

Impact of storm-burning on *Melaleuca viridiflora* invasion of grasslands and grassy woodlands on Cape York Peninsula, Australia

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Abstract This paper examines invasion of grasslands on Cape York Peninsula, Australia, by *Melaleuca viridiflora* and other woody species, and the role of storm-burning (lighting fires after the first wet season rains) in their maintenance. Trends in disturbance features, fuel characteristics, ground layer composition, and woody plants dynamics under combinations of withholding fire and storm-burning over a 3-year period were measured on 19 plots in three landscape settings. Population dynamics of *M. viridiflora* are described in detail and 20-year population projections based on transition matrices under different fire regimes generated. Numerous *M. viridiflora* suckers occurred within the grass layer, increasing each year regardless of fire regime, and were rapidly recruited to the canopy in the absence of fire. Storm-burning had little impact on fuel, ground layer or woody plant composition, but maintained open vegetation structure by substantially reducing recruitment of *M. viridiflora* suckers to the sapling layer, and by reducing the above-grass-layer abundance of several other invasive woody species. Population projections indicated that withholding fire for 20 years could cause a sevenfold increase of *M. viridiflora* density on Ti-tree flats, and that annual to triennial storm-burning should be effective at maintaining a stable open vegetation structure. These findings argue against vegetation thickening being an inevitable consequence of climate change. We conclude that a fire regime that includes regular storm-burning can be effective for maintaining grasslands and grassy woodlands being invaded by *M. viridiflora*.

Key words: encroachment, fire, grassland, habitat restoration, *Melaleuca viridiflora*, storm-burn, transition matrices, vegetation thickening.

INTRODUCTION

Across the globe, invasion by woody species has caused a loss of grasslands and thickening of grassy woodlands (Archer *et al.* 1995). The resulting changes in the tree-grass balance have implications for the conservation of grassland-dependent species (e.g. Jansen *et al.* 1999; Garnett & Crowley 2000), pastoral production (Dyer & Stafford Smith 2003); hydrology (Huxman *et al.* 2005) and global carbon budgets (Gifford & Howden 2001; Burrows *et al.* 2002; Henry *et al.* 2002). Loss of grasslands and vegetation thickening have been variously linked to changing fire regimes, herbivore grazing and atmospheric CO₂ fertilization (Archer *et al.* 1995; Bond & Midgley 2000; van Langevelde *et al.* 2003). While different causal factors may be at play in each situation, woodland expansion or thickening has often been associated with a reduction in fire frequency or intensity, sometimes in association with cattle grazing (Archer 1995; Bowman

et al. 2001; Roques *et al.* 2001; Sharp and Whittaker 2003; Kerby *et al.* 2006). The reinstatement of pre-pastoral fire regimes has been proposed as a potential tool for managing vegetation structure (O'Reagain & Bushell 2002; Grice 2006).

Across northern Australia, pre-pastoral fire regimes were characterized by fires being lit through much of the year by indigenous people, although with considerable regional variation (Preece 2002). This was the case on eastern Cape York Peninsula (Crowley & Garnett 2000), where the rise in pastoralism saw intentional fires being largely restricted to the early dry season, and several years often passing between fires (Stanton 1992; Crowley & Garnett 2000). This change in fire regime was accompanied by a loss of grasslands at around 5% per decade in the late 20th century, primarily as a result of invasion by *Melaleuca viridiflora* (Myrtaceae) (Neldner *et al.* 1997; Crowley & Garnett 1998). Both indigenous people and non-indigenous pastoralists on Cape York Peninsula recognized the benefits of storm-burning (the practice of lighting fires within 2–3 days after the first storms of the wet season) for maintaining open vegetation structure, but its

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practice had declined by the early 1990s (Crowley & Garnett 2000; Bassani *et al.* 2006). Both on Cape York Peninsula and elsewhere in Australia, use of storm-burning by indigenous land managers appears to have predominated on floodplains (Russell-Smith *et al.* 1997; Bassani *et al.* 2006), which are areas subject to invasion by *Melaleuca* species (Crowley & Garnett 1998; Sharp & Bowman 2004). Renewed interest in storm-burning as a means of halting or reversing invasion of grasslands by *M. viridiflora* (Garnett & Crowley 1997) saw the landholders on Artemis station reinstate storm-burning as a vegetation management tool (Crowley *et al.* 2004). This paper reports on the monitoring undertaken to assess this shift in management. It examines the population dynamics of invading *M. viridiflora*, reports on the efficacy of storm-burning at maintaining the open structure of grasslands and grassy woodlands, and develops 20-year population projections for *M. viridiflora* under different storm-burning frequencies.

METHODS

Study area

This study was undertaken on Artemis station in east-central Cape York Peninsula, within an area defined by 14°51'–15°00'S and 143°30'–143°36'E. The region has a warm monsoonal climate, with most rain falling between December and May. The 10-year annual rainfall average at Artemis homestead (14°58'S, 143°35'E) from April 1993 to March 2002 was 1109 mm, and the average wet season duration (defined as the period between the first and last fall of at least 20 mm/day, but ignoring such falls separated by more than one month) was 4.2 months. The 88-year annual average rainfall at nearby Musgrave (14°47'S, 143°30'E) was 1166 mm, with the highest rainfall recorded being 2163 mm (186% Musgrave average) in 1973/4 (Crowley & Garnett 2001; <http://www.longpaddock.qld.gov.au>). The study period encompassed three wet seasons of above-average rainfall (Artemis: 1998/99, 1632 mm (147% average); 1999/2000, 1267 mm (114%); and 2000/2001, 1376 mm (124%)). The 1999 and 2000 calendar years were the third and eighth wettest years on record at Musgrave. The duration of the wet season between each monitoring period was also longer than average (Artemis: 1998/1999, 5.9 months (142% average duration); 1999/2000, 5.7 months (136%); and 2000/2001, 4.3 months (103%)).

Ti-tree woodlands dominated by *M. viridiflora*, *M. nervosa*, *M. stenostachya*, *M. citrolens* and *M. foliolosa*, and grasslands being invaded by these species covered

15.4% of a 297 km² study area on Artemis station in 2002 (S. T. Garnett, unpubl. data, 2002) and 14.2% of Cape York Peninsula in 1995 (Neldner & Clarkson 1995); uninvaded grasslands covered 1.8% of the Artemis study area and 6.1% of the peninsula. The studies reported here were undertaken in three grass-dominated settings prone to invasion by *M. viridiflora*, with or without other species (Crowley & Garnett 1998; Fig. 1), referred to here as Mixed flats (regional ecosystem 3.3.14; Neldner 1999), Ti-tree flats (3.3.59) and Hill sites (3.3.16). Mixed and Ti-tree flats occur in drainage depressions that typically hold standing water for 4–6 months of the year. The Hill sites are saturated by groundwater seepage for up to 4 months a year. Deep duplex sodic soils (hydrosol) over colluvium predominate on the flats. The Hill sites are characterized by moderately deep duplex soils, merging into gradational yellow soils (kandosol), with angular quartz gravel common in some areas (Biggs & Philip 1995).

