ELEPHANTS, FIRE, AND FROST CAN DETERMINE COMMUNITY STRUCTURE AND COMPOSITION IN KALAHARI WOODLANDS

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Abstract. Fire, elephants, and frost are important disturbance factors in many African savannas, but the relative magnitude of their effects on vegetation and their interactions have not been quantified. Understanding how disturbance shapes savanna structure and composition is critical for predicting changes in tree cover and for formulating management and conservation policy. A simulation model was used to investigate how the disturbance regime determines vegetation structure and composition in a mixed Kalahari sand woodland savanna in western Zimbabwe. The model consisted of submodels for tree growth, tree damage caused by disturbance, mortality, and recruitment that were parameterized from field data collected over a two-year period. The model predicts that, under the current disturbance regime, tree basal area in the study area will decline by two-thirds over the next two decades and become dominated by species unpalatable to elephants. Changes in the disturbance regime are predicted to greatly modify vegetation structure and community composition. Elephants are the primary drivers of woodland change in this community at present-day population densities, and their impacts are exacerbated by the effects of fire and frost. Frost, in particular, does not play an important role when acting independently but appears to be a key secondary factor in the presence of elephants and/or fire. Unlike fire and frost, which cannot suppress the woodland phase on their own in this ecosystem, elephants can independently drive the vegetation to the scrub phase. The results suggest that elephant and fire management may be critical for the persistence of certain woodland communities within dry-season elephant habitats in the eastern Kalahari, particularly those dominated by Brachystegia spiciformis and other palatable species.

Key words: Baikiaea plurijuga; Brachystegia spiciformis; coppiced scrub; disturbance; elephants; fire; frost; herbivory; Kalahari sand woodlands; Zimbabwe.

INTRODUCTION

It is well established that disturbance plays a fundamental role in structuring savannas (Walker 1987, Higgins et al. 2000, van Langevelde et al. 2003), but relatively little is known about how multiple disturbances influence tree community composition and structure in this biome. In particular, there is a critical need to understand and predict how elephants, the dominant herbivores in many African savannas, interact with the effects of fire and other agents to cause vegetation change. This is because elephants, fire, and to a lesser extent frost, can have profound effects on tree cover, through which they may indirectly affect ecosystem function (Hoffmann et al. 2002, Jackson et al. 2002), biodiversity (Cumming et al. 1997), and the welfare of local communities (Piearce 1986). To a greater or lesser extent, these disturbance agents are under human control, so the development of tools that predict vegetation change as a function of management

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decisions is an important goal. This paper addresses this challenge by presenting the results of a simulation model that analyzes the effects of elephants, fire, and frost on the structure and composition of the tree community in a Kalahari woodland savanna in southern Africa.

Studies of disturbance in savannas often focus on fire, particularly its role in facilitating tree-grass coexistence (Menaut et al. 1990, Higgins et al. 2000, van Langevelde et al. 2003, Sankaran et al. 2004). In many African savannas, however, elephants (Loxodonta africana) may play an equal if not greater role than fire in regulating tree cover, but despite a large body of work conducted on their impact (Buechner and Dawkins 1961, Laws 1970, Dublin et al. 1990, Ben-Shahar 1993, Van de Vijver et al. 1999, and many others), considerable uncertainty remains about how elephants and fire directly and indirectly modify vegetation structure and species composition. Addressing these questions requires the use of models, both because savanna tree dynamics can be too slow to be effectively captured with experimental studies of short duration, and because such studies cannot adequately incorporate the spectrum of disturbance scenarios of interest.

