Potential Key Drivers of Thicket Expansion in Savanna

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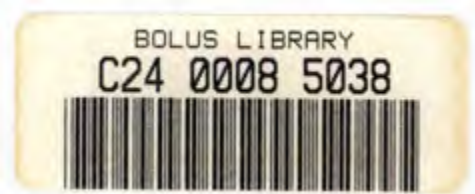
Abstract

The invasion of grasslands by woody plants and their increase in savannas is a global phenomenon. There has been a lot of work on the ecology of savanna trees, but very little on the drivers of the increase of non-savanna (forest and thicket) vegetation within savannas. The switch from savanna to closed canopy thicket represents a biome switch for the system and is therefore of concern to land and conservation managers. Data on height growth, root suckering and fire damage were collected for two thicket forming species. A simulation model was developed to evaluate the effect of different biotic and abiotic factors on the spread of a thicket clump in savanna in the Hluhluwe Game Reserve, South Africa. The amount of damage from fire suffered by a thicket clump is increased by higher fire intensity and decreased by larger clump area or greater pre-burn mean clump height. A sensitivity analysis indicated that increased height and area growth rates and decreased fire frequency allows thicket expansion to occur and that data on these is essential for predicting the expansion of thicket clumps. Predictions from the model suggest that a thicket clump's situation within the landscape is important and that spatial modelling, incorporating fire spread and fire refugia such as river banks is necessary to further improve understanding of thicket expansion.

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Introduction

The invasion of grasslands by woody plants and their increase in savannas is a global phenomenon. Often termed 'bush encroachment', it has been described in Southern Africa, North America, Australia and South America. Bush encroachment is of concern to ranchers, conservation managers and eco-tourism businesses. In South Africa the invasion of savannas by woody vegetation has potentially large impacts on the eco-tourism value of our savanna national parks because game viewing is harder in woodlands than in savannas.

Most research work into the patterns and possible mechanisms driving the increase in woody vegetation cover has focussed on the co-existence of C_4 grasses and microphyllous arborescent species e.g. *Acacia spp.* in Southern Africa and *Prosopis spp.* in the southern United States. There are many hypotheses as to the possible causes of bush encroachment; increased CO_2 (Bond and Midgley, 2000), reduced fire frequencies and or intensities (Higgins et al, 2000; Briggs et al. 2005), heavy grazing (Archer, 1995), increased rainfall (Sankaran et al. 2005) and a lowering of the water table (King 1987). Many of these hypotheses have been evaluated for microphyllous savanna trees and modelling exercises (e.g. Higgins et al. 2000) have helped to elucidate some of the key drivers of the recruitment and establishment of trees in savanna systems. Sankaran et al. (2005) argue for the suggestion by Bond et al. (2003) of 'stable' and 'unstable' savannas. In stable savannas water availability places an upper bound on the potential maximum tree cover, whereas in unstable savannas, with higher water availability, tree cover is not limited by access to water with the result that tree cover may be at or close to 100 percent. In therefore disturbances, in the form of fire and herbivory, that are important in determining the cover of trees and grasses in the system.

Despite the large literature on tree-grass coexistence in savannas, there has been relatively little work done on the increase in non-savanna vegetation cover (forest/thicket) in savanna systems. Unlike savanna, forest and thicket have a grass layer that, if present, is discontinuous and because of this is less likely to allow the spread of fire (Stauffer and Aharony, 1992). Secondary succession in savanna is often associated with a transition from microphyllous trees to a more closed, broadleaf thicket or woodland (Smith and Goodman 1986,1987; Franco-Pizana, 1996). Smith

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and Goodman, (1987) suggested that microphylls act as nurse plants for thicket forming species and Archer et al. (1988) described them as nucleation sites for the formation of thicket clumps in grassland. Smith and Goodman (1986) and Brown and Archer (1995) suggest that broadleaved individuals eventually overtop and shade out the microphylls, which senesce and die, resulting in a closed canopy woodland. Brown and Archer (1989), however, showed that this facilitation did not extend beyond the germination and establishment stage of a shrub seedling. Also in disagreement with microphylls facilitating broadleaved recruitment, Skowno et al. (1999), working in a mesic subtropical savanna, state that broadleaved thicket forming species (*Euclea divinorum* and *Euclea racemosa*) are not facilitated by mature *Acacia nilotica* individuals and instead suggest that these species are present in the grass and therefore fire layer as saplings due to their having relatively slower growth rates. Slower growth rates make the thicket species less likely than acacias to grow tall and escape the fire layer during inter fire periods. A decrease in fire frequency, however, could lead to an escape event and consequently the formation of a euclea thicket, which would shade out savanna grasses and prevent recruitment of shade-intolerant acacias.

In the Hluhluwe game reserve, South Africa, the increase in thicket species in savanna has been noted as a problem by managers since the 1930's (King, 1987) and has resulted in the formation of closed canopy thicket over substantial areas of the northern section of the park (Watson and Macdonald 1983; King 1987). It is thought that the growth and coalescence of the broadleaf shrub and tree (thicket) clumps that are present in open savanna in Hluhluwe may lead to the formation of this closed canopy thicket, similar to the coalescence of thicket clumps described by Archer et al. (1988) and Briggs et al. (2005) for the south-western United States. There is a change in the species composition of the grass layer from savanna to thicket and Skowno and Bond (2003) describe a change in the bird species composition between thicket and savanna in Hluhluwe. This change to thicket could therefore represent a complete biome switch with severe implications for managers mandated to conserve the current biodiversity of the park. Various interventions such as the mechanical removal of shrubs and poisoning have been undertaken, but have failed to halt the thicket's expansion (Wigley, 2007). As has been the case internationally, much of the research

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focus in Hluhluwe has been on savanna trees, with little work done on the expansion and contraction of non-savanna vegetation within the system.

Modelling is a useful tool that forces integrative thinking and allows the dissection of a problem by predicting the effects of key parameters that may then be tested in the field. Simulation models have proved valuable in elucidating the complex dynamics of savannas (e.g. Higgins et al. 2000; Bond et al. 2003; van Langvelde et al., 2003). We developed a simulation model of a broadleaved savanna thicket clump in order to answer the following questions. What are the key drivers of thicket clump expansion? Are these the same as those suggested for microphyllous bush encroachment? What management actions might be most effective in combating thicket expansion in Hluhluwe?

Study species

Maytenus senegalensis and *E. divinorum* are the two major broadleaf thicket forming species in Hluhluwe. King (1987) describes them as pioneer species for bush encroachment in the park. *E.divinorum* thicket has established and excluded savanna grasses over periods of possibly less than a decade in Hluhluwe (Skowno et al. 1999). The model therefore focuses on thicket clumps where one of these two species is the major component of the vegetation and is parameterised using height and area growth value for these two species.

E. divinorum is an evergreen multi-stemmed shrub or small tree (up to 8m) that grows at low altitudes in tropical and sub-tropical Africa and is a strong resprouter, able to survive damage by fire, and has the ability to root sucker (Pooley 1993; Coates - Palgrave 1984). *M. senegalensis* is an evergreen multi-stemmed shrub or small tree (up to 4m). It is capable of resprouting and can root sucker at least up to 2 m (pers. obs.). Black rhino feed on the bark and leaves (Pooley, 1993). Both species have fleshy bird dispersed fruits and, unlike acacias, flower and fruit within the flame zone.

Savanna tree and thicket clump ecology

Key differences exist between the ecology of savanna trees and thicket clump vegetation. Escape from the flame zone is a key life history stage in savanna tree ecology. The amount of fire damage (topkill) experienced by savanna trees is related

to their height and to fire intensity (Trollope, 1984). Once an individual has grown tall enough to be relatively undamaged by the fire intensities experienced at a site they are able to develop a large canopy on which to bear flowers and fruits. High height growth rates are in important in enabling saplings to escape and an erect pole-like sapling growth form is common in many savanna trees. Saplings trapped within the flame zone, termed 'Gulliver's' by (Bond and van Wilgen, 1996), generally do not reproduce and maintain large below-ground carbon stores that enable them to resprout and grow rapidly in height after fire (Bond and Midgley, 2000). Over time, increasing numbers of saplings may become trapped within the flame zone with the result that escape at a site occurs in cohorts during periods of low fire frequency or intensity. Based upon this, Higgins et al. (2000), suggest that acacia recruitment in savannas fits a storage effect model (Chesson and Huntly, 1989) where reproductive potential is stored between generations, allowing the population to recruit strongly when conditions are favourable. In contrast, many thicket clump species are able to flower and fruit within the flame zone therefore weakening the storage effect by allowing more even rates of recruitment amongst periods of high and low disturbance. Vigorous root suckering also allows for the lateral spread of thicket forming species, with short intervals between saplings. Unlike savanna trees, this allows thicket clumps to expand in area before escaping the flame zone. The amount of fire damage suffered by a thicket clump may therefore depend not only on its height, but also on its area. Clumps with a large area would be expected to suffer less damage at their centre than smaller clumps, for a given fire intensity. Data on the height growth rates and root suckering distances of thicket forming species or determinants of the fire damage suffered by thicket clumps was not available and therefore, before a simulation model could be built, a number of these variables needed to be parameterised.