Monitoring plots

To assess the rate of *M. viridiflora* invasion and the impact of storm-burning on grassland and grassy woodland composition and structure, 14 monitoring plots were established in 1997 and five in 1998, with at least six plots in each setting (Fig. 1). We selected plots with a sparse canopy (<5%), and a continuous grass layer, and where the majority of woody plants were suckers within the grass layer and/or adult plants in the canopy. Plots were typically on the interface between grassland and open woodland, with *M. viridiflora* occurring in a narrow band, 50–200 m wide, with grassland down-slope and eucalypt woodland up-slope. At four sites, the drainage depression was uniformly covered with Ti-tree suckers, although open grassland persisted down-stream. Mixed flats had the highest diversity of other subcanopy species, and Ti-tree flats the lowest (Appendix S1). No plot was truly independent, as decisions of the landholders to graze cattle in any paddock, or to leave them in unfenced areas, necessarily impacted on the stocking rate in all other parts of the property. Where plots in a single setting were in an unfenced part of the property or situated in the same paddock, they were at least 0.14 km apart, but, more often, over 0.5 km apart, and thus treated as independent. These sites were monitored annually, at intervals of between 11 and 13 months.

Each plot was 50 m × 4 m, oriented parallel to the boundary between grassland and woodland, or north-south where there was no clear boundary, and permanently marked with steel pickets. Plots were visited annually for monitoring for 3 years between June and

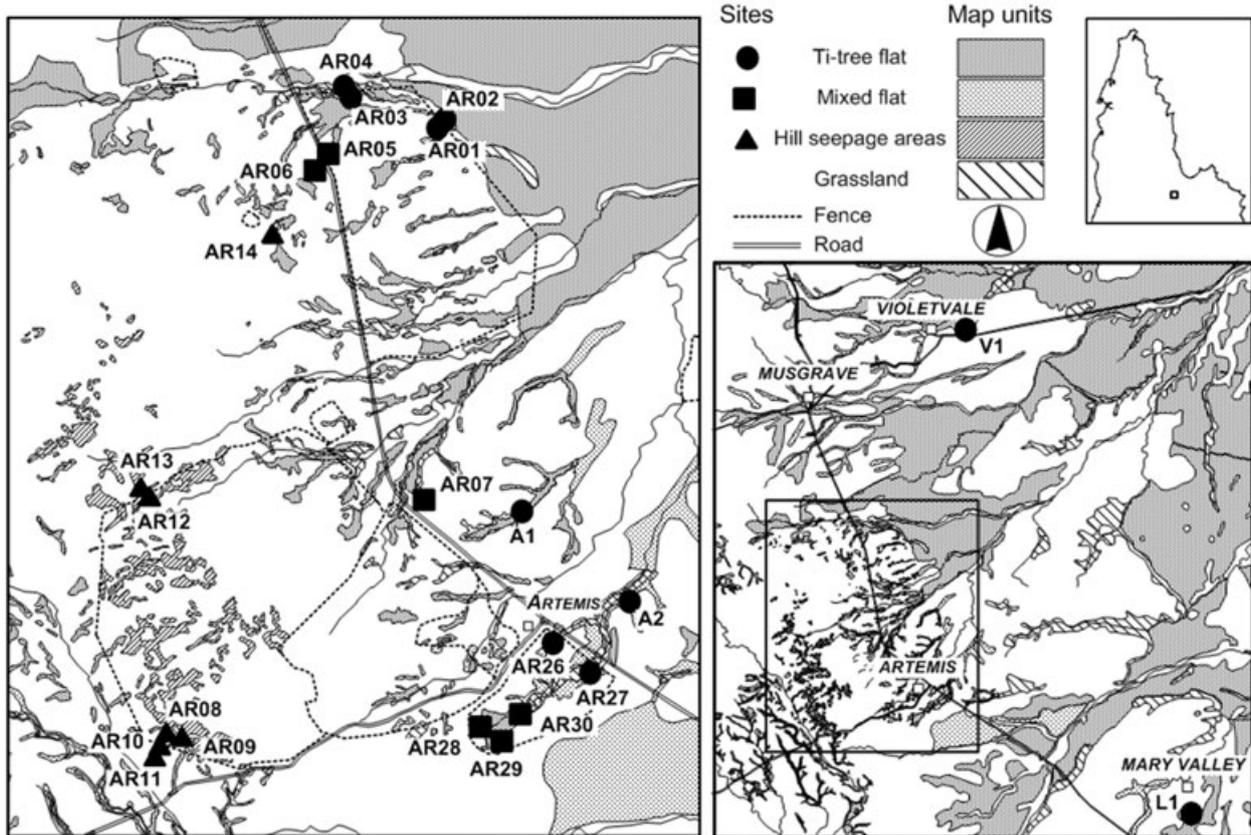


Fig. 1. Location of study sites in relation to grassland and *Melaleuca*-dominated communities.

August. Additional annual growth rate information was collected from tagged *M. viridiflora* plants in the sucker to canopy layers at two additional Ti-tree flat sites within the study area (A1 & A2), and single sites at nearby Lakefield National Park (L1) and Violetvale (V1) between 1993 and 1995. These sites were included to increase the representation of otherwise poorly represented size-classes.

Fire treatments

The location of trials on a working cattle property prevented randomization of treatments. Each year, plots were either left unburnt or storm-burnt (fire lit within about 72 h of the first substantial wet season rain) by the landholders as part of their property management. Each plot was burnt by a separate ignition, mostly on the same day within a single year, and each fire was treated as independent of all other burns. A single late dry season wildfire burnt through the majority of plots on the Mixed and Ti-tree flats on 24 October 2000, so transitions in these plots between 2000 and 2001 were eliminated from the study.

Disturbance, fuel conditions and ground layer plants

Frequency of the perennial grasses *Alloteropsis semialata*, *Sorghum plumosum* and *Heteropogon triticeus* and annual grasses *Schizachyrium* spp. was recorded at twenty 0.25 m × 0.25 m quadrats located at 2.5 m intervals along the central axis in each plot, along with the three dominant ground layer taxa in each quadrat (based on above-ground biomass) and percentage of bare ground (including partially incorporated litter). Fuel depth was recorded at 50 points inside each plot using the disk and stick method (Trollope & Potgieter 1986). Fuel load for each setting was estimated visually in May 2003 (Johnson 2002). Disturbance features (fire, cattle, pig and freshwater crab damage and/or signs) were recorded on each visit.

