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Peter W. J. Baxter and Wayne M. Getz. 2005. A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecological Applications* 15:1331-1341.

Appendix A. Model equations and parameters. _____

Nine stage classes of tree, the i -th of which (in cell x at time t) has number of individuals $w_{x,i}(t)$ ($i = 1, 2, \dots, 9$), are modeled, based on height. We define a tenth vegetation class, $w_{x,10}(t)$, denoting the grass biomass (kg) in cell x at time t . These classes may be represented by the column vector

$$\mathbf{w}_x(t) = (w_{x,1}(t), \dots, w_{x,10}(t))',$$

where ' denotes the transpose of a vector.

(See Box 1 for a flow-chart depicting the model procedure.)

Rainfall

To account for rainfall seasonality (Solbrig et al. 1996) and the southern Africa 20-year wet-dry cycles (Tyson and Dyer 1978, Gertenbach 1980), we model the rainfall in year $[t, t+2]$ as a sine-wave plus noise overlaid in the long term, normalized to take the value of 1:

$$r(t) = \max\left(0, 1 + \eta \sin \frac{\pi(t+1)}{2\omega} + z(t)\right), \quad t \text{ even (start of wet season),}$$

$$r(t) = 0, \quad t \text{ odd (start of dry season),}$$

where η is the amplitude (relative to the long-term mean) of wet-dry cycles of period ω years, and $z(t)$ is a stochastic variable accounting for interannual variation around these cycles.

Wet season woody plant dynamics

The change in the woody population during a wet season starting from time t is given by:

$$w_{x,i}(t+1) = (g_{x,i-1}w_{x,i-1}(t) + (1 - g_{x,i})w_{x,i}(t))(1 - k_{x,i}(t)), \quad i = 2, 3, \dots, 9,$$

where $w_{x,i}(t)$ is the number of individuals in cell x of woody class i at the start of the wet season, $h_{x,i}(t)$ is loss of individuals due to encroachment by growth and expansion of larger individuals, and $g_{x,i}(t, \mathbf{w}_x, r)$ is the transition rate from class i to class $i+1$ for that cell and season. The seedling class ($i = 1$) is given by

$$w_{x,1}(t+1) = (g_{x,0}c_x(t) + (1 - g_{x,1})w_{x,1}(t))(1 - h_{x,1}(t)),$$

where $g_{x,0}$ is the proportion of these which successfully recruit. $c_x(t)$ is the expected number of new seedlings emerging in cell x at time t :

$$c_x(t) = m \left[(1 - \delta)(w_{x,8}(t-1) + w_{x,9}(t-1)) + \frac{\delta}{4} \sum_{z \text{-neighbour of } x} (w_{z,8}(t-1) + w_{z,9}(t-1)) \right],$$

where m is the fecundity of mature trees, and δ is a dispersal parameter representing the proportion of seedlings parented by individual trees from the four neighboring cells.

The transition rate from class i to $i+1$ is given by:

$$g_{x,i}(t) = \min(\chi_{x,i}(t), \lambda_{x,i}(t)), \quad 0 \leq i \leq 8,$$

where $\lambda_{x,i}(t)$ is the maximum proportion of class i that can grow to class $i+1$ without causing the cell x to overfill. $\chi_{x,i}(t)$ represents the underlying growth rate adjusted for competition and rainfall:

$$c_{x,0}(t) = r(t)c_x(t),$$

$$c_{x,i}(t) = r(t)g_i f_{x,i}(\mathbf{w}_x(t)), \quad 1 \leq i \leq 8,$$

where γ_i is the underlying growth rate from class i to $i+1$ and $\phi_{x,i}(\mathbf{w}_x(t))$ is a "competition coefficient" (sensu [Getz and Haight 1989](#)). We approximate competitive effects by aggregating on a per-area basis:

$$\phi_{x,0}(t) = \phi_{x,1}(t) = 1 - \left(a_{x,10}(t) + \sum_{j=1}^7 a_{x,j}(t) \right),$$

$$\phi_{x,i}(t) = 1 - \sum_{j=i}^9 a_{x,j}(t), \quad i = 5, 6, 7, 8,$$

where $a_{x,i}(t)$ represents the proportion of area (in cell x at time t) controlled by class i , i.e.,

$$a_{x,i}(t) = \alpha_i w_{x,i}(t), \quad 1 \leq i \leq 9,$$

and α_i is the "resource area" (ha; [after Kiker 1998](#)) occupied by one individual of class i . Automatic growth within sapling classes means that $\phi_{x,i}(t) = 1$ for $i = 2, 3, 4$.

