

L. D. Prior · D. M. J. S. Bowman · B. W. Brook

## Growth and survival of two north Australian relictual tree species, *Allosyncarpia ternata* (Myrtaceae) and *Callitris intratropica* (Cupressaceae)

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**Abstract** *Allosyncarpia ternata* (an angiosperm) and *Callitris intratropica* (a gymnosperm) are two fire-sensitive tree species of the Australian monsoonal tropics. Studies using historical aerial photography have revealed recent expansion of *A. ternata* rainforests. There has simultaneously been a widespread collapse of *C. intratropica* populations in northern Australian savannas, presumably because of cessation of traditional Aboriginal landscape burning. To explain the demography behind these contrasting trends, stand structure, survival, and growth of the two species were recorded over a 16-year period at the boundary of a rainforest patch and also in adjacent savanna, in Kakadu National Park. Ages of the largest trees of each species, estimated by using a Bayesian analysis of tree-diameter increments, were approximately 433 years for *A. ternata* and 235 years for *C. intratropica* on the rainforest boundary, and 417 years for *C. intratropica* in the adjacent savanna. Densities of juveniles (seedlings and re-sprouts <0.5 m high) were 325–6,000 times higher for *A. ternata* than for *C. intratropica*. Life-table calculations indicated there was sufficient recruitment of *A. ternata*, but not *C. intratropica*, to overcome observed mortality rates and maintain a stable population. This is almost certainly because *A. ternata* re-sprouts prolifically after fire whereas *C. intratropica* is an obligate seeder. These results highlight the critical need for careful fire management to maintain populations of a characteristic Australian gymnosperm over much of its range.

**Keywords** Survival · Recruitment · Seasonal tropics · Growth rate · Tropical tree

L. D. Prior (✉) · D. M. J. S. Bowman · B. W. Brook  
School for Environmental Research,  
Charles Darwin University,  
Darwin, NT 0909, Australia  
E-mail: lynda.prior@cdu.edu.au  
Tel.: +61-8-89467711  
Fax: +61-8-89467720

### Introduction

Landscape fire is a pervasive feature of the Australian environment. This disturbance seems to be responsible for the overwhelming importance, over most of the continent, of the family Myrtaceae, which has undergone massive phylogenetic radiation to dominate fire-prone environments (Bowman 2000). This family contributes the largest component of woody biomass in much of northern Australia, despite having generally lower photosynthetic rates and growth rates than non-myrtaceous species, which are usually dominant in fire-protected environments, for example rainforests (Prior et al. 2004). A few primitive myrtaceous species, for example *Allosyncarpia ternata*, are rainforest trees, however, survivors from a time when the Australian continent was wetter and less fire-prone than it is today (Ladiges et al. 2003). *Allosyncarpia* is endemic to the Arnhem Land Plateau in Australia's Northern Territory. The mono-specific genus is a primitive member of the eucalyptus group, and closely related to two other relictual rainforest taxa—one that occurs in eastern Indonesia and New Guinea and the other in Queensland, Australia (Ladiges et al. 2003). Increasing aridity in northern Australia during the Oligocene isolated Arnhem Land from the wet tropics of north eastern Queensland, segregating the ancient rainforest biota (Ladiges et al. 2003). The increasing aridity that favoured the evolution of the fire-tolerant eucalypts was associated with the decline of gymnosperms, which are now a minor component of the Australian flora. The notable exception is the ancient Australian endemic conifer genus *Callitris*, which is widespread in dry forests and woodlands through most of the continent (Bowman and Harris 1995). Bowman and Harris (1995) suggested that because *Callitris* includes some xerophytic species, its present fragmentary distribution is unlikely to be because of aridification of the continent but, rather, is related to the effect of fire. In the context of their

contrasting biogeographic histories, the north Australian species *A. ternata* and *Callitris intratropica* are of fundamental interest because they are both fire-sensitive relictual species that occur within a wider landscape subject to very frequent fires.

*Allosyncarpia ternata* is a large spreading tree, 15–30 m high, with a broad, dense evergreen crown, which frequently forms closed-canopy stands, which are termed “rainforest” in Australia. *A. ternata* is endemic to the Arnhem Land Plateau in the Northern Territory and, despite its restricted geographic distribution, is found in a variety of topographic settings with contrasting micro-climates, from ravines to sandstone cliffs and hilltops (Fordyce et al. 1995). *Allosyncarpia* forests have a fragmented distribution and are often found in broken, rocky country where fires are less frequent and intense, but they are occasionally found in areas with no topographic fire protection (Bowman 1991). Like most rainforest species in northern Australia, *A. ternata* is relatively fire-sensitive, grows mainly in areas where fire is infrequent (Russell-Smith 1991; Bowman 1991), and suffers elevated mortality with recurrent fires (Bowman 2000). Although fire kills seedlings and may damage and eventually kill older trees, most trees re-sprout prolifically after fire (Bowman 1991, 1994; Fordyce et al. 1997, 2000).

