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CLIMATIC, VEGETATION AND EDAPHIC INFLUENCES ON THE PROBABILITY OF FIRE ACROSS MEDITERRANEAN WOODLANDS OF SOUTH EASTERN AUSTRALIA

Running heading: Time since fire and fire probability in mallee woodlands and heathlands

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Abstract

Aim:

We investigated how the probability of burning is influenced by time since fire (TSF) and gradients of climate, soil and vegetation in the fire-prone Mediterranean-type climate mallee woodlands of south eastern Australia. This provided insight into processes controlling contemporary fuel dynamics and fire regimes across biogeographic boundaries, and consequent effects of climate change on potential shifts in boundaries between fuel systems and fire regimes, at a sub-continental scale.

Location:

South eastern Australia.

Methods:

We used a Bayesian framework to examine the effects of combinations of rainfall, vegetation and soil type on the hazard of burning and survival parameters of the Weibull distribution. These analyses identified the nature of environmental controls on the length of fire intervals and the age-dependence of the hazard of burning.

Results:

Higher rainfall was consistently associated with shorter fire intervals. However, within a single level of rainfall, an interaction between soil and vegetation type influenced the length of fire intervals. Higher fertility sands were associated with shorter fire intervals in grass-dominated communities, while lower fertility sands were associated with shorter fire intervals in shrub-dominated communities. The hazard of burning remained largely independent of TSF across the region; only in shrub-dominated communities at high rainfall did the hazard of burning markedly increase with TSF.

Main conclusions:

Rainfall had a dominant influence on fire frequency in the Mediterranean climate mallee woodlands of south eastern Australia. Predicted changes in the spatial distribution and amount of rainfall therefore have the potential to drive changes in fire regimes. However, the effects of soil fertility and rainfall on fire regimes do not align on a simple productivity gradient. Reduced soil fertility may favour plant traits that increase rates of woody litter fuel accumulation and flammability, which may alter the over-riding influence of rainfall gradients on fire regimes.

INTRODUCTION

Fuel dynamics and resultant fire regimes may change in the future due to global change, but the nature of these changes are poorly understood (Matthews *et al.*, 2012). Higher atmospheric CO_2 and changes to temperature and precipitation as a result of climate change may influence plant growth and consequent fuel dynamics, but such changes will vary across regions and among plant species (Lenihan *et al.*, 2008; Pausas & Paula, 2012). A fundamental understanding of how fuel dynamics can influence contemporary fire regimes is needed to predict how fire regimes may respond to global change and to management practices such as fuel treatment (Bradstock *et al.*, 2012; Matthews *et al.*, 2012; King *et al.*, 2013).

The influence of fuel accumulation on fire regimes can be inferred from the nature of hazard functions (McCarthy *et al.*, 2001). These functions relate the instantaneous probability of burning to the post-fire age of the fuel complex, which can be estimated by time since fire (TSF) in landscapes. In systems where fire is dependent on fuel age, the probability of fire in young fuels is likely to be low and increase over time if fuels accumulate in a regular manner. By contrast, in systems where fire is independent of fuel age, the probability of fire is unrelated to TSF. This could arise in systems where irregular events, such as periods of high rainfall, promote fire through a rapid response of ephemeral vegetation to suitable conditions (McCarthy *et al.*, 2001; Pausas & Paula, 2012). These examples indicate contrasting types of fuel dynamics, where, respectively, fuel may or may not accumulate with TSF. Models of the probability of burning with TSF for a given system can be used to characterise patterns of fire interval distributions and quantify the role of TSF in determining fire regimes (McCarthy *et al.*, 2001).

Moisture and soils will influence vegetation community structure and composition, which in turn may influence the probability of fire. For example increased productivity, as a function of increasing moisture, is often associated with increased fire frequency (i.e. the productivity-fire frequency model; Bond & Keeley, 2005; Pausas & Bradstock, 2007; Krawchuk & Moritz, 2011; Gibson *et al.*, 2014). While considerable attention has been devoted to the influence of climatic moisture on fire occurrence (Bond & Keeley, 2005; Pausas & Paula, 2012), less is known about the way that variations in soil characteristics (e.g. texture and fertility) may influence this relationship. For example, lower soil fertility at any given level of rainfall may increase the cover of woody plant with sclerophyllous leaves, increasing the flammability of vegetation (Keeley *et al.*, 2011; Lehmann *et al.*, 2011; Gibson *et al.*, 2014). Soil type therefore may play a role, in interaction with moisture, in determining fuel types and resultant fire probability.

Gradients in rainfall, vegetation and soil in southern Australia can be used to examine the effect of differing fuel systems on the probability of burning (e.g. O'Donnell *et al.*, 2011a). In arid ecosystems of southern Australia, the fuel system is dominated by ephemeral herbage and grasses that respond rapidly to infrequent and sporadic periods of heavy rainfall. As a result, fire frequency is relatively low (Allan & Southgate, 2002; Letnic & Dickman, 2006). In temperate sclerophyllous shrublands, woodlands and forests near the coast in southern Australia, spatially continuous surface litter fuels accumulate in a regular manner and fire occurs more frequently than in arid climates (Gill & Catling, 2002; Russell-Smith *et al.*, 2007; Bradstock, 2010). Mallee communities in the Mediterranean-type climate region of south eastern Australia occupy a transitional zone between these contrasting ecosystems and fuel types.

Previous research in the Mediterranean-type climate region of south eastern Australia indicated that area burned and fire frequency were positively correlated with rainfall along a north to south gradient of woodland and shrubland vegetation types situated on oligotrophic, aeolian-derived sandy soils (Pausas & Bradstock, 2007). These trends in fire possibly correspond with a transition in vegetation composition and structure from dominance of the understory by grasses to dominance by shrubs as rainfall increases (Krawchuk & Moritz, 2011; Gibson *et al.*, 2014). Thus a corresponding shift in fire regime characteristics could be anticipated in response to this change in the nature of surface fuel along the rainfall gradient. However, possible effects of rainfall are partially confounded by the low fertility of the sandy substrates on which these woodlands and shrublands are situated (Blackburn & Wright, 1989). Such a trend in soil fertility has the potential to reduce productivity (Paoli *et al.*, 2008), favour woody, sclerophyllous species (Mills *et al.*, 2012) and alter resultant effects of rainfall on fire regimes.