The expansion limiting coefficients, $\lambda_{x,i}$ involve projecting total possible recruitment and then reducing that recruitment, in order of trees, shrubs, saplings, seedlings, in case of overflow:

$$\lambda_{x,7}(t) = \frac{1 - a_{x,8}(t) - a_{x,9}(t)}{\alpha_8 w_{x,7}(t)}.$$

This allows us to calculate $g_{x,7}(t)$ and then proceed through the stage-classes (dropping the x and t arguments for convenience):

$$\lambda_5 = \frac{1 - a_6 - \alpha_7(1 - g_7)w_7 - \alpha_8 g_7 w_7 - a_8 - a_9}{\alpha_6 w_5},$$

$$\lambda_4 = \frac{1 - a_2 - a_3 - a_4 - \alpha_5(1 - g_5)w_5 - \alpha_6 g_5 w_5 - a_6 - \alpha_7(1 - g_7)w_7}{\alpha_2 w_1},$$

$$\lambda_0 = \frac{1 - \alpha_1(1 - g_1)w_1 - \alpha_2 g_1 w_1 - a_2 - a_3 - a_4 - \alpha_5(1 - g_5)w_5 - \alpha_6 g_5 w_5 - a_6 - \alpha_7(1 - g_7)w_7 - a_{10}}{\alpha_1 c(t)}.$$

We set $\lambda_i = 1$ for those height classes deemed not to expand laterally upon growth to the next class, i.e., $i = 2, 3, 4, 6, 8$.

We introduce h_i as a "crowding coefficient", representing the proportion of plants overcrowded by the individuals growing from class i to $i+1$:

$$h_6 = h_7 = \frac{(\alpha_8 - \alpha_7)g_7 w_7}{1 - a_8 - a_9},$$

$$h_2 = h_3 = h_4 = h_5 = \frac{(\alpha_6 - \alpha_5)g_5 w_5}{1 - a_6 - \alpha_7(1 - g_7)w_7 - \alpha_8 g_7 w_7 - a_8 - a_9},$$

$$h_1 = \frac{(\alpha_2 - \alpha_1)g_1 w_1}{1 - a_2 - a_3 - a_4 - \alpha_5(1 - g_5)w_5 - \alpha_6 g_5 w_5 - a_6 - \alpha_7(1 - g_7)w_7}.$$

We update grass cover to account for changes in woody vegetation, elephant grazing, and rainfall:

$$\alpha_{x,10}(t+1) = r(t) \left(1 - \sum_{i=1}^7 \alpha_{x,i}(t) \right) (1 - u_{x,10}(t) (1 - h_{x,1}(t) - h_{x,5}(t))), \quad t \text{ even,}$$

where $u_{x,10}(t)$ is the proportion of the grass in cell x grazed by elephants. The grass biomass then increases by the productivity of the area $\alpha_{x,10}(t+1)$, adjusted for wet season senescence ([Illius and O'Connor 2000](#)) and for elephant grazing:

$$w_{x,10}(t+1) = s_{10}^W r(t) (1 - u_{x,10}(t)) (w_{x,10}(t) + \gamma_{10} \alpha_{x,10}(t+1)),$$

where γ_{10} is annual grass productivity (kg/ha), and s_{10}^W is wet-season persistence ("survival") of grass biomass.

