Modeling the Impact of the African Elephant, *Loxodonta africana*, on Woody Vegetation in Semi-Arid Savannas

by

Peter William Joseph Baxter

B.A. (University of Dublin, Trinity College) 1996

A dissertation submitted in partial satisfaction of the requirements for the degree of

Doctor of Philosophy
in

Environmental Science, Policy and Management

in the

GRADUATE DIVISION

of the

UNIVERSITY OF CALIFORNIA, BERKELEY

Committee in charge:

Professor Wayne M. Getz, Chair
Professor Dale R. McCullough
Professor Cheryl J. Briggs

Summer 2003

The dissertation of Peter William Joseph Baxter is approved:

Chair Date

Date

Date

University of California, Berkeley

Summer 2003

Modeling the Impact of the African Elephant, *Loxodonta africana*,
on Woody Vegetation in Semi-Arid Savannas

by

Peter William Joseph Baxter

Abstract

Modeling the Impact of the African Elephant, *Loxodonta africana*, on Woody Vegetation in Semi-Arid Savannas

by

Peter William Joseph Baxter

Doctor of Philosophy in

Environmental Science, Policy and Management

University of California, Berkeley

Professor Wayne M. Getz, Chair

Concerns over elephant impacts to woody plants in African savannas have highlighted shifts in vegetation community composition with implications for possible reductions in biodiversity.

I developed a grid-based savanna model that differs from previous elephant-vegetation models by accounting for tree demographics, tree-grass interactions, stochastic environmental variables (fire and rainfall) and spatial contagion of fire and tree recruitment. The vegetation component of the model produces long-term tree-grass coexistence and realistic fire frequencies. The tree-grass balance of the model is more sensitive to changes in rainfall conditions and tree growth rates while less sensitive to fire regime. Introducing elephants into this model savanna has the expected effect of reducing tree cover, although at an elephant density of 1.0 per square kilometer, woody plants still persist for over a century. I tested the effect of plant responses to elephant

impact: faster growth was a more successful strategy than elephant-enhanced germination or adult resilience to impact.

I elaborated the model by including a second, more “r-selected” tree species to investigate the effects of elephant impacts on species composition within the tree community. The model produces similar dynamics when run with either tree species alone; when both species are included it replicates ecological succession, with competitive exclusion of the early-successional species by the later-successional species on a timescale of centuries. Increases in growth, fecundity or survival of the early-successional species increase the likelihood of its persistence over 500 years. Inclusion of the faster-growing tree species in the model enables both species to survive greater elephant densities. Spatial heterogeneity of the woody plant component increases with elephant density. I examined the interaction of the two tree strategies – adult resilience and elephant-enhanced germination – with elephant preference for either species. Adult tree resilience was the more successful strategy and may act synergistically between tree species. Fire suppression also moderates the effects of elephant damage.

I conclude that while elephants may cause woodland to decline, they may also enhance biodiversity at lower densities, and increase spatial heterogeneity. Conservation workers should be conscious of the array of species types and their interactions when planning to manage savannas and/or elephant populations for biodiversity.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter Two

Chapter Three

LIST OF EXPLANATORY BOXES

LIST OF TABLES

ACKNOWLEDGEMENTS

This dissertation is the product of (exactly!) six years' work on three continents, and there are many people who deserve thanks for helping this man from Dublin study African savannas in California. I've stood on the shoulders of many giants.

Enormous thanks must first go to my advising professor, Wayne Getz, who always had faith in me, and was a shining beacon of inspiration throughout the process. His astonishing mind is matched only by his genuine concern for his students' welfare and success.

Also at Berkeley, I'd like to thank the members of my committees for their guidance and nurturing throughout my graduate career – Tracy Benning, John Harte, Ye Qi, but primarily Cherie Briggs and Dale McCullough, who've been available and helpful since I first got here. My lab-mates and fellow students also provided many hours of discourse and assistance. Nelleke van Deusen-Scholl found the time to teach me Afrikaans (and Dutch) for a year and made it thoroughly enjoyable: *Baie dankie*!

In South Africa, many scientists were willing to share their time and valuable experience with me. Norman Owen-Smith was the main driving force behind the study, and provided hours of stimulating discussion and guidance. Johan du Toit generously hosted me at the University of Pretoria's Mammal Research Institute, and I benefited from fruitful discussions with him and the MRI students. Tim O'Connor provided great insights into savanna vegetation; Kevin Duffy and Bruce Page did the same for elephants. Angela Gaylard, Michele Hofmeyr, Steve Higgins and Nick Zambatis brought me out on fieldwork so that a modeler could see what the bushveld is really like, and how an elephant or a tree might experience it. The scientific staff at Kruger National Park provided useful feedback, especially Harry Biggs, Ian Whyte and Nick Zambatis. I also benefited from discussions with William Bond, Bruce Brockett, Beukes Enslin, Kay Hiscocks, Olga Jacobs, Wayne Matthews, Sue Milton, Mike Peel, Frank Schurr, Gerhard Strydom, Winston Trollope, Brian van Wilgen, Petri Viljoen, Dave Ward and Ed Witkowski.

These and others provided comments and advice on manuscripts, thanks especially to Cherie Briggs, Paul Cross, Kevin Duffy, Johan du Toit, Steve Higgins, Jamie Lloyd-Smith, Dale McCullough, Tim O'Connor, Norman Owen-Smith, Jessica Redfern, Sadie Ryan, Chris Wilmers and George Wittemyer. I'm grateful to Bruce Brockett, Beukis Enslin, Tim O'Connor, Max Rietkerk and Winston Trollope for access to unpublished material.

My South African travels were enormously assisted, and made much more enjoyable, by my cousins, especially Mike and Janet Britton who provided me with a real home-away-from-home in Jo'burg on many occasions – and great travel assistance too. The Latillas in Witbank were a welcome rest stop going to and from the Kruger Park (thanks again for the van Wyk "Trees of KNP", Cecilia) and Patrick and Richard showed me the highlife in Durban. Other warm welcomes (when I wasn't getting lost) were provided by Derek and Doreen Gallagher, the Ellenbergers and John Matison. Wayne also makes it into the South African acknowledgement section – thanks to himself and Jenny for putting up with Jenny and I for a great month in Stellenbosch.

Personal support has been immensely important during this long process. In the USA, the Getz Lab has always been a great place to work so thanks to all my lab colleagues past and present (especial thanks to Wes for all the encouraging phone calls as well as the guiding hand as I found my feet here). Logan was the first fellow student I met at Berkeley and has proved a great friend ever since. He and others in my ESPM cohort – Dave, Lisa, Lori, Stacey – convinced me that it wasn't so bad to be far from home. Hermann, Jason, Sadie, Virginia and Wendy have all added music to my life. Simon has been a great mate, lucid, encouraging and generous. Thanks to the many cool people I've shared houses with. The administrative staff in Mulford and Wellman Halls helped me through many a bureaucratic hiccup. Many thanks also to Mary Mendoza-Newman and Tina Liu. And again I must thank the Getzes; Wayne and his family have really made me feel like one of their own. Thanksgivings won't be the same in future.

Despite my wanderlust, Ireland will always be home and so I go *trasna na dtonnta* to acknowledge my family and friends. The contribution my immediate family has made is hard to sum up; feeding, sheltering and chauffeuring only scratch the surface. The little things always make an impression so thanks for the cuppas and the car, Miriam, the myriad postcards, Mum (guess where I get the wanderlust from), and the pints and sectretarial service, Paul.

Peter was one of my greatest sources of support and advice throughout the Ph.D., thanks for blazing the trail. Conor and Fiona have been just amazing, with a Homely House worthy of Rivendell. Thanks to Ger and family for the phone calls; to Marie, "Mrs. Mac" and Rosalie for the divine intervention; to John, Kieran and Naomi for dropping by; to Darragh, Maria and Peter for the accommodation; to Derek for the phone calls and credit. Thanks to all the Gang because yiz're just brilliant. Looking forward to seeing you all soon.

Over any six-year period, life goes on, and ends for some. Unfortunately I won't be able to celebrate with Eileen, my aunt and godmother, or Eran, my friend and colleague, but they're fondly remembered – my life is richer for having known them. My late father kept the buttons from his first mail-boy uniform to remind him of where he started out, so Dad, I'll try to keep my feet on the ground too, even as I reach for the stars.

Finally, my love and thanks to Jenny Dowse who has been a constant source of joy and a rock of support, buoying me up and urging me on even during the roughest times – a true friend (and a great traveling companion!). Thanks with all my heart for your love and perseverance Jen – I look forward immensely to our long-term reunion.

This work was supported in part by a Foreign Language and Area Studies Fellowship and an Andrew and Mary Rocca Travel Scholarship, and by NSF grant DEB-0090323 to W. M. Getz. I would also like to thank South African National Parks and the Scientific Services Division of the Kruger National Park for facilitating my research.

Go raibh míle maith agaibh go léir.

Berkeley, August 14th 2003.

Grey as a mouse, big as a house,

Nose like a snake, I make the earth shake,

As I tramp through the grass; trees crack as I pass.

With horns in my mouth I walk in the South,

Flapping big ears. Beyond count of years

I stump round and round, never lie on the ground,

Not even to die. Oliphaunt am I,

Biggest of all, huge, old, and tall.

If ever you'd met me you wouldn't forget me.

If you never do, you won't think I'm true;

But old Oliphaunt am I, and I never lie.

J. R. R. Tolkien

Chapter One

Elephant-vegetation interactions in African savannas.

Peter W. J. Baxter

Introduction

The African elephant (*Loxodonta africana* Blumenbach) is the largest extant land mammal, with recorded body mass of up to 6,000 kg for males, and 2,800 kg for females. Accordingly, its dietary intake is considerable (typically 1% (dry weight) of body mass daily) and the resulting effects on vegetation can be dramatic (Owen-Smith 1988). Pronounced reductions in trees and other woody plants have been experienced across the continent, including Cameroon, Tanzania, and South Africa (Barnes 1983a, Pamo and Tchamba 2001, Jacobs and Biggs 2002a). Conservationists and reserve managers have expressed concern about loss of rare or vulnerable trees and a possible concomitant loss of biodiversity. This has led to the paradoxical situation whereby managers of reserves with high elephant densities develop plans to limit or reduce population numbers of an endangered species (Barnes 1983b, Caughley *et al.* 1990).

While poaching for ivory has caused precipitous declines in elephant populations (Laws 1970, Caughley *et al.* 1990, Prins and van der Jeugd 1993, Leuthold 1996), annual rates of population increase can be in excess of 5% (Cumming 1981, Tchamba 1995, Tafangenyasha 1997), with a theoretical maximum of 7% (Calef 1988). Local population densities up to 12.12 individuals per km^2 have been recorded (Ruess and Halter 1990). As elephants experience human-caused habitat reduction, elimination of migration routes and disturbance (including poaching), previously wide-ranging populations may become confined ("compressed") within reserves inducing sudden changes in vegetation (Buechner and Dawkins 1961, Field 1971, Barnes 1983b, Lewis 1986, Mapaure and Mhlanga 2000, Pamo and Tchamba 2001). Laws (1970) argued that while elephant conversion of woodland should lead to increased elephant grazing and dispersal, poorer condition and thus eventual regulation of their population, compression interacts with elephant longevity to prevent such natural population regulation occurring (see also Lewis 1986).

Elephant feeding patterns

The level of impact of high elephant densities is governed by elephant feeding behavior acting in concert with other ecological and environmental factors. Elephants are mixed feeders, ingesting both grass and browse in varying proportions. Woody plants contain higher levels of crude protein than grasses in the dry season (Field 1971), so that browsing allows elephants to maintain body condition year-round (Williamson 1975). Elephants thus tend to increase the percentage of browse (when available) in their diet, causing most damage to woody plants, in the dry season (Barnes 1982, Glover 1963, Field and Ross 1976, Kalemera 1989, Bowland and Yeaton 1997). Browsing may also be increased as elephants take refuge in woodlands as a response to human disturbance (Lewis 1986, de Boer *et al.* 2000). The overall proportion of browse in the diet has been recorded at levels up to 98.8%, in Hwange National Park, Zimbabwe (Williamson 1975). Napier Bax and Sheldrick (1963) report that elephant diet is more diverse in the dry season than the wet season but de Boer *et al.* (2000) found that the diet became narrower at the late dry season. Intake of wood and bark tends to increase as the dry season progresses (Barnes 1982, Lewis 1986).

Preferred feeding height tends to be below 2m, the height of the browsed plants being somewhat greater (Jachmann and Bell 1985, Ruess and Halter 1990, Smallie and O'Connor 2000). Plants shorter than 1m tend to be ignored, and other height classes utilized in proportion to their availability (Croze 1974b, Kalemera 1989). Other workers have found a preference for adult trees (Barnes 1982, Okula and Sise 1986, Swanepoel and Swanepoel 1986), which may entail switching from stem and leaf browsing to bark stripping as height increases beyond 4m (Smallie and O'Connor 2000).

Depending on the root system of the tree species, it may be uprooted frequently (*Combretum apiculatum, C. zeyheri, Acacia nigrescens, Terminalia sericea*) or merely browsed (*Sclerocarya birrea, A. tortilis, C. imberbe*) (van Wyk and Fairall 1969). Uprooting of adult trees by elephants may serve a social purpose (Lamprey *et al.* 1967, Guy 1976) but is chiefly associated with gaining access to fruit and leaves on the upper branches (Croze 1974a, Jachmann and Bell 1985, Mwalyosi 1987). Trees can survive toppling and regenerate if even half of their root system remains intact (Croze 1974b). Other elephant damage to trees includes felling, bark damage and stem breakage resulting from scratching-post behavior to shed ticks (Buss 1961).

Patterns of damage may be distributed differently by sex. Barnes (1982) notes that elephant cows moved more between plants than bulls, and breeding herds tend to be more selective than bulls in feeding patch and plant choice, apparently to minimize fiber intake (Stokke 1999). Duffy *et al.* (2002) advocate that managers should focus on numbers of male elephant, as mature bulls are responsible for the most of the tree toppling; Stokke and du Toit (2000) found that bulls topple five times as many trees as family units.

Damage rates to vegetation can vary greatly by elephant density. Elephant densities of approximately 1 per km^2 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). In general, elephant populations, or localized concentrations thereof, which exceed 2 km^{-2}, cause damage to almost every individual tree (Buechner and Dawkins 1961, Ben-Shahar 1998, Jacobs and Biggs 2002b).

Dietary preferences

While being bulk feeders, elephants still demonstrate distinct preference or avoidance for different plant species, which in turn affects (along with the individual species responses to utilization, see below) the extent and pattern of any vegetation change that may occur with elephant utilization of a habitat.

Preferentially utilized trees include those that provide shade or fruit (e.g. *Acacia albida* (Barnes 1983a) and marula, *Sclerocarya birrea* (Coetzee *et al.* 1979, Duffy *et al.* 2002)), nutrients – such as calcium and nitrogen (*Sterculia* spp and baobab, *Adansonia digitata* (Napier Bax and Sheldrick 1963)) and others (Williamson 1975, Hiscocks 1999) – or simply those individuals that are more exposed or accessible (Pamo and Tchamba 2001). Bowland and Yeaton (1997) found that elephants had a four-fold preference for trees from later successional stages (*Acacia caffra* and broadleaves) to earlier successional trees such as *A. nilotica*. Latex-bearing species such as *Euphorbia candelabrum* are generally avoided (Field 1971).

As a result, elephant damage tends not to be distributed among species in proportion to their relative abundance. For example, elephant damage around Lake Kariba, Zimbabwe, revealed that in *Colophospermum mopane* (mopane)-dominated woodland, elephants used mopane, *Combretum* spp and *Croton gratissimus* roughly in proportion to their occurrence, but that in *Combretum* woodland elephants selected mopane in preference to the other two species; *Meiostemon tetrandrus* was avoided, even in *Meiostemon*-dominated woodland (Jarman 1971). Similarly, Ben-Shahar (1998) found that although *Brachystegia* woodlands in northern Botswana had higher elephant densities, mopane woodlands experienced more elephant damage. Mopane is generally considered a preferred species (Williamson 1975, Ben-Shahar 1998), with coppiced trees often being continually pruned (Lewis 1991, Ben-Shahar 1993, Smallie and O'Connor 2000). Other workers, however, have argued that elephant dependence on mopane is over-emphasized (Lewis 1986, Styles and Skinner 2000; see also Anderson and Walker 1974). *Acacia tortilis*, the iconic savanna "umbrella thorn" tree is also generally considered a preferred species (Guy 1976, Ruess and Halter 1990, Ben-Shahar 1993; but see Smallie and O'Connor 2000). The baobab *Adansonia digitata* is frequently utilized for its soft pulpy wood in the dry season (Weyerhaeuser 1995).

Interactions with other ecological and environmental factors

Fire, other browsers, drought and soil/nutrient conditions and other factors can exacerbate the extent and pattern of elephant damage to species.

Fire. Vegetation shifts from woodland to grassland have most often been attributed to the joint action of elephants and fire (Napier Bax and Sheldrick 1963, Lawton and Gough 1970, Barnes 1983b, Pellew 1983, Leuthold 1996). While elephants can impact large or small trees, fire normally acts to suppress re-establishment of the damaged plants to reproductive heights (Buechner and Dawkins 1961, Lamprey *et al.* 1967, Thomson 1975, Norton-Griffiths 1979, Guy 1981, Trollope *et al.* 1998, Jacobs and Biggs 2002a), often acting in concert with other browsers (Field and Ross 1976, Pellew 1983, Ruess and Halter 1990, Jacobs and Biggs 2002a). Mosugelo *et al.* (2002) reason that elephant damage may additionally affect non-selected woody species (e.g. *Baikiaea plurijuga*) by opening the woodland canopy and increasing fire frequency. Ben-Shahar's (1996b) model suggests that *Brachystegia plurijuga* woodlands in northern Botswana, while less at risk from elephant impacts than mopane woodlands, are in "precarious" condition due to their fire-susceptibility. Fire manipulation has therefore been advocated and employed successfully to manage elephant effects on savannas, using either fire suppression to mitigate damage (van Wyk and Fairall 1969, Pellew 1983, Trollope *et al.* 1998, Mapaure and Campbell 2002), or controlled burns to alter elephant browsing patterns (Lewis 1987b, Kennedy 2000).

Herbivores. Other browsers act in similar fashion to fire by preventing elephant-impacted plants from regenerating to adult heights (Field and Ross 1976, Lewis 1991), the principal agents being giraffe *Giraffa camelopardalis* (Norton-Griffiths 1979, Pellew 1983, Ruess and Halter 1990) and impala *Aepyceros melampus* (Lewis 1987a, Prins and van der Jeugd 1993, Mosugelo *et al.* 2002). Other impacts reported include hedging by eland *Tragelaphus oryx* (Styles and Skinner 2000) and debarking by buffalo *Syncerus caffer* and kudu *T. strepsiceros* (Mapaure and Campbell 2002). The browsing guild itself can be negatively affected by reduction of woodland by elephants (Napier Bax and Sheldrick 1963, Addy 1993)

Water. Extended dry seasons or prolonged droughts can compromise tree viability (Scholes 1985) and amplify negative elephant effects (van Wyk and Fairall 1969), perhaps even moreso than fire (Tafangenyasha 1997). Elephants may also intensify use of browse in dry periods (Barnes 1982) or alter habitat use patterns (Napier Bax and Sheldrick 1963, Leuthold 1977). Vegetation change often decreases as distance to water increases (van Wyk and Fairall 1969, Calenge *et al.* 2002, Mosugelo *et al.* 2002). The concentration of elephant populations around permanent water sources in the dry season can lead to "damage epicenters" (Laws 1970, Field and Ross 1976). Ben-Shahar (1993), however, found significant correlations of increased damage to *Acacia erioloba*, *Colophospermum mopane* and *Terminalia sericea* with proximity to temporary water sources, but not with proximity to permanent water.

Soil nutrients. Elephant impact may be associated with nutrient-rich soils (Nellemann *et al.* 2002, but see Ben-Shahar and Macdonald 2002), and woodland response to utilization also varies with soil conditions. On clayey, poorly drained soils, trees are more vulnerable and tree density is reduced (McShane 1989, Lewis 1991, Jacobs and Biggs 2002b) whereas on sandy, well-drained soils coppice regrowth is supported and high browsing pressure sustained for longer, though potentially leading to more dramatic eventual crashes (McShane 1989, Lewis 1991). In the Kruger National Park, South Africa, woody cover increased by 12% between 1940 and 1998, whereas cover decreased by 64% on basalt substrates over the same period (Eckhardt *et al.* (2000); see also Trollope *et al.* 1998).

Other factors. Elephant damage to bark increases tree vulnerability to infestation by woodboring insects (Bostrychidae, Lucanidae) and fungi (Thomson 1975, Jacobs and Biggs 2002b). Flooding can kill directly (Lawton and Gough 1970) but also affects elephant habitat use, making riparian grass unavailable and increasing browsing intensity (Kalemera 1989).

Plant resilience to impacts

Savanna plants have nevertheless evolved with elephants (and fire, etc.) and many species demonstrate adaptations to cope with impacts. Survival and regeneration is common where some of the bark (Mwalyosi 1987) or root system (Croze 1974b) remains intact. Hence, although Jacobs and Biggs (2002b) record 99% of *Sclerocarya birrea* (marula) individuals with “extreme damage”, 78% of these were re-sprouting (“coppicing”). Furthermore, browsing can stimulate rapid regrowth by reducing intershoot competition for nutrients (du Toit *et al*. 1990), for example Mwalyosi (1990) records 59.7 cm annual growth of elephant-utilized *Acacia tortilis* in the absence of fire. This facilitates overall resilience of woodland, so that woody cover can increase even with elephant densities over 1 km^{-2} (Mapaure and Campbell 2002); interacting factors such as fire or browsing, however, can impede this resilience (Norton-Griffiths 1979).

Jachmann and Bell (1985) note that elephants capitalize on the strong coppicing ability of damaged plants to maintain selected tree species at optimal height for browsing, while allowing non-selected species to grow to canopy height. A striking example of resilience is found in mopane *Colophospermum mopane*, which forms almost monospecific communities where it occurs (Anderson and Walker 1974) and is highly selected by elephants (Williamson 1975, Ben-Shahar 1996b, Tafangenyasha 1997). Coppiced mopane buds early, and continues to produce accessible nutritious leaves even when heavily browsed (Styles and Skinner 2000); Lewis (1991), Mapaure and Mhlanga (2000) and Smallie and O’Connor (2000) found that elephants selectively utilized mopane plants that had coppiced after previous utilization.

Vigorous growth ability can compensate for heavy elephant impacts (e.g. *Acacia tortilis*, Mwalyosi 1990), particularly in wet years (Mosugelo *et al.* 2002). Guy (1989) concludes that woodlands in Sengwa Wildlife Research Area, Zimbabwe, can continue supporting 0.67 elephants km^{-2} as woody production exceeds elephant damage (although with a concomitant shift towards unpalatable, fire-resistant species). Leuthold (1996) documents increase of trees and shrubs in 76% of study sites in Tsavo National Park, Kenya, following an 80% reduction in the elephant population due to ivory poaching, the regeneration fuelled by long-lived seedbanks (>20 years) or zoodispersal. In Sengwa Wildlife Research Area, Zimbabwe, woodland recovery followed a reduction in fire frequency combined with a reduction in elephant density from culling and poaching (Mapaure and Campbell 2002). Ben-Shahar's (1996a) logistic model with constant rate of biomass removal by elephants predicts a "complete regain" of *C. mopane* biomass in northern Botswana within 10 years if elephant browsing were halted, but Pellew's (1983) height-structured model suggests management efforts should be concentrated more on encouraging regeneration (by limiting giraffe and fire effects) rather than limiting elephant-induced mortality.

Patterns of vegetation change

In concert with environmental factors, elephants can nonetheless precipitate declines in tree populations or marked changes in community composition. For example, Swanepoel and Swanepoel (1986) report baobab *Adansonia digitata* mortality of 15.5% over 6 months at an elephant density of 2 km^{-2} in the Zambezi Valley, Zimbabwe and Field (1971) reports a yearly decline in large trees of 14.6% in the Queen Elizabeth

National Park, Uganda, as the elephant density approached 1.7 km^{-2}. Marked declines can occur even at lower elephant densities. A sudden increase of elephant density to 0.135 per km^2 in Serengeti National Park, Tanzania, led to a decline of large trees at an annual rate of 6% (Lamprey *et al.* 1967). Figures for overall woodland reduction can mask more serious rates of individual species decline; for example, Field and Ross (1976) record a 1.6-1.8% overall loss of trees from Kidepo Valley National Park, Uganda, in 20 years, while *Acacia gerrardii* declined by 23% in 3 years.

Palatable species such *Acacia tortilis, A. xanthophloea* (Ruess and Halter 1990), *A. dudgeoni* (Jachmann and Croes 1991), *Brachystegia boehmii* (Guy 1989) *Colophospermum mopane* (Tafangenyasha 1997), *Commiphora* spp and the baobab, *Adansonia digitata* (Leuthold 1996) have declined while less preferred species (e.g. *Julbernardia globiflora* (Guy 1989); see also Jachmann and Croes 1991) or disturbance-tolerant species such as *Lonchocarpus laxiflorus* (Buechner and Dawkins 1961) and *Combretum mossambicense* (Anderson and Walker 1974, see also Simpson 1978) increase. The nature and extent of species change also depends on habitat type (Anderson and Walker 1974, Guy 1981).

Elephant utilization can alter the vertical structure of the woody plant community, commonly manifested as reduced tree density and increased shrub density (Leuthold 1977, Guy 1989). For example, Pellew (1983) records a reduction in the proportion of mature *Acacia tortilis* (>6m in height) in the Serengeti National Park, Tanzania, from 48% to 3% of the population between 1971 and 1978, by which time individuals below 3m in height comprised 94% of the population. As mentioned above continued browsing may trap plants in more accessible size-classes (Jachmann and Bell 1985, Mapaure and

Mhlanga 2000), although Lewis (1991) argues that such shrublands are unstable, prone to crashes when nutrients are eventually depleted under persistent elephant utilization. Others have noted little structural change even with pronounced impacts (Jachmann and Croes 1991, Weyerhaeuser 1995), and Mwalyosi (1990) reports selective browsing for *Acacia tortilis* shrubs in Lake Manyara National Park, Tanzania, effecting a shift towards an older population structure.

