodlands of the region is *Coptotermes acinaciformis* (Froggatt), accounting for more than 90% of the pipes in trees growing in natural areas (Andersen *et al.* 2005, Braithwaite *et al.* 1988, Fox & Clark 1972, Hodda 1992). The species usually enters living trees from underground or occasionally through broken stems caused by mechanical injury or fire. They extend galleries through the heartwood, occasionally into the sapwood, producing a hollow pipe the entire length of the bole (Andersen *et al.* 2005) and even into smaller branches and throughout the larger root system (Werner & Murphy 2001, and unpubl. data).

The presence of external signs of wood-boring termites does not mean that termites are still present, as termites abandon trees periodically (Andersen & Lonsdale 1990, Hodda 1992). Although we do not have estimates of how many of our trees contained living colonies, in similar savanna woodlands near Darwin, Fox & Clark (1972) found that only 73% of the 1414 piped eucalypts still had active colonies, somewhat higher than the 57% found in piped rain-forest trees of the Amazon Basin (Apolinário

& Martius 2004). In this paper, we have not tried to determine termite numbers, but have focused instead on the growth and survival responses of trees to the piping, and from which we can show significant relationships among tree size, pipe ratio, species and eco-taxonomic group, growth and survival.

Although live termites were often encountered during our coring of trees, this per se was not considered a reliable indicator of termite activity that could potentially affect tree growth. For example, a dying tree might show signs of termite infestation, but no longer have live termites in it; alternatively, a newly infested tree yielding live termites might not yet have a detectable pipe. Due to time constraints, baits were not employed, and termite species were not identified. Nevertheless, in this case, we are quite confident that the main species responsible for piping was *Coptotermes acinaciformis*.

Tree species and eco-taxonomic groups

The 16 tree species in the study plots were grouped into two eco-taxonomic types for analyses, based on evolutionary and ecological affinities (e.g. morphology, phenology, distribution, life cycle, deciduousness, growth patterns, height, dominance) (Werner 2005, Williams *et al.* 1997, Wilson *et al.* 1996) (Table 1).

(1) Eucalypts (*sensu lato*): Species of the dry-fruited Myrtaceae subfamily Leptospermoideae, restricted to the

Australasian flora. The canopy stratum of these savannas is almost totally dominated by this group; on the study site, they comprise > 70% of the mature trees (Werner 2005). The species at our study site were predominantly evergreen, but many of the other tropical eucalypt species are deciduous or semi-deciduous during the dry season (Williams *et al.* 1997).

(2) Pantropical genera: Species of genera with wide-ranging pantropical or Old World tropical distributions, such as *Buchanania*, *Gardenia*, *Planchonia* and *Terminalia*. In the Australian savannas they are smaller in stature at full maturity than the eucalypts, and make up most of the mid-canopy stratum. A few of the species (e.g. *Erythrophleum chlorostachys*) have the ability to produce large trees and become semi-deciduous, but as a rule, the Pantropics group are dry-season deciduous (Williams *et al.* 1997).

The few arborescent monocots (palms) and other Australian affinities on the Werner (2005) site were few and otherwise considered inappropriate for coring.

Statistical analyses

Our analytical approach was to employ multi-model inference based on information theory and model averaging. A set of candidate models was developed to describe relationships between each response variable and possible explanatory variables; each candidate model set included a 'null' model, which describes the case where none of the possible explanatory variables has an effect. Akaike's information criterion for small sample sizes (AICc) was used to rank and weight the models (Burnham & Anderson 2001). The AICc identified the model(s) most strongly supported by the data based on the bias-corrected, maximised log-likelihood of the fitted model and a penalty for the number of parameters used (Burnham & Anderson 2002). The Akaike weights represent the weight of evidence in favour of a particular model as being the best model in the set. Designation of a single 'best' model is often unsatisfactory when there are several models receiving similar levels of support, but model averaging can provide a more stable and less biased estimate of effect size than any single best model. All analyses were performed using the R statistical package v. 2.2.0 (http://www.r-project.org/foundation/).

We used this multi-model approach to assess the major influences on the frequency and severity of termite piping in savanna trees, and to determine how much the piping affected tree growth and survival. We hypothesized that responses would differ for the two major eco-taxonomic groups (i.e. eucalypts vs. Pantropics), and may also differ among species. Analysis of species effects was possible only for the four most abundant species, all eucalypts *sensu lato*: *Corymbia bella*, *C. porrecta*, *Eucalyptus miniata* and *E. tetrodonta*. Specifically, we investigated: (1) Frequency of piping in relation to tree size (diameter at breast height, dbh) and either eco-taxonomic group or species. (2) Piped diameter in relation to dbh and either eco-taxonomic group or species. For these analyses, we used only piped trees to avoid problems with zero-inflated data. As expected, pipe diameter responses were dominated by dbh. In further analyses we therefore scaled piped diameter by dividing by dbh, and termed this pipe ratio. (3) Pipe ratio in relation to dbh and either eco-taxonomic group or species. For these analyses, we again used only piped trees. When pipe ratio was the response variable, an arcsine-square root transformation was used to normalize these proportional data and improve model fit. However, when pipe ratio was an explanatory variable ((4) and (5) below), the untransformed data produced a better model fit. (4) Annual dbh increment (averaged over 2 y) in response to dbh, pipe ratio and either eco-taxonomic group or species. (5) Tree survival over 4 y in response to dbh, pipe ratio and either eco-taxonomic group or species.