Elephants are a keystone species in the ecosystems they inhabit because their large size allows them (in the

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absence of human intervention) to escape predators and proliferate in a short period of time to the point of significantly altering their environment, primarily by toppling trees and opening up the canopy of forests and savannas (Laws 1970). This direct effect is accompanied by a second, indirect role: elephants can promote the spread of fire by facilitating grass growth as the canopy is removed (Buechner and Dawkins 1961, Laws 1970). Fire is regarded as a key factor in the maintenance of many savannas, where regular burns may maintain the vegetation in an open scrub phase dominated by coppiced shrubs and grasses (Childes and Walker 1987, Dublin et al. 1990, Hoffmann 1999). Frost also plays an important role in some tropical savannas (Brando and Durigan 2004), including the Kalahari sand woodland savannas of southern Africa (Calvert 1986, Childes and Walker 1987), but its effects have received little attention to date. Like fire, frost can damage and kill above-ground plant tissues and even cause widespread changes in savanna vegetation (Rushworth 1975, Childes 1984). Its interaction with fire and elephant damage could be significant because, as frequent burns and tree toppling open up the canopy, trees are increasingly exposed to damaging temperatures at cold times of the year (Rushworth 1975, Childes 1984). Frost can also have a reciprocal effect: by raising the height of fuel loads, ground fires can extend into tree crowns, causing extensive mortality (Calvert 1986).

Most models that have examined the role of disturbance in savannas have tended to rely on fragmented data sources to produce parameters, often from multiple studies and habitats (Higgins et al. 2000, van Langevelde et al. 2003, Baxter and Getz 2005). As a result, they do not control for unmeasured variables that may differ among studies, and they are not always suited to express predictions in probabilistic terms. In particular, comprehensive data sets are rarely available for a single site, and thus it is not possible to perform a comparative analysis of the role of different disturbance types, or the synergistic effects between them. Finally, models that have examined the elephant-fire interaction have tended to focus on the issue of tree-grass coexistence, often ignoring variation in response to disturbance among tree species (Hochberg et al. 1994, Higgins et al. 2000, van Langevelde et al. 2003, Baxter and Getz 2005), which may be just as important for ecosystem function as the tree–grass dichotomy.

The approach used in the present study was to design a simulation model fully parameterized with data obtained from a single field study in the Kalahari sand ecosystem of western Zimbabwe. This ecosystem presents an ideal case study for the analysis of multiple disturbance effects in savannas, due to the high elephant population density present within much of its extension and the occurrence of frequent fires and killing frost events (Calvert 1986, Childes and Walker 1987). The primary objectives of the study were to (1) investigate the relative impact of elephant damage, fire, and frost on the structure and species composition of Kalahari sand vegetation, (2) analyze interactions among disturbance types, and (3) make quantitative predictions of vegetation change, particularly in the extent of mature woodland, as a function of the disturbance regime.

SAVANNA DYNAMICS MODEL

Study system

The simulation model was parameterized with data collected in a 1500-ha focal block within an area denominated Farm 41, a protected area of mixed Kalahari sand woodland savanna located at 18°38' S and 26°55' E on the eastern boundary of Hwange National Park (Hwange hereafter) in western Zimbabwe, described in detail elsewhere (Holdo 2003, Holdo and McDowell 2004). In terms of tree-species composition, it is representative of the extensive Baikiaea plurijuga-Terminalia sericea Kalahari sand woodlands that occur throughout much of southern Africa, but also includes species more typical of the Miombo woodlands that predominate farther east, in particular Brachystegia spiciformis. Rainfall at the nearby park headquarters averages 650 mm/yr, with a coefficient of variation of 28% (Hwange park records). Most of the area was selectively logged for Baikiaea plurijuga between 1920 and 1927 (Childes 1984), and at present the vegetation ranges structurally from coppiced scrub to mature Brachystegia woodland, with most of it being somewhere in between these two phases. This inbetween stage is denominated here as "transitional" woodland, because vegetation in this phase appears to be in the process of becoming either mature woodland or coppiced scrub, both of which can be stable over long periods of time (Childes 1984).

Model description

A computer simulation was used to model vegetation dynamics as a function of elephant, fire, and frost effects. The model is stochastic and discrete in time and tracks the fate of individual trees of 10 common species in a 1-ha square with boundaries that wrap around into a torus to eliminate edge effects. The species are Baphia massaiensis, Baikiaea plurijuga, Brachystegia spiciformis, Burkea africana, Combretum collinum, C. zeyheri, Erythrophleum africanum, Ochna pulchra, Pterocarpus angolensis, and Terminalia sericea. At every iteration of the simulation, each tree is cycled through a sequence of submodels: frost, elephant, and fire damage, topkill (mortality of aboveground tree biomass), whole-tree mortality, resprouting, growth, and recruitment (Fig. 1; Appendix). The effect of each submodel on a given tree is a function of environmental variables (e.g., elephant population density, the occurrence of an ignition event), state variables (e.g., tree diameter), and submodel parameters (Fig. 1; Appendix). The equations used in the submodels and all their parameters were produced from a data set obtained from monitoring individual trees over two years in vegetation plots set up in Farm