Effects of storm-burning on fuel depth and bare ground cover between 1998 and 1999 were assessed using repeated-measures ANOVA. Influence of storm-burning on changes in average fuel depth and average cover of bare ground between 1998 and 1999 and between 1999 and 2000 was assessed using adjusted G-tests (rows × columns test of independence with Williams' correction to counter higher than expected

type I errors; Sokal and Rohlf 1995). Effect of storm-burning on changes in frequency and dominance of perennial grasses between 1998 and 2000 was assessed using repeated-measures ANOVA.

Woody plants

On each visit, location of all woody plants within the plot was recorded in relation to a central 50 m tape using a coordinate measurement system (Back *et al.* 1997), along with species identity and height in meters rounded to 0.05 m. Changes in frequency and rank after 2 years for each of three fire regimes (UU: unburnt in subsequent years; SU, storm-burnt in first year, unburnt in the second year; SS: storm-burnt in consecutive years) were described for all woody species found above the grass layer. Plant frequency in plots was too low for statistical comparisons for all species except *M. viridiflora*. Relative growth rate (RGR) of *M. viridiflora* was calculated as the height increment between visits divided by height on the initial visit, and adjusted to a 12-month RGR, by assuming 14% of annual growth occurs in each wet season month and 2% in each dry season month between measurements, based on measurements taken of 160 plants at four additional sites within the study area (Eleven Mile Flat 14°56'S, 143°33'E; Emu Creek 15°00'S, 143°30'E; Fourteen Mile Flat 14°57'S, 143°35'E and Seventeen Mile Flat 14°59'S, 143°36'E) between 1993 and 1995.

Population projections for *Melaleuca viridiflora*

In order to develop population transition frequency tables for *M. viridiflora*, five life-stage classes were

identified using a combination of morphological characteristics and average annual RGR in the absence of fire (Caswell 2001; Hibbard *et al.* 2003; Fig. 2). These classes were advanced seedlings (Se): new plants that were less than 0.2 m high, had soft, immature foliage and a single slender stem indicating an absence of a developed lignotuber; suckers (Su): plants with sclerophyllous, mature foliage that did not exceed grass height (Hill sites: ≤ 0.4 m; Mixed flats: ≤ 0.45 m; Ti-tree flats ≤ 0.5 m), with one to many stems and thickened bases suggestive of a developed lignotuber, with average RGR approaching zero; saplings (Sa): plants that were taller than the grass height, with one to many stems, and average RGR of 0.16–0.87 per year (max height: 1.5 m); subcanopy (Sb): plants below the canopy, whose height could be measured to at least a 0.1 m accuracy (max height: 4 m), and average RGR of 0.02 to 0.13 per year; and canopy (C): plants approaching or within canopy (>4 m), with average RGR approaching zero. Plants either persisted in a class, or moved between classes through growth or regression, or were lost to the population through mortality. Therefore, these divisions were also used as fate classes, with the addition of death as a final fate class (D).

Separate matched-pair *t*-tests were used to assess the change in the number of above-grass-layer *M. viridiflora* (combining Sa, Sb and C) for all plots that remained unburnt for either a 12- or 24-month period. Influence of storm-burning on the change in the number of above-grass-layer *M. viridiflora* was tested using separate repeated-measures ANOVAs for 1998–1999 and 1999–2000. Kruskal–Wallis ANOVA was used to assess the influence of storm-burning on the rate of change in the number of above-grass-layer *M. viridiflora* plants in each plot over a 2-year period.

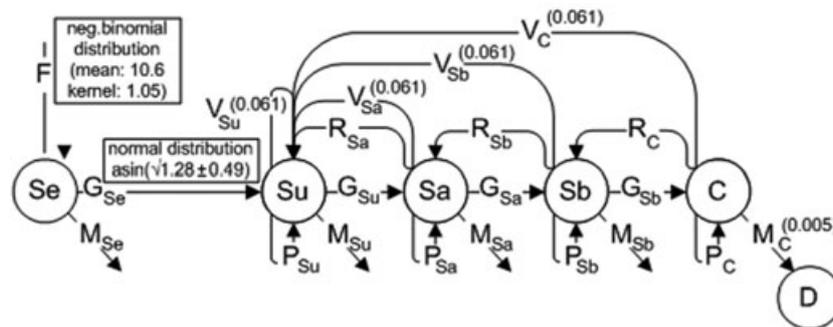


Fig. 2. Theoretical life cycle for *Melaleuca viridiflora*, showing transitions between classes (Se, advanced seedlings; Su, suckers; Sa, saplings; Sb, subcanopy; C, canopy). Plants may persist in a class (P), or move between classes through growth (G) or regression (R), or be lost to the population through mortality. New stems may enter the population either as advanced seedlings (at a rate of F, independent of existing plants) or vegetative suckers (at a rate of V, proportional to existing plants), both of which are uninfluenced by setting or treatment. Rates of accession and loss for each class were calculated separately for each setting and treatment, except those of F, V and G_{Se}, which were set at constant values. Mortality of canopy plants was increased by 0.005 over observed values to account for stochastic deaths not observed over the study period.

Matrices for each of the two treatments (unburnt or storm-burnt) in each setting were populated by combining all transition data for a single size-class, across sites and years. Transition frequency tables (Caswell 2001) for *M. viridiflora* classes Su to C in the absence of fire and following storm-burning were constructed from annual growth data for each setting, and adjusted G-tests were used to examine the influence of fire on the fate of individuals in each stage class (adding 0.5 to each cell before analysis to avoid zero-cell errors; (Caswell 2001) using PopTools (Hood 2003).

Twenty-year population projections were constructed for a theoretical *M. viridiflora* population in a grassland edge community (with densities of plants derived from the average densities found in the monitoring plots on the first visit: 350 suckers, 30 saplings, 25 subcanopy plants and 30 canopy plants per hectare) under four different frequencies of storm-burning (never, triennial, biennial, annual) using Monte-Carlo simulations with 1000 iterations in PopTools (Hood 2003). For these projections, transition between Su, Sa, Sb and C was treated as fixed variables, influenced only by treatment, appearance of Su was treated as a fixed variable influenced by density of existing plants, and transitions to and from Se, and loss of C were treated as stochastic processes, with their values in any one transition being randomly selected from the appropriate distributions, as explained below (Fig. 2).

Seedling recruitment and survival was based on measurements from across all settings, years and fire treatments, as insufficient data were available to assess significance of observed differences. Numbers of advanced seedlings recorded at a site approximated a negative binomial distribution (mean = 10.6/ha, kernel = 1.05) (based on maximum likelihood across varying kernel values), and was not significantly correlated with number of mature trees ($r = 0.03$, $n = 52$, $F = 0.06$, $P = 0.814$). Seedling survival approximated a normal distribution after angular transformation with a mean of 0.83 (angular transformed data: mean = 1.28, SD = 0.49).