Intensity of elephant habitat use and the emergent spatial patterns of change in vegetation, reflect the distribution of elephants across the heterogeneous savanna landscape (van Wyk and Fairall 1969, Thomson 1975, Swanepoel and Swanepoel 1986, Steyn and Stalmans 2001). Absolute elephant density can thus be a "relatively meaningless" guide to expected outcomes (Steyn and Stalmans 2001; see also Anderson and Walker 1974), while even seemingly identical areas can experience very different impacts (Duffy *et al.* 2002). Elephants have been reported to move up to 80km in response to localized rainfall (Leuthold and Sale 1973) and, as mentioned above, available water can concentrate elephant impacts (van Wyk and Fairall 1969, Laws 1970, Swanepoel and Swanepoel 1986, Pamo and Tchamba 2001), as can localized nutrient-rich soil in rugged terrain (Nellemann *et al*. 2002).

Spatial distribution of tree use can be contagious, with preferred and/or fruiting trees forming focal points for elephant damage (Lamprey *et al.* 1967, Croze 1974b, Mwalyosi 1987, Calenge *et al.* 2002). In the Kruger National Park, South Africa, an enclosure to protect the roan *Hippotragus equines* population has also served as an incidental elephant-free refuge for the marula, *Sclerocarya birrea* (Jacobs and Biggs 2002a).

Effects on biodiversity

Elephants play an important role in savanna ecology, especially with regard to nutrient cycling, gap formation, and seed dispersal (Lewis 1987a, Owen-Smith 1988). The consequences of elephants' presence in the ecosystem (or under semi-artificial conditions such as in fenced reserves) may therefore have implications, both positive and negative, for biodiversity. For example Anderson and Coe's (1974) study of elephant dung demonstrates its use as food for baboons and birds but mainly for both adult and larval beetles (and thus also as an oviposition site), with an estimated 16,000 beetle individuals removing 1.5kg of dung in two hours. Elephants facilitate the dispersal and germination of fruit-bearing trees. A notable case is the marula, *Sclerocarya birrea*, the fruit of which is highly selected by elephants, its germination greatly enhanced by passage through the elephant gut and deposition in dung (Lewis 1987a). Structural changes in woodland can benefit smaller browsers by increasing availability of food and cover (van Wyk and Fairall 1969, Lawton and Gough 1970). Mwalyosi (1990) also argues that canopy-thinning of *Acacia tortilis* woodland by elephants is a positive phenomenon, increasing gap dynamics, landscape diversity, and browse productivity.

Heavily utilized areas, however, have been shown to have reduced biodiversity in terms of birds and ants (Cumming *et al.* 1997). Lock (1993) relates increases in woody plant cover and species diversity to a decline in elephant populations between 1970 and 1988 in Queen Elizabeth National Park, Uganda. Field (1971) reports a 46.3% increase in elephant numbers over 15 years, causing a 36.9% decrease in buffalo (*Syncerus caffer*) as tree cover declined and the resultant drop in soil moisture allowed short palatable grasses such as *Panicum maximum* to be replaced by unpalatable, disturbance-tolerant

Hyparrhenia filipendula. Musgrave and Compton (1997), however, found no detrimental elephant effects on the insect community, with plants which were browsed by elephants showing higher mean levels of insect herbivory than those not utilized by elephants. High elephant densities in northern Botswana were found to substantially change bird species composition without a dramatic loss of species richness (Herremans 1995); however, woodland changes favored migrant birds over native Afrotropical species.

Elephants may also impact other herbivores more directly by competing for food; for example Napier Bax and Sheldrick (1963) attribute the death "in large numbers" of black rhinoceros *Diceros bicornis* to their being outcompeted for browse in a 1961 drought. Field and Ross (1976) found that elephant and giraffe diets converged as the dry season progressed to share the same important species. Analyzing data from 31 ecosystems in eastern and southern Africa, Fritz *et al.* (2002) found that abundance of megaherbivores such as elephants lowers the abundance of mesobrowsers and meso-mixed-feeders, but not mesograzers.

Implications for conservation management

While it remains unknown how elephants and plants coexisted historically, theories have concentrated on the "compression" hypothesis (Lamprey *et al.* 1967, Lewis 1986), the existence of multiple stable states (Dublin *et al.* 1990, Dublin 1995), or long-term cycles reminiscent of predator-prey dynamics (Caughley 1976). Lewis (1991) emphasized the interaction of soil type with elephant-vegetation dynamics. Sustainable elephant densities or carrying capacities have been proposed within the range of 0.3-0.6

individuals per km^2 (Glover 1963, van Wyk and Fairall 1969, Fowler and Smith 1973, Jachmann and Croes 1991), while Ben-Shahar (1996b) predicts mopane woodland withstanding elephant densities of up to 11 per km^2.

The creation of zones and elephant-free reserves within parks has been suggested to protect species and habitats of concern (Lawton and Gough 1970, Whyte *et al.* 1999, Johnson *et al.*1999). Barnes (1983a) discusses the relative benefits of management options to control the effects of elephants impacts, viz. manipulating water supply, fire control, reducing human pressure, culling, laissez-faire, and even poaching as an unauthorized means of elephant population control. While culling is certainly an effective means of elephant population control, it can have variable results: Cumming (1981) describes a culling program in Sebungwe region of Zimbabwe targeted to selectively protect particular vegetation zones, which was only partially successful, although culling in Gonarezhou National Park led to recovery of the woody vegetation. Random culling can increase group size, ultimately causing more damage (e.g. 500 elephants utilizing an area over 10 days can have much greater impacts than 50 elephants over 100 days; Laws 1970). Barnes (1983a) employed simple, deterministic models to suggest that large culls were needed to stabilize or reverse woody plant decline in Ruaha National Park, Tanzania. He notes, however, that the benefit/cost ratio of culling declines rapidly with time, the situation often being already irredeemable when the problem is first noted, although controlling immigration also can add to the effectiveness of culling (Barnes 1983a).

Fire suppression is often thought a necessary accessory to elephant population control (Glover 1963, Thomson 1975, Pellew 1983), as it facilitates the regeneration of damaged individuals and increase in browsing fauna (van Wyk and Fairall 1969). Lewis (1987b) found that elephants move out of burned areas in the early dry season due to the reduction in grass forage and suggests early dry-season burning as a means of repelling elephants from heavily impacted sites. A number of authors have emphasized the need for consideration of ecosystem complexity and varying species responses to any management policies implemented (Barnes 1983a, Pellew 1983, Lewis 1987b).

This dissertation aims not to test hypotheses of elephant-vegetation interactions but rather to produce realistic savanna models (dealt with in detail in Chapter 2) capable of providing insight into community-level changes in woody plants subject to elephant impacts. We simulate savanna dynamics by including species of woody plant and grass and explore their coexistence and community-level responses to changes in assumptions or parameters. We pay particular attention to variations in growth, fecundity and survival rates of the woody plant species, and their interaction with rainfall, fire and elephants. The research is driven by the formulation of a new elephant management plan (Whyte *et al.* 1999) to address concerns over elephant impacts in Kruger National Park, South Africa (Trollope *et al.* 1998). In the absence of detailed vegetation demographic data for Kruger Park, the models presented in subsequent chapters are generalized and applicable to most African savannas when suitable data become available.

Chapter Two

An African savanna model:

effects of tree demography, rainfall, fire and elephants.

Peter W. J. Baxter and Wayne M. Getz.

Abstract

Recent concerns over elephant impacts to woody plants in southern African savannas have highlighted a possible loss of species diversity, including the potential loss of associated fauna due to a reduction in both structural and species diversity of trees. We present a grid-based model of elephant-savanna dynamics, which differs from previous elephant-vegetation models by accounting for woody demographics, tree-grass interactions, stochastic environmental variables (fire and rainfall) and spatial contagion of fire and tree recruitment. The model output provides three-dimensional information on the long-term trajectory of a savanna by detailing height structure as well as spatial pattern. The vegetation component of the model produces long-term tree-grass coexistence and the emergent fire frequencies match those reported for southern African savannas. The tree-grass balance of the model is more sensitive to changes in rainfall conditions and woody growth rates while less sensitive to fire regime.

Introducing elephants into this model savanna had the expected effect of reducing woody plant cover, mainly via increased adult tree mortality, although at an elephant density of 1.0 per square kilometer, 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 utilization, mimicking a more resilient tree species, mitigated the detrimental effect of elephants on the woody population to some extent. (2) Coupling germination success (increased seedling recruitment) to elephant browsing patterns was even more resilient, and (3) a faster-growing woody component allowed some woody plant persistence for at least a century at a density of three elephants km^{-2}. Given the lack of data regarding woody plant species in southern African savannas,

managers should be cognizant of different tree species attributes when considering whether or not to act on perceived elephant threats to vegetation.

Introduction

Savannas occupy 54% of southern Africa and 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 and herbivory (Scholes and Walker 1993, Solbrig *et al*. 1996, Rutherford 1997, Scholes 1997).

The reasons for coexistence of trees and grasses in savannas have been debated for decades. Trees impede grass domination through rainfall interception, litter accumulation, shading or rooting-zone competition, and in turn grasses can negatively impact upon tree populations by preventing seedling recruitment and providing fuel for fire, thus inducing mortality or suppression of woody individuals (Scholes and Archer 1997). Walter (1971) formulated the first coexistence hypothesis, based on moisture availability with reference to rooting-depth. He proposed that as rainfall increases, grasslands undergo transition to woodlands, because the availability of water in the lower soil horizons allows trees to establish deeper roots and survive drought conditions. The hypothesis was supported by Walker and Noy-Meir's (1982) simple model, which demonstrated a single stable equilibrium under those assumptions. Further conceptual models built in soil moisture and other physical properties of soil, as well as nutrient availability, fire and herbivory (see Belsky (1990) for a concise review). Field studies have since cast doubt on the existence of separate niches in the rhizosphere (Knoop and

Walker 1985, Scholes and Walker 1993, Belsky 1994). Savannas are now seen as inherently stable but non-equilibrial, kept in a state of tree-grass coexistence by disturbances such as fire, drought and herbivory (Scholes and Walker 1993, Higgins *et al*. 2000, Jeltsch *et al*. 2000), and thus not predictable by a simple model (Scholes and Archer 1997, Jeltsch *et al*. 2000). The recent work of Higgins *et al*. (2000), for example, shows that disturbance, translating into opportunistic recruitment events, may play the critical role in maintaining tree-grass coexistence, and Hochberg *et al*. (1994) argued that a patchy distribution of small, internally oscillatory sub-systems of trees may be sufficient to secure the persistence of both trees and grasses. Van Langevelde *et al*. (2003) have shown, however, that a deterministic model incorporating infiltration rates, fire and herbivory can produce realistic savanna behavior. Jeltsch *et al*. (2000) urged a shift in focus to examine the mechanisms that may buffer the coexistence condition at the boundaries of change into tropical forest or grassland, i.e., what mechanisms may prevent the *non*-existence of savannas.

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 1996a and b, Duffy *et al*. 1999, 2000), it has been argued that non-spatial models are inadequate to describe a system defined by heterogeneous vegetation (Jeltsch *et al*. 2000). Recent attempts 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). While some models only achieved tree-grass coexistence within narrow or extreme parameter ranges (Menaut *et al*. 1990, Jeltsch *et al*. 1996), others have found that, for example, widespread seed availability assists tree persistence, and spatial attributes of reproduction (dispersal, clumping) can further enhance the likelihood of coexistence (Hochberg *et al*. 1994, Jeltsch *et al*. 1998).

Most of these spatial vegetation models have sought to explore coexistence processes by modeling very localized plant environments, and so have been individual-based models (IBMs), or grid-based approximations to IBMs, operating at a spatial resolution of 0.3-5.0m 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). Our aim in this paper is to produce a model savanna sufficiently broad in scale to realistically and usefully explore elephant impacts while still capturing the essential underlying vegetation processes, rather than to investigate mechanisms for tree-grass coexistence. Therefore we eschew IBMs in favor of a set of interrelated population models, each representing the dynamical processes occurring in a one-hectare cell of a one-square-kilometer block of 100 such cells. Such blocks can then be scaled up to model even larger areas in which the basic environmental drivers may vary from block to block.

Elephants have major ecological effects on savanna dynamics, playing significant roles in nutrient cycling, seed dispersal and the provision of space for new germinants (Lewis 1987a, 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 however lead to a decrease in other species: it is acknowledged that the present spatial restriction ("compression") placed upon elephant populations by fenced nature reserves and/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 1983b), or be followed by a transition to shrubland due to the prevention, by elephants and/or other browsers, of tree recruitment (Leuthold 1977, Pellew 1983, Jachmann and Bell 1985, Smallie and O'Connor 2000).

It is not known how elephant populations historically coexisted with today's extant woody plant species, and the dynamic properties governing the elephant-woodland interaction are poorly understood. Traditionally their coexistence was thought to be equilibrial (Lawton and Gough 1970, Fowler and Smith 1973). Caughley (1976) applied a predator-prey model to the elephant-tree interaction and found that the system could be cyclic, with an oscillatory period of approximately 200 years. Laws (1970) reasoned that compression would disrupt any natural cyclic behavior, while a recent parameterization of the Caughley model (Duffy *et al*. 1999) has reasserted the possibility of a fixed-point equilibrium. Others have proposed the existence of multiple equilibria (Dublin *et al*. 1990, Dublin 1995), with fire and other herbivores acting as other major factors influencing vegetation state.

High levels of elephant utilization may compromise the viability of some woody plant populations (Swanepoel and Swanepoel 1986), resulting in community changes coupled with a possible loss of species diversity (Cumming *et al*. 1997) and/or structural diversity (Trollope *et al*. 1998). Concern has been expressed over further ramifications for other fauna. In the Zambezi Valley, Zimbabwe, Cumming *et al.* (1997) documented lower species richness of birds, ants and "total animals" (ants, bats, birds and mantises) in elephant-impacted sites than in non-impacted sites. Herremans (1995) recorded substantial changes in bird species composition in northern Botswana due to habitat modification by elephants, but noted that bird species richness may be increased if elephant impacts remained patchy. Rare antelope species such as bushbuck (*Tragelaphus scriptus*) are also adversely affected by the reduction in cover and quality browse (Addy 1993).

While elephant utilization of woody plants may leave the species composition of woodlands unchanged, the structural composition may be considerably altered (Jachmann and Bell 1985). Some models of elephant-vegetation interactions ignored this vertical structuring of the woody community (Caughley 1976, Duffy *et al*. 1999, Duffy *et al*. 2000). Others (Pellew 1983, Dublin *et al*. 1990, Ben-Shahar 1996b) 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, shrubland and grassland states, as driven by elephants, fire and rainfall levels, however 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).

The Model

I. Model Structure

Any modeling exercise requires decisions as to which is the appropriate scale of resolution to encompass enough necessary information without becoming intractable (Starfield and Bleloch 1986). We chose a spatial extent of 1 km^2 to enable management issues to be addressed, with a spatial grain of one hectare to maintain a reasonable scale for modeling plant competition and fire events, while assuming uniform water and nutrient distribution within our 1 km^2 area. The timescale of models requires similar trade-offs: the timescale of vegetation changes usually exceeds management time horizons (Weber *et al*. 1998) and this is particularly the case when dealing with long-lived organisms such as trees and elephants. Using a time-step of 6 months (to reflect the strong seasonality characteristic of savannas; Solbrig *et al*. 1996), we simulated the vegetation-only component of our model for 500 years to investigate the effects of parameter combinations on long-term coexistence. For the combined elephant-savanna model, we reduce the timescale to 100 years after elephant introduction, to better reflect the shorter-term concerns of park managers striving to maintain biodiversity. 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). Our model is easily extended to consider several co-dominant species of trees, as well as the question of persistence of rare tree species. While we attempted to model our savanna on the Kruger National Park in South Africa, lack of data, on woody plants in particular, resulted in our employing data from African savannas in general.

The model habitat.

A representative 1 km^2 patch of a model savanna ecosystem was generated by linking together 100 one-hectare cells in a 10×10 grid. Hochberg *et al*. (1994) found that this spatial extent is sufficient to produce smooth and predictable dynamics. One-hectare cells are denoted below with the index $x = 1, \ldots, 100$ and only a single 1 km^2 patch is considered. With appropriate computing power, the model is easily extended to cover many 1 km^2 patches, each allowed to vary with respect to underlying water and nutrient regimes and including linkages due to fire contagion and seed dispersal. 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 (see below). 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: in the field this assumption may mimic the presence of roads or boundary fences so we do not employ a torus or a reflecting boundary; sensitivity testing of this assumption revealed no substantial difference in results). Moisture availability (as driven by rainfall in the model) and nutrient availability are both major influences on savanna dynamics (Belsky 1990, Scholes and Archer 1997). We assume these factors are homogeneous across the grid and are implicitly incorporated in model parameter values. Future applications of our model at larger spatial scales will vary parameter values across grid cells to reflect heterogeneity in moisture and nutrient availability associated with different soil types. Other impacts not explicitly modeled include other (non-elephant) herbivores (which may act synergistically or antagonistically with elephant impact; Pellew 1983, Lewis 1987a, Ben-Shahar 1993), and other environmental factors such as frost (Scholes and Walker 1993), lightning, wind-throw, disease (Spinage and Guinness 1971, Croze 1974b, Ben-Shahar 1993) and insects (Scholes and Walker 1993, Jacobs 2001).

Time.

The model is simulated using discrete time-steps (denoted by t) of half-years, reflecting annual wet and dry seasons of six months each. Initial conditions are given by $t=0$, and as the model starts in a wet season, the passage of any year can be represented by a wet season commencing at an even value of t followed by a dry season commencing at an odd value of t.

Vegetation structure.

As noted above, structural diversity is an important component of savanna biodiversity. Therefore it is appropriate to develop demographic models emphasizing changes and transitions in the vertical woody structure. Nine stage classes of tree, the i-th of which (in cell x at time t) has number of individuals $w_{x,i}(t)$ ($i = 1, 2, \ldots, 9$), are modeled, based on height. Although woody vegetation attributes are often measured using above-ground biomass, canopy cover or stem diameter, elephant utilization of woody plants is often measured with reference to tree height. We do not explicitly model seed production, survival and germination but rather use potential seedlings per tree to derive an expression for the first woody plant class $w_{x,1}(t)$, in terms of the state of other variables at earlier time steps. Further, we define a tenth vegetation class, $w_{x,10}(t)$, denoting the grass biomass (measured in kg) in cell x at time t. These classes may be more concisely represented by the column vector

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

where ' denotes the transpose of a vector. The nine woody stage classes in turn represent four broader classes (“metaclasses”): seedlings are <15cm tall ($i = 1$), four sapling classes ($i = 2, \ldots, 5$) are <1m tall (individuals advancing automatically between these subject to sufficient rainfall), two shrub-sized classes of 1-2m ($i = 6$) and 2-3m ($i = 7$; i.e., up to fire escape height; Pellew 1983), and two tree classes of 3-5m ($i = 8$) and >5m ($i = 9$; beyond browsing height). An individual in each of these metaclasses is assumed to control a resource area of 0.01, 1, 9 and 25 m^2, respectively (after Kiker 1998) (Note 1 $m^2 = 10^{-4}$ ha). Area covered by grass is also tracked, and the area of cell x covered at time t by individuals in class i is given by $a_{x,i}(t)$, $i = 1, \ldots, 10$.

Vegetation vital rates.

Plant growth depends on annual rainfall (adjusted for vegetation type) and competition. Competition occurs within and between woody plants and grass and is modeled within each cell on a per-area basis, assuming each category controls a fixed area of “resource space." Growth is therefore constrained by the amount of available resource space for expansion (Smith and Goodman 1986, Shackleton 1997).

Plant mortality depends on rainfall, fire and herbivory by elephants. A certain proportion of woody plants whose above-ground tissue is destroyed by fire (or elephant browsing) can resprout, due to below-ground tissue storage. These are modeled as reverting to the previous stage-class. Model sensitivity to this resprouting parameter is tested as savanna plants show much variation in their coppicing ability (Gignoux *et al.* 1997).

Elephant population.

The model simulates only one representative square kilometer, so that it does not make sense to couple the modeled vegetation to elephant population dynamics. Rather, we assess the impact of elephants visiting our one representative square kilometer: that is, elephants are dealt with as a time-varying input into the model, and different scenarios may be analyzed. In the context of modeling impacts on vegetation in a park fenced to contain elephants, the model can include a description of elephant demography. In this paper we limit our analysis to various constant elephant "stocking densities" (as did Pellew 1983, Starfield *et al.* 1993 and Barnes 1994).

Elephant impacts.

In southern Africa, elephants transfer the focus of their foraging from grass to browse during the dry season, the timing of this shift depending largely on rainfall which determines the amount of quality grazing remaining at the end of the wet season (Field

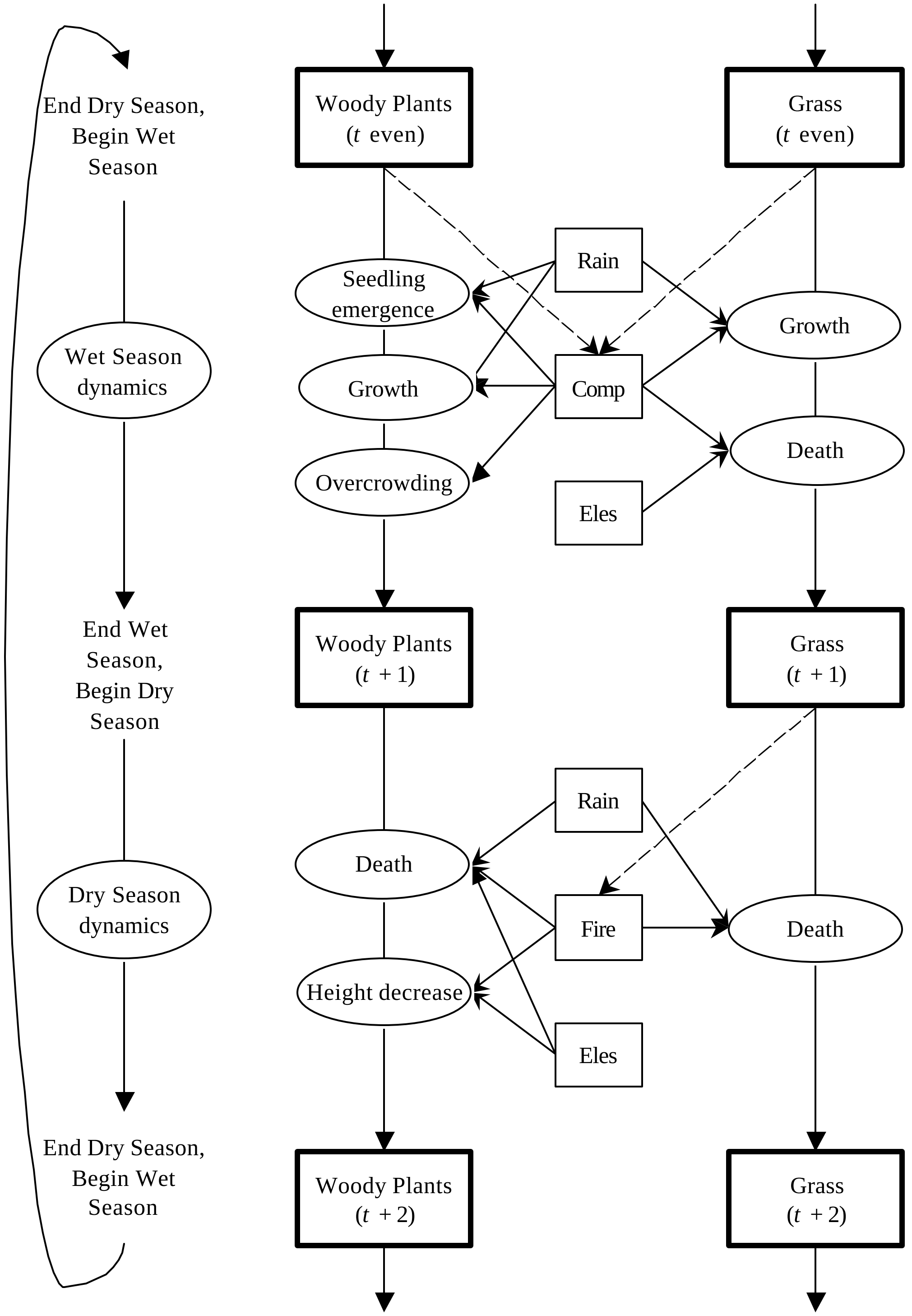
1971). In this model, elephants are assumed to graze exclusively in the wet season and to browse exclusively in the dry season (Guy 1976, Meissner *et al*. 1990) although a more general feeding pattern can be introduced when biological data becomes available to justify the additional complexity in the model. Pushing-over and uprooting of trees improves food availability to elephants in the dry season (Jachmann and Bell 1985). Kalemera (1989) found that elephant dry-season foraging in Lake Manyara National Park, Tanzania, consisted mainly of browsing, with grazing predominating at the lakeshore where woody plants are scarce. Jarman (1971), studying herbivore diets at Lake Kariba, in present-day Zimbabwe, found that elephant grazing, although generally low, was concentrated exclusively in the wet season.

II. Model Procedure/Implementation

(See Box 1 for a flow-chart depicting the model procedure, described in detail below.)

Rainfall.