FIG. 1. Flowchart for the Kalahari sand woodland simulation model. Using an annual time step, state variables are updated in the sequence depicted by subjecting each tree to the submodels shown. Input and output variables are given for each submodel (some variables relating to tree allometry are omitted for clarity). Variables, submodel equations, and parameters are described in the Appendix.

41 and surrounding areas in 2001. Maximum likelihood methods were used to select the best functions for each submodel and to estimate parameters and their error estimates (Pacala et al. 1996). Field methods and parameter estimation are described in (Holdo 2005*a*, *b*, 2006*a*, *b*) and in the Appendix. Most parameters are species specific, but some are common to two or more species. Where data gaps occurred (e.g., lack of growth data for undamaged *Pterocarpus angolensis*), parameter values from similar species were used. In the fire estimator, species were grouped into five functional classes because of low sample sizes for some species (Holdo 2005*b*).

The model uses an annual time step, but assumes, for simplicity, that the various processes modeled occur in a fixed sequence within each step (Fig. 1). In this ecosystem, disturbance events occur mainly during the dry season, between May and October, whereas growth and recruitment occur primarily in the wet season, from November to April (Fig. 1). If frost and/or fire occur in any given year, the former tends to occur early in the dry season, in the colder months, whereas fires are more likely late in the season when fuels are dry (Rushworth 1975, Childes and Walker 1987); this sequence is reflected in the model structure (Fig. 1).

Three of the submodels (frost, fire, and growth) contain functions that depend on tree neighborhoods (e.g., effects of tree cover on frost damage and growth rates), so the model is spatially explicit, with continuous x, y coordinates for each tree. These coordinates are

used to determine whether a given tree is shaded by a larger tree in the fire submodel (Fig. 1, Appendix), since fire damage is considerably lower under the tree canopy, where grass growth is suppressed (Holdo 2005b), and to calculate a neighborhood basal area (within 25×25 m subplots) in the frost submodel, given that the analysis of field data indicated a decline in frost damage with neighborhood basal area (Holdo 2006a). There was little empirical support for competitive effects among neighboring trees based on the analysis of growth data (Holdo 2006b), but an analysis of spatial structure provided indirect evidence for inter-tree competition (Holdo 2005a), so density dependence was incorporated at the stand level. This is implemented in the model by multiplying an empirical function for tree growth (with species, basal diameter, and damage as covariates) by 1 $-(b/b_{MAX})^2$, where b is total basal area (m²/ha) within the 25 \times 25 m neighborhood of the tree, and b_{MAX} is the maximum basal area that can be supported by the simulated environment (m²/ha; Fig. 1; Appendix).

The model is fully stochastic: each submodel produces a mean value for the process in question, which in turn is used to generate a random deviate (the outcome of the submodel) to be passed on to the next submodel in the sequence (Fig. 1). Most of the submodels have binary outcomes (e.g., a tree is either damaged or undamaged as a result of disturbance), and binary random deviates are generated by comparing a uniform random variable u (ranging between 0 and 1) with the expected value of F (the

probability of frost damage) in the frost submodel, given a number of covariates (Fig. 1), is p_F (Appendix). If u < p_F , F = 1, otherwise F = 0. A Gaussian error is assumed for tree growth (Holdo 2006b), with the stochastic portion of the growth term z for each tree being drawn from a normal distribution with a variance term σ^2 that was estimated empirically (Appendix). A Poisson distribution is assumed for seedling recruitment (Ribbens et al. 1994; Appendix). In addition to the stochastic nature of each submodel, at the beginning of each time step the occurrences of frost or fire events (represented by e_{FR} and e_{FI} in Fig. 1) are treated as stochastic processes with mean return intervals $t_{\rm FR}$ and $t_{\rm FI}$ (in years), respectively (Appendix). For example, the probability of a frost event with mean return interval of two years is 0.5; this mean value is used at each time step to generate a random variable e_{FR} .