Appearance of new suckers was based on measurements from across all settings, years and fire treatments. The number of new suckers found each visit was related to the total number of pre-existing plants (including pre-existing suckers; Visit 2: $r = 0.72$, $n = 19$, $F = 18.6$, $P = 0.000$; Visit 3: $r = 0.75$, $n = 19$, $F = 22.2$, $P = 0.000$; Visit 4: $r = 0.74$, $n = 14$, $F = 14.1$, $P = 0.003$). Suckering did not appear to be influenced by storm-burning (unburnt plots: 0.10 ± 0.09 new suckers/existing plants, $n = 28$; burnt plots 0.11 ± 0.10 new suckers/existing plants, $n = 24$), and pattern of suckering across sites was significantly different from that of pig digging ($G(\text{adj.}) = 339$, d.f. = 43, $P = 0.000$). Fewer new suckers were found each visit (new suckers = $0.34 \times \text{old suckers}^{-1.21}$, d.f. = 2,

$F = 1229$, $P = 0.001$). While it is possible that some suckers were overlooked on the first and second visit, it is difficult to argue that all new suckers had been overlooked previously, especially by the third and fourth visit. The number of new suckers recorded on the fourth visit was therefore assumed to closely represent the actual vegetative suckering rate. Rate of new vegetative suckering was thus set at 0.061 new suckers/per pre-existing plant across settings and fire regimes.

The only recorded mortality of *M. viridiflora* canopy plants in the study was on Ti-tree flats after storm-burning at a rate of 0.023/year. In order to account for stochastic deaths not observed over the study period, a lifespan of 200 years was assumed for mature trees once they reach the canopy in the absence of fire, so observed annual mortality rate of canopy plants was increased by 0.005 for all settings and treatments.

To help separate the contribution of seedling recruitment, vegetative suckering and fire regimes on vegetation thickening, projections were run with seedling recruitment alone, vegetative suckering alone and both seedling recruitment and vegetative suckering. No plots had sufficiently high density of trees to allow us to investigate density dependence, so density dependence could not be incorporated into the population projections. Nevertheless, two density-dependent factors should be considered when assessing the results. First, regardless of fire treatments, after an initial expected increase in seedling recruitment in response to an increase in seed producing plants (L. D. Prior, pers. comm., 2007), recruitment of seedlings to the population and subsequent growth rates are likely to be reduced as stem density increases competition (Silva Matos *et al.* 1999). Second, because grass biomass (and hence fuel load) decreases with stem density (Scholes & Archer 1997; Dyer & Stafford Smith 2003; Scholes 2004), it is likely that the impact of storm-burning would decrease at higher stem densities, and that eventually burning of any kind would become impossible because of a lack of fuel. A density of 670 above-grass-layer *M. viridiflora* stems per hectare measured in a 100-m² invaded plot within the study area in 1993 was used to provide an indication of the densities that can be reached before competition leads to population thinning

RESULTS

Disturbance, fuel conditions and ground layer plants

Other than fire, the only disturbance that featured in more than two plots each year was pig damage. Pig activity peaked in 2000, following extremely wet conditions. In the 14 plots monitored across the

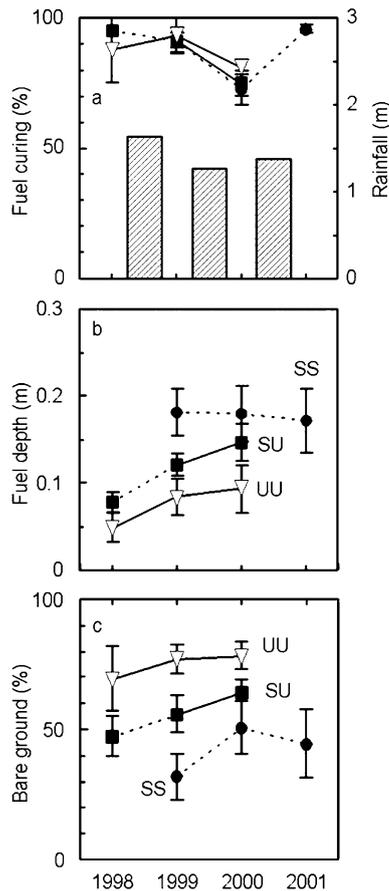


Fig. 3. Changes in fuel conditions in relation to rainfall and fire history. Sites are grouped according to fire history: (∇) unburnt twice ($n = 4$), (\blacksquare) storm-burnt, then unburnt ($n = 10$), (\bullet) and storm-burnt twice in succession ($n = 5$). Dotted lines (...) indicate that plots were burnt between monitoring periods; solid lines (—) that plots remained unburnt.

4 years, pig diggings were recorded in 7% of plots in 1998 (extent of diggings: $1.8 \pm 6.7\%$), 7% of plots in 1999 ($0.4 \pm 1.3\%$), 71% of plots in 2000 ($10.7 \pm 14.3\%$) and 57% of plots ($10.0 \pm 16.9\%$) in 2001.

All ground layer fuels were at least 50% cured on each visit and pattern of curing was similar between burnt and unburnt plots (Fig. 3). Fuel depth was similar on Ti-tree flats and Mixed flats, being approximately double that on Hill sites. The reverse was true for bare ground. These features combined to produce a fuel load that was at least three times greater on the Mixed flat and Ti-tree flats than on the Hill sites. Although fuel depth increased significantly between 1998 and 1999 ($F = 24.2$, d.f. = 1,12, $P = 0.000$), repeated-measures ANOVA found no significant differences attributable to fire treatment ($F = 2.41$, d.f. = 1,12, $P = 0.146$). Repeated-measures ANOVA indicated that area of bare ground was stable between 1998 and 1999 ($F = 1.17$, d.f. = 1,12, $P = 0.301$) and was

not influenced by storm-burning ($F = 4.04$, d.f. = 1,12, $P = 0.067$). Adjusted G -tests did not detect any significant influence of storm-burning on fuel characteristics.

In most cases, frequency of recording perennial grass taxa as present or dominant showed similar trends in storm-burnt and unburnt plots, and no significant differences between treatments were detected by repeated-measures ANOVAs ($P > 0.05$). The only major change was the appearance of *Alloteropsis semi-alata* and its subsequent increase on twice storm-burnt plots (Table 1). Of the 14 most abundant ground layer taxa, only *Leptocarpus* spp. consistently decreased in relative importance after storm-burning, and increased in the absence of fire. Conversely, *Aristida* spp. consistently increased on storm-burnt plots, and decreased in the absence of fire. Least changes in rank occurred on twice storm-burnt plots. No abundant taxon disappeared during the study. Mean change (\pm SD) in rank of all ground layer taxa over 2 years was $3.0 (\pm 2.5)$ for unburnt plots, $2.5 (\pm 1.7)$ for once-burnt plots and $2.8 (\pm 3.1)$ for twice-burnt plots.