The southern African lowveld region experiences two seasons, wet and dry. (Solbrig *et al*. (1996) note that rainfall seasonality is the sole constant climate characteristic of tropical savannas.) We incorporate this seasonality by iterating our model using 6-month time steps and we assume that each year's rainfall falls entirely in the wet season. In southern Africa, rainfall also follows a pronounced "quasi 20-year oscillation" of relatively wet and dry periods (Tyson and Dyer 1978, Gertenbach 1980). Thus we model



Box 1. Schematic flowchart of the model. Note that rainfall ("Rain") occurs yearly (in the wet season), but affects both wet and dry season dynamics. Competition ("Comp") is modeled as competition for space; see text for details. Grass "death" refers to senescence and burning of above-ground tissue and uprooting of tufts by elephants ("Eles").

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 (i.e., changes in biological rates as a function of relative rainfall levels are scaled to long term average rates), although our model could just as easily be run using real rainfall time series applicable to any region being specifically modeled in future studies. Specifically, we set relative rainfall $r(t)$ to be:

$$
\begin{aligned}
r(t) &= \max\left(0, 1 + h\sin\frac{p(t+1)}{2w} + z(t)\right), && t \text{ even (start of wet season)},\\
r(t) &= 0, && t \text{ odd (start of dry season)} \quad ,
\end{aligned}
$$

where h is the amplitude (relative to the long-term mean) of wet-dry cycles of period w years (doubled above to take our 6-monthly seasonal time step into account), and $z(t)$ is a stochastic variable accounting for interannual variation around these underlying cycles. We assume that for each even t the value of $z(t)$ is drawn from the same distribution (i.e., $z(t)$ is i.i.d); see the subsection on stochasticity below for further details. 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). Obviously if we string together thousands of 1 km^2 plots to represent a more extensive area then rainfall can vary from plot to plot with a suitable correlation between neighboring plots.

Wet season dynamics.

Wet season woody plant dynamics.

All growth and reproduction is assumed to occur in the rainy season (see Box 1). The change in the woody population during a wet season starting from time t is given by:

$$w_{x,i}(t+1) = \left(g_{x,i-1}w_{x,i-1}(t) + \left(1 - g_{x,i}\right)w_{x,i}(t)\right)\left(1 - h_{x,i}(t)\right), \qquad i = 2, 3, \ldots, 9 \ ,$$

where $w_{x,i}(t)$ represents the number of individuals in cell x of woody class i at the beginning of the wet season, $h_{x,i}(t)$ is loss of individuals due to encroachment by the growing and expansion of larger individuals, and $g_{x,i-1}$ is the transition rate from class i–1 to class i for that cell and season. In general, $g_{x,i-1}$ will depend not only on t, but also on the current vegetation $\mathbf{w}_x(t)$ as well as on rainfall: i.e., $g_{x,i-1} = g_{x,i-1}(t, \mathbf{w}_x, r)$. The seedling class ($i$ = 1) is given by

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

where $c_x(t)$ is the expected number of new seedlings emerging in cell x at time t, and $g_{x,0}$ is the proportion of these which successfully recruit (see below; the zero-subscript refers to a notional class of presumptive seedlings). The seed bank is not explicitly modeled (Menaut *et al*. 1990), rather the expected number of emerging seedlings depends on the adult tree population at the end of the previous wet season (i.e., which ran from t–2 to t–1) and is given by

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

where m is the fecundity of mature trees (classes 8 and 9; individuals <3m in height are assumed to be non-reproductive, and we make no distinction between seed-production of the two adult classes $i = 8$ and $i = 9$). The dispersal parameter d represents the proportion of seedlings parented by individual trees from the four neighboring cells. If applied to a specific site this equation could be modified to account for a more complex, and even directional, dispersal gradient.

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

$$g_{x,i}(t) = \min\,(c_{x,i}(t),\; l_{x,i}(t)), \qquad\qquad 0 \le i \le 8,$$

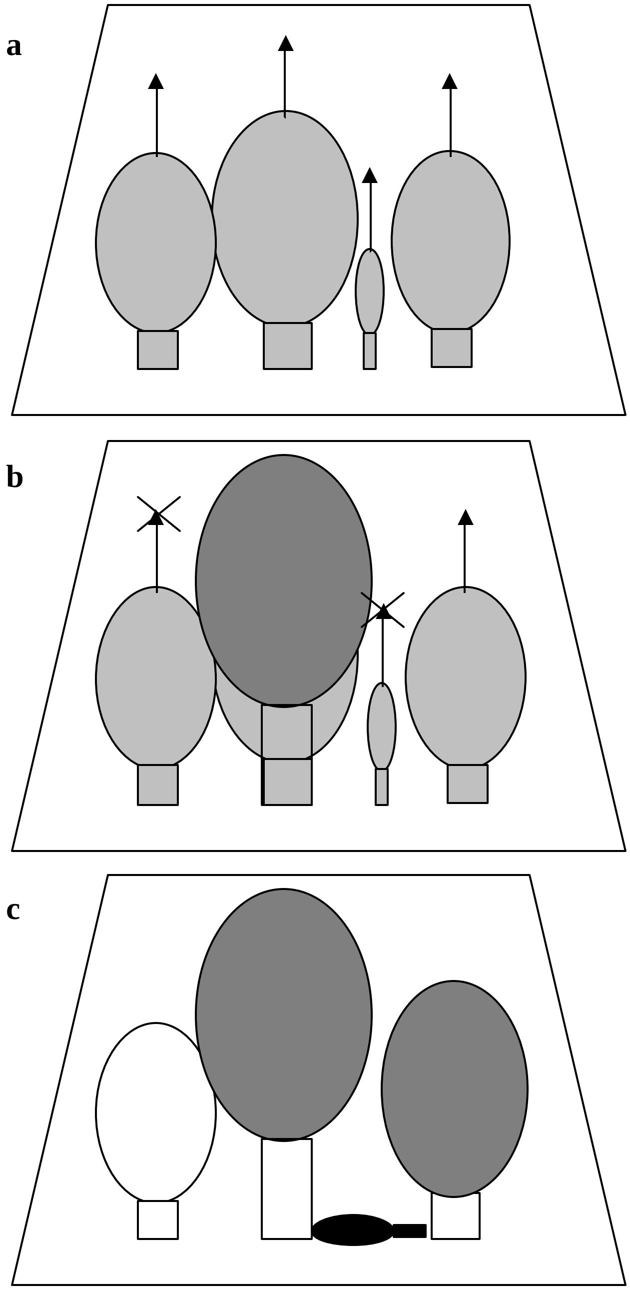
where $c_{x,i}(t)$ represents the underlying growth rate adjusted for competition and rainfall, and $l_{x,i}(\mathrm{t})$ is the maximum proportion of class i that can grow to class i+1 without causing the cell x to overfill. The growth algorithm is schematically depicted in Box 2. For seedling establishment, the proportion recruited is given by

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

and for plants already established ($i \ge 1$), the adjusted growth rate is given by

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

where g_i is the underlying growth rate from class i to i+1 and $f_{x,i}(\mathbf{w}_x(t))$ is the proportion of those overcoming competition for space and resources. Within the sapling classes, growth is assumed to be automatic, so that $f_{x,i}(t) = 1$ for $i = 2, 3, 4$. For other woody



Box 2: Woody plant growth algorithm

(a) schematically depicts the woody component of a section of the savanna at the start of the wet season. From left to right we have classes i = 6, 7, 4 and 6, i.e., three shrubs and a sapling. These strive to advance to classes 7, 8, 5 and 7 respectively, (i.e., one tree and three shrubs), and would do so at rate $g(i)$ if there was no crowding, and average rainfall.

(b) shows the effect of the parameter l: priority is given to the larger individuals and because the i=7 shrub grows into a tree (i=8), the growth of some other individuals is reduced. This is done on a per-area basis.

(c) shows the implementation of the parameter h: if the area is still overcrowded then self-thinning is induced. Priority is again given to the more mature individuals, so that in this case the sapling is killed.

classes ($i \leq 9$), $f_{x,i}(t)$ is defined below. First, recall that we define "resource areas," α_i, in terms of the area (in hectares) occupied by one individual of class i. Then let $a_{x,i}(t)$ represent the total proportion of area (in cell x at time t) controlled by all individuals of class i, i.e.,

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

Calculation of $a_{x,10}(t)$, the area covered by grass, is elaborated in the subsection on wet season grass dynamics below. Next we consider competition for light, nutrients and water, and calculate $f_{x,i}(t)$, the "competition coefficient" (*sensu* Getz and Haight 1989). Little is known about inter-plant competition in savannas (Scholes and Archer 1997, Higgins *et al*. 2000). Smith and Goodman (1986) demonstrated strong effects of nearest-neighbor distance on canopy cover and growth of savanna trees. Thus we approximate competitive effects by aggregating on a per-area basis:

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

$$f_{x,i}(t) = 1 - \sum_{j=i}^{9} a_{x,j}(t), \qquad \mathrm{i} = 5, 6, 7, 8.$$

Effectively, we assert that recruitment of seed (again employing the notional class $i = 0$) into seedlings, and of seedlings into saplings, will be limited by competition from existing seedlings, saplings, shrubs and grass. Growth of individuals in classes $i = 5, \ldots, 8$ (i.e., growth of saplings to shrubs, and so on up to mature trees) is assumed to be limited by competition from individuals in equal or higher stage classes (Menaut *et al*. 1990; also see Getz and Haight (1989) for tree classes with competition treated by canopy cover).

The expansion limiting coefficients, $l_{x,i}$, come into play in situations of strong woody dominance coupled with excellent growth conditions. Because we allow the more mature individuals to dominate, and thus grow in preference to smaller individuals, the coefficients $l_{x,i}$ involve projecting total possible recruitment and then reducing that recruitment, in order of trees, …, seedlings, in case of overflow (see Box 2). To derive the recruitment equations presented below, we have assumed that seedlings and saplings can grow under tree-canopies but that shrubs cannot. Thus, to grow into seedlings, seeds can use bare ground or space under trees but not under existing seedlings, saplings, shrubs or grass. Similarly, seedlings can only expand under trees or over bare ground to grow into saplings, saplings can only expand over seedlings or grass to grow into shrubs, and the expansion space available for the shrub class $i = 7$ to grow into trees equals all but the existing trees. In the case of growth of shrubs to trees, $l_{x,7}$ is simply the available area for new trees divided by $a_8 w_{x,7}(t)$, the area which would be taken up by shrubs currently in class $i = 7$, were they all to become trees (i.e., if the growth rate equaled 1). As we assume mature trees can dominate over all other classes, the available area for recruitment is given by total area, less area already occupied by adult trees, giving

$$l_{x,7}(t) = \frac{1 - a_{x,8}(t) - a_{x,9}(t)}{a_8 w_{x,7}(t)}.$$

This allows us to calculate $g_{x,7}(t)$ and thus determine the actual number of recruits to the tree stage and then proceed to calculate the available space for sapling recruitment to shrubs and so on (dropping the x and t arguments for convenience):

$$l_5 = \frac{1 - a_6 - a_7(1 - g_7)w_7 - a_8 g_7 w_7 - a_8 - a_9}{a_6 w_5},$$

$$l_1 = \frac{1 - a_2 - a_3 - a_4 - a_5(1 - g_5)w_5 - a_6 g_5 w_5 - a_6 - a_7(1 - g_7)w_7}{a_2 w_1},$$

$$l_0 = \frac{1 - a_1(1 - g_1)w_1 - a_2 g_1 w_1 - a_2 - a_3 - a_4 - a_5(1 - g_5)w_5 - a_6 g_5 w_5 - a_6 - a_7(1 - g_7)w_7 - a_{10}}{a_1 c(t)}.$$

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

Any given level of growth, g_i, may also entail shading out other plants in the same or lower height class and so we introduce h_i as a “crowding coefficient,” representing the proportion of plants overcrowded by the individuals growing from class i to i+1 (see Box 2). Again using per-area aggregation, we set h_i as the ratio of the extra area now occupied by the grown individuals (i.e., area encroached over), to the total area occupied by those plants which can be crowded out by their growth, i.e., the area which had been available for the expansion of the growing individuals (the numerator of the l_i above). Since we assume that crowding of shrubs is experienced equally by both shrub classes, and likewise for the sapling classes, this gives us (again space subscripts and time arguments are understood):

$$h_6 = h_7 = \frac{(a_8 - a_7) g_7 w_7}{1 - a_8 - a_9},$$

$$h_2 = h_3 = h_4 = h_5 = \frac{(a_6 - a_5) g_5 w_5}{1 - a_6 - a_7 (1 - g_7) w_7 - a_8 g_7 w_7 - a_8 - a_9},$$

$$h_1 = \frac{(a_2 - a_1) g_1 w_1}{1 - a_2 - a_3 - a_4 - a_5 (1 - g_5) w_5 - a_6 g_5 w_5 - a_6 - a_7 (1 - g_7) w_7}.$$

Note that we don't need any crowding coefficient for recruitment to the seedling class as this growth just "encroaches" over bare ground. Also note that h_1 and h_5 are applied to crowding out the grass layer too (see below).

Wet season grass dynamics.

We also model wet season grass growth in terms of area covered and biomass. The area covered by grass is updated to account for changes in the woody vegetation cover (including woody growth during the wet season), reduced by the level of elephant grazing (it is assumed that elephants uproot whole grass tufts when grazing; Owen-Smith 1988, Kalemera 1989) and adjusted for rainfall amount:

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

where $u_{x,10}(t)$ represents the proportion of the grass in cell x grazed by elephant. As discussed above we reduce the grass area by the proportion of extra ground shaded out by individuals growing into the first sapling and shrub classes (i.e., entering classes $i = 2, 6$). Although we allow grass to occupy the sub-canopy space beneath adult trees in this model, Midgeley *et al.* (2001) have hypothesized that grass growing under adult acacias is more palatable, and is thus grazed down to such a level that its contribution to fuel for fires becomes insignificant. The area occupied by grass is rainfall-dependent as it is assumed that grass tufts expand or shrink in higher or lower rainfall conditions, which may be important in seedling recruitment dynamics.

The grass biomass then increases by the productivity of the area $a_{x,10}(t+1)$, adjusted for wet season senescence (Illius and O'Connor 2000) and for elephant grazing:

$$w_{x,10}(t+1) = s_{10}^{W} r(t)\left(1 - u_{x,10}(t)\right)\left(w_{x,10}(t) + g_{10} a_{x,10}(t+1)\right),$$

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

Elephant grazing

Elephants are assumed to visit each cell in proportion to the relative amount of grass biomass present. Let $l(t)$ be the elephant density (numbers per hectare) at time t and I_g be the elephant intake rate of grass in units of kg/elephant/wet-season. Then the elephant utilization of cell x is given by:

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

Note that we project grass biomass forward in time in the calculation of $u_{x,10}(t)$ to allow initial grass recovery from dry season burns, senescence etc.

Dry season dynamics.

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

$$w_{x,i}(t+1) = F_i(\mathbf{w}_x(t), s_i, r(t-1), l(t)), \qquad t \text{ odd},$$

where s_i represents the mean survival rate of woody class i, and recalling that $r(t–1)$ is the rainfall from the previous wet season and $l(t)$ is the density of elephants (number per hectare) at time t. Here 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.,

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

$$f_{\text{ele},i} \equiv f_{\text{ele},i}(\mathbf{w}_x(t), l(t), f_{\text{surv},i}),$$

$$F_i = f_{\text{fire},i} \equiv f_{\text{fire},i}(\mathbf{w}_x(t), f_{\text{ele},i}).$$

We now consider each of the functions $f_{\text{surv},i}$, $f_{\text{ele},i}$ and $f_{\text{fire},i}$ in turn.

Woody plant survival.

A certain proportion of subadult woody plants die, depending on the rainfall for that year. We also assume that mature trees are fairly resilient to short-term fluctuations in rainfall, but will experience increased mortality in droughts lasting more than two years (Scholes 1985):

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

$$f_{\text{surv},i}(r(t-1), s_i, w_{x,i}) = (s_i - m^r_{8-9} x(t)) w_{x,i}\ , \qquad \mathrm{i} = 8, 9.$$

where m^r_{8-9} is additional mortality experienced by mature trees in drought conditions, weighted for drought severity (calculated from a three-year running mean, i.e., through wet seasons at t–5, t–3 and t–1) using the function $x(t)$:

$$?(t) = \frac{k^z}{\left(\sum_{y=t-5}^{t} \frac{r(y)}{3} \right)^z + k^z}.$$

Given this form, we see that the function x maps the three-year mean relative rainfall to points on the interval [0, 1], where the parameter z describes the steepness of the drought response (cf. density response in Getz 1996), and the constant k is the value of the three-year mean which causes 50% of the additional drought-related mortality. Recall that $r(t) = 0$ for odd values of t (dry seasons) so that in the above summations $r(y) = 0$ for $y = t, t-2, t-4$.

Elephant browsing.

Jachmann and Bell (1985) found that in the Kasungu National Park, Malawi, the number of trees used by elephants increased with tree density (up to densities of 300 trees ha^{-1}). Elephants are thus assumed to browse in each cell, with the total browsing pressure in a cell depending on that cell's "attractiveness" (a preference-weighted sum of its woody plant availability) relative to the others'. Within each cell elephants browse on the different size-classes in proportion to each class's availability, with the exception of the tallest and shortest sizes (Croze 1974b). Lewis (1987a) also found that elephants tend not to browse seedlings, and in fact may make a positive contribution to recruitment by assisting in dispersal of drupes such as the marula, *Sclerocarya birrea*. Using the vector notation $\mathbf{w}_x(t)$ for each cell's woody structure, $\mathbf{f}_{\text{ele}}$ for the column vector $(f_{\text{ele},1}, f_{\text{ele},2}, \ldots, f_{\text{ele},9})'$, and employing $\mathbf{u}_x(t)$, an elephant-utilization vector for cell x (see below), we can express the effect of elephant browsing on the woody vegetation as:

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

where $\mathbf{U}_x(t)$ is a 9×9 diagonal matrix with the elements of utilization vector $\mathbf{u}_x(t)$ on the diagonal, $\mathbf{I}$ is the (9×9) identity matrix and $\mathbf{E}$ is an elephant-effect matrix mapping the rates of death and stunting resulting from elephant utilization.

The utilization profile of the vegetation within each cell is measured with the 9-element column vector $\mathbf{u}_x(t)$, which is composed of the elements $u_{x,i}(t)$, representing the proportion of each stage-class used. This is calculated as a weighted sum of the woody vegetation, with the perceived "preference-value" of each stage-class (v_i) providing the weights. As utilization of adult trees differs from that of size-classes <3m, we consider adult utilization separately from that of saplings and shrubs. We assume that within our square kilometer of interest, elephants allocate their foraging effort between cells in proportion $p_x(t)$ to the cells' perceived attractiveness, and that within each cell they then forage on each stage-class in proportion $p'_{x,i}(t)$ to each stage class's presence (also weighted by the preference value), where

$$p_x(t) = \frac{\sum_{k=1}^{7} v_k w_{x,k}(t)}{\frac{1}{n}\sum_{z=1}^{n}\sum_{k=1}^{7} v_k w_{z,k}(t)},$$

$$p'_{x,i}(t) = \frac{v_i w_{x,i}(t)}{\sum_{k=1}^{7} v_k w_{x,k}(t)}, \qquad 1 \le i \le 7$$

and n is the number of cells in the grid (n = 100). (Note that $v_1 = 0$ as we assume seedlings are not utilized.) Thus the proportion of individuals utilized in each cell, of each stage class <3m is:

$$u_{x,i}(t) = l(t) I_{1-7} p_x(t) p'_{x,i}(t) \frac{1}{w_{x,i}(t)}, \qquad w_{x,i}(t) > 0,\ \ 1 \le i \le 7,$$

which simplifies to

$$u_{x,i}(t) = l(t) I_{1-7} \frac{n v_i}{\sum_{x=1}^{n} \sum_{k=1}^{7} v_k w_{x,k}(t)}, \qquad w_{x,i}(t) > 0, \quad 1 \le i \le 7,$$

where $I_{1\text{-}7}$ is the elephant intake rate of sub-adult woody vegetation, in units of plants per elephant per dry season. Similarly, we calculate the proportion of adult trees utilized as:

$$u_{x,i}(t) = l(t) I_{8-9} \frac{n v_i}{\sum_{x=1}^{n} \sum_{k=8}^{9} v_k w_{x,k}(t)}, \qquad w_{x,i}(t) > 0, \quad i = 8, 9.$$

where $I_{8\text{-}9}$ is the elephant intake rate of adult trees (again in units of plants per elephant per dry season). If $w_{x,i}(t) = 0$ then we also set $u_{x,i}(t) = 0$. We then compose $\mathbf{u}_x(t)$ as the vector corresponding to the $u_{x,i}(t)$'s:

$$\mathbf{u}_x(t) = \left(u_{x,1}(t), u_{x,2}(t), \ldots, u_{x,9}(t)\right)'.$$

The elephant-effect matrix **E** is a 9×9 matrix which adjusts the woody vegetation for the impact of elephant browsing, incorporating both mortality and sub-lethal effects. Broken stems may either die or resprout. Resprouting saplings are assumed to re-enter the seedling height class, similarly shrubs are reduced to sapling height and trees may be reduced to sapling or shrub height. To reflect accelerated growth of coppiced individuals due to below-ground stored tissue, plants re-entering the sapling or shrub metaclasses are assigned to the highest cohort ($i = 5$ or $i = 7$) within those strata.

$$\mathbf{E} = \begin{pmatrix} \mu_1^e & -r_{21} & -r_{31} & -r_{41} & -r_{51} & 0 & 0 & 0 & 0 \\ 0 & \mu_2^e + r_{21} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mu_3^e + r_{31} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mu_4^e + r_{41} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mu_5^e + r_{51} & -r_{65} & -r_{75} & -r_{85} & 0 \\ 0 & 0 & 0 & 0 & 0 & \mu_6^e + r_{65} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mu_7^e + r_{75} & -r_{87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu_8^e + r_{85} + r_{87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu_9^e \end{pmatrix},$$

where m_i^e is the proportion of those in class i, utilized by elephants, which die, and r_{ik} is the proportion of class i which are reduced in height to class k following utilization. Note that not all browsing results in death or stunting (if $m + r < 1$).

Fire.

Burning is assumed to take place 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).

Grass biomass provides fuel for fires and in our model the probability of fire occurring is linearly related to grass biomass. This is a close approximation to the logistic regression formula produced by van Wilgen *et al*. (2000) from Kruger National Park fire history data. 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

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

where R_x is a uniform random variable drawn on [0, 1] for each cell x, and y is a constant which scales biomass to a fire probability. The spread of fire is modeled by repeating this procedure (drawing another random number for comparison) for every non-burning cell with a burning neighbor, for each burning neighbor. For example, if a non-burning cell x has two burning neighbors, then two further values of R_x are drawn and compared with $y\, w_{x,10}(t)$. The procedure is further repeated until no additional cells burn. As we employ dissipative boundary conditions (see Model Structure, above), fires cannot wrap around to the other side of the grid as would happen in a toroidal model.

Fire intensity is also assumed to be linearly related to grass biomass (Trollope 1984b, Higgins *et al*. 2000), and is modeled relative to the biomass yielding maximum intensity:

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

where $b_x(t)$ is the fire intensity relative to that yielded by a grass biomass of $w_{\max}$. Other variables such as heat yield, rate of spread, relative humidity, fuel moisture and wind speed (Trollope 1984b, Higgins *et al*. 2000) can also affect fire intensity but we ignore these factors in this model.

Woody plants have their above-ground stems burned which may cause death or resprouting. The proportion, $t_{x,i}(t)$, of those in class i experiencing topkill is calculated as follows:

$$t_{x,1}(t) = b_x(t),$$

$$t_{x,i}(t) = \min\left(1, \frac{b_x(t)\,w_{x,10}(t)}{w^*}\right), \qquad 2 \le \mathrm{i} \le 5$$

$$t_{x,i}(t) = m^{b}_{6-7}\, b_x(t), \qquad i = 6,\ 7$$

$$t_{x,i}(t) = m^{b}_{8-9}\, b_x(t), \qquad i = 8,\ 9,$$

where w^* is the grass fuel required to kill 100% of saplings, and m^{b}_{6-7} and m^{b}_{8-9} are the topkill rates of shrubs and mature trees, respectively, under maximum intensity fires. These equations assume that all seedlings are killed by fire (Jeltsch *et al*. 1996) and that above-ground tissue death is proportional to fire intensity for all other stage-classes. Although our tree class has been defined based on the fire-escape height (≥3m; Pellew 1983), we allow for some mortality from fires which may be linked to, for example, scarring of bark by porcupine (Yeaton 1988). The woody vegetation is adjusted for topkill from fires as follows:

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

where k_i is the proportion of top-killed plants in stage-class i that resprout following fire; these are assumed to enter the next lowest stage-class due to strong regrowth enabled by below-ground biomass reserves.

Dry season grass dynamics.

Dry season grass dynamics are comparatively simple – we assume that grass burns entirely in fires, and senesces (again depending on annual rainfall) in the absence of fire:

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

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

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

III. Model Parameterization

For a list of all parameters (and their default or initial values where appropriate) and other symbols used, see Table 1.

Table 1. Parameters and variables used (in alphabetical order). See text for details of parameter estimation. 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.

Symbol	**Description**	**Units**	**Values**
$a_{x,i}(t)$	area controlled by woody vegetation classes in cell x at time t	ha	
	$i = 1$,		*0.0012*
	$2 \le i \le 5$,		*0.1996*
	$i = 6, 7$,		*0.2075*
	$i = 8, 9$.		*0.0918*
$a_{x,10}(t)$	grass coverage in cell x at time t	ha	*0.5000*
b_x	fire indicator for cell x	binary	0
c_x	potential seedlings emerging in cell x	plants	0
$\mathbf{E}$	elephant browsing effect matrix	–	*
$F()$	dry-season woody plant function comprised of f_{ele}, f_{fire}, f_{mort}.	–	*
$f_{\text{ele}}()$	dry-season elephant impact function for woody plants	–	*
$f_{\text{fire}}()$	dry-season fire-impact function for woody plants	–	*
$f_{\text{surv}}()$	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 ($1 \le i \le 9$), grass biomass ($i = 10$)	–	*
I_g	elephant intake rate of grass, wet season only	kg/ele/season	4600
$I_{1\text{-}7}$	elephant utilization of sub-adult woody plants, dry season only	plants/ele/season	5667
$I_{8\text{-}9}$	elephant utilization of trees, dry season only	plants/ele/season	1000
k	value of mean relative rainfall resulting in 50% of maximum drought-related tree mortality (m_m^r)	–	0.8
$l(t)$	elephant density at time t	individuals/ha	*0.0*
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)	–	*1.0*
s_i	survival of woody class i	–	
	$i = 1$,		0.950
	$2 \le i \le 5$,		0.990
	$i = 6, 7$,		0.994
	$i = 8, 9$.		0.995

Table 1 (continued).

