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A MODEL-FRAMED EVALUATION OF ELEPHANT EFFECTS ON TREE AND FIRE DYNAMICS IN AFRICAN SAVANNAS

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Abstract. There is a concern that high densities of elephants in southern Africa could lead to the overall reduction of other forms of biodiversity. We present a grid-based model of elephant–savanna dynamics, which differs from previous elephant–vegetation models by accounting for woody plant demographics, tree–grass interactions, stochastic environmental variables (fire and rainfall), and spatial contagion of fire and tree recruitment. The model projects changes in height structure and spatial pattern of trees over periods of centuries. The vegetation component of the model produces long-term tree–grass coexistence, and the emergent fire frequencies match those reported for southern African savannas.

Including elephants in the savanna model had the expected effect of reducing woody plant cover, mainly via increased adult tree mortality, although at an elephant density of 1.0 elephant/km^2, woody plants still persisted for over a century. We tested three different scenarios in addition to our default assumptions. (1) Reducing mortality of adult trees after elephant use, mimicking a more browsing-tolerant tree species, mitigated the detrimental effect of elephants on the woody population. (2) Coupling germination success (increased seedling recruitment) to elephant browsing further increased tree persistence, and (3) a faster growing woody component allowed some woody plant persistence for at least a century at a density of 3 elephants/km^2. Quantitative models of the kind presented here provide a valuable tool for exploring the consequences of management decisions involving the manipulation of elephant population densities.

Key words: African savanna; herbivory; Loxodonta africana; *plant demography; spatial model; tree–grass coexistence; woody plants.*

INTRODUCTION

Savannas occupy 60% of sub-Saharan Africa. They are typified by the coexistence of woody plants and grasses, with the relative (and wide-ranging) proportions of each being influenced predominantly by water availability, fire, nutrients, herbivory, and people (Scholes and Walker 1993, Solbrig et al. 1996, Rutherford 1997, Scholes 1997). Many mechanisms have been proposed for tree–grass coexistence in savannas, from equilibrial niche partitioning via rooting-zone competition for available moisture (Walter 1971, Walker and Noy-Meir 1982), to nonequilibrial stability via disturbance (Higgins et al. 2000) and state-and-transition (Westoby et al. 1989) dynamics.

African elephants (*Loxodonta africana*) have major ecological effects on savanna dynamics, playing significant roles in nutrient cycling, seed dispersal, and the provision of space for new germinants (Lewis 1987, Owen-Smith 1988). Despite their overall endangered status, extensive protected areas and effective control of poaching in southern Africa have led to the success of elephant conservation in the region (Douglas-Hamilton 1987). Continued increase of elephant populations may lead to a decrease in other species: it is argued that the present spatial restriction of elephant populations by fenced nature reserves or external human pressures exacerbates their impact on woody plants (Laws 1970, Lewis 1986, Hoare 1999, Pamo and Tchamba 2001). The habitat modification that results, particularly at high elephant densities, has altered the compositional, structural, and possibly functional diversity of ecosystems (Buechner and Dawkins 1961, Dublin et al. 1990, Cumming et al. 1997). Loss of canopy trees may imperil the woody plant population in the absence of recruits (Barnes 1983), or be followed by a transition to bushland (i.e., shrub-dominated vegetation) due to the prevention, by elephants, fire, or other browsers, of tree recruitment (Leuthold 1977, Pellew 1983, Jachmann and Bell 1985, Smallie and O'Connor 2000).

While most attempts at modeling elephant–savanna interactions have ignored spatial heterogeneity (Caughley 1976, Pellew 1983, van Wijngaarden 1985, Dublin et al. 1990, Ben-Shahar 1996*a*, *b*, Duffy et al. 1999, 2000), it has been argued that nonspatial models are inadequate to describe a system defined by heterogeneous vegetation (Jeltsch et al. 2000). Recent attempts

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at modeling savanna vegetation dynamics (without elephants) have acknowledged the importance of space in ecological processes (Menaut et al. 1990, Hochberg et al. 1994, Jeltsch et al. 1996, Simioni et al. 2000). Most of these spatial vegetation models have been individual-based models (IBMs), or grid-based approximations to IBMs, exploring tree–grass coexistence processes by modeling very localized plant environments and operating at a spatial resolution of 0.3–5.0 m sided cells. While such models are useful in considering fine-scale drivers of tree–grass coexistence, they are not readily expandable for considering the action of megaherbivores such as elephants and not necessarily appropriate for application to management (also see Getz and Haight 1989). Other larger scale multilayered models such as the Coughenour SAVANNA model (Kiker 1998, Ludwig et al. 2001, Boone et al. 2002) are less amenable to testing a wide range of scenarios. In this paper we develop a savanna model sufficiently broad in scale to explore elephant impacts usefully while still capturing the essential underlying vegetation processes. We use a set of interrelated population models, each representing the dynamical processes occurring in a 1-ha cell of a 1-km^2 block of 100 such cells.

While elephant impacts on woody plants may leave the species composition of woodlands unchanged, the structural composition may be considerably altered (Jachmann and Bell 1985, Trollope et al. 1998). Some models of elephant–vegetation interactions have ignored this vertical structuring of the woody community (Caughley 1976, Duffy et al. 1999, 2000). Others (Pellew 1983, Dublin et al. 1990, Ben-Shahar 1996*b*) have modeled the effects of elephants and fire on height-structured populations, but excluded the effects of climate, grass, competition, and density dependence. The elephant–trees–grass–grazers model produced by van Wijngaarden (1985) included woody plant structure at a coarse level (trees and shrubs) but not rainfall variability or fire. Starfield et al. (1993) used frame-based modeling to track broad-scale qualitative shifts between woodland, bushland, and grassland states, as driven by elephant, fire, and rainfall levels, but this approach lacked the detailed, quantitative information provided by a demographic model. Here we present a spatial elephant–vegetation model, which has a realistic vegetation component, taking into account a height-structured woody plant population operating in competition with grass, and affected by key environmental variables (water and fire). Our objective was to produce a model with a sufficient level of realism to investigate the impacts of elephants on savanna structure while maintaining enough flexibility to be adaptable to a variety of savanna ecosystems.