In this study we investigated how fire probability and fire intervals responded to gradients of climate and variations in soil and vegetation attributes in the Mediterranean-type climate woodlands ("mallee" vegetation, Noble & Bradstock, 1989) of south eastern Australia. We used fire history data for the region to test the prediction that the probability of burning would become more frequent as rainfall increases. We also examined how the relative abundance of grass and woody shrub components and sand types of differing fertility may alter the over-riding influence of rainfall on fire regimes. We predicted that fire probability would be more dependent on TSF in mallee communities with a prominent shrub layer and on low fertility sands (i.e. dominance of woody litter fuels) than communities with a grassy understory and those situated on higher fertility sands.

MATERIALS AND METHODS

Study Area

The study was carried out in two Mediterranean-type climate regions in south eastern Australia (Fig. 1); i) the Murray Lowlands from south-west New South Wales (NSW), to central-west Victoria; ii) the Eyre Peninsula, including Kangaroo Island in South Australia. These regions span wide rainfall gradients (≈200-600mm/yr) and a variety of vegetation types (ANVA, 2001) including mallee woodlands and mallee heathlands. Mallee woodlands are extensive in the north of each region (200-350mm/year). This vegetation type is dominated by shrub-like, multi-stemmed *Eucalyptus* species (i.e. mallee growth habit; Burbidge, 1950), with an understory containing perennial hummock grasses (*Triodia* sp.), along with sclerophyllous shrubs, such as species of *Acacia*, *Beyeria*, *Chenopodium*, *Dodonea*, *Eremophila*, *Halgania*, *Leptospermum* and *Westringia*; (Westbrooke *et al.*, 1998). Ephemeral grasses and herbs become abundant following periods of heavy rainfall (e.g. *Austrostipa* sp., *Zygophyllum* sp.). Mallee heathlands, dominated by multi-stemmed *Eucalyptus* spp. are extensive across the south of the study area (350-600mm/yr) with a relatively dense understory dominated by sclerophyllous shrubs (e.g. species of *Acacia*, *Baeckea*, *Eremophila*, *Grevillea*, *Leucopogon*, *Templetonia* and *Melaleuca*). Hummock and ephemeral grasses are sparse or absent in this community (Bradle, 2010). Along with changes in mean annual rainfall, seasonality of rainfall changes across the study region from semi-arid in the north, where rainfall and plant growth are not strongly seasonal, to a more temperate, Mediterranean-type climate with peaks of growth in winter and spring (Hutchinson *et al.* 2005).

Mallee woodlands and mallee heathlands occur on undulating dune fields of aeolian sands that are either solonised brown earths (red sands) or solodised solonetz (yellow sands) (NRIC, 1991). The red sands are alkaline with poor to moderate fertility and commonly support semi-arid mallee, while the yellow sands are relatively more acidic, less fertile and more coarse than the red sands and commonly support temperate mallee heathlands (Blackburn & Wright, 1989). The characteristics and distribution of these contrasting sand types reflects differences in origin; red sands derived from alluvial and subsequent Aeolian origins are prevalent in the north of both study regions, whereas yellow sands formed by marine processes are common in the south (Wasson, 1989). Mallee woodlands occur mainly on red sands in the drier north (Table 1), while mallee heathlands occur mainly on yellow sands across the wetter south (Table 1). However, there are more limited instances where mallee woodlands occur on yellow sands and where mallee heathlands occur on red sands (Table 1).

Data compilation

Approximately 6300 points, spaced at a minimum of 1km apart, were randomly generated and used as sampling points in conservation reserves across the study area, totalling 53,366km^2 (see Fig. S1-S9, Appendix S1), using Hawth's Tools in ArcGIS 9.2. At each point, the length of fire intervals, average annual rainfall, vegetation and soil type were estimated. Data sampling was constrained within large tracts of native vegetation situated within national parks and conservation reserves (Fig. 1).

Fire interval data were determined by overlaying fire history maps, obtained from state government agencies; New South Wales Office of Environment and Heritage, (NSW OEH), Victorian Department of Sustainability and Environment (Vic DSE), and South Australian Department of Environment, Water and Natural Resources (SA DEWNR). The spatial resolution of fire history data varies, due to different methods of data capture (e.g. satellite imagery, GPS and hand drawn maps). The first recorded fires in the Victorian and South Australian database occurred in 1932, while in NSW the first recorded fires occurred in 1935. However, the completeness and accuracy of the fire history record in each state is considered more reliable from 1970 (see Fig. S10-S18, Appendix S2). For the Murray Lowland region, fire history data derived from satellite imagery interpreted by the Mallee Fire Group at LaTrobe University was used, with a minimum spatial resolution of 50m (Haslem *et al.*, 2011). The years of wildfire occurrence that intersected each random sampling point were ordered chronologically, and the length of the intervals between fires were calculated. Prescribed burns were excluded from the analysis as these fires represented a negligible component of total burn area (< 1% of the burnt area in any given year) and tend to have greater patchiness and uneven coverage within the mapped fire scar, compared to wildfires. At a small portion of points, the fire intervals could therefore be overestimated.

Intervals bounded by a fire of unknown date (i.e. either because the period of observation began after the previous fire occurred or terminated before the next fire occurred) are considered 'censored' intervals or incomplete data (Polakow & Dunne, 1999; Moritz *et al.*, 2009). Estimates of fire return interval vary widely depending on whether censored data are included or not (Kraaij *et al.*, 2013). For example, if censored data are excluded from such analyses, the length of fire intervals will be generally underestimated (Moritz *et al.*, 2009; O'Donnell *et al.*, 2011a; Kraaij *et al.*, 2013). O'Donnell *et al.*, (2011a) noted that exclusion of censored data would effectively result in a study that was confined to a subset of samples that were relatively frequently burnt resulting in inaccurate characterisation of fire regimes for the entire study domain. Alternatively, Fernandes *et al.*, (2012) argued that analyses based on uncensored data may provide a more accurate depiction of fire recurrence and risk in those areas inherently more prone to burning.

Our initial exploratory analyses, using only uncensored data, confirmed this bias (authors' unpublished results). Thus analyses using censored data were warranted based on the general principle that inclusion of censored data, and resultant estimated intervals, would provide a more thorough characterisation of the fire regime. Our study also builds on the precedent for use of censored data in past studies in temperate, shrub-dominated Mediterranean climate landscapes (e.g. Moritz *et al.*, 2009; Kraaij *et al.*, 2013), including examples such as O'Donnell *et al.*, (2011a) with strong floristic, edaphic and climatic affinities to our study area.

