The influences of climate, habitat and fire on the distribution of cockatoo grass (*Alloteropsis semialata*) (Poaceae) in the Wet Tropics of northern Australia

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Abstract. Cockatoo grass (*Alloteropsis semialata* (R.Br.) A. Hitchc.) is considered a keystone species in northern Australian ecosystems as it provides a food resource for many species, including several endangered vertebrates. This study examined both local and regional environmental factors influencing cockatoo grass distribution and abundance in the Wet Tropics of north Queensland, Australia. Local distribution and abundance were investigated in the sclerophyll ecotone between open woodland and tall open forest, because little is known about cockatoo grass distribution within this habitat; also, the endangered northern bettong (*Bettongia tropica*) is restricted to this habitat and depends on cockatoo grass for its survival. Regional-scale modelling of distribution was undertaken to examine the climatic tolerances of cockatoo grass in Queensland. Density of cockatoo grass was negatively related to litter cover, soil moisture, and the presence of two dominant grass species, *Themeda triandra* [Forssk.(R.Br.) Stapf] and *Cleistochloa subjuncea* (C.E.Hubb.). Soil nutrients (N, C, S, and C : N ratio) were positively related to density of cockatoo grass. A late dry season experimental burn demonstrated that cockatoo grass had high survival to fire, with increased density and flowering in response to fire. Regional-scale modelling using climate variables indicated that cockatoo grass is more suited to the drier end of the sclerophyll habitat range. Cockatoo grass in the woodland-forest ecotone in the Wet Tropics appears to be influenced by several environmental features associated with the ground layer. The species benefits from the reduction in litter cover and competing grass species that result from management actions such as prescribed burning. Understanding of the factors limiting this species, both at a local and regional scale, can be used to guide management of this ecotone habitat for both cockatoo grass and the survival of other species that depend on it.

Introduction

Cockatoo grass (*Alloteropsis semialata* (R.Br.) A. Hitchc.) is a widespread species native to northern Australia, New Guinea and Melanesia (Bostock and Holland 2007), and also occurs throughout parts of Africa and Asia (Crowley and Garnett 2001). In Australia, its seeds and culms provide food resources for many animal species, such that it is considered to be a keystone species sustaining biodiversity in savanna ecosystems of northern Australia (Crowley 2008). Several bird species, such as the golden-shouldered parrot (*Psephotus chrysopterygius*), and the Gouldian finch (*Erythrura gouldiae*) (Crowley and Garnett 2001; Dostine et al. 2001; Abell et al. 2006; Crowley 2008) depend on cockatoo grass. The endangered marsupial, the northern bettong (*Bettongia tropica*), depends on the culms of cockatoo grass when availability of its main food source, truffles, is low during the late dry season (Johnson and McIlwee 1997; Abell et al. 2006). Northern bettings live close to the wet sclerophyll-rainforest ecotone, where cockatoo grass is generally less abundant than it is in dry *Eucalyptus* woodland, probably as a result of shading by wet sclerophyll vegetation (Vernes 1999, 2003; Abell et al. 2006; Mathams 2008). Information on the ecological factors limiting the distribution and abundance of cockatoo grass in this ecotone is therefore crucial for an understanding of limits to the distribution of the northern bettong.

Although it is rarely the dominant grass species, healthy populations of cockatoo grass are thought to indicate a healthy ecosystem with an appropriate fire management and minimal grazing impacts (Crowley 2008; Mathams 2008). Fire has been shown to advantage cockatoo grass in savanna environments (Woinarski et al. 2004; Crowley et al. 2009; Scott et al. 2009; Russell-Smith et al. preprint) over other, more competitive, perennial grasses, but little is known about this species in closed forest systems such as wet sclerophyll forest. A reduction of frequency and intensity of fires since European settlement has facilitated a transition of wet sclerophyll habitats towards a denser mid-canopy structure as a result of encroachment of pioneer rainforest vegetation and an increase in abundance of *Allocasuarina* spp. (Withers and Ashton 1977; Withers 1978; Kellman 1986; Harrington and Sanderson 1994; Lunt 1998; Abell et al. 2006). Where fire has been absent for long
periods, vegetation change in the ground layer has also been observed, with an increase in shade-tolerant sedge species and rainforest vines (Everson et al. 1988). This may suppress cockatoo grass, which is a poor competitor (Walker et al. 1997; Crowley and Garnett 2001).