The Model

Our model links 100 1-ha cells in a 10 × 10 grid, to maintain a reasonable scale for modeling plant competition and fire events and to produce smooth and predictable dynamics (Hochberg et al. 1994). We assume uniform water and nutrient distribution across the resulting 1-km^2 area. Each hectare cell consists of a tree–grass community that, we assume, experiences uniform fire intensity and herbivory. The cells are linked spatially by seed dispersal and fire contagion. A cell's neighbors are defined as those cells immediately to the north, south, east, or west, with cells on the edge having fewer neighbors (i.e., dissipative boundary conditions).

A flow diagram outlining the progression of the model is given in Fig. 1. The model is simulated using discrete, half-year time steps (denoted by t), reflecting annual wet and dry seasons characteristic of savannas (Solbrig et al. 1996), although some savanna ecologists (e.g., Starfield et al. 1993) recognize three seasons: hot–wet, cold–dry, and hot–dry. In southern Africa, rainfall has a component of ''quasi 20-year oscillation'' of relatively wet and dry periods (Tyson and Dyer 1978, Gertenbach 1980), which we also include in the model. The rainfall is applied evenly over the entire grid; this is a reasonable assumption, given the size of our representative plot (du Toit et al. 1990). In our model, fire is assumed to occur only in the dry season. Although timing of burning can be important (particularly with reference to whether woody plants have produced new shoots yet or not; Frost and Robertson 1987, Enslin et al. 2000), our resolution of time into biannual units does not permit us to account explicitly for this subtlety (rather, the effect is averaged into the parameter values).

Although woody vegetation attributes can be measured using aboveground biomass, canopy cover, or stem diameter, elephant use of woody plants is often measured with reference to tree height. Therefore, we use height to demarcate nine stage classes of woody plant ($1 \leq i \leq 9$), which in turn represent four broader classes (metaclasses): seedlings are <15 cm tall (i = 1), saplings (i = 2, . . . , 5) are <1 m tall, two shrub-sized classes of 1–2 m (i = 6) and 2–3 m (i = 7; i.e., up to fire escape height; Pellew 1983), and two tree classes of 3–5 m (i = 8) and >5 m (i = 9; beyond browsing height). We use four sapling classes as a device to prevent seedlings entering the shrub metaclass within two years, and so individuals advance automatically through classes i = 2, . . . , 5 subject to sufficient rainfall. We employ a 10th vegetation class to record grass biomass. We also track area covered by woody plants and grass. An individual in each of the woody metaclasses is assumed to control a ''resource area'' of 0.01, 1, 9, and 25 m^2, respectively (after Kiker 1998). Rather than using the −3/2 self-thinning rule (Yoda et al. 1963, Westoby 1977), we follow other spatial models of savannas by assuming a linear relationship between height and neighborhood extent (Menaut et al. 1990, Higgins et al. 2000).

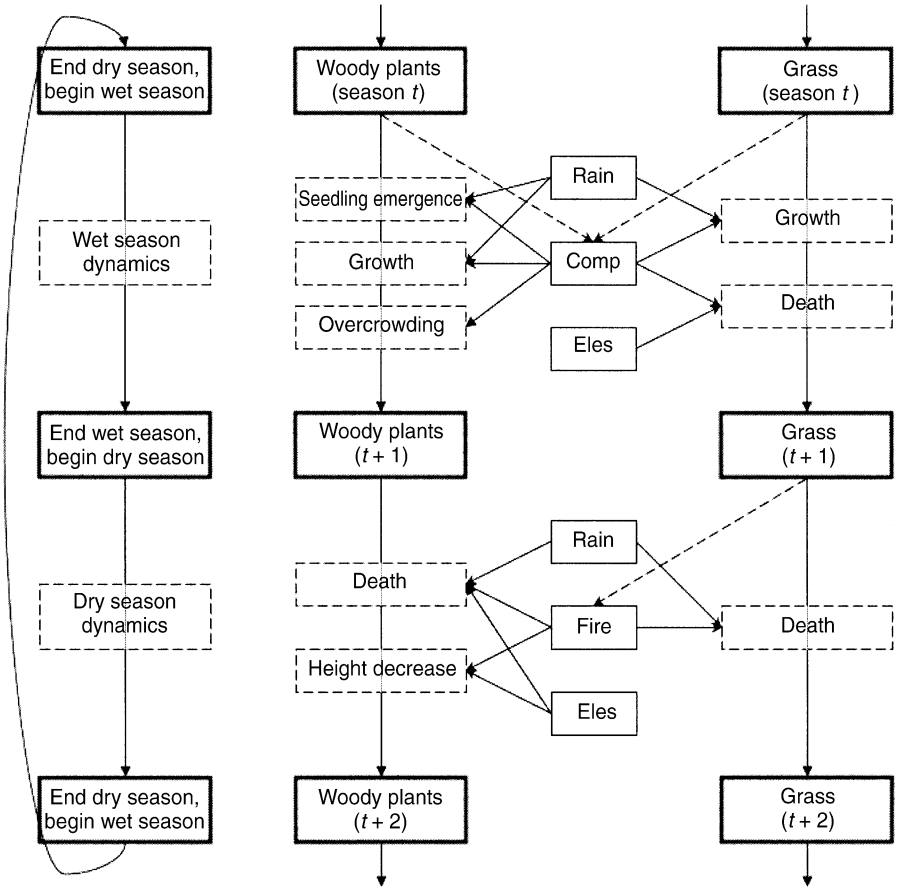

FIG. 1. Schematic flowchart of the model. Note that annual rainfall (Rain) occurs in the wet season but affects both wet-season and dry-season dynamics. Competition (Comp) is modeled as competition for space; see Appendix for details. Grass ''death'' refers to senescence and burning of aboveground tissue and uprooting of tufts by elephants (Eles).