Approximately 73% of all fire intervals included in the dataset were censored (i.e. minimum estimates of fire intervals), with 27% of fire intervals bounded by known dates (i.e. measured intervals). However, the distribution of censored data was uneven across the study area with mallee heathlands and mallee woodlands having relatively low and high proportions, respectively, of censored data (Table 2). Inclusion of censored data in analyses therefore eliminated biases arising from unequal proportions of censored data within the study area (e.g. major underestimation of fire intervals in mallee woodlands; Table 2), if only uncensored data was used. The minimum possible fire-interval was therefore estimated on this basis (i.e. the time between the year of fire and the beginning or end of the records).

Rainfall, vegetation and soil data at each point were estimated using the enumeration function of Hawth's Tools. Average annual rainfall across the study area was determined using the spatial map of ANUCLIM version 6.0 (Hutchinson, 2004), which estimates a mean annual precipitation surface for Australia based on weather station records from 1975 to 2005. As an alternative to rainfall we considered using an ANUCLIM moisture index which incorporates evaporation. The average annual moisture index, mean moisture of the high quarter and mean moisture of the low quarter were all found to be highly correlated with mean annual precipitation ($P < 0.0001$, $r > 0.8$). As a result rainfall rather than the moisture index was used in the analyses on the basis of simplicity, as recommended by Wintle *et al.*, (2005).

Vegetation mapping was obtained from the relevant state government agencies (unpublished data from the NSW OEH, Vic DSE, and SA DEWNR). Vegetation types that were included in the analysis were either mallee woodlands or mallee heathlands. Soil mapping was obtained from the digital Atlas of Australian Soils (Bureau of Rural Sciences, 1991). Soil types that were included were categorised as either red (including brown) or yellow (including pale coloured) siliceous sands. These datasets had a minimum spatial resolution of 250 metres.

Spatial autocorrelation was tested for using the Moran's *I* spatial autocorrelation to ensure the assumption of independence of sampling points could be maintained (Legendre, 1993). Moran's *I* values range from −1 (dispersion) to +1 (clustering), with values close to zero indicating a random spatial pattern (Diniz *et al.*, 2003). Moran's *I* values were calculated for fire interval data for the sampling points within each park across the study area (15 parks in total). To maximise the sample size while minimising the effects of spatial autocorrelation, points were selected to be a minimum of 1km apart to maintain Moran's *I* values of < 0.2.

Statistical Analysis

The generalised Weibull distribution has been extensively used in fire-interval analyses (Johnson & Gutsell, 1994; O'Donnell *et al.*, 2011a). The cumulative mortality function of the Weibull distribution, *F(t),* represents the probability that a fire will have occurred at or before time 't' and takes the form:

$$F(t) = Pr(T \geq t) = 1\text{-}e^{-(t/b)\wedge c}$$

where T denotes the time or interval at which a fire occurs, *t* is time since the last fire in years, *b* is the Weibull scale parameter and *c* is the Weibull shape parameter. The hazard function, *λ(t)*, of the Weibull distribution represents the probability of burning with respect to TSF and takes the form:

$$\lambda(t) = ct^{c-1}/bc$$

where *t* is time since the last fire in years, *b* is the scale parameter and *c* is the shape parameter. In both instances, the b parameter is related to the expected length of fire interval that will be exceeded approximately 37% of the time and the *c* parameter captures how the hazard of burning changes with TSF. When $c = 1$, the hazard of burning does not change with time since fire, when $1 < c < 2$, the hazard of burning grows at a diminishing rate, and when $c = 2$, the hazard of burning increases linearly with time (Johnson & Gutsell, 1994; O'Donnell *et al.*, 2011a). Given that censored data were included, values of *b*, the estimates of potential fire intervals were not measured intervals. High proportions of censored data also tend to increase the Weibull *b* parameter (with wider CIs) and lower Weibull *c* parameter close to zero (with narrower CIs) (Moritz *et al.*, 2009).

We used a Bayesian framework with uninformative priors to test the effect of various models containing all additive combinations of the factors of rainfall, vegetation and soil type on the hazard and mortality parameters of the Weibull distribution (see Table 2). Interactive models were not considered due to degrees of freedom limitation. Bayesian models with uninformative priors are numerically similar to maximum likelihood models used for analyses of fire-interval information containing incomplete (censored) data (Polakow &

Dunne, 1999; O'Donnell *et al.*, 2011a). We used Markov chain Monte Carlo (MCMC) methods to calculate the model parameters (Spiegelhalter *et al.*, 2002). To ensure the MCMC was sampled from the posterior distribution, it was necessary to discard the initial samples in the Markov chain. We initially considered 110,000 samples and discarded the first 10,000. The Bayesian models were batch run in the OpenBUGS program, version 2.2.0 (Thomas *et al.*, 2006). We used the Deviance Information Criterion (DIC) (Spiegelhalter *et al.*, 2002) to assess the effects of differing explanatory variables on the fire parameters (response variables). Models containing sets of explanatory variables with changes in DIC of greater than 10 points of the best model were considered to have essentially no support (McCarthy, 2007). Within a model, we regarded parameter estimates as significant at the $P = 0.05$ level when the 95% credible intervals (CIs) did not overlap zero. Similarly, significant differences between parameter estimates were regarded when the 95% CIs did not overlap (McCarthy, 2007).

RESULTS

The preferred model to explain variation in fire intervals with the most support contained all three explanatory factors; rainfall, vegetation and sand type. All remaining models had DIC values > 90 points higher than the best model and thus were not considered further. All three predictor variables were included within the best model, as none of the 95% CIs of their coefficients overlapped zero (Table 3).

The b-parameter estimate (the length of the fire interval that will be exceeded approximately 37% of the time) varied under each combination of soil, vegetation and rainfall (Table 3, Fig. 2, Fig. S19 Appendix S3). Higher rainfall was associated with shorter fire intervals in all soil and vegetation combinations. Fire intervals were significantly shorter with higher rainfall in each of the two dominant soil and vegetation combinations; red sand/mallee woodlands and yellow sand/mallee heathlands ($P < 0.05$, Table 3, Fig. 2).

