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Environmental and demographic correlates of tree recruitment and mortality in north Australian savannas

Lynda D. Prior [a,*], Brett P. Murphy [b], Jeremy Russell-Smith [b,c]

[a] School for Environmental Research, Charles Darwin University, Darwin, Northern Territory 0909, Australia
[b] Bushfires NT, Northern Territory Government, Winnellie, Northern Territory, Australia
[c] Tropical Savannas Management Cooperative Research Centre, Charles Darwin University, Darwin, Northern Territory, Australia

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ABSTRACT

Tropical savannas cover approximately 20% of the earth's land area, and therefore represent an important carbon store. Under scenarios of future climate change it is thus important to understand the demographic processes determining tree cover, namely tree recruitment, growth and mortality. This study measured tree recruitment and mortality in 123 (0.08 h) plots in Kakadu, Nitmiluk and Litchfield National Parks, in the Australian monsoonal tropics, over two consecutive 5-year intervals. Plots were located in two important habitats, both dominated by eucalyptus—lowland savanna and savanna growing on sandstone plateaux. All trees with diameter at breast height (DBH) $\geq$5 cm were tagged and identified. Recruitment was calculated as the proportion of tagged trees present at the end of an interval that were not present at the beginning. There were a total of 6666 and 6571 tree-intervals for mortality and recruitment, respectively. We used Akaike Information Criterion (AIC)-based model selection and multi-model inference to relate tree mortality and recruitment to fire frequency, mean annual rainfall (MAR), stand basal area, tree density and eco-taxonomic group. Recruitment decreased with tree density in both savanna types, and in lowland savanna, with the frequency of fires. In sandstone savanna, recruitment increased with MAR. Effects of fire on recruitment were better explained by season than severity of fire, while fire severity had a stronger influence on mortality. Mortality decreased with tree size up to about 25 cm DBH, but increased sharply when DBH exceeded 50 cm. Mortality increased with stand basal area, and increased with the frequency of late dry season fires in lowland savanna only. There was little evidence that mortality was affected by the frequency of early dry season fires or MAR. Both recruitment and mortality rates were higher for *Acacia* and Proteaceae species than for pantropical or Myrtaceae (including *Eucalyptus*) species. We identified several negative feedbacks, mediated by changes in tree density and stand basal area that help confer long-term stability to savanna tree cover. Nonetheless, changes such as a long-term increase in MAR or an increase in frequency or severity of fires are likely to result in changes in tree density, stand basal area and therefore carbon storage potential of savannas.

1. Introduction

Tropical savannas are characterised by a continuous understorey of C_4 grasses and a scattered overstorey of trees, and occur in areas with strongly seasonal rainfall that falls predominantly in the summer months (Walker, 1987). Globally, savannas cover approximately 20% of the land surface, are home to 20% of the human population, and generate almost 30% of the net primary productivity (Scholes and Walker, 1993; Young and Solbrig, 1993). The balance between tree and grass cover has profound impacts on savanna ecosystem function, affecting carbon, nutrient and hydrological cycles (Scholes and Archer, 1997; Simioni et al., 2003). Thus, it is important that we understand the processes controlling tree recruitment, growth and mortality in these environments.

Tree cover, and hence woody biomass, of arid and semi-arid savannas is determined largely by mean annual rainfall (MAR) (Sankaran et al., 2005). In African savannas with MAR above 650 mm, canopy closure is possible, and disturbance is required for the coexistence of trees and grasses (Sankaran et al., 2005). Thus, mesic savannas are 'disequilibrium' systems, and have been successfully described using demographic-bottleneck models (Higgins et al., 2000; Sankaran et al., 2004). The key feature of

* Corresponding author. Tel.: +61 8 8946 7711; fax: +61 8 8946 7720.
E-mail address: lynda.prior@cdu.edu.au (L.D. Prior).

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these models is that grasses persist in mesic savannas because inter-annual climatic variability and/or disturbances such as fire and grazing limit tree seedling germination, establishment and/or transition to mature size classes (Sankaran et al., 2004). Model simulations by Higgins et al. (2000) showed that savanna tree dynamics are characterised by long periods of slow decline in adult stems punctuated by occasional recruitment events. They concluded that understanding grass-tree interactions in savanna requires consideration of the long-term effects of life history–disturbance interactions on demography.

Unlike growth, which is a continuous process, both mortality and recruitment are infrequent events that occur only once in the life of a tree. They therefore need to be measured over large spatio-temporal scales to reliably estimate their rates. Tree mortality rates under a range of fire and herbivory regimes have been reported for savannas in Australia (Williams et al., 1999) and elsewhere (Trapnell, 1959; Thomson, 1975; Birkett and Stevens-Wood, 2005). However, while the adverse effects of fire on establishment and recruitment of savanna trees are well documented (Hoffmann, 1996, 1998, 2000; Setterfield, 2002; Werner et al., 2006), recruitment rates have seldom been quantified, especially in relation to fire.