Plant establishment and growth are assumed to occur in the wet season, and depend on annual rainfall and competition. Competition occurs within and between woody plants and grass and is modeled within each cell on a per-area basis, constraining growth with reference to the available resource space (Smith and Goodman 1986, Shackleton 1997). Plant mortality depends on rainfall, fire, and herbivory by elephants. In our model, woody plant mortality is limited to the dry season but grass senesces in both seasons. A certain proportion of woody plants whose aboveground tissue is destroyed by fire (or elephant browsing) can resprout. These are modeled as reverting one stage class (or more, in the case of elephant damage). Elephants are assumed to graze exclusively in the wet season and to browse exclusively in the dry season (Guy 1976, Meissner et al. 1990), visiting each cell in proportion to its forage content.

Finally, we ignore species differences between the hundreds of savanna tree and grass species, opting instead to model single ''generic'' tree and grass species (Hochberg et al. 1994). While we base our savanna model on the Kruger National Park in South Africa, paucity of data on woody plant height growth rates resulted in our employing data from African savannas in general (Baxter 2003). For details of equations used in the model, a list of all parameters, their default or initial values, and other symbols used, see the Appendix.

The model commences in a wet season, in the first year of a wet cycle. Each hectare cell contains the same initial vegetation structure: 50% grass cover, and 50% woody cover based on the right eigenvector (stable stage distribution; Caswell 2001) of the Lefkovitch matrix obtained from the growth and survival rates. We simulated the vegetation-only component of our model for 500 years to ensure long-term tree–grass coexistence. For the combined elephant–savanna model, we reduced the timescale to 100 years after elephant introduction, to better reflect the shorter-term concerns of park managers.

RESULTS

The model was used to simulate the trajectory of the system under several different scenarios represented by different sets of parameters. For each parameter set the

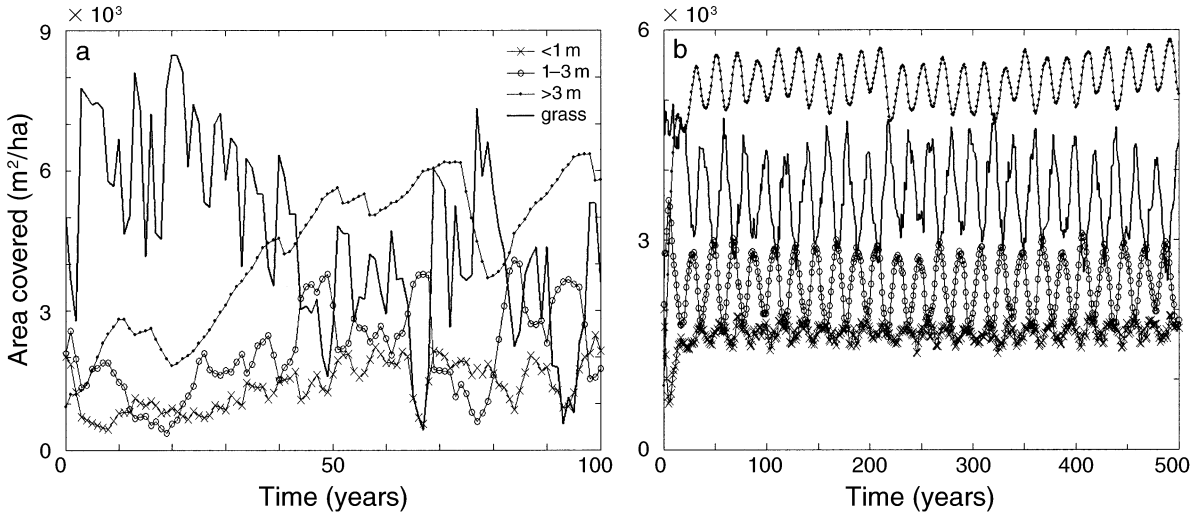

FIG. 2. Model results using the default parameter set, showing the mean area covered by woody plants in juvenile (<1 m high, i.e., seedlings and saplings), shrub (1–3 m), and tree (>3 m) classes, and by grass. Elephant density is zero throughout. (a) Output from a single stochastic run over 100 years, representing the mean output across the 10 × 10 grid (100 cells). (b) Mean output from 100 stochastic runs across the 10 × 10 grid, over 500 years.

model was run 100 times, each set initiated with the same random seed to ensure comparability of results. We first present model results in terms of area covered by woody ''juveniles'' (seedlings and saplings combined), shrubs, trees, and grass. Output represents the state of the savanna at the end of the wet season in the relevant year, i.e., after growth has taken place but before dry-season mortality, fire, and elephant browsing occurs. As juveniles and grass are permitted to grow under tree canopies, the areas of the vegetation classes may sum to >10 000 m²/hectare. Fig. 2a shows the output (mean of 100 cells) for a single simulation of 100 years using the default parameter values and without elephants. There is a strong stochastic signal in the output, and so we present the subsequent vegetation results as output averaged over the 100 cells and 100 simulations (each point on the graph thus representing the mean of 10 000 data points). Fig. 2b shows this mean output for the default model parameters over 500 years. Trees persisted with grass in each of the 100 runs averaged in the figure; the sinusoidal pattern in the trajectories is emphasized due to the synchrony of the underlying wet–dry cycles in the models. Sensitivity tests were conducted on key parameters (rainfall, fire, growth) and are presented elsewhere (Baxter 2003).