Generalized linear mixed effects models (GLMMs) or linear mixed effects models, with plot as a random factor, were used for all analyses. Binomial GLMMs with a logit link were used to investigate frequency of piping and tree survival, linear mixed effects models for piped diameter, pipe ratio and growth. The interaction between dbh and either eco-taxonomic group or species was included in all the above analyses. The candidate model sets are listed in Tables 2, 3 and 4. We used the weighted averaged coefficients of all models receiving $\geq 10\%$ of the AIC_c weight to calculate the predicted values presented in figures and tables.

RESULTS

Evidence of termites

Of hollow trees, 91% showed one or more of the external signs of termite activity (65% of trees had termite nests and/or exit holes). Fewer than 10% of hollow trees showed no external evidence of termites, and almost all of these were smaller trees that died over the next 4 y. Of trees with solid cores, 66% showed at least one of the signs of termite activity (42% with nests and/or exit holes). Only 34% of these trees were completely free of any sign of termites.

Of the trees with hollow cores at breast height (used in this analysis), 85% also had a piped centre at ground level, with the ground-level pipe somewhat larger in diameter than at breast height, but proportional to diameter of the tree at each level. Of the trees with solid cores at breast height, 29% had a hollow centre at ground level; these hollows were very small, both in absolute terms

and relative to size of tree, and perhaps reflected new infestations.

In sum, almost all of the trees piped at breast height showed external evidence of termite activity, compared with only two-thirds of the unpiped trees, some of which had small hollows at ground level only.
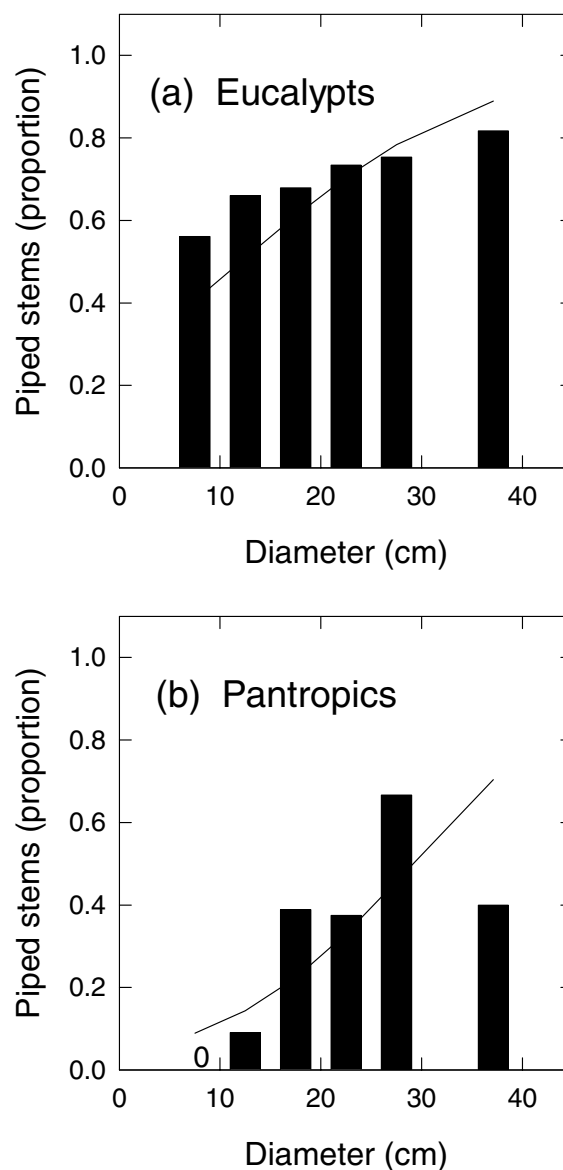
Frequency of piping

Over all sampled trees, 66% had piped stems (Table 1). The frequency of piping was strongly dependent on both tree size (dbh) and eco-taxonomic group (eucalypts vs. pantropics) (Figure 1, Table 2). In general, trees of larger size classes had a higher proportion of trees piped than did smaller size classes, and eucalypts had a higher proportion piped than did pantropics for a given size category (Figure 1). Further, there was some evidence for the two groups having a different slope of the relationship between frequency of piping and tree size (i.e. the model with Group × dbh received 43% support). The Pantropics were less likely to be piped, overall, but had a steeper increase in frequency of tree piping with size (Figure 1).