Elephant grazing

Elephant use of cell x is in proportion to the relative amount of grass biomass present:

$$u_{x,10}(t) = l(t) I_g \frac{w_{x,10}(t) + \gamma_{10} r(t) \left(1 - \sum_{i=1}^7 \alpha_{x,i}(t) \right)}{\sum_{z=1}^{100} \left(w_{z,10}(t) + \gamma_{10} r(t) \left(1 - \sum_{i=1}^7 \alpha_{z,i}(t) \right) \right)},$$

where $l(t)$ is elephant density (numbers/hectare) at time t , and I_g is the elephant intake rate of grass (kg/elephant/wet-season).

Dry season woody plant dynamics

In our model, woody plant mortality, elephant browsing and fire are limited to the dry season (see Box 1):

$$w_{x,i}(t+1) = F_i(w_x(t), s_i, r(t-1), l(t)), \quad t \text{ odd,}$$

where s_i is the mean survival rate of woody class i , and F_i is a concatenation of the functions, $f_{\text{surv},i}$, $f_{\text{ele},i}$ and $f_{\text{fire},i}$, that incorporate the effects of mortality, elephant browsing and fire respectively: i.e.,

$$f_{\text{surv},i} \equiv f_{\text{surv},i}(w_{x,i}(t), r(t-1), s_i)$$

$$f_{\text{ele},i} \equiv f_{\text{ele},i}(w_x(t), l(t), f_{\text{surv},i}),$$

$$F_i = f_{\text{fire},i} \equiv f_{\text{fire},i}(w_x(t), f_{\text{ele},i})$$

Woody plant survival

We assume that survival of subadult woody plants depends on the rainfall for that year, but that mature trees only experience increased mortality in droughts lasting more than two years ([Scholes 1985](#)):

$$f_{\text{surv},i}(r(t-1), s_i, w_{x,i}) = s_i r(t-1) w_{x,i}, \quad i = 1, \dots, 7,$$

$$f_{\text{surv},i}(r(t-1), s_i, w_{x,i}) = (s_i - \mu_{8-9}^{\zeta} \xi(t)) w_{x,i}, \quad i = 8, 9$$

where μ_{8-9}^{ζ} is additional mortality experienced by mature trees in drought conditions, weighted for drought severity using the function $\zeta(t)$:

$$\zeta(t) = \frac{k^{\zeta}}{\left(\frac{\sum_{y=1}^3 r(t-2y+1)}{3} \right)^{\zeta} + k^{\zeta}},$$

where ζ describes the steepness of the drought response (cf. density response in [Getz 1996](#)), and k is the value of the three-year mean which causes 50% of the drought-related mortality.

Elephant browsing

Using vector notation, the effect of elephant browsing on the woody vegetation is:

$$\mathbf{f}_{\text{ele}}(l(t), \mathbf{w}_x) = (\mathbf{I} - \mathbf{E} \cdot \mathbf{U}_x(t)) \mathbf{w}_x,$$

where μ_i^e is the proportion of those in class i killed by elephants, and ρ_{ik} is the proportion of class i which are reduced in height to class k following browsing.

Fire

The occurrence of fire in each cell is recorded by the binary variable $b_x(t)$ and the condition for a cell burning ($b_x(t) = 1$) is

$$\begin{aligned} b_x(t) = 1 & \quad \text{if} & \quad R_x < \psi w_{x,10}(t), \\ b_x(t) = 0 & \quad \text{if} & \quad R_x \geq \psi w_{x,10}(t), \end{aligned}$$

where R_x is a uniform random variable drawn on $[0, 1]$ for each cell x , and ψ is a constant which scales biomass to a fire probability. This linear relationship between grass biomass and fire probability is a close approximation to the logistic regression formula produced by van [Wilgen et al. \(2000\)](#) from Kruger National Park fire history data. The spread of fire is modeled by repeating this procedure for every non-burning cell with a burning neighbor, for each burning neighbor, until no additional cells burn. We assume that fire intensity is linearly related to grass biomass ([Trollope 1984](#), [Higgins et al. 2000](#)):

$$\beta_x(t) = \frac{b_x(t) w_{x,10}(t)}{w_{\max}},$$

where $\beta_x(t)$ is the fire intensity relative to that yielded by a grass biomass of w_{\max} .