It is unclear to what extent altered fire regimes may have affected cockatoo grass within this ecotonal habitat. Although individual plants tolerate dry season fires because their tillers can survive long periods in dormancy, seeding early in the wet season, and the lacking persistent seed bank, makes cockatoo grass affected cockatoo grass within this ecotonal habitat. Although cockatoo grass, which is a poor competitor (Walker et al. 1988), and the combination of changes in fire regime, grazing pressure, and shading could prevent the regeneration of cockatoo grass, with the authors already noting declines within Allocasuarina forest in some areas within a decade.

The aim of this study was to investigate the distribution and abundance of cockatoo grass in the ecotone between wet sclerophyll forest and dry woodland on the margins of the Wet Tropics region in north Queensland. Specifically, we asked the following questions: (i) where does cockatoo grass grow in relation to habitat features such as soil, light, habitat structure, and vegetation communities within this habitat; (ii) what is the relationship between cockatoo grass and other grass species in the wet sclerophyll ecotone; and (iii) how is this affected by a single late dry season fire? To answer these questions, we first conducted a site-scale survey of cockatoo grass in Allocasuarina/sclerophyll woodlands. In addition, we explore the relationship between regional-scale climatic factors and the distribution of this species within the Wet Tropics.

Materials and methods

Study sites

The study was conducted at the Mt Zero-Taravale wildlife sanctuary (Australian Wildlife Conservancy) on the Coane Range, north-east Queensland (146°11' E, 19°07'S). Four treatment and control sites (Site 1: 146°09'E, 19°03'S, altitude 855 m; Site 2: 146°10'E, 19°02'S, altitude 801 m; Site 4: 146°11'E, 19°07'S, altitude 850 m; Site 5: 146°10'E, 19°04'S, altitude 900 m) were selected to examine the relationship between cockatoo grass density and habitat features within the wet sclerophyll ecotone and to conduct an experimental burn. A fifth site (Site 3: 146°11'E, 19°08'S, altitude 796 m) did not contain cockatoo grass, either before or after the experimental burns, and was not included in any analysis.

Each site contained three 50 x 20-m replicate plots, and was isolated from the surrounding habitat by fire breaks created by a road grader. Sites were chosen in similar habitat types located 500 m apart to maintain independence, and situated in areas suitable for performing containable experimental burns. The sites fell along a gradient from tall open forest to medium woodlands situated on granite-derived soils (Stanton 2007). All sites were located in wet/mesic sclerophyll Allocasuarina habitat types, which occur on the transition between tall open forest and open woodland. Dominant tree species in the canopy were Eucalyptus resinifera, Syncarpia glomulifera, Corymbia intermedia, E. reducta, E. portuensis, and C. leptoloma, C. reducta and C. abergiana (Stanton 2007). All sites have Allocasuarina torulosa trees and saplings in the sub-canopy and understorey.

Each site was selected for known or suspected presence of cockatoo grass. The dominant grass species at most sites was Themeda triandra [Forssk.(R.Br.) Stapf] and/or Cleistochloa subjuncea (C.E.Hubb.). Other common grass species occurring throughout the sites included Imperata cylindrica and Panicum spp.

Sampling methods

Environmental data

Environmental data (11 variables) were collected for each of the three plots in each of the four treatment sites in a pre-burn survey (in November, n = 12; Site 3 excluded). Unforeseen problems prevented the control plots from being sampled in this pre-burn survey. Variables were recorded along a permanent 20-m transect established within each plot. Data consisted of measurements taken from the centre of each transect as well as estimates of percentage cover over the whole transect.