Elephant influence

We next modeled the effects of introducing an elephant population at year 101 (i.e., allowing 100 years for initial transient dynamics to decay). The population is assumed to remain at a constant density, or at least to visit our 1-km² patch with constant intensity. Fig. 3 depicts the mean trajectories arising from introducing 0.5 and 1.0 elephants/km². Fig. 4a shows the vegetation composition 100 years after introduction of elephant populations from 0 to 3 individuals/km².

Fig. 4b–d shows the results of three different assumptions for the same elephant population ranges. To account for variation in tree species' vulnerability to elephant browsing (e.g., Hiscocks 1999) we examined the outcome of assuming lower mortality of toppled and bark-stripped adult trees (40% mortality instead of the default of 80%; Fig. 4b). As fruit production and ingestion were not modeled directly, in Fig. 4c we account for the role of elephants in promoting germination (Lewis 1987, Cochrane 2003) by increasing the woody plant fecundity by a factor of $(1 + l(t))$, e.g., doubling the potential number of viable seedlings produced per tree when elephant density ($l(t)$) is 1 elephant/km². As vertical growth rates for woody plants are not well studied (Baxter 2003), we also tested the sensitivity of the model to a doubling of growth from 30 to 60 cm annual height increase (e.g., Knoop and Walker 1985, Mushove and Makoni 1993), shown in Fig. 4d. All of these results demonstrate that, while plant characteristics may somewhat mitigate the deleterious effect of elephants on woody cover, the magnitude of the elephant impacts has a controlling effect on the outcomes. We also examined patterns of ''quasi-removal'' (analogous to quasi-extinction; Ginzburg et al. 1982), which we define as occurring when less than one adult tree per hectare remains in a single simulation. Our default assumptions predict a 78% likelihood of tree quasi-removal within a century at 1 elephant/km², reducing to 35% for the reduced tree mortality scenario, 26% for elephant-enhanced fecundity, and 1% for annual woody growth of 60 cm.

Spatial consideration: woody dominance patterns

For elephant-affected savannas, it is interesting to examine transitions between different vegetation states.

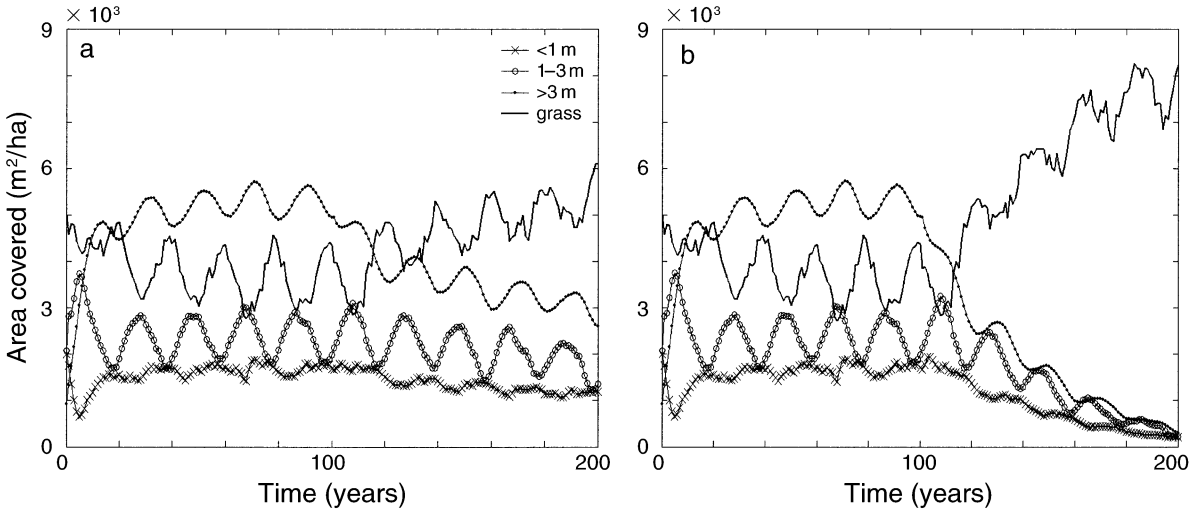

FIG. 3. Effects of elephant introduction at constant stocking density on mean area covered by woody plants (size classes as in Fig. 2) and by grass. Mean trajectories following introduction (at year 101) of elephants at constant densities of (a) 0.5 individuals/km^2 and (b) 1.0 individuals/km^2.