Symbol	**Description**	**Units**	**Values**
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 utilization 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	–	
	$i = 1$		0
	$i > 1$		1
$w_{x,i}(t)$	number of woody plants of class i, in cell x, at time t ($1 \leq i \leq 9$)	individ'ls	
	$i = 1$,		*1211.4*
	$i = 2$,		*767.8*
	$i = 3$,		*507.2*
	$i = 4$,		*335.0*
	$i = 5$,		*386.4*
	$i = 6$,		*168.1*
	$i = 7$,		*62.4*
	$i = 8$,		*28.4*
	$i = 9$.		*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	individ'ls	*
x	cell index ($1 \leq x \leq 100$)	–	*
a_i	area controlled by one individual of class i	ha	
	$i = 1$,		1×10^{-6}
	$2 \leq i \leq 5$,		1×10^{-4}
	$i = 6, 7$,		9×10^{-4}
	$i = 8, 9$.		25×10^{-4}
b_x	relative fire intensity in cell x	–	*
g_i	expected transition rate (under mean, uncrowded conditions) from i to $i+1$	–	
	$1 \leq i \leq 4$,		1.000
	$i = 5$,		0.353
	$i = 6$,		0.300
	$i = 7$,		0.300
	$i = 8$.		0.150
g_{10}	net annual grass productivity under mean rainfall	kg/ha	2400
d	proportion of seedlings dispersing to neighboring cells	–	0.05
e_g	proportion of grass grazed by elephants in wet season	–	*

Table 1 (continued).

Symbol	**Description**	**Units**	**Values**
z	drought severity steepness control (shape parameter)	–	50
h	amplitude of wet-dry rainfall cycles, relative to long-term mean	–	0.13
k_i	resprouting rate of woody class i following fire ($2 \le i \le 7$)	–	0.9
$l_{x,i}$	expansion-limiting coefficient for woody class i in cell x	–	*
$m_{6\text{-}7}^{b}$	shrub topkill under maximum intensity fire	–	0.80
$m_{8\text{-}9}^{b}$	mature tree mortality under maximum intensity fire	–	0.02
m_i^{e}	mortality of class i plants utilized by elephants	–	
	$i = 1$		1.00
	$2 \le i \le 5$		0.25
	$i = 6, 7$		0.25
	$i = 8, 9$		0.80
$m_{8\text{-}9}^{r}$	additional drought mortality for mature trees	–	0.05
x	drought severity coefficient	–	*
p_x	proportion of elephant foraging allocated to cell x	–	*
$p'_{x,i}$	proportion of elephant foraging allocated to class i in cell x	–	*
r_{ik}	proportion of class i reduced to class k after elephant utilization	–	
	$2 \le i \le 5$ ($k = 1$)		0.5
	$i = 6, 7$ ($k = 5$)		0.5
	$i = 8$ ($k = 5$)		0.1
	$i = 8$ ($k = 7$)		0.1
s_r	standard deviation in annual rainfall relative to long-term mean	mm	0.30
t_i	topkill rate of woody class i due to fire	–	*
$f_{x,i}$	competition coefficient applied to growth rate of woody class i	–	*
$c_{x,i}$	net growth rate of woody class i given sufficient area for expansion	–	*
y	scaling constant converting grass biomass to fire probability	kg^{-1}	10^{-4}
w	period of wet-dry rainfall cycles	years	20

Woody demographic parameters

Growth.

Values for growth of savanna trees vary widely, and are measured in a variety of ways. Rutherford (1981) reports a mean height increase of 4% for unburned trees at Nylsvley Nature Reserve, South Africa. Du Toit *et al*. (1990) recorded 15.3 cm and 31.2 cm net annual shoot extension of *Acacia tortilis* and *A. nigrescens* respectively in the Kruger National Park, South Africa, changing to 10.7 cm and 35.9 cm respectively near to waterholes. Pellew (1983) found mean annual growth of *A. tortilis* in the Serengeti, Tanzania, to be 16.5 cm and 44.2 cm, with and without giraffe browsing respectively. Lewis (1987b) measured mean annual growth in coppiced *Colophospermum mopane* trees in Luangwa Valley, Zambia, as 13.4-19.2 cm.

Mushove (1993) achieved mean shoot heights of around 10 cm after two months' growth of *C. mopane* seedlings in a nursery. Mushove and Makoni (1993) cut *C. mopane* trees and recorded the resultant coppice-shoot growth over the following growing season as about 50 cm (dry season experiment) and 30 cm (wet season experiment), the results also depending on height of cutting and stump thickness. Smith and Shackleton (1988) recorded *Acacia tortilis* seedling growth of 10-16 cm after 6 weeks under various light treatments. Knoop and Walker (1985) measured shoot growth at irregular intervals at Nylsvley, finding growth in the range of 3-33 cm for *A. tortilis* and 3-15 cm for *A. nilotica*, over intervals of approximately 3-10 months, with this growth almost doubling where herbaceous vegetation had been removed. Herlocker estimated annual growth of young *A. tortilis* as 30 cm (Croze 1974b).

Here we assume that woody plants grow by a vertical height of 30 cm yr^{-1} under mean conditions, and calculate the underlying transition rates g_i by assuming equal size distribution within each height class. The transition rate from some height d_1 to height d_2 (in cm) is thus the proportion of the range (d_1, d_2) that lies within (d_1+30, d_2), or simply $1 - 30/(d_2 - d_1)$. Recalling that stages 2-4 are "waiting" stages with automatic growth within the sapling metaclass, this gives us values of $g_i = 1$ for $1 \leq i \leq 4$, and $g_i = 0.353$, 0.3, 0.3, 0.15 for $i = 5, 6, 7, 8$ respectively.

Fecundity.

In this paper we model fecundity as "viable seedlings produced per tree" rather than explicitly modeling seed production and survival. Values for seedling production also vary widely in the literature. Desmet *et al*. (1996) provide a fecundity value of 0.028 (including coppicing) for a matrix population model of *Pterocarpus angolensis*. Smit and Rethman (1998) found a mean establishment rate (including first year survival) of 0.064 (within a range of 0-0.222) for *Colophospermum mopane* seedlings in South Africa. Ben-Shahar (1996b, 1998), working in Botswana, measured *C. mopane* seedling per tree rates as 1.13 and 1.73, close to the value of 1.7 used by Pellew (1983) to model *Acacia tortilis* dynamics in the Serengeti. The recent model of Higgins *et al*. (2000) used 4 viable seeds per plant per year. Kiker (1998) modeled a monthly seedling production rate in the range of 0.15-0.40 per tree.

Other work has provided much higher estimates for seedling production, however. Witkowski and Garner (2000) counted number of viable seedlings for *Acacia nilotica*, *A. tortilis* and *Dichrostachys cinerea* at Nylsvley, South Africa which, coupled with O'Connor's (1995) probability of establishment gives seedling production per tree as anywhere within the range of [232, 4627]. Shackleton (1997) measured seedling production over two years in 6.25 m^2 quadrats which scales up to 720 and 1024 seedlings produced per hectare.

We choose a value of $m = 50$ for the number of potential seedlings per tree per year. Incorporating this value, and the model's growth and survival rates, into a Lefkovitch matrix gives a dominant eigenvalue of 1.5, i.e., potential population growth of 50% yr^{-1}, however this neglects the effects of competition (intraspecific and interspecific from grass) and environmental variability (fire and rainfall). Duffy *et al*. (1999) used an overall intrinsic tree population growth rate of 2.5% in their elephant-tree models.

Survival.

Savanna trees are generally well suited to harsh environments, with adaptations for disturbances and stresses from fire, herbivory, drought and low soil fertility, thus overall tree survival rates tend to be almost 100% (ranging from 94.4% (Shackleton 1997, and references therein) to 99.5% (Tafengenyasha 1997); see also Norton-Griffiths 1979, Rutherford 1981, Wiegand *et al*. 2000). Mortality tends to decrease with age, so that survival rates for seedlings are lower than those for mature individuals. Estimates for seedling survival range from close to zero for some sites (O'Connor 1995) up to 0.99 (Dublin 1995, Ben-Shahar 1996b). Shackleton (1997) measured seedling survival in two consecutive years as 0.981 and 0.873, for a mixture of species. We use $s_1 = 0.95$ in this model. For sapling survival we use $s_i = 0.99$, $2 \le i \le 5$, after O'Connor (1998), which was based on 9-year *Colophospermum mopane* drought mortality. The lowest estimate of sapling survival comes from Desmet *et al*. (1996), who measured survival of

Pterocarpus angolensis individuals <1m high as 0.78. The same authors also gave shrub survival for *P. angolensis* as 0.948-0.969 (Desmet *et al*. 1996), but again we adopt the value for *C. mopane* from O'Connor (1998), of s_6, s_7 = 0.994. For adult trees, we use an underlying rate of 0.005 for age-related mortality, giving s_8, s_9 = 0.995. Hochberg *et al.* (1994) used a value of 0.985 to model adult survival in Lamto, Cote d'Ivoire, and Desmet *et al*. (1996) measured *P. angolensis* adult survival as 0.944. Croze (1974b) estimated non-elephant mortality to adult *Acacia* spp in Serengeti National Park, Tanzania, as roughly 1% yr^{-1}. *C. mopane* survival estimates include 0.99 (Dublin 1995, Ben-Shahar 1996b) and O'Connor (1998) who failed to find any adult mortality during a 9-year drought. We set adult tree mortality in a full-scale drought ($x = 1$) to $m^r_{8-9} = 0.05$ (Scholes 1985). We use a drought mortality half-saturation value of $k = 0.8$ (so that a three-year average relative rainfall of 80% will result in drought-related mortality of $m^r_{8-9}/2$) and a use quite a steep drought mortality onset curve by choosing a high value for the shape parameter, $\zeta = 50$.

Grass parameters

Production.

Owen-Smith and Danckwerts (1997) provide an annual biomass production figure of 2,600 kg ha^{-1} for the Kruger National Park (mean rainfall = 575 mm yr^{-1}), with about 6.5% of this being grazed. Grass production is highly dependent on soil and climatic properties and can vary between 500-4000 kg ha^{-1} for southern African savannas (Owen-Smith and Danckwerts 1997). Here we use a figure of g_{10} = 2,500 kg ha^{-1}, to reflect the production level, net of grazing, at about 550-600 mm yr^{-1} mean rainfall.

Survival.

Illius and O'Connor (2000) modeled grass senescence using a senescence rate of 0.03 per day. Silva (1987) recorded *Andropogon semiberbis* mortality in a western Venezuelan savanna over two years as 0.81-0.47 (dry seasons, successive years) and 0.22-0.24 (wet seasons). Scholes (1985) measured grass mortality in a drought year as 0.07-0.29, 0.74-0.97 and 0.82-0.86 (clay, sand/clay and sandy soils respectively) in Klaserie, South Africa. We use rates of s_{10}^{W} = 0.8 (wet season) and s_{10}^{D} = 0.2 (dry season) for grass biomass persistence ("survival").

Elephant parameters

Distribution of impact by plant height.

Croze (1974b) found elephant utilization of tree height classes in the Serengeti, Tanzania, was in proportion to availability, except for the largely ignored <1m range. Pellew (1983) also found that elephants tended not to eat stems <1m high. Kalemera (1989) notes that elephants rarely ate small *Acacia tortilis* seedlings and Mwalyosi (1987) found that smaller *A. tortilis* trees at Manyara, Tanzania, were less susceptible to elephant-induced mortality.

Other authors, however, recorded elephants predominantly foraging at lower heights. Guy (1976) found that 59.8% and 81.7% of feeding took place at heights below 1.2m and 2m, respectively. Smallie and O'Connor (2000) found that elephants preferentially chose branches <1m high in the Venetia mopaneveld, while preferring trees <2m high for return visits. Both Caughley (1976), working in the Luangwa Valley, Zambia, and Mapaure and Mhlanga (2000), working on islands in Lake Kariba, Zimbabwe, recorded greater rates of elephant utilization of *Colophospermum mopane* occurring to thinner stems. Jachmann and Bell (1985) found that in the Kasungu National Park, Malawi, the preferred elephant feeding height (of preferred species) was between 1-2m (the height of impacted plants being thus somewhat higher), while for less preferred species, height classes were utilized in proportion to abundance – this would then result in maintenance of preferred species at the preferred feeding height. Jachmann and Croes (1991) found a preferred feeding level of 2-3 m. Trees over this height (and below 7m), however, were more likely to be knocked over (Jachmann and Bell 1985).

For adult trees of species that grow much higher than those modeled here, special consideration is required. For example, Jacobs (2001) studying marula (*Sclerocarya birrea*) adults in the Kruger National Park, South Africa, found that the proportion of trees that were damaged by elephants tended to decrease with increasing height, and that the predominant damage type tended to switch from stem breakage to bark stripping as height increased. Croze (1974a) found that elephant browsing height may extend up to 6m, with trees higher than 6m tending to be uprooted. Jacobs (2001) found less elephant damage to marula trees >8m in height, and a greater occurrence of "extreme damage" in the 2-8m individuals.

Here we consider utilization of adult trees separately from utilization of the shrub and sapling metaclasses. We assume that plants <3m high (and >15cm, i.e., excluding seedlings) are selected in proportion to the abundance of each class ($2 \leq i \leq 7$), and similarly we assume that impact on adult trees is proportional to the abundance of each class ($i = 8, 9$).

Intake.

Based on observed tree uprooting rates of one per 25-40 hours observation in the Seronera woodlands, Tanzania, (Croze 1974a), Croze (1974b) gives a rough toppling rate of 5.25 trees per elephant per week. Guy (1976) found toppling rates of 3 and 9 trees per day (by females and males respectively) in the Sengwa Research Area, Zimbabwe, with no toppling occurring in the wet season – for a 1:1 sex ratio this approximates to 1095 adult trees toppled per elephant per year. The model of Duffy *et al*. (1999) uses 1200 trees.(elephant.km^2.yr)$^{-1}$ as the maximum "predation" rate (in a Holling (1959) type II function with a half-saturation constant of 15: implying that intake remains in the order of 1200 for most of the range of tree density). We set $I_{8\text{-}9}$ = 1000 adult trees toppled per elephant per dry-season. Assuming this figure represents 15% of plant utilization (Guy 1976, Stokke and du Toit 2000), then we set $I_{1\text{-}7}$ = 5667 plants per elephant per dry-season. For a 183-day dry season, we therefore have a rough visitation rate of (1000+5667)/183 = 36.43 plants per day (5.5 trees and 31 saplings/shrubs), which seems reasonable: Stokke and du Toit (2000) recorded handling times of 18 minutes and 7.11 minutes for males and females, respectively, to complete browsing on two woody plants in immediate succession.

For grass intake, we use the estimate of Owen-Smith (1982; after Laws *et al*. 1975), of 0.8-1.0% body mass intake per day, with a mean elephant body mass of 2800 kg, giving I_g = 4600 kg per elephant per wet-season.

Distribution of impact intensity/Plant response given that an impact has occurred.

Death: Barnes (1985) reported decreases of 45%, 72% and up to 100% in densities of *Adansonia digitata* (baobab), *Acacia albida* and *Commiphora ugogensis* respectively in Ruaha National Park, Tanzania, between 1976 and 1982, at an elephant density of approximately 4.1 km^{-2}. Jacobs' (2001) study of marula (*Sclerocarya birrea*) adults in the Kruger National Park, South Africa, found an overall mortality incidence of 7%, which she ascribed mainly to elephant damage (marula is highly favored by elephants). Dublin *et al*. (1990) used the same rate to model annual tree mortality under high elephant densities. Elephant impact can be highly variable and opportunistic, e.g., Dublin (1995) reported that within a single 24-hour period, 6 bulls killed 34% *Acacia gerrardii* and injured 22% in a 2 km^2 area. Elephant effects can also be exacerbated by drought conditions, for example Lewis (1991) reported an account of 100% die-off of heavily-browsed *Colophospermum mopane* in a drought year (at a density of 6.7 elephants.km^{-2}).

Hiscocks (1999) surveyed trees in the Sabi Sand Wildtuin, South Africa, following the removal of a fence separating the reserve from the adjacent Kruger National Park (KNP) and found that in 1996 and 1998, of a total of 972 browsed trees >3m tall, 285 (29.3%) had died. For the shrub genus *Grewia* (<3m tall), 119 had died out of 398 browsed (29.9%). Engelbrecht (1979) studied *Acacia nigrescens* in the north of KNP and found 583 elephant-damaged trees out of a total of 951 trees, of which 264 trees (45%) were gored and ring-barked, ultimately resulting in their death. Mapaure and Mhlanga (2000), working on islands in Lake Kariba, Zimbabwe, provide data showing that on average, 17.6% of elephant-damaged *C. mopane* individuals died, although this varied widely (3-67%) between islands. Croze (1974b) found that 44% of elephant utilization of *Acacia* spp resulted in removal of >75% of the canopy, which was to likely result in mortality in 55-80% of cases (this damage-class included toppled trees and Croze used 100% mortality in his subsequent analysis). We assume that toppled adult trees experience 80% mortality ($m_8^e = m_9^e = 0.8$), and set the mortality of browsed shrubs and saplings to 25% ($m_i^e = 0.25, 2 \leq i \leq 7$).

Tree stunting (a net reduction in height, i.e., taken to include both browsing down to another height class and browsing followed by resprouting) is determined as the proportion escaping death while being more than lightly browsed. Lewis (1987b) found mean height reductions of 0.4-7.3 cm in coppiced mopane trees in Luangwa Valley, Zambia, due to dry season elephant utilization, depending on fire regime and extent of elephant utilization. Wackernagel (1993) surveyed elephant damage to the woody plant community in Linyanti/Chobe, Botswana, and provides figures for frequency and intensity of damage. For all species combined, approximately 25% experienced little or no damage, with 9.5% and 64.6% of impacted individuals experiencing medium and heavy damage respectively. This pattern also occurs for the two most abundant non-riverine species in the sample, *Colophospermum mopane* (11.2%, and 62.9% medium and heavy damage respectively) and *Combretum mossambicense* (3.0%, 69.7%). If we assume that 25% of browsed individuals experience little damage, and 25% die (as discussed above), the remaining 50% will resprout into the next lowest metaclass, i.e., $r_{i1} = 0.5$ for $2 \leq i \leq 5$ and $r_{i5} = 0.5$ for $i = 6, 7$. For toppled trees, we divide the surviving 20% equally between the sapling and shrub metaclasses ($r_{i5} = r_{i7} = 0.1$, $i = 8, 9$).

Fire parameters.

Van Wilgen *et al*. (2000) used fire records from the Kruger National Park, South Africa, to parameterize a logistic regression formula relating the probability of fire occurrence to grass biomass in kg ha^{-1} (w_{10} in our model) for 1995 and 1996, with the latter year providing the better statistical fit:

$$\text{P(fire)} = \frac{e^{0.0005w_{10}-2.7431}}{1+e^{0.0005w_{10}-2.7431}},$$

This formula is almost linear over most of the biological range of biomass and here we use the rough approximation P(fire) = $w_{10}/10000$ (i.e., $y = 10^{-4}\ \text{kg}^{-1}$), which also ensures that a fire can't occur if there is no grass fuel present ($w_{10} = 0$ gives P(fire) = 0.0605 in the above). Our value of $y = 10^{-4}$ gives somewhat lower fire occurrence probabilities (P(fire) = 1 when $w_{10} = 10000$ kg ha^{-1}) than those used by Weber *et al*. (1998) to model grazing pressure on a Kalahari shrubland (P(fire) = 1 when $w_{10} = 3000$ kg ha^{-1}).

Trollope (1993) states that a grass fuel load of 4000 kg ha^{-1} is required to produce an "intense" fire. We use $w_{\text{max}} = 5000$ kg ha^{-1}, which is twice the annual grass production under mean conditions, i.e., $n_{\text{max}} = 2g_{10}$. Using this biomass with the equation and mean values given by Higgins *et al*. (2000) for fuel moisture, wind speed and relative humidity, yields an intensity of 3686 kWm^{-1}.

Woody plant response to fire.

Topkill. Jacobs and Biggs (2001) found marulas up to 1.5m to be highly susceptible to fire, with the tallest tree affected by fire being 2.7m and impact increasing with fire intensity. Trollope and Tainton (1986) found that woody plants up to 2m high exhibited greater than 40% mortality in intense fires (>2500 kWm^{-1}). Trollope (1984a) noted 100% of saplings (<50cm) being top-killed in medium-intensity fires; Menaut *et al.* (1990) also employed this result in their model, with each fire completely burning the aboveground shoots, so that each individual reverted to the previous stage-class after coppicing. We use a fuel load of w^* = 2500 kg as the grass biomass necessary to cause 100% sapling topkill.

Dublin (1995) used a rate of 90% for topkill of shrubs (i.e., rate of reversal to a sapling) by fire. Norton-Griffiths (1979) used rates of 28-68% for topkill of shrubs, depending on height and species. Trollope (1974; reviewed in Trollope 1982) provided a figure of 80.8% topkill of trees and shrubs, comprised of 71.5% coppicing and 9.3% mortality. Trollope (1999) depicted topkill rates of 30-97% (decreasing with increasing height) for plants between 1-3m. We use a shrub topkill rate under maximum fire intensity of m^b_{6-7} = 0.8.

We also include a small level of fire-caused adult tree mortality (m^b_{8-9} = 0.02) to take into account possible previous bark damage from porcupine (Yeaton 1988).

Resprouting. Savanna plants have evolved with fire and therefore show high levels of fire-resilience, a common strategy being high proportions of woody plants resprouting, following topkill by fires, although this ability of course varies by species (Gignoux *et al.* 1997, Gadd *et al.* 2001). This change in height can be modeled as topkill followed by resprouting (as in this paper) or as a combined stunting effect. Dublin (1995) used stunting rates of 90% and 95% for saplings and shrubs respectively in a model of the Masai-Mara *Acacia tortilis* population. In a similar model, Ben-Shahar (1996b) used maximum shrub stunting rates of 1% for *Acacia erioloba* and *Colophospermum mopane*, but 31% for *Baikiaea plurijuga*; maximum stunting rates for the <1m class were 15%, 50% and 70% (*A. erioloba*, *C. mopane* and *B. plurijuga* respectively). Other authors (see references in Frost and Robertson 1987) give fire-induced mortality rates typically in the order of 10%. Higgins *et al*. (2000) use a value of 0.9 as a maximum probability of height-dependent resprouting, with their resultant resprouting rates falling between 0.89-0.90 for all heights up to 3m. Therefore for simplicity we use the same value of $k_i = 0.9$ for all saplings and shrubs ($2 \leq i \leq 7$). As noted in the previous section (Model Procedure/Implementation: dry season dynamics), we set $k_1 = k_8 = k_9 = 0$.

Stochasticity

In order to ensure comparability of results, the random number generators were reseeded with the same fixed random seed before simulation of each different parameter set. The model is deterministic except for the variables R_x in the fire component, discussed above, and $z(t)$ in the rainfall equation. The value for $z(t)$ is drawn from a normal distribution with zero mean and variance of s_r^2. Rainfall in the Kruger National Park exhibits pronounced extended wet and dry periods, of approximately 10 years each (Gertenbach 1980); thus we use a period of $w = 20$ years, i.e., a predominantly wet decade followed by a dry decade and so on. The amplitude of the cycles is set to $h = 0.13$ (i.e., mean rainfall cycles between 87% and 113% of the overall mean; Gertenbach 1980) and the variability around the resultant sinusoidal cycles is set to $s_r = 0.3$ (Nicholson 1993).

Initial conditions.

The model is started in the wet season of the first year of a wet cycle. Each hectare cell contains the same initial vegetation structure: 50% grass cover and 50% woody cover. The grass biomass is assumed to be 1200 kg, roughly equivalent to one average year's production over half a hectare (i.e., $g_{10}/2$). The initial woody structure is determined from the right eigenvector of the Lefkovitch matrix obtained from the growth and survival rates, i.e., the stable class distribution that would result from a linear woody-only model (Caswell 2001) ignoring competition, density dependence, fire etc. For sensitivity analyses (except sensitivity to growth rates) the model is run for 100 years to allow initial transient dynamics to fade before adjusting the parameter(s) in question.

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 model was run 100 times, initiated with the same random seed as described above. 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 more than 10,000 m^2 per hectare. Figure 1A shows the output (mean of 100 cells) for a single simulation of 100 years using the default parameter values and without elephants.