Data collection and results

Thirty-four thicket clumps were sampled for fire damage after management burns in the reserve. A number of measures of clump size were taken (fig. 1). The middle height of a clump is a significant predictor of a clump's mean height (P<0.01, d.f. = 31, R^2 = 0.74; eqn 5 in table 1). Using the methods of Williams et al. (2003) A post-hoc estimate of fire intensity for each burn was calculated from the mean char height (the height just below the lowest leaf that is not burnt by fire) of the six *Acacia karoo*

individuals closest to the thicket clump. This was done to get as good an estimate as was possible of the fire intensity just prior to the clump burning. The relationship between char height and fire intensity for Hluhluwe was calibrated using experimental fires, where measures of intensity were taken while the fire was burning (fig. 2).
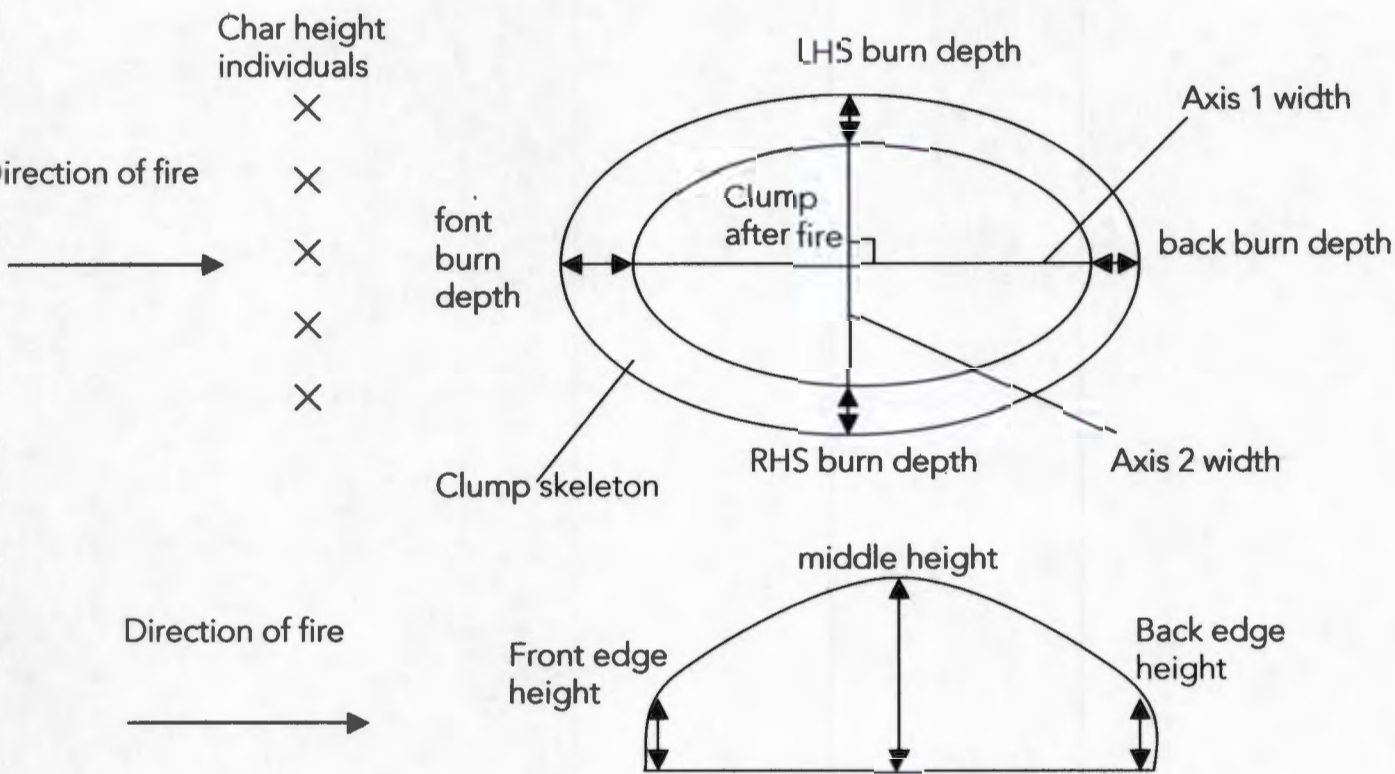

Figure 1. Measurements of clump size and damage from fire that were recorded.
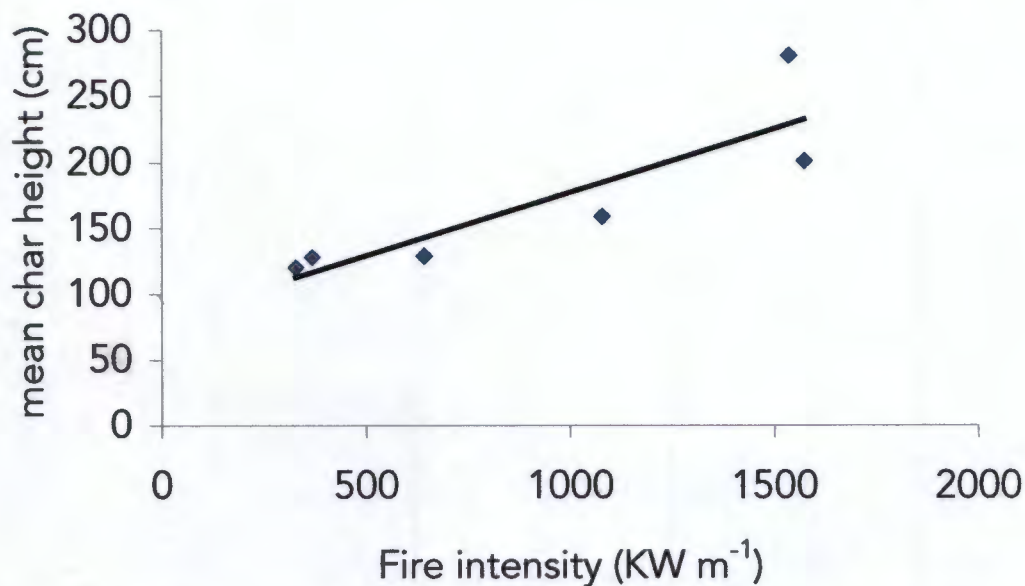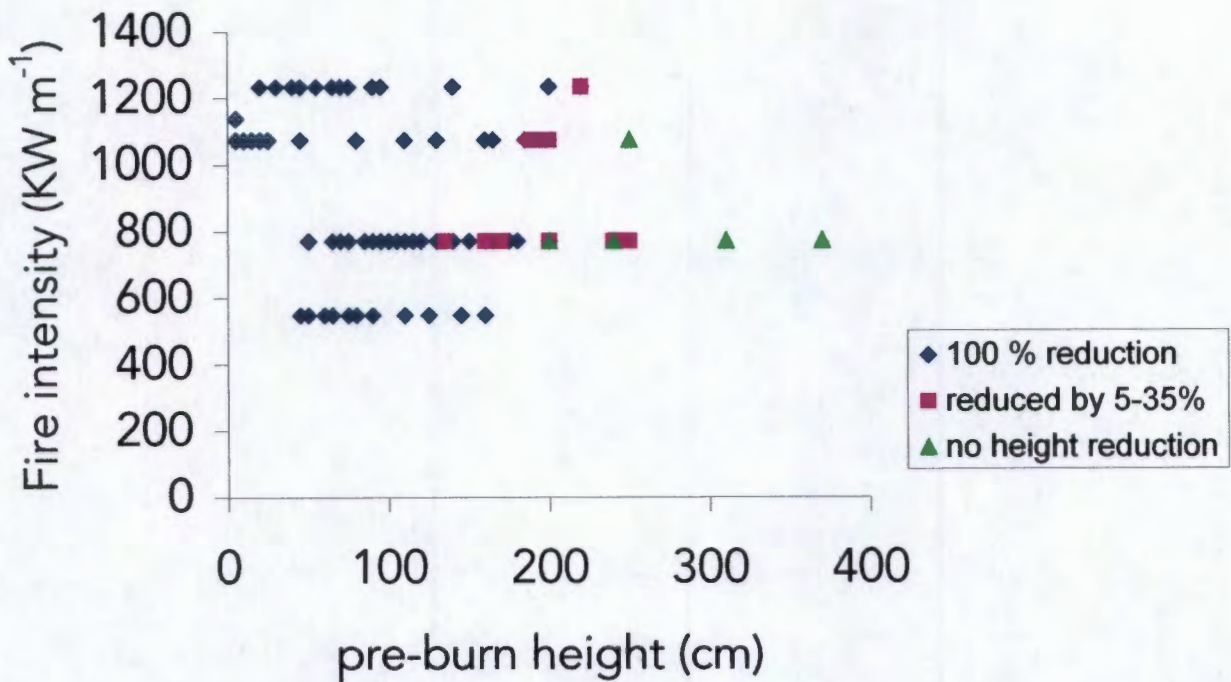
Figure 2. The effect of fire intensity on mean char height ($y = 0.096x + 81.23$); $R^2 = 0.76$.