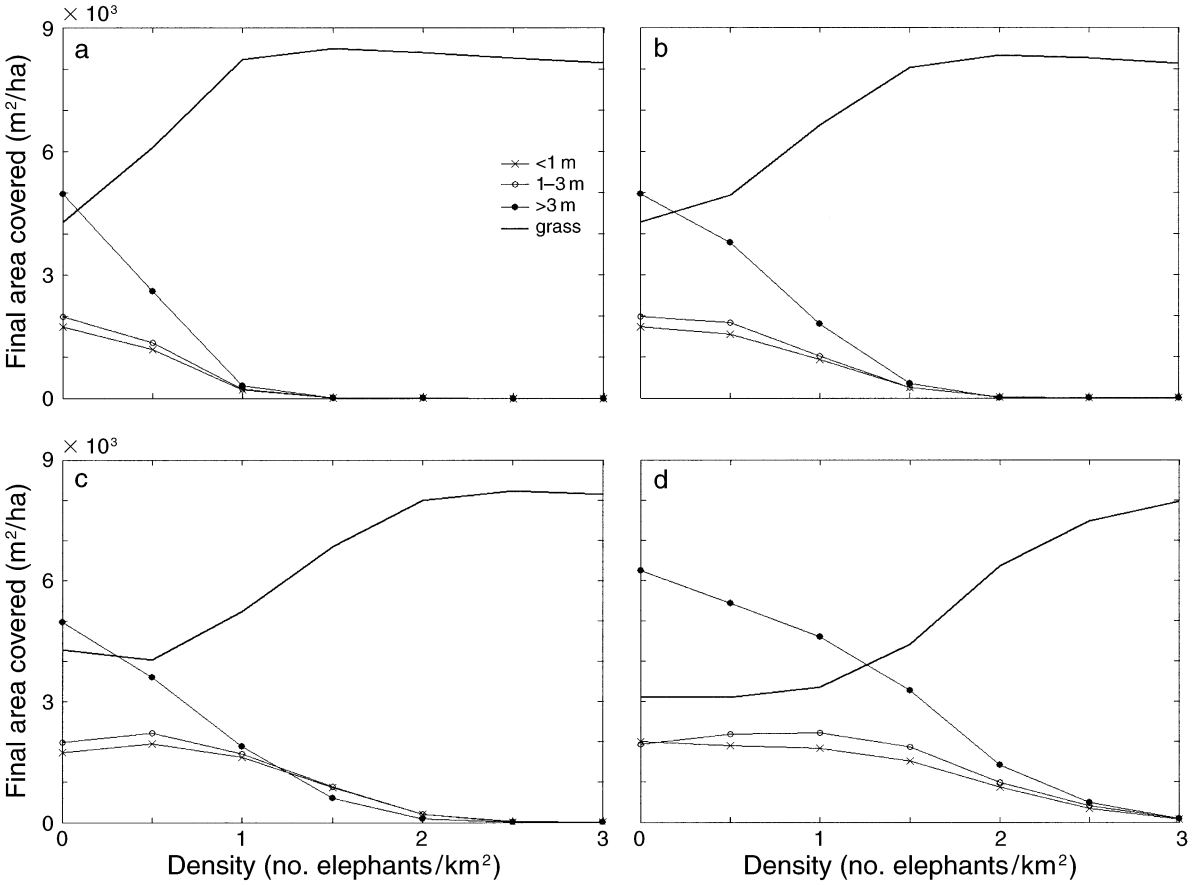

FIG. 4. Sensitivity of vegetation composition to elephant population densities, 100 years after elephant introduction: (a) default parameters; (b) assuming lower elephant-induced mortality to adult trees ($\mu_i^e = 0.4$, $i = 8, 9$), where e denotes elephant browsing as the source of mortality and i denotes the woody plant stage class; (c) allowing for elephant-assisted seedling establishment by increasing the fecundity parameter (m) to $[1 + l(t)]m$, where $l(t)$ is elephant density (individuals/km^2) at time t; and (d) assuming annual woody growth of 60 cm. All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates, which are set at year 0.