The frequency of piping was also strongly dependent on species of eucalypt (Table 3). *Eucalyptus miniata* was notable for piping being present in 90% of the trees across all size categories, even the smallest trees. In contrast, the piping frequency of *E. tetrodonta* was approximately 70% of smallest trees (< 10 cm dbh), increasing with dbh to 95% of larger trees (< 30 cm dbh). Similarly, piping frequency of *Corymbia porrecta* was approximately 50% in the smallest trees to > 90% in the largest trees. In *C. bella*, the only eucalypt dominant in lower topography, there was markedly less piping (< 40% even in the largest trees), most likely due to less favourable underground conditions (several months per year of water-logged soils) than that required for the initial infestation by tree-piping termites.

Pipe diameter and pipe ratio

Over the total stand of trees (piped and unpiped), the cross-sectional area of stem tissue lost to piping was 7.8% and 1% for eucalypts and pantropics, respectively (Table 1).

Considering only those trees that were piped, pipe diameter was influenced by dbh, eco-taxonomic group and their interaction, as indicated by the global model receiving strong support (Table 2). The increase in pipe diameter with size was greater for the eucalypts than the pantropics (Figure 2a). The pipe ratio increased only slightly with tree dbh, and was somewhat larger in the eucalypts than the pantropics (Figure 2b), but effects were weak (Table 2).

Figure 1. Frequency of piped stems for six tree size classes (5–10; 10–15; 15–20; 25–30; and > 30 cm dbh) for the two major eco-taxonomic groups in northern Australia: eucalypts (a) and species of pantropical genera (b). Bars show actual numbers. There were totals of 478 eucalypt stems and 63 pantropical stems; 0 indicates that no pantropical stems in the smallest dbh class were piped. Lines show the weighted model averaged proportion of piped stems.

There was some evidence for differences in pipe diameter among the four eucalypt species, as indicated by the global model receiving strong support (Table 3). However, dbh of the tree had overriding importance, and the differences between species were subtle, the most obvious one being that pipe diameter was larger in *C. porrecta* than the other species, but only for trees larger than 25 cm dbh. Of trees that were piped, the two *Corymbia* species showed a steep increase in pipe ratio with dbh, but pipe ratio in the two *Eucalyptus* species was

Table 2. AICc weights (wi) of models in candidate sets used to compare effects of initial dbh, eco-taxonomic group, and their interaction on (1) frequency of termite piping in trees, (2) pipe diameters of trees piped by termites, (3) pipe ratio (piped diameter: tree dbh). AICc weight indicates the likelihood of the particular model being the best in the candidate set; AICc weights sum to 1 over a particular model set. The operator '+' indicates that only additive effects of the explanatory variables are in the model whereas the operator '×' indicates both main effects and interactions Those values > 0.10 are shown in bold, and these models were used to calculate model averaged coefficients. Explained deviance (expdev) is per cent deviance explained by the model. NA is not applicable.

Response variable	Frequency		Pipe diameter		Pipe ratio	
Model	wi	expdev	wi	expdev	wi	expdev
Group × initial dbh	**0.568**	11	**0.668**	8.8	**0.322**	6.0
Group + initial dbh	**0.432**	11	**0.328**	8.7	**0.653**	5.9
initial dbh	< 0.001	6.7	0.004	8.2	0.002	2.1
Group	< 0.001	5.1	< 0.001	0.2	0.024	3.5
Null	< 0.001	NA	< 0.001	NA	< 0.001	NA

totally insensitive to dbh (this accounts for the interaction term in Table 3).

Tree growth rates

Growth increased with dbh and decreased with an increasing pipe ratio (Table 4; Figures 3a and 3b). The effect of pipe ratio was demonstrated in the actual overall growth rate of all eucalypt trees that had no hollows, which averaged $0.19 \, \text{cm y}^{-1}$, compared with $0.14 \, \text{cm y}^{-1}$ and $0.10 \, \text{cm y}^{-1}$ for piped trees with 20–30% and 30–40% of their diameters hollowed out, respectively (Figure 3a). Average growth rate was negative for eucalypt trees with more than 40% of their diameter hollowed out (Figure 3a) (negative values can be obtained in several ways, including failure to recover from the nadir of diameter that occurs during the dry season, part of a natural seasonal fluctuation in dbh; Werner & Murphy 2001). The effects of both dbh and pipe ratio were clear in the modelling, which predicted the growth rate of a 10-cm tree without termites to be $0.13 \, \text{cm y}^{-1}$, with steady decreases with increasing pipe ratio, down to $-0.23 \, \text{cm y}^{-1}$ with 80% of the stem piped. In a 25-cm tree, the comparison is $0.24 \, \text{cm y}^{-1}$ vs.

$-0.11 \, \text{cm y}^{-1}$ and in a 40-cm tree, $0.36 \, \text{cm y}^{-1}$ vs. $0.00 \, \text{cm y}^{-1}$ (Figure 3b).

The range in growth rates (averaged over 2 y) of individual trees without hollows was quite variable, from -1.5 to $1.3 \, \text{cm y}^{-1}$. From modelled data, average growth increments were in the range of 0.14 to $0.23 \, \text{cm y}^{-1}$; these increments are well within the ranges of the increments reported in longer-term studies of Werner (2005) and Prior et al. (2006).