The best regression model for clump area fire damage was selected by comparing the R^2 values between models. A linear regression equation containing the pre-burn area of the clump, the pre-burn mean height of the clump and the fire intensity as the predictor variables was selected ($P<0.01$, d.f. = 30, $R^2 = 0.72$; eqn 4 in table 1). An increase in either the pre-burn area (fig. 3a) and/or the pre-burn mean height (3b.) of a thicket clump, for a given fire intensity, is associated with a decrease in the percentage of the clump that is burnt by fire.
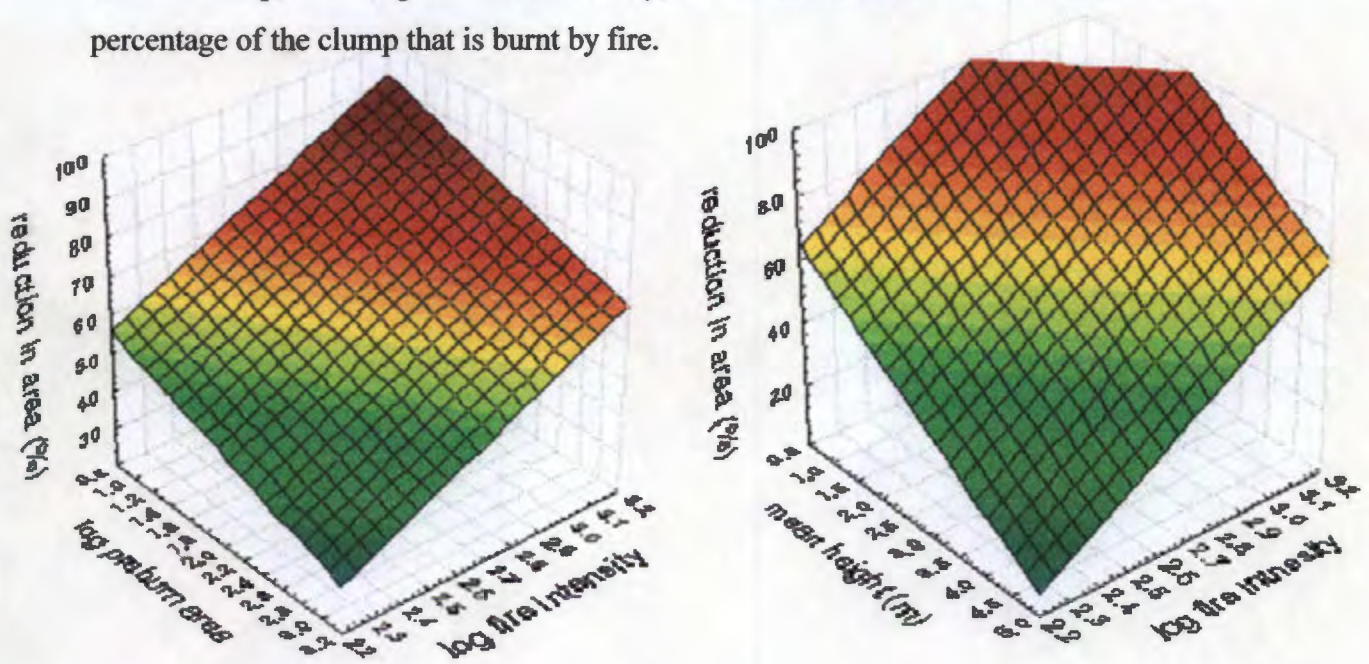
Figure 3. The percentage reduction in clump area as influenced by fire intensity and (a) pre-burn area (b) pre-burn mean height.

A relationship for the reduction in the height of a thicket clump as a result of fire was derived from data on height reduction for 80 *M. senegalensis* after experimental burns in Hluhluwe (fig. 4.). A threshold is reached at around 2.5 m where any height reduction is avoided.

Figure 4. The effect of fire intensity and pe-burn height on the percentage reduction in the height of *M. sengalensis* individuals.

Height growth rates were estimated from data on two years of growth without exposure to fire or browsing for *M. senegalensis* in Hluhluwe. The relationship between current height and height growth was obtained using 90th percentile quantile regressions in Blossom version w2003.02 (U.S. Geological Survey) to give an estimate of the maximum height growth associated with each height (fig. 5).
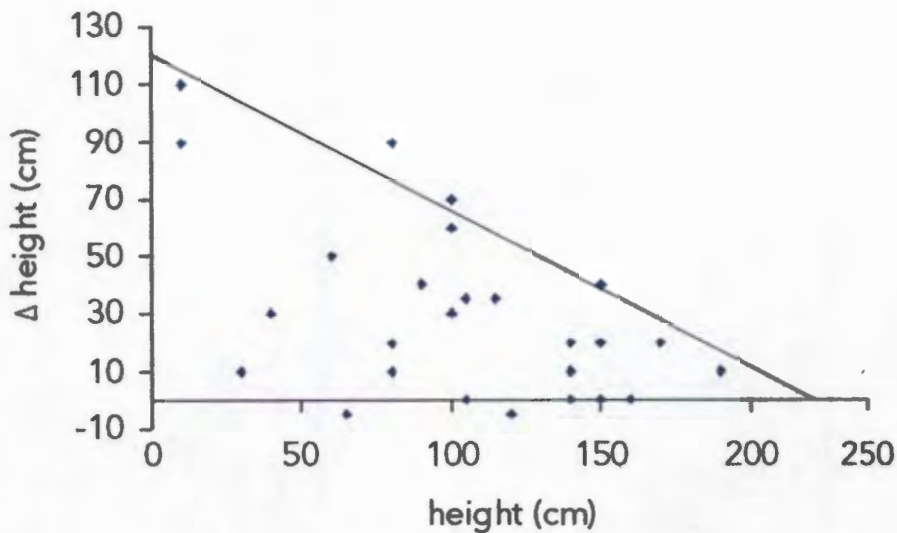
Figure 5. The line indicates the 90th percentile of height growth (Δ height = 115 − 0.5*height, p<0.01) for *M. senegalensis* individuals not exposed to fire or herbivory.

The distances over which *E. divinorum* and *M. senegalensis* could root sucker were assessed by digging up individuals of the two species. Root suckering distances of 0.8 m, 1.6 m and 2 m were observed for *M. senegalensis* with no root suckering being observed for individuals of *E. divinorum*. Attempts to parameterise clump area growth rates using aerial photography were unsuccessful.

