

Impacts of changed fire regimes on tropical riparian vegetation invaded by an exotic vine

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Abstract Riparian habitats are highly important ecosystems for tropical biodiversity, and highly threatened ecosystems through changing disturbance regimes and weed invasion. An experimental study was conducted to assess the ecosystem impacts of fire regimes introduced for the removal of the exotic woody vine, *Cryptostegia grandiflora*, in tropical north-eastern Australian woodlands. Experimental sites in subcatchments of the Burdekin River, northern Queensland, Australia, were subjected to combinations of early wet-season and dry-season fires, and single and repeated fires, with an unburnt control. Woody vegetation was sampled using permanent quadrats to record and monitor plants species, number and size-class. Sampling was conducted pre-fire in 1999 and post-fire in 2002. All fire regimes were effective in reducing the number and biomass of *C. grandiflora* shrubs and vines. Few woodland or riparian species were found to be fire-sensitive and community composition did not change markedly under any fire regime. The more intense dry-season fires impacted the structure of non-target vegetation, with large reductions in the number of sapling trees (<5 cm d.b.h.) and reductions in the largest tree size-class and total tree basal area. Unexpectedly, medium-sized canopy trees (10–30 cm d.b.h.) appear to have been significantly benefited by fires, with decreases in number of trees of this size-class in the absence of fire. Although the presence of *C. grandiflora* as a vine in riparian forest canopies changed the nature and intensity of crown combustion patterns, this did not lead to the initiation of a self-perpetuating weed–fire cycle, as invaders were unable to take advantage of gaps caused by fire. Low intensity, early wet-season burning, or early dry-season burning, is recommended for control of *C. grandiflora* in order to minimize the fire intensity and risk of the loss of large habitat trees in riparian habitats.

Key words: *Cryptostegia grandiflora*, fire response, plant invader, riparian plant community, tropical savanna.

INTRODUCTION

Riparian plant communities are biologically diverse, but are also among the most threatened ecosystems across the globe. Threats to riparian communities are partly due to high rates of disturbance, and also high plant available resources here (Gregory *et al.* 1991; Stohlgren *et al.* 1998; Brown & Peet 2003). Riparian communities are subject to natural disturbance because of water movement and flooding, have high deposition of nutrients, and are foci for agricultural/pastoral disturbances because of high productivity and access to water. Presumably because of high rates of disturbance and elevated resources, riparian habitats are major foci for plant invasions (Pysek & Prach 1993; Lonsdale 1999). A number of experimental studies have linked disturbance and resource availability directly to habitat invasibility (Burke & Grime 1996;

Davis *et al.* 2000; Thompson *et al.* 2001). Plant invasion globally has been found to be higher in species rich and resource rich environments, including riparian habitats (Pysek & Prach 1993; Stohlgren *et al.* 1998; Lonsdale 1999).

So what happens if disturbance is introduced into riparian habitats specifically for the control/removal of plant invaders? Does further disturbance in an already disturbed environment lead to a benefit to resident native biodiversity, or simply to reinvasion by target or additional invaders? It is a moot point whether the effects of disturbance associated with weed control activities are indeed beneficial to the plant communities we are trying to protect.

Cryptostegia grandiflora R.Br. is one plant invader for which control associated disturbance may be detrimental to riparian vegetation. *Cryptostegia grandiflora* is a prominent invader of riparian habitats throughout tropical north-eastern Australia (Tomley 1998) and continues to invade in other northern regions. *Cryptostegia grandiflora* is apparently associated with far-reaching consequences for biodiversity in these habitats (McFadyen *et al.* 1991; Grice 2006). *Cryptostegia grandiflora* causes significant and broad-scale

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change in vegetation structure from savanna woodland/open forest to exotic vine thicket, and is believed to smother and kill established trees (Tomley 1998). Important tropical vegetation types, including gallery forests, rainforest and riparian forest, are threatened by *C. grandiflora* invasion (McFadyen *et al.* 1991; Fensham 1996). A number of vertebrate and invertebrate taxa actively avoid *C. grandiflora* plants and litter (Valentine 2006; Valentine *et al.* 2007), leading to the hypothesis that dominance by this species in large areas may have negative impacts on the fauna of tropical riparian zones. Riparian communities make a disproportionate contribution to overall biodiversity in northern Australian savannas (Douglas *et al.* 2003). This is despite riparian habitats covering less than 1% of the area of these landscapes. As such riparian habitats are important foci for conservation and biodiversity values in Australian tropical savannas, and threats to these environments should be minimized if possible.

Control techniques available for *C. grandiflora* involve disturbance. Mechanical techniques potentially destabilize riverbanks, and chemical and biological control methods selectively remove invader biomass (Vitelli 1995; Mackey *et al.* 1996; Tomley 1998), possibly resulting in competitive release of plant available resources. Prescribed burning for the control of *C. grandiflora* (Grice & Brown 1996; Grice 1997; Bebawi *et al.* 2000) is also likely to be associated with significant disturbance of riparian communities. The limited data available for fire responses in Australian tropical riparian vegetation suggest there might be dramatic negative impacts of burning here (Douglas *et al.* 2003; Douglas & Setterfield 2004). The effectiveness of fire in reducing *C. grandiflora* density (Grice 1997), plus the hypothesis that reduced fire frequency led to *C. grandiflora* invasion in the first place (Grice *et al.* 2000), has, however, led to increasing use of fire for the control of this species, particularly in pastoral environments where *C. grandiflora* has production and management impacts (Tomley 1998). The question remains – does the implementation of prescribed fire in potentially fire-sensitive vegetation types lead to ecosystem benefits or costs in riparian landscapes? Fire impacts in riparian vegetation could potentially have greater impacts on biodiversity than those associated with the target invader itself.

So what might be the impacts of prescribed burning for *C. grandiflora* control in tropical riparian vegetation? And can potential impacts be minimized? Based on previous fire experiments (Williams *et al.* 1998, 1999, 2003; Williams & Lane 1999) we predict that lower-intensity fires, conducted in the early dry season (or during the wet season), would result in fewer impacts than late dry-season fires. We would also predict greater impacts in riparian than in woodland vegetation, based on impact comparisons within the

Kapalga fire experiment in the Northern Territory (Williams *et al.* 1999; Douglas *et al.* 2003; Douglas & Setterfield 2004; Andersen *et al.* 2005). More intense fires in riparian habitats might be predicted to result in selective removal of very large and very small juvenile trees, thereby simplifying community structure, as found in previous burning studies (Williams *et al.* 1999; Russell-Smith *et al.* 2003a; Vigilante & Bowman 2004; Woinarski *et al.* 2004). Prescribed fires may also influence plant assemblages, with more fire-sensitive species (e.g. rainforest species) being selectively removed or reduced in density (Bowman *et al.* 1990; Fensham *et al.* 2003; Russell-Smith *et al.* 2004; Woinarski *et al.* 2004). In addition, removal of established plants might lead to further establishment/invasion by *C. grandiflora*, or any of a number of exotic woody species known to occur in tropical riparian vegetation, or to increases in colonizing native species (e.g. *Acacia* spp.) in the same areas. In terms of general plant ecological theory, removal of some of the dominant competitive species (C) in riparian habitats might lead to a competitive release and an increase in plant available resources (Grime 1988; Grime *et al.* 1997; Caccianiga *et al.* 2006), which in turn might lead to establishment of early succession or disturbance tolerant species (ruderals, R), including exotic and colonizing species. Such changes would result in floristic and structural change in riparian plant communities.

In this study we report on the impacts of low intensity (early wet season), moderate intensity (mid-dry season) and repeated burning for *C. grandiflora* control at sites in the greater Burdekin catchment of north-eastern Queensland, Australia. Target riparian communities comprised grassy woodlands typical of surrounding savannas, through to true riparian forests, and included elements of closed broadleaf tropical forest (Rogers *et al.* 1999; Sattler & Williams 1999). Presence of a complex of exotic woody species (e.g. *C. grandiflora*, *Ziziphus mauritiana*, *Lantana camara* and *Parkinsonia aculeata*) and exotic herbaceous species in these habitats (Mackey *et al.* 1996; Rogers *et al.* 1999; Grice 2006), highlights the potential for proliferation of non-native or early successional elements in these environments. In this paper we report on prescribed burning impacts on woody plant communities within riparian plots.

MATERIALS AND METHODS

Study sites

Three sites were chosen on tributaries of the Burdekin River south-east of Charters Towers: One Mile Creek (20°14'10"S, 146°40'35"E), Bend Creek (20°16'07"S, 146°37'48"E) and Cornishman Creek (20°12'18"S,

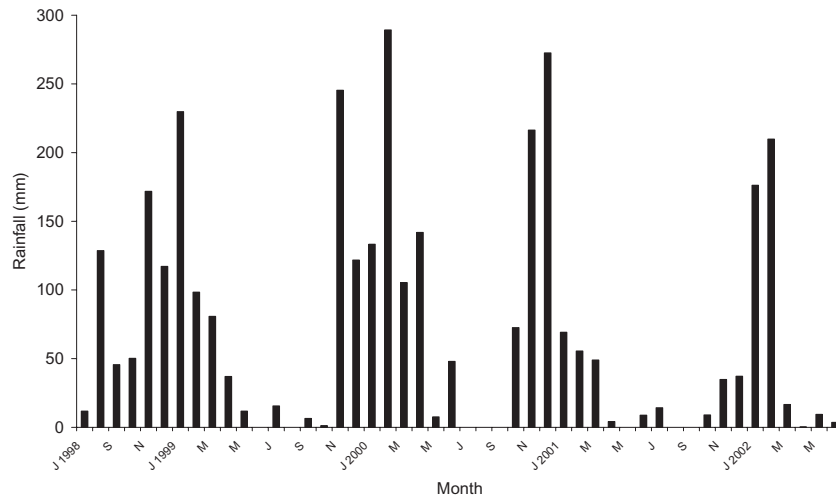


Fig. 1. Monthly rainfall data from Charters Towers, from July 1998 through until June 2001, during the period the prescribed burning experiment was run.

146°27'15"E). Sites were within granodiorite landscapes (Rogers *et al.* 1999) and were situated on two commercial grazing leases. The sites fall within Province 4 of the Einasleigh Upland vegetation region (Sattler & Williams 1999) and were dominated by *Eucalyptus crebra* and *Corymbia erythrophoia* woodland/savanna vegetation. Sites were chosen with at least 3 km of creek frontage with continuous rubber vine populations and were divided into five landscape size experimental plots, which were randomly assigned to one of five prescribed burning treatments. Burn treatments were – control (unburnt), single wet-season burn, double wet-season burn, single dry-season burn and double dry-season burn. As a result of dramatically reduced grass fuel loads in 2001/2002 owing to drought and increased grazing (Fig. 1), the second dry-season burn had to be abandoned. We have included data from these plots within analyses to provide a duplicate set of dry-season burns for analysis.