A distinction is made in the model between basal and stem resprouting. Following a disturbance event, damaged trees may either be topkilled or resprout from remaining aboveground parts. Those that are topkilled may either die or resprout basally from belowground structures. This distinction may be critical in savannas because basal and stem resprouting may have very different outcomes for a tree in terms of the probability of escaping disturbance (Bond and Midgley 2001). Whereas basal resprouting is equivalent to "resetting" a tree to the smallest size class, coppied trees that retain part of their original stem are less susceptible to future disturbance events than topkilled trees (Holdo 2005b, 2006a). This is because frost and fire damage are strongly correlated with tree diameter (Hoffmann 1999, Holdo 2005b, 2006a). The model thus keeps track of several state variables, such as main stem diameter (d), damage to the main stem (C), and diameter (r) of the largest resprout, if any (Fig. 1; Appendix).

Variation in rainfall is not explicitly included in the model, despite the importance of soil moisture as a factor influencing savanna structure (Scholes and Archer 1997, Sankaran et al. 2005), for several reasons. First, a primary objective of the study was to understand the role of disturbance and the consequences of manipulating the disturbance regime in a specific study site. It was considered desirable to assume for the time being that rainfall may be treated as a constant rather than a variable, to retain a manageable number of variables to be manipulated in the simulation. The model also assumes that the main effect of rainfall in this system is to control the maximum basal area b_{MAX} that can be supported by the environment, while disturbance determines the ability of the vegetation to reach b_{MAX} (Appendix). Second, analysis of a limited (but highly variable) temporal sequence of growth data suggested that systematic interannual variation in rainfall is not correlated with changes in tree growth rate (Holdo 2006b). Thus, given the data, there was no support for the inclusion of a rainfall term in the growth submodel. Variation in rainfall is likely to be important, but its effects may not be captured by a single variable: growth in Kalahari sand trees can be highly stochastic (Childes 1984, Holdo 2006*b*), with the effects of variation in soil moisture operating at small spatial scales (Caylor and Shugart 2004). Given that the field study included both wet and dry years (964, 392, and 475 mm recorded at Hwange park headquarters for the 2000–2001, 2001– 2002, and 2002–2003 seasons, respectively), it is therefore assumed that some of the interannual variation in growth caused by climatic stochasticity is captured by the error term for each individual tree in the growth submodel. Full descriptions of the submodels, ancillary functions, and their parameters are given in the Appendix.

Simulation scenarios

The model was run for different combinations of elephant population density (δ_E) and fire and frost return intervals (t_{FR} and t_{FI}) with the purpose of determining changes in Kalahari sand vegetation under contrasting disturbance regimes over 50 years. In the simulations, δ_E was deterministic (because there was no error estimate for elephant population density), while fire and frost events were treated as realizations of stochastic processes. For each set of conditions simulated, the model was initialized by sampling trees with replacement from the F41 data set so that the initial conditions represented a sample of the vegetation in its present state. The same initial conditions were used for any given set of model runs. The number of trees sampled was chosen to ensure that the basal area of the simulated woodland was approximately equal to the mean basal area of the plots sampled. The main output variables generated were tree basal area and crown cover and tree density for trees >20 cm in diameter. To predict vegetation change under the present-day disturbance regime, fire and frost events and elephant population density were either included or excluded from the simulation in a factorial design (producing eight disturbance scenarios). A constant elephant population density was assumed (fixed at 2001-2003 levels, for which $\delta_E = 1$), so that no feedback from vegetation on the elephant population was modeled. For cases in which $\delta_{\rm E} < 1$, the probability of toppling or ringbarking (girdling) in the elephant damage submodel was assumed to decline linearly with $\delta_{\rm E}$ (Appendix). The mean frost return interval $t_{\rm FR}$ (four years) was estimated by combining the known recent history of the study site (R. M. Holdo, personal observation) with a long-term data set from nearby Hwange compiled by Dudley (1999). Similarly, Hwange records indicated a mean fire return interval $t_{\rm FI}$ of three or four fires per decade during the 20th century in this area (Childes 1984), so $t_{\rm FI}$ = 3 yr was used. To further investigate the effect of changes in elephant numbers and fire and frost return intervals on vegetation, and to analyze interactions among disturbance types, simulations were conducted with a range of values of $\delta_{\rm E}$ (0, 0.1, 0.5, and 1), $t_{\rm FI}$ (1, 2,