Woody plants

Over 2 years without fire, frequency of woody plants found above the grass layer increased for *M. viridiflora*, *M. citrolens*, *Grevillea pteridifolia*, *G. glauca* and *Alphitonia obtusifolia*. One year after storm-burning, the above-grass-layer frequency of *M. viridiflora*, *G. pteridifolia* and *Dendrolobium umbellatum* had declined (Table 2). After two consecutive storm-burns, above-grass frequency of *M. viridiflora*, *M. nervosa*, *G. pteridifolia* and *Asteromyrtus symphyocarpa* decreased, and *Glochidion* sp. and *Acacia leptostachya* were eliminated from this stratum. Of the species that were reduced in number by storm-burning, only for *G. pteridifolia*, *A. symphyocarpa* and *D. umbellatum* was the decrease enough to reduce the rank of the species relative to other taxa. Thus most species that increased in the absence of fire were reduced or eliminated from above-grass level by storm-burning. No species was completely eliminated from all plots by storm-burning, but *D. umbellatum*, *A. leptostachya* and *G. glauca* were eliminated from one quarter to one half of the plots in which they had originally been recorded. *Acacia holosericea* and *Atalaya variifolia*, found only below grass height at the start of the monitoring, were eliminated after one or two storm-burns. *Acacia holosericea* also disappeared from one unburnt plot.

Population projections for *Melaleuca viridiflora*

In all settings, most plants remained in the same stage class from one year to the next in the absence of fire

Table 1. Changing rank of the 14 most abundant ground layer taxa based on frequency measures

Species	UU		SU		SS	
	Rank (1998)	Change	Rank (1998)	Change	Rank (1999)	Change
<i>Schizachyrium</i> spp.	1	0	1	0	4	+1
<i>Eriachne stipacea</i>	8	+3	3	+1	1	0
<i>Scleria rugosa</i>	9	0	2	-1	2	0
<i>Rhynchospora</i> spp.	3	-5	4	-2	6	0
<i>Fimbristylis</i> spp.	12	0	7	+3	3	-1
<i>Aristida</i> spp.	2	-1	6	+1	12	+2
<i>Ectrosia</i> spp.	7	-2	8	-3	10	+1
<i>Chloris truncata</i>	-	0	5	-2	14	0
<i>Ischaemum fragile</i>	-	0	17	+5	5	0
<i>Eremochloa bimaculata</i>	4	-8	11	-5	7	0
<i>Leptocarpus</i> spp.	6	+3	10	-3	14	-5
<i>Eragrostis</i> spp.	-	0	13	+5	8	-5
<i>Alloteropsis semialata</i>	9	+3	15	+6	-	+
<i>Sorghum plumosum</i>	16	-2	8	-1	-	0

Taxa are presented in order of the abundance over all plots. Positive changes indicate increases in relative importance; negative changes indicate decreases. SS, storm-burnt in consecutive years; SU, storm-burnt in first year, then unburnt; UU, unburnt throughout.

(Table 3). However, for each stage class, recruitment to taller classes exceeded both regressions to smaller classes and deaths, leading to a thickening of the above-grass layer. Over ca 12 months without fire, there was a median increase of 20% in the number of above-grass-layer *M. viridiflora* across all plots and all years (Fig. 4a), an increase of 3%, if suckers are included. A significant increase was found in the total number of *M. viridiflora* plants in plots that remained unburnt between 1999 and 2000 ($t = 2.20$, d.f. = 13, $P = 0.047$). This increase was even more significant when the suckers were excluded ($t = 3.35$, d.f. = 13, $P = 0.005$). In the four plots that remained unburnt for 2 years, there was a median increase of above-grass-layer *M. viridiflora* of 44% (Fig. 5). Even with the small sample size, matched-pairs t -test indicated that this increase was significant ($t = 5.25$, d.f. = 3, $P = 0.013$). Too few sites remained unburnt for single-year assessment to be made between 1998 and 1999 or between 2000 and 2001.

In storm-burnt plots, most plants were also retained in their original stage class from year to year, but the number of regressions and deaths out-numbered new recruits in all stage class from suckers to the sub-canopy (Table 3). A significantly greater proportion of saplings was reduced to the sucker stage class on storm-burnt plots than on unburnt plots, while only in Mixed flats did a significantly smaller proportion of suckers progress to taller stage classes on burnt plots than on unburnt plots. In combination, these differences meant that storm-burning had a significant impact on fate of individuals across the whole population in all settings (Table 4). Storm-burning significantly affected the rate of change in abundance of

above-grass-layer *M. viridiflora* plants in each plot over a 2-year period (Kruskal–Wallis test: $H = 10.9$, d.f. = 2, $P = 0.004$; Fig. 5). Storm-burning also significantly reduced the total number of above-grass-layer *M. viridiflora* (Fig. 4b). This effect is also indicated by a significant interaction between fire treatment and number of above-grass-layer plants in repeated-measures ANOVAs in both 1998 to 1999 ($F = 9.3$; d.f. = 1,12; $P = 0.010$); and 1999 to 2000 ($F = 14.4$; d.f. = 1,17; $P = 0.002$). These changes resulted in the retention of canopy plants, but a more open mid-storey, as can be seen after two consecutive storm-burns on the Mixed flat in Figure 6.

Twenty-year population projections of *M. viridiflora* indicated that density of above-grass-layer plants is likely to increase fastest on Mixed flats, and be slowest on Ti-tree flats (Fig. 7). Production of new suckers and seedling recruitment should have negligible influence on the rate of vegetative thickening in the first 5 years, with projected trends in the above-grass-layer plants the result of the growth of pre-existing plants. When recruitment of advanced seedlings is included, but no vegetative increase in sucker number, twenty-year projections suggest a near doubling of density on Ti-tree flats, a tripling on Hill sites and a fivefold increase on Mixed flats. The rates of thickening are even higher when projections include vegetative suckering, but no seedling recruitment. When both suckering and seedling recruitment are incorporated into the projections, projected 20-year increases range from threefold on Ti-tree flats to sevenfold on Mixed flats; the maximum density predicted (ca 620 stems per hectare) being similar to the 670 stems per hectare recorded on an invaded flat within the study area.