Vegetation sampling

Woody vegetation was sampled within experimental plots using a series of transects, five in each plot. Transects were run perpendicular to and across the main creek line at each site to sample a cross section of riparian habitats from open woodland vegetation, to that of levee and creek bank habitats. Transects were permanently marked with steel pickets placed 100 m or more out from the top of the defined creek banks on both sides of the creek and also on the creek banks themselves. In woodland habitats, which were extensive, woody vegetation was recorded every 50 m in 10 m radius circles (woodland samples). In defined creek bank habitats, 10 m radius sampling circles were

placed every 20 m (riparian samples). As a result of narrowness and potential under-sampling of riparian landscapes at one of the sites (One Mile Creek), two quadrats were placed on each side of the creek running parallel and 5 m in from the bank. Five transects in total, >70 m apart, were used to sample vegetation within each plot. Subsidiary creeks and gullies were avoided in sampling. Plots ranged in area from 9 to 40 ha depending on the difficulty of the terrain, the meandering of the main creeks, and the topography.

Vegetation was sampled by identifying, counting and recording stem size into classes for all shrubs and trees within 10 m of the point on the transect. Woody plant species were identified using field keys (Anderson 1993; Townsend 1997), and (Brooker & Kleinig 2004) or were sent to the Brisbane herbarium (BRIS) for identification if unknown. Size-classes were as follows: shrubs (<3 m high); trees >3 m high, class 1 (<5 cm d.b.h.); class 2 (5–10 cm d.b.h.); class 3 (10–30 cm d. b.h.); class 4 (30–50 cm d.b.h.); and class 5 (>50 cm d.b.h.). Woody vegetation sampling was undertaken early in the dry season in April 1999 before prescribed burn implementation and in April 2002 after the final fires had occurred.

Implementation of fire regime

Two single grader width fire breaks (6 m wide) were run around treatment plots. These were *c.* 50 m apart. The vegetation between these breaks was burnt before the main plot fires to protect experimental treatments and the properties on which sites were established. Drip torches were used to allow continuous fire lines to be ignited. All fires were lit initially on the down-wind edges of the plots after assessment of the prevailing

wind direction. This was to allow a safety back-burn of another *c.* 50 m to be made inside the plot so that surrounding areas were more fully protected from the head fire once it was lit. When sufficient fire break was established through back-burning, the upwind edges of the plots were lit to allow a head fire to run through most of the plot. As we were using fire as a control for rubber vine, any major unburnt patches, particularly along creek-lines, were lit separately. Fires were lit for wet-season burns after significant rainfall had occurred, from 8 to 10 December 1999 and in 20–21 November 2001. Dry-season burns were conducted from 30 to 31 August and from 5 to 7 September 2000 when rains had ceased and grass fuel had cured sufficiently to allow reasonably intense fires, but before fire-bans were imposed.

Herbaceous fuel loads were determined on the morning of the fire for prescribed burns in 2000 and 2001. Following one transect, fire disc meter measurements were taken every 10 m. Such measurements involve determination of the vertical distance to the ground of a metal disc of 0.33 m² dropped from a height of 1.5 m into a grass sward. This is essentially a measure of resistance of the grass, which represents an estimation of the relative amount of grass biomass. To calibrate disc measurements with grass biomass a set of 12 standards were harvested in each plot, where all herbaceous biomass under the disc was cut at ground level, dried and weighed. The standards were chosen to represent the full range of grass biomass observed, and regression equations used to calculate mean biomass across plots. Pre-fire biomass was estimated in 1999 using herbaceous biomass values from the end of the previous wet season (Radford *et al.* unpubl. data, 1999) with a correction factor for the percentage dry-season weight off-take through grazing. Off-take rates were estimated from paired end of wet-season herbaceous biomass measurements and pre-fire disc measurements for wet-season burns in 2001.

Weather data on the days that prescribed burns were conducted, including temperature, relative humidity and wind speed, were obtained from the Bureau of Meteorology for the Charters Towers weather station which is *c.* 35 km north of the study area.

An estimate of Byram fire intensity (Byram 1959) of prescribed burns was made using the equation $I = 500 \times W \times R$; where I = Intensity (kW m⁻¹); W = fuel biomass (tonnes ha⁻¹) and R = rate of spread (km h⁻¹) (Williams & Cook 2001). 'R' was estimated using average wind speeds recorded at Charters Towers on the day of the prescribed burn, and the relationship between fire and wind speed developed by Cheney and Sullivan (1997). 'W' was based on grass biomass as measured above. The value of 500 is a constant based on the heat off-put from burning grass fuels in northern Australia (Williams *et al.* 1998; Williams & Cook 2001). The equation used to esti-

mate Intensity is a simplified version of equations used for fires in northern Australian savannas by Williams *et al.* (1998, 1999). Estimated fire intensity ranged from as low as 720 kW m⁻¹, up to 6200 kW m⁻¹. For the sake of classification, we consider fires <2000 kW m⁻¹ of low intensity and >2000 kW m⁻¹ moderate. This is on the basis that fires >2000 kW m⁻¹ fully consume ground level fine fuels in tropical savanna vegetation, whereas less intense fires are more patchy and result in only partially burnt understorey vegetation (Williams & Cook 2001). High-intensity fires (>8000 kW m⁻¹), where combustion of all canopy fuels occurs (Williams & Cook 2001), were not characteristic of experimental fires overall, although some dense riparian forest patches and rubber vine thickets appeared to have burnt at high intensities according to this definition. Intensity estimates made in this study were only directly relevant to grass fuels, and are not considered accurate when large amounts of woody fuels are present (Dyer *et al.* 2001).

Statistical analysis

Each woody plant species was analysed separately for change in numbers from pre-fire (1999) to post-fire (2001) using a split plot design analysis of variance (MINITAB). This design used Sites S as blocks ($n = 3$), with Treatment Plots Tr ($n = 5$) and Time T (pre- and post-fire, $n = 2$) being the other two factors. $Site \times Tr \times T$ was used as the error term in this analysis. Significant Treatment Plot \times Time interactions ($Tr \times T$) were taken as primary evidence of a significant response to fire regime. In addition, Tukey's pairwise comparisons were used to identify significant differences among burn treatment pairs where Time was a significant term in the analysis.

To test for fire sensitivity of woody plant communities as a whole, a number of additional analyses were completed. Responses of broad plant functional groups were investigated. This was done in two ways. First, all species within defined functional groups were added together and analysed using split plot ANOVA as above. In addition, multivariate analysis of variance (MANOVA) was used to test whether species composition within these functional groups changed with respect to fire regime. Functional groups were *Eucalyptus/Corymbia* spp. trees (>3 m high); *Eucalyptus/Corymbia* spp. juveniles (shrubs <3 m high), Legumes, which included all *Acacia* spp. and *Albizia* spp.; Woodland Mid-storey trees (e.g. *Grevillea*, *Bursaria*, *Atalaya*); Woodland shrubs (*Carissa*, *Breynia*, *Grewia*, *Erythroxylum*); Riparian canopy trees (*Melaleuca*, *Casuarina*, *Lophostemon*); Riparian mid-storey trees (*Planchonia*, *Santalum*, *Petalostigma*, *Pleiogynium*); and Exotic shrubs (*Cryptostegia*, *Ziziphus*, *Lantana*). Functional groups were defined according to their

habitat distribution or ecological role (e.g. ridge habitats with open grassy woodland vegetation *vs.* riparian thicket vegetation, from either levee or creek bank habitats) and structural form (canopy tree, mid-story tree, shrub) at the study sites.

Woody plant community response to burning treatments was tested using Non-Metric Multi-Dimensional Scaling (NMDS). Plot level multivariate species abundances before and after fire treatments were compared. NMDS reduces the magnitude of the effects of more numerous species on the overall analysis by automatically reducing multiple axes to the same dimensions, thereby assigning equal weight in the analysis to abundant and less abundant species. Only species occurring in more than half of the experimental plots were included within this analysis. All abundances were log_e transformed and converted to proportional values relative to the maximum before analysis.

Analysis of structural change of vegetation with fire regime was undertaken by using data collected on number of plants of each size-class within quadrats for each plot (see Vegetation Sampling). Each size-class was analysed using split plot ANOVA as described above for analysis of species-specific responses. Because of greater replication with combined species data, four factors including Site, Treatment plots, Time and Landscape (Woodland or Riparian) were used in the split plot design, again site being the block factor and being used as the error term in the analysis ($Site \times Tr \times T \times L$).

RESULTS

Vegetation description

A total of 84 shrub and tree species, and 26 101 individual plants were recorded and monitored in 567 10-m radius circles at three sites from 1999 to 2001. The majority of canopy species recorded within experimental plots were either *E. crebra* or *Corymbia erythrophloa*, with *Carissa ovata*, and juveniles of *Eucalyptus* spp. and *Corymbia* spp. dominating the native component of the shrub layer (plants <3 m high). Other common canopy species in woodland environments were *Eucalyptus brownii*, *Eucalyptus persistens*, *Eucalyptus platyphylla* and *Corymbia aparrerinja* ssp. *dallachiana*. Within riparian habitats (levee and creek bank) *Melaleuca fluviatilis*, *Melaleuca leucodendra*, *Melaleuca bracteata*, *Casuarina cunninghamiana* and *Corymbia tessellaris* were common canopy species. Other important, but less common mid-canopy or shrub species included *Acacia* spp., *Atalaya hemiglauca*, *Maytenus cunninghamii*, *Eremophila mitchellii*, *Erythroxylum australe*, *Petalostigma pubescens*, *Pleiogynium timorense* and *Santalum lanceolatum*. Initial

mature tree densities (d.b.h. > 10 cm) were 87 ha⁻¹ in woodland and 128 ha⁻¹ in riparian habitats, with small trees (d.b.h. < 10 cm) 176 and 169 ha⁻¹. Shrub densities were between 469 ha⁻¹ and 252 ha⁻¹ in woodland and riparian habitat, respectively. Total tree basal area was 3.4 m² ha⁻¹ in woodland areas and 6.4 m² ha⁻¹ in riparian habitats. The exotic invasive shrub/vine, *C. grandiflora*, was at high densities relative to native species. *Cryptostegia grandiflora* density ranged 300–500 ha⁻¹ in woodland areas, and 2500–5000 ha⁻¹ in riparian forest habitats (defined by creek banks).