The conifer *C. intratropica* (Cupressaceae) grows 15–18 m high and is found across much of tropical Australia. It is fire-sensitive and an obligate seeder. Whereas mature trees have thick bark and can survive mild but not intense fires, seedlings cannot survive even the coolest fires (Bowman and Panton 1993). Populations can thus survive mild fires occurring every 2–8 years, but not more frequent or more intense fires (Price and Bowman 1994). Cessation of Aboriginal land management has led to a decline of *C. intratropica* in much of its former range, and it currently persists only in rainforest margins and savanna micro-sites such as in rocky crevasses or among boulders or drainage lines that protect seedlings from fire (Bowman et al. 2001). Both *C. intratropica* and *A. ternata* have been used as bio-indicators of altered fire regimes (Yates and Russell-Smith 2003; Russell-Smith et al. 1998; Sharp and Bowman 2004), and changes in their distribution, density, and stand structure are consequently of substantial interest to land managers responsible for maintaining an intact ecosystem.

There is concern that both *C. intratropica* and *A. ternata* populations are under threat from repeated wildfires in the surrounding wooded savanna (Bowman 1994; Bowman et al. 2001). A preliminary study by Bowman (1994) showed 36% of *A. ternata* stems died over a 4-year period in which two wildfires occurred, and matrix-model-based sensitivity analyses derived from estimates of annual fecundity, mortality, and growth rates of *C. intratropica* in the surrounding savanna predicted the stand would become extinct if such a regime was sustained for 325 years (Bowman et al. 2001). A more recent study using historical and recent aerial

photography has, however, revealed overall expansion of *Allosyncarpia* forests in Kakadu National Park of 20% over the last 40 years (D.M.J.S. Bowman and J.K. Dingle, submitted for publication). Demographic analyses are required to explain the apparent contradiction that a fire regime that has caused the collapse of *C. intratropica* populations has simultaneously enabled the expansion of fire-sensitive *Allosyncarpia* forests (D.M.J.S. Bowman and J.K. Dingle, submitted for publication).

Our study measured the growth, mortality, recruitment, and changes in stand structure of *A. ternata* and *C. intratropica* trees in a rainforest patch in Kakadu National Park over a 16-year period. The rainforest, known locally as Round Jungle, is dominated by *A. ternata*, but many other rainforest species also occur within its core, and *C. intratropica* is also found in the rainforest and especially on the boundary. Round Jungle receives no topographic fire protection, and Bowman (1991) proposed that the enhanced water supply arising from deeper soils and hence a larger soil volume enables closed-canopy *Allosyncarpia* forest to grow here. Analysis of aerial photography showed the size of Round Jungle has been stable, fluctuating by only 5% over four decades from 131 ha in 1964 to 138 ha in 2004 (D.M.J.S. Bowman and J.K. Dingle, submitted for publication). The earlier demographic work on *A. ternata* and *C. intratropica* at Round Jungle was based on measurements made over a few years only (Bowman 1991, 1994; Bowman et al. 2001) whereas the current study spanned 16 years to determine whether the populations of both species are stable.

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## Methods

### Site description

The study area was a rainforest patch known as Round Jungle (13°17'S, 132°38'E), in Kakadu National Park in the seasonal tropics of northern Australia (Fig. 1). Mean annual rainfall for the nearest town, Jabiru, is 1,485 mm, of which 98% falls in the wet season months between October and April (Bureau of Meteorology 2006, [http://www.bom.gov.au/climate/averages/tables/cw\\_014198.shtml](http://www.bom.gov.au/climate/averages/tables/cw_014198.shtml)). Temperatures are high throughout the year, and the annual mean for Jabiru is 28.8°C. Round Jungle is approximately 1.5 km in diameter and is located on well-drained soils deeper than those of the surrounding savanna (Bowman 1991). It is made up of a mosaic of intergrading stands, some of which are co-dominated by a variety of monsoon forest species and have dense, closed-shrub understoreys (Bowman 1991). Others are mono-specific stands of *A. ternata*, with open understoreys. Near the rainforest boundary, many stands are co-dominated by savanna tree species, for example *Eucalyptus tetradonta*, with grassy understoreys. *C. intratropica* trees are found both inside the

rainforest, and in the surrounding savanna. The forest boundary is abrupt, and easily distinguished from the surrounding savanna on aerial photographs (Fig. 1).

#### Remote sensing of patch size and fire activity

Aerial photography from each of the years 1964, 1984, 1991, and 2004 was viewed at a scale of 1:5,000 and used to map the boundary of Round Jungle. The 1991 photography was ortho-rectified and photography from the other years was geo-rectified to the 1991 photos. A GPS was used to map the perimeter and ground-truth the aerial photographic analyses, as described in D.M.J.S. Bowman and J.K. Dingle (submitted for publication). A fire index based on the number of fires over the period 1984–2004 apparent on Landsat satellite imagery was derived at 100 m resolution (1984–1994) or 25 m resolution (1994–2004) for the Round Jungle area (Edwards et al. 2003).