Vegetation and soil type influenced the length of fire intervals in complex ways. Within a single level of rainfall and soil type, vegetation type had contrasting effects on the length of fire intervals. Mallee heathlands had significantly shorter fire intervals than mallee woodlands when on yellow sand (at 400 and 500mm/yr, $P < 0.05$, Table 3, Fig. 2), whereas on red sand, mallee heathlands had significantly longer fire intervals than mallee woodlands (at 300 and 400mm/yr, $P < 0.05$, Table 3, Fig. 2). Within a single level of rainfall and vegetation type, soil type had contrasting effects on fire-intervals. Mallee heathlands on red sands had significantly longer fire intervals than mallee heathlands on yellow sands at 400 and 500mm/yr (i.e. at 400 and 500mm/yr, $P < 0.05$, Table 3, Fig. 2). By contrast, mallee woodlands on red sands had significantly shorter fire intervals than mallee woodlands on yellow sands at 400mm/yr ($P < 0.05$, Table 3, Fig. 2).

The complex interactions of rainfall, vegetation and soil type on the length of fire intervals (b-parameter estimate) were reflected in the fire interval probability models. Increased rainfall consistently increased the probability of fire occurring at or before a given time (Fig. 3). Higher rainfall also increased the hazard of burning, irrespective of TSF (Fig. 4). The interaction of vegetation and soil type at any given level of rainfall influenced the probability of fire, whereby lower soil fertility (i.e. yellow compared to red sands), corresponded with a higher probability of fire in mallee heathlands, and a lower in the probability of fire in mallee woodlands (Fig. 3). While this pattern occurred across rainfall levels, the effect was more pronounced at high rainfall (i.e. 400-600mm/yr).

The c-parameter estimate (dependency of fire-intervals on TSF) was not significantly different among rainfall categories, but varied between the combinations of soil and vegetation (Table 3). Fire intervals were independent of fuel age in mallee woodlands on red sand ($c = 1$) and tended to be relatively more dependent on TSF in each of the other soil and vegetation combinations ($c > 1$). Fire intervals were significantly more dependent on TSF in yellow sand/mallee heathlands compared to red sand/mallee woodlands ($P < 0.05$, Table 3).

The hazard of burning remained largely independent of TSF in the majority of rainfall, vegetation and soil combinations (Fig. 4). There tended to be slight increases in the hazard of burning with TSF in each combination of vegetation and soil type at > 300mm/year rainfall, except for mallee woodlands on red sand. However, only in mallee heathlands on yellow sands at 500mm/year did the hazard of burning increase with TSF, with an increase from 2% to 4% in the hazard of burning from 1 to 200 years since fire.

DISCUSSION

Productivity and fire regimes

Rainfall had an overarching influence on fire frequency in the Mediterranean climate mallee woodlands of south eastern Australia. The length of the fire interval that will be exceeded approximately 37% of the time decreased with higher levels of rainfall, as predicted on the basis of general relationships between productivity and fire (Bond & Keeley, 2005; Pausas & Bradstock, 2007). In addition, higher levels of rainfall corresponded with in a change in the probability of fire with TSF. The probability of burning was independent of TSF in red sand/ mallee woodlands, which is dominant in the drier north of the region, but had a positive relationship with TSF in the yellow sand/ mallee heathlands, which dominates the wetter south. Such a response was consistent, as predicted, with an overall contrast between dominance of herbaceous fuels in the north to woody litter and foliage fuels in the south (Pausas & Bradstock, 2007; Gibson *et al.*, 2014), and a greater influence of TSF on the probability of burning due to patterns of litter fuel accumulation with time since fire.

Soil fertility also had a strong influence on the probability of fire, but the nature of this influence differed between vegetation types. Fire intervals in mallee woodlands were shorter compared with mallee heathlands on the relatively high fertility sands. In mallee heathlands fire intervals with a greater dependence on TSF at high rainfall (> 400mm/yr) occurred on yellow sands with lower soil fertility. Therefore, the effects of soil fertility and rainfall on fire regimes did not align in terms of effects on potential productivity. This result indicates that models which attempt to predict large-scale fire patterns solely on the basis of moisture variations (e.g. Pausas & Paula, 2012) are potentially subject to inaccuracy in regions with high variation in soil fertility. Integration of effects of different influences on 'productivity' is therefore needed to more completely understand its relationship with fire regimes.

A possible explanation for the complexity of the observed relationship is that the effect of soil fertility on the selection of plant traits and the corresponding influence on fire may override effects that ensue from the influence of rainfall on fire (e.g. lower soil fertility favours woody shrubs with small sclerophyllous leaves, increasing fire propensity; Ojeda *et al.*, 2010; Keeley *et al.*, 2011; Gibson *et al.*, 2014).

The overall trend toward longer intervals and lower hazard of burning with TSF (i.e. Weibull *b* and *c* parameters respectively) at low rainfall levels was most likely an outcome of the use of high proportions of censored data in samples from low rainfall sites (Table 2). By contrast, it was less likely that general trends in hazard of burning and fire intervals were influenced by use of censored data, due to the more even spread of such data across the soil types (Table 2). While conclusions concerning effects of rainfall were contingent on inclusion of censored data we considered these to be robust, given the likelihood of major underestimation that would have occurred if such data were excluded for low rainfall levels.

Age dependency of burning and fuel systems

Previous research within the mallee woodlands on red sand from 200-350mm/yr provided evidence that shrub cover increased while grass cover declined from north to south with increasing rainfall (Gibson *et al.*, 2014). This change in the relative mix of grass and woody shrub cover with rainfall corresponds with a decrease in the length of fire-intervals (i.e. higher fire frequency, Fig. 2). There was no change in the dependency of fire intervals on TSF across this same range (i.e. within semi-arid mallee woodlands on red sand from 200-350mm/yr; Fig. 4). Higher dependency on TSF at the wetter end of the gradient in these woodlands was expected but it was possible woody shrub cover at the wetter end remained insufficient to exert a TSF effect on fire intervals.