Soil was collected from each plot at the centre of the 20-m transect during each sampling period. Soil samples were analysed for the soil nutrients (mg/g) nitrogen (N), carbon (C), sulfur (S), and the C : N ratio. Mean soil moisture was determined for each plot (mL/g) for each survey from wet and dry weights. Soil samples were sieved to 2 mm to separate earth material from gravel. Soil N, C, and S were determined with an Elementar Vario Max CNS Analyser (Elementar, Hanau Germany) by the Sediment Laboratory, School of Earth and Environmental Sciences, James Cook University, Townsville. Soil variables were collected during all surveys.

Each of three plots in all of the five treatment sites were assessed for the presence and density of cockatoo grass pre-burning within 20 1-m² quadrats placed every 1 m on alternate sides of a permanent 20-m transect. All individual cockatoo grass plants in the plots were tagged to assess post-fire survivorship. Cockatoo grass plants develop subterranean tillers (Crowley and Garnett 2001), which are shoots that sprout from the base of the plant. Any vegetative growth of cockatoo grass observed within a permanent 10-cm-diameter plot around each plant was regarded as being from the same individual plant. Each plant was marked within a sub-quadrat using an individually numbered tag attached to a 10-cm ring encircled around the base of the plant and secured using a metal peg to allow survivorship to be measured as presence or absence of a living individual plant in each marked sub-quadrat throughout the survey, and calculated as the number of cockatoo grass plants in each survey over the initial population density of each plot. All individual cockatoo grass plants that were flowering along transects were recorded. The 20 1-m² quadrats were also assessed for percentage of total grass cover, total grass density, T. triandra cover, and C. subjuncea cover. Density was measured as the number of individual plant stems or shoots within the quadrat. Percentage projected foliage cover for the ground layer was visually estimated as a percentage, giving an indication of ecological dominance for each species. Dominant ground cover species (T. triandra and C. subjuncea) for each plot were then combined and averaged to represent the total cover and density measure per plot. In addition, percentage litter cover and litter
layer depth (cm) were measured, as an average of 13 random samples per plot.

**Experimental burn**

An experimental burn was undertaken of all four treatment sites in November 2007. This burn was of low to moderate intensity across plots, with flame height varying from 0.3 to 6.0 m (*Allocasuarina* flare-ups accounted for larger flames). Unfavourable weather prevented Site 5 from being burnt; so this site was removed from all post-burn analysis. The control plot in Site 4 was inadvertently burnt in November 2008, so was excluded from analysis using data from this sampling period. To assess recovery of cockatoo grass, treatment sites were resampled in April and November 2008. Control plots were also sampled in these periods. To determine how immediate survival was affected by the experimental burn, survival was assessed 1 week post burn. Control sites were assessed for flowering at the post-burn/wet survey and the 1-year post-burn survey. Cockatoo grass survival in the unburnt control plots was assessed at the 1-year post-burn survey for direct comparison with the treatment sites.

**Analysis**

Environmental variables collected from the treatment sites in the pre-burn habitat surveys were examined to test for site-specific features associated with cockatoo grass density. Correlations between the 11 variables were measured using a Spearman rank correlation matrix in order to reduce the number of correlated variables. Pairs of variables with high Spearman pair-wise correlation coefficients \((r > 0.5)\) were reduced to a single variable to represent the pair by giving one variable priority (as per Graham 2003). All variables were standardised before further analysis.