Climate and fire variables

Rainfall was higher and of longer duration for the 1998/1999 and the 1999/2000 wet season than it was in the succeeding years of the study (Fig. 1). Significant rainfall (>10 mm) occurred for 9 months in 1998/1999 but only 6 months in 2000/2001. Total accumulated rainfall was well above the average for Charters Towers (mean = 660 mm) in 1998/1999 (983 mm) and 1999/2000 (1116 mm), and below average in 2001/2002 (511 mm).

Wet-season fires were of lower intensity than dry-season fires in this study (Table 1). Wet-season fires were conducted after a number of rainfall events at the start of the rainy season so that soil moisture was high and some green grass growth had been initiated. These fires were slow and patchy, which necessitated separate internal ignition of many rubber vine patches to get fires to progress. Individual experimental fire intensity estimates in wet-season fires (Table 1) ranged from low to moderate, but on average were of low intensity (<2000 kW m⁻¹). In contrast, dry-season fires were generally of moderate intensity (2000–8000 kW m⁻¹) despite relatively low grass biomass (<2 t ha⁻¹) by Australian tropical savanna standards (Johnson 2002) during much of the study (Table 1). These fires resulted in more complete ignition of grass fuels and much less patchiness of burnt and unburnt areas as observed in the wet season. There was no need during dry-season fires to individually light rubber vine clumps to achieve ignition. With the wet-season burning we were only able to achieve a full opening up of the rubber vine canopy with the second wet-season burn.

It should be noted that tree canopy fires in this study were observed only in riparian forest vegetation, and only in association with rubber vine towers (plants climbing over established canopy trees), whereas elsewhere in experimental plots fires were restricted to the grass and shrub vegetation layers. High shrub, small tree and rubber vine tower biomass within riparian landscapes, constituted much greater combustible fuel loads than grass fuels. *Cryptostegia grandiflora* in particular was observed to be highly flammable and

Table 1. Weather data from nearby Charters Towers, grass fuel loads, estimated fire spread rates and estimated fire intensity for prescribed burns undertaken within this experiment

Season	Site	Plot	Year	Temperature (maximum)	Relative humidity (%)	Wind speed (9 AM) (km h ⁻¹)	Wind speed (3 PM) (km h ⁻¹)	Estimated spread rates (km h ⁻¹)	Grass fuels – Mean ± SE (tonnes ha ⁻¹)	Intensity (kw m ⁻¹)
Wet	One mile	2	1999	31	36	4	8	1.5–3.5	1.79 (±0.17)	1350–3140
Wet	One mile	4	1999	31	36	4	4	1.5	2.34 (±0.22)	1760
Wet	Bend	2	1999	33	37	8	4	1.5–3.5	1.74 (±0.17)	1305–3480
Wet	Bend	4	1999	33	37	8	8	3.5	1.79 (±0.17)	3130–3580
Wet	Cameron	2	1999	33	37	4	4	1.5	1.68 (±0.16)	1260
Wet	Cameron	4	1999	34	37	4	4	1.5	1.78 (±0.17)	1330
	Mean							2.1	1.85	1943
Dry	One mile	3	2000	34	26	11	11	5.0	1.58 (±0.16)	3950
Dry	One mile	5	2000	34	26	17	9	4.0–7.0	1.58 (±0.16)	3160–5530
Dry	Bend	1	2000	31	35	11	4	1.5–5.0	1.61 (±0.17)	1210–4830
Dry	Bend	5	2000	30	36	17	17	8.0	1.55 (±0.23)	6200
Dry	Cameron	3	2000	32	19	4	4	1.5	1.64 (±0.15)	1230
Dry	Cameron	5	2000	35	15	5	5	2.0	1.82 (±0.16)	1820
	Mean							4.3	1.63	3505
Wet	One mile	4	2001	36	31	4	11	1.5–5.0	1.26 (±0.15)	950–3160
Wet	Bend	2	2001	36	31	4	4	1.5	1.65 (±0.20)	1240
Wet	Cameron	4	2001	35	31	4	5	1.5–2.0	0.96 (±0.13)	720–960
	Mean							2.3	1.29	1484

may have had higher-intensity fires than other canopy fuels based on flame height. *Cryptostegia grandiflora* tower and canopy ignition/scorch was common in riparian habitats.

Species-specific fire response

Most plant species showed significant response to Site and/or Treatment plot, indicating pre-existing spatial differences in vegetation (Table 2). In contrast, only a minority of species showed a direct response to imposed fire regime indicated either by a significant Treatment × Time effect, or by significant Time effects and a significant Tukey's pairwise comparison between treatments. Only two species, *Acacia salicina* and *Acacia holosericea*, showed an increase in number after a single fire (Treatment × Time response, Table 2) (Fig. 2a,c). These species also both declined in numbers after two wet-season fires, suggesting mortality of new seedlings (Fig. 2a,c). Another nine species showed overall response to Time, however, only for *C. grandiflora*, the target invader, can this be unambiguously (statistically) be related to fire regime – both repeated wet-season and dry-season burning leading to a reduction in numbers of between 66% and 75% (Fig. 2f). For *Acacia leptostachya*, *C. ovata*, *Maytenus cunninghamii* and pooled paperbark species (*Melaleuca leucodendra*, *M. fluviatilis* and *M. nervosa*) change in numbers in some plots may be related to fire regime (Fig. 2d,e,h,i). *A. leptostachya* showed an overall decrease in density in experimental

plots, however, all plants recorded in dry-season plots died (Fig. 2c). Observations of charred standing dead *A. leptostachya* plants following dry-season fires, whereas living plants remained in other plots suggest fire-related mortality. *Carissa ovata* showed a large increase in plant numbers in unburnt and dry-season burnt plots (50–100%), but not in wet-season burnt plots (Fig. 2e). *Maytenus cunninghamii* showed a relative increase in numbers (approx. 50%) in control plots, while in twice burnt wet-season plots there was a 50% decrease in numbers, suggesting a fire suppression effect on recruitment of this species (Fig. 2h). There was a near significant Treatment × Time response for this species (Table 2). Significant Time-related differences for *Corymbia aparrerinja* ssp. *dallachiana* (Table 2) appeared not to be related to fire regime (Fig. 2g). Similarly, Time-related differences observed for *Solanum torvum* and *Jasminum didymium* ssp. *racemosum* (Table 2) were unrelated to fire regime, with the former species increasing, and the latter decreasing generally in all treatments. Near significant fire regime responses were observed for the small number of *Acacia aulacocarpa* plants (Table 2), with fewer plants recorded when burnt twice, and also after dry-season burning in one replicate (Fig. 2b).

We recorded fire responses for a number of additional plant species that could not be included in statistical analyses because of lack of replication at the treatment or site level. Apparently, fire-resistant species included *Eucalyptus brownii*, *E. persistens*, *Breynia oblongifolia*, *Corymbia clarksoniana*, *Lophoste-*

Table 2. Analysis of variance table with *F*-ratios for effects of Sites (Block), Plots (to which burning treatments were applied) and Time (before and after treatments applied) on plant number and species richness

Variable	Site (Block) (d.f. = 2)	Treatment (d.f. = 4)	Site × Treatment (d.f. = 8)	Time (d.f. = 1)	Site × Time (d.f. = 2)	Treatment × Time (d.f. = 4)
Legumes						
<i>Acacia bidwillii</i>	5.41*	0.71	2.64	2.33	0.10	1.03
<i>A. farnesiana</i>	7.02*	4.23*	6.97**	1.84	1.68	1.51
<i>A. salicina</i>	2.33	5.52*	3.18~	9.37*	1.27	5.12*
<i>A. aulacocarpa</i>	4.75*	1.57	1.91	4.96~	2.43	3.58~
<i>A. holosericea</i>	64.12***	2.09	1.45	21.37**	2.84	4.06*
<i>A. leptostachya</i>	9.00**	2.51	6.70**	6.19*	2.35	1.83
<i>A. excelsa</i>	0.90	3.01	4.97*	0.10	1.97	0.70
<i>Albizia basaltica</i>	5.14*	1.87	3.12~	4.81~	0.85	1.36
Total	8.77*	1.07	4.20*	1.21	3.57	0.54
MANOVA	13.31~	2.08	4.10**	7.40	1.83	2.15
Eucalyptus/Corymbia						
<i>Eucalyptus crebra</i>	56.89***	16.61**	28.24***	1.34	3.82~	1.57
<i>E. platyphylla</i>	10.61**	1.46	0.86	0.86	0.78	1.08
<i>Corymbia erythrophloia</i>	18.31**	2.71	2.64	0.34	0.07	0.25
<i>C. tessellaris</i>	33.00***	3.80~	4.22**	2.40	1.75	0.94
<i>C. aparereinja</i> ssp. <i>dallachiana</i>	52.67***	11.02**	16.42***	11.59**	13.87**	1.91
<i>Eucalyptus/Corymbia</i> spp. (<2 m high)	8.78*	9.76**	10.23**	11.35*	0.59	1.63
Total	1.74	3.64~	12.85**	9.81*	8.71*	0.97
MANOVA	22.27**	3.51*	4.17**	2.58	1.12	0.88
Sub-dominant woodland trees						
<i>Atalaya hemiglauc</i>	16.05**	11.55**	2.43	1.10	1.21	1.04
<i>Bursaria incana</i>	3.48	3.27~	4.71*	<0.00	0.10	0.52
<i>Eremophila mitchellii</i>	59.22***	1.82	25.12***	1.75	0.85	0.41
<i>Erythrina vespertilio</i>	2.97	2.04	1.17	0.03	6.70*	0.51
<i>Grevillea striata</i>	0.96	3.36~	6.00*	1.12	0.12	0.02
<i>Canthium attenuatum</i>	10.25**	1.30	1.27	0.02	0.42	1.04
<i>Canthium vacciniifolium</i>	4.95*	1.03	1.46	0.05	0.82	2.24
<i>Ehretia membranifolia</i>	71.68***	1.89	17.97***	2.12	0.61	2.11
Total	3.51	4.17*	6.44**	2.04	0.05	1.16
MANOVA	113.87**	4.45~	2.96*	0.63	0.74	0.93
Woodland shrubs						
<i>Capparis lasianthera</i>	1.26	1.75	3.14~	0.90	0.89	1.74
<i>Carissa ovata</i>	74.03***	18.74***	11.52**	36.34***	3.57	1.37
<i>Erythroxylem australe</i>	6.21*	11.02**	2.22	0.05	1.20	0.42
<i>Maytenus cunninghamiana</i>	43.59***	3.57~	9.24**	6.40*	3.27	3.62~
<i>Geijera salicifolia</i>	8.09*	1.30	3.06~	<0.00	0.48	1.45
<i>Fluggea virosa</i> ssp. <i>melanthoides</i>	4.33~	3.24~	3.25~	0.13	2.43	0.91
<i>Eustrephus latifolius</i>	20.57**	0.86	0.95	1.96	1.13	1.09
<i>Jasminum didymum</i> spp. <i>racemosum</i>	6.79*	2.71	1.00	31.04**	6.79*	2.71
Total	7.70*	3.28~	3.93*	0.73	2.17	0.78
MANOVA	535.42**	36.62***	21.85***	999.42*	56.63*	9.64**
Riparian canopy trees						
<i>Casuarina cunninghamiana</i>	195.09***	0.99	2.44	3.47	1.32	1.14
<i>Melaleuca leucodendra</i> <i>/fluvialis/nervosa</i>	24.29***	2.45	1.66	5.45*	0.29	1.57
<i>Melaleuca bracteata</i>	283.57***	1.58	3.86*	3.17	0.80	1.84
Total	24.59***	2.99	1.10	5.48*	0.16	0.95
MANOVA	92.42***	1.09	2.44*	1.95	0.97	1.36
Riparian understorey trees						
<i>Alphitonia excelsa</i>	16.02**	1.67	0.63	1.81	1.17	0.48
<i>Petalostigma pubescens</i>	22.89***	4.72*	2.47	1.17	4.13~	0.64
<i>Planchonia careya</i>	124.75***	10.64**	14.05**	5.18~	12.72**	0.42
<i>Santalum lanceolatum</i>	14.92**	12.23**	10.22**	0.04	1.45	0.59
<i>Ficus opposita</i>	147.62***	2.15	1.80	0.11	1.14	1.34
<i>Pleiogynium timorense</i>	47.96***	19.47***	24.28***	0.51	0.39	0.71
Total	20.19**	16.06**	6.03*	0.14	1.94	1.05
MANOVA	42.78***	6.70**	5.13**	5.82	1.29	0.71
Exotic shrubs						
<i>Cryptostegia grandiflora</i>	38.58***	0.71	1.27	89.51***	2.83	3.65~
<i>Ziziphus mauritiana</i>	25.92***	2.03	6.12*	0.71	0.12	2.19
<i>Lantana camara</i>	32.23***	2.64	4.62*	2.06	0.33	1.06
<i>Solanum torvum</i>	10.30**	0.80	1.29	11.06*	6.43*	0.25
Total	38.68***	1.18	1.44	85.97***	2.58	4.33*
MANOVA	25.63***	1.85	3.70**	51.18***	1.49	2.62*