The strength of the TSF effect on fire in mallee heathlands on yellow sand was also weak. Other Mediterranean-type shrubland ecosystems have reported weak to moderate c parameter estimates (i.e. $c < 2.5$; Moritz *et al.*, 2004; O'Donnell *et al.*, 2011a). In these systems, fuel most rapidly accumulates in the immediate post-fire period (e.g. < 10 - 20 years). Beyond this time period fuel accumulation rate declines and the consequent influence of TSF on the probability of fire continues to diminish. Although there was an increase in the hazard of burning with TSF in yellow sand/mallee heathlands at high rainfall (Fig. 4), the magnitude of this effect was small (i.e. a maximum increase of < 4% on the hazard of burning). Most fires in mallee heathlands were likely to be more strongly influenced by the occurrence of extreme fire weather and dry conditions in the antecedent year (i.e. low fuel moisture content) than by the age and spatial patterns of fuels, as in other Mediterranean-type shrubland ecosystems (Moritz *et al.*, 2004; van Wilgen *et al.*, 2010). In general, we note the lack of a strong effect of TSF at high rainfall levels is a robust result, given that censored data was either absent or negligible across all plant community and soil types (Table 2). Compelling evidence of strong, implied effects of fuel accumulation on fire regimes in these shrub dominated systems is therefore lacking.

Future implications

Prescribed burning for hazard reduction is unlikely to be effective at reducing the probability of fire, given that the probability of fire is unrelated to TSF in mallee woodlands and only weakly related to TSF in mallee heathlands on yellow sands. Historically most of the area burned in mallee woodlands of the Mediterranean region of southern Australia is due to a small number of fires that burn large areas (authors' unpublished data), which is consistent with reports in other crown-fire ecosystems around the world (Moritz, 1997; Johnson *et al.*, 2001). In addition, the majority of fires in mallee woodlands have occurred shortly following extreme *La Niña* years (authors' unpublished data; Bradstock & Cohn, 2002; O'Donnell *et al.*, 2011b), which is likely to be due to the rapid response of ephemeral herbaceous fuels creating an increase in biomass available for burning. Therefore, strategic prescribed burning, particularly during periods following heavy rainfall, may provide critical fuel breaks to protect long unburnt vegetation in this community (Willson, 1999). Previous research in mallee woodlands of this region highlights the importance of the long-term development (i.e. > 100 years) of some critical habitat resources, such as the mature canopy layer and tree hollows (Haslem *et al.*, 2011). Therefore, fire management that protects long un-burnt mallee vegetation would also be advantageous for fauna habitat conservation.

Given the strong influence of rainfall on fire intervals in the Mediterranean region of south eastern Australia, changes in climate-related factors that are predicted to occur in the future have the potential to drive changes in fire regimes. For example, a 20% reduction in mean annual rainfall, which is in the range projected to occur in this region by 2070 (Suppiah *et al.*, 2007), would correspond with an increase in mean fire intervals by approximately 15 years in yellow sand/mallee heathland and 64 years in red sand/mallee woodland. Temperatures are also likely to increase, possibly leading to a higher incidence of extreme fire weather, as evident in the study regions in the last few decades (Clarke *et al.*, 2012). Such effects may ultimately lead to a decrease in mean fire intervals via an increase in area burned.

Changes in temperature and moisture, as well as further increases in atmospheric CO_2, may affect different species in different ways. Warmer, drier conditions may provide a relative advantage to plants that use the C_4 photosynthetic pathway (*Triodia* sp.) compared to plants that use the C_3 pathway, such as woody shrubs and *Austrostipa* spp., the major contributors to ephemeral fuels (Sage *et al.*, 1999). As such, shifts in the patterns of fire intervals as a result of changes in temperature and moisture may not be linear across the grass and shrub dominated communities. Furthermore, elevated CO_2 may be more beneficial to C_3 plants compared to C_4 plants (Bond & Midgley, 2012; Wang *et al.*, 2012), which may ameliorate any potential relative advantage of C_4 plants under warmer, drier conditions. Given the divergent effects of soil fertility on fire intervals in mallee woodlands (dominated by *T. scariosa* plus ephemeral grasses following heavy rainfall) compared to mallee heathlands (shrub dominated), elevated CO_2 has the potential to interact with soil fertility to influence the growth of grass and shrub species in different ways. Further research is required to quantify the effects and interactions between moisture, temperature and CO_2 and soil fertility on the relative growth and abundance of the C_4 grasses and C_3 shrubs and grasses in this region. This would provide important insight into potential consequences of climate change on fuel dynamics and corresponding changes in fire regimes across the Mediterranean mallee woodlands of south eastern Australia in the future.

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SUPPORTING INFORMATION

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

Appendix S1: Decadal sequence of fire history maps across the study area since 1930 (Fig. S1-S9)

Appendix S2: Maps vegetation type at each random sampling point in each park or reserve included in the analysis (Fig. S10-S18)

Appendix S3: Cumulative probability curves of fire interval distributions, based on empirical fire history data (Fig. S19)

BIOSKETCH

The research team represents a collaborative venture between government and academic researchers funded by an Australian Research Council Linkage grant. The team is devoted to understanding the role of fire in determining ecological diversity in dry, shrub-dominated environments and harnessing such knowledge to improve the management of fire in conservation reserves. The scope of this work includes quantification of fire regime patterns and processes, the ecology and population genetics of key plant and animal taxa and application of population models to explore fire management scenarios that enhance population viability.

Author contributions: All authors contributed to conceiving the ideas; R.K.G. collected the data; R.K.G, T.P. and R.A.B. analysed the data; and R.K.G. and R.A.B. led the writing.

Table 1 Summary of the relative proportion of the landscape that each vegetation/soil complex occupies, within the dry (<300mm/yr) and wet (>300mm/yr) regions of the study area. Bold values indicate the cases where >50% of the landscape is occupied.

	Relative proportion of the landscape (%)	
Vegetation/soil complex	***< 300mm/yr***	***> 300mm/yr***
Red sand/ Mallee woodlands	**68.11**	3.31
Yellow sand/ Mallee woodlands	11.62	20.08
Red sand/Mallee heathlands	5.28	14.22
Yellow sand/ Mallee heathlands	14.99	**62.39**

Table 2 Summary of the proportion of censored fire intervals across vegetation, sand and rainfall categories, included in analyses.

	Mallee Woodlands		***Mallee Heathlands***	
Rainfall	***Red sand***	***Yellow sand***	***Red sand***	***Yellow sand***
200	90.84	92.47	0.00	0.00
300	56.03	85.22	45.45	67.48
400	100.00	80.93	0.00	49.74
500	0.00	100.00	0.00	0.00

Table 3 Estimated Weibull parameters, b (the fire interval, in years, that will be exceeded ca. 37% of the time) and c, (a measure of the dependence of fire intervals on fuel age) for each of the soil, vegetation, and rain categories in the study region in south-eastern Australia, including the mean, standard deviation (Std. Dev.), the median, upper (97.5 percentile) and lower (2.5 percentile) 95% credible intervals. The parameter estimate is considered significant at the p = 0.05 level when the 95% credible intervals (CIs) do not overlap 0. Significant differences at the p = 0.05 level between combinations of soil, vegetation and/or rainfall occur when 95% CIs do not overlap each other (e.g. the lower CI of x > upper CI of y). Different superscript letters indicate significant differences in parameter estimates among classes at the p = 0.05 level.