On average, eucalypts grew slightly faster than pantropics (Table 4). When unpiped, the difference was $0.018 \, \text{cm y}^{-1}$, but given a pipe ratio of 0.2, the difference was only $0.007 \, \text{cm y}^{-1}$. Within the eucalypts, C. porrecta and E. tetrodonta grew faster than C. bella and E. miniata when not piped, but there were pronounced species × piping interactions (Table 4). While piping scarcely affected growth rates of E. miniata, overall, it was associated with markedly reduced growth in the other eucalypt species.

Tree survival

The overall 4-y survival rate of eucalypt trees was 88.9%, and of pantropical trees, 82.5%. Survival increased with

Table 3. AICc weights (wi) of models in candidate sets used to compare effects of initial tree dbh, species (four major eucalypt species were included in this analysis), and their interaction on (1) frequency of termite piping in trees, (2) pipe diameters in those trees piped by termites, (3) pipe ratio. AICc weight indicates the likelihood of the particular model being the best in the candidate set; AICc weights sum to 1 over a particular model set. The operator '+' indicates that only additive effects of the explanatory variables are in the model whereas the operator '×' indicates both main effects and interactions. Those values > 0.10 are shown in bold, and these models were used to calculate model averaged coefficients. Explained deviance (expdev) is per cent deviance explained by the model. NA is not applicable.

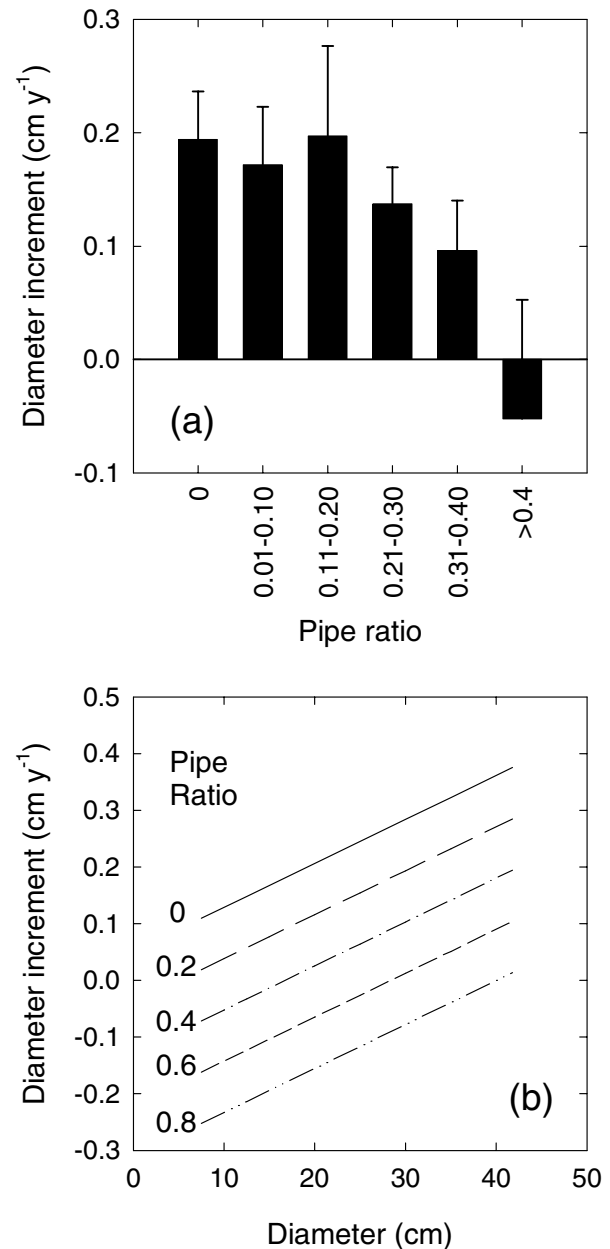| Response variable	Frequency		Pipe diameter		Pipe ratio	
Model	wi	expdev	wi	expdev	wi	expdev
Species × initial dbh	**0.563**	18	**0.944**	8.9	**0.926**	8.0
Species + initial dbh	**0.435**	16	0.009	8.1	0.010	3.4
initial dbh	0.001	13	0.047	8.0	0.060	2.7
Species	< 0.001	5	< 0.001	0.8	0.001	1.5
Null	< 0.001	NA	< 0.001	NA	0.002	NA
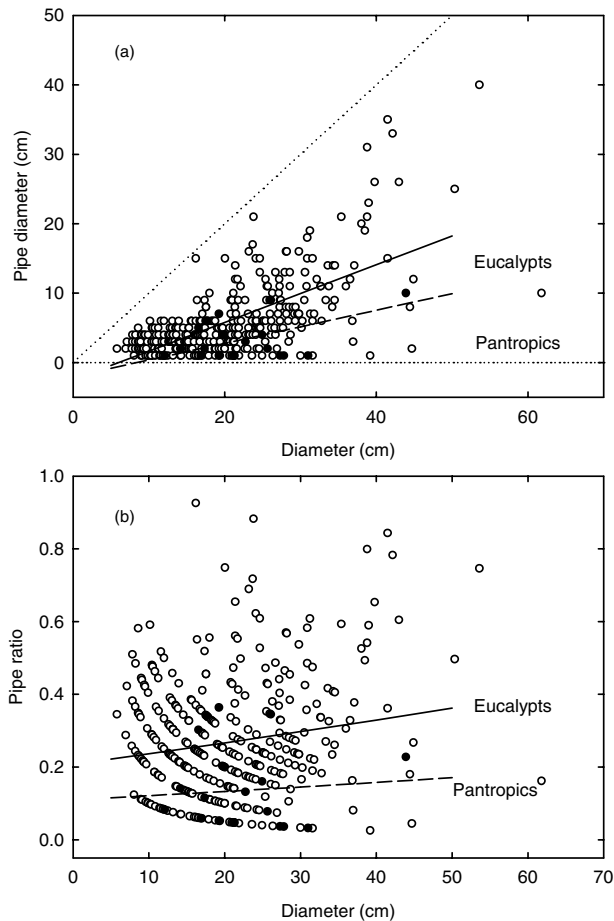
Figure 2. Relationships between pipe diameter and tree dbh (a) and pipe ratio and tree dbh (b) for eucalypts (open circles) and pantropics (closed circles) in northern Australia savanna woodland. Model predicted values are indicated by the dashed (eucalypts) and solid (pantropics) lines. The dotted lines in (a) indicate the bounds of possible values. The series of hyperbolae in (b) appear because pipe diameter was measured on a discrete scale (to the nearest cm); for example, when a pipe diameter of 1 cm is divided by many corresponding dbh values, a hyperbola is generated.