Table 2. Mean frequency and change in rank of species in the canopy/subcanopy under different fire regimes, along with the number and extent of regional ecosystems (REs) containing these species on Cape York Peninsula (SS: storm-burnt in consecutive years; SU, storm-burnt in first year, then unburnt; UU: unburnt throughout)

Species	Increaser species [†]	UU			SU			SS			Regional representation [‡]		
		Frequency (plants per plot)		Rank change	Frequency (plants per plot)		Rank change	Frequency (plants per plot)		Rank change	REs	Area (ha)	%
		Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
<i>Melaleuca viridiflora</i>	++	8.75	13.25	0	6.3	5.9	0	15.2	11.6	0	52	4 139 036	36.5
<i>Grevillea pteridifolia</i>	++	0.25	0.75	0	0.2	0.1	v	2.2	1.8	0	8	359 970	3.2
<i>Melaleuca nervosa</i>	+	-	-	-	-	-	-	1.6	1.4	0	14	1 881 170	16.6
<i>Asteromyrtus symphyocarpa</i>	+	-	-	-	-	-	-	0.8	0.2	v	7	386 010	3.4
<i>Dendrobium umbellatum</i>	+	-	-	-	0.2	0.1	v	-	-	-	7	411 610	3.6
<i>Glochidion</i> sp.	+	-	-	-	-	-	-	0.2	0	v	0	0	0
<i>Acacia leptostachya</i>	+	-	-	-	-	-	-	0.2	0	v	2	39 600	0.3
<i>Melaleuca citrolens</i>	+	0.25	0.5	v	-	-	-	-	-	-	4	97 150	0.9
<i>Grevillea glauca</i>	-	1.25	1.5	^	0.1	0.1	^	-	-	-	24	4 439 250	39.2
<i>Alphitonia obrusifolia</i>	-	0.25	0.5	v	0.1	0.1	^	-	-	-	19	1 038 790	9.2
<i>Petalostigma banksii</i>	-	1.5	1.25	v	0.1	0.1	^	0.4	0.4	^	22	1 740 250	15.3
<i>Melaleuca stenostachya</i>	-	-	-	-	0.3	0.3	0	-	-	-	14	910 565	8.0
<i>Corymbia clarksoniana</i>	-	-	-	-	0.2	0.2	0	-	-	-	39	3 994 201	35.2
<i>Corymbia dallachiana</i>	-	-	-	-	0.2	0.2	0	-	-	-	8	261 140	2.3
<i>Petalostigma pubescens</i>	-	-	-	-	0.2	0.2	0	-	-	-	7	1 071 420	9.4
<i>Dolichandrone heterophylla</i>	-	-	-	-	0.1	0.1	^	-	-	-	3	344 980	3.0
<i>Eucalyptus cullenii</i>	-	-	-	-	0.1	0.1	^	-	-	-	16	1 102 270	9.7
<i>Neofabricia njoebergii</i>	-	-	-	-	0.1	0.1	^	-	-	-	2	214 490	1.9
<i>Corymbia confertiflora</i>	-	-	-	-	-	-	-	0.2	0.2	^	4	493 080	4.3
<i>Eucalyptus chlorophylla</i>	-	-	-	-	0.8	0.9	0	-	-	-	13	875 470	7.7

[†]++, increases in absence of fire, based on this study; +, increases in absence of fire, based on anecdotal observations; -, no evidence of increases in absence of fire. [‡]Based on number and area of Cape York Peninsula REs for which the species is listed as a characteristic species (Neldner 1999).

Table 3. Transition matrices describing the fate of individual *Melaleuca viridiflora* in unburnt and storm-burnt stands on Mixed flats, Ti-tree flats and Hills

Year 2	Year 1							
	Unburnt				Storm-burnt			
	Suckers (Su)	Saplings (Sa)	Subcanopy (Sb)	Canopy (C)	Suckers (Su)	Saplings (Sa)	Subcanopy (Sb)	Canopy (C)
Mixed flats								
Su	168	3	0	0	379	67	15	0
Sa	38	41	0	0	19	17	17	0
Sb	0	15	4	0	0	0	22	0
C	0	0	2	23	0	0	3	60
Dead	13	1	0	0	16	0	2	0
Ti-tree flats								
Su	302	6	0	0	501	70	13	1
Sa	14	40	0	0	14	42	10	0
Sb	0	7	41	0	0	8	111	1
C	0	0	1	57	0	0	2	86
Dead	16	1	0	0	22	3	0	2
Hills								
Su	289	5	1	0	140	11	1	0
Sa	36	49	2	0	11	19	0	0
Sb	0	12	84	0	0	1	40	0
C	0	0	4	13	0	0	2	8
Dead	15	2	0	0	13	1	1	0

Cells above the diagonal represent movement to a smaller stage class; below the diagonal represent movement to a taller stage class. Rate of accession to the sucker layer in Year 2 across all settings is shown in Figure 2.

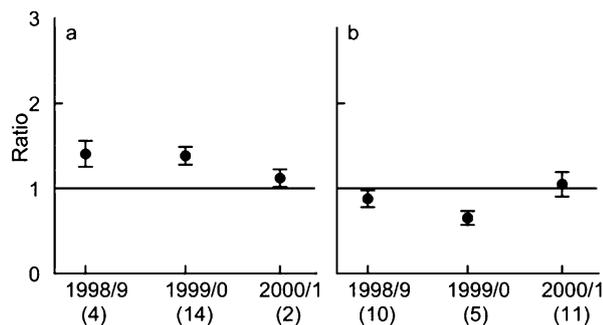


Fig. 4. Ratio between the number of above-grass-layer *Melaleuca viridiflora* before and after a one-year period with (a) no fire and (b) storm-burning. Number of plots is indicated in brackets.

Twenty-year projections indicate that annual storm-burning should lead to a slow loss of *M. viridiflora* above the grass layer on Mixed flats and on Ti-tree flats, and population stabilization in Hill sites (Fig. 8). The projections also indicate that stability should be achieved on Mixed flats by biennial storm-burning and on Ti-tree flats by biennial to triennial storm-burning.

DISCUSSION

Replacement of grasslands on Cape York Peninsula by Ti-tree woodlands is well documented (Neldner *et al.*

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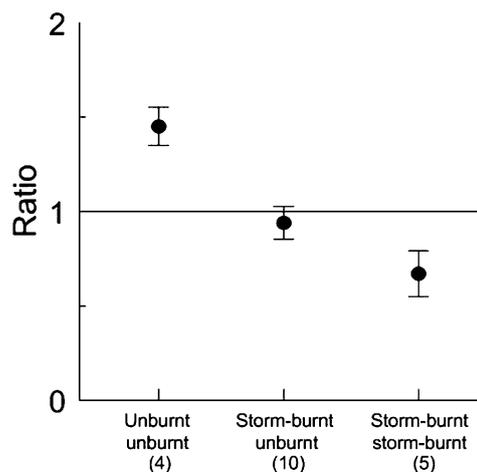


Fig. 5. Ratio between the number of above-grass-layer *Melaleuca viridiflora* plants before and after a 2-year period, showing successive storm-burning in successive years as critical to woody reduction. Number of plots is indicated in brackets.