Model Parameters			Mean	Std. Dev.	Lower CI (2.5pc)	Median	Upper CI (97.5pc)
Red Sand	Mallee woodland	b-param. (200mm rain)[a]	509.000	119.100	318.600	494.700	783.000
		b-param. (300mm rain)[b]	191.200	36.590	130.500	187.400	272.300
		b-param. (400mm rain)[d,e]	73.370	18.590	44.020	71.010	116.400
		c-param[x].	1.020	0.047	0.930	1.020	1.113
	Mallee heathland	b-param. (300mm rain)[a,]	632.000	225.600	312.500	591.800	1182.000
		b-param. (400mm rain) [a]	422.100	138.600	221.500	398.600	756.600
		b-param. (500mm rain) [a,b]	282.700	87.350	154.900	268.300	492.400
		b-param. (600mm rain) [a,b]	190.000	56.990	105.900	180.500	326.900
		c-param[x,y].	1.164	0.073	1.027	1.164	1.312
Yellow Sand	Mallee woodland	b-param. (300mm rain)[a,b]	468.400	145.200	252.000	444.400	813.000
		b-param. (400mm rain)[b,c]	225.400	55.650	137.600	217.400	353.600
		b-param. (500mm rain)[b,c]	109.900	25.780	68.560	106.900	169.300
		c-param[x,y].	1.138	0.065	1.014	1.137	1.267
	Mallee heathland	b-param. (300mm rain)[a,b]	324.200	46.370	243.900	321.100	425.200
		b-param. (400mm rain)[c,d]	117.600	12.380	95.530	117.000	143.800
		b-param. (500mm rain)[e]	42.950	5.388	33.480	42.540	54.380
		c-param[y].	1.193	0.028	1.139	1.192	1.247

1 FIGURES

Fig. 1 Location of the Mediterranean climate region of south eastern Australia, with the National Parks and Nature Reserves included in the study, classified by soil type. Grid reference datum is GDA 1994, Lambert Conformal Conic projection.

Fig. 2 Mean estimate of Weibull parameter b (the length of the fire interval that will be exceeded ca. 37% of the time, in years) for each combination of sand and vegetation type (mallee woodlands, M.W. and mallee heathlands, M.H.) for the rainfall categories in which they occur. Error bars represent 95% credible intervals. Different superscript letters indicate significant differences in parameter estimates among classes at the $p = 0.05$ level.

Fig. 3 Weibull cumulative mortality functions for each combination of sand and vegetation type (mallee woodlands, M.W. and mallee heathlands, M.H.) for the rainfall categories in which they occur, based on the Weibull parameter estimates (Table 2). The mortality function describes the probability that a fire will occur before or at time t.

Fig. 4 Weibull hazard functions for each combination of sand and vegetation type (mallee woodlands, M.W. and mallee heathlands, M.H.) for the rainfall categories in which they occur, based on the Weibull parameter estimates (Table 2). The hazard function reflects the influence of TSF on the probability of burning.

Mean estimate of Weibull parameter c (the dependence of fire intervals on TSF) for each combination of sand and vegetation type (mallee woodlands, M.W. and mallee heathlands, M.H.). Error bars represent 95% credible intervals. Different superscript letters indicate significant differences in parameter estimates among classes at the $p = 0.05$ level.