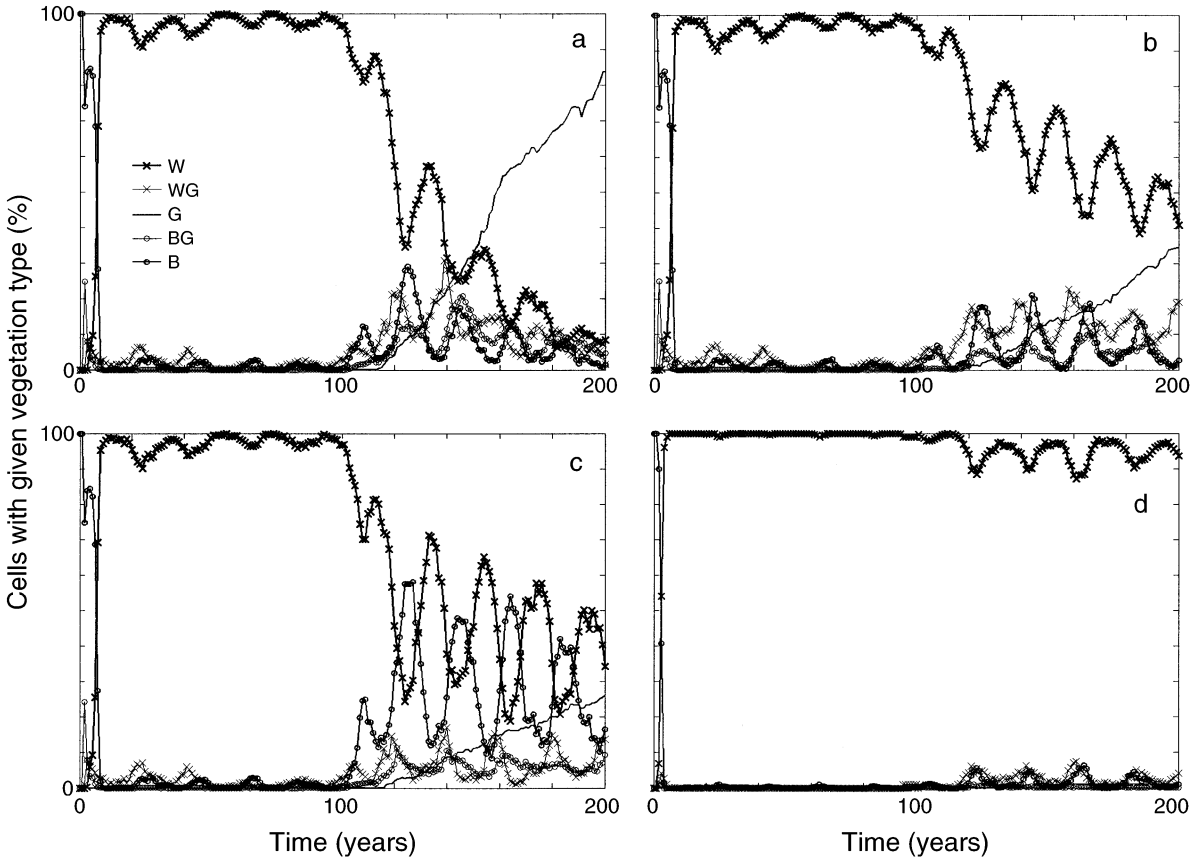

FIG. 5. Mean percentage of cells with given vegetation types for introduction (at year 101) of elephants at constant densities of 1.0 individual/km^2. Vegetation types (after Pratt et al. 1966) are woodland (W), wooded-grassland (WG), grassland (G), bushed-grassland (BG), and bushland (B). The different dominance profiles represent (a) default parameters (corresponding to the trajectory in Fig. 3b), (b) reduced adult mortality from elephant impacts (μ_i^e = 0.4, i = 8, 9), (c) extra fecundity assumption (increasing the fecundity parameter (m) to $[1 + l(t)]m$, where $l(t)$ is elephant density at time t), and (d) annual woody plant growth of 60 cm. All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates, which are set at year 0. Points represent means of 100 runs over a 10 × 10 grid.

We choose an elephant density of 1 individual/km^2 for illustrative purposes as densities close to this value have been reported as causing both little damage to trees (4.7% damaged, Anderson and Walker 1974; 18%, Birkett 2002) and extensive damage (77.6%, Mapaure and Mhlanga 2000; 87.2%, Thomson 1975). Pratt et al. (1966) provide a classification for savanna vegetation, whereby woodland and bushland represent trees and shrubs (respectively) being the dominant woody plant forms, and comprising >20% of the cover. We apply this classification, defining grassland as woody canopy cover of <5% and wooded-grassland and bushed-grassland as intermediate vegetation states (see also White 1983). Fig. 5 shows mean trajectories of these vegetation states for the four elephant–savanna scenarios dealt with in Fig. 4, for an elephant population of 1 individual/km^2, viz.: default parameters (Fig. 5a, vegetation cover trajectory also shown in Fig. 3b), reduced adult mortality from elephant impact (Fig. 5b), extra fecundity due to elephant-assisted germination (Fig. 5c), and higher woody plant growth rates (Fig. 5d). Further, for each of the five vegetation classes some runs result in 0% or 100% cover, so that the mean output shown can also be interpreted as the likelihood of achieving a given state. While broadly reflecting the trends of the mean vegetation cover trajectories, Fig. 5 also demonstrates that while these mean trajectories may display an overall woody dominance or otherwise, the actual spatial representation of woody-dominated cells may be more or less than expected. For example, comparing Figs. 3b and 5a (the default assumptions with 1 elephant/km^2), we see just 7.6% woody cover on average after 100 years (757 m^2 = 213 m^2 juvenile cover + 231 m^2 shrub cover + 313 m^2 tree cover), while only 83.7% of cells are classified as grassland and 8.5% of cells can still be classified as (mature-tree-dominated) woodland.

Fire dynamics

We also record the occurrence of fire events, and calculate fire return period (FRP) per iteration as the total number of potential fires (i.e., per cell, per year:

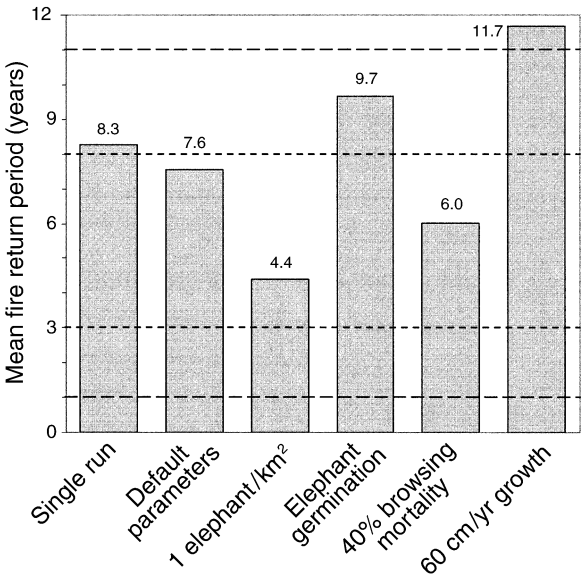

FIG. 6. Mean fire return periods for selected runs: single stochastic run; default model parameters (mean of 100 runs); introduction of 1 elephant/km^2; 1 elephant/km^2 with elephant-assisted seedling establishment; 1 elephant/km^2 with lower elephant-induced mortality to adult trees ($\mu_i^e = 0.4$, $i = 8$, 9); 1 elephant/km^2 with annual woody growth of 60 cm. All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates, which are set at year 0. Fire return periods indicate the mean interval between fires after parameters are adjusted. Horizontal lines represent typical (long-dashed lines) and mean (short-dashed lines) ranges of fire return periods reported for the Kruger National Park, South Africa (Trollope 1993).