FIG. 2. Simulated change in tree basal area (means for five runs) over 50 years in a mixed Kalahari sand woodland savanna with different disturbance regimes. When included in a given scenario, values for frost (t_{FR}) and fire (t_{FI}) mean return intervals are four and three years, respectively, and elephants are at present-day population density.

3, 5, 10 yr, and no fire), and t_{FR} (2, 4, 10, 20, and no frost).

Error analysis

To test the robustness of model predictions given the uncertainties in the data, an error analysis was conducted in which estimation error in all submodel parameters was propagated through the simulation with a bootstrapping procedure. The entire data set was resampled with replacement 2000 times to generate sets of maximum-likelihood parameter estimates for each submodel. This procedure generates a distribution of parameter values that estimates the multivariate error distribution of the parameters obtained from the original data set (Burnham and Anderson 1998). When the different sets of parameter values are run through the model, a distribution of model output results that reflects the uncertainty in the parameter estimates (Pacala et al. 1996). The model was run for 50 years under the present disturbance regime ($\delta_{\rm E} = 1$, $t_{\rm FR} = 4$ yr, and $t_{\rm FI} = 3$ yr) for the 2000 parameter combinations, and the median, interquartile range, and 95% confidence interval were computed for each output variable.

RESULTS

Vegetation structure under the present-day disturbance regime

The addition or subtraction of disturbance factors showed marked effects on tree cover, particularly for elephant damage (Fig. 2). Without elephants, fire, and frost, the model predicted the development of mature woodland within 25 years (Fig. 2). At current disturbance frequencies, frost only slightly delayed the development of woodland in the absence of elephant herbivory or fire, and fire had a similar effect, though its effect was more marked than that of frost (Fig. 2). In contrast, elephants were predicted to independently impede woodland formation, maintaining the vegetation in its present transitional stage between scrub and woodland (Fig. 2). Pairwise combinations of disturbance types showed much stronger effects, particularly when elephants were included, and tended to drive the system away from a woodland state. Fire and frost (without elephants) exerted a much stronger effect combined than alone, suggesting a strong synergistic interaction between them (Fig. 2). When elephants, fire, and frost were included in the model simultaneously (the present-day conditions), the vegetation tended to revert to a scrub phase, with lower basal area than at present (Fig. 2). The simulation predicted that total basal area would decline by about two-thirds over the next 50 years (with most of the decline occurring in the first decade) if the presentday disturbance regime were to remain unaltered and that the decline would reach an asymptote in the scrub phase (Fig. 2). The error analysis suggested that the prediction of a decline in tree basal area under these conditions was fairly robust, given that, for most sets of bootstrapped parameters, the vegetation followed a similar trajectory (Fig. 3). The upper limit of the distribution of tree basal area had a long tail, however, and decomposition of the model results by species suggested that this uncertainty was driven primarily by Baikiaea plurijuga (Fig. 3), a slow-growing, unpalatable species not favored by elephants.

Vegetation structure as a function of the disturbance regime

When the three disturbance types were tested at a range of values, as opposed to simply being present or absent, it was possible to examine their interactions in greater detail. The results suggested pairwise interactions among each of the factors (Fig. 4). A synergistic



FIG. 3. Projected change in basal area based on 2000 iterations of a 50-year simulation using bootstrapped sets of model parameters ($t_{\text{FR}} = 4 \text{ yr}$, $t_{\text{FI}} = 3 \text{ yr}$, and $\delta_{\text{E}} = 1$). The median (thick solid line), interquartile range (thin solid lines), and the 95% confidence interval (dashed lines) are shown.

fire–frost interaction was indicated by the fact that, in the absence of fire, frost had little or no effect on basal area, but as fire frequency increased, the impact of frost also increased (Fig. 4). Similarly, for a given fire-return interval, the slope of the relationship between frost and basal area depended on elephant population density, indicating a frost–elephant interaction (Fig. 4). A similar fire–elephant interaction was implied. Elephant impact also varied in a nonlinear fashion with population density: there was a marked difference between $\delta_E = 0$ and $\delta_E = 0.5$, but little further change as δ_E increased to present-day levels (Fig. 4).