Fig. 1

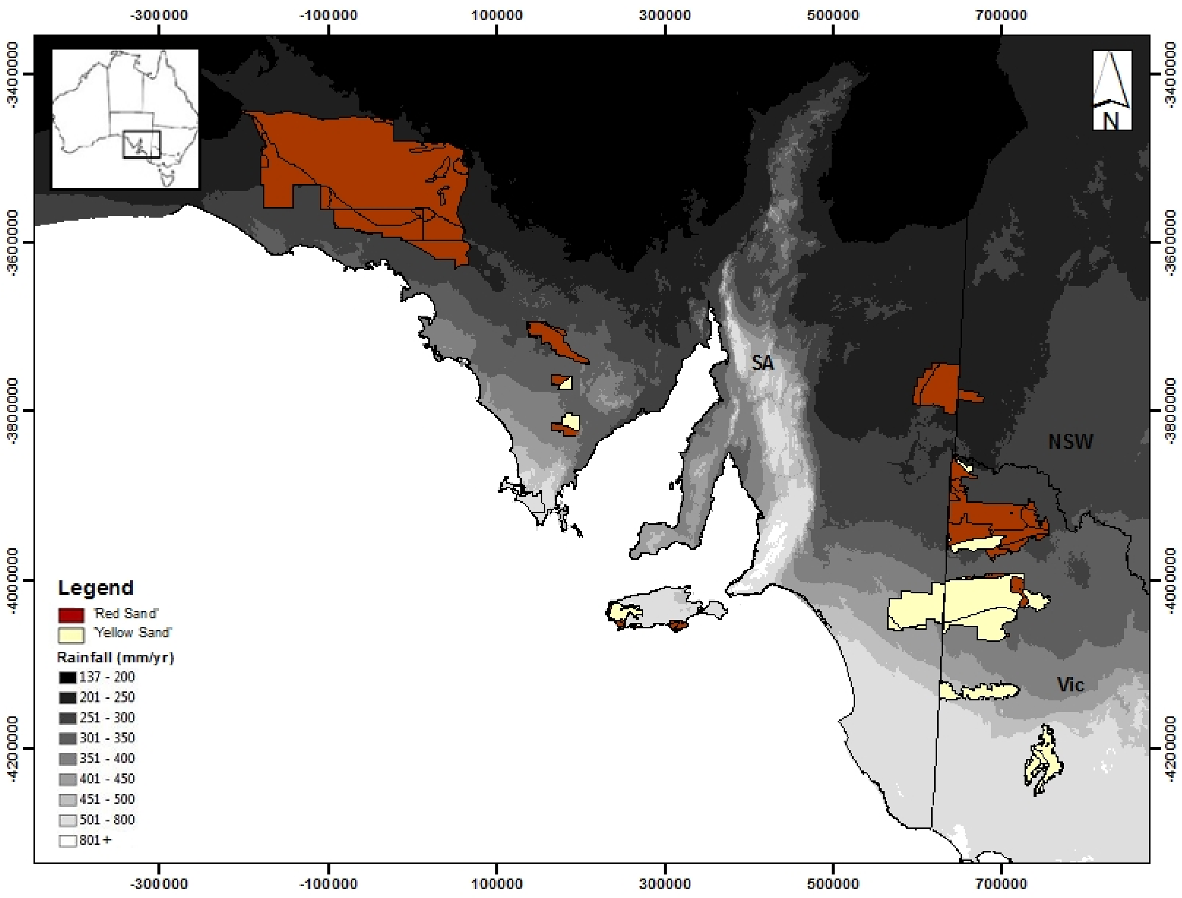

-300000
-100000
100000
300000
500000
700000
-3400000
-3600000
-3800000
-4000000
-4200000
N
SA
NSW
Vic
Legend
'Red Sand'
'Yellow Sand'
Rainfall (mm/yr)
137 - 200
201 - 250
251 - 300
301 - 350
351 - 400
401 - 450
451 - 500
501 - 800
801 +

Fig. 2

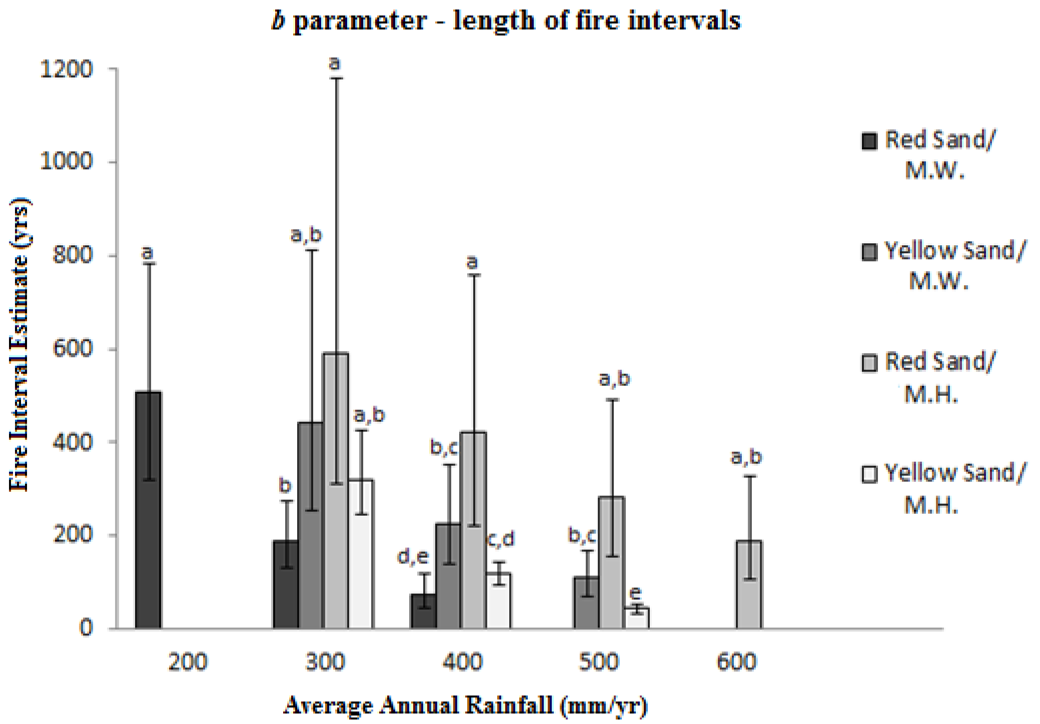

b parameter - length of fire intervals
Fire Interval Estimate (yrs)
0
200
400
600
800
1000
1200
a
b
a,b
a
a,b
d,e
b,c
a
c,d
b,c
a,b
e
a,b
200
300
400
500
600
Average Annual Rainfall (mm/yr)
Red Sand/ M.W.
Yellow Sand/ M.W.
Red Sand/ M.H.
Yellow Sand/ M.H.