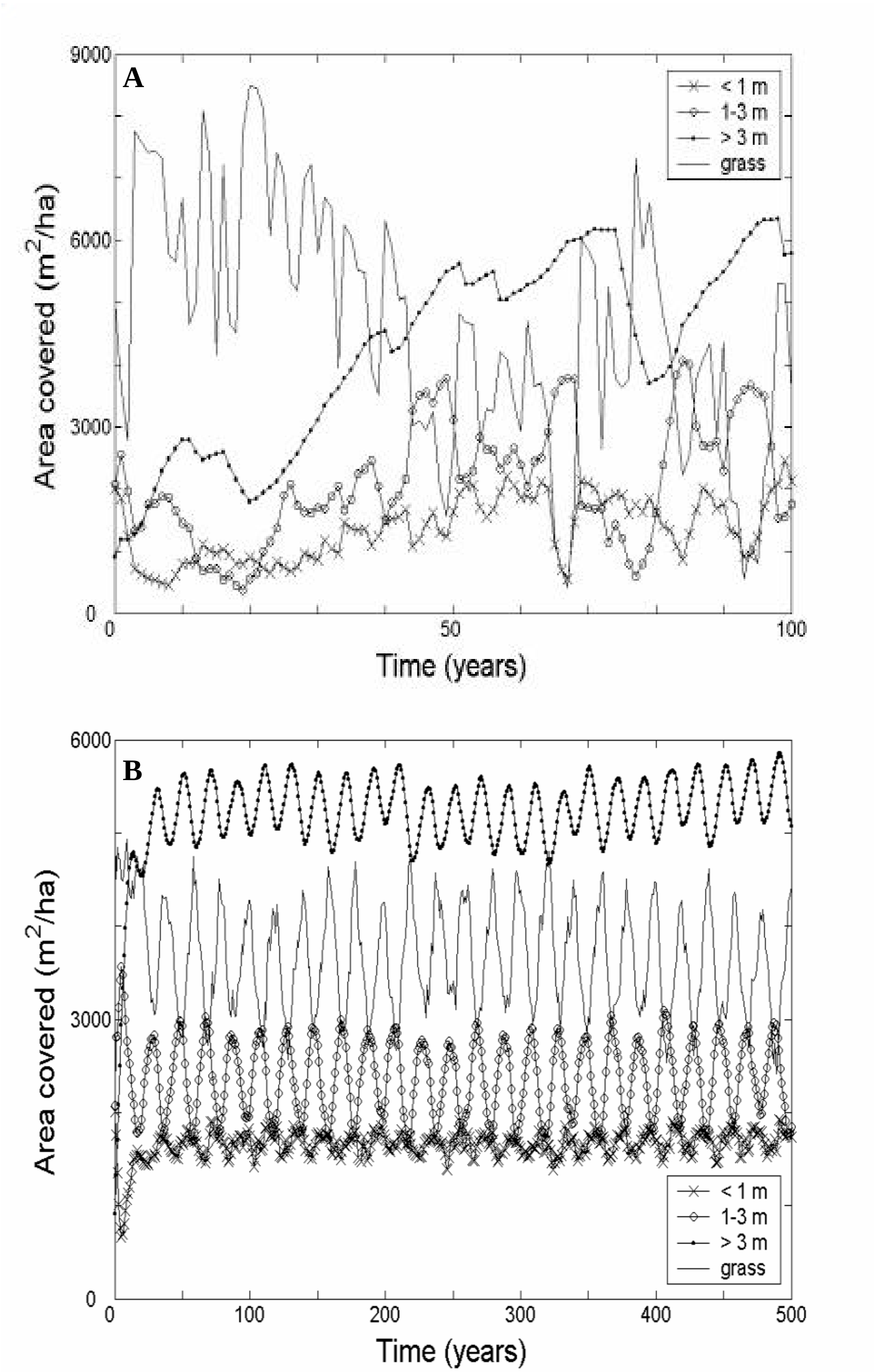


Figure 1. Model results using the default parameter set, showing the mean area covered by woody plants in “juvenile” (<1m high, i.e., seedlings and saplings), shrub (1-3m) and tree (>3m) classes, and by grass. A: Output from a single stochastic run over 100 years, representing the mean output across the 10 × 10 grid (100 cells); B: Mean output from 100 stochastic runs across the 10 × 10 grid, over 500 years.

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). Figure 1B shows this mean output for the default model parameters over 500 years. An overall long-term coexistence between the woody and grass components is clearly demonstrated, with a pronounced sinusoidal pattern reflecting the underlying wet-dry cycles. This coexistence occurred for each of the 100 runs averaged in the figure.

Model Sensitivity

We tested the model's sensitivity to changes in the following key variables: mean annual rainfall, probability of fire (y) for a given grass biomass, coppicing ability k_i following topkill by fire, and vertical growth of woody plants (affecting the transition rates g_i). In each case (except the fourth, demographic assertion) we allowed the model to run using the default parameter values for 100 years, allowing the initial transience to dissipate, before altering the test parameter.

Rainfall regime was altered first by simply multiplying $r(t)$ by 1.1 or 0.9 after 100 years, to give a "wet" and a "dry" scenario. (Nominally we refer to these perturbations as a 10% increase or decrease in rainfall, although actual averages will be more of an increase and less of a decrease because $r(t)$ is constrained to be nonnegative.) The periodicity (w) or amplitude (h) of long-term cycles were not altered, nor was the standard deviation of annual rainfall (s_r). The mean trajectories obtained are shown in Figure 2. Although tree-grass coexistence still persists, the dominance shifts from trees to grass as conditions get drier. Figure 3A demonstrates this shift by plotting the

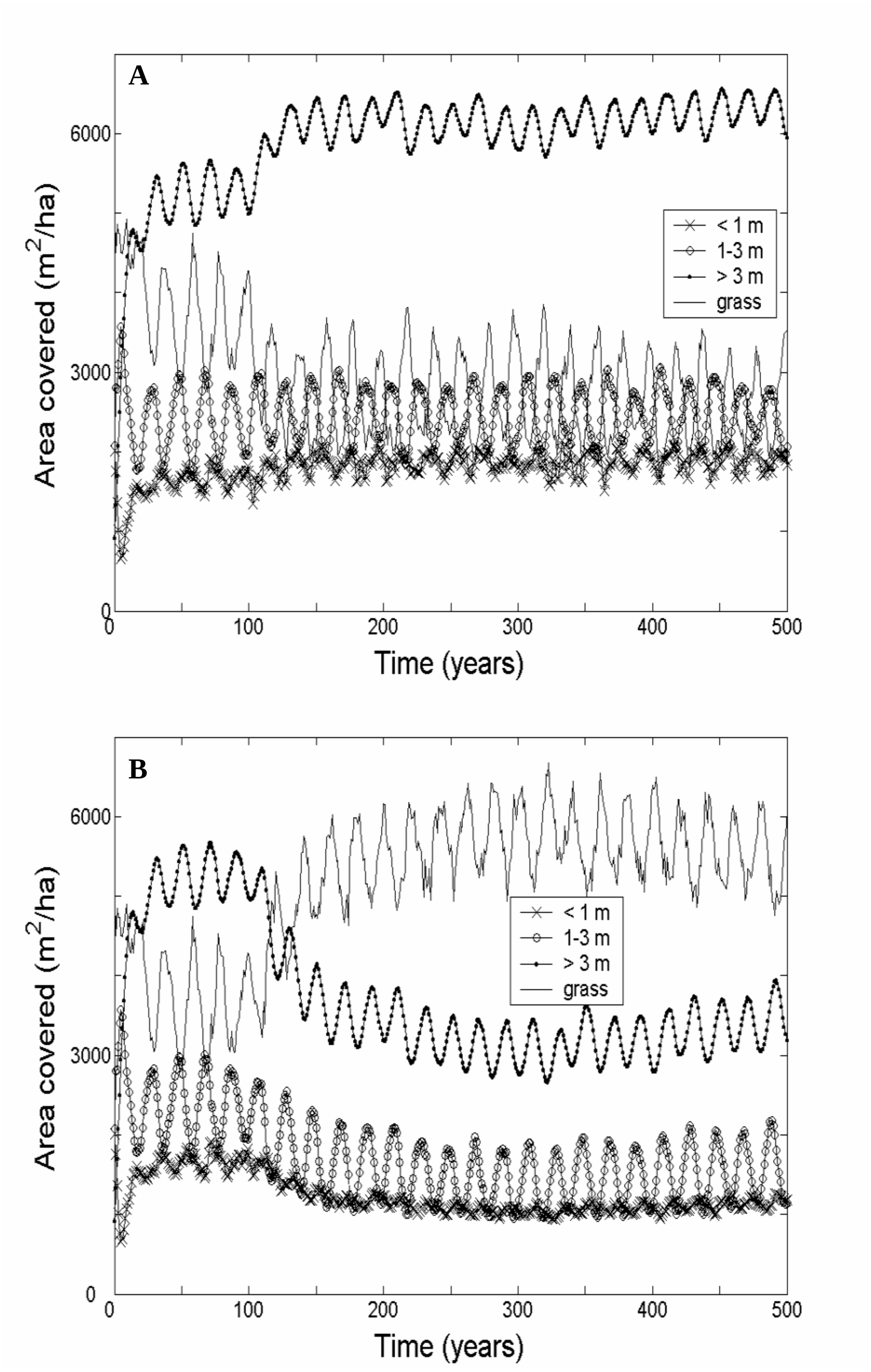


Figure 2. Mean trajectories for (A) wet (110% mean annual rainfall) and (B) dry (90% mean annual rainfall) scenarios. Rainfall is adjusted after year 100 to allow initial transient dynamics to fade.

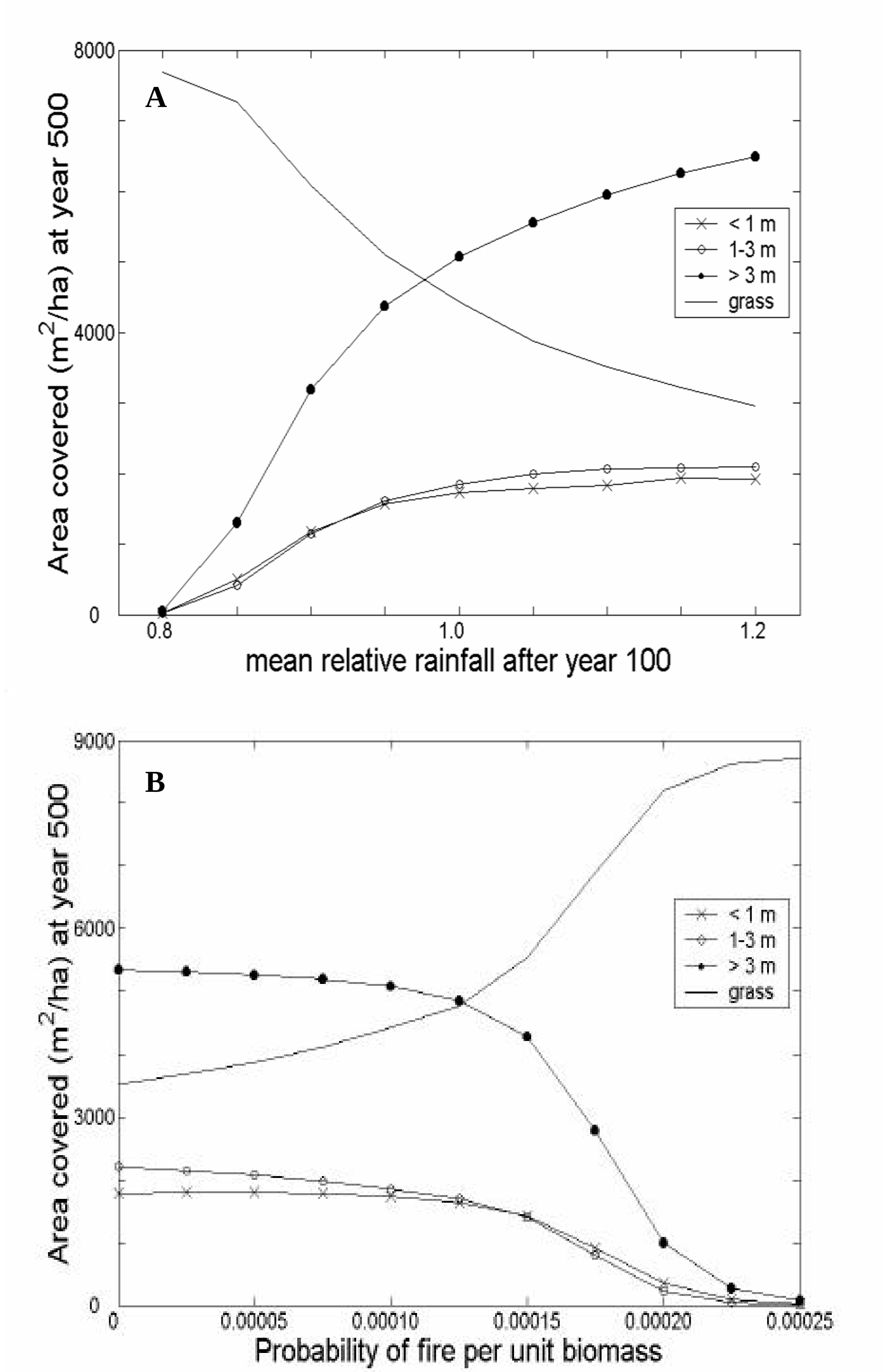


Figure 3. Sensitivity of final vegetation composition to changes in (A) mean relative rainfall (default value 1.0), (B) y, the probability of fire occurrence relative to grass biomass (default value 0.0001), (C) resprouting rates (k_i) of shrubs and saplings (default value 0.9) and (D) annual woody-plant vertical growth (default value 30 cm yr^{-1}). All parameter adjustments take place at year 101, except for growth rates which are fixed throughout. Mean area covered by each stratum after 500 years is plotted, (n=10000 for each point: 100 runs × 100 cells).

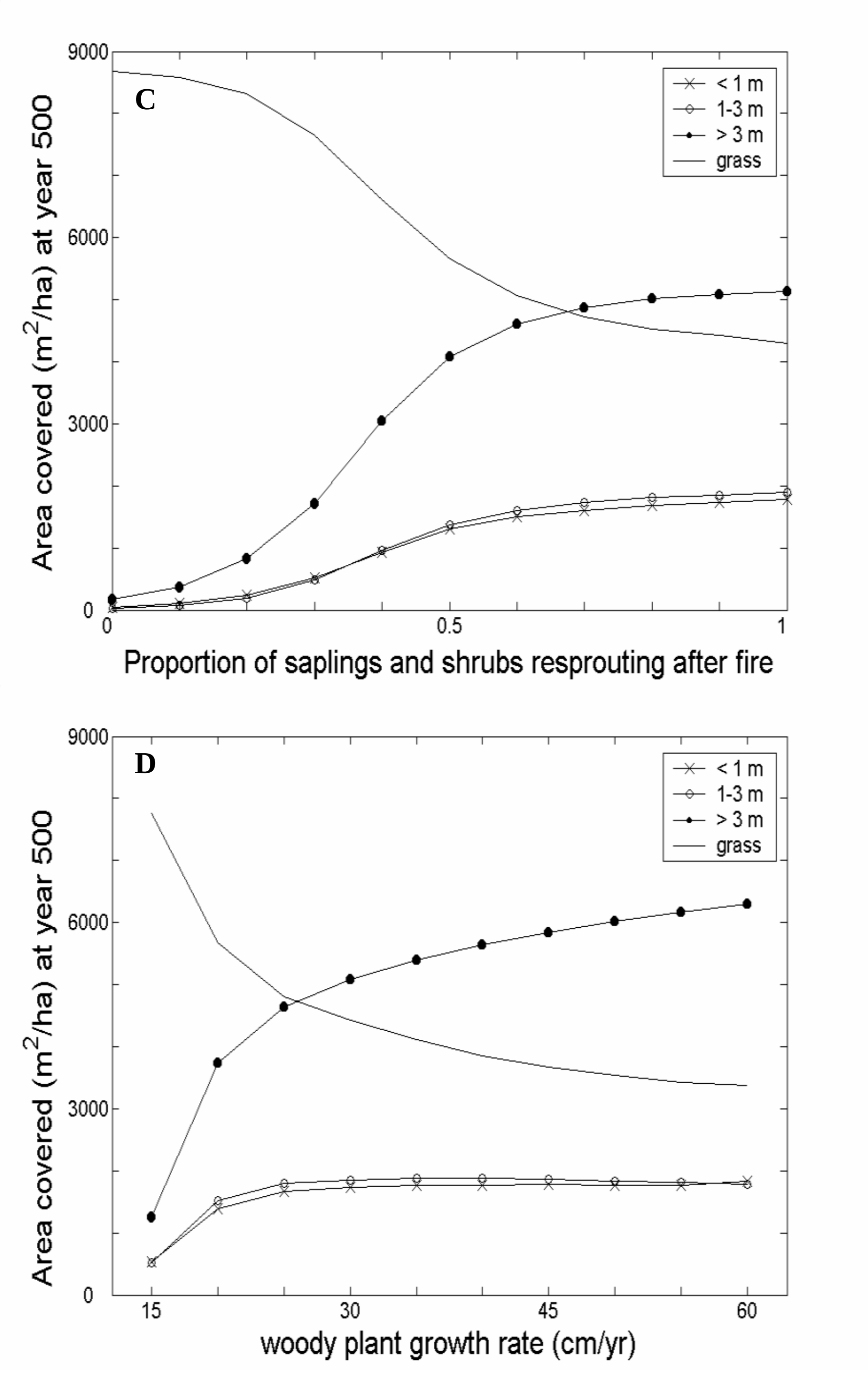


Figure 3 (continued).

vegetation end-points (vegetation state 400 years after the rainfall change was instigated) for rainfall regimes between 80% and 120% of the default model.

Figures 3B-D present results in the same fashion for sensitivity to fire probability, coppicing ability and woody plant growth rate. As sensitivity to the probability of fire occurrence (y) for a given grass biomass was very slight near the default value of $y = 10^{-4}$ kg^{-1} (Figure 3B) we also focused on the sensitivity of woody plant response to fire in terms of coppicing ability, k_i (Figure 3C). We kept all k_i values equal for the classes allowed to coppice ($2 \leq i \leq 7$) and altered all values together, again after the initial 100 year transitory period. Figure 3C shows the mean final state of vegetation as the proportion coppicing in each class $2 \leq i \leq 7$ was altered from 0 to 100%. Woody plant dominance increases as fire frequency, or susceptibility to fire, reduces. Sensitivity to the value used for woody plant growth (the default g_i were based on a vertical height increase of 30cm) is shown in Figure 3D; as would be expected, faster woody plant growth leads to more tree dominance while slower growth leads to exclusion by grasses.

Elephant influence

We next modeled the effects of introducing an elephant population at year 101 (i.e., again 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 km^2 patch with constant intensity. Figure 4 depicts the mean trajectories arising from introducing 0.5 and 1.0 elephants per km^2. Figure 5A shows the vegetation composition 100 years after introduction of elephant populations from 0-3 km^{-2}.

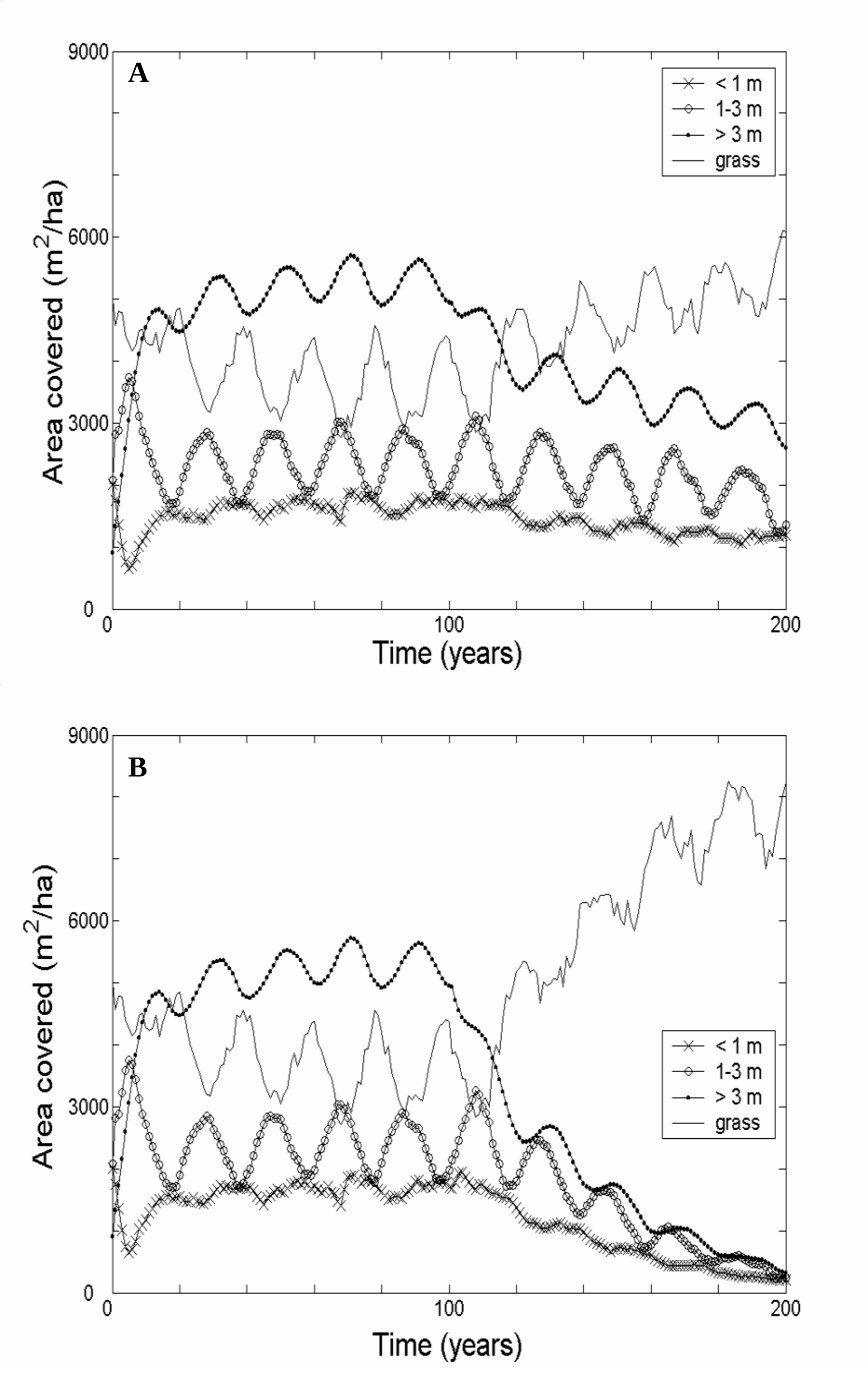


Figure 4. Effects of elephant introduction at constant stocking density. Mean trajectories following introduction (at year 101) of elephants at constant densities of (A) 0.5 km^{-2} and (B) 1.0 km^{-2}.

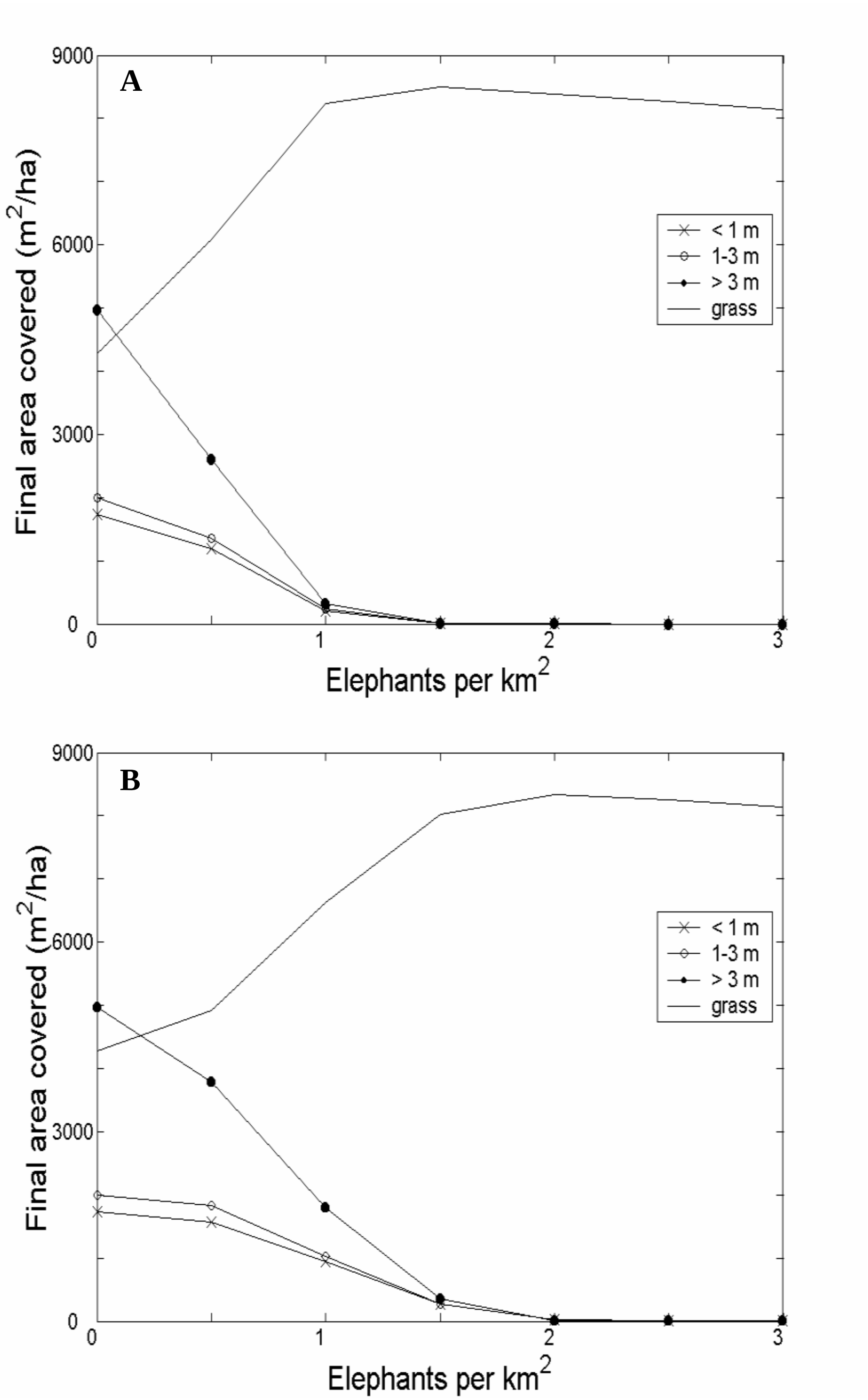


Figure 5. Sensitivity of vegetation composition to elephant population densities, 100 years after elephant introduction: (A) default parameters; (B) assuming lower elephant-induced mortality to adult trees ($m_i^e = 0.4$, $i = 8, 9$); (C) allowing for elephant-assisted seedling establishment by increasing the fecundity parameter (m) to $(1 + l(t))m$, where $l(t)$ is elephant density (individuals.km^{-2}) at time t; (D) 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.