50 000 in the 100-cell model run for 500 years) divided by the total number of actual fires, i.e., (fire frequency)$^{-1}$. In total, 668 471 cells burned in 100 runs of our 500-year, 100-cell default model, with an harmonic mean of 6604 fires per simulation, representing a mean FRP of 7.6 years. FRPs for a selection of scenarios are depicted in Fig. 6. These reflect the relative tree–grass balances resulting from each scenario, with more grass-dominated results yielding more fires and thus shorter FRPs.

DISCUSSION

The results presented previously indicate that the model is sufficiently detailed to address an array of ecological questions regarding the competitive interplay of the grass and woody components of a savanna system, and how this interplay is further impacted by elephant herbivory.

Default tree–grass balance

In their review of tree–grass competition in savannas, Scholes and Archer (1997) concluded that a balanced competition model should predict one of two states: dense woodland with sparse grass, or dense grassland with no trees. The output of this model meets this requirement (Fig. 2). In the default model, mean density of adult trees in years 480–500 (219.8 individuals/ha, mean cover of 5494.0 m^2/ha; see Fig. 2b), is in close agreement with tree densities found in the Klaserie Nature Reserve, South Africa (mean density 258) individuals/ha, with means for 10 vegetation types varying from 144 to 431/ha; Witkowski and O'Connor 1996). Calculating mean densities from the area covered gives densities in years 480–500 of 5180.5, 1658.1, 268.3 and 219.8 individuals/ha of the seedling, sapling, shrub, and tree metaclasses, respectively; the strong right skew of this distribution suggests the ''Gulliver'' strategy of persistence whereby many individuals remain at low heights, held in check by herbaceous-layer competition and resprouting continuously after fires, until an opportunity for recruitment to higher classes occurs (Bond and van Wilgen 1996).

The typical range of fire return periods for the Kruger National Park in South Africa is 1–11 years with a mean of three years for sourveld and eight years for sweetveld (Trollope 1993), although some locations in the park can go up to 40 years without a fire (van Wilgen et al. 2000). Our use of fire probabilities based on van Wilgen et al. (2000) has generated the realistic stochastic fire regime in this model (Fig. 6), whereas other savanna models have forced fire to occur every year (e.g., Menaut et al. 1990, Jeltsch et al. 1996, Simioni et al. 2000), a regime which when applied in the field (i.e., controlled burning every year) tends to lead to exclusion of trees (Shackleton and Scholes 2000). Jeltsch et al. (1997) also generated realistic fire frequencies using a probabilistic fire submodel for Kalahari thornveld.

Elephant effects

The trajectories in Fig. 3 show the typical ''elephant problem'' (Glover 1963, Caughley 1976, Barnes 1983) of decreased woody presence involving a loss of tall trees and eventual recruitment failure. Although reports of extreme, acute elephant damage to woodland areas are common (e.g., Field 1971, Croze 1974, Leuthold 1977, Norton-Griffiths 1979, Hiscocks 1999), our model provides a somewhat milder scenario and a longer-term perspective: despite a seemingly alarming initial response to elephant introduction, recruitment of smaller woody plants into the gaps left by adult trees tempers the overall decline of the woody species. The model of Pellew (1983) suggests that the roles of other browsers (specifically giraffe) and fire may be important in preventing recovery to the adult height class, eventually causing the woody species to succumb (see also Bond and Loffell 2001). van Wijngaarden (1985) modeled the introduction of elephants to a semiarid savanna and predicted that the ensuing drop in woody plants would produce a decline in the browsing guild. Conversely, recruitment or recovery into higher stage classes could be facilitated by heavy grazing reducing the frequency and intensity of fire, or by asynchrony in elephant impacts. In our model, the initial rapid decline

in woodlands tails off as the mature trees decline, and their canopy position is filled by the waiting shrubs. The signal of the wet–dry cycle is still evident, indicating more pronounced woody plant declines in drier years, consistent with field observations (Laws 1970, Leuthold 1977).

Savanna tree species differ greatly in levels and types of elephant browsing and in their response to this use (Anderson and Walker 1974, Croze 1974, Leuthold 1977, Jachmann and Bell 1985, Hiscocks 1999). As we have modeled one generic savanna tree species, we cannot expect the results to apply uniformly across the full range of woody species. By changing certain assumptions we can get an indication of the range of responses for different species types, and a broader feel for how the savanna as a whole may respond to elephant populations, without resorting to a complex (and less tractable) multispecies model. Figs. 4 and 5 depict how changes in plant properties can alter the fate of vegetation composition and structure. The default elephant–savanna model is summarized in Fig. 4a for constant elephant densities of 0–3 individuals/km^2. Although elephant densities tend to lie below 2 individuals/km^2, densities in excess of 5 elephants/km^2 have also been reported (Laws 1970, Owen-Smith 1988, Lewis 1991, Ben-Shahar 1996*b*). In our model, higher elephant populations increased levels of grass cover at the expense of woody plants and resulted in higher likelihood of tree quasi-removal over time. Specifically, the results suggest that elephant densities of 1 individual/km^2 or greater will result in inevitable reduction in woodland, with almost 80% probability of tree quasi-removal within a century. Our model does not account for the possibility that, under heavy elephant pressure, alternative tree species that are quicker growing, less palatable, or more resistant to elephant damage than the modeled species, may invade to produce a higher woody component than predicted by our results (Jachmann and Croes 1991). Mapaure and Campbell (2002) found that while elephant densities and woody cover were strongly negatively correlated in Sengwa Wildlife Research Area, Zimbabwe, with woody cover decreasing by 28.4% between 1958 and 1996, woody cover increased in 1993–1996 by 1.6% per year with elephant densities of between 1 and 2 individuals/km^2, with a possible shift in woodland species composition. Ben-Shahar (1996*b*) produced a size-structured model (based on Dublin et al. 1990) of woodland dynamics in northern Botswana and found that under mean fire and elephant impact conditions, woodlands would not start to decrease until elephant densities exceeded 9 individuals/km^2 for *Baikiaea plurijuga* woodlands, 11 individuals/km^2 for *Colophospermum mopane* woodlands and not at all for the *Acacia erioloba* community; however his model neglected the contributory roles of environmental variability and grass competition.