The woody vegetation is adjusted for fire effects as follows:

$$f_{\text{fire},i}(w_{x,i}(t)) = (1 - \tau_{x,i}(t)) w_{x,i}(t) + \kappa_{i+1} \tau_{x,i+1}(t) w_{x,i+1}(t),$$

where κ_i is the proportion of top-killed plants in stage-class i that resprout following fire. The proportion of woody plants in class i experiencing topkill is given by $\tau_{x,i}(t)$:

$$\tau_{x,1}(t) = b_x(t),$$

$$\tau_{x,i}(t) = \min \left(1, \frac{b_x(t)w_{x,10}(t)}{w^*} \right), \quad 2 \leq i \leq 5,$$

$$\tau_{x,i}(t) = \mu_{6-7}^{\beta} \beta_x(t), \quad i = 6, 7,$$

$$\tau_{x,i}(t) = \mu_{8-9}^{\beta} \beta_x(t), \quad i = 8, 9,$$

where w^* is the grass fuel required to kill 100% of saplings, and μ_{6-7}^{β} and μ_{8-9}^{β} are the topkill rates of shrubs and mature trees, respectively, under maximum intensity fires.

Dry season grass dynamics

We assume that grass burns entirely in fires, and otherwise senesces (depending on rainfall):

$$\alpha_{x,10}(t+1) = (1 - b_x(t))\alpha_{x,10}(t), \quad t \text{ odd},$$

$$w_{x,10}(t+1) = r(t-1)s_{10}^D(1 - b_x(t))w_{x,10}(t),$$

where s_{10}^D is the dry-season persistence ("survival") of grass biomass.

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TABLE A1. Parameters and variables used (in alphabetical order). For parameters, roman type indicates default values and italics indicate initial conditions. Asterisks in the "Values" column are used to indicate functions, calculated in the course of each simulation. Parameters values were derived from an extensive review of the African savanna literature ([Baxter 2003](#)).

Symbol	Description	Units	Values
$a_{x,i}(t)$	area controlled by woody vegetation classes in cell x at time t	$i = 1,$ $2 \leq i \leq 5,$ $i = 6, 7,$ $i = 8, 9.$ ha	<i>0.0012</i> <i>0.1996</i> <i>0.2075</i> <i>0.0918</i>
$a_{x,10}(t)$	grass coverage in cell x at time t	ha	<i>0.5000</i>
b_x	fire indicator for cell x	binary	0
c_x	potential seedlings emerging in cell x	plants	0
E	elephant browsing effect matrix	—	*
$F()$	dry-season woody plant function comprised of $f_{ele}, f_{fire}, f_{mort}$.	—	*
$f_{ele}()$	dry-season elephant impact function for woody plants	—	*
$f_{fire}()$	dry-season fire-impact function for woody plants	—	*
$f_{surv}()$	dry-season survival function for woody plants	—	*
$g_{x,i}$	realized transition rate from class i to $i+1$ for cell x	—	*
$h_{x,i}$	crowding coefficient resulting from growth to class $i+1$ in cell x	—	*
i	vegetation class index: woody classes ($1 \leq i \leq 9$), grass biomass ($i = 10$)	—	*
I_g	intake rate of grass by elephants, wet season only	kg/ele/season	4600
I_{1-7}	elephant use of sub-adult woody plants, dry season only	plants/ele/season	5667
I_{8-9}	elephant use of adult trees, dry season only	plants/ele/season	1000
k	value of mean relative rainfall resulting in 50% of the maximum drought-related tree mortality (μ_m^r)	—	0.8
$l(t)$	elephant density at time t	individuals/ha	<i>0.0</i>
m	fecundity of mature trees	seedlings/tree/yr	50
n	number of hectare cells in grid	—	100
R_x	uniform random variable drawn from U(0, 1)	—	*
$r(t)$	rainfall relative to the long-term mean (=0 for dry seasons)	—	<i>1.0</i>