*0.05 < *P* < 0.01, **0.01 < *P* < 0.001, ****P* < 0.001, ~near significant (0.075 < *P* < 0.05). Values presented are *F*-values and significance is shown by symbols (see legend).

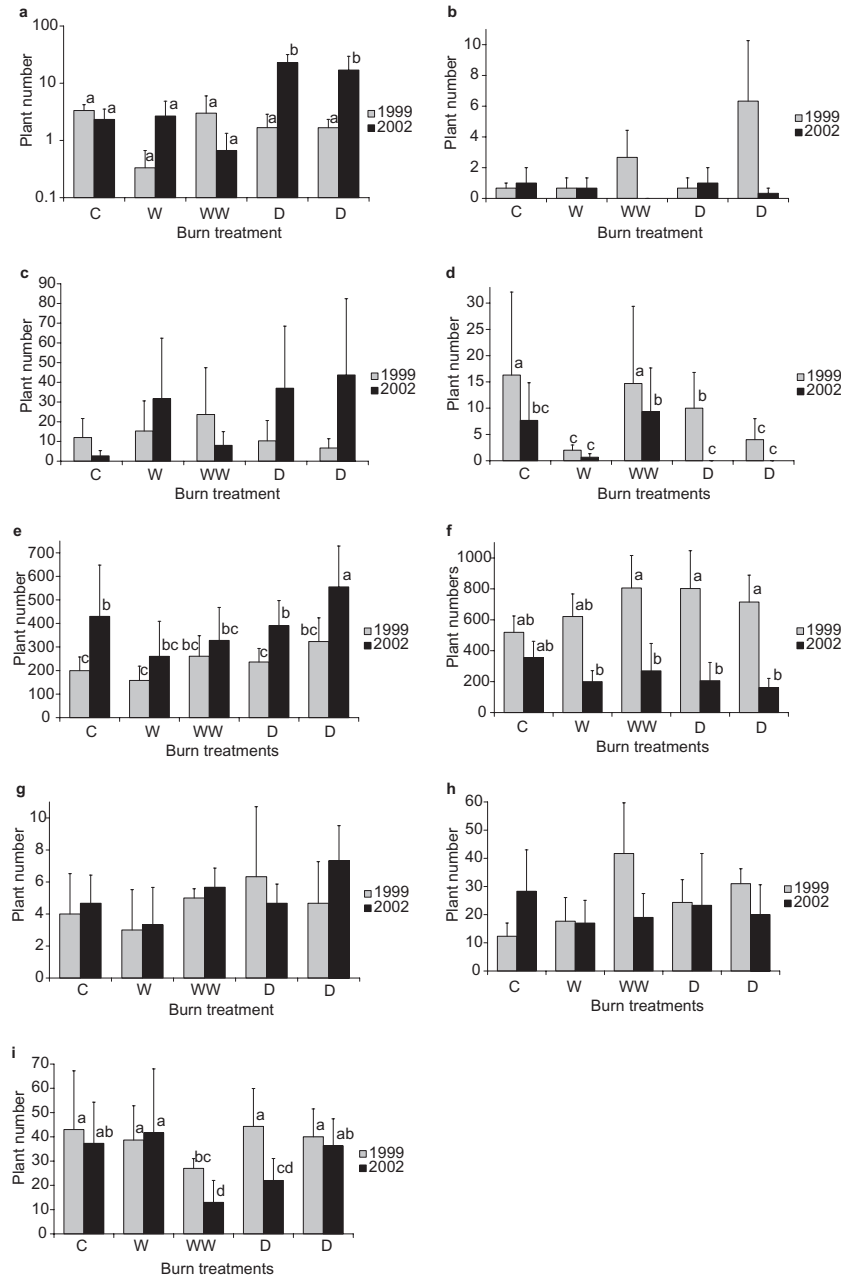


Fig. 2. Mean plant number, and standard error of the mean (vertical bars) for (a) *Acacia salicina*, (b) *A. aulacocarpa*, (c) *A. holocserisea*, (d) *A. leptostachya*, (e) *Carissa ovata*, (f) *Cryptostegia grandiflora*, (g) *Corymbia aparrerinji* ssp. *dallachiana*, (h) *Maytenus cunninghamii* and (i) *Melaleuca* spp. (paperbarks including *M. leucodendra*, *M. fluviatilis* & *M. nervosa*), before (grey) and after (black) prescribed burning treatments had been applied. Letters denote the significance of differences between mean values. Treatments compared are Control (C), burnt once in Wet Season (W), burnt Twice in Wet Season (WW) and Burnt Once in the Dry Season (D).

mon suaveolans, *Lysophyllum hookeri*, *Ventilago viminalis*, *Lagumaria patersonii*, *Larsenaikia achreata*, *Capparis canescens*, *Carissa lanceolata*, *Grevillea parallela* and the exotic cactus *Eriocerus martinii*. Additional species recorded in burnt plots in 2002, and therefore unaffected by fire, included *Acacia elachanatha* and *Senna gaudichaudii*. Species present but with fewer plants observed post-fire included *Pandanus spiralis*, *Heliotro-*

pium indicum, *Diospyros compacta*, *Callicarpa candicans*, *Dodonaea viscosa*, *Dodonaea stenophylla*, *Clerodendron floribundum* and *Flindersia dissosperma*.

Although there were pre-existing differences in plant species richness among sites and treatment plots, there was no response of species richness to either wet or dry season prescribed burning treatments in this study (Table 2).

Functional group fire-response

Of functional groups represented in plant communities at experimental sites, only *Eucalyptus/Corymbia* spp. (juveniles and trees), riparian trees and exotic shrubs showed significant numerical response over Time (Table 2). *Eucalyptus/Corymbia* spp. juveniles (<2 m high) showed a significant increase in numbers with a single wet-season fire, and with a single dry-season fire (one replicate only) (Fig. 3b). *Eucalyptus/Corymbia* spp. trees (>2 m high) showed a negative response to being burnt twice in the wet season, and to dry-season burning in one replicate (Fig. 3a). Riparian trees (*Melaleuca* spp., *Casuarina* spp.) showed significant decreases in plant number in all treatments except single wet-season fire (Fig. 3c). The response of exotic shrubs was identical to that of *C. grandiflora*, with all burning treatments leading to a reduction in plant number (Fig. 2f). This was likely to reflect the numerical dominance by rubber vine in this group. Woodland shrubs and exotic shrub functional groups showed an overall change in species composition in response to burning treatments (Time and Treatment × Time MANOVA response) (Table 2).

Community composition response to fire regime

Minimal change occurred within experimental plots from 1999 to 2002 irrespective of fire treatment (Fig. 4) suggesting that fire had little overall floristic effect on plant communities at these sites. The largest differences among plots corresponded to species differences between the three study sites (Blocks) and were apparent in 1999 before application of treatments (Table 3). The lack of a clear trend from initial to post-treatment states with respect to the NMDS Axes made it impossible to identify the species responses most closely related to community fire responses.