Selected variables were then used as independent variables in a Generalised Linear Model to explain cockatoo grass density. As cockatoo grass density was count data, the Poisson distribution was used with a log-link function. A Kullback-Leibler information-theoretic method to model relationships was undertaken to construct all possible model configurations (best subsets), using the Akaike Information Criterion (AIC) as an objective means of model selection (Burnham and Anderson 2002). This is not a hypothesis testing method, but rather a model selection method that uses Akaike model weights \((w_i)\), or relative strengths of evidence, to determine the most parsimonious models (Burnham and Anderson 2002). All analyses were conducted in R (version 2.10.0, [http://www.r-project.org](http://www.r-project.org), accessed 20 April 2011), with use of the MuMln R package (http://cran.r-project.org/web/packages/MuMln/index.html, accessed 20 April 2011). To correct for bias \((n/K < 40)\), the second-order information criterion \((\text{AIC}_c)\) was used for each model (Burnham and Anderson 2002). The best-supported model was selected as the \(\text{AIC}_{c\min}\) (the model with the lowest \(\text{AIC}_c\) value). Plausible models were presented if they fell within 2 \(\text{AIC}_c\) units \((\Delta)\) of the \(\text{AIC}_{c\min}\), although models within 4–7 \(\text{AIC}_c\) units \((\Delta)\) were retained as they still contain support (Burnham and Anderson 2002). The relative likelihood, or weight of evidence for that model being the most parsimonious model, was calculated for each model in the set using \(w_i\). Model weights vary from 0 (no support) to 1 (complete support).

Evidence ratios were calculated from model weights to determine if one model was convincingly better than the others or if a 95% confidence set of models was needed (Burnham and Anderson 2002). A measure of model fit is provided as the percent deviance explained.

In addition, to determine the relative importance of each variable contributing to model building, model averaging was conducted. Variable importance was assessed as the sum of the weight scores \((w_i)\) for each model of which the variable was a component, with values closer to 1 being relatively more important and values above 0.5 considered good (Ritchie et al. 2009). Akaike \(w_i\) were used to weight the parameter estimates and variance \((s.e.)\) associated with each model. The parameter estimates are reported with confidence intervals, to show whether or not the estimate of effect size overlapped zero. The magnitude (impact on model building) and direction of the effect (positive or negative) are indicated by the direction and magnitude of the parameter estimate.

For analysis of grass data post burn, all grass data distributions were tested for normality by Shapiro–Wilk (SW-W). The distribution of cockatoo grass density was non-normal (SW-W = 0.76, \(P = 0.00005\)) and was transformed \([\log(x + 1)]\) for nested ANOVA analysis (SW-W = 0.95, \(P = 0.18\)). Control sites were included in data analysis only for post-burn surveys. Cockatoo grass survival was uniformly high and approaching 1. Data were then compared between all surveys to determine if time from burn influenced survival, as well as between sites, and plots to determine if site-specific factors influenced survival. To determine if treatment sites differed from control sites, a comparison with control sites was undertaken for 1 year post fire (Sites 1 and 2 only as Site 4 had been inadvertently burnt by this time). To examine if cockatoo grass flowering differed between control and treatment sites, a Chi-square test for homogeneity \((\chi^2)\) was used.

The distributions of total density and cover \((T. triandra\) and \(C. subjuncea\) combined) were non-normal (total cover: SW-W = 0.70, \(P = 0.00001\); and total density: SW-W = 0.91, \(P = 0.05\)), and could not be normalised by transformation. To test for variation in total density and cover among treatment sites, plots and surveys, a Kruskal–Wallis one-way non-parametric analysis of variance (ANOVA, H) was used.

**Regional-scale modelling**

To determine large-scale controls on cockatoo grass distribution a species distribution model was generated using location records from across Queensland. Location records were obtained from the Queensland Herbarium and supplemented with opportunistic data collected by the author and records obtained in other studies from the Wet Tropics region (Abell et al. 2006; Mathams 2008). Cockatoo grass has a broad distribution and its climatic tolerances may not be completely captured by Queensland records, but we felt that a distribution model based on Queensland records would indicate what climatic factors might influence its occurrence in wet sclerophyll communities in Queensland.