1997; Crowley & Garnett 1998), and this study confirms rapid population growth of *M. viridiflora* in seasonally wet environments in the absence of fire. This growth may have been exacerbated by the wetter-than-average years that prevailed during the study, through elevated levels of seedling germination and survival, suckering and/or plant growth. Exceptionally wet con-

Table 4. Statistics describing the significance of the effect of storm-burning on the fate of individuals in each stage class (Su to C), and in the population as a whole (total)

Class	G (adj.)	d.f.	P-value
Mixed flats			
Su	22.81	4	0.000 [†]
Sa	78.78	4	0.000 ^{††}
Sb	6.18	4	0.186
C	0.50	4	0.974
Total	108.26	16	0.000
Ti-tree flats			
Su	1.69	4	0.792
Sa	30.33	4	0.000 ^{††}
Sb	7.22	4	0.125
C	0.89	4	0.927
Total	40.13	16	0.000
Hills			
Su	3.38	4	0.496
Sa	10.95	4	0.027 ^{††}
Sb	1.93	4	0.750
C	0.12	4	0.998
Total	16.37	16	0.175

[†]Reduced recruitment to taller classes. ^{††}Increased regression to smaller classes.

ditions promoting seedling germination have also been linked to *Melaleuca* thickening on floodplains in the Victoria River District (Sharp & Bowman 2004). Seedling recruitment, in particular, may have been inflated in this study – no *Melaleuca* seedlings were found in numerous plots in the same study area in the drier-than-average years between 1992 and 1996 (authors' unpublished observations). If so, vegetation thickening may be either moderated or reversed in dry years (Fensham & Holman 1999; Fensham *et al.* 2005). Nevertheless, a 10% loss of grasslands occurred between 1969 and 1988, a period that included similar numbers of wetter-than-average and drier-than-average wet seasons (Crowley & Garnett 1998).

Population growth may also have been inflated by the presence of grazing animals, which elsewhere have been shown to exacerbate thickening by reducing fuel loads (Archer 1995; Sharp & Whittaker 2003; Kerby *et al.* 2006). As *M. viridiflora* is not grazed by cattle (authors' unpublished observations), possibly because its leaves contain unpalatable and/or toxic oils (Allen *et al.* 1978), any level of grazing should favour it over more palatable species, including both grasses and shrubs. Grazing was not controlled in this study and would have reduced the grass cover in many plots, thereby reducing competition with *Melaleuca* seedlings and suckers. Certainly disturbance through trampling and grazing cattle and rooting by pigs may have exacerbated the resprouting of *M. viridiflora* suckers, whose shallow roots seem to sucker whenever they are damaged (Anning 1980). Failure to account for

density-dependent effects may also have inflated the population projections produced here. Despite these limitations, plant densities that were predicted by the 20-year population projections were no greater than the highest densities of Ti-trees observed in the study area (see *Methods*). Moreover, similar rates of invasion have been demonstrated using transition matrices to model invasion of Texan grasslands by Mesquite *Prosopis glandulosa* (Hibbard *et al.* 2003). So while the projections are probably at the top end of the likely range, we maintain that they provide useful tools to assess the impact of storm-burning on vegetation structure.

The population projections indicated that storm-burning indeed slowed, and in some cases reversed vegetation thickening by *M. viridiflora*. It primarily did so by arresting the progression of suckering plants to the canopy. Sucker death was rare, the suckers being extremely durable – in a separate trial suckers survived scorching with a blow torch that raised temperatures 10 cm below ground to 60°C (authors' unpublished observations). The increase in the sucker bank observed in this study indicates that even a small leakage of suckers through to canopy height will lead to substantial vegetation thickening, even under biennial to triennial burning. Elsewhere, fire has been shown to promote suckering (Hoffmann 1999), and unpublished observations by the authors indicate that this is the case for *M. viridiflora* in the months following most fires. However, the results of the current study indicate that, within a full year of a storm-burn, sucker production was no greater in storm-burnt than in unburnt sites. Suppression of suckers may be related to the timing of the fire, when high soil moisture and subsequent rains favour regeneration of grasses, and when site saturation and flooding bring other challenges, such as algal or fungal attack and plant submersion (Lockhart *et al.* 2004). Even for a moderately flood-tolerant species, such as *M. viridiflora* (Franklin *et al.* 2007), survival can be reduced with extent and duration of plant submergence (Sieg & Wolken 1999; Amlin & Rood 2001).

Once *M. viridiflora* suckers or seedlings grow above grass height, the invasion process can be effectively interrupted only before they reach the subcanopy. Rate of movement through this 'top-kill' zone (Sa class in this paper) is recognized as influencing vegetation thickening in savannas worldwide (Bond & Midgley 2000; Bond & Archibald 2003). Storm-burns were most effective at top-killing plants in the Sa class on Mixed flats (80%), followed by Ti-tree flats (59%), and least in Hill sites (38%). This corresponded to differences in fuel loads that were at least three times greater on the flats sites than on the Hill sites (Appendix S1; <http://www.ecolsoc.org.au/What%20we%20do/Publications/Austral%20Ecology/AE.html>), and hence with differences in fire intensity (Williams *et al.* 1998). Differences in fuel load are most likely to be related to the



Fig. 6. Grassy woodland being invaded by *Melaleuca viridiflora* before (a) and after (b) storm-burning in two consecutive years.

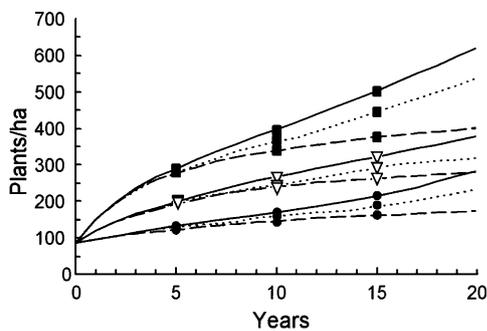


Fig. 7. Projections of the density of *Melaleuca viridiflora* above the grass layer in the absence of fire on (■) Mixed flats, (▽) Hills and (●) Ti-tree flats, assuming (—) 0.061 new suckers per plant and 10.6 new seedlings per hectare, (---) new suckers only, and (.....) new seedlings only.

different species present in the ground layer, with smaller-statured grasses growing on the shallow gravelly soils on the hill sites, but may also have been influenced by differential grazing pressure. However, as *M. viridiflora* growth was not similarly stunted by poor soil conditions, maintaining an open vegetation structure on Hill sites required more frequent use of storm-burning. Ti-tree flats, with the slowest tree growth and relatively high fuel loads, required the lowest storm-burning frequency to maintain an open structure. We therefore conclude that site factors other than dominant tree species must be taken into account when recommending fire regimes.