s_i	survival of woody class i	$i = 1,$ $2 \leq i \leq 5,$ $i = 6, 7,$ $i = 8, 9.$	—	0.950 0.990 0.994 0.995
s_{10}^D	dry season survival (non-senescence) of grass		—	0.2
s_{10}^W	wet season survival (non-senescence) of grass		—	0.8
t	time index		half-year	*
\mathbf{U}_x	diagonal matrix with \mathbf{u}_x on the diagonal		—	*
\mathbf{u}_x	elephant woody plant use vector for cell x		—	*
$u_{x,i}$	elephant browsing intensity on woody class i in cell x (dry seasons)		—	*
$u_{x,10}$	elephant grazing intensity in cell x (wet seasons)		—	*
v_i	elephant preference weighting for woody class i	$i = 1,$ $2 \leq i \leq 9.$	—	0 1
$w_{x,i}(t)$	number of woody plants of class i ($1 \leq i \leq 9$), in cell x , at time t	$i = 1,$ $i = 2,$ $i = 3,$ $i = 4,$ $i = 5,$ $i = 6,$ $i = 7,$ $i = 8,$ $i = 9.$	individuals	1211.4 767.8 507.2 335.0 386.4 168.1 62.4 28.4 8.3
$w_{x,10}(t)$	biomass of grass in cell x at time t		kg	1200
w_{\max}	grass biomass yielding maximum intensity fire		kg	5000

w^*	grass fuel required for a fire to kill 100% saplings	kg	2500
$\mathbf{w}_x(t)$	vector of woody structure in cell x at time t	individuals	*
x	cell index ($1 \leq x \leq 100$)	–	*
$z(t)$	rainfall random variable drawn from $N(0, \sigma_r^2)$	–	*
α_i	area controlled by one individual of class i	$i = 1,$ $2 \leq i \leq 5,$ $i = 6, 7,$ $i = 8, 9.$ ha	1×10^{-6} 1×10^{-4} 9×10^{-4} 25×10^{-4}
β_x	relative fire intensity in cell x	–	*
γ_i	expected transition rate (under mean, uncrowded conditions) from i to $i+1$	$1 \leq i \leq 4,$ $i = 5,$ – $i = 6,$ $i = 7,$ $i = 8.$	1.000 0.353 0.300 0.300 0.150
γ_{10}	net annual grass productivity under mean rainfall	kg/ha	2500
δ	proportion of seedlings dispersing to neighboring cells	–	0.05
ζ	drought severity steepness control (shape parameter)	–	50
η	amplitude of wet-dry rainfall cycles, relative to long-term mean	–	0.13
κ_i	resprouting rate of woody class i following fire	$i = 1,$ – $2 \leq i \leq 7,$ $8 \leq i \leq 9.$	0.0 0.9 0.0
$\lambda_{x,i}$	expansion-limiting coefficient for woody class i in cell x	–	*
μ_{6-7}^b	shrub topkill under maximum intensity fire	–	0.80
μ_{8-9}^b	mature tree mortality under maximum intensity fire	–	0.02
μ_i^e	mortality of class i plants browsed by elephants	$i = 1,$ –	1.00 0.25 0.25

		$2 \leq i \leq 5,$ $i = 6, 7,$ $i = 8, 9.$	0.80
μ_{8-9}^r	additional drought mortality for mature trees	—	0.05
ξ	drought severity coefficient	—	*
π_x	proportion of elephant foraging allocated to cell x	—	*
$\pi_{x,i}$	proportion of elephant foraging allocated to class i in cell x	—	*
ρ_{ik}	proportion of class i reduced to class k after elephant use	$2 \leq i \leq 5 (k = 1),$ $i = 6, 7 (k = 5),$ $i = 8 (k = 5),$ $i = 8 (k = 7).$	0.5 0.5 0.1 0.1
σ_r	standard deviation in annual rainfall relative to long-term mean	mm	0.30
τ_i	topkill rate of woody class i due to fire	—	*
$\phi_{x,i}$	competition coefficient applied to growth rate of woody class i	—	*
$\chi_{x,i}$	net growth rate of woody class i given sufficient area for expansion	—	*
ψ	scaling constant converting grass biomass to fire probability	kg^{-1}	10^{-4}
ω	period of wet-dry rainfall cycles	years	20

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