For most scenarios, the model produced similar results regardless of the output variable, whether it be basal area, crown cover, or tree density (Fig. 4). This correlation broke down at low disturbance rates (no elephants, infrequent fire and/or frost). Under these conditions, the model predicted that the system would achieve its maximum basal area b_{MAX} , a closed woodland, but with lower crown area and large tree density than in the frequent fire scenario (Fig. 4). This paradox, which may or may not parallel reality, is a result of competition: with no disturbance, even-aged stands take longer to thin out as a result of competition; conversely, when fire is present but elephants are excluded, fast growing species such as *Brachystegia spiciformis* are able to reach the canopy, and fire thins

out the population, so that a number of individuals experiencing reduced competition are able to dominate.

Community composition as a function of the disturbance regime

The model predicted strong differences in species responses to disturbance after 50 years and marked effects of the disturbance regime on community composition (Figs. 5 and 6). Results for three key species are shown in Fig. 5. Baikiaea plurijuga, which is unpalatable to elephants but susceptible to fire and frost (Holdo 2005a), was predicted to become increasingly dominant as elephant population density increases and frost and fire frequency decline (Fig. 5). The roles of frost and fire were also enhanced as elephant population density increased: even though Baikiaea is seldom directly affected by elephant browsing, the reduction in tree cover at high population density leads to enhanced frost and fire damage. As a result, Baikiaea was predicted to benefit from reduced competition when elephants were present, but only when frost and fire were infrequent (Fig. 5a). Brachystegia spiciformis, which is palatable and fast growing (Holdo 2006a, b), was strongly affected by elephants: it dominated when elephants were absent, but was suppressed as the elephant population increased (Fig. 5). Terminalia sericea was never predicted to be dominant, regardless of the disturbance regime. At high elephant population densities, Terminalia was sup-



FIG. 4. (a) Basal area, (b) crown area, and (c) density of large trees (dbh > 20 cm) as a function of elephant population density (δ_E) and fire- and frost-return intervals after 50 years (values plotted are means for five runs). The return interval ∞ is equivalent to no disturbance.

pressed by herbivory, and when elephants were absent, *Terminalia* increased in basal area, but was overtaken by species that grow faster and/or reach larger sizes (Holdo 2006b), such as *Brachystegia* and *Baikiaea* (Fig. 5). To a greater or lesser extent, other species fell into one of these categories (Fig. 6): in the absence of disturbance, faster growing species such as *Baphia massaiensis*, *Burkea africana*, and *Combretum collinum* became increasingly common (Fig. 6d); under the present disturbance regime, most species declined, but unpalatable ones such as *Erythrophleum africanum* and *Ochna pulchra* comprised an increasingly greater proportion of the total basal area (Fig. 6c).

DISCUSSION

Changes in vegetation structure under the current disturbance regime

Elephants are the principal drivers of vegetation change in the mixed woodlands of the study site. Fire, and to a lesser extent frost, are important accessory agents that become increasingly important as the landscape shifts from mature and transitional woodland to scrub. This key role of elephants is supported by previous assessments of their impact on vegetation (Guy 1989, Conybeare 1991, Ben-Shahar 1996, Mosugelo et al. 2002). Conybeare (1991) previously reported a decline in tree cover in Hwange in areas with high elephant population densities. The model results suggest that this trend is likely to continue. The finding that trees are unlikely to be driven to local extinction can be attributed to their marked ability to resprout following disturbance. In contrast, in other savannas trees can be completely excluded by grasses as a result of disturbance (Buechner and Dawkins 1961, Laws 1970, Higgins et al. 2000, van Langevelde et al. 2003).