This study casts no light on the influence of storm-burns on seedling germination or recruitment. However, it is likely that seedlings would be killed by fires in the first year or so after germination (Fensham & Fairfax 2006). If so, then the fires following a heavy or extended wet season will be particularly important for minimizing seedling recruitment. Ti-tree invasion of grasslands on Cape York Peninsula is most pronounced on two National Parks purchased in the 1970s (Stanton 1992; Crowley & Garnett 1998). This

decade not only included only four of the ten wettest years on record, and one of the three shortest dry seasons on record, but was a time when the Queensland National Parks and Wildlife Service had a policy of excluding all fires (Stanton 1992), and actively discouraged burning on adjacent properties (T. Shepherd, pers. comm., 1992). It is therefore possible that many of the sites currently experiencing Ti-tree invasion were colonized during this period.

This study indicates that storm-burning has minimal impact on the ground layer, including its production of fuel. Its one demonstrated effect was to favour the ecological keystone species *Alloteropsis semialata* (Crowley, 2008), promoting its presence and abundance. Storm-burns have been shown to synchronize flowering and promote seed production of this species (Crowley & Garnett 2001). Promotion by fire is consistent with previous studies, showing that *A. semialata* is advantaged by disturbance (Walker *et al.* 1997). Storm-burning did not exhibit any of the adverse community-level effects described for late dry season fires (Lonsdale & Braithwaite 1991): there was no evidence in this study of canopy loss, death of large trees or a shift in woody vegetation composition. When combined with the restricted extent of the fires, this means that storm-burning should also have far less impact than late dry season fires on flower or seed production of canopy trees (Setterfield 1997), or on fauna that rely on unburnt vegetation for shelter and prey (Griffiths & Christian 1996).

Atmospheric carbon fertilization has also been mooted as a contributing factor to accelerated growth of C_3 plants in relation to C_4 grasses, increasing the probability of leakage to the canopy (Bond & Midgley 2000; Reich *et al.* 2001). However, this would not explain why one suite of woody C_3 species that includes *M. viridiflora* should be more advantaged by atmospheric carbon fertilization than any other C_3 plant in the study area (Bond & Midgley 2000; Reich *et al.* 2001). Moreover, observations of dense Ti-tree suckers in the grass layer of this region over 100 years

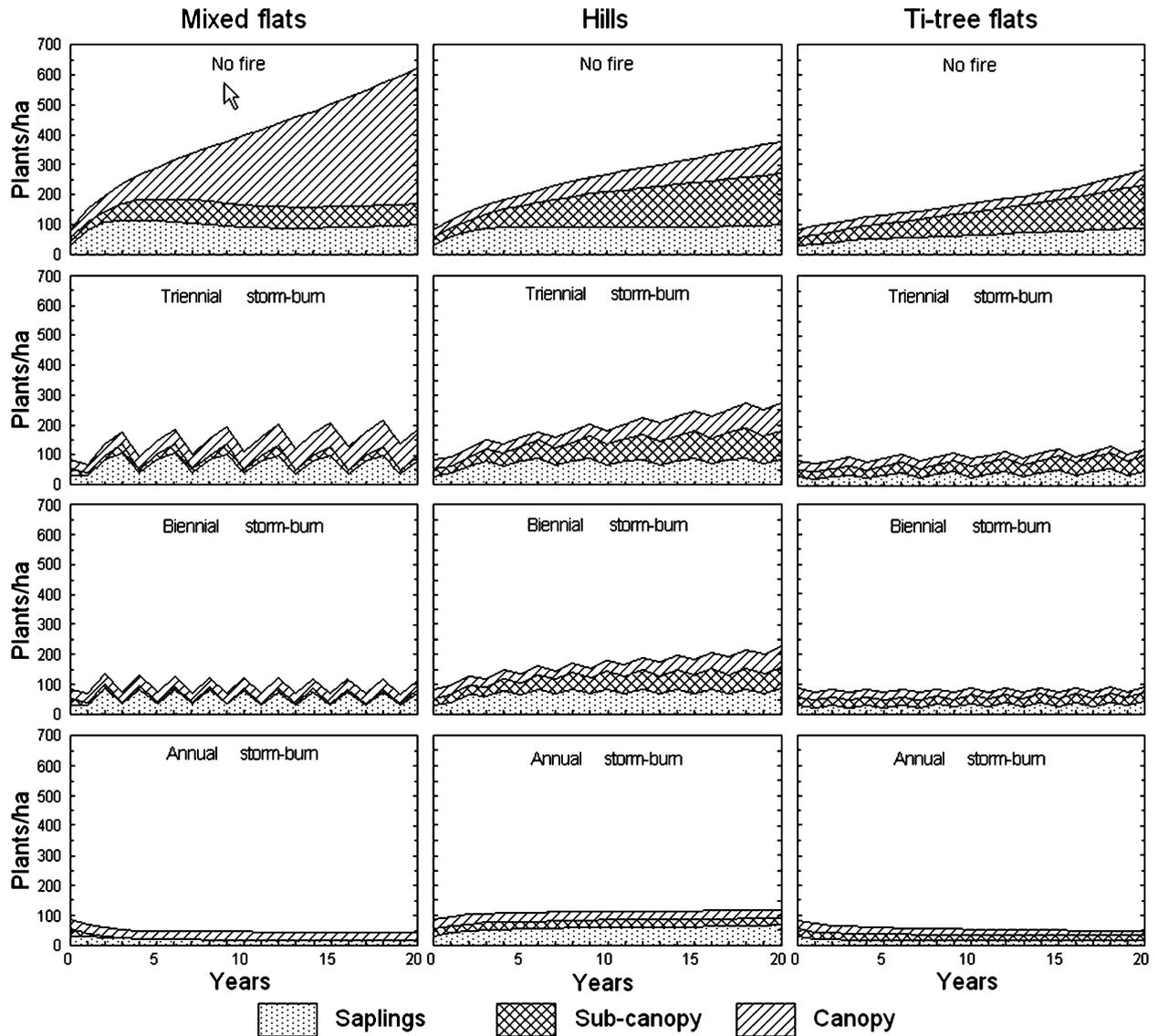


Fig. 8. Projected population structure of *Melaleuca viridiflora* above the grass layer in three different settings with four different management regimes.

ago (Byerley 1867) are more suggestive of a dynamic system maintained by fire than a recent process initiated by escalating carbon fertilization. This is not to say that carbon fertilization is not contributing to vegetation thickening in northern Australia. Rather, we contend that invasion of grasslands by *Melaleuca* species can be explained without recourse to this factor, and can be at least arrested, if not reversed by re-instituting storm-burning as a key feature of management in these ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristics of the three settings studied.

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