Climate data were entered as long-term climate means, derived from ANUCLIM 5.1 (McMahon et al. 1995) software using monthly averages and an 80-m DEM resampled from ~250 m (GEODATA 9 Second DEM Version 2; Geoscience
Values represent the number of parameters (smallest AICc, in descending order). The four highest ranked models are shown (between $K$ and 7 of AICc). Variable codes refer to: LC, litter cover (%); GD, grass density (per m$^2$); N, nitrogen (mg/g); CC, Cleistochloa subjuncea percentage cover (%); LL, litter layer depth (mm)

<table>
<thead>
<tr>
<th>Model</th>
<th>Variable</th>
<th>Log(L)</th>
<th>AICc</th>
<th>$\Delta$</th>
<th>$w_i$</th>
<th>% Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>LC</td>
<td>GD</td>
<td>CC</td>
<td>6</td>
<td>-30.04</td>
<td>88.88</td>
</tr>
<tr>
<td>2</td>
<td>LC</td>
<td>GD</td>
<td>N</td>
<td>5</td>
<td>-35.56</td>
<td>91.18</td>
</tr>
<tr>
<td>3</td>
<td>LC</td>
<td>LL</td>
<td>GD</td>
<td>5</td>
<td>-36.48</td>
<td>92.95</td>
</tr>
<tr>
<td>4</td>
<td>LC</td>
<td>LL</td>
<td>GD</td>
<td>N</td>
<td>-33.23</td>
<td>95.34</td>
</tr>
</tbody>
</table>
Table 2. Model averaging results for relative importance of contributing variables to Poisson generalised linear models using Akaike’s information criterion for cockatoo grass density (per m$^2$)

Values represent the relative importance of each variable ($w_i$), average estimates (estimate), standard errors (s.e.), and upper and lower confidence intervals (CI).

<table>
<thead>
<tr>
<th>Variable</th>
<th>$w_i$</th>
<th>Estimate (s.e.)</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.71</td>
<td>0.23</td>
<td>1.17</td>
<td>2.24</td>
</tr>
<tr>
<td>Grass density (%)</td>
<td>1.0</td>
<td>-1.77 (0.17)</td>
<td>-2.56</td>
<td>-0.99</td>
</tr>
<tr>
<td>Litter cover (%)</td>
<td>1.0</td>
<td>-1.62 (0.001)</td>
<td>-2.01</td>
<td>-1.23</td>
</tr>
<tr>
<td>Nitrogen (mg/g)</td>
<td>0.88</td>
<td>0.32 (0.07)</td>
<td>0.17</td>
<td>0.48</td>
</tr>
<tr>
<td>Cleistochloa subjuncea cover (%)</td>
<td>0.67</td>
<td>-0.33 (0.16)</td>
<td>-0.67</td>
<td>0.02</td>
</tr>
<tr>
<td>Litter layer (mm)</td>
<td>0.08</td>
<td>-0.03 (0.06)</td>
<td>-0.15</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Fig. 1. Cockatoo grass density (per m$^2$) for burn treatments versus control plots by survey. Survey 1: pre-burn; survey 2: post-burn/post-wet; survey 3: 1 year post burn. (Survey 1 omitted for control sites). Error bars represent standard error.

Table 3. Cockatoo grass density (per m$^2$) by site and survey period, including survey average grouped as treatment or control sites

Mean and standard error (s.e.) are presented. Pre-burn surveys were not conducted for control sites (indicated in the table as –).