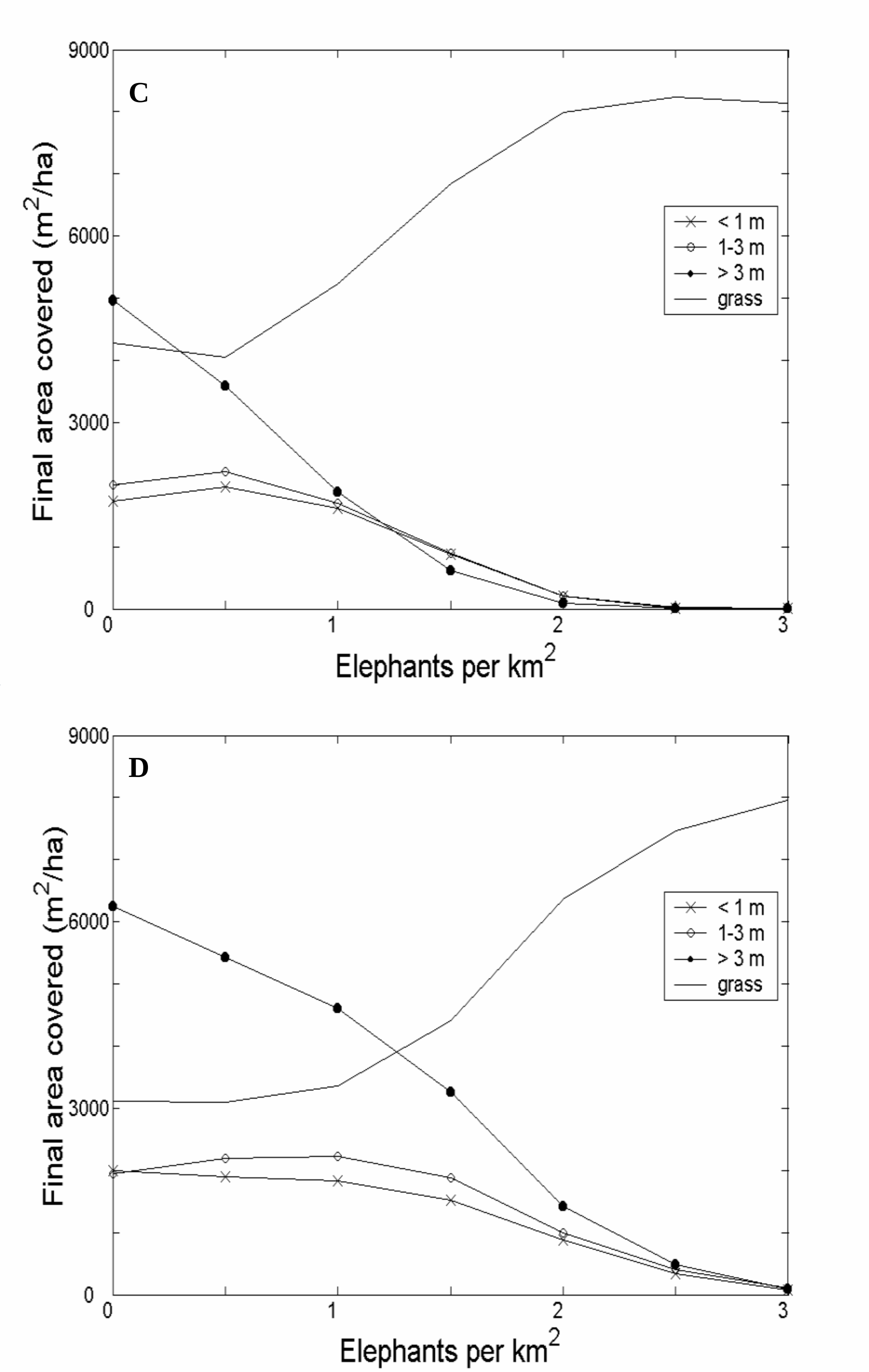


Figure 5 (continued).

Figures 5B-D show the results of three different assumptions for the same population ranges. As the model was sensitive to certain levels of resilience to fire (as measured by coppicing rate, Figure 3D), we also tested the effect of increased resilience to elephant utilization. The outcome of assuming lower mortality of toppled and bark-stripped adult trees ($m_i^e = 0.4$ instead of the default of 0.8) is shown in Figure 5B. We also took into account Lewis's (1987a) assertion (and that of many field biologists) that elephants are important facilitators of plant recruitment by scarring seed testae in the digestive tract and depositing it in nutrient-rich dung. Figure 5C shows the effect of increasing the fecundity measure m by a factor of $(1 + l(t))$, e.g., doubling the potential number of viable seedlings produced per tree when elephant density is 1 km^{-2}. As vertical growth rates for woody plants are not well studied (see Model Parameterization, above), we also tested the sensitivity of the model to a doubling of growth: from values of g_i based on a 30 cm annual height increase to 60 cm (Figure 5D). All of these results demonstrate that, while elephants generally have a deleterious effect on woody cover, the precise interaction of elephant pressure with tree demographics can play a role of great importance in the long-term vegetation profile of a savanna.

Spatial consideration: woody dominance patterns.

The mean trajectories shown in Figures 1B, 2 and 4 are averaged not just over 100 stochastic simulations, but also over the 100 cells in our 1 km^2 grid. Thus we also depict these results by examining the extent of woody plant dominance throughout the grid. We describe a cell x as having low, medium or high levels of dominance by woody plants if the sum of woody cover ($a_{x,1} + \ldots + a_{x,9}$) comes to more than ¼, ½ or ¾ of a hectare respectively (these measures are somewhat arbitrary because as noted earlier the model allows seedlings, saplings and grass to grow under adult tree canopies so that at any stage the vegetation cover may sum to more than one hectare).

Figures 6 and 7 represent the changes in woody dominance through time for some of the scenarios covered above. Output from the vegetation-only model for the default, 110% rainfall and 90% rainfall scenarios is depicted in Figures 6A-C respectively. Figure 7 shows the dominance trajectories for the four elephant-savanna scenarios dealt with in Figure 5, for an elephant population of 1 km^{-2}, viz.: default parameters (7A; vegetation cover trajectory also shown in Figure 4B), reduced adult mortality from elephant impact (7B), extra fecundity due to elephant-assisted germination (7C) and higher woody plant growth rates (7D). While broadly reflecting the trends of the mean vegetation cover trajectories, Figures 6 and 7 also demonstrate 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 figures 4D and 7A (the default assumptions with one 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 2.7% of cells still have more than 75% woody cover (7500 m^2).

Quasi-removal risks

We also examined patterns of quasi-removal of trees, which we define here as less than one adult tree per km^2. Figure 8 shows the proportions of simulations which resulted in quasi-removal for the four elephant-savanna scenarios (default (8A), reduced tree

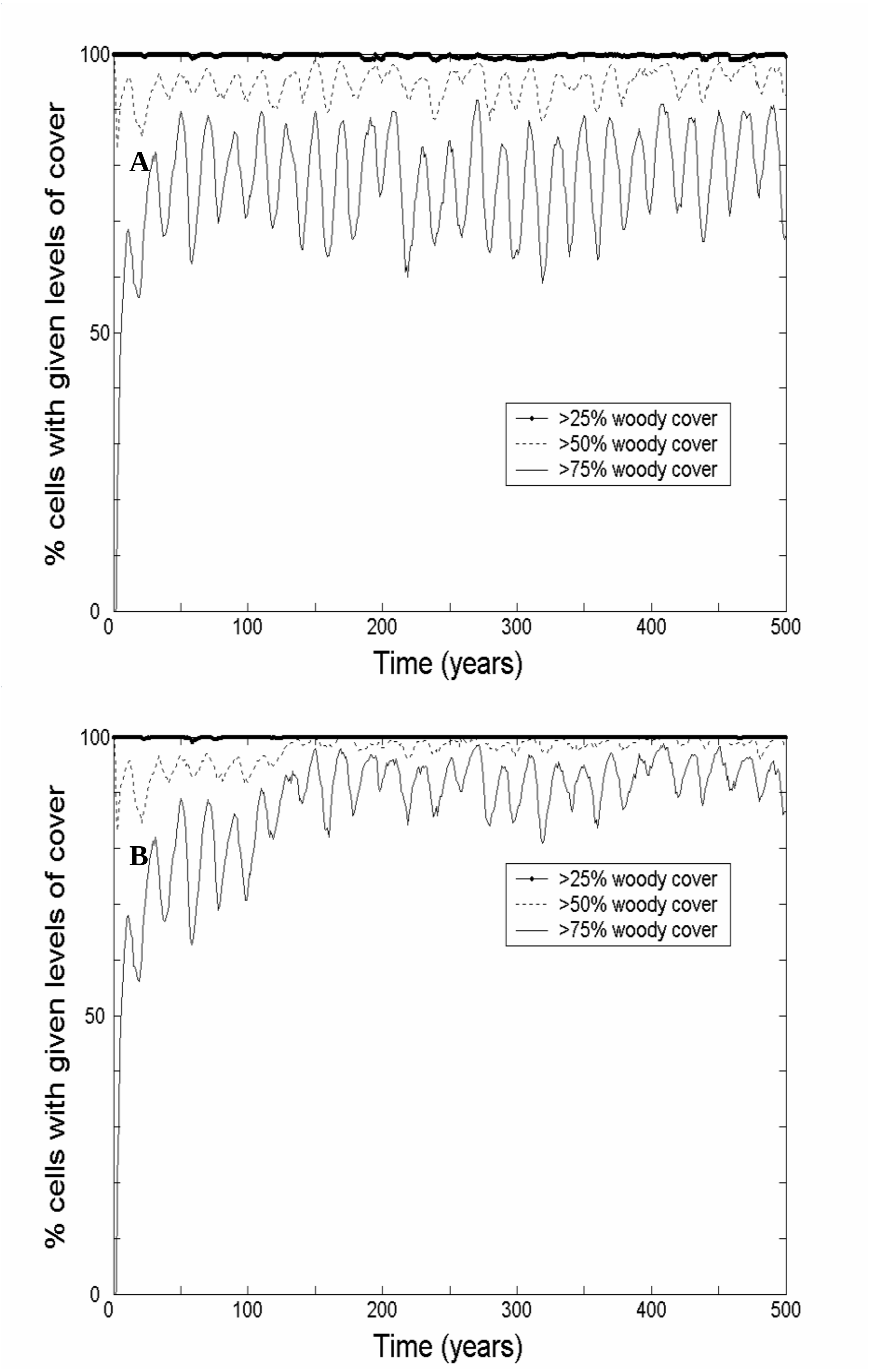


Figure 6. Mean percentage of cells with >25%, 50% or 75% woody cover for (A) default, (B) 110% rainfall and (C) 90% rainfall scenarios (corresponding to the mean trajectories shown in figures 1B, 2A and 2B).

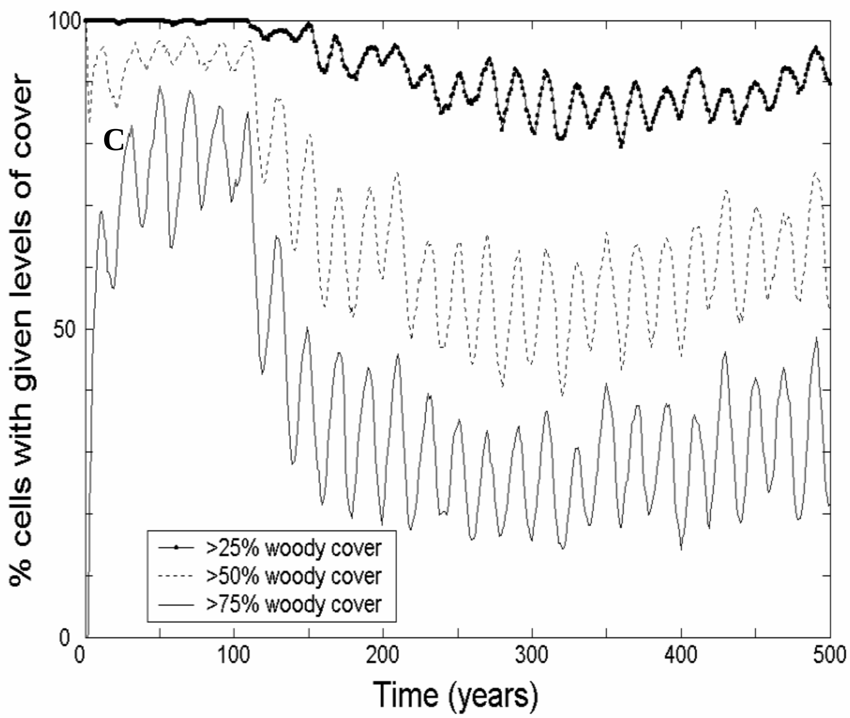


Figure 6 (continued).

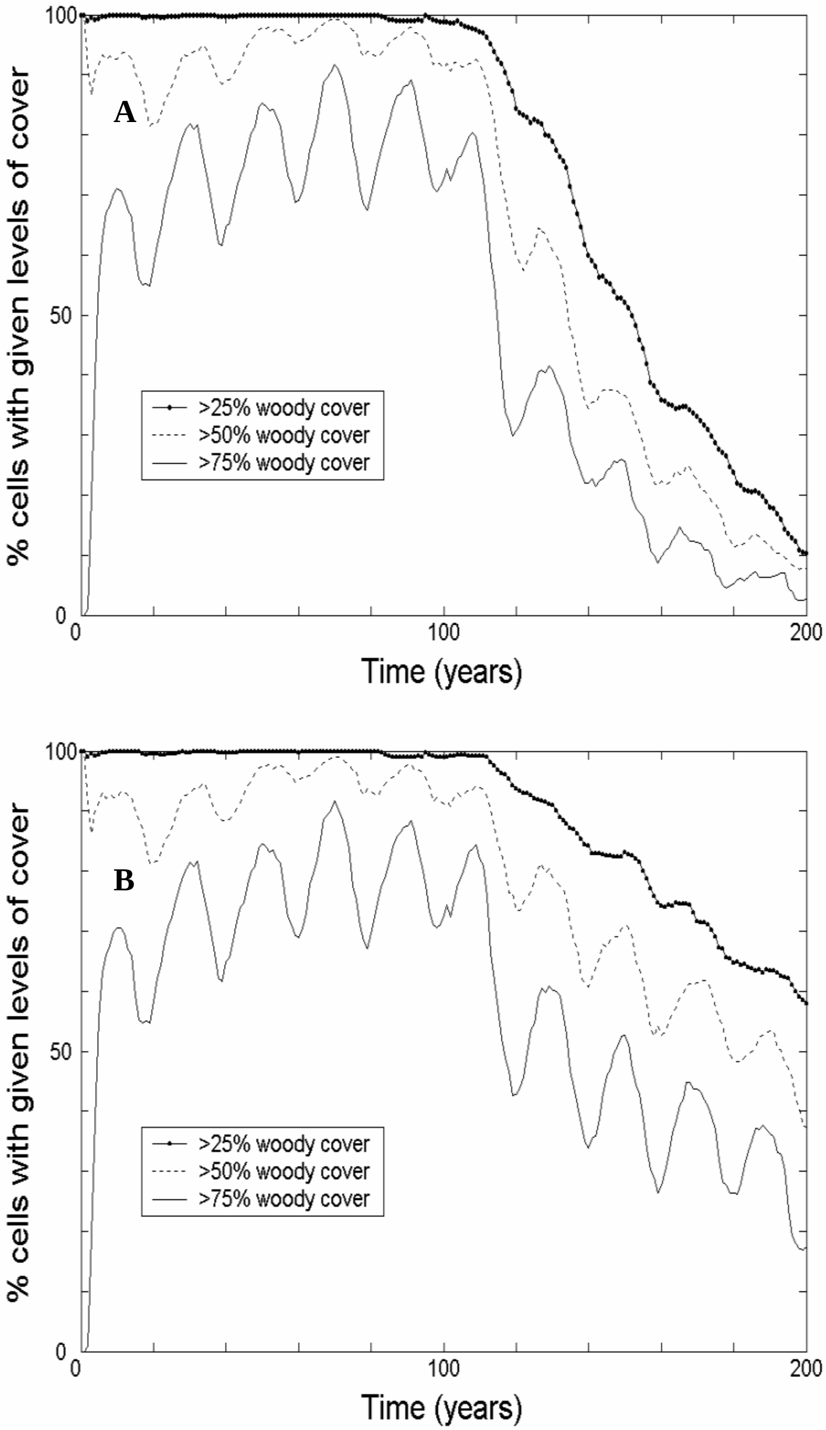


Figure 7. Mean percentage of cells with >25%, 50% or 75% woody cover for introduction (at year 101) of elephants at constant densities of 1.0 individuals.km^{-2}. The different dominance profiles represent (A) default parameters (corresponding to the trajectory in figure 4(b)), (B) reduced adult mortality from elephant impacts ($m_i^e = 0.4$, $i = 8, 9$). (continued)

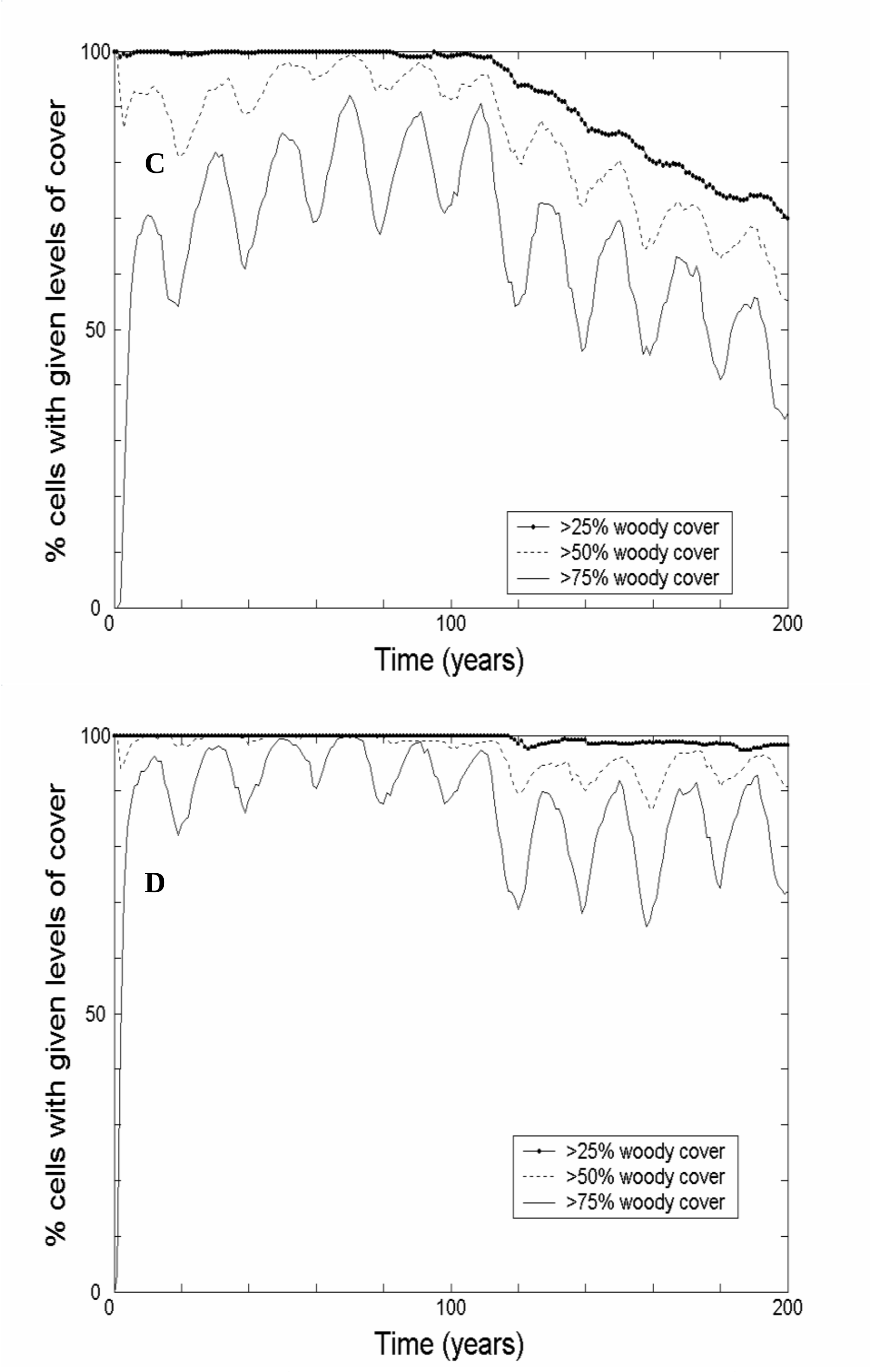


Figure 7 (continued). (C) extra fecundity assumption (increasing the fecundity parameter (m) to $(1 + l(t))m$, where $l(t)$ is elephant density at time t) and (D) annual woody plant growth of 60 cm. All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates which are set at year 0. Points represent mean of 100 runs over a 10 × 10 grid.

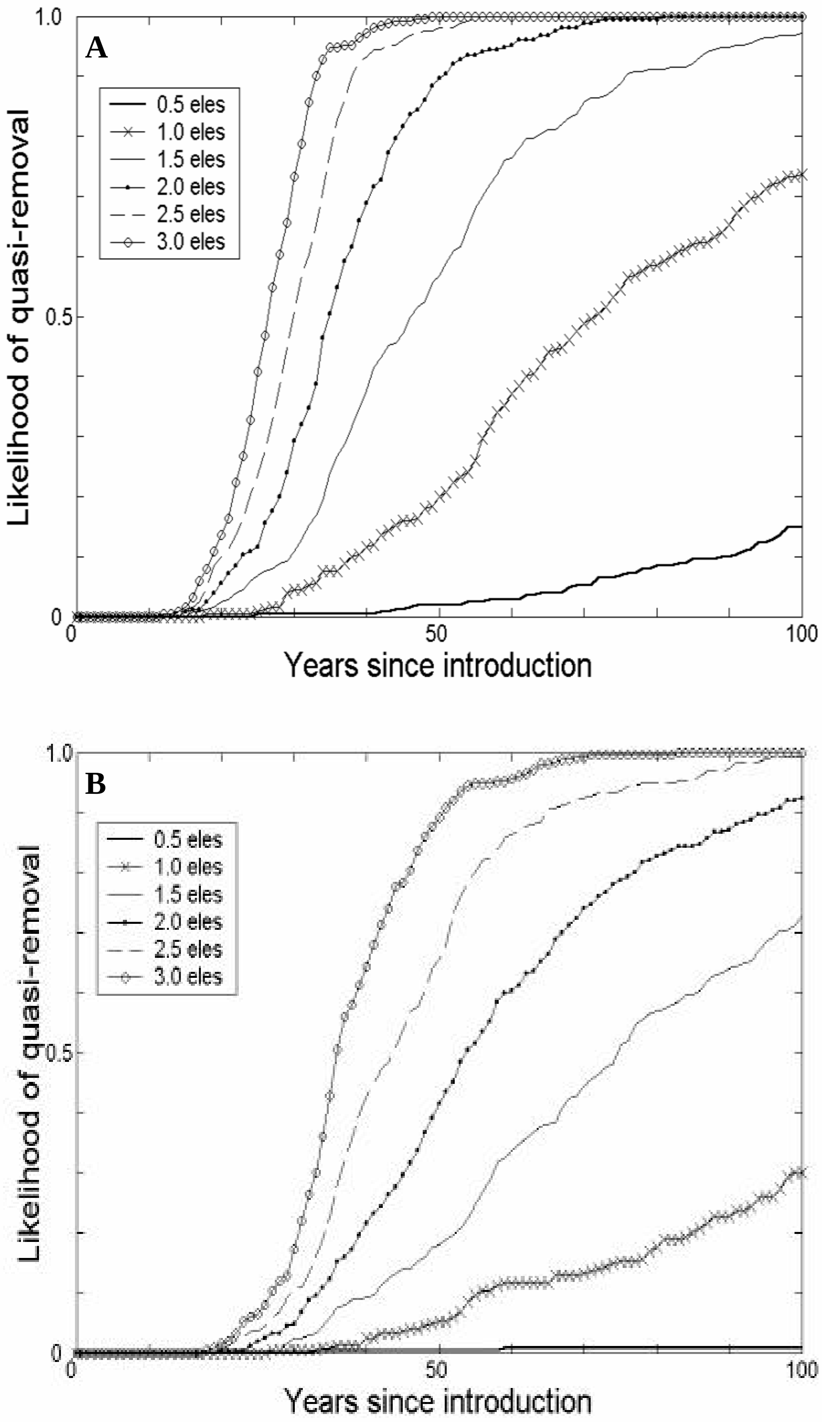


Figure 8. Likelihood of quasi-removal (defined as less than one adult tree per km^2) for constant elephant densities of 0.5-3.0 individuals per km^2. The different dominance profiles represent (A) default parameters, (B) reduced adult mortality from elephant impacts ($m_i^e = 0.4$, $i = 8, 9$). (continued)

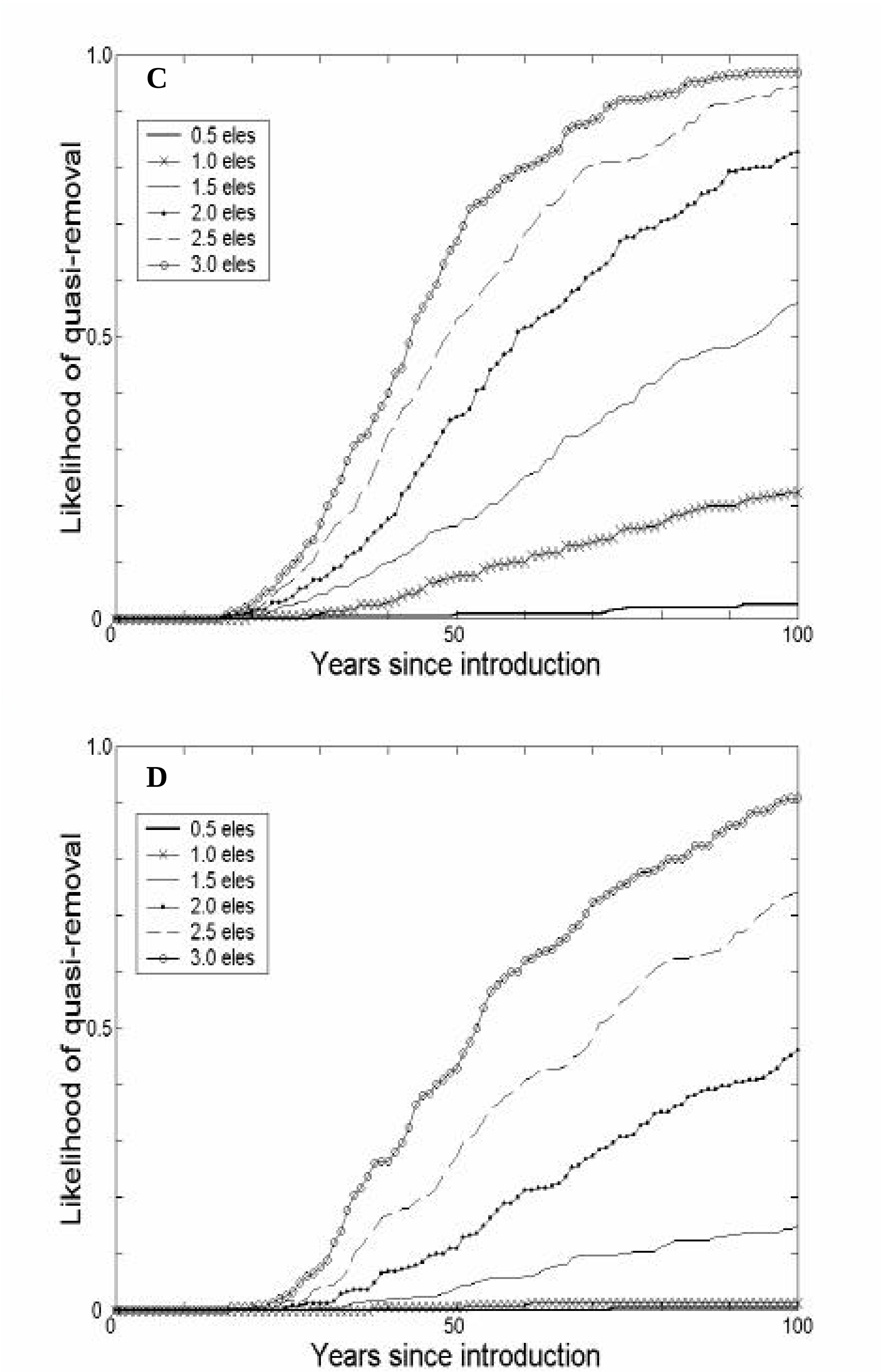


Figure 8 (continued). (C) extra fecundity assumption (increasing the fecundity parameter (m) to $(1 + l(t))m$, where $l(t)$ is elephant density at time t) and (D) annual woody plant growth of 60 cm. All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates which are set at year 0. Points represent mean of 250 runs over a 10 × 10 grid.

mortality (8B), elephant-enhanced fecundity (8C), and annual woody growth of 60cm (8D)), for constant elephant populations between 0.5 and 3.0 individuals km^{-2} (250 simulations each). Thus we see that while our default assumptions predict a 15% chance of tree quasi-removal within a century of 1 elephant km^{-2} (Figure 8A), this likelihood is reduced almost to zero for a faster-growing tree species (Figure 8D).