Interactions among disturbance types

The relationship between elephant browsing and fire and frost is probably primarily one of facilitation. By reducing crown cover, elephants allow fire and frost to gradually increase in intensity, until a threshold is passed



FIG. 5. Basal area (means for five runs) as a function of elephant population density and fire- and frost-return interval after 50 years for (a) *Baikiaea plurijuga*, (b) *Brachystegia spiciformis*, and (c) *Terminalia sericea*. Note differences in the vertical-axis scales.

and elephant browsing no longer becomes necessary to suppress growth. The manipulation of fire and frost frequency in the simulation shows a strong interaction between these two factors and relatively weak independent effects of each in the absence of elephant browsing. These synergistic effects may be caused either by the higher mortality of burned trees following frost, or by an increased susceptibility to frost resulting from a reduction in canopy cover driven by fire. The former effect, caused by the accumulation of standing dead biomass following frost, is a potentially critical factor in this system. Childes (1984) points out that late dry-season fires frequently occur in areas recently affected by frost: extensive burns followed killing frosts in Hwange in 1972, 1974, and 1979, suggesting that the co-occurrence of these two factors in a single season is not uncommon. Despite the importance of the fire-frost interaction, however, the estimation of this effect in the current study was based on a relatively small data set (Holdo 2005b); more research is required on the relationship between the extent of frost damage and the subsequent level of fire-induced mortality, and on the environmental factors that predict the occurrence of frost, which is highly patchy across the landscape (Childes 1984, Holdo 2005*a*). The frost-fire interaction becomes stronger as elephant population density increases. For *Baikiaea*, this is driven by two factors: when fire and frost increase in frequency, the negative effect of elephants on tree cover exacerbates the impact of the former; when fire and frost decrease in frequency, elephant suppression of *Brachystegia* leads to reduced competition, allowing *Baikiaea* to become the canopy dominant.

Changes in community composition

The impact of disturbance on Kalahari sand community composition appears to be strongly modulated by the marked differences in susceptibility among species to different disturbance types. *Baikiaea plurijuga*, for example, is unpalatable to elephants (Holdo 2003, 2005*a*), and the impact of elephants on this species



FIG. 6. Simulated change in basal area of 10 tree species (means for five runs) over 50 years under the present-day disturbance regime (a and c) and without disturbance (b and d). For the disturbance scenario, $t_{FR} = 4$ yr, $t_{FI} = 3$ yr, and $\delta_E = 1$. Species key: BAMA, *Baphia massaiensis*; BAPL, *Baikiaea plurijuga*; BRSP, *Brachystegia spiciformis*; BUAF, *Burkea africana*; COCO, *Combretum collinum*; COSP, *Combretum* spp.; ERAF, *Erythrophleum africanum*; OCPU, *Ochna pulchra*; PTAN, *Pterocarpus angolensis*; TESE, *Terminalia sericea*.

appears to be an indirect one, mediated primarily through facilitation of fire and frost and through the removal of faster-growing palatable competitors such as Brachystegia. An analysis of field data suggested a potential trade-off between competitive ability and sensitivity to disturbance (R. M. Holdo, unpublished data). The two extremes of this tradeoff are Ochna pulchra and Brachystegia spiciformis. The latter grows about 10 times faster than the former, but Ochna is unpalatable to elephants and highly resistant to both frost and fire (Holdo 2005a, b). As a result, lowdisturbance scenarios favor the development of Brachystegia woodland, whereas in the long term, a highdisturbance scenario is probably conducive to the proliferation of scrub vegetation dominated by species such as Ochna pulchra, a scenario that is already being observed in areas of Hwange that experience frequent fires, killing-frost events, and high elephant numbers (A. M. G. Conybeare, unpublished data).

The shifts in community composition with the disturbance regime have potentially important implications for ecosystem function. Slow-growing, unpalatable species, such as *Ochna pulchra*, have high levels of condensed tannins and waxier leaves than more palatable species. The eventual dominance of the community by these species may lead to changes in nutrient cycling as the litter layer becomes dominated by recalcitrant material (Pastor and Cohen 1997); the amount of palatable food for small selective browsers such as impala may also decline, leading to changes in the diversity of the animal community.