<table>
<thead>
<tr>
<th></th>
<th>Pre-burn Mean (s.e.)</th>
<th>Post-burn/wet Mean (s.e.)</th>
<th>1 year post Mean (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Treatment site</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T1</td>
<td>0.53 (0.09)</td>
<td>0.17 (0.17)</td>
<td></td>
</tr>
<tr>
<td>T2</td>
<td>2.9 (0.43)</td>
<td>1.47 (0.03)</td>
<td></td>
</tr>
<tr>
<td>T4</td>
<td>9.25 (2.21)</td>
<td>3.4 (0.79)</td>
<td></td>
</tr>
<tr>
<td>Survey average</td>
<td>1.53 (0.69)</td>
<td>4.23 (1.45)</td>
<td>1.68 (0.52)</td>
</tr>
<tr>
<td>(b) Control site</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1</td>
<td>–</td>
<td>0.68 (0.41)</td>
<td>0.62 (0.35)</td>
</tr>
<tr>
<td>C2</td>
<td>–</td>
<td>0.57 (0.3)</td>
<td>0.85 (0.45)</td>
</tr>
<tr>
<td>C4</td>
<td>–</td>
<td>9.22 (3.63)</td>
<td>–</td>
</tr>
<tr>
<td>Survey average</td>
<td>–</td>
<td>3.49 (1.78)</td>
<td>0.73 (0.26)</td>
</tr>
</tbody>
</table>

individuals indistinguishable. Maximum total cover measured at all sites never exceeded 50%.

Survival of tagged cockatoo grass plants was highest immediately after the burns, 1 week post fire (survival proportion: 0.99 ± 0.01), followed by the post-burn wet season surveys (survival proportion: 0.97 ± 0.02) and less survival 1 year post fire (survival proportion: 0.92 ± 0.03) ($H_{2,27} = 7.12$, $P = 0.03$). No variation between sites ($H_{2,27} = 1.28$, $P = 0.53$) or plots ($H_{2,27} = 2.79$, $P = 0.25$) was found. There was no significant difference between control and treatment sites ($H_{1,12} = 1.76$, $P = 0.18$) although control sites had a slightly higher survival (control 0.97 ± 0.02, treatment 0.94 ± 0.02).

In the post-burn/wet survey, only treatment (burnt) sites were observed with flowering cockatoo grass. In the treatment sites, 16 plants were observed flowering on the measured transects out of a total of 722 counted cockatoo grass plants. No flowering cockatoo grass plants were found in the surrounding unburnt vegetation. Control sites had 628 cockatoo grass total plants over all of the measured transects, with zero flowering; cockatoo grass flowering therefore differed between treatment (burn) and control (unburnt sites) ($\chi^2 = 13.79$, $P \leq 0.05$). Flowering in November 2008 was only observed in control Site 4, which was accidentally burned just before the 1-year post surveys. Previous observations have also noted cockatoo grass flowering in sites that had been burnt, but not within immediately adjacent unburnt sites (separated by a road as a fire break) containing a thick grass sward dominated by T. triandra (B. Bateman, pers. obs.).

**Regional-scale modelling**

The Maxent model examining the relationship between climatic variables and cockatoo grass density had good discrimination (AUC = 0.81) and should be considered useful in its predictive performance (Elith et al. 2006; Guisan et al. 2007). The variable with highest contribution to the model was the maximum temperature of the warmest period (59.8%), followed by temperature seasonality (14.5%) and precipitation of the driest quarter (8.5%). From the records obtained within Queensland, it appears that cockatoo grass can persist over large maximum temperature ranges, from 22 to 38°C (Fig. 2a). However, probability of occurrence begins to decline above 30°C, and the highest probability of occurrence is close to 26°C.

Temperature seasonality appears to limit cockatoo grass on either end of the extremes, from 20°C to 220°C (CV) being the full range this species experiences in Queensland. Probability of occurrence is highest at around 90°C (Fig. 2b).

Cockatoo grass occurs where precipitation of the driest quarter ranged from 0 to 400 mm, with probability of occurrence greatest between 200 and 250 mm (Fig. 2c).

Despite cockatoo grass records being sourced only from within Queensland, it appears that the large-scale model presented here captures the near full range of tolerances for the climate variables most important to model development of this species.