Model components

The objective of the model is to evaluate the effect of different biotic and abiotic factors on the spread of a thicket clump within a savanna matrix. The major components of the model are shown in Figure 6.: Circles represent parameter inputs; rectangles represent correlative relationships and rounded squares represent mechanistic relationships in the model. The model is driven by inputs of mean annual rainfall, fire weather data, the level of grazing, the level of grass decay and the maximum height and area growth values for a thicket clump. The time step in the model is years. The outputs of the model are the area and the mean height of a thicket clump at the end of each year. A year in the model comprises of a wet growing season, in which rainfall and then plant growth occurs, followed by a dry season in which fires may occur. A list of the equations for the processes outlined below can be found in table 1.
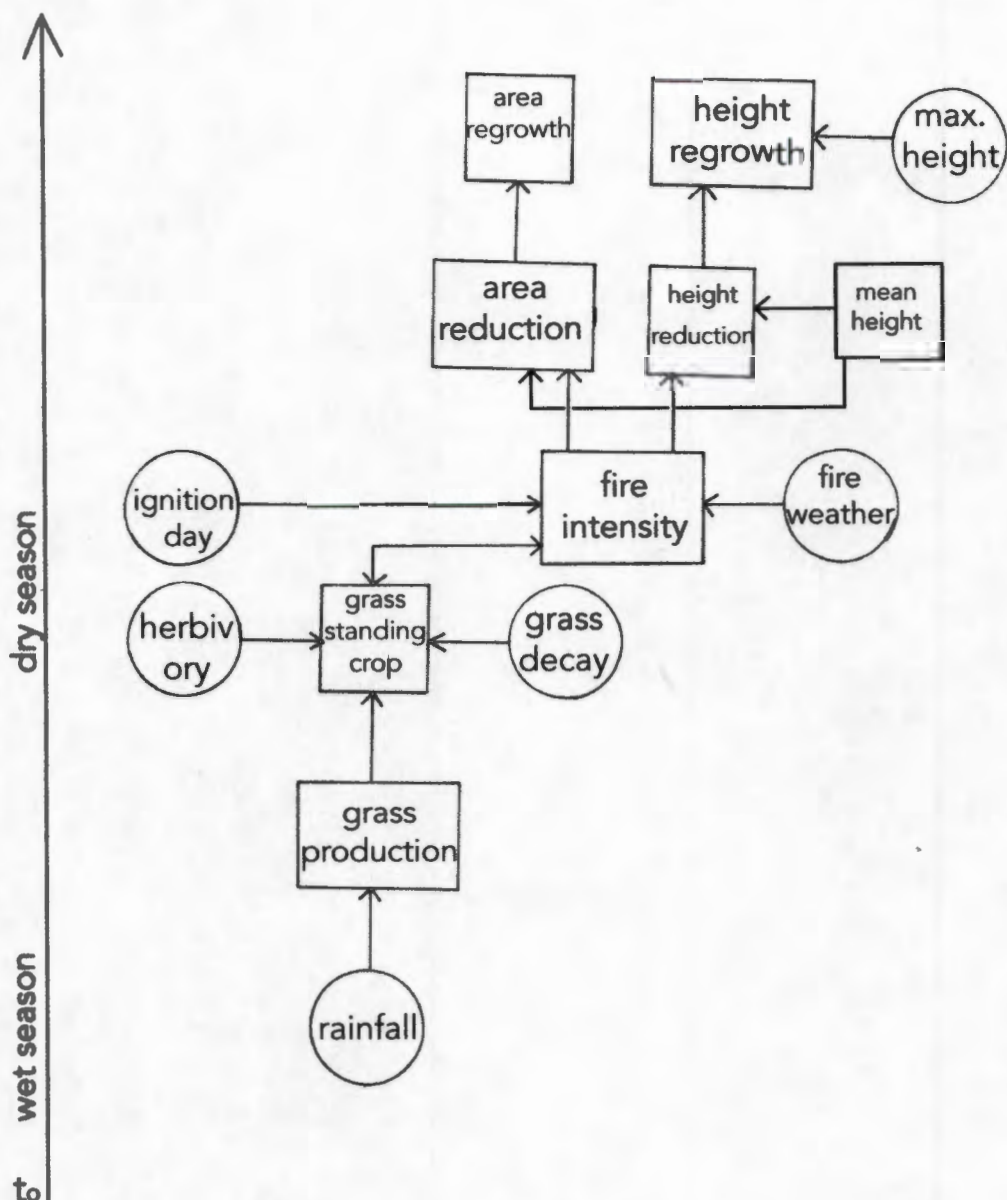
Figure 6. The major processes in the model are shown above; circles represent parameter inputs, rectangles represent correlative relationships and squares, represent mechanistic relationships in the model.

GRASS and FIRE

The model initiates at the beginning of the wet growing season by generating the rainfall for that year (t_0 in fig. 1). Rainfall is modelled as having both a stochastic and a periodic aspect (1 in table 1). The periodic aspect of rainfall for the North East of South Africa can account for up to 30% of the variation in mean annual rainfall with the length of one period being around 18years (i.e. 9 years of above average rainfall

followed by nine years of below average rainfall) (Tyson, 1986). The mean and standard deviation of annual rainfall were calculated from monthly rainfall data collected at Egodeni (n=67) on the North Western boundary of the park (Lynch 2003).

The mass of the grass standing crop (kg ha^{-1}) at the end of the wet season is determined by the amount of rainfall (eqn 2 in table 1). The effect of rainfall on grass productivity can be described as a positive linear relationship (Higgins et al. 2000). The resultant grass standing crop is then consumed by grazers (kg ha^{-1} day^{-1}) to yield the mass that is available as fuel for fire. The standing crop is exposed to grazing until the day within the dry season on which a fire is ignited. The ignition day, the number of days after the onset of the dry season after which a fire occurs, is determined by sampling from a random distribution following Higgins et al. (2000). Ideally the mean and standard deviation of this distribution would be obtained from the distribution of fire days within the dry season. For this model, however, we used the distribution from Higgins et al. (2000) for Southern African savannas. Grass production and consumption by herbivores are separated in time in the model with any temporal heterogeneity in grazing being ignored.

Fire intensity is determined by the fire weather (relative humidity and wind speed), the fuel moisture content and the fuel load on the day of the fire. Relative humidity and wind speed are sampled from normal distributions and fuel moisture content is a fixed value. A regression model developed by Trollope (1998) is used to predict fire intensity (3 in table 1). This model explained 56% of the variance in fire intensity when tested against independent fire behaviour data (Trollope, 1998). Van Wilgen and Scholes (1997) estimated that fire intensity must be at least 150 KW.m^{-1} for fires to spread in savanna. If the fire intensity is less than this, then the fire intensity in that year is set to zero. Fire does spread if the grass standing crop is less than 1000kg ha^{-1} (Trollope, 1993)

When there is no fire the grass standing crop is carried over to the next year. It decays (kg ha^{-1}day^{-1}) until the onset of the following wet season. The standing crop at the beginning of the following year's dry season is then the new mass of grass produced plus what remains of the carry-over from the previous year. It is assumed that for

burns of above 150 KW m^{-1} in intensity there is complete combustion of the grass layer. This is not so in reality as low intensity burns will leave patches of grass unburnt (Williams et al. 2003). The negative effect of self-shading from grass carry-over on grass productivity (reference) is accounted for by limiting the standing crop in any year to a maximum of 12 t ha^{-1}.

THICKET

The thicket clump is modelled as an elliptical cylinder (fig. 7a). The area of the clump is decreased by fire. A linear regression model describes the relationship between the area of the clump that is burnt by fire and the predictor variables: pre-burn clump area, pre-burn mean height and the fire intensity. The mean height of a clump may decrease or increase as a result of fire (fig. 7c). It increase because individuals in the portion of the clump undamaged by fire, towards the centre, are taller than those that are burnt on the periphery of the clump (fig. 2). The post-fire height of the clump is separated out into an unburnt and a burnt portion. The height reduction experienced by the portion of the clump that is burnt is dependent on the pre-fire mean height of the clump (fig. 4). So if the clump has a mean height of less than 2 m before fire, the fire-damaged portion of the clump will resprout from a height of 0 m (fig. 4 and fig. 7c). The post-fire height of the unburnt portion of the clump will be higher than the pre-fire mean height of the clump (fig. 7c). This is because thicket clumps generally increase in height towards their centre (fig. 1). The height of the unburnt portion is predicted from the pre-fire mean height (eqn 5 in table 1, see also data collection). The unburnt portion of the clump will therefore begin to grow in height from the middle height (2 m in fig. 2c.). New area growth of the clump has an initial height of 0m (fig. 7c). The pre-fire mean height for the following year is the mean of the burnt, unburnt and new area heights of the clump after resprouting and growth.
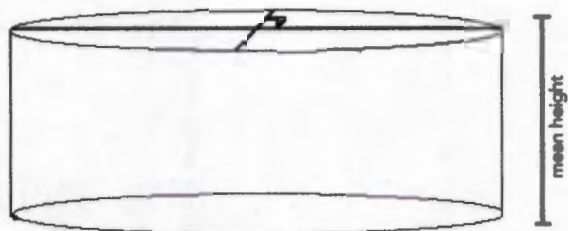
Figure 7a. The cylindrical form used to describe a thicket clump in the model
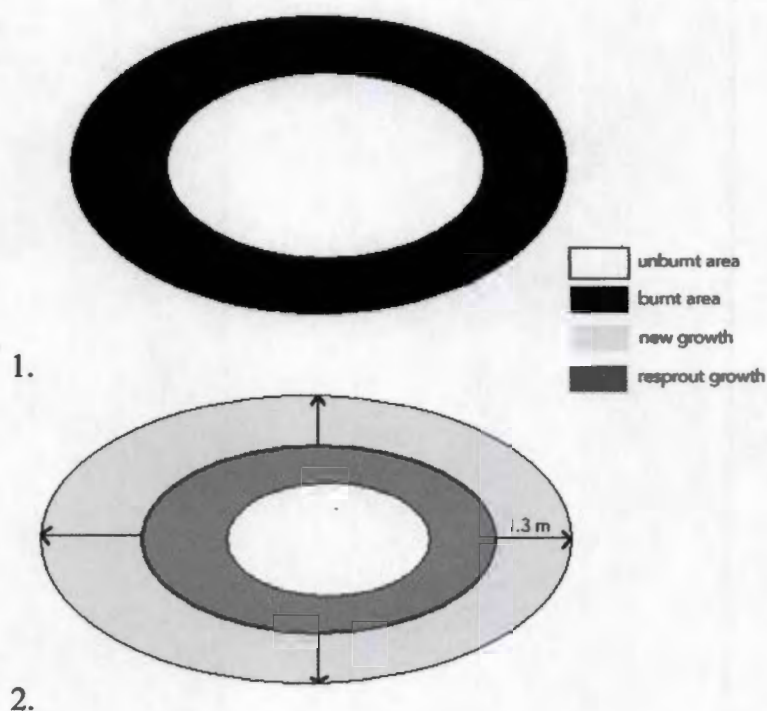
Figure 7b. (A) the area of a clump damaged by fire and (B) clump area growth.
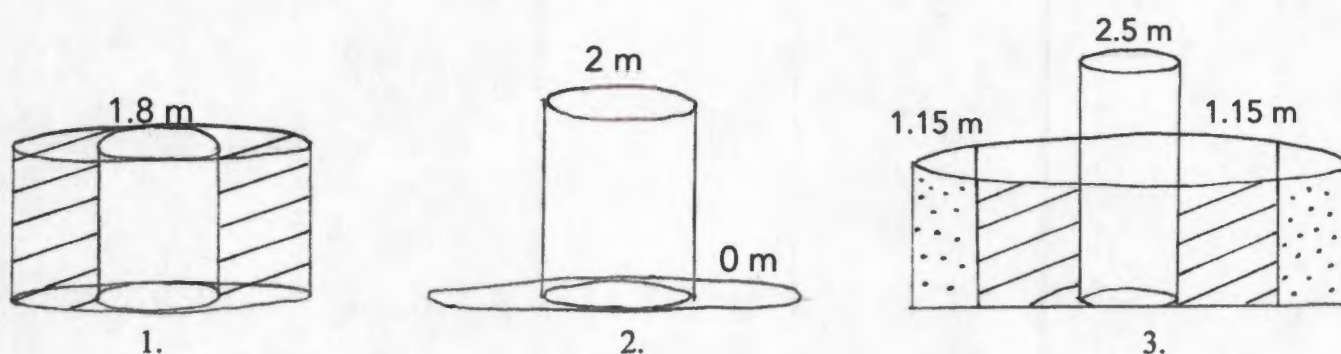
Figure 7c. (1) pre-burn mean clump height, (2) undamaged height increased to the middle height (2 m; obtained using eqn 5 in table 1) and resprout height (0 m) and (3) undamaged height growth (2.5 m) and the height of resprouts and new individuals (1.15 m) after growth. The three heights measures in 3. will be used to obtain the new mean height.