Vegetation structural response to fire regime

Two vegetation components, medium trees and total basal area, showed a direct and significant response to fire regime indicated by a Treatment Plot × Time response (Table 4). Monitored medium trees decreased in number in control (unburnt) and single wet-season burnt plots, while increasing relative to pre-fire numbers in more severely burnt plots (dry-season or double wet-season burns), which suggests a benefit to this size-class through burning (Fig. 5d). A significant decrease in basal area took place in one duplicate of the dry-season burning treatment (Fig. 5h), although small numbers of trees in the large size-class which most contributed to this basal area

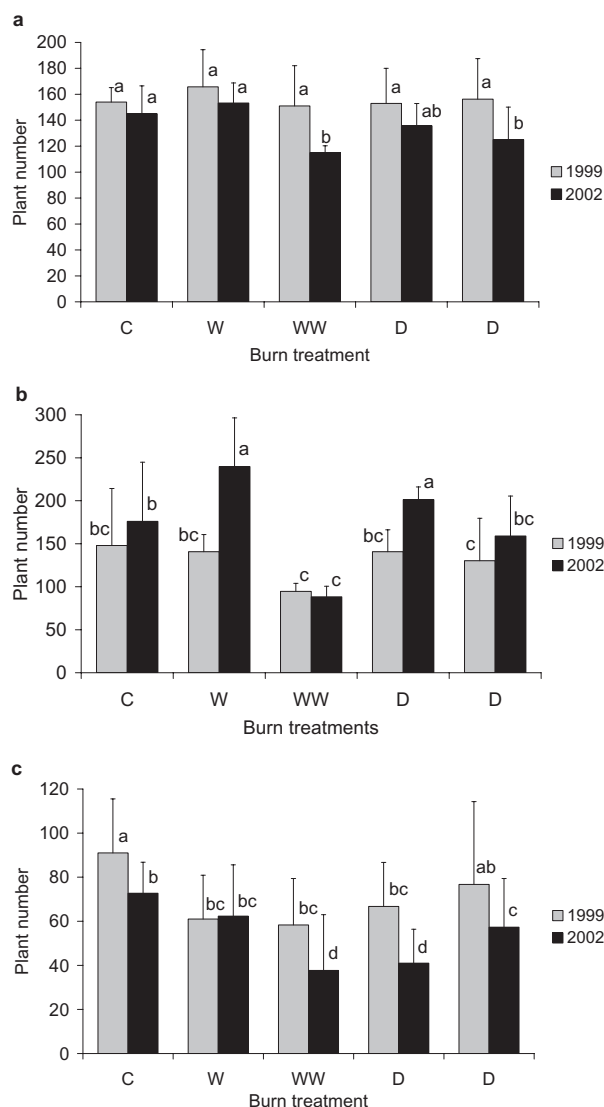


Fig. 3. Mean plant number, and standard error of the mean (vertical bars) for (a) *Eucalyptus* spp. and *Corymbia* spp. trees (>2 m high), (b) *Eucalyptus* spp. and *Corymbia* spp. juveniles (<2 m high) and (c) total riparian trees (*Melaleuca* spp., *Casuarina cunninghamiana*, *Lophostemon suaveolans*), before (grey) and after (black) prescribed burning treatments had been applied. Letters denote the significance of differences between mean values. Treatments compared are Control (C), burnt once in Wet Season (W), burnt Twice in Wet Season (WW) and Burnt Once in the Dry Season (D).

response (Fig. 5f) meant that the response of this size-class was non-significant (Table 4). In addition, shrubs, saplings, small trees, rubber vine towers and total tree numbers showed significant responses to Time suggesting a possible fire response (Table 4). Pairwise tests showed an increase in shrub density in the unburnt control plots and dry-season burnt plots (one replicate only), but no change was recorded for the wet-season burning treatments (Fig. 5a). Sapling

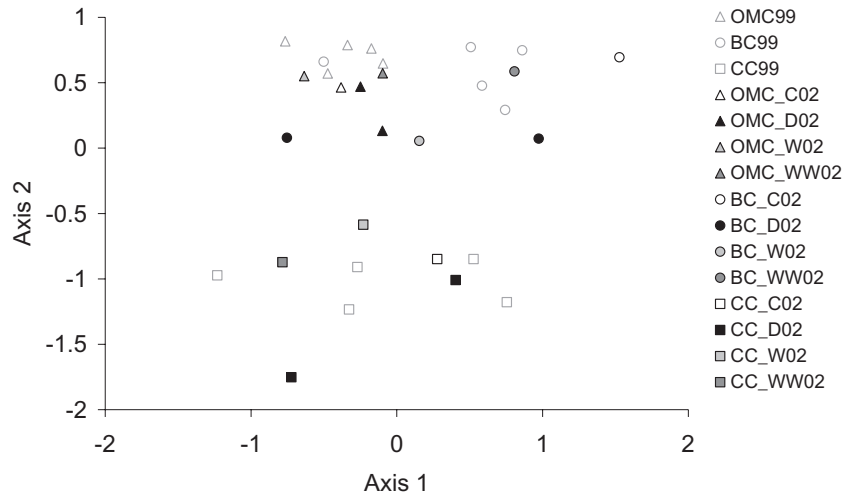


Fig. 4. Non-Metric Multidimensional Scaling (NMDS) of variation in plant assemblages among plots before and after experimental fire regimes were imposed. Pre-fire plot data represented by clear symbols with grey outline, control (unburnt) plots by clear symbols with black outline, single wet-season fire by pale grey, double wet-season fire by dark grey and dry-season fire by solid black symbols. The different shape symbols (triangle, circle and square) represent the different study sites (Blocks). All data was log_e transformed before NMDS analysis. The stress value for NMDS was 0.16.

Table 3. Plant species correlations (Kendal’s rank tau values) for the Non-Metric Multi Dimensional Scaling (NMDS) scatter plots shown in Figure 4

Axis 1	tau	Axis 2	tau
Positive		Positive	
<i>Pleiogynium timorense</i>	0.655	<i>Casuarina cunninghamii</i>	0.576
<i>Eriocercus martini</i> [†]	0.540	<i>Alphitonia excelsa</i>	0.561
<i>Lysophyllum hookeri</i>	0.531	<i>Ficus opposita</i>	0.544
<i>Coymbia tessellaris</i>	0.517	<i>Canthium vacciniifolium</i>	0.442
<i>Lophostemon suaveolans</i>	0.510	<i>Melaleuca bracteata</i>	0.408
<i>Acacia farnesiana</i> [†]	0.433	<i>Atalaya hemiglauca</i>	0.407
		<i>Albizia basaltica</i>	0.401
		Negative	
		<i>Acacia holosericea</i>	-0.660
		<i>Eucalyptus brownii</i>	-0.574
		<i>Pandanus spiralis</i>	-0.551
		<i>Ehretia membranifolius</i>	-0.514
		<i>Eucalyptus normantensis</i>	-0.507
		<i>Eucalyptus platyphylla</i>	-0.469
		<i>Planchonia careya</i>	-0.428
		<i>Larsenaikia acreata</i>	-0.419
		<i>Eremophila mitchellii</i>	-0.415
		<i>Melaleuca nervosa</i>	-0.412

[†]Exotic species. Only correlation >0.400 are shown in this table.

number decreased significantly in plots burnt twice in the wet season and in the dry season (one replicate only) (Fig. 5b). Small trees increased in number when unburnt (control), when burnt once in the wet season, and in one of dry-season replicates, whereas elsewhere they remained unchanged (Fig. 5c). Total tree numbers decreased significantly overall to being burnt twice during the wet season and in one of the duplicates of the dry-season burn (Fig. 5h). Rubber vine

tower density decreased under all but the single wet-season burning treatment and the control treatment (Fig. 5i).

Little differentiation in total and exotic species richness could be explained by the effects of burning treatment over time, with the majority of the differentiation being partitioned among landscapes, pretreatment plot effects, and interactions including these factors (Table 4). Total and exotic species richness was higher

Table 4. Analysis of variance showing *F*-ratios for effects of Sites (Block), Treatment, Landscape and Time (before and after treatments applied) on structural vegetation components

Variable	Time (T) d.f. = 1	Site (S) d.f. = 2	Tr d.f. = 4	Ldsc (L) d.f. = 1	T*S d.f. = 2	T*Tr d.f. = 4	T*L d.f. = 1	S*Tr d.f. = 8	S*L d.f. = 2	Tr*L d.f. = 4	T*Tr*L d.f. = 4	T*S*Tr d.f. = 8	T*S*L d.f. = 2	S*Tr*L d.f. = 8
Shrubs	34.64***	0.20	2.73	2.71	12.50**	2.98	3.50	2.06	11.09**	1.05	0.72	4.70*	0.79	1.30
Saplings	67.16***	7.86*	1.82	9.09*	8.52*	2.53	8.00*	3.69*	2.79	0.66	1.07	3.87*	3.53	0.96
Small trees	19.80**	29.03**	2.48	75.00***	16.63**	3.21	7.36*	7.28**	20.60**	2.43	1.38	4.38*	0.48	2.97
Medium trees	0.00	16.06**	20.09***	54.07***	3.61	5.67*	1.22	11.69***	29.61***	4.63*	2.06	3.40	5.89*	6.83**
Large trees	3.17	2.31	2.35	19.02**	3.20	1.06	0.08	1.53	0.19	0.52	1.29	0.43	0.32	0.81
Very large trees	4.38	2.81	1.44	57.53***	1.14	2.94	1.68	0.76	0.45	1.10	0.86	1.46	0.82	0.30
Rubber vine towers	25.46**	4.88*	0.73	46.07***	0.03	0.76	1.47	1.23	0.56	0.38	0.83	0.39	2.13	0.18
Total trees	53.92***	5.65*	1.44	5.35*	8.96**	2.08	9.41*	3.61*	5.51*	0.79	3.78*	0.83	0.64	3.13
Total basal area	1.56	6.20*	0.06	71.45***	0.10	3.85*	3.15	0.93	1.86	1.22	1.80	1.02	0.77	0.01
Total species richness	2.62	1.41	9.98***	177.42***	3.32*	1.70	13.00***	2.46*	11.92***	6.47***	0.31	0.66	3.82*	1.48
Exotic species richness	4.04*	4.09*	5.06***	306.92***	0.33	0.32	17.47***	4.32***	7.80***	1.57	1.06	2.41*	2.45	2.62**

Values presented are *F*-values and significance is shown by symbols (see legend Table 2).

in creek bank habitat plots (8.3 and 1.2 spp. per quadrat, respectively) than in ridge plots (5.9 and 0.6). An overall reduction in exotic species richness occurred during the period of the study irrespective of fire regime (0.91–0.75 spp. per quadrat). There was a fire-related decrease in mean species richness (per quadrat) after two wet-season burns, and after a dry-season burn (one duplicate only) (Fig. 5j) and this was likely attributed to the loss of *C. grandiflora*. There was a significant positive relationship between exotic and native plant species richness in ridge/levee quadrats in 1999 ($F = 11.65$; $P = 0.001$; $R^2 = 0.029$), but not once experimental disturbance treatments were imposed in 2002 ($F = 2.17$; $P = 0.142$). There was no relationship between exotic and native species richness for creek bank habitat quadrats either before ($F = 0.16$; $P = 0.692$) or after ($F = 1.48$; $P = 0.225$) experimental treatments were imposed.