Figure 3. Growth (dbh increment) of eucalypts in northern Australia savanna woodland. Actual dbh increments, averaged over a range of pipe ratios (a) and modelled values of dbh increment as a function of dbh, for a range of pipe ratios (b).

tree dbh (Figures 4 and 5) and decreased with pipe ratio (Table 4; Figure 5).

For eucalypts, by way of example using modelled data, the survival rate of 10 cm trees without piping was 85%, and this steadily decreases with increasing pipe ratio, down to 46% survival for 10-cm trees where 80% of the stem is hollow. For 25-cm eucalypt trees, the comparison in survival between zero and 80% piping was 95% vs. 84%, respectively. Of 40-cm eucalypt trees, survival was 97–99% without much difference among pipe ratios (Figure 5). As stated in the methods, these data do not include any effects of fire.

In contrast, for pantropics, using modelled data, the survival rate was between 80–90%, increasing slightly with dbh, but no real difference between zero and 20% piping (Figure 5). Sample sizes were very small, however;

further, no pantropics had pipe ratios > 0.4, so we did not extrapolate the example beyond pipe ratio of 0.2.

There was also some evidence for small differences between eucalypt species in survival (Table 4). Actual overall 4-y survival was 90% for both *E. tetrodonta* and *E. miniata,* 81% for *C. porrecta* and 94% for *C. bella.* However, the predicted survival, after controlling for dbh and pipe ratio among the four species, was highest in *E. tetrodonta* (average 92%) and lowest in *E. miniata* (average 89.5%).

Table 4. Growth and survival of trees: AICc weights (wi) of models in candidate sets used to compare effects of pipe ratio (ratio pipe diameter: tree dbh), initial dbh (1985) and ecotaxonomic group or species (four major eucalypt species) on (1) growth rate of trees and (2) survival of trees over 4 y. Results of several analyses are included in this table, and the explanatory factor in each case is either Group or Species. AICc weight indicates the likelihood of the particular model being the best in the candidate set; AICc weights sum to 1 over a particular model set. The operator '+' indicates that only additive effects of the explanatory variables are in the model whereas the operator '×' indicates both main effects and interactions. Those values > 0.10 are shown in bold, and these models were used to calculate model averaged coefficients. Explained deviance (expdev) is per cent deviance explained by the model. This is not listed for growth models, where explained deviance was small; for the global models it was 2.0% for the Group analysis, and 5.3% for the Species analysis. GrSp indicates Group or Species, depending on analysis (see headers). NA is not applicable.

| Response variable | Growth | | Survival | | | |
| | w_i | | w_i | | expdev (%) | |
Model	Group	Species	Group	Species	Group	Species
initial dbh + GrSp × Ratio	**0.108**	**0.805**	**0.232**	0.016	9.0	14
initial dbh + GrSp + Ratio	**0.246**	< 0.001	**0.399**	**0.319**	8.8	14
initial dbh + GrSp	0.001	< 0.001	0.073	0.019	7.4	11
initial dbh + Ratio	**0.583**	0.001	**0.192**	**0.621**	7.9	12
initial dbh	0.003	< 0.001	**0.103**	0.024	7.1	8.9
GrSp × Ratio	0.007	**0.192**	< 0.001	< 0.001	1.4	4.0
GrSp + Ratio	0.015	< 0.001	< 0.001	< 0.001	0.88	3.7
GrSP	0.001	< 0.001	< 0.001	< 0.001	0.50	2.7
Ratio	0.034	0.001	< 0.001	< 0.001	0.13	1.1
Null	0.002	< 0.001	< 0.001	< 0.001	NA	NA