The fire-damaged and undamaged portions of the clump resprout and/or grow in the wet season following fire. Height growth rates vary inversely with clump height (eqn 7 in table 1 and fig. 1). Shackleton (1997) showed that maximum tree height and stem growth rates in savannas are affected by nutrient and moisture availability, but these effects are not explicitly considered in this model. A sensitivity analysis of growth rates does, however, allow some examination of these factors.

The area of a clump grows predominantly as a result of the establishment of new broadleaf saplings beyond the perimeter of the clump from root suckering and/or seedling establishment and not from increases in canopy diameter. Individuals towards the centre of the clump are therefore modelled as growing tall and not expanding outwards. Field excavations showed that *M. senegalensis* individuals could establish saplings at distances of up to 2 m through root suckering. Post fire, the two axes of the clump were each increased by the same set distance each year and the new total area of the clump calculated (fig. 7b). An increase of 2 m in axis length corresponds to an increase of 1m at each edge, so for a 1.3 m edge expansion on each side you need a total increase in axis length of 2.6 m. The relative growth rate in area of smaller clumps in the model is an order of magnitude more than that of larger clumps.

Table 1. Equations describing the major processes within the model.

$R = N(R_x, R_{sd}) + \sin(2\prod y/z)m; \quad R>0$	(1) rainfall
$G_t = pR - ht_d + j(G_{t-1}-d)$	(2) grass biomass
$F = 2729+0.8684G_t-530\sqrt{M} -0.907D^2-596/W$	(3) fire intensity
$\log B = 2.3813-0.1H_t-3.2529(1/\log A_t)+$	(4) area of clump burnt
$2.6(1/\log A_t-0.62)i+0.5007F$	
$K = 0.4676+1.0391H_t$	(5) undamaged height
$H_{pt} = 0$ if $H_t <2$ m; $H_{pt} = H_t - 0.35H_t$ if $2m<H_t <2.5$ m;	(6) height reduction
$H_{pt} = H_t$ if $H_t >2.5$ m	
$H_{t+1} = H_{pt} + (1-H_{pt}/H_{max})g_h$	(7) height growth
$H_{t+1} = (H_{t+1\ ub} + H_{t+1b} + H_{t+1ng})/3$	(8) mean height
$\log A_{tg} = 0.4604*\log A_{t-1}+0.4443$	(9) area growth
$A_t = A_{tg} + A_{t-1}$	(10) new area

R, annual rainfall; N, normal distribution; R_x, mean annual rainfall, R_{sd}, std deviation of mean annual rainfall; y, simulation year; z, period length in rainfall; m, strength of periodicity; G_t, grass fuel load in year t; p, grass productivity coefficient; h, grazing rate; t_d, ignition day; j = 1 if grass is carried over, else 0; d, rate of decay; F, fire intensity; M, fuel moisture content; D, relative humidity; W, wind speed; B, area of clump burnt by fire; H_t, pre-fire mean height this year; A_t, pre-fire area of clump this year; i =1 if 1/logA>0.62, else 0; K, post-fire undamaged height; H_{pt}, post-fire height; H_{t+1}, next year's height; H_{max}, maximum height; g_h, maximum height growth rate; H $_{ub}$, unburnt height after growth ; H $_b$, height of resprout growth; H $_{ng}$, height of new growth; A_{tg}, area growth this year; A_{t-1}, post-fire area of clump last year.

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Model Behaviour

The analysis of the model is separated into two sections. The first examines whether the model predicts the expansion of a thicket clump using the default parameter values (table 2). The second tests the sensitivity of thicket clump expansion to selected model parameters in an attempt to identify the key drivers of thicket clump expansion. The model was initialised using the best parameter estimates available (table 3). These estimates were set as the default values for the model parameters for subsequent analyses. The model was run for 2000 years to remove any effect of the initial conditions. The escape probability for a thicket clump was calculated as the number of runs, out of 100, in which a clump reached a size of 2000 m^2.

Two thousand m^2 was selected as the escape size for two reasons. Firstly, clumps are relatively fireproof, experiencing little fire damage from all, but the highest fire intensities once they reach 2000 m^2. When clumps of this size do experience fire damage, generally, with the default lateral growth rate of 1.3 m year^{-1}, they are able to resprout and grow enough during the following wet season to recover any area lost to fire. Secondly, thicket clumps of this size will have begun to coalesce with neighbouring clumps to form closed canopy thicket and exclude savanna species. Generally, clumps of 2000 m^2 will have diameters of 40 m-50 m and thicket clumps in the field are spaced at intervals of about 50 m-70 m (pers. obs.). Therefore, assuming thicket clumps expand evenly on all sides, thicket clumps with a diameter of over 40 m, in an area where neighbouring clumps have experienced similar conditions and so expanded similarly, will be of a size where they have grown to occupy half of the space between themselves and neighbouring clumps. They will therefore begin to coalesce with their neighbours who will also have expanded to occupy half of the space. The escape probability can therefore be interpreted as the probability of a switch to closed canopy thicket.

Table 2: parameter names, symbols and default values used in the simulation runs.

Symbol	Name	Default value
R_x	mean annual rainfall	883mm
R_{sd}	std deviation of mean annual rainfall	248mm
z	period length in rainfall	18 years
m	strength of periodicity	188mm
p	grass productivity coefficient	$3.369 \ kg \ ha^{-1} \ mm^{-1}$
h	grazing rate	$7 \ kg \ ha^{-1} \ day^{-1}$
t_{dx}	mean ignition day (Julian day)	150 days
t_{dsd}	standard deviation in ignition day	50 days
d	rate of decay	$1 \ kg \ ha^{-1} \ day^{-1}$
M	fuel moisture content	30%
D_x	mean relative humidity	20%
D_{sd}	standard deviation of relative humidity	20%
W_x	mean wind speed	$5 \ km \ h^{-1}$
Ws_d	standard deviation of wind speed	$5 \ km \ h^{-1}$
H_{max}	maximum height *M.senegalensis*	4 m
H_{max}	maximum height *E.divinorum*	8 m
g_h	maximum height growth rate	$1.15 \ m \ year^{-1}$
A_{tg}	area growth	axes expansion of 1.3 m at each edge

p, m, t_{dx} and $t_{dsd,}$ H and D obtained from Higgins et al. (2000)