Our default conditions assume 80% mortality to adult trees following bark-stripping or toppling by elephants. Figs. 4b and 5b allow for less vulnerability, either in terms of different forms of impact or increased browsing tolerance, by halving this mortality rate to 40%. Under this assumption, some woody cover remains for a century even at elephant densities of 1.5 individuals/km^2, and 100 years after the introduction of 1 elephant/km^2, 41.0% and 2.7% of cells remain in the woodland and bushland states, respectively (cf. 8.5% and 1.4% for the default model).

Our model does not explicitly consider the proportion of elephant use taking the form of frugivory, which results in far less damage than leaf/stem-browsing (Jachmann and Bell 1985), and may even be beneficial to the tree population by assisting in dispersal and germination of drupes such as the marula, *Sclerocarya birrea* (Lewis 1987). Croze (1974), Pellew (1983), and Lewis (1991) concur that the role of continued recruitment in the face of elephant impacts is more beneficial to population persistence than adult survivorship. Figs. 4c and 5c demonstrate that this effect can indeed allow longer woody plant persistence, for elephant densities up to 2 individuals/km^2 (and with 34.2% and 16.6% of cells classified as woodland and bushland, respectively, after a century of 1 elephant/km^2). Although the role of elephants in dispersing seeds is not explicitly modeled, we recall that elephant habitat use is modeled to reflect tree density. Thus, relatively tree-rich cells, in addition to producing more seeds, will attract greater elephant use, which may further facilitate seedling emergence.

In a similar fashion, Figs. 4d and 5d highlight the effect that a woody plant's underlying growth rate may have on its population-level response to elephant impacts. African elephants have commonly been found to eat well over 100 plant species (Guy 1976 and references therein), and given the wide variation in woody species' growth, and response to fire, browsing, and other factors (Baxter 2003), there is obviously a need for detailed studies of the effects of elephants on woody species of different functional types. The implication is that as elephant browsing persists, slow-growing or particularly vulnerable species may in time be replaced by faster growing or more elephant-tolerant species. However, while an initial expectation might be that elephants may thus cause rare and favored tree species to decline and face extinction, the recent model of Duffy et al. (2000) suggests that the abundance of another tree species may divert elephant attention and energy needs from the rare species, its rarity itself providing a refuge. Our model results show that even with densities of up to 3 elephants/km^2, a faster growing tree species may still persist for $>$100 years, with 94% of cells still classified as woodland after a century of 1 elephant/km^2. The striking difference between the 30 and 60 cm/yr growth scenarios emphasizes that, in addition to the need for growth data, variation between different species' growth rates must be taken into account when managing savannas.

As well as the overall decline in woody plants produced by our model, the vertical structure becomes less adult tree dominated at higher elephant densities, reflecting a shift toward a bushland state within the increasingly grass-dominated community. This is particularly the case for the elephant-enhanced fecundity scenario (Figs. 4c and 5c). Continued elephant browsing of woody plants has been shown to lead to more shrub-dominated communities (Anderson and Walker 1974, Guy 1981, Jachmann and Bell 1985, Smallie and O'Connor 2000); however any trend toward bushland in the results presented here occurs only as part of an overall shift toward grassland. The species-specific ability of trees to coppice following impacts from elephants or fire, leading to dense bushland, may also reflect underlying soil type (Lewis 1991), which we do not explicitly consider here.

As with any model, the work presented here is based on many assumptions and approximations: uniform environmental substrate and topology; strict seasonal dynamics; and simplification of the vegetation, fire, and elephant components. Future variants of the model will address some of these simplifications. We nevertheless believe that this model provides a valuable tool for savanna management: neither site specific nor vague, with appropriate data it can be readily adapted to apply to different savanna ecosystems.

Conclusions

We have produced a versatile savanna model, parameterized from empirical sources, at a level of spatial resolution appropriate to exploring the community-level response to elephant impacts. Output from the model provides three-dimensional information about the long-term trajectory of a savanna by detailing changes in vertical structure as well as in spatial patterns of dominance. The introduction of elephants into the model at densities above $1/km^2$ leads to a loss of woodlands; however this trajectory may be mitigated in the case of faster tree growth, decreased vulnerability to heavy browsing, or an elephant-associated increase in seed germination. Although developed primarily as a tool for investigating elephant impacts, the model can also be used to investigate the behavior of systems involving different environmental conditions and tree functional types and to explore other scenarios such as changes in fire management or rainfall regime. As southern Africa faces great uncertainty in the coming decades, with issues such as climate change and population growth having uncertain implications for the future of natural areas, judicious and prudent management of biodiversity, necessarily using models such as the one presented here, is of the utmost importance.

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APPENDIX

Details of the equations used in the savanna model, a list of all parameters, their default or initial values, and other symbols used are available in ESA's Electronic Data Archive: *Ecological Archives* A015-035-A1.