#### Abundance and size class distributions

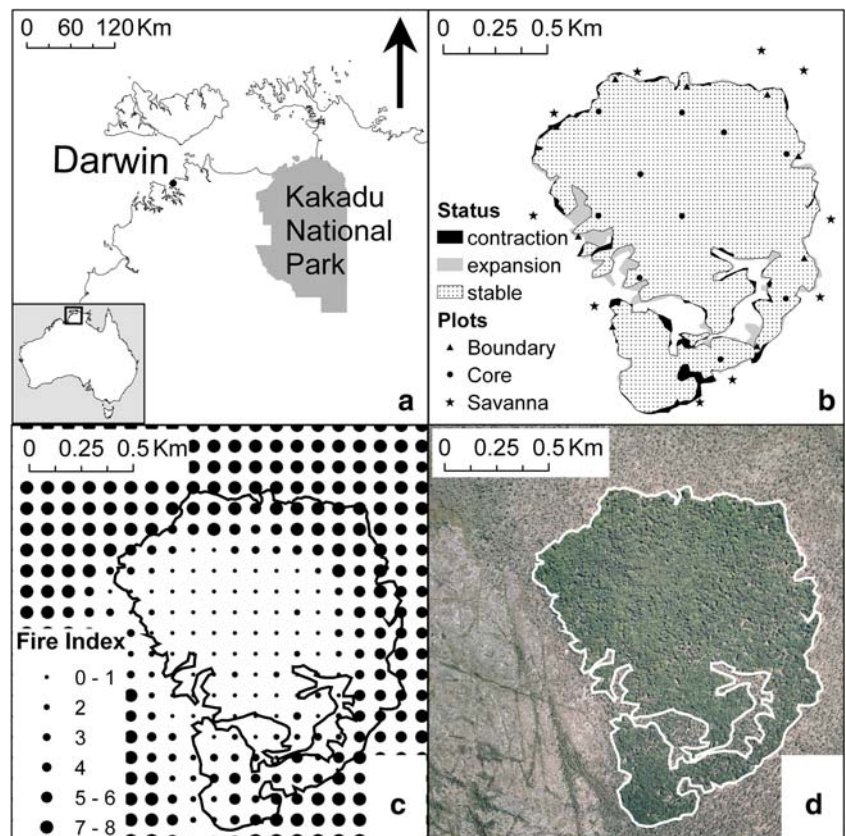
Ten plots, each 50 m×20 m, were located in each of the following habitat types (i.e. 1 hectare total per habitat type):

- 1 on the boundary between the rainforest patch and savanna (these were a sub-plot or all of the ten permanent plots used in a previous study, in which all *A. ternata* and *C. intratropica* trees within these marked plots were tagged in 1989) (Bowman 1994)
- 2 inside the core of the rainforest patch
- 3 in the savanna, 30–260 m (average 100 m) distant from the rainforest boundary.

Plots in the rainforest core were randomly pre-selected and located with a GPS; approximate locations for those on the boundary and in surrounding savanna were identified to provide representative coverage, and plots were randomly located within these areas. In August 2005, species and diameter at breast height (DBH) were recorded for all trees > 2 m high in these 30 plots. Tree density and stand basal area were calculated for each species within each plot. Density of seedlings < 0.2 m high was estimated for a 2-m-wide strip along 120 m of the perimeter of each plot, and density of seedlings 0.2–2 m high was recorded for the entire plot. Density of *C. intratropica* juveniles (saplings plus seedlings) and trees in the savanna was compared with that in a 250 m×15 m transect near Round Jungle in 1998 (data recalculated from Bowman et al. 2001).

Frequency distributions of six size classes were calculated for *A. ternata* and *C. intratropica* in the boundary and core plots. These were compared with the

**Fig. 1** **a** Location of Round Jungle, in Kakadu National Park, Northern Territory, Australia. **b** Map of Round Jungle, showing areas where rainforest is stable (dotted), contracting (black) or expanding (grey). Locations of rainforest core (circles), boundary (triangles), and savanna (stars) plots are also shown. **c** Fire activity index derived from Landsat satellite imagery in the preceding 10 years is indicated by the size of the circles. Fire activity was much lower within the rainforest than on the boundary, or in the surrounding savanna. **d** Aerial photograph of Round Jungle, which can be clearly discerned from the surrounding savanna



corresponding distributions in 1989, when 103 plots of dimensions 10 m×20 m were measured (recalculated data from Bowman 1991).

### Tree growth and survival of tagged stems

In August 1989, ten plots, ranging in size from 0.1 to 0.62 ha and totalling 1.68 ha, were marked on the boundary between the rainforest patch and the surrounding savanna. Within these plots, a total of 361 *A. ternata* stems and 125 *C. intratropica* stems > 1 cm DBH were marked with numbered aluminium tags, and the DBH of each was recorded. In July 1993, an additional 223 *C. intratropica* stems in savanna adjacent to the rainforest were tagged and measured. At the same time, plots were revisited and previously tagged trees were recorded as dead, alive, or missing (Bowman 1994). In August 2005, the plots were again searched to record dead and missing stems (“Statistical analysis” section), and to record DBH of the survivors.