DISCUSSION

Major trends in riparian vegetation with and without fire

The overall vegetation community trends attributable to experimental fire treatments were relatively minor during the 4 years of the study. Neither burning nor control treatments led to appreciable divergence of plant communities from that recorded pre-fire in 1999 (Fig. 4). None-the-less some important changes were observed both for experimentally burnt, and for unburnt plots. In control plots (without fire) there were increases in shrub (plants <4 m) and small tree (5–10 cm d.b.h.) density (Fig. 5, Table 4), increases in the shrub species *C. ovata*, *M. cunninghammii* and *Solanum torvum*, and changes in overall shrub species composition (Fig. 2, Table 2). In addition, medium-sized trees (10–30 cm d.b.h.), some *Acacia* spp. and riparian trees overall decreased in abundance in the absence of fire (Figs 2,5, Tables 2,4). In contrast, in burnt plots there were reductions in *C. grandiflora*, *C. grandiflora* towers, some *Acacia* spp., adult *Eucalyptus/Corymbia* spp., sapling trees (<5 cm d.b.h.), total tree basal area and total species richness in some burnt treatments. Increases in numbers of some *Acacia* spp. (e.g. *A. holosericea*), medium-sized trees (10–30 cm d.b.h.) and *Eucalyptus/Corymbia* juveniles (<2 m high), also resulted from burning (Figs 2,3,5, Tables 2,4). Changes were more severe/significant associated with moderate intensity (dry-season burnt) burnt plots (Table 1) and in plots burnt twice. For instance, reductions in tree basal area (Fig. 5, Table 4), *C. grandiflora* (Fig. 2, Table 2) and total species richness (Fig. 5, Table 4) were greater after

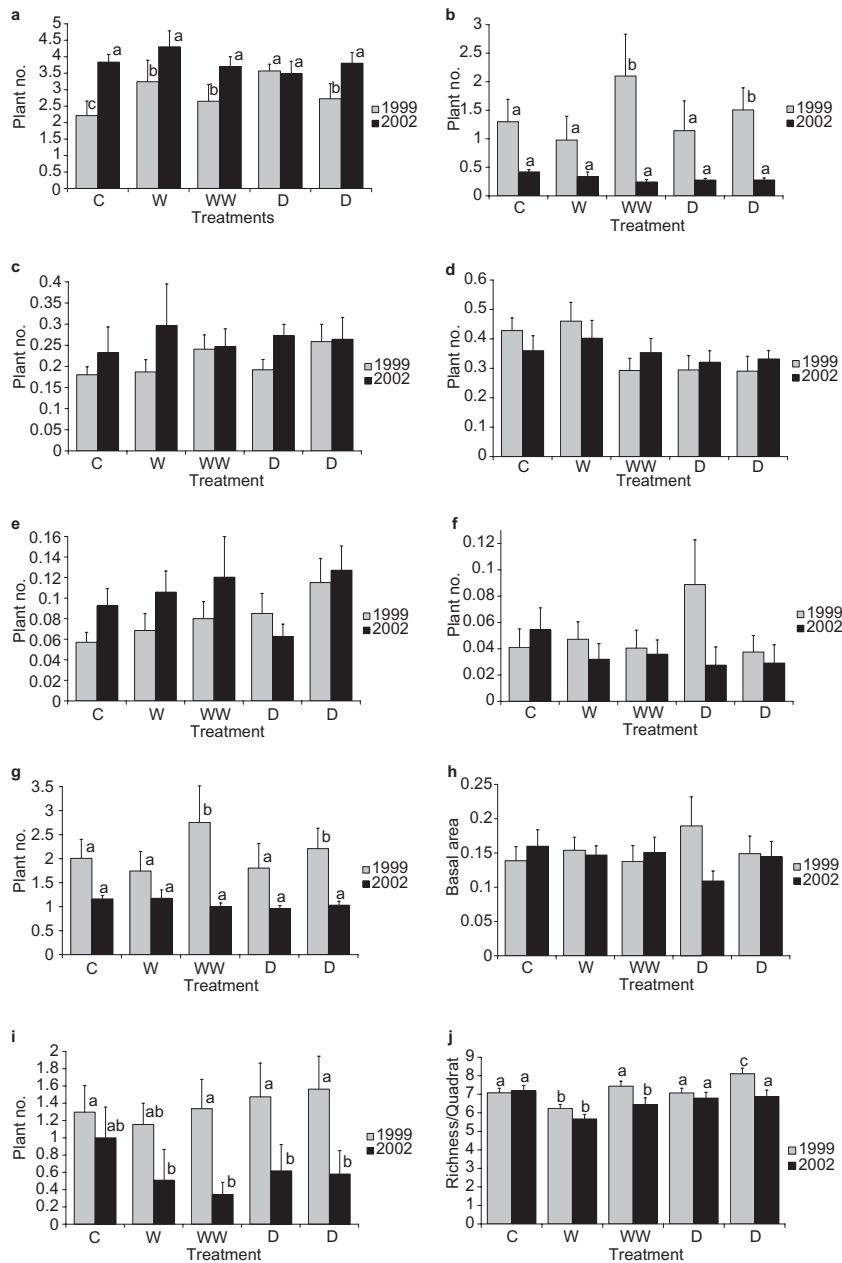


Fig. 5. Mean plant density, and standard error of the mean (vertical bars) for (a) all shrubs (species growing to <4 m or tree species <2 m), (b) sapling trees (tree species >2 m high and <5 cm d.b. h.), (c) small trees (5–10 cm d.b.h.), (d) medium trees (10–30 cm d.b.h.), (e) large trees (30–50 cm d.b.h.), (f) very large trees (>50 cm d.b.h.), (g) total trees (trees >2 m high), (h) estimated total tree basal area (m² ha⁻¹), (i) density of *Cryptostegia grandiflora* towers, before (grey) and after (black) prescribed burning treatments had been applied, and (j) species richness in experimental quadrats. Letters denote the significance of differences between mean values. Treatments compared are Control (C), burnt once in Wet Season (W), burnt Twice in Wet Season (WW) and Burnt Once in the Dry Season (D).

moderate intensity dry-season fires than after low intensity early wet-season fires (Table 1).

None of the plants communities, even under the do-nothing treatment, can therefore be said to be entirely stable over the 4 years of this experimental study. What does this mean, and are these results consistent with previous studies in northern Australia?

Does reduced rainfall explain trends in unburnt habitats?

It is clear from climatic data for the district during the study period that rainfall varied markedly from the beginning to the end of the experiment. Rainfall in the first 2 years of the study was >300 mm above average

for the region (mean = 660 mm), and in the final year, rainfall was >100 mm less than average (Fig. 1). Are underlying vegetation trends in this study in unburnt plots associated with change from relatively wet to relatively dry conditions?

Declines in medium-sized and riparian trees in unburnt plots may be related to drought mortality and greater competition. Widespread tree mortality, particularly of *E. crebra*, was recorded in the region during droughts in the early 1990s (Fensham & Holman 1999; Fensham *et al.* 2003, 2005). Mortality was highest for mature established trees during drought periods, and smaller establishing trees were relatively resilient (Fensham & Holman 1999; Rice *et al.* 2004). This is consistent with observations of reduced density of medium trees in the non-burnt controls in this study, at the same time that small tree density increased (Fig. 5). Selective mortality of larger *E. crebra* trees during droughts in the 1990s is thought to be due to greater vulnerability to xylem cavitation in larger trees (Rice *et al.* 2004). Reduced density of medium established trees in unburnt plots is consistent with mortality following drought. Higher competition from greater shrub and small tree density, higher *C. grandiflora* density (Fig. 5) and higher grass biomass (I.J. Radford unpubl. data 2001) in unburnt plots, may have also contributed to tree mortality (Russell-Smith *et al.* 2003a; Jurskis 2005). In contrast, in burnt plots, presumably with lower competition from grasses, small trees, *C. grandiflora* and shrubs, there was actually a slight increase in medium tree density (Fig. 5) suggesting that active growth of trees from smaller size-classes may have occurred in these plots.

Tree community structural trends in the context of regional patterns

Broad trends in riparian vegetation during the period of the study do not conform to the hypothesis that tree density is generally increasing in Queensland savannas under pastoralism. This is despite rainfall well above average in the first 2 years of the study. The generalization has been made that tree density has increased with increased intensity of pastoralism in Queensland rangelands (Burrows 2002; Burrows *et al.* 2002). The mechanism for this is thought to be intensification of cattle industries leading to greater biomass off-take by herbivores leading to reduced fire frequency/intensity (Ash *et al.* 1997). Reduced fire frequency/intensity resulting from grazing is known to lead to reduced mortality and increased recruitment of trees and shrubs, and therefore increasing woody community density (Ash *et al.* 1997; Werner 2005). This phenomenon has been observed in tropical savannas globally (Molelele & Perkins 1998). Yet, in spite of this theory, total tree

density at these sites actually decreased in the absence of fire during the study (Figs 3,5). Results like this, albeit over short time frames and at only three sites, and also recent studies in longer term trends in woody vegetation (Krull *et al.* 2005), calls into question the generality of increases in tree density across north-eastern savannas under cattle grazing enterprises.

Shrub dynamics

Shrub communities are relatively dynamic components of woody plant communities in northern Australian savannas (Edwards *et al.* 2003), although links with fire regime are not always as obvious as for trees (Russell-Smith *et al.* 2003a; Andersen *et al.* 2005). The obvious exception to this is fire-sensitive obligate seeding species in some sandstone areas that are threatened by increases in severity (intensity or frequency) of fires (Russell-Smith *et al.* 1998, 2002). In this study there was a trend towards increasing shrub density in all but one set of the dry-season burning treatment (Fig. 5), evidence that shrub communities changed floristically (Table 2), and evidence that general increases in density for some species (e.g. *M. cunninghamii*, *C. ovata*) were suppressed by some fire treatments. In this study, fire-related effects on the most common shrub elements of riparian plant communities appeared to be minor compared with changes occurring independently of fire.

One caveat to shrub dynamic interpretations here should be made in regard to multistemmed shrubs within experimental plots (e.g. *C. ovata* and juvenile *Eucalyptus/Corymbia* spp.). Observed increases for these species may be due to greater ability to see ground level rooting at the end of the study compared with the initial record. Significant reductions in herbaceous biomass in the final year of this study (I.J. Radford, unpubl. data 2001) may have increased the ability to accurately count basal stems. This is likely due to reduced rainfall in the final wet season, and through removal of herbaceous biomass through burning and selective grazing. Increased ability to see ground level vegetation may therefore have contributed to increases in numbers of shrubs counted in 2002. This issue could be addressed in future studies by individually tagging shrubs before imposition of experimental burning treatments. These artefacts, however, apply only to a few species in the study as most were single stemmed or had only few stems. Conversely, apparently single clumps of *C. ovata* could contain as many as 30 rooting nodes.