**Discussion**

In this ecotone habitat, the density of cockatoo grass was negatively related to litter cover and soil moisture, as well as
to the presence of two dominant grass species, *T. triandra* and *C. subjuncea*. Grass species have been shown to be suppressed by litter cover deposited by woody plants in such habitat types (Scott 2008). Shading and litter cover reduce light levels at the grass layer, influence temperature and soil moisture levels, have chemical and mechanical effects, and can suppress establishment, germination, growth, biomass, reproductive allocation and production for some grasses (Jensen and Gutekunst 2003; Scott 2008). Fire can influence the litter layer and shading, with infrequent fires promoting shading and litter accumulation (Scott 2008). In a greenhouse experiment Scott (2008) found that growth of cockatoo grass was suppressed by the litter layer, with less seedling emergence in litter treatments than in non-litter treatments, especially when sown under the litter layer. Early successional species, such as cockatoo grass, tend to be out-competed by later successional species with larger seeds (Jensen and Gutekunst 2003); larger seed size confers an advantage for later successional species in both plant germination and establishment under litter layers and shading conditions. Density of cockatoo grass was negatively related to cover and density of two dominant grass species in this study, *C. subjuncea* and *T. triandra*. Tall perennial grasses, such as *T. triandra*, with long growing periods and high potential growth rate, expanded tussock structure, and which deposit a dense layer of ground litter, are likely to be strong competitors for water and nutrients (Grime 1973; Walker et al. 1997; Lunt 2003; Cole and Lunt 2005). *T. triandra* quickly dominates the landscape in the absence of biomass reduction due to burning, grazing, or some other management, out-competing inter-tussock species such as cockatoo grass (Walker et al. 1997; Morgan and Lunt 1999; Lunt 2003).

In the absence of fire or other disturbances, *Allocasuarina* spp. can invade and form dense stands, causing the decline of eucalypts and increase shading of the ground layer (Withers and Ashton 1977; Withers 1978; Kellman 1986; Lunt 1998; Abell et al. 2006). Saplings of *A. torulosa* become less sensitive to fire after reaching 200 cm in height (Kellman 1986). *Allocasuarina* spp. drop high volumes of needles under their canopy (Withers and Ashton 1977), and this litter layer has an allelopathic effect and can physically restrict the germination and seedling establishment of other species (Withers 1978; Abell-Davis 2008). The direct impact of *Allocasuarina* needles on cockatoo grass was not studied during this experiment, but few grass species were seen to grow under dense *Allocasuarina* needle litter. The thick needle bed associated with encroaching *A. torulosa* pockets and associate canopy cover had a lower diversity of grass species than did adjoining woodlands. The absence of cockatoo grass in sites where it had been previously recorded (McIlwee and Freeman 1998) within the study area coincides with an increase in density of *A. torulosa* within a decade (B. Bateman, pers. obs., M. Parsons, pers. obs.).

The negative relationship found between cockatoo grass density and soil moisture is consistent with previous studies in the Wet Tropics. Mathams (2008) surveyed cockatoo grass across an environmental gradient from wet sclerophyll to dry sclerophyll habitat, and found that it was least abundant in wettest habitat types with highest soil moisture, ground cover, and densities of *Allocasuarina* species, while abundance increased with number of *Eucalyptus* species, in more open grassy habitats. This was similar to the findings of Abell et al. (2006) and Vernes (2003) and suggests that cockatoo grass prefers soils under *Eucalyptus* trees, as leaf litter under eucalypts creates hydrophobic soils (Scott 2000; Doerr et al. 2006).

Density of cockatoo grass was positively related to N along with C and S. Cockatoo grass produces more biomass at higher N levels, allowing for more storage in the corn and for sexual reproduction, which is an advantage after fire in the absence of competition for light when the high assimilation and fast growth rates conferred by this corn facilitate re-sprouting and recruitment (Ripley et al. 2008). Nitrogen concentration is often higher in the litter layer, where it may be mobilised through low decomposition rates preventing replenishment of soil nutrients (Chen et al. 2001; Parsons and Congdon 2008; Prusty et al. 2009). As litter layer depth and litter cover were both negatively related to cockatoo grass density, litter nutrient mobilisation could be negatively influencing soil nutrient levels. Fire may play a key role in releasing some of this N for availability, at least in the short term (Wan et al. 2001).