The stability of the stand structures was explored for *A. ternata* and *C. intratropica*. Trees were assigned to three size classes: ≤ 5 cm DBH (“small” trees), 5–10 cm DBH (“medium” trees) and > 20 cm DBH (“large” trees). Recruitment of both species was estimated from the number of untagged trees that had become established in the permanent boundary plots—most were in the “small” class but some were in the “medium” size class. On the basis of the recruitment into the “small” and “medium” size classes, and the proportion of trees moving from one size class to another, or that died, we used standard life-table analysis (Carey 1993) to calculate the proportion of trees required in the “small” size class in order to maintain a stable equilibrium population size (i.e. when instantaneous rate of increase ( $r$ ) calculated from recruitment and mortality equalled zero). This was compared with the observed proportion of trees in the “small” size class in 1989 and 2005.

### Statistical analysis

Growth was calculated for tagged trees as the increase in overbark DBH. Some of the negative growth values almost certainly resulted from measurement error. We chose to include these in the analyses, however, because the error was in both directions and thus they did not bias the results (but did increase uncertainty in the predictions). The alternative was to arbitrarily delete certain values, but there was no sound logical or theoretical basis on which to decide which should be culled or retained. A Bayesian linear regression analysis implemented in the OpenBUGS v2.1 implementation of WinBUGS (Spiegelhalter et al. 2005) was used to investigate the relationship between DBH growth increment and initial tree size for any of the three groups of trees (*A. ternata* on the boundary, *C. intratropica* on the boundary or *C. intratropica* in the adjacent savanna).

No prior information was available to characterise the relationship between growth and tree size for *A. ternata* and for this species a vague uniform prior was used for the intercept ( $a$ ), slope ( $b$ ) and a vague gamma distribution for the precision ( $\tau$ ). For *C. intratropica*, however, Prior et al. (2004) studied the growth of 12 individuals of this species at the Berry Springs Nature Park, Northern Territory, measured between May 2000 and May 2002. These trees were growing on a sand ridge in an area similar climatically to Round Jungle. From this work we were able to estimate a normal prior estimate of  $a$  (mean = 0.241, standard error = 0.067) and  $b$  (−0.011, 0.0057). Posterior distributions were generated by WinBUGS using 100,000 Markov chain Monte Carlo samples after discarding an initial 10,000 samples as a “burn in” (required to ensure an appropriate posterior probability distribution is being sampled by the Markov chain, because the initial estimates of the model parameters may not lie within the posterior). Parameter estimates for the regressions were based on the mean of the posterior Bayesian estimates and 95% credibility intervals were estimated from the 2.5th and 97.5th percentiles of the distribution.

Survival was calculated from the proportion of stems tagged in 1989 or 1993 that were subsequently recorded as alive, dead, or missing in 2005. The large number of missing stems was dealt with in two ways:

- 1 they were excluded from the analysis, which provided an upper bound for survival; or
- 2 they were treated as dead, which provided the lower bound for survival.

Annualised survival ( $S_A$ ) was calculated as

$$S_A = \left[ \frac{NA_{2005}}{NT} \right]^{(1/Y)} \quad (1)$$

where  $NA_{2005}$  = the number of stems alive in 2005,  $NT$  = the number of stems initially tagged, and  $Y$  = the number of years between monitoring. Annualised survival is equal to (1 − annualised mortality), and was preferred in this instance because it provides a more intuitive expression of long-term persistence of individual trees (proportion surviving any defined number of years).

Our final step was to use the results of the Bayesian regression of annual DBH growth increment versus tree size to estimate the probability distribution of number of years required for trees to reach a “large” girth (set arbitrarily at 100 cm for *Allosyncarpia* and 40 cm for *Callitris*). This was achieved using an individual-based model written in *R* v2.2 (<http://www.r-project.org>) to project stochastically the fate of 10,000 simulated trees and record the time it took for each modelled tree to achieve the threshold DBH. The percentiles of the resultant frequency distribution were used to define the 95% confidence bounds. This method is superior to a

projection based on the mean of the regression because it accounts fully for the variable and autocorrelated growth of individual trees over their lifetime.

## Results

### Remote sensing of boundaries and fire

Analysis of aerial photography showed that changes to the boundary of Round Jungle during the period 1964–2004 have been minor, with very small areas of both expansion and contraction (Fig. 1). Using Landsat satellite imagery, we detected very little evidence of fire in the core of the rainforest, but there was evidence of frequent fire in the savanna surrounding Round Jungle: much of this savanna was burnt seven or more times in the 10 years studied (Fig. 1).