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: 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 6603.76 fires per simulation, representing a mean FRP of 7.57 years. FRPs for a selection of scenarios are depicted in Figure 9. These reflect the relative tree/grass balances resulting from each scenario, with more grass-dominated results yielding more fires and thus shorter FRPs.

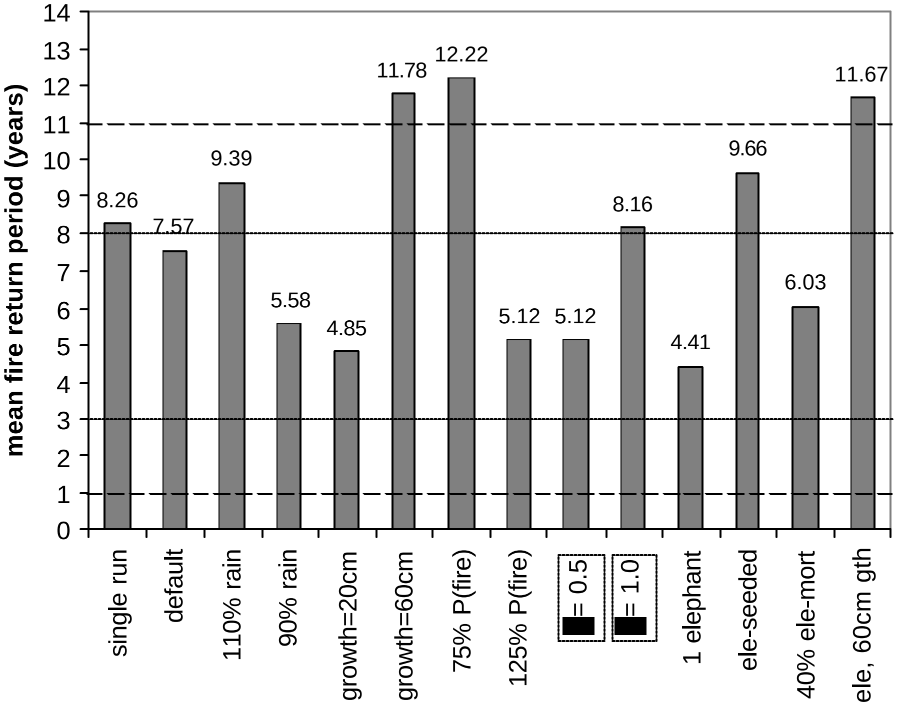


Figure 9. Mean fire return periods for selected runs, viz.: single stochastic run; default model parameters (mean of 100 runs); 110% rain; 90% rain; annual woody growth of 20 cm; annual woody growth of 60 cm; 75% fire probability ($y = 0.75 \times 10^{-4}$), $y = 1.25 \times 10^{-4}$); reduced coppicing ability reduced to κ=0.5; κ=1.0; introduction of one elephant km^{-2}; 1 elephant km^{-2} with elephant-assisted seedling establishment; 1 elephant km^{-2} with lower elephant-induced mortality to adult trees ($m_i^e = 0.4$, $i = 8, 9$); 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 (– –) and mean (--) ranges of fire return periods reported for the Kruger National Park, South Africa (Trollope, 1993).

Discussion

The results presented above indicate that the model is sufficiently detailed to address a rich array of ecological questions regarding the competitive interplay of the grass and woody components of a savanna system: specifically, how this competitive interplay is explicitly impacted by precipitation, fire, and elephant herbivory. Other factors, such as soil type and non-elephant herbivory, are implicitly incorporated into the model through our choice of parameter values. In the discussion presented here, we review our results in the context of our explicit factors, bearing in mind that implicit factors can be made explicit in the model should we want to address ecological or management questions relating directly to these factors.

Default tree-grass balance

In their comprehensive 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. Shackleton (1997) summarized various studies and concluded that 67% woody productivity is about the expected level for savannas. The output of this model concurs with these two observations (Figures 1-3). In the default model, mean density of adult trees in years 480-500 (219.8 individuals per hectare; mean cover of 5494.0 $m^2 ha^{-1}$, see Figure 1B), is in close agreement with tree densities found in the Klaserie Nature Reserve, South Africa (mean density 258 ha^{-1}, with means for ten vegetation types varying from 144-431 ha^{-1}; Witkowski and O'Connor 1996). Furthermore, the long-term tendency of juveniles, shrubs and trees to cover roughly 1800, 2500 and 5500 m^2 (per hectare), with seedlings comprising approximately 3% of the juvenile cover, respectively translates into 5400, 1750, 280 and 220 individuals in the seedling, sapling, shrub and tree metaclasses: their mean densities in years 480-500 are 5180.5, 1658.1, 268.3 and 219.8 individuals per hectare respectively. The strong left skew of this distribution allows for 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).

Rain/Fire sensitivity

The model of Higgins *et al*. (2000) demonstrates the important role of disturbance in maintaining tree-grass coexistence. The larger-scale demographic model we present here supports that view yet arrives at strikingly different dynamics. In our case the overriding disturbance factor comes not from fire but from drought. The incidence of extra tree mortality in drought years ($z = 0.05$) rises sharply as rainfall declines (the proportions of 3-year rainfall averages falling below 80% mean annual rainfall in our simulations are 10, 15 and 25% for 110, 100 and 90% rainfall respectively). This extra tree mortality is mitigated by strong recruitment of juveniles, in much the same way as Higgins *et al*.'s variability in fire intensity can allow stems to opportunistically recruit beyond the fire escape height – i.e., increased recruitment following disturbance allows tree persistence.

A further difference in the two models' predictions is the community shift under changes in rainfall regime: Higgins *et al*. (2000) predict grass biomass increasing with mean annual rainfall, producing fires of greater intensity and allowing grass dominance, whereas this paper has shown increased woody dominance under wetter conditions.

Higgins *et al*. invoke higher fire intensity in wet conditions, a result of higher grass biomass, as a cause of woody decline; although increased humidity may offset this effect. Our results demonstrate, however, that reduced tree mortality in the concomitant absence of drought, and increased tree growth, can offset such fire intensities. In our model, fire intensity does indeed increase with rainfall (not shown), but a protracted increase in mean rainfall allows the fire intensity effect (which should lead to grass dominance) to be counteracted by increased woody plant survival and recruitment. Jeltsch *et al*.'s (1996) model also found that increased rainfall led to higher tree cover due to improved recruitment, and the deterministic models of Walker and Noy-Meir (1982) and van Langevelde *et al*. (2003) also predict a shift from grassland to savanna to woodland as moisture availability increases.

This model and those of Higgins *et al*. (2000) and van Langevelde *et al*. (2003) are in agreement that reduced rainfall decreases woody plant dominance, via recruitment limitation and extra incidence of drought-related mortality (this model). Viljoen (1988) suggested that reduction in the woody component of the Kruger National Park's marula-knobthorn (*Sclerocarya birrea - Acacia nigrescens*) savanna between 1944-1981 was due mainly to an extended drought in the 1960's, interacting with elephant and fire effects.

Walker and Noy-Meir (1982), Belsky (1990) and Behnke and Scoones (1993) produce phase diagrams of expected savanna composition with rainfall and nutritional gradients (on a regional scale) which suggest that a progression to either state (grassland or woodland) may be feasible, depending on the region, species composition and soil nutrient levels – which are not explicitly considered here.

The stochastic fire regime in our default model gives a mean fire return period (FRP) of 7.57 years, changing to 9.39 and 5.58 years under wet (110% rainfall) and dry (90% rainfall) scenarios as grass cover decreases and increases respectively (see Figure 9 for more examples). The typical range of FRPs for the Kruger National Park in South Africa is 1-11 years with a mean of 3 years for sourveld and 8 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). It is very reassuring that we can stochastically generate fire events and produce realistic results 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*. (1997a) also generated realistic fire frequencies using a probabilistic fire submodel for Kalahari thornveld.

Hochberg *et al*. (1994) found that yearly fires were not sufficient to exclude trees from a model savanna, yet our model suggests that trees may be excluded by choosing very high values for y, the probability of fire per kg of grass biomass (Figure 3B). Nevertheless the model is quite insensitive to reasonable changes in y (Figure 3B: compare endpoints for 75% and 125% fire probability). Hochberg *et al*. (1994) also found that the equilibrium level of trees was insensitive to fire regime, unless fire mortality of seedlings was greater than 98%. This insensitivity may arise because the result of reducing fire frequency is to allow grass fuel to build up, leading to increased fire intensity and woody plant mortality when the fire eventually occurs. The tree-grass balance is also quite robust to variation in the woody plants' response to fire, as demonstrated by the relative insensitivity to the proportion coppicing k_i ($2 \le i \le 7$), shown in Figure 3C. Most savanna tree species have high rates of resprouting so that the rapid fall-off in woody plant cover as the k_i decrease below 0.5 may indicate that $k_i <<$ 0.5 is unlikely for savanna species, unless vulnerability to fire is reduced or compensated for by some extra feature such as higher seed production (ignored at this juncture) (Gignoux *et al*. 1997, Bond and Midgeley 2001). Higgins *et al*. (2000) also found that coexistence was unlikely once the coppicing rate fell below 0.6.

As would be expected, enhanced woody plant growth leads to an increase in woody cover at the expense of grass (Figure 3D), the higher growth rates allowing woody plants to compete more strongly with grass and to reach the fire escape height more quickly. This extra woody cover is manifested as an increase in adult trees at the expense of grass cover (even though grass is allowed to grow under tree canopies), with the subadult metaclasses being relatively unaffected as a result of their quicker turnover to reach the adult class. As knowledge of woody plant growth rates for African savannas is lacking or ambiguous even within a single species (see Model Parameterization, above), this strong shift in the tree-grass balance within a reasonable range of growth estimates demonstrates the importance of obtaining pertinent demographic data. Of course, by modeling one generic tree species we have neglected the possible influence of interactions between fast and slow-growing tree species which may also differ in other life-history strategies such as survival or fecundity. Neither have we allowed for faster growth of coppiced individuals, due to stored reserves, which would favor the woody plant component (Menaut *et al*. 1990).

Elephant effects

The trajectories in Figure 4 show the typical “elephant problem” (Glover 1963, Caughley 1976, Barnes 1983b) 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 (for example Field 1971, Croze 1974b, 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 back up 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 semi-arid savanna, however, and found that the ensuing drop in woody plants produced 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 to linked km^2 patches of a larger model. 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 (our output shows the savanna at the end of the wet season, i.e., following woody growth and prior to fire and elephant damage). 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 utilization and in their response to this utilization (Anderson and Walker 1974, Croze 1974b, 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) multi-species model. Figures 5, 7 and 8 depict how changes in plant properties can alter the fate of vegetation composition and structure. The default elephant-savanna model is summarized in Figures 5A and 8A for constant elephant densities between 0-3 km^{-2}. Although elephant densities tend to lie below 2 km^{-2}, densities in excess of 5 km^{-2} have also been reported (Laws 1970, Owen-Smith 1988, Lewis 1991, Ben-Shahar 1996b). 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 km^{-2} or greater will result in inevitable reduction in woodland, with over 70% 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% yr^{-1} with elephant densities of between 1 and 2 km^{-2}, with a possible shift in woodland species composition. Ben-Shahar (1996b) 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 km^{-2} for *Baikiaea plurijuga* woodlands, 11 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 (we assume 25% of elephant utilization of adults is negligible so that this 80% mortality applies to the remaining heavily-impacted 75% of those utilized – see Model Parameterization, above). Figures 5B, 7B and 8B allow for less vulnerability, either in terms of different forms of impact and/or increased resilience to utilization, by halving this mortality rate to $m_i^e = 0.4$, ($i = 8, 9$). Under this assumption, some woody cover remains for a century even at elephant densities of 1.5 km^{-2}, and 100 years after the introduction of 1 elephant km^{-2}, 37% of cells still have woody cover of more than 5000 $\mathrm{m}^2\,\mathrm{ha}^{-1}$ (c.f. 8% for the default model).

Our model does not explicitly consider the proportion of elephant utilization 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 increasing recruitment by assisting in dispersal and germination of drupes such as the marula, *Sclerocarya birrea* (Lewis 1987a and this paper). Croze (1974b), 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. Figures 5C, 7C and 8C demonstrate that this effect can indeed allow longer woody-plant persistence, for elephant densities up to 2 km^{-2} (and with 55% of cells still having woody cover of more than 5000 m^2 ha^{-1} after a century of 1 elephant km^{-2}). Although the role of elephants in dispersing seeds was not explicitly modeled, we can rationalize by noting that our elephants will preferentially visit those cells which have a higher tree representation, thus are more likely to defecate in those cells which are modeled as producing more seedlings anyway, i.e., higher tree density in cell x leads to increased elephant time spent in cell x, resulting in greater fecal deposits in cell x, culminating in an increase in seeds deposited in cell x. The key (implicit) assumption is time spent in each cell, although we do not necessarily imply that the deposited seeds originate from trees within that actual cell – they may even have been introduced from outside the grid, but we assume an overall balance of distribution. Of course, in areas of more- or less-elephant-favored vegetation, a source-sink dynamic may occur; this possibility is outside the scope of this paper and would also operate at a larger spatial scale than is appropriate for this model.

In a similar fashion, Figures 5D, 7D and 8D 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, response to fire, browsing, etc. (see Model Parameterization, above), 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 utilization persists, slow-growing or particularly vulnerable species may in time be replaced by faster-growing or more resilient 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 under densities of up to 3 elephants km^{-2}, a faster-growing tree species may still persist for over 100 years, with 91% of cells still having woody cover of more than 5000 m^2 ha^{-1} after a century of 1 elephant km^{-2}. The striking difference between the default and 60cm-growth scenarios emphasizes that, in addition to the obvious need for growth data, variation between different species' growth rates must be taken into account when managing savannas, particularly with respect to decisions regarding elephant populations.

As well as the overall decline in the tree species produced by our model, the vertical structure becomes less adult tree dominated at higher elephant densities, reflecting a shift towards a shrubland woody structure within the increasingly grass-dominated community. This is particularly the case for the elephant-enhanced fecundity scenario (Figure 5C). Continued elephant utilization 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 towards shrub-domination of the woody component in the results presented here occurs only as part of an overall shift towards grassland. The ability of trees to coppice following impacts from elephants or fire, leading to dense shrubland, is dependent on underlying soil type (Jachmann and Bell 1985, Lewis 1991, Trollope *et al*. 1998). We do not explicitly consider this factor here, although the model is easily extended to specific edaphic conditions by adjusting the parameters for grass productivity, woody growth rate and drought-response.

The quasi-removal curves shown in Figure 8 reflect the same patterns seen in figures 5 and 7 for different elephant-plant interaction assumptions, with higher elephant populations producing more grass-dominated savannas, while woody plant populations are more likely to persist if resilience to impacts, elephant-mediated germination or higher growth rates are accounted for. Presentation of results in such a format emphasizes some of the greatest of southern African savanna management concerns: the persistence of species and structural diversity in the presence of a globally endangered (IUCN status EN-A1b) but locally destructive megaherbivore. As such it allows management decisions regarding elephant impacts to be more informed: deciding whether or not to introduce elephants into a reserve, or to attempt population manipulation by contraception, translocation or culling (Barnes 1983b, Whyte *et al.* 1999).

As is the nature of any model, the work presented here is based on many assumptions and approximations, which may affect the results to greater or lesser extents: for example, the assumption of a uniform environmental substrate and topology across the grid; strict seasonal partition of vegetation increase, decrease and utilization by elephants; simplification of fire timing and of elephant population structure and dynamics, habitat use and feeding patterns. Future variants of the model will address some of these simplifications. Nevertheless, we 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. It shows reasonable savanna dynamics, allows for a wide range of assumptions, parameters and scenarios to be tested, and provides a panoply of results which are merely summarized here. Management discussions involving long-lived organisms must inevitably rely on models such as the one presented here to perform meaningful thought-experiments and make informed decisions (Starfield and Bleloch 1986).

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 model responds in reasonable fashion to variations in rainfall and fire dynamics. The introduction of elephants into the model demonstrates a possible loss of woodlands – however this trajectory may be mitigated in the case of faster tree growth, decreased vulnerability to heavy utilization, 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 is of the utmost importance. This research suggests that further work on woody plant demographics is essential before decisions are made based on the putative impacts of elephants on savanna systems, particularly if those decisions involve culling elephants.

Acknowledgements

We thank P. Cross, K. Duffy, J. du Toit, S. Higgins, J. Lloyd-Smith, D. McCullough, T. O'Connor, N. Owen-Smith, J. Redfern, S. Ryan and C. Wilmers for valuable comments on an earlier draft of this paper, and M. Rietkerk for access to an unpublished (van Langevelde *et al*) paper. The authors would like to thank South African National Parks and the Scientific Services Division of the Kruger National Park for facilitating parts of this study. PWJB would also like to thank the Mammal Research Institute, University of Pretoria, for use of their facilities. The work was supported by a Foreign Language and Area Studies Fellowship and Andrew and Mary Rocca Travel Scholarship (PWJB) and by NSF grant DEB-0090323 (WMG).

Chapter Three

Effects of elephant impacts on two competing tree species in an African savanna model: insights into coexistence and management.

Peter W. J. Baxter and Wayne M. Getz.

Abstract

High densities of elephants in African savannas have been blamed for shifts in vegetation community composition, with reductions in populations of rare, vulnerable and/or palatable trees. Here we present a savanna simulation model which seeks to investigate under what situations, in terms of plant characteristics and elephant feeding preferences, such community changes may take place. We adapted an existing tree-grass savanna model by including a second tree species to investigate the effects of elephant impacts on species composition within the woody community. The model allows for spatial and vertical vegetation structure, and includes realistic environmental variability via stochastic fire and rainfall processes. The two tree species vary with respect to their growth, fecundity and survival and differ in the degree to which they are "r- vs K-selected." The model produces similar tree-grass dynamics when run with either species alone, and when both species are included produces an initial period of dominance by the early-successional species followed by its eventual competitive exclusion by the later-successional species on a timescale of centuries. We examined how variation in parameters of one species affected its coexistence or competitive exclusion in the savanna without elephants. Increases in any or all of growth, fecundity or survival of the early-successional species increased the likelihood of its persistence over 500 years. For selected parameter combinations, we investigated the effects of introducing an elephant population on long- and short-term trajectories of the plant community. The presence of the faster-growing plant species in the model enabled both species to survive greater elephant densities. As elephant densities are increased, the savanna community changes from tree dominance to grassland while the tree community shifts towards the more "r-selected" species. Spatial heterogeneity increases with elephant density and time. We tested the effect of plant responses to elephant impact (resilience of adult trees and elephant-enhanced germination), and examined the interaction of these strategies with varying elephant preference for either species. Resilience to impact (reduced mortality following impact) was the more successful strategy and may act synergistically between tree species. Fire suppression also mitigated the effects of elephant damage, confirming its useful role in management strategies. We conclude that while elephants may cause woodland to decline, they can also enhance biodiversity at lower densities, and increase spatial heterogeneity. Conservation workers should be conscious of the array of species types and their interactions when planning to manage savannas and/or elephant populations for biodiversity.

Introduction

The "elephant problem," in which high densities of elephant (*Loxodonta africana*) in African savannas have severe impacts on woody vegetation, has been an issue of concern and research for many decades (e.g. Glover 1963, Caughley 1976, Barnes 1983b). Faced with severe impacts, and their concomitant implications for biodiversity loss (Cumming *et al.* 1997, Fritz *et al.* 2002), managers of reserves seek to make informed decisions regarding possible control of elephant populations (Whyte *et al*. 1999), including reduction by culling, which in turn may have repercussions on the regional and global elephant population (Barnes 1983b). Here we present a savanna model designed to give detailed information about species, structural, and spatial changes resulting from elephant impacts.

Field research has elucidated the multi-faceted nature of elephant impacts and the complex ecological interactions which may lead to changes in species and structural diversity of woody plants. Extremely high rates of decline in adult trees have been recorded under certain conditions. For example Field (1971) reports a decline in large trees of 14.6% per annum from Queen Elizabeth National Park, Uganda, as the elephant population increased to 1.7 individuals km^{-2} and Swanepoel and Swanepoel (1986) report baobab (*Adansonia digitata*) mortality of 15.5% over 6 months at an elephant density of 2 km^{-2} in the Zambezi Valley, Zimbabwe. Reports of tree loss rates of 6% per annum are common (Lamprey *et al.* 1967, Pellew 1983, Mwalyosi 1987).

Due to the strong regeneration capability of savanna trees following damage by elephants or fire, structural conversion of woodland to shrubland may occur as regenerating plants get trapped in a shrub-like state by burning or browsing (Guy 1989, Leuthold 1977, Lewis 1991, Pellew 1983). The lowering of canopy height, and the relative nutrient richness of regrowth shoots favors continued browsing by elephants and other herbivores, resulting in prolonged maintenance of shrubland as adult reestablishment is suppressed (Jachmann and Bell 1985, Mapaure and Mhlanga 2000, Smallie and O'Connor 2000, Styles and Skinner 2000). However, recurrent fire can prevent reestablishment of adult trees, leading to eventual population decline (Buechner and Dawkins 1961, Napier Bax and Sheldrick 1963, Lamprey *et al.* 1967, Field 1971, Field and Ross 1976, Norton-Griffiths 1979, Guy 1981, Pellew 1983, Jacobs and Biggs 2002a) although the interactions of elephant and fire damage are not always synergistic (Ben-Shahar 1993, 1996b, Mapaure and Mhlanga 2000).

Other factors interacting with elephant damage include soil type (McShane 1989, Lewis 1991, Jacobs and Biggs 2002b, Trollope *et al.* 1998) and catenal position (Styles and Skinner 2000, Nellemann *et al.* 2002) which affect plant growth patterns and nutrient content, thus affecting tree susceptibility and resilience to elephant utilization. Reestablishment of adult trees can be impeded by other browsing mammals, most notably giraffe (Norton-Griffiths 1979, Pellew 1983, Ruess and Halter 1990) but also impala (Lewis 1987a, Prins and van der Jeugd 1993) and other antelope (Styles and Skinner 2000 (eland), Mapaure and Campbell 2002 (debarking by buffalo and kudu)). Elephant impacts can also be exacerbated by drought conditions (Napier Bax and Sheldrick 1963, Leuthold 1977, Tafangenyasha 1997, Mosugelo *et al.* 2002) and by attack by insects and fungi (Thomson 1975).