Fire-related impacts on riparian vegetation

The three primary fire-related impacts on riparian vegetation were reduced density of some tree size-classes,

decreases in density of the exotic species *C. grandiflora*, and increases in density of some native ruderal species. Loss of very large trees in some dry-season burnt plots, and loss of saplings in dry season and repeatedly burnt plots (Fig. 5), are consistent with previous studies showing a consistent relationship between tree mortality and fire intensity and frequency both in woodland (Williams *et al.* 1998, 1999; Russell-Smith *et al.* 2003a) and in riparian habitats (Douglas *et al.* 2003; Douglas & Setterfield 2004). Fire-related losses of large trees, along with tree basal area reductions, may have important implications for ecosystem function (e.g. hydrology, creek bank stability), competition dynamics (e.g. invasion and recruitment) and habitat for fauna (e.g. tree hollows). The role of large trees in riparian function and habitat provision are unknown in these tropical riparian ecosystems. Trees with hollows, however, are known to provide habitat for arboreal mammals and bird species in many Australia ecosystems (Gibbons & Lindenmayer 2002) including the tropics (McFadyen *et al.* 1991; Tidemann *et al.* 1992, 1999).

Consistent with previous studies (Grice 1996, 1997; Bebawi *et al.* 2000), *C. grandiflora* was significantly reduced in density (Fig. 2) and stature/biomass (Fig. 5) after fire. Greater impacts on this species were associated with higher intensity dry-season fires and with repeated fires. This reduction is likely to be due to fire-related mortality (Grice 1997), although we cannot verify this directly as individual plants were not marked pre-fire. Such a reduction in the density and biomass of *C. grandiflora* is likely to lead to direct benefits in some associated native species in riparian habitats. Valentine (2006) and Valentine *et al.* (2007) found that native skinks avoided *C. grandiflora* dominated habitats, and that *C. grandiflora* significantly changed invertebrate composition. A number of arboreal riparian mammal and bird species are thought to be threatened by *C. grandiflora* dominance (Chippendale 1991; McFadyen *et al.* 1991) and may be benefited by reduced density of this invader, if damage to major habitat trees can be minimized through the use of low intensity burns.

Experimental fires at these sites did not lead to widespread establishment of major native ruderal or disturbance tolerant species, although some species increased after fire. Single dry-season fires led to major increases in some native *Acacia*, in particular *A. salicina* and *A. holosericea*, but also apparent decreases in others (e.g. *A. leptostachya*). Increases were likely to result from recruitment events, although we have no direct data on this. Fire, however, is known to stimulate seed germination of many Australian *Acacia* spp. (Bradstock & Auld 1995). Density decreases in *Acacia* spp. after moderate intensity dry-season fires appear to be attributable directly to fire-related mortality, with dead *Acacia* trees/shrubs clearly present in sampling plots post fire. There seems to have

been little effect of wet-season burns, or repeated burning, on *Acacia* numbers, suggesting that low-intensity fires are insufficient to induce significant germination or mortality. Relatively low density, and restricted distribution of *Acacia* spp. at experimental sites, has meant that fire-related changes in their populations had little overall influence on broader riparian vegetation communities.

The weed–fire cycle

Fire treatment did not lead to major recruitment events for any of the exotic species within the study area. No seedlings of either *C. grandiflora* or other exotic woody species were observed during the study, and this may be related to effective reduction in recruitment, in the case of the former species, as a result of biocontrol agent impacts on seed production (Mo *et al.* 2000; Volger & Lindsay 2002; Radford 2003). There is therefore little evidence that burning in riparian zones in the presence of exotic woody species will lead to irreversible vegetation and ecosystem degradation in these landscapes because of prescribed fire disturbance (although impacts on herbaceous exotic species are yet to be analysed).

Fire can lead to significant impacts on native ecosystems not only through fire induced recruitment events, but also through alteration of fire intensity and frequency in target habitats, leading to greater impacts on dominant established native species. Change of vegetation flammability and impacts because of weed presence, known as the weed–fire cycle (Brooks *et al.* 2004), has been documented for a number of exotic species in Australian rangelands (Butler & Fairfax 2003; Rossiter *et al.* 2003). Changes in flammability and initiation of weed–fire cycles are well documented for invasive grass species globally (D’Antonio & Vitousek 1992) and there are a number of Australian examples of this phenomenon (Rossiter *et al.* 2003). However, exotic vines, such as *C. grandiflora*, can also lead to significant changes in fire regime. This is particularly in relation to changes in the distribution of flammable fuels relative to native species. For instance, fuel ladders (vines and towers into the canopy) and increased flammable fuels leading up to and including tree canopies could increase fire intensity here (Brooks *et al.* 2004). Although there was evidence that canopy fire intensity may have been increased in some parts of the study area because of *C. grandiflora* fuel ‘ladders’ and penetration of vine fuels into the canopy itself, this did not lead to widespread fire mortality-related collapse of forest populations. *Cryptostegia grandiflora* vine presence in forest canopies may, however, have elevated mortality of large riparian trees in dry-season burnt plots, and as discussed this may have important consequences for biodiversity in riparian habitats.

Wet versus dry-season burning

Few studies have reported on the response of plant species in tropical savannas to fire in the build-up storm, or in the wet season. This is despite considerable evidence that fires at this time of year are natural because of lightning ignitions, occurred under indigenous fire management (Haynes 1985; Fensham 1997; Yibarbuk *et al.* 2001; Preece 2002), and are conducted for management purposes to the present day (Craig 1997, 1999; Russell-Smith *et al.* 2003b; Felderhoff & Gillieson 2006). In this study, wet-season burning had lower impacts than dry-season burning, and impacts were consistent with the lower estimated fire intensity during the wet (Williams *et al.* 1998, 1999). There was no evidence of additional impacts to woody communities because of burning plants when they were green. This study provides the first published data that we are aware of on the impacts of wet-season burning in tropical woody vegetation. Previous wet-season fire impact studies have focused on herbaceous species (Smith 1960; Stocker & Sturtz 1966; Williams & Lane 1999). The main disadvantage with timing of prescribed burning during the wet was failure of a single wet-season fire to achieve statistically significant reductions in *C. grandiflora* plant or tower density (Figs 2,5). As shown in this study, however, two prescribed burns during the wet season were able to achieve the same reductions in *C. grandiflora* density as a single dry-season burn, but without non-target effects on large trees in riparian zones. For this reason an important recommendation arising from this study is that prescribed burning for the control of *C. grandiflora* should be conducted when fire intensity is low either during the wet or in the early dry-season period.

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REFERENCES

Andersen A. N., Cook G. D., Corbett L. K. *et al.* (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecol.* **30**, 155–67.

Anderson E. R. (1993) *Plants of Central Queensland*. Queensland Department of Primary Industries, Brisbane.

Ash A. J., McIvor J. G., Mott J. J. & Andrew M. H. (1997) Building grass castles: integrating ecology and management of Australia's tropical tallgrass rangelands. *Rangel. J.* **19**, 123–44.

Bebawi F. F., Campbell S. D., Lindsay A. M. & Grice A. G. (2000) Impact of fire on rubber vine (*Cryptostegia grandiflora* R.Br.) and associated pasture and germinable seed bank in a sub-riparian habitat of north Queensland. *Plant Prot. Q.* **15**, 62–6.

Bowman D. M. J. S., Panton W. J. & McDonough L. (1990) Dynamics of forest clumps on Chenier Plains, Cobourg Peninsula, Northern Territory. *Aust. J. Bot.* **38**, 593–601.

Bradstock R. A. & Auld T. D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *J. Appl. Ecol.* **32**, 76–84.

Brooker M. I. H. & Kleinig D. A. (2004) *Field Guide to Eucalypts. Volume 3, Northern Australia*. Bloomings Books, Melbourne.

Brooks M. L., D'antonio C. M., Richardson D. M. *et al.* (2004) Effects of invasive alien plants on fire regimes. *Bioscience* **54**, 677–88.

Brown R. L. & Peet R. K. (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology* **84**, 32–9.

Burke M. J. W. & Grime J. P. (1996) An experimental study of plant community invasibility. *Ecology* **77**, 776–90.

Burrows W. H. (2002) Harry Stobbs Memorial Lecture, 2002. Seeing the wood (land) for the trees – an individual perspective of Queensland woodland studies (1965–2005). *Trop. Grassl.* **36**, 202–17.

Burrows W. H., Henry B. K., Back P. V. *et al.* (2002) Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. *Global Change Biol.* **8**, 769–84.

Butler D. W. & Fairfax R. J. (2003) Buffel Grass and fire in a Gidgee and Brigalow woodland: a case study from central Queensland. *Ecol. Manage. Restor.* **4**, 120–5.

Byram G. M. (1959) Combustion of forest fuels. In: *Forest Fire Control and Use* (ed. K. P. Davis) pp. 61–89. McGraw-Hill, New York.

Caccianiga M., Luzzaro A., Pierce S., Ceriani R. M. & Cerabolini B. (2006) The functional basis of a primary succession resolved by CSR classification. *Oikos* **112**, 10–20.

Cheney N. P. & Sullivan A. (1997) *Grassfires. Fuel, weather and fire behaviour*. CSIRO Publishing, Melbourne.

Chippendale J. F. (1991) *Potential Returns to Research on Rubber Vine (Cryptostegia Grandiflora)*. Department of Agriculture. University of Queensland, Brisbane. pp. 88.

Craig A. B. (1997) A review of information on the effects of fire in relation to the management of rangelands in the Kimberley high-rainfall zone. *Trop. Grassl.* **31**, 161–87.

Craig A. B. (1999) Fire management of rangelands in the Kimberley low-rainfall zone: a review. *Rangeland J.* **21**, 39–70.

D'Antonio C. M. & Vitousek P. M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23**, 63–87.

Davis M. A., Grime P. J. & Thompson K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88**, 528–34.

Douglas M. M. & Setterfield S. A. (2004) Catchment cover and stream water quality in an Australian tropical savanna: rapid recovery after a change to a less intense fire regime. *Ecol. Manage. Restor.* **5**, 136–8.