DISCUSSION

Frequency and degree of piping

The frequency of piped eucalypts in this study is very similar to the frequency found in 1972 by Fox & Clark (1972) when comparable data are used. The 1972 study measured only trees > 15.2 cm in dbh, over five species, and found that 84% of the trees were piped. In our study, we found that excluding all eucalypts < 15.2 cm dbh and *C. bella*, a species not included in the Fox & Clark (1972) study, yielded 85.2% piping frequency among the remaining (n = 256) trees. These overall frequencies are only slightly greater than the values obtained by Braithwaite (1985) for trees > 10 cm dbh, who reported piping frequencies of 79%, 70% and 66% for *E. miniata*, *E. tetrodonta* and *C. porrecta*, respectively.

The fact that pantropical trees are less likely to have termite-piped stems than are eucalypts, across all size classes (Table 2; Figure 1), could be due to (1) pantropical trees in general suffering fewer termite infestations and/or (2) rates of infestation by termites being no different, but juvenile (< 1.4 m height) pantropical trees that become infested could be more likely to die before reaching sapling stages and are not registered in this sort of study. In the latter case, the fact that few sapling-sized (dbh 10 cm) pantropical trees die when piped (Figure 4) would simply reflect strong individual trees. We cannot separate these two possibilities.

The fact that diameter of tree is only very weakly related to pipe ratio, but strongly related to frequency of piping, is an important contrast. Assuming that tree diameter reflects time (age), then the probability of having termite pipes increases over time, whereas the amount of stem tissue lost is not merely a matter of time and/or age of the individual trees. Once termites enter a tree, their ability to pipe that tree depends on a number of factors, including vigour of the host tree.

Growth and survival

That initial dbh is positively related to growth (Prior *et al.* 2006, Werner 2005; Werner & Murphy 2001) and survival (Lonsdale & Braithwaite 1991, Prior *et al.* 2006, Werner 2005, Williams *et al.* 1999) of the savanna trees of this region has been reported previously. However, the fact that termites may mediate the relationship between initial tree size and growth and between initial tree size and survival has not been reported previously. The role of tree-piping termites in mediating these relationships can now be added to a growing list of factors, including fire, grazing, precipitation, and competition from ground level vegetation.