Fig. 3

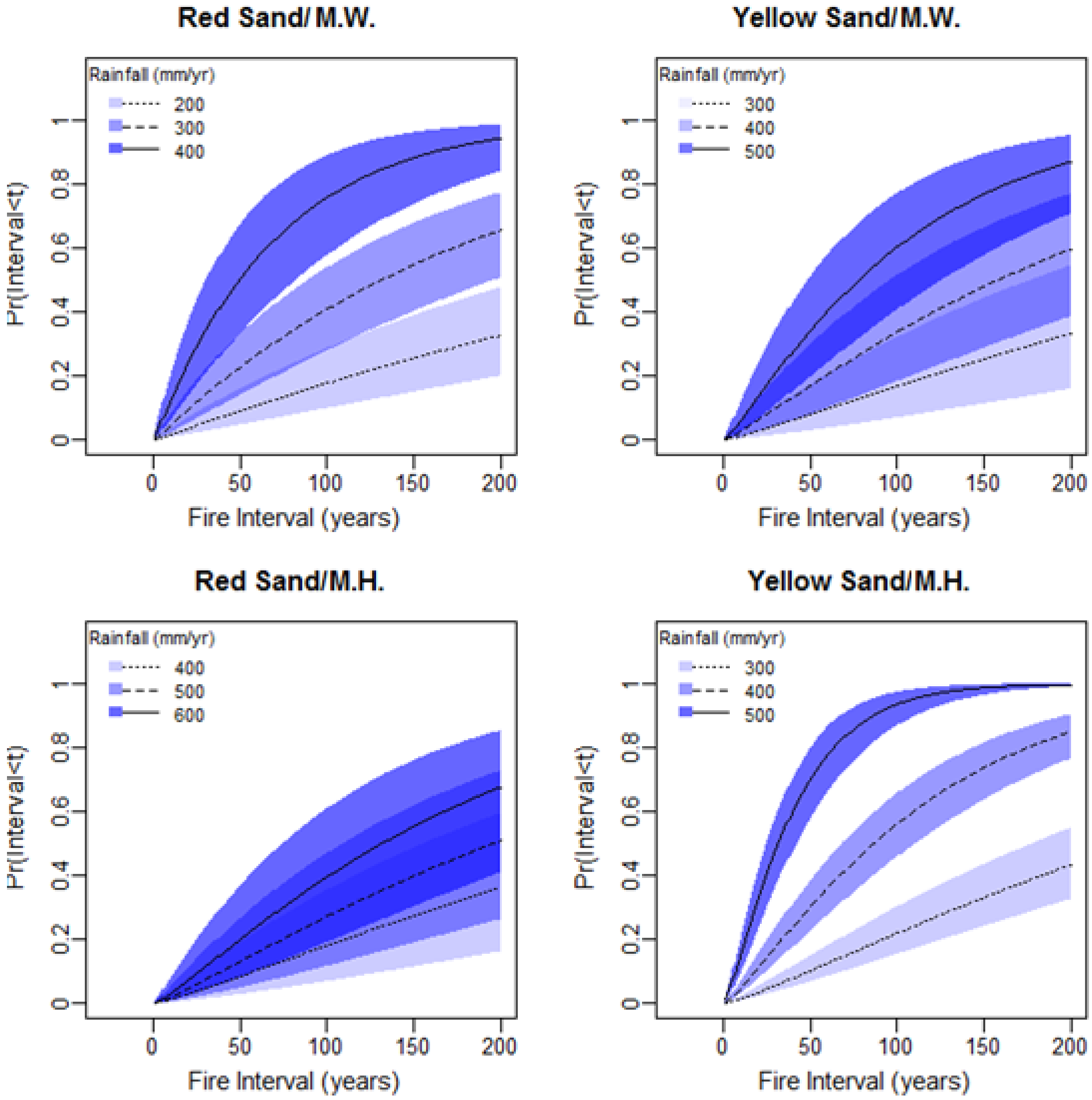
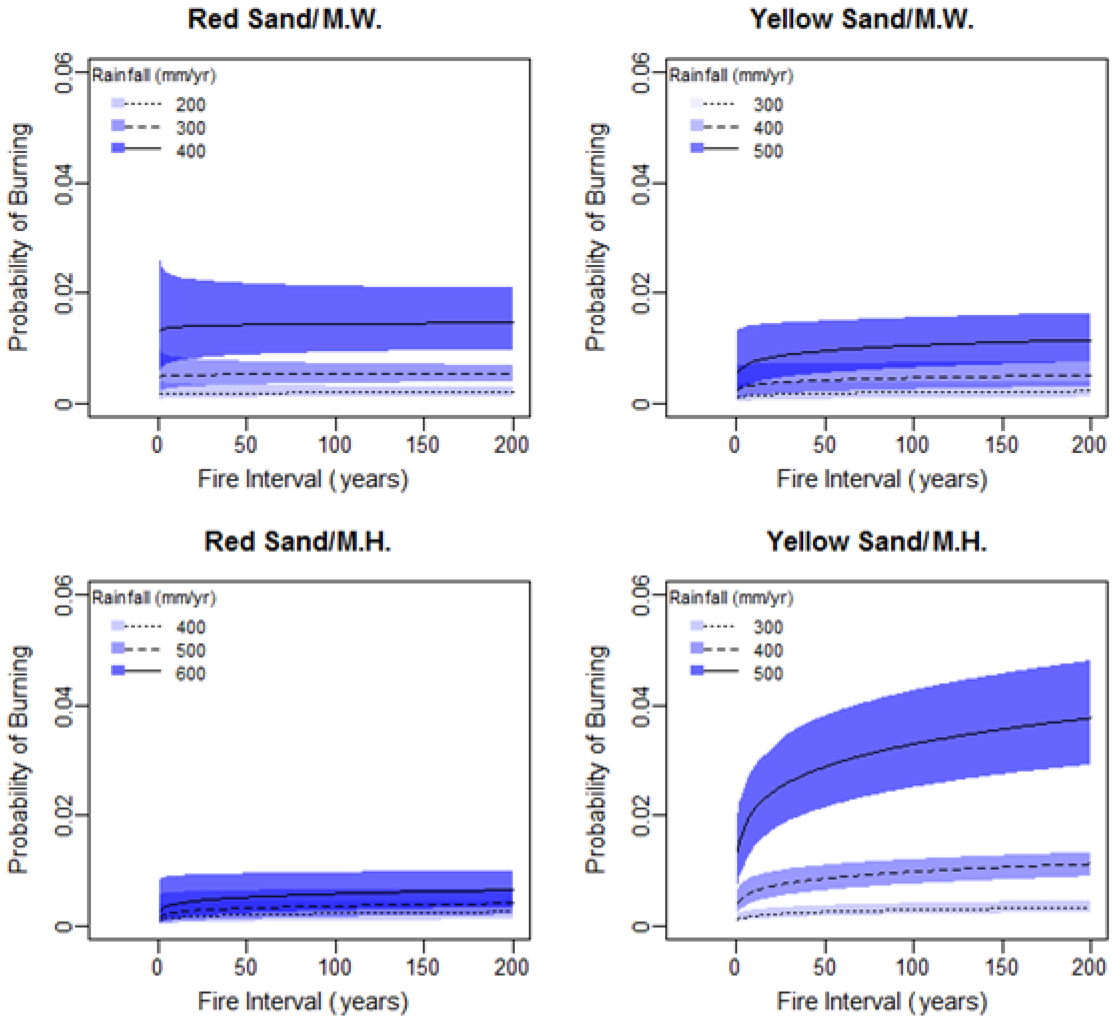

Red Sand/ M.W.
Rainfall (mm/yr)
200
300
400
Pr(Interval<t)
Fire Interval (years)
Yellow Sand/M.W.
Rainfall (mm/yr)
300
400
500
Pr(Interval<t)
Fire Interval (years)
Red Sand/M.H.
Rainfall (mm/yr)
400
500
600
Pr(Interval<t)
Fire Interval (years)
Yellow Sand/M.H.
Rainfall (mm/yr)
300
400
500
Pr(Interval<t)
Fire Interval (years)

Fig. 4


Red Sand/M.W.
Yellow Sand/M.W.
Red Sand/M.H.
Yellow Sand/M.H.
Probability of Burning
0 0.02 0.04 0.06
Fire Interval (years)
0 50 100 150 200
Rainfall (mm/yr)
200 300 400
300 400 500
400 500 600
300 400 500