- Douglas M. M., Townsend S. A. & Lake S. (2003) Streams. In: *Fire in Tropical Savannas: The Kapalga Experiment* (eds A. N. Andersen, G. D. Cook & R. J. Williams) pp. 59–78. Springer-Verlag, New York.
- Dyer R., Jacklyn P., Partridge I., Russell-Smith J. & Williams D. (2001) *Savanna Burning: Understanding and Using Fire in Northern Australia*. Tropical Savanna CRC, Darwin.
- Edwards A., Kennett R., Price O., Russell-Smith J., Spiers G. & Woinarski J. (2003) Monitoring the impacts of fire regimes on vegetation in northern Australia: an example from Kakadu National Park. *Int. J. Wildland Fire* **12**, 427–40.
- Felderhoff L. & Gillieson D. (2006) Comparison of fire patterns and fire frequency in two tropical savanna bioregions. *Austral Ecol.* **31**, 736–46.
- Fensham R. J. (1996) Land clearance and conservation of inland dry rainforest in north Queensland, Australia. *Biol. Conserv.* **75**, 289–98.
- Fensham R. J. (1997) Aboriginal fire regimes in Queensland, Australia: analysis of the explorer's record. *J. Biogeogr.* **24**, 11–22.
- Fensham R. J. & Holman J. E. (1999) Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *J. Appl. Ecol.* **36**, 1035–50.
- Fensham R. J., Fairfax R. J., Butler D. W. & Bowman D. M. J. S. (2003) Effects of fire and drought in a tropical eucalypt savanna colonized by rain forest. *J. Biogeogr.* **30**, 1405–14.
- Fensham R. J., Fairfax R. J. & Archer S. R. (2005) Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *J. Ecol.* **93**, 596–606.
- Gibbons P. & Lindenmayer D. (2002) *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing, Collingwood.
- Gregory S. V., Swanson F. J., McKee W. A. & Cummins K. W. (1991) An ecosystem perspective of riparian zones. *Bio-science* **41**, 540–51.
- Grice A. C. (1996) Seed production, dispersal and germination in *Cryptostegia grandiflora* and *Ziziphium mauritiana*, two invasive shrubs in tropical woodlands of northern Australia. *Aust. J. Ecol.* **21**, 324–31.
- Grice A. C. (1997) Post-fire regrowth and survival of the invasive tropical shrubs *Cryptostegia grandiflora* and *Ziziphium mauritiana*. *Aust. J. Ecol.* **22**, 49–55.
- Grice A. C. (2006) The impacts of invasive plant species on the biodiversity of Australian rangelands. *Rangeland J.* **28**, 27–35.
- Grice A. C. & Brown J. R. (1996) The population ecology of the invasive tropical shrubs *Cryptostegia grandiflora* and *Ziziphium mauritiana* in relation to fire. In: *Frontiers of Population Ecology* (eds R. B. Floyd, A. W. Sheppard & P. J. De Barro) pp. 589–97. CSIRO, Melbourne.
- Grice A. C., Radford I. J. & Abbott B. N. (2000) Regional and landscape-scale patterns of shrub invasion in tropical savannas. *Biol. Invasions* **2**, 187–205.
- Grime J. P. (1988) The C-S-R model of primary plant strategies – origins, implications and tests. In: *Plant Evolutionary Biology* (eds L. D. Gottlieb & S. K. Jain) pp. 371–93. Chapman & Hall, London.
- Grime J. P., Thompson K., Hunt R. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**, 259–81.
- Haynes C. D. (1985) The pattern and ecology of *munwag*: traditional Aboriginal fire regimes in north-central Arnhemland. *Proc. Ecol. Soc. Aust.* **13**, 203–14.
- Johnson A. (2002) *North Australian Grassland Fuel Guide*. Tropical Savanna Cooperative Research Centre, Darwin.
- Jurskis V. (2005) Eucalypt decline in Australia, and a general concept of tree decline and dieback. *For. Ecol. Manage.* **215**, 1–20.
- Krull E. S., Skjemstad J. O., Burrows W. H. *et al.* (2005) Recent vegetation changes in central Queensland, Australia: evidence from Delta 13 C and 14 C analyses of soil organic matter. *Geoderma* **126**, 241–59.
- Lonsdale W. M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**, 1522–36.
- McFadyen R. E., Chippendale J. F. & Tomley A. J. (1991) Rubber vine (*Cryptostegia grandiflora*) the most critical weed of concern to conservation in Australia. Paper was presented to the Conservation Biology Conference, University of Queensland, Brisbane.
- Mackey A. P., Carston K., James P. *et al.* (1996) *Rubber Vine (Cryptostegia Grandiflora) in Queensland*. Department of Natural Resources, Queensland.
- Mo J., Trevino M. & Palmer W. A. (2000) Establishment and distribution of the rubber vine moth, *Euclasta whalleyi* Popescu-Gorj and Constantinescu (Lepidoptera: Pyralidae) following its release in Australia. *Aust. J. Entomol.* **39**, 344–50.
- Moleele N. M. & Perkins J. S. (1998) Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana. *J. Arid Environ.* **40**, 245–53.
- Preece N. (2002) Aboriginal fires in monsoonal Australia from historical accounts. *J. Biogeogr.* **29**, 321–36.
- Pysek P. & Prach K. (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *J. Biogeogr.* **20**, 413–20.
- Radford I. J. (2003) Demography, fecundity and natural enemy dynamics of rubber vine (*Cryptostegia grandiflora*) in riparian and upland sites of north Queensland. *Plant Prot. Q.* **18**, 138–42.
- Rice K. J., Matzner S. L., Byer W. & Brown J. R. (2004) Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* **139**, 190–8.
- Rogers L. G., Cannon M. G. & Barry E. V. (1999) *Land Resources of the Dalrymple Shire*. Department of Natural Resources, Brisbane.
- Rossiter N. A., Setterfield S. A., Douglas M. M. & Hutley L. B. (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Divers. Distrib.* **9**, 169–76.
- Russell-Smith J., Ryan P. G., Klessa D., Waight G. & Harwood R. (1998) Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. *J. Appl. Ecol.* **35**, 829–46.
- Russell-Smith J., Ryan P. G. & Cheal D. C. (2002) Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, intervals, patchiness. *Biol. Conserv.* **104**, 91–106.
- Russell-Smith J., Whitehead P. J., Cook G. D. & Hoare J. L. (2003a) Response of *Eucalyptus*-dominated savanna to frequent fires: lessons from Munmarlary, 1973–96. *Ecol. Monogr.* **73**, 349–75.
- Russell-Smith J., Yates C., Edwards A. *et al.* (2003b) Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable management. *Int. J. Wildland Fire* **12**, 283–97.
- Russell-Smith J., Stanton P. J., Whitehead P. J. & Edwards A. (2004) Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-east Australia. I. Successional processes. *J. Biogeogr.* **31**, 1293–303.

- Sattler P. & Williams R. (1999) *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency, Brisbane.
- Smith E. L. (1960) Effects of burning and clipping at various time during the wet season on tropical tall grass range in Northern Australia. *J. Rangeland Manage.* **13**, 197–203.
- Stocker G. C. & Sturtz J. D. (1966) The use of fire to establish Townsville lucerne in the Northern Territory. *J. Exp. Agric. Anim. Husbandry* **6**, 277–9.
- Stohlgren T. J., Bull. K. A., Otsuki Y., Villa C. A. & Lee M. (1998) Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecol.* **138**, 113–25.
- Thompson K., Hodgson J. G., Grime J. P. & Burke M. J. W. (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *J. Ecol.* **89**, 1054–60.
- Tidemann S. C., Boyden J., Elvish R., Elvish J. & O'Gorman B. (1992) Comparison of breeding sites and habitat of two hole-nesting estrildid finches, one endangered, in northern Australia. *J. Trop. Ecol.* **8**, 373–88.
- Tidemann S. C., Lawson C., Elvish R., Boyden J. & Elvish J. (1999) Breeding biology of the Gouldian Finch *Erythrura gouldiae*, an endangered finch of northern Australia. *EMU* **99**, 191–9.
- Tomley A. J. (1998) *Cryptostegia grandiflora* Roxb. ex R.Br. In: *The Biology of Australian Weeds* (eds F. D. Panetta, R. H. Groves & R. C. H. Shepherd) pp. 63–76. R.G and F.J Richardson, Melbourne.
- Townsend K. (1997) *Field Guide to Plants of the Dry Tropics*. Society for Growing Australian Plants, Townsville Branch Inc, Aitkenvale.
- Valentine L. E. (2006) Habitat avoidance of an introduced weed by native lizards. *Austral Ecol.* **31**, 732–5.
- Valentine L. E., Roberts B. & Schwarzkopf L. (2007) Mechanisms driving avoidance of non-native plants by lizards. *J. Appl. Ecol.* **44**, 228–37.
- Vigilante T. & Bowman D. M. J. S. (2004) Effects of fire history on the structure and floristic composition of woody vegetation around Kalumburu, North Kimberley, Australia: a landscape-scale experiment. *Aust. J. Bot.* **52**, 381–404.
- Vitelli J. S. (1995) Rubber vine. In: *Exotic Woody Weeds and Their Control in North West Queensland* (ed. N. March) pp. 14–17. Isa Printing Service, Mount Isa.
- Volger W. & Lindsay A. (2002) The impact of the rust fungus *Maravalia cryptostegiae* on three rubber vine (*Cryptostegia grandiflora*) populations in tropical Queensland. In: *Proceedings 13th Australian Weeds Conference* (eds H. S. Jacob, J. Dodd & J. H. Moore) pp. 180–2. Plant Protection Society of WA, Perth.
- Werner P. A. (2005) Impact of feral water buffalo and fire on growth and survival of mature savanna trees: an experimental field study in Kakadu National Park, northern Australia. *Austral Ecol.* **30**, 625–47.
- Williams D. & Cook G. (2001) Savanna fire regimes. In: *Savanna Burning* (eds R. Dyer, P. Jacklyn, I. Partridge, J. Russell-Smith & D. Williams) pp. 15–28. Tropical Savanna CRC, Darwin.
- Williams R. J. & Lane A. M. (1999) Wet season burning as a fuel management tool in wet-tropical savannas: applications at Ranger Mine, Northern Territory, Australia. In: *Proceedings of the VI International Rangeland Congress*, Vol. 2 (eds D. Eldridge & D. Freudenberger) pp. 972–7. VI International Rangeland Congress, Inc, Townsville.
- Williams R. J., Gill A. M. & Moore P. H. R. (1998) Seasonal changes in fire behaviour in a tropical savanna in northern Australia. *Int. J. Wildland Fire* **8**, 227–39.
- Williams R. J., Cook G. D., Gill A. M. & Moore P. H. R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Austral Ecol.* **24**, 50–9.
- Williams R. J., Woinarski J. C. Z. & Andersen A. N. (2003) Fire experiments in northern Australia: contributions to ecological understanding and biodiversity conservation in tropical savannas. *Int. J. Wildland Fire* **12**, 391–402.
- Woinarski J. C. Z., Risler J. & Kean L. (2004) Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecol.* **29**, 156–76.
- Yibarbuk D., Whitehead P. J., Russell-Smith J. *et al.* (2001) Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *J. Biogeogr.* **28**, 325–43.