### Density and basal area of abundant species

A total of 54 species was recorded in the core, boundary, and savanna plots; the 22 species present in at least three plots are listed in Table 1. *A. ternata* was the most abundant species within the rainforest and on the boundary, and *C. intratropica* was the second most abundant in both environments (Table 1). *E. tetradonta* was the most abundant species in the savanna. Stem

**Table 1** Density in the rainforest core, boundary, and savanna plots of the 22 species occurring in at least three plots (50 m×20 m), listed in order of decreasing density in the rainforest

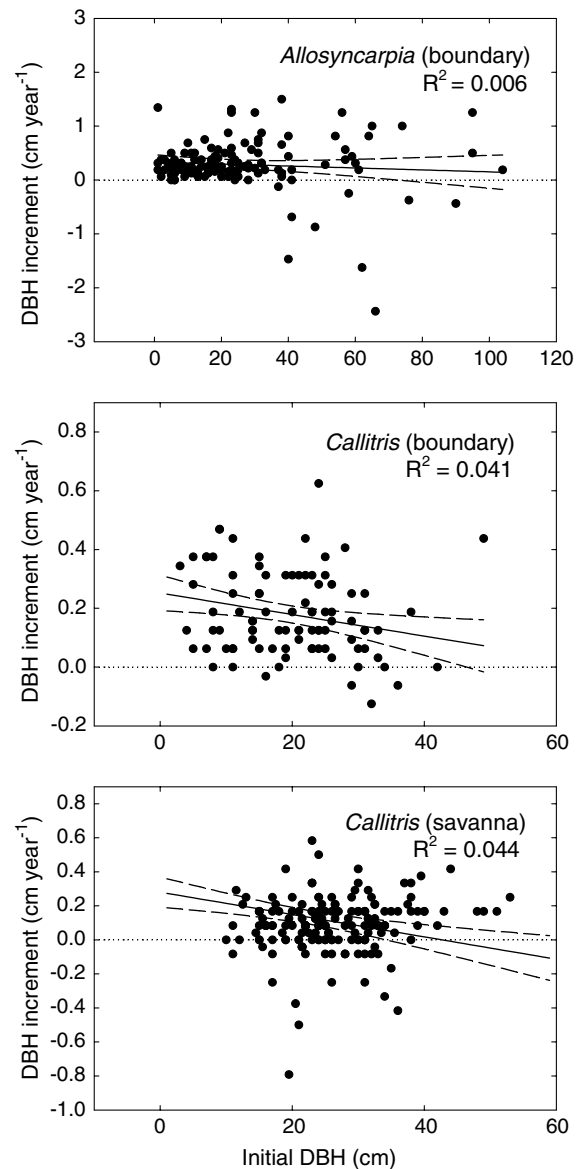
Species	Density (stems per ha)		
	Core	Boundary	Savanna
<i>Allosyncarpia ternata</i>	560	257	–
<i>Callitris intratropica</i>	58	107	6
<i>Pouteria sericea</i>	58	9	–
<i>Carpentaria acuminata</i>	55	–	–
<i>Denhamia obscura</i>	21	2	1
<i>Drypetes deplanchei</i>	16	1	–
<i>Notelea microcarpa</i>	10	2	–
<i>Eucalyptus tetradonta</i>	7	95	122
<i>Canarium australianum</i>	7	1	–
<i>Terminalia carpentariae</i>	4	6	3
<i>Erythrophleum chlorostachys</i>	4	4	–
<i>Owenia vernicosa</i>	3	4	7
<i>Acacia lamprocarpa</i>	3	1	3
<i>Petalostigma pubescens</i>	2	13	7
<i>Buchanania obovata</i>	2	11	27
<i>Grevillea heliosperma</i>	1	11	3
<i>Acacia torulosa</i>	1	8	8
<i>Pogonolobus reticulatum</i>	1	7	–
<i>Persoonia falcata</i>	1	3	5
<i>Eucalyptus miniata</i>	–	13	71
<i>Grevillea pteridifolia</i>	–	13	14
<i>Acacia platycarpa</i>	–	1	7
Density—all species	869 (141)	597 (94)	360 (46)
Basal area—all species (m <sup>2</sup> ha <sup>-1</sup> )	22.9 (2.2)	14.6 (2.1)	5.4 (0.8)

Total stem density and basal area of all species, with standard errors in brackets, are also shown

density and total basal area were highest in the rainforest and lowest in the savanna (Table 1).

### Growth and survival of tagged trees

Tree growth rate as measured by DBH increment was negatively (but not strongly) affected by tree size for all three populations of tagged trees (Fig. 2). In none of the three populations did the 95% credibility intervals of the slopes overlap with zero, showing that the decline in



**Fig. 2** Increment in DBH versus tree size for the three groups of tagged trees: *Allosyncarpia ternata* on the boundary and *Callitris intratropica* on the boundary and in the adjacent savanna. In each case the *solid line* represents the mean prediction of the Bayesian regression and the *dotted lines* are the 95% credibility intervals of the regression line. Trees on the boundary were measured over a 16-year interval and those in the savanna over a 12-year interval

growth increment with size was a real effect. We note that the negative relationship between DBH increment and size illustrated in Fig. 2 is not valid for cross-sectional area increment; a Bayesian regression of annualised growth in cross-sectional area versus tree size yielded a positive relationship for all three populations (regression data not shown). Tree biomass theoretically scales to  $(\text{DBH})^{8/3}$  (Enquist et al. 1998), so the relationship between biomass increment and tree size would also be positive. The stochastic individual-based model suggests that a large *A. ternata* tree of 100 cm DBH would require an average of 433 years (413–455; 95% credibility interval), plus the time needed to reach 1.5 m in height, to attain this size. Similarly, the larger-sized individuals of *C. intratropica* in the boundary plots and the savanna had DBHs exceeding 40 cm, corresponding to ages of 235 (230–239; 95% CI) and 417 (389–456; 95% CI) years, respectively.