The model predicts that thicket clumps will not escape under the default parameter conditions. The area of the thicket clump is less than 20 m^2 for the majority of the duration of the model run (fig. 8.). The clump does expand, however, up to 600 m^2 for brief periods of about twenty years. This fits with observations from aerial photographs taken between 1937 and 2004 that show *M. senegalensis* clumps in open savanna, in Hluhluwe, expanding and contracting over time. The expansions of the thicket clump coincide with successive years of low fire intensity or no fire.
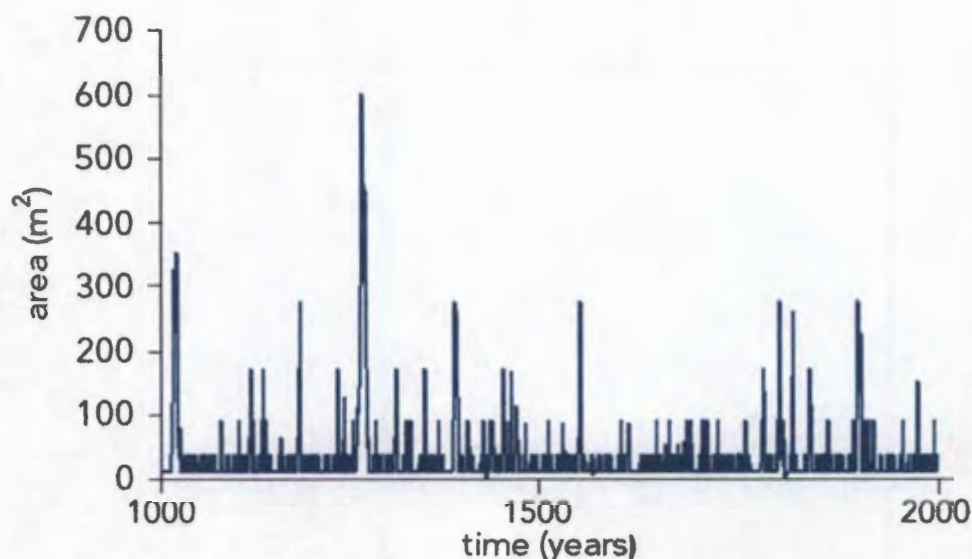
Figure 8. One thousand year trajectory of thicket clump area for a single simulation run. Data for the last 1000 years of the run is shown to remove any effect of the initial conditions. The model was initiated with the default parameter values (table 1).

Sensitivity analysis

Testing the sensitivity of thicket clump area to a range of potential key drivers helps to elucidate which of these have a significant effect on thicket clump expansion and how thicket clumps may respond to environmental change. Sensitivity of thicket expansion to selected model parameters was tested by varying the parameters from their default values. The model was run for 2000 years and escape probabilities were calculated as detailed earlier. Since there are 18 parameters in the model a full sensitivity analysis is impractical and so sensitivity analyses were only performed on hypothesized key drivers of thicket expansion.
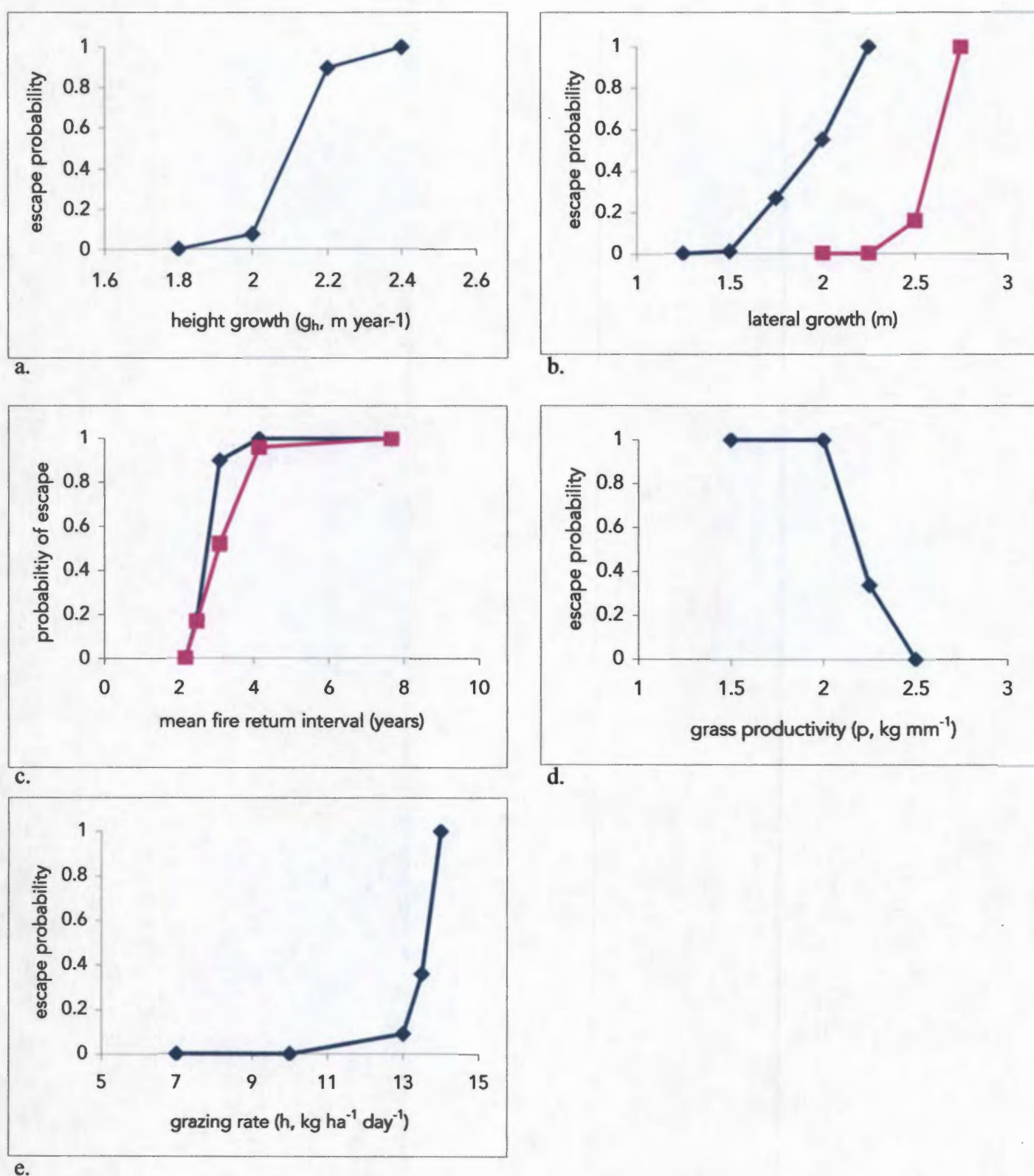
Figure 9. Sensitivity the escape probability (probability of thicket expansion) to variation in key model parameters. All other parameters are set to their default values (table 2). *E.divinorum* (blue) and *M. sengalensis* (pink).

Height is an important predictor of the probability of being topkilled by fire for savanna trees, with taller individuals having lower probabilities of being topkilled by fire (Trollope, 1984). Increasing maximum height to up to 15 m did not increase the chances of thicket clump escape for either of the two species. Maximum height does, however, have a positive effect on escape probability as is shown in the sensitivity analysis of height growth rates (fig 9a.). In *M. senegalensis*, increasing height growth rate has no effect on escape probability, but an increase in height growth does increase the escape probability for the taller *E. divinorum* thicket clumps. The low maximum height of *M. senegalensis*, allows even the tallest individuals to be damaged by fire, with the model predicting that *M. senegalensis* clumps do not expand by escaping fire damage through growing tall. The prediction that euclea thicket clumps escape when their height growth rate is increased, supports the suggestion by Skowno et al. (1999) that eucleas in Hluhluwe are trapped in the fire layer due to their having slower height growth rates relative to acacias. The euclea height growth rates predicted for thicket clump expansion by the model are much higher than those recorded for saplings of the savanna trees *Acacia nigrescens* and *Terminalea sericia* in an arid and mesic savanna respectively (February, Bond and Higgins unpublished, 2007). Savanna acacia height growth rates may be higher in mesic savanna, although little effect on growth rate is observed in acacias with either an increase or a decrease of 50 percent in water availability (Bond, pers. comm.). This suggests that it is unlikely that *E. divinorum* thicket clumps expand solely due to height growth.

An increase in lateral growth rate has a positive effect on escape probability (fig 9b). Again, *E.divinorum* thicket increases in escape probability at lower lateral growth rates than *M.senegalensis*, due its greater height. Archer et al. (1995b) suggested that increased atmospheric carbon dioxide did not drive bush encroachment. This study,however, did not consider the effects of CO_2 on resprouting ability, a key trait in high disturbance systems such as savannas. Bond and Midgley (2000) hypothesized that elevated atmospheric CO_2 could assist saplings to accumulate the belowground carbon stores they need to grow rapidly to escape the grass layer. Field excavations in Hluhluwe showed *M.senegalensis* to have large underground storage organs and root suckers. Increased CO_2 levels may therefore promote, already vigorous, resprouting and root suckering in this species, enhancing thicket clump expansion. In conflict with the literature, no substantial underground storage organs or root suckers were found for *E. divinorum* (n = 5, also S. van Rensburg pers. com.). The effect of increased CO_2 would therefore be predicted to be less for euclea thicket clumps both in resprouting and root suckering.