Overwhelmingly, the presence of termite-pipes is negatively correlated with size-dependent incremental growth, especially in eucalypts, and with the probability of survival of small trees. Further, the relationship is strongly in proportion to the degree of piping. For eucalypts, the crucial period for growth and survival seems to be when trees are small. When trees are less than 20 cm dbh, any piping greater than 60% of the diameter (pipe ratio ≥ 0.60) is accompanied by very little or no growth (Figure 3) and less than 75% probability of survival
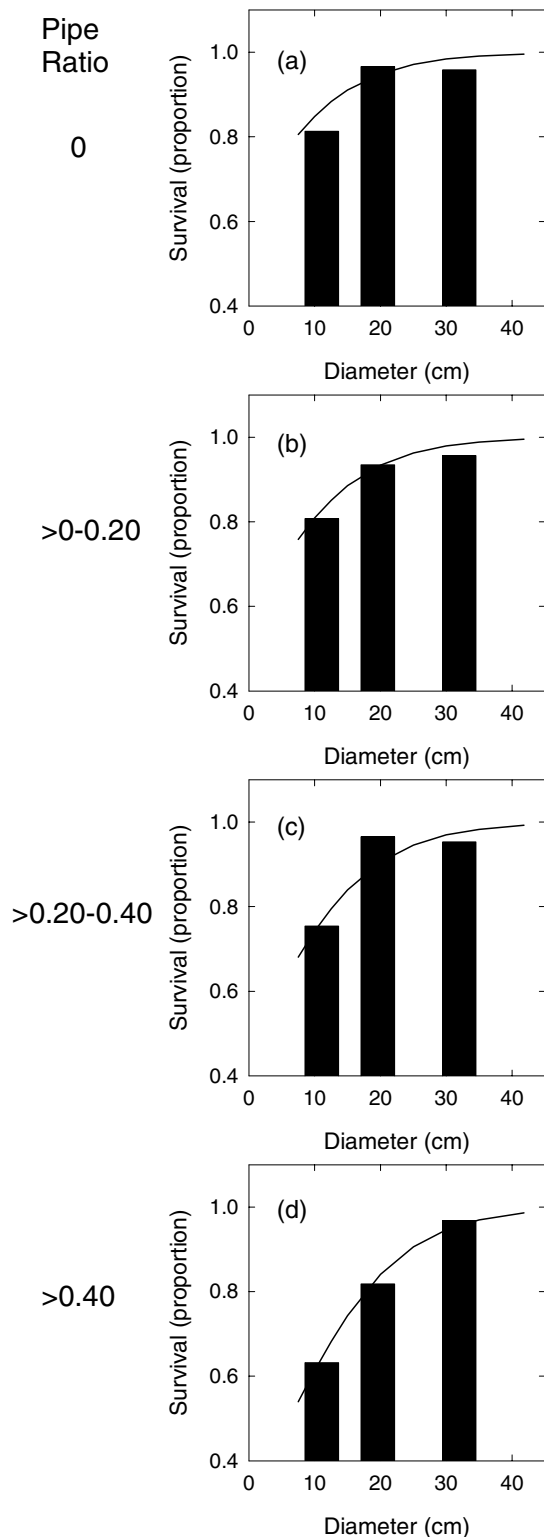
Figure 4. Survival (proportion) of eucalypts in northern Australia savanna woodland for three dbh classes (< 15 cm dbh, 15–25 cm dbh and > 25 cm dbh) and four pipe ratio classes (zero piping, > 0–0.20, > 0.20–0.40 and > 0.40). Only classes containing >10 individual trees are shown. Bars show actual values, and lines show the weighted model averaged proportion of trees that survived.
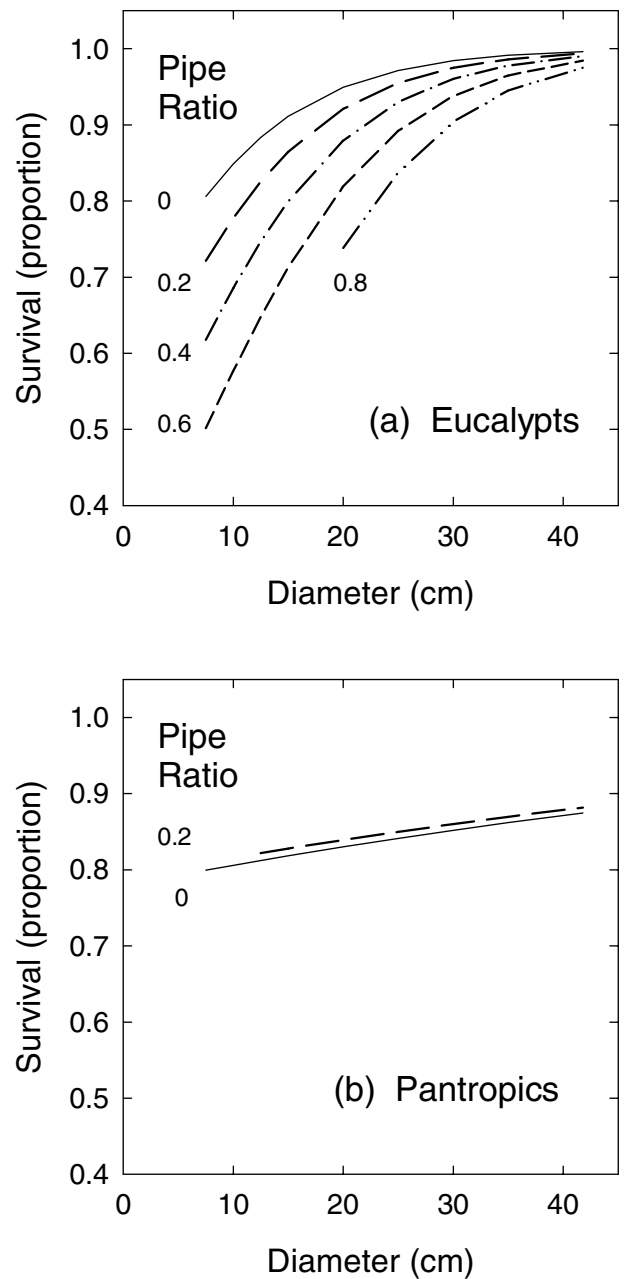
Figure 5. Survival (proportion) of eucalypts (a) and of pantropics (b) in northern Australia savanna woodland: modelled values of survival as a function of tree dbh, for a range of pipe ratios. Few pantropics had a pipe ratio > 0.2, and there was none > 0.4. No eucalypts < 20 cm dbh had a pipe ratio > 0.6.

(Figure 5). When trees are even smaller, say, 10 cm dbh, any piping greater than 60% of the diameter (6 cm), stops growth, and reduces survival to approximately 55%. Once a eucalypt achieves a dbh greater than 30 cm, growth rate continues to increase compared to smaller sizes, but the probability of death becomes almost independent of degree of piping. In fact, the middle size (20–35 cm dbh) individuals of these eucalypts seem to

be the healthiest with regard to a composite of growth, survival, response to fire and flowering (Werner, unpubl. data). In the population dynamics of eucalypts, we would expect higher turnover rates in the smaller size classes of *E. miniata* than of *E. tetrodonta* or *C. porrecta*, because of the higher incidence of piping in small *E. miniata* trees. This possibility has not been calculated or investigated in the field.