Annual survival rates of large trees were high, approximately 0.98–0.99 for both species (Table 2). Survival patterns were different for the two species: survival rates were generally higher for *C. intratropica* than for *A. ternata*, especially for small trees (Fig. 3; Table 2). Whereas survival rate of small *C. intratropica* trees was only slightly less than that of medium and large trees, it was much lower for small than for medium or large *A. ternata* trees (Fig. 3; Table 2). One hundred and two trees, representing 15% of all tagged trees, could not be relocated. These were mostly small *A. ternata* trees. Whether missing trees were excluded from the analysis or treated as dead did not affect the relative rankings of the species and size classes (see below).

#### Size class distributions, recruitment, and population stability

The size class distributions of both species in the permanent boundary plots and in the core of the rainforest, in 1989 and in 2005, are shown in Fig. 4. Most of the *A. ternata* trees were in the “small” (1–5 cm DBH) size class, but for *C. intratropica*, “medium” trees (6–20 cm DBH) predominated. In the boundary plots, there were many more “small”, but fewer “large”, *A. ternata* trees in 2005 than in 1989. There were also more “small” and “large” *C. intratropica* trees in the boundary plots in 2005 than in 1989. In contrast, stand structure of *A. ternata* in the core plots was similar between years, but there were fewer “small” and “medium”, and more “large” *C. intratropica* trees in 2005. There were only six *C. intratropica* trees and no juveniles (< 2 m high) found in the 1 ha of savanna plots in 2005, compared with nine trees and 38 juveniles found in 0.38 ha in 1998; these numbers are too small for meaningful size class comparisons between the years, however.

*Allosyncarpia ternata* seedling densities were extremely high, especially in the rainforest core ( $\sim 47,000 \text{ ha}^{-1}$ ; Table 3). *C. intratropica* seedling densities were lower by 3–4 orders of magnitude. Sapling (trees 0.2–2 m tall)

densities were also much higher for *A. ternata* than for *C. intratropica* (Table 3).

In the permanent boundary plots there was recruitment of 189 “small” and 53 “medium” *A. ternata* trees  $\text{ha}^{-1}$ , and 3 “small” and 1 “medium” *C. intratropica* trees  $\text{ha}^{-1}$  at the end of a 16-year period (plus an unknown number of recruits that emerged and subsequently died unobserved during the period between visits). Life-table calculations showed that to achieve population stability ( $r=0$ ) in the boundary plots, 57.5% *A. ternata* and 30.8% *C. intratropica* trees must be in the small size class—a lower proportion than this does not provide sufficient recruitment to overcome the mortality rates whilst a higher value would impel population growth. The observed figures were higher than this for *A. ternata* (67% in 1989 and 81% in 2005) but considerably lower for *C. intratropica* (1.7% in 1989 and 5.6% in 2005).

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## Discussion

The demographic analyses show there has been substantial recruitment into the “small” size class of *Allosyncarpia* in both the rainforest core and the boundary over the last 16 years, which is more than is required to maintain the population. This is consistent with the observed expansion of *Allosyncarpia* forest in Kakadu National Park (D.M.J.S. Bowman and J.K. Dingle, submitted for publication). There are two sources of recruits:

- the very dense seedling populations that arise from episodic seeding, and can persist in a suppressed state for many years in the absence of fire, and
- the prolific re-sprouts that occur after fire (Fordyce et al. 2000).

Seedlings are probably the most important source in the rainforest core, which is seldom burnt, but the re-sprouts are likely to predominate on the boundary, which is subject to more frequent fires (Table 3). Very dense re-sprouting was observed around fire-killed or -damaged large *A. ternata* trees on the boundary. This ability of *A. ternata* to re-sprout after fire is critical in maintaining and perhaps even increasing the area of *Allosyncarpia* forest in a competitive but fire-prone environment. Nonetheless, there was substantial mortality of all size classes, and some evidence of a decline in the numbers of large *A. ternata* trees on the boundary (Fig. 4). It is, therefore, likely that a long-term change in stand structure is occurring on the dynamic boundaries of these forests, with more small trees and fewer large trees making up the population.

The long-term outlook for *C. intratropica* in this area is, by contrast, bleak, despite high survival rates of adult trees. This is because the observed rate of recruitment into the “small” size class in the boundary plots was very

**Table 2** Survival rate of tagged trees over a 16-year period (*A. ternata* and *C. intratropica*—boundary) and a 12-year period for *C. intratropica*—savanna

	Size class (cm DBH)	Annual survival rate	
		Lower bound	Upper bound
<i>A. ternata</i> —boundary	≤ 5	0.830	0.855
	5–20	0.966	0.979
	> 20	0.977	0.982
<i>C. intratropica</i> —boundary	≤ 5	0.925	0.934
	5–20	0.988	0.989
	> 20	0.980	0.983
<i>C. intratropica</i> —savanna	≤ 5	0.954	0.982
	5–20	0.983	0.988
	> 20	0.989	0.994