Model limitations

Two potentially important factors omitted from the model are rainfall and modeling of grass dynamics. Although the inclusion of explicit terms for rainfall in the simulation submodels was not supported by the available data, considering the consequences of variation in rainfall on model outcome may be important for effectively extrapolating model results beyond the study site used for model parameterization. It is well established that rainfall and soil moisture are key determinants of vegetation structure in savannas (Childes and Walker 1987, Scholes and Walker 1993, Sankaran et al. 2005), but further work is needed to incorporate rainfall-disturbance interactions (e.g., fire mortality in drought years) into savanna models. The present modeling framework could potentially be expanded by adding terms for rainfall to the growth, mortality, and recruitment submodels.

The model also ignores grass dynamics, assuming that grass cover (and thus fuel) is indirectly controlled by tree cover (R. M. Holdo, *unpublished data*). One limitation of this approach is that it does not consider the buildup of grass litter than can occur in the time between successive fires, and thus the model assumes that fires have the same intensity, regardless of their frequency. This assumption is reasonable for medium to long fire-return intervals, given that grass-litter buildup begins to March 2007

saturate after about three years (McNaughton 1985). For shorter intervals, the model results may be less reliable, but one- and two-year fire-return intervals are relatively uncommon in this ecosystem (Childes 1984). Perhaps more importantly, the fire and frost submodels were fitted to a small number of fires (all occurring in the same year) and a single frost event, so there is no provision in the model for variation in fire or frost intensity from year to year. Further research on the extent of this variation is required to incorporate this uncertainty into the simulation.

Elephant population dynamics were not considered in the model. On the one hand, the elephant population in the study site is likely to continue to rise beyond its present size, as it has shown no tendency to slow down over the past two decades (Martin et al. 1992, Blanc et al. 2002). On the other, the model ignores feedback of the vegetation on the elephants themselves, which might be expected to move to relatively unexploited areas as the availability of palatable tree species declines over time. The extent to which this is possible, however, may be limited by the availability of dry-season water supplies, which are intensively managed in Hwange.

Implications for management

The results of the study have important implications for management policy, given that elephant populations and fire are partly under human control. The fact that the model has been parameterized for a variety of tree species means that it can potentially be applied to a range of other woodland savanna ecosystems, from *Brachystegia*-dominated Miombo (Frost 1996) to *Burkea–Ochna* broad-leaved savanna (Scholes and Walker 1993), after additional terms have been added to some of the submodels to account for geographical variation in climate, as outlined above.

It should be considered that the model was based on a site characterized by a very high elephant population density. Although the absolute elephant population density was not quantified in the study site, it is probably within the upper range of values for adjacent Hwange, where the latest census yielded an estimate of 3 elephants/km² (Blanc et al. 2002). Elephant population density in this ecosystem can fluctuate widely depending on the distribution of water supplies (Williamson 1975, Martin et al. 1992), and more remote areas of the region, which lack dry-season water sources, experience lower population densities than this average, and thus there is less impact on vegetation.

The applicability of the model results for the Hwange ecosystem are also likely to be strongly dependent on the distribution of *Brachystegia spiciformis*, which is common in the study site, but less so in the greater Hwange ecosystem, where *Baikiaea plurijuga* dominates. In areas of Hwange where mature *Baikiaea* woodland remains, relatively little change in vegetation structure (but a strong shift in species composition favoring unpalatable species) may occur under the present disturbance regime. As mature *Baikiaea* trees succumb to age-related mortality, the system may eventually shift to a stable scrub phase as slow-growing, immature trees are prevented from escaping the fire/frost trap, but this would depend on proximity to populated areas outside the national park, as there is a strong gradient in firereturn interval between the unpopulated western reaches of the park and the eastern section (Childes 1984). In areas that are not *Baikiaea* woodland, rapid change may be expected as elephants topple or ringbark (girdle) sensitive species like *Brachystegia* and *Pterocarpus* and fire and frost become more intense as canopy cover is reduced.

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APPENDIX

Model equations and parameters (Ecological Archives A017-020-A1).