Field observations have highlighted elephant-induced changes in community structure as palatable abundant tree species are selectively reduced (Guy 1981, Ruess and Halter 1990, Leuthold 1996, Tafangenyasha 1997) and savannas become dominated by woody species which are unpalatable (Guy 1989, Jachmann and Croes 1991, Leuthold 1996) or disturbance-tolerant (Buechner and Dawkins 1961, Simpson 1978, Ben-Shahar 1996b). Elephants demonstrate distinct dietary preferences for particular species (e.g. marula *Sclerocarya birrea*; Duffy *et al.* 2002), while avoiding others such as latex-bearing *Euphorbia candelabrum* (Field 1971). Bowland and Yeaton (1997) recorded elephants preferring later successional species such as *Acacia caffra* and broadleaved trees, while avoiding early successional species such as *A. nilotica*. Preferences may vary with habitat, location or season. For example, elephant preference for *Colophospermum mopane* has been recorded (Jarman 1971, Ben-Shahar 1993, 1998, Smallie and O'Connor 2000) whereas others have found relatively low occurrence of *C. mopane* in the diet (Anderson and Walker 1974, Lewis 1986, Styles and Skinner 2000). *Delonix elata* is not typically eaten but may become heavily utilized in drought conditions (Agnew 1968, Leuthold 1977).

In contrast to the emphasis of field observations on vegetation community-level changes, attempts at modeling elephant impacts have focused mainly on single-species responses, with shifts in species composition only implied. For instance the frame-based model of Starfield *et al.* (1993) assumed that different woody species dominated as the vegetation community shifted from prevailing woodland to bushland conditions (frames), but did not consider inter-specific dynamics between woody plants. Recent work by Duffy *et al.* (2000), however, employs a Lotka-Volterra model to suggest that a rare tree species, in competition with an abundant tree species favored by elephants, may find a functional refuge as elephants suppress the more abundant species. The only elephant-vegetation models to dynamically link elephant population dynamics to vegetation have been those based on Lotka-Volterra predator-prey models (Caughley 1976, Duffy *et al.* 1999, 2000; see also the vegetation-mesoherbivore-macroherbivore model of van de Koppel and Prins (1998)). Other previous elephant-savanna models have been logistic vegetation models with harvesting by input elephant populations (Barnes 1983a, Ben-Shahar 1996a), and discrete models of structured woody vegetation with fixed levels of fire and non-elephant herbivory (Norton-Griffiths 1979, Pellew 1983, Dublin *et al*. 1990, Dublin 1995, Ben-Shahar 1996b, Birkett 2002). None of the above models, however, include grass dynamics, competing species of woody plant, or spatial attributes; and the lack of credible savanna vegetation dynamics in elephant impact models to date has been emphasized (Chapter 2). Ben-Shahar (1996a) modeled different scenarios of fixed rainfall but otherwise rainfall variation has also been neglected. Van Wijngaarden's (1985) model of the Tsavo ecosystem in Kenya partitions woody plants into tree and shrub layers and includes elephant and other herbivore populations dynamically linked to the vegetation state (grazing capacity). Variation in rainfall and spatial distribution of impacts are not taken into account, however, and fire is introduced on a fixed five-yearly basis.

These factors – multiple plant species, vertical and spatial structure, environmental (rainfall and fire) variability – have been included more frequently in models constructed to investigate the roles of other processes in savanna dynamics, e.g. cattle grazing (Jeltsch *et al.* 1997a, 1997b, Weber *et al.* 1998), carbon and water flux (Simioni *et al.* 2000) and fire and other disturbances (Menaut *et al.* 1990, Hochberg *et al.* 1994, Wiegand *et al.* 1997, Jeltsch *et al.* 1996, 1998 Higgins *et al.* 2000). Heretofore, the models that have proved more successful in replicating savanna dynamics have either been individual-based models (Menaut *et al.* 1990, Hochberg *et al.* 1994, Higgins *et al.* 2000) or models operating at a fine-grained scale (up to 25-m^2 patches: Hochberg *et al.* 1994, Jeltsch *et al.* 1996, 1997a, 1997b, 1998, Weber *et al.* 1998, Wiegand *et al.* 1997). These two approaches do not lend themselves readily to informing management decisions. Some simpler non-spatial models have also provided useful insights into savanna processes such as tree-grass coexistence and the role of herbivory (Noy-Meir 1982, Walker and Noy-Meir 1982, van Langevelde *et al.* 2003) but lack sufficient detail to gain insight into elephant effects on the vertical structuring of woody plants.

Here we include a second tree species in an existing elephant-savanna model (Chapter 2), that includes rainfall and fire variability, spatial and vertical vegetation structure, and tree-grass competition, to obtain a model capable of addressing several critical issues regarding the management of elephant populations. Relative to most other savanna vegetation models, our model employs a large spatial grain and extent while maintaining reasonable assumptions, and produces credible vegetation dynamics. Thus it provides a suitable platform for investigating the impacts of elephant on vegetation at the community level. Inclusion of the additional tree species allows more detailed insight into community dynamics than possible with previous models. Output is presented on timescales that inform managers of expected species-shifts under various plant life-history trade-offs and elephant pressures.

Methods

Our model is developed from a previous single-tree-species version (Chapter 2), with the only major structural difference being the inclusion of a second woody species. Growth and reproduction of woody plants and grass depend on stochastic annual rainfall and competition, which is modeled on a per-area basis. Natural rates of senescence and mortality are augmented by drought, fire and elephant herbivory. Fire and elephant impacts may also cause a net reduction in size of woody plants, as a result of top-kill and resprouting. Seed dispersal, stochastic fire spread and elephant herbivory are included as spatial processes. The model equations and parameters are given in the Appendix (see Chapter Two for detailed description of model development, assumptions and parameterization). In our parameterization, the two woody species differ only in growth, fecundity and survival rates. We explore the response of the vegetation community to changes in these rates for the additional species, and, for selected parameter combinations, the response of the community to elephant impacts and strategies of resilience to those impacts.

Vegetation structure.

In development of our model, we consider two tree species, denoted v and w, and one biomass component for grass, denoted by y, in the vegetation component of the savanna. We partition space into a 10×10 grid of 1-hectare (10000 m^2) cells. We emphasize changes and transitions in the vertical woody structure by dividing v and w each into nine height classes of tree, the i-th class of which, in cell x at time t, has number of individuals $v_{x,i}(t)$ or $w_{x,i}(t)$ ($i = 1, 2, \ldots, 9$). These classes are more concisely represented by the column vectors

$$\mathbf{v}_x(t) = (v_{x,1}(t), \ldots, v_{x,9}(t))',$$

$$\text{and} \quad \mathbf{w}_x(t) = (w_{x,1}(t), \ldots, w_{x,9}(t))'$$

where ' denotes the transpose of a vector. The nine stage classes for each woody species represent four broader classes ("metaclasses"): seedlings are <15cm tall ($i = 1$), four sapling classes ($i = 2, \ldots, 5$) are <1m tall (surviving individuals advancing automatically between these subject to sufficient rainfall), two shrub-sized classes of 1-2m ($i = 6$) and 2-3m ($i = 7$; i.e., up to fire escape height; Pellew 1983), and two tree classes of 3-5m ($i = 8$) and >5m ($i = 9$; beyond browsing height). An individual in each of these metaclasses is assumed to control a resource area of 0.01, 1, 9 and 25 m^2, respectively (after Kiker

1998). Further, we define $y_x(t)$ as the grass biomass (measured in kg) in cell x at time t. Area covered by grass is also tracked, and the area of cell x covered at time t by individuals in class i ($i = 1, \ldots, 9$), is given by $a_{x,v,i}(t)$, $a_{x,w,i}(t)$ and $a_{x,y}(t)$, for woody species v and w, and grass, respectively.

Choice of parameters for woody species.

The parameters selected for species w are the default values of the tree species in Chapter Two. As noted in Chapter Two there has been little consistency in demographic rates recorded for woody savanna species and so we vary the parameters for species v freely, and investigate the competitive tradeoffs of growth, survival and fecundity strategies. Our default parameters for species v were chosen so that its trajectory in the single tree-species savanna model would closely match that of species w.

We contrasted two life-history strategies in the parameterization of the woody species vital rates: species v invests more strongly in reproduction and fast growth than species w, which invests more strongly in survival (for convenience we follow the traditional caricature of this trade-off as r- vs K-selected species). We chose parameters for species v that produce a similar dominant eigenvalue (λ1.5) of its Lefkovitch matrix to that of species w. Simulations indicated mean life expectancies (in the absence of reproduction, competition and disturbance) of 12.7 and 192.6 years for individuals of species v and w, respectively.

Model Simulations

We seeded the random number generator to allow replication of runs and improve comparison between sets. We ran at least 25 replicates of each parameter combination, but more (100) for runs requiring less memory or execution time speed allowed. The model was started at the start of the wet season in the first year of a wet phase in the 20-year wet/dry cycle. Initial vegetation structure was identical for all grid-cells, and comprised of 5000 m^2 grass cover (1250 kg biomass), and 5000 m^2 woody cover, divided equally among the woody species and split according to the left eigenvector corresponding to the dominant eigenvalue of either woody species.

We chose a timescale of 500 years to examine behavior of the savanna vegetation while varying the parameters for species v. Although our initial trials showed that some parameter sets took many millennia (>20000 years) to reach a steady state, we verified that the state of the populations after 500 years approximates a quasistationary distribution (Nåsell 2001), sufficiently well for questions addressed in this paper. For management-oriented questions involving elephant impact we chose a timescale of 100 years, after allowing an initial transitory period of 100 years prior to elephant introduction which was sufficient to eliminate the influence of initial conditions on our analysis. We performed extensive vegetation-only simulations, varying growth, survival and fecundity of species v to explore its fate matched against species w. For selected species v growth-fecundity-survival parameter combinations we investigated the effect on the model savanna of introducing various (constant) elephant densities. We explored further plant strategies for the default parameter sets, namely increased resilience to elephant impacts and elephant-enhanced germination (see also Chapter 2), and the interaction of these strategies with elephant preference for either woody species. We examined changes in spatial heterogeneity over elephant density and time, and explored the possibility of mitigating elephant damage through fire suppression.

Results

Model output, given as area covered (m^2 per 1-ha grid-cell) is aggregated within woody species into juvenile (<1m height), shrub (1-3m) and adult tree (>3m) strata, and for most of the results is presented as either total or percentage area covered by species *v*, species *w*, and grass. For brevity, we refer to "woody plant species" as "tree species" and use "adult trees" for woody plants >3m in height in future.

To confirm correspondence with our original single-tree-species model, and between our two model tree species, we obtained single-species trajectories for species *v* (Figure 1A) and species *w* (Figure 1B), by setting the initial density of the other species to zero. Both species demonstrate long-term tree-grass coexistence. Moreover, trees and grass coexisted for each of the 100 random simulations for either woody species.

Including both tree species together in the model produced the trajectories shown in Figure 2A (area covered by species and stratum) and Figure 2B (total area covered by each species). Although species *v* dominates in the first five decades, ultimately it is competitively excluded by species *w* and the overall vertical savanna structure (not shown) approaches that of Figure 1B.

We next explored the sensitivity of the competitive outcome between species *v* and *w* to the growth, survival and fecundity parameters of species *v*. We kept these parameters fixed throughout for species *w*, the model species from Chapter 2, but allowed the parameters for species *v* to vary. Growth of species *v* was varied between 25 and 65 cm per annum (species *v* and *w* defaults were 60 and 30 cm per annum, respectively), and *v*'s fecundity was varied between 40 and 125 seedlings per tree per annum (species *v* and *w* defaults were 100 and 50 seedlings per tree per annum, respectively). We varied *v*'s survival rates over five levels, $\mathbf{s}_i$, i=1, …,5, setting $\mathbf{s}_i = ((5-i)\mathbf{s}_1 + (i-1)\mathbf{s}_5)/4$ (i.e. $\mathbf{s}_1 \eta \mathbf{s}_v$ and $\mathbf{s}_5 \eta \mathbf{s}_w$, the default *v* and *w* survival rates; see Appendix, with $\mathbf{s}_2$-$\mathbf{s}_4$ interpolating between these). The dominant eigenvalues associated with these survival vectors (with otherwise baseline values for growth and fecundity) are $\lambda(\mathbf{s}_1) = 1.528$, $\lambda(\mathbf{s}_2) = 1.592$, $\lambda(\mathbf{s}_3) = 1.656$, $\lambda(\mathbf{s}_4) = 1.719$ and $\lambda(\mathbf{s}_5) = 1.783$.

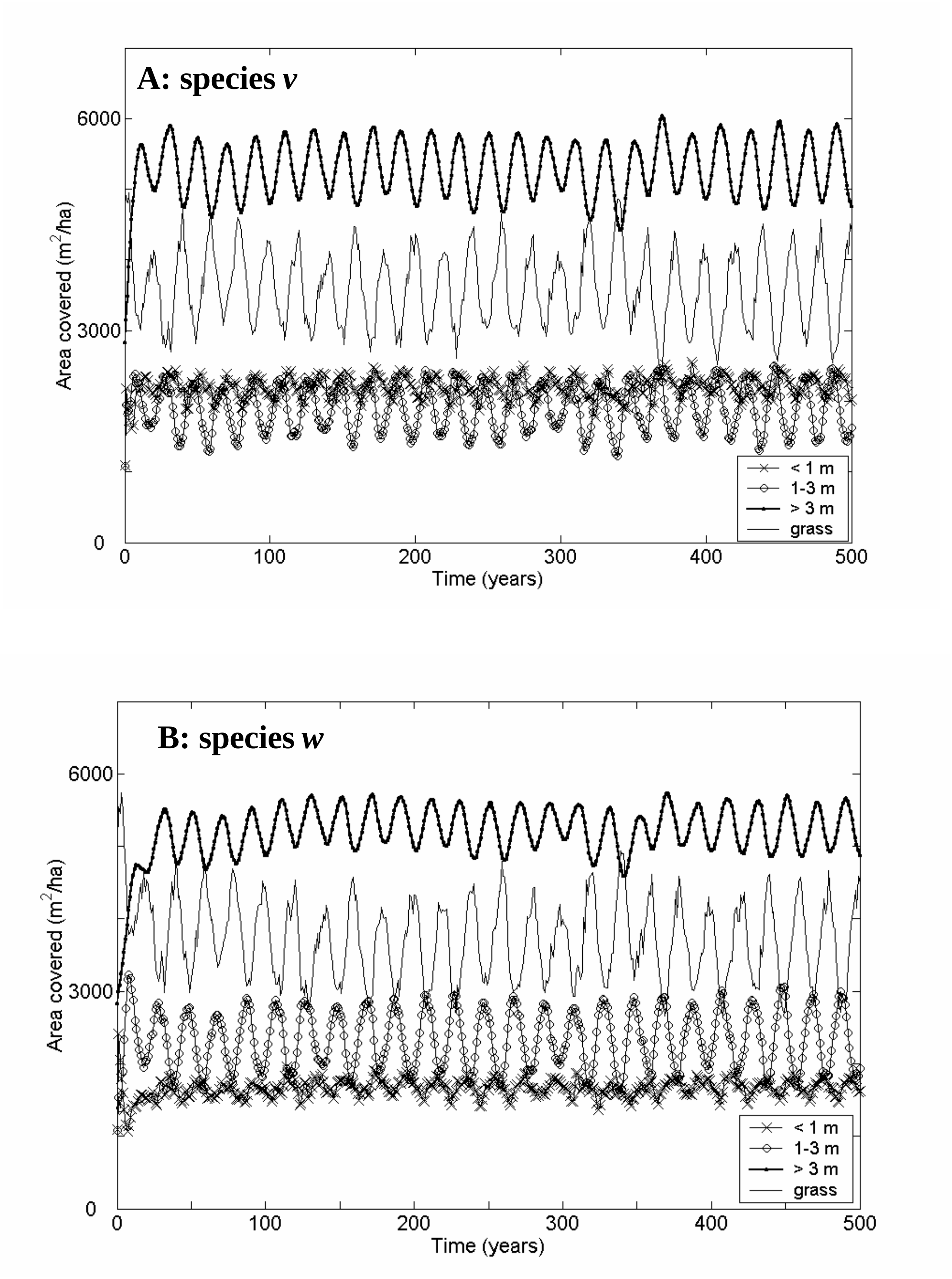


Figure 1. Trajectories for savanna model with only one woody species (the alternative species set to zero). A: species *v*, the growth/reproduction investing species; B: species *w*, the survival-investing species (cf. Chapter 1). Output is recorded at the end of wet seasons only, mean of 100 runs and grid-cells shown.

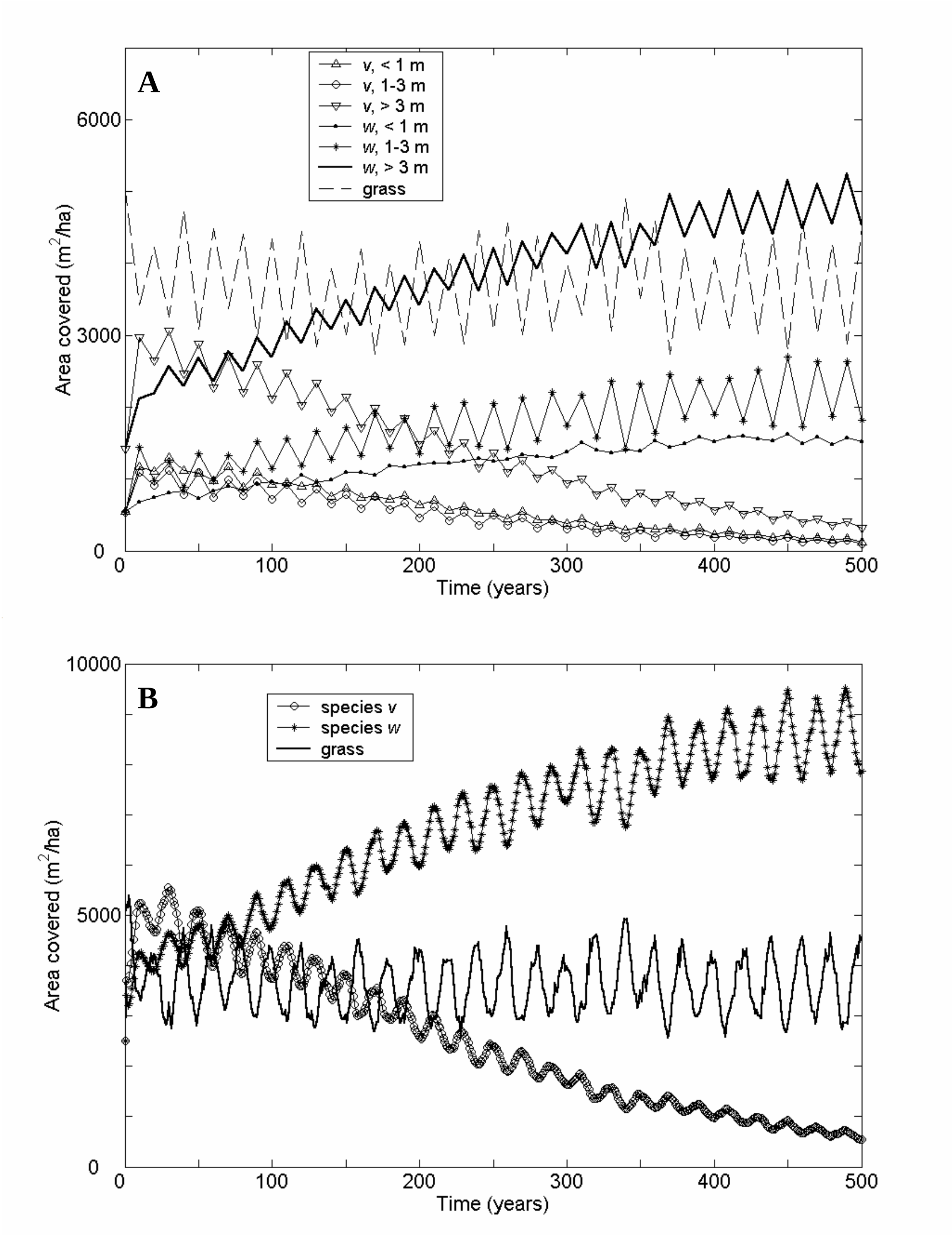


Figure 2. Trajectories for savanna model with both woody species starting at 25% cover each (with 50% initial grass cover). A: Output of species and structure; B: Total aggregated cover for each species. Mean of 100 runs and grid-cells shown.

Figures 3A and 3B show the percentage of area covered by *v* and *w* after 500 years, as *v*'s growth, fecundity and mortality parameters are varied. Figures 3C and 3D show how the persistence to year 500 of *v* and *w* changes with *v*'s parameters where "persistence" in this case is defined as at least 0.5 m^2 cover per hectare (= one sapling, after rounding the results to the nearest sapling). Species *v* persistence and cover is enhanced by its increased growth, fecundity or survival and species *w* persistence and cover is diminished. At least one tree species persists in all parameter combinations.

To examine the effect of introducing an elephant population (at constant density) to the savanna, we chose selected growth-fecundity-survival parameter combinations of species *v*. Specifically we examined the trade-off in vital attributes as species *v* approached a species *w* strategy, by reducing either growth or fecundity to species *w* levels while increasing survival to intermediate levels (growth-fecundity-survival parameter combinations of {60 cm yr^{-1}, 100 seedlings $tree^{-1}$ yr^{-1}, $\mathbf{s}_1$}, {30, 100, $\mathbf{s}_3$}, {60, 50, $\mathbf{s}_3$} and {30, 50, $\mathbf{s}_5$}); the two intermediate cases had dominant eigenvalues (density-independent case) of 1.549 and 1.477, and simulated life expectancies of 36.5 and 28.4 years, respectively. The elephant population was introduced at year 100, to allow for initial transient dynamics in the tree-grass balance to fade, although the tree component of the savanna is still in transition from domination to exclusion of species *v* (cf. Figure 2). Figures 4A-D show the state of the savanna after 500 years for various elephant densities introduced at year 100 (i.e. 400 years of elephant presence), for comparison with Figures 3A and 3B. Figures 4E-H shows the vegetation state 100 years after elephant introduction, a more meaningful time-frame for managers. Woody cover of both species decreases with increasing elephant densities although for low elephant

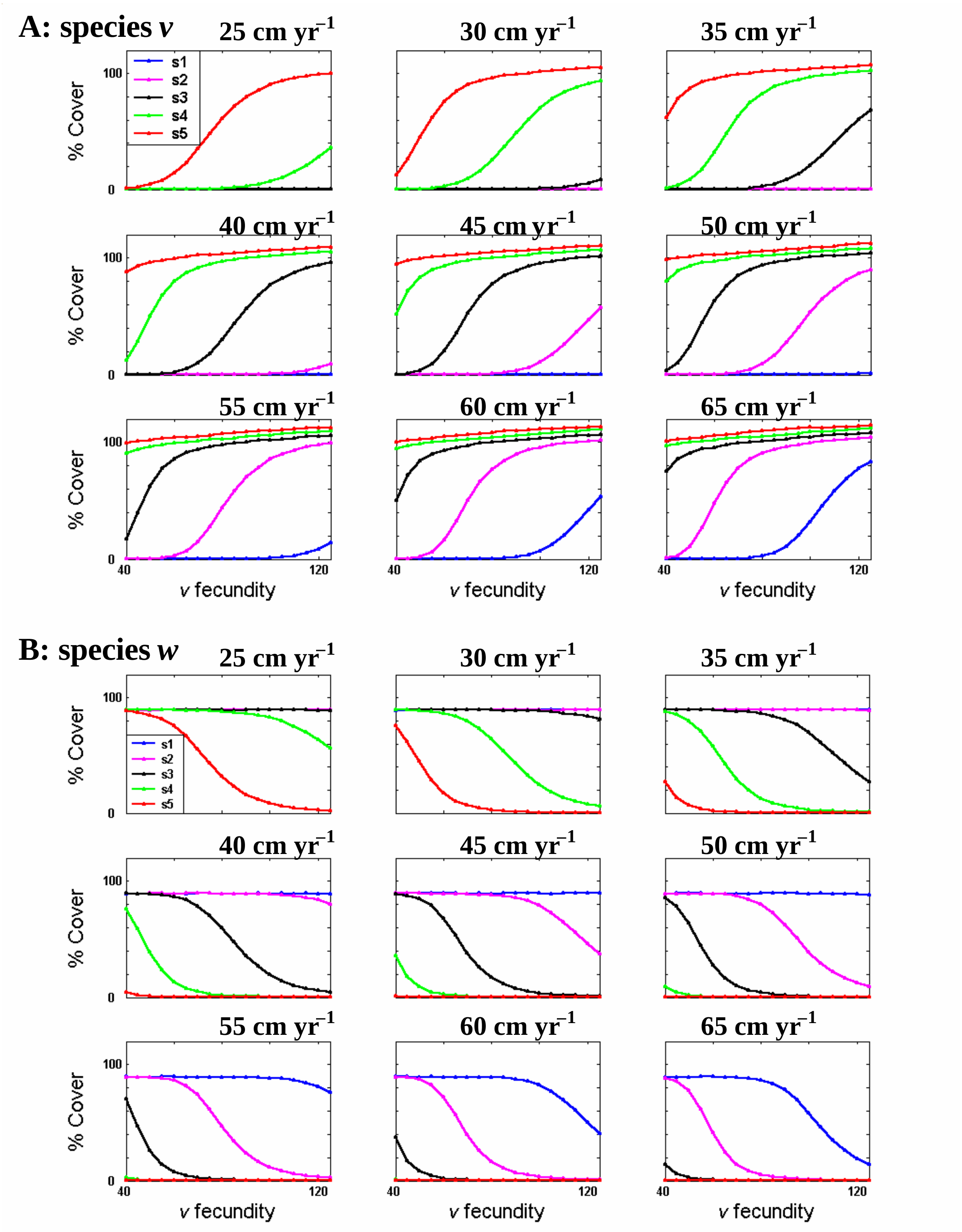