The lower bound for survival rate was determined by assuming all missing trees were dead, and the upper bound by excluding all missing trees from the analysis. Small trees are those with diameter at breast height (DBH) ≤ 5 cm, medium trees are those with DBH between 5 and 20 cm, and large trees are those with DBH > 20 cm

low and the proportion of “small” trees was well below that required to maintain a stable population. Consistent with this finding, a paucity of seedlings was detected in any of the savanna, boundary, or rainforest core. *C. intratropica* is a long-lived, obligate seeder that does not have a seedbank (Stocker 1966) and requires a fire-free interval of at least 2 years for any seedlings to grow to a size that can survive the mildest fires (Bowman and Panton 1993). This requirement, combined with the long life span and low annual mortality rates of large *C. intratropica* trees, means that declines in density of these trees may be slow but insidious, and difficult to reverse without active fire management in the areas within which they occur. The apparent increase in density of *C. intratropica* in the small (1–10 cm DBH) and large (> 30 cm DBH) size classes (Fig. 4) on the relatively fire-protected rainforest boundary highlights the sensitivity of this species to slight differences in fire regimes.

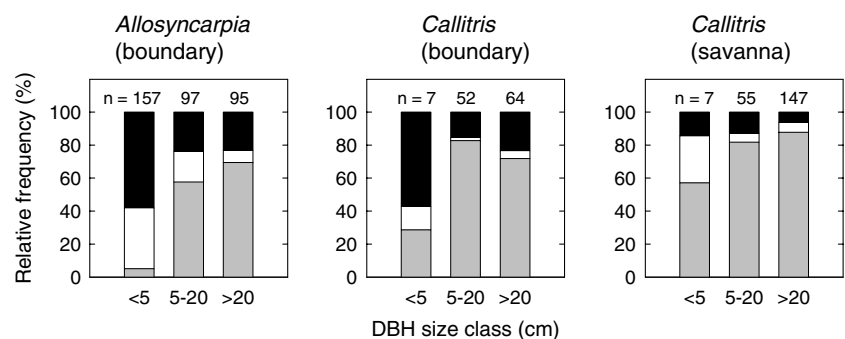
Large *A. ternata* trees are invariably hollowed out by termites (Insecta: Isoptera, various genera), so it is not possible to estimate their ages by dendrochronology. The growth measurements reported here are the only ones of which we are aware for *A. ternata*, and, for the first time, they enabled us to estimate the age of some of

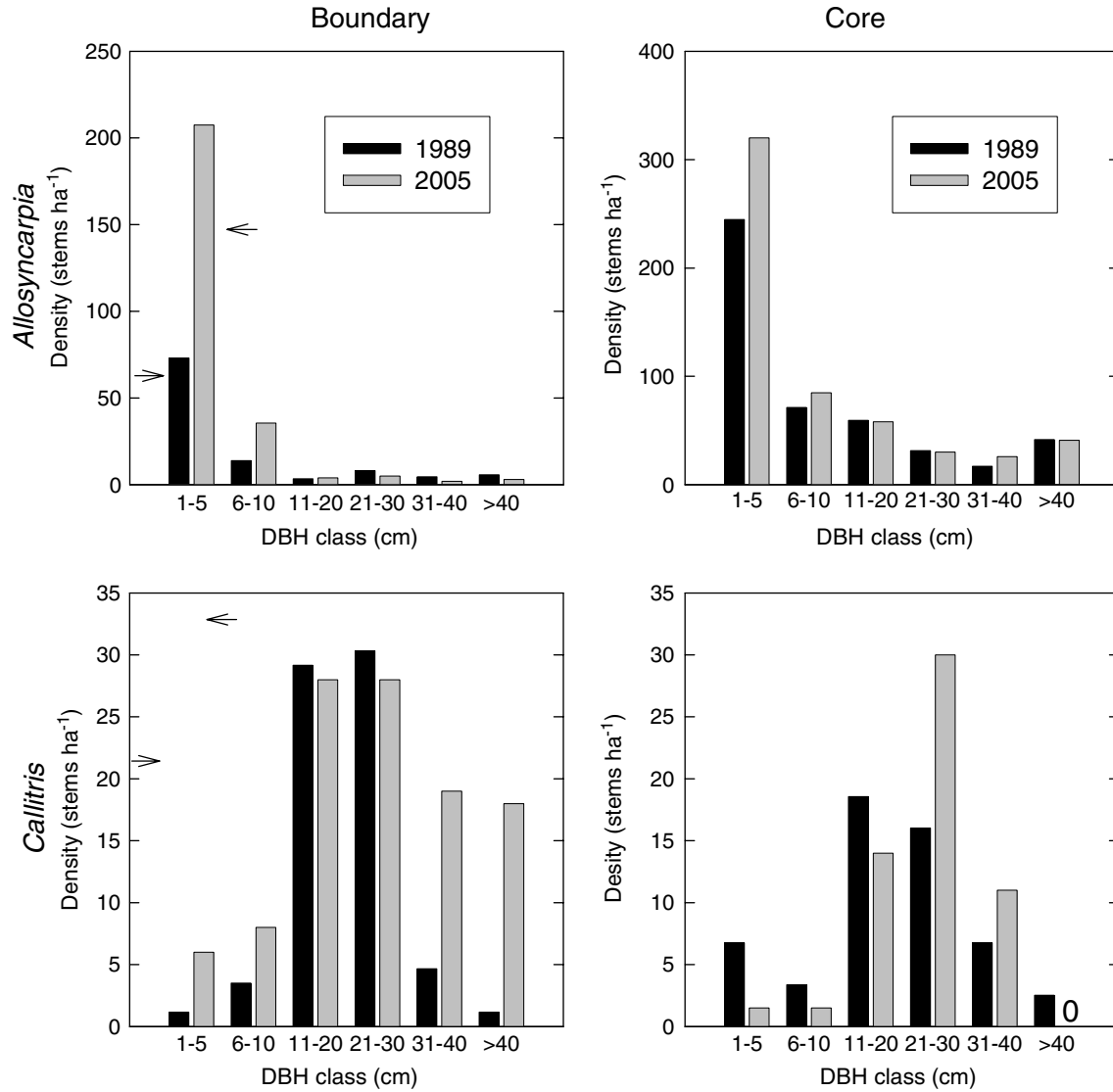
the largest trees in each habitat type. Interestingly the mean posterior estimates of the regression for *C. intratropica* implies a decline in DBH beyond a size of 41 cm, yet the largest tree observed had reached 59 cm. This paradox suggests the current fire regime under which the savanna *C. intratropica* have grown over the last 12 years is less forgiving than that in which the largest individuals must have grown during their earlier life (i.e. before European fire management).