In all cases, the smallest trees tolerate only the lowest percentage loss of stem to termites. The cause and effect of this relationship is unknown, i.e. whether termite piping causes reduced tree growth and survival, or a poorly growing tree is more likely to suffer a successful termite infestation. We suggest that in the eucalypts, the termite piping is more likely the cause of the reduced growth and survival since there is no relationship between dbh (age/time) and pipe ratio but both growth and survival decrease proportionally with pipe ratio regardless of size of tree; this is in contrast to the pantropics where termite piping is more likely related to tree poor health or senescence since pipe ratio increases with dbh (age/time) and is high only for the largest trees. It must be noted that our study was done on sites and during a time interval that did not experience fire or severe wind velocities. However, we know that the largest trees in eucalypt populations suffer the highest in high winds (Werner & Shirley unpubl. data) and following late-dry-season fires (Lonsdale & Braithwaite 1991, Stocker 1976, Werner 2005, Williams *et al.* 1999). It is most probable that the degree of piping would interact with fire and wind in toppling or otherwise killing these largest trees.

Termites as releasers of nutrients and the adaptation hypothesis

To the extent that the termites return heartwood materials to circulation, they are decomposers, but to the extent that they also eat sapwood, they are parasites. The dual role is especially true for *Coptotermes acinaciformis* of north Australia, which commonly consumes sapwood. Obviously from this study, the presence of termite piping, even if pipe ratio is small and sapwood remains intact, does not produce growth and survival rates greater than that of trees that do not have termite piping. The degree to which the negative relationships are due to the direct action of termites and/or other commonly associated microbial and fungal decay agents and other wood-feeding insects, or are simply a consequence of poor tree health and vigour, is unknown. Braithwaite (1985), in a broad-scale survey within Kakadu National Park, found the frequency of tree hollows was negatively correlated with total soil phosphorus and total soil nitrogen. It is possible that the trees were less robust on poorer soils and more vulnerable to termite infestation.

According to a hypothesis first proposed by Janzen (1976), the rotting heartwood at the centre of living trees may provide nutrients, especially nitrogen, derived from animal defecation and microbial activity, and suggested that the central rotting could be an adaptive trait, providing advantage to an individual tree. If so, then the higher frequency of piped trees on poorer soils in Kakadu (Braithwaite 1985) might indicate advantage to the piped trees; unfortunately, growth and survival rates are unknown. Certainly, termite cavities in north central Australian trees provide shelter and nest sites for other organisms, including reptiles, birds and mammals (Andersen & Braithwaite 1996, Andersen *et al.* 2005, Braithwaite *et al.* 1988), which in turn bring nutrients to the tree hollows. However, there is no measure of the degree to which any released or added nutrients benefit the tree from which the nutrients originate, nor whether the piped trees grow faster than they would have had they not been piped. On the contrary, from our study, it is very clear that any enhancement from nutrient recycling or nutrient enrichment is outweighed by overall negative growth and survival compared with unpiped trees of the same size growing in the same plots. Hence, we argue, the presence of the tree-piping termites is highly unlikely to confer a relative adaptive advantage.

Birkill (1985), in a field study of termites at Manbullo Station 250 km south of Darwin, Australia, reported a low return of nitrogen to living plants through termite activity, with most released nitrogen lost to predation, nuptial flights, and especially, to heavy rains that do not allow capture by the local vegetation. We suggest, further, that any nutrients released into the soil are likely to be captured by herbaceous understorey, the major competitor of canopy trees (Werner 2005, Werner *et al.* 2006). The herbaceous understorey grows rapidly during the wet season when the leaf area index (LAI) of grasses is 2–3, compared with only 0.95 for trees (O'Grady *et al.* 2000), presumably reflected in corresponding higher nutrient uptakes by grasses. The seasonal rapid growth of the herbaceous understorey vegetation would further compound any deleterious effects of termite piping and/or poor tree health.

It has been suggested that unpiped trees might benefit from termite-piped trees nearby. That may be so, but the effect would be indirect, through a shift in competitive relationships, with an advantage accruing to the unpiped trees. Other mechanism(s) might also operate to give the net effect we have recorded in this study. These might include further negative effects of fungi (e.g. clogging xylem) as well as the greater chance of death due to fire or wind. Even though the mechanism(s) underlying the negative relationship between termite-piping and growth and survival of the host trees is unknown, the net effect on the individual tree is the same – not good.

Termites do have positive effects on the entire woodland system, for example they increase biodiversity through provision of food and shelter for other organisms, and increase the rate of nutrient cycling in an area. That termites create hot-spots of nutrients in the landscape has been demonstrated often, mainly in Africa and Australia (mainly for mounding-building termites; reviewed in Andersen & Braithwaite 1996); however, the overall role of termites in depleting soils of nutrients and carbon (through respiration into the atmosphere) may be large enough to create an overall negative effect on the system (Birkill 1985, Jones 1990, Schaefer & Whitford 1981). As to advantages on longer time scales, e.g. to the persistence of tree populations as a whole, or to the quasi-stable nature of savanna biomes, we believe too little information is available to speculate.

ACKNOWLEDGEMENTS

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