From a 5-year fire and savanna response experiment at Kapalga, northern Australia, Williams & Prior (unpublished data) found that annual proportional recruitment was 0.083 in the unburnt treatment, compared with 0.026 in the annual late fire treatment, equivalent to 108 and 18 new trees $ha^{-1}\,y^{-1}$, respectively. Sato (1996), cited by Hoffmann and Solbrig (2003) found that in an area of Brazilian savanna that initially contained 1212 trees, during two fire cycles of 2 years each there were only 37 new recruits to the >5 cm diameter at breast height (DBH) size class, equating to an annualised proportional recruitment rate of 0.008. Marín et al. (2005) measured recruitment rates of 0.025 and 0.040, respectively in deciduous and gallery forest in Nicaragua.

Here we report rates of tree recruitment and mortality over a 10-year period in mesic savanna in three National Parks in Northern Australia. This complements the analysis of tree growth by Murphy et al. (personal communications) from the same dataset. We examine the relationship between both recruitment and mortality, and fire frequency, MAR, tree density, stand basal area, tree size and eco-taxonomic group in two major habitat types, lowland woodland and sandstone plateau woodland.

2. Methods

2.1. Study area

The study was undertaken in Kakadu (19,092 km^2), Nitmiluk (2924 km^2) and Litchfield (1464 km^2) National Parks, in the Northern Territory, Australia. The regional climate is characterised by marked rainfall seasonality, with over 90% occurring in the summer, wet season months of November through March. While rainfall varies considerably from year to year, the wet season is reliable (McDonald and McAlpine, 1990). MAR declines from over 1500 mm in the northwest to about 1000 mm in the southeast of the study area. Temperatures are high, with monthly average maximum temperatures over 30 °C throughout the year.

The climate is conducive to high fire frequencies, with the hot wet season promoting prolific grass growth, and the long, warm dry season promoting grass curing (Gill et al., 1996). The rapid accumulation of grass fuels following a fire means that fires may recur at a site every 1–2 years. Over the decade 1995–2004, 40%, 46% and 64%, respectively of Kakadu, Nitmiluk and Litchfield National Parks were burnt each year (Northern Territory Bushfires Council unpublished data).

The landforms and vegetation of the study area are described by Russell-Smith and Edwards (2006), and for the Kakadu region by Wilson et al. (1990), Russell-Smith (1995) and Russell-Smith et al. (1995). Briefly, vegetation of the three parks is predominantly eucalyptus-dominated savanna woodland. The dominant regional landform is the rugged Arnhem Land Plateau, which is mostly less than 400 m elevation. Soils, where present, are typically skeletal and infertile sands. The lowland landform included in this study comprises an undulating Cainozoic plain that stretches away from the plateau margins. Lowland soils are predominantly kandosols, and consist of deeply laterised, predominantly coarse-grained sediments, with low nutrient availability throughout the profile (McKenzie et al., 2004).

2.2. Measurements of tree recruitment and mortality

A network of permanent plots was established in the three parks in 1995 to examine the impact of fire on vegetation, and to involve park staff and Aboriginal traditional owners in the fire-monitoring program (Russell-Smith and Edwards, 2006; Murphy et al., personal communications). Each plot was 40 m × 20 m. Detailed vegetation information for trees, shrubs and ground cover was recorded at the time of plot establishment, and twice thereafter, at approximately 5-yearly intervals. This paper reports rates of tree mortality and recruitment during the two intervals at a total of 73 lowland plots (71 in the second interval) and 50 plots on the sandstone plateau (Table 1).

Within each 800 m^2-monitoring plot, all live adult trees (DBH > 5 cm) were permanently marked with metal tags, and the species and DBH were recorded. At the end of both 5-year intervals, DBH was remeasured and deaths of tagged trees were recorded. New trees with DBH > 5 cm were tagged and DBH measured; we define these new trees as recruits.

For mortality analyses, we used all trees that were present at the start of the first interval, and scored the response as 1 if it had died at the end of the 5-year interval, and 0 if it did not. We repeated this for the second interval; there were thus two observations for most trees. Similarly, recruitment was assessed on all trees present at the end of an interval. If a tree was not present at the start of an interval, it was scored 1 (a recruit), and 0 if it was present. Each observation consisted of one tree in one interval; there was a total of 6572 observations for recruitment and 6666 for mortality.

Table 1
Habitat characteristics

	Habitat	
	Lowland	Sandstone
Number of plots	73[a]	50
MAR (mm)	1266 (16)	1235 (25)
Early fire frequency (proportion of years)	0.446 (0.033)	0.372 (0.036)
Late fire frequency (proportion of years)	0.115 (0.018)	0.150 (0.024)
Initial basal area ($m^2\,ha^{-1}$)	7.65 (0.48)	7.73 (0.56)
Final basal area ($m^2\,ha^{-1}$)	7.73 (0.48)	7.06 (0.55)
Initial tree density (ha^{-1})	352 (21)	338 (24)
Final tree density (ha^{-1})	372 (25)	280 (23)
Mean DBH (cm)	13.3 (0.14)	14.6 (0.2)

Number of plots and mean values (and standard errors) of mean annual rainfall (MAR), early and late dry season fire frequencies, basal area at the start and end of the study, tree density at the start and end of the study, and tree diameter at breast height (DBH) averaged over the study period.

[a] Measurements for two plots were not available in the second interval.