*Allosyncarpia* forests are expanding throughout their limited range on the western edge of the Arnhem Land Plateau whereas *C. intratropica* populations are declining over large areas of northern Australia. This difference is best explained by considering their comparative life-histories. Despite being relatively fire-sensitive, *A. ternata* can re-sprout after fire. *C. intratropica*, in contrast, cannot re-sprout after fire and requires several fire-free years for seedlings to re-establish. These demographic differences have been of critical importance in determining population trends after the breakdown of traditional burning practices by the indigenous people of the region (Bowman et al. 2001). Furthermore, higher atmospheric CO<sub>2</sub> levels caused by industrially driven global climate change may also have significantly contributed to the expansion of *A. ternata* populations (D.M.J.S. Bowman and J.K. Dingle, submitted for publication). Higher CO<sub>2</sub> may have changed the demographic effects of fire disturbance by increasing growth and assimilation rates and thereby altered the competitive balance between different tree species of these rainforests and surrounds. Faster-growing seedlings have a greater likelihood of recruitment by escaping the “fire trap” and higher assimilation enables seedlings to accumulate sufficient below-ground carbohydrate stores to re-sprout after destruction of above-ground biomass.

In tropical savannas, where trees and grasses coexist, potential maximum tree cover is determined by moisture availability, but disturbances such as fire and anthropogenic activity keep tree cover below that maximum (Bond et al. 2005; Sankaran et al. 2005). The Australian seasonal tropics, unlike those of other continents, contain sparse human populations, and natural vegetation is largely intact—human influences on the biota have been largely restricted to the use of fire, low-intensity cattle-grazing in some regions, and

**Fig. 3** Observations in 2005 of fate of trees tagged in 1989 (boundary plots) and 1993 (savanna plots). Grey indicates trees were still alive, white is missing and black is confirmed dead. Annualised survival rates based on these data are shown in Table 2





**Fig. 4** Size class distributions of *Allosyncarpia ternata* and *Callitris intratropica* trees at the boundary, and in the rainforest core, in 1989 (black bars) and 2005 (grey bars). The areas sampled were different in the two years. The arrows in the boundary plots

indicate the number of “small” trees required for population stability based on life-table analysis. These are calculated as a percentage of total tree numbers, so as absolute densities they differ between years

possibly global atmospheric change. Northern Australia therefore offers the rare opportunity to study changes in vegetation over large areas not subject to

timber harvesting or land clearing for agriculture, but experiencing major changes in fire regimes because of the breakdown of traditional Aboriginal burning practices and global climate change. Here, our demographic measurements have documented the shifts in population structure that underlie the contrasting landscape-scale dynamics of *A. ternata* and *C. intratropica*. It seems that Aboriginal fire management, most probably fortuitously, had caused populations of these relict trees to exist in a finely balanced state—the cessation of this management regime is driving the demographic changes we have documented. Thus our results also emphasise the need for careful fire management to maintain populations of the important and characteristic Australian gymnosperm *C. intratropica* over much of its range.

**Table 3** Mean seedling (< 0.2 m high) and sapling (0.2–2.0 m high) densities in the boundary and rainforest core plots

	Density (ha <sup>-1</sup> )			
	Rainforest core		Boundary	
	Seedling	Sapling	Seedling	Sapling
<i>A. ternata</i>	47,146 (6,624)	549 (116)	13,186 (4,874)	981 (259)
<i>C. intratropica</i>	4.2 (4.2)	4.0 (2.2)	37.5 (25.2)	6 (6)

Standard errors of the means are shown in parentheses

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