To our knowledge, this is the first study on the impact of fire on cockatoo grass at the wetter end of its environmental range. Cockatoo grass had high survival (≥92%) through the late dry season following an experimental burn, similar to unburnt plots. High survival was probably mediated through dry season dormancy, as early senescence in combination with an underground carbohydrate storage base tends to make the species resistant to burning (Everson et al. 1988; Crowley and Garnett 2001). Cockatoo grass is resistant to fire when the bulk of its biomass is underground, with quick recovery attributed to the
reallocation of belowground biomass for regrowth (Ripley et al. 2010). Data from this study also indicate that fire promotes flowering in cockatoo grass. Crowley and Garnett (2001) found that foliage removal (such as caused by fire or grazing) stimulates and synchronises flowering in this species and promotes seed production. Flowering and seed production are highest in the first wet season after burning, possibly stimulated by the removal of competing plants and/or the release of nutrients from the destruction of competing plants, rank grass and litter grass species (Lunt and Morgan 2002; Williams et al. 2005).

Flower production in grasses may also be driven by light availability and release from competition as a dense, closed grass layer reduces flowering productivity (Lunt and Morgan 2002).

In the present study, fire had a positive impact on density of cockatoo grass, particularly in the first wet season after the burn, and elevated levels were still evident 1 year later. A reduction in cockatoo grass density was observed 1 year after the burn for both treatment and control in accord with other studies that have shown a positive relationship of cockatoo grass to fire frequency (Woinarski et al. 2004; Crowley et al. 2009; Scott et al. 2009; Russell-Smith et al. preprint). This is also consistent with the relationship found in this study between cockatoo grass and C. subjuicea and T. triandra.

As fire frequency influences biomass accumulation and structural dominance, short fire intervals may be needed to facilitate the coexistence of subordinate grass species such as cockatoo grass (Lunt and Morgan 2002). Fire intervals of 5 years are suggested to maintain T. triandra while allowing inter-tussock flora to co-exist (Morgan and Lunt 1999), and might benefit cockatoo grass as it experiences a boom 2–4 years post disturbance (Walker et al. 1997). As this study examined only a single late dry season fire within this ecotone habitat, future studies will need to be conducted using a variety of fire regimes over a long time period to fully understand the relationship of cockatoo grass and fire, and to develop an appropriate fire frequency management regime.

At the larger scale, both temperature and precipitation appear to limit cockatoo grass, although it has broad tolerances. The climate model identified a broad niche which encompasses the conditions suitable for both the sclerophyll to savanna habitats within which this species occurs with the wetter end of the sclerophyll woodland gradient being less favourable than the drier end of this spectrum. This is also consistent with the species being less abundant in wet sclerophyll vegetation containing Allocasuarina. Cockatoo grass distribution is limited at either end of this gradient by wetter conditions adjacent to rainforest habitats as well as by hotter and drier conditions of inland savannas. The persistence of cockatoo grass is largely dependent on vegetative growth, which depends on moisture availability (Crowley and Garnett 2001). Abundance of the C₄ form of cockatoo grass found in Australia (a C₃ form of this species is found in South Africa) is likely to be limited by drought and arid conditions, as investment in belowground biomass storage hinders recovery during drought (Ripley et al. 2007, 2008; Ibrahim et al. 2008).

The influence of fire and grazing pressure, factors likely to influence the distribution of this species, were not included in the regional-scale modelling of cockatoo grass distribution as data currently available at this scale are too coarse for useful model inputs. To improve the climate-based predictions presented here, a more detailed model could be developed using finer-scale fire histories. Factors such as fire frequency, fire weather, grazing pressure, and their likely interactions could be integrated to develop a more useful model of cockatoo grass distribution.

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