The model accurately demonstrates that thicket expansion is a rapid event (fig. 10). In the model it is possible for closed canopy *M. senegalensis* thicket to form in only 60 years. The short escape time predicted for thicket clumps agrees with observations by Skowno et al. (1999) and Wigley (2007; fig. 11), that the expansion of thicket in Hluhluwe is swift and occurs at the decadal scale.
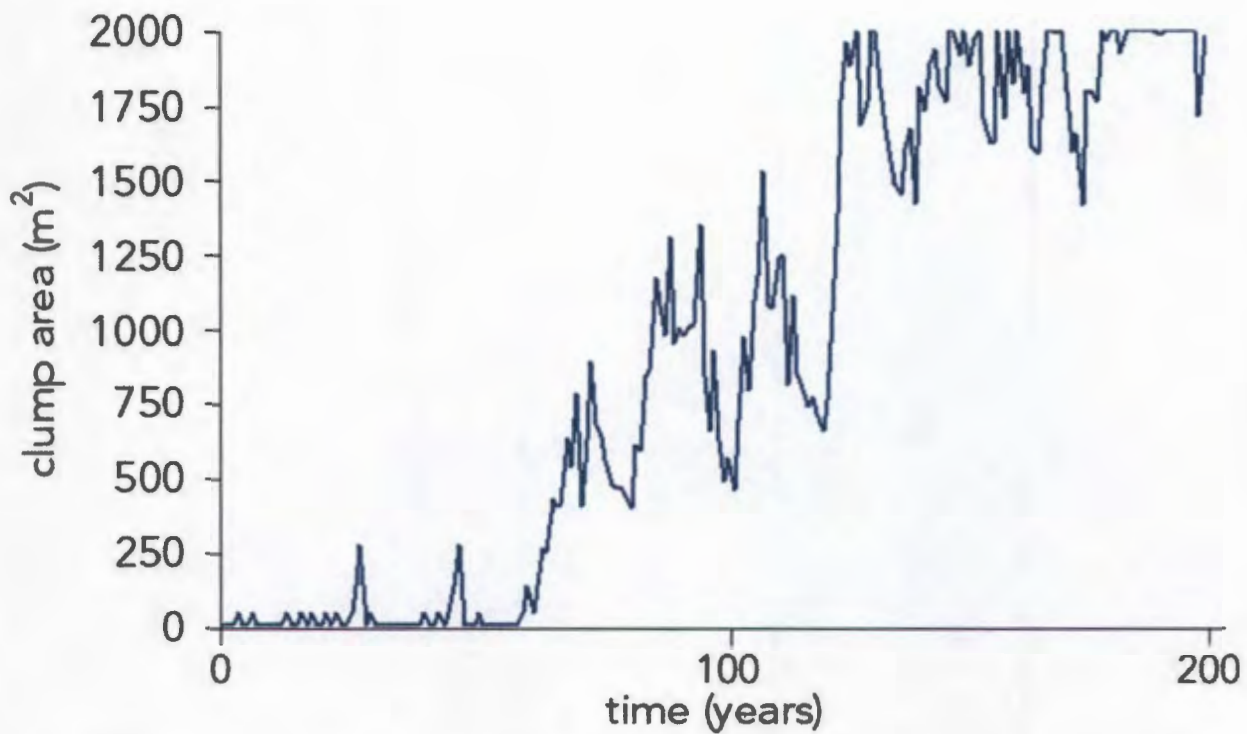
Figure 10. Thicket clump escape trajectory for an *M. senegalensis* clump with a lateral growth rate of 2.5m year^{-1}. During the first four years of the escape no fires occurred.
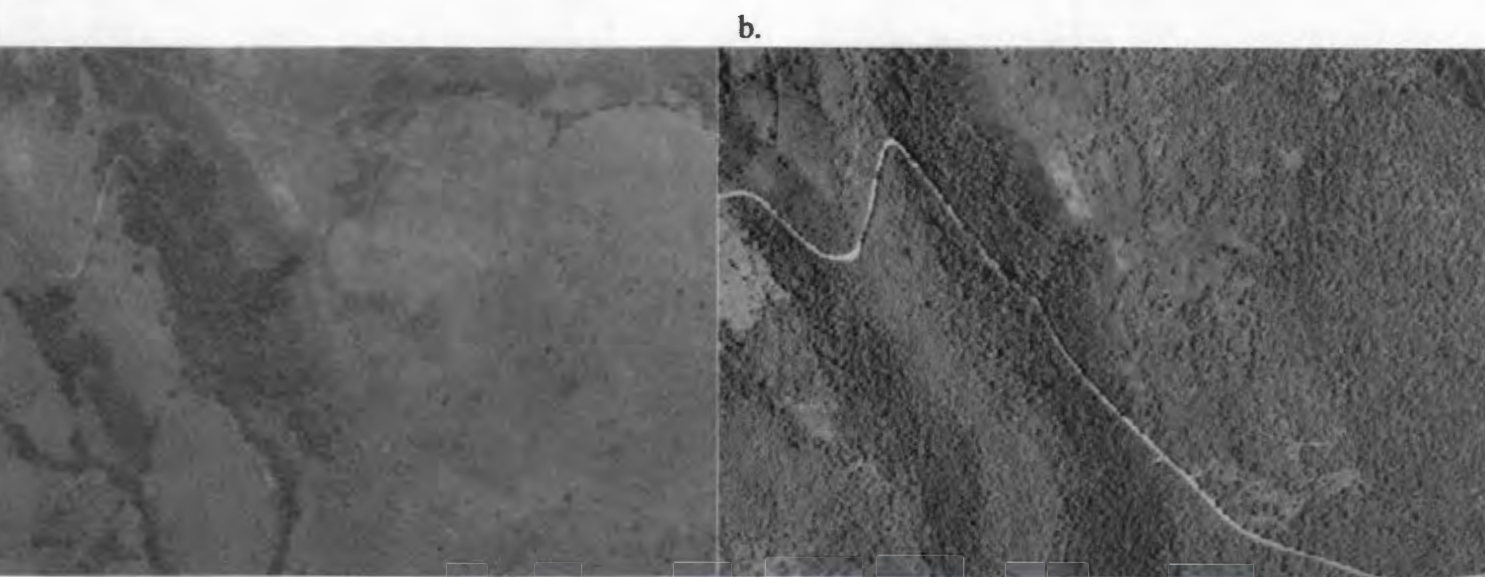

Figure 11. Aerial photographs of the same area (a) in 1937 before thicket expansion and (b) in 2000 after thicket had expanded. Images from Wigley (2007).

Increasing the variance in fire intensity (by changing variation in rainfall, fire weather and ignition day) does not allow thicket clumps to escape. Escape probability remained at zero, even when the variance in fire intensity was an order of magnitude larger than that for the default parameters. The model was also run using a fire intensity distribution approximating that which would occur under current management burning practices in the reserve (Zululand Tree Project, unpubl.) and a fire return interval of two years to evaluate the effect of current burning practices on thicket expansion. There was no increase in the probability of escape for either *M. senegalensis* or *E. divinorum* under this fire regime. Increasing the mean fire return interval, however, does increase the escape probability of thicket clumps (fig 9c). The median fire return interval for Hluhluwe for the period 1955-1995 was 1.3 years (Balfour and Howison, 2001). Thicket clumps of both species begin to escape at mean fire return intervals of above 2.2 years. Therefore the model predicts that thicket expansion will have occurred in the areas shown (fig. 12), where the median fire return interval was above 2.2 years. *E. divinorum* escapes better at slightly higher fire frequencies than *M. senegalensis*, again due the difference in maximum height. The predicted thicket expansion is outwards from areas of thicket and forest that were already present along drainage lines. Briggs et al. (2005), also found this for the expansion of thicket in North American prairie grasslands.

Decreasing grass productivity positively influences thicket expansion (fig. 9d). This is because there is less fuel for fire with the result that fires are both less intense and, important in this model, less frequent. An increase in herbivory rate (fig. 9e) also increases escape probability by reducing the available fuel load. This agrees with observations that high grazing pressure promotes bush encroachment (Archer 1995;

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Roques et al, 2001). Briggs et al. (2005), proposed that a reduction in fire frequency and intensity was the reason for shrub-encroachment into prairie grassland. They suggested that this was as a result of stock farming causing the reduction of fuel loads through grazing and fragmenting the landscape, thereby reducing fire spread.
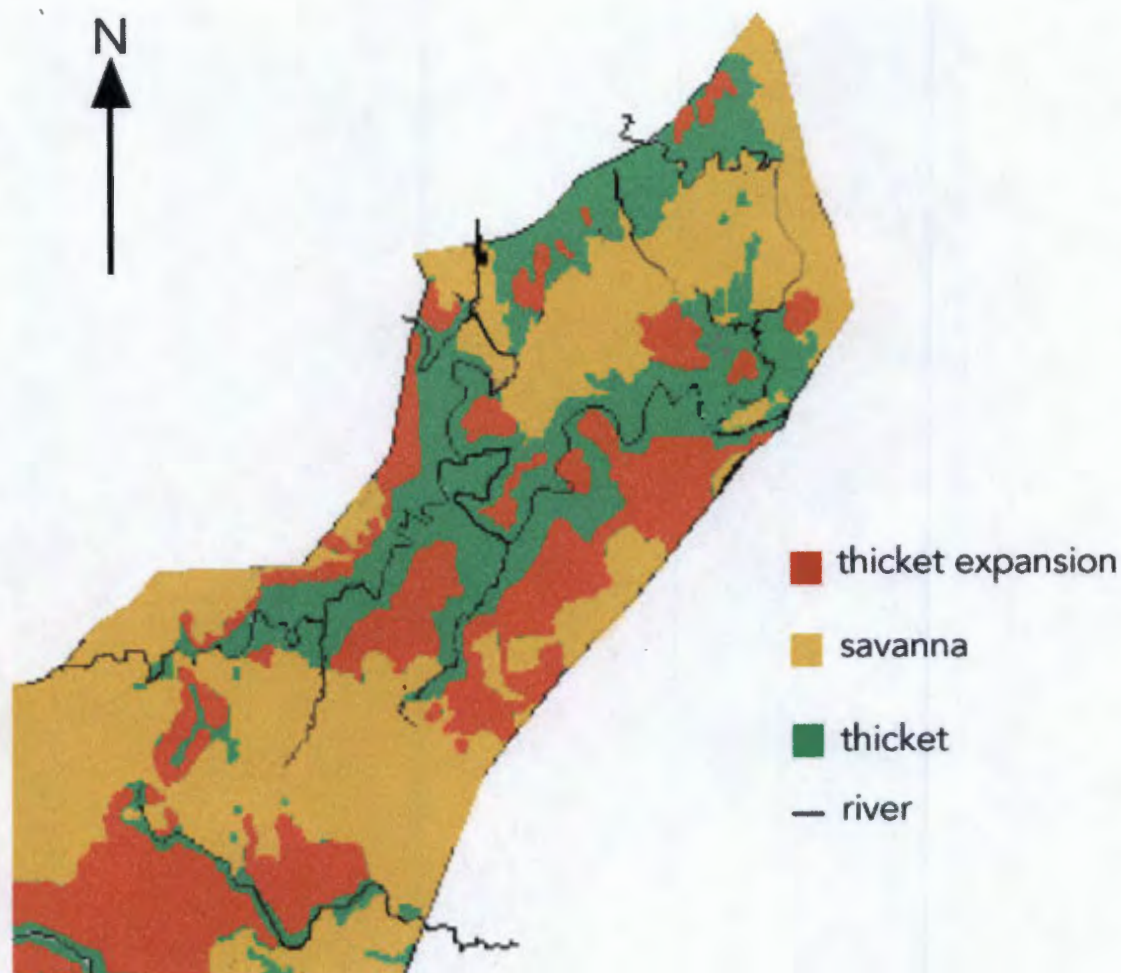
Figure 12. Areas within Hluhluwe where thicket is predicted to have expanded (red) based on median fire return interval data. Thicket and savanna refer to areas that were categorized as these vegetation types by Whately and Porter (1983). Map adapted from Balfour and Howison (2001).

The coefficient of variation of mean annual rainfall (between 0.1 and 0.6) and the stochasticity of mean annual rainfall do not have any influence on thicket expansion in the model. A decrease in mean annual rainfall, increases escape probabilities due to

the negative impact on grass production and therefore fuel. The model, however, does not include any restriction on thicket clump growth at low water availabilities and so not much insight can be gained into the range of mean annual rainfall over which thicket expansion can occur, other than to say that dry years in the rainfall record may promote thicket expansion through their negative impact on fuel loads. An increase in winter rainfall in Hluhluwe may also promote thicket expansion by increasing fuel moisture levels in the dry season and so reducing fire frequency. Savanna grasses in Hluhluwe were able to green quickly in response to winter rainfall and subsequent fires did not ignite easily and were of low intensity (pers. obs.).

Conclusions

The key drivers of thicket clump expansion predicted by the model are: reduced fire frequency, increased growth rates (height and area), increased grazing pressure and decreased grass productivity. Increased variance in fire intensity not increasing the probability of thicket clump expansion is possibly a result of the model predicting too great reduction in area for a given fire intensity. The model assumes that the area regrowth of a thicket clump occurs from portion of the clump that is not burnt by fire. In reality, however, after a low intensity fire, individuals that were burnt may be able to recover quickly and expand the clump through root suckering in the same season. A better measure of the reduction in area of a clump would be to record the proportion of a clump that did not resprout after fire. While, due to time constraints, this was not possible for this project, these measurements would improve the predictive accuracy of the model.

Modelling is beneficial in highlighting key parameters where further data collection would facilitate a better understanding of the system. It needs to be established whether *E. divinorum* is capable of root suckering and over what distances root suckering may occur in this species as well as over what distances they do occur in *M. senegalensis*. Improved estimates of the height growth rates for taller thicket forming species need to be obtained as height growth in these species can influence the probability of thicket expansion. The history of a site (past parameter values) is important, as simulation models are sensitive to the initial conditions. In dynamic global vegetation models (e.g. Woodward and Lomas, 2004), the model is run until selected parameter values are reached and only then are simulation runs begun. Running the model for 2000 years was done to remove the effect of the initial conditions. If the fire intensity record for the 20th century were known and not simulated from the values of other parameters the model would be better able to approximate reality and make predictions about thicket expansion at the beginning of the 21st century. Without knowing the history of a site, the start time of the model cannot be set to correspond to a specific calendar year to reflect current changes in the system. The model does, however, make testable predictions about the sensitivity of thicket clump expansion to changes in key parameters and over what time scales thicket expansion may occur. Further research could test these predictions by mapping the parameter estimates associated with thicket expansion in the model and assessing whether this corresponds to the expansion of thicket in temporal and geographical space.

The spatial changes in savanna dynamics such as fire, as savanna vegetation becomes more fragmented due to the expansion of thicket clumps are important in

understanding thicket expansion. Percolation theory (Stauffer and Aharony, 1992), which deals with the transport of a fluid through a randomly distributed media, predicts that fire may stop moving through a landscape when a threshold cover of non-flammable vegetation is reached (Nahmias et al, 2000; Favier, 2004). Broadleaved thicket clump shrubs, trees and the shade tolerant understorey grass, *Panicum maximimum*, found in thicket clumps in thicket clumps, are less flammable (pers. obs.) than the savanna grass layer. The branches of *E. divinorum* are used to beat out fires (Pooley, 1993). Thicket clump expansion may therefore prevent fire spreading in a landscape before thicket clumps coalesce completely. This in turn would enhance the expansion rate of the thicket. The threshold parameter values for thicket clump escape may therefore be lower than those predicted by the current model. A lower escape threshold could explain the observation of even more rapid thicket expansion within Hluhluwe (Skowno et al. 1999), than that currently predicted by the model. Situation also seems to be important in thicket clump expansion with the model predicting that thicket expansion has taken place along rivers (fig. 12). Conversion to a spatial modelling framework (e.g. Favier et al. 2004b) is needed to incorporate and evaluate these effects.

Understanding the mechanisms driving the reduction in savanna in Hluhluwe is important in being able to manage a savanna ecosystem. The model predicts that park managers in Hluhluwe should focus on burning frequently to control thicket clump expansion. *E.divinorum* is predicted to be the dominant thicket forming species, due to its greater maximum height. This fits with observations by park staff and researchers that *E. divinorum* is the more aggressive of the two thicket encroachment species (van Rensburg pers. comm.). Efforts to halt thicket expansion should focus

more on this species than *M. senegalensis*. Harvesting of *E. divinorum* by local communities on the park's boundary is not likely to prove successful in combating thicket expansion as *E. divinorum* is not used as fuel wood (Coates-Palgrave, 1984; Pooley, 1993). Archer et al. (1989), state that the inertia of a closed canopy thicket system is too great for it to be reverted to savanna through burning alone. The model predictions agree with this and would suggest mechanical clearing followed by burning to reduce the thicket area. Predictions from a spatial model could inform the pattern of mechanical clearing to affect the best spread of fire through thicket patches that have been fragmented by clearing.

The expansion of woody vegetation in grasslands and savannas is a global phenomenon and therefore may have global change drivers. If elevated CO_2 does enhance the resprouting ability of thicket species, as hypothesized by Bond and Midgley (2000), then this would be a key global change driving the expansion of thicket and as such, one that conservation managers cannot directly address. The model has been consistent with other frequently suggested drivers of woody expansion such as high grazing rates and reduced fire frequency have also been suggested by this model. The use of spatial modelling is now needed to evaluate these hypotheses for the expansion of forest and thicket in a framework that can incorporate observed expansions of thicket from drainage lines and the effects of coalescing clumps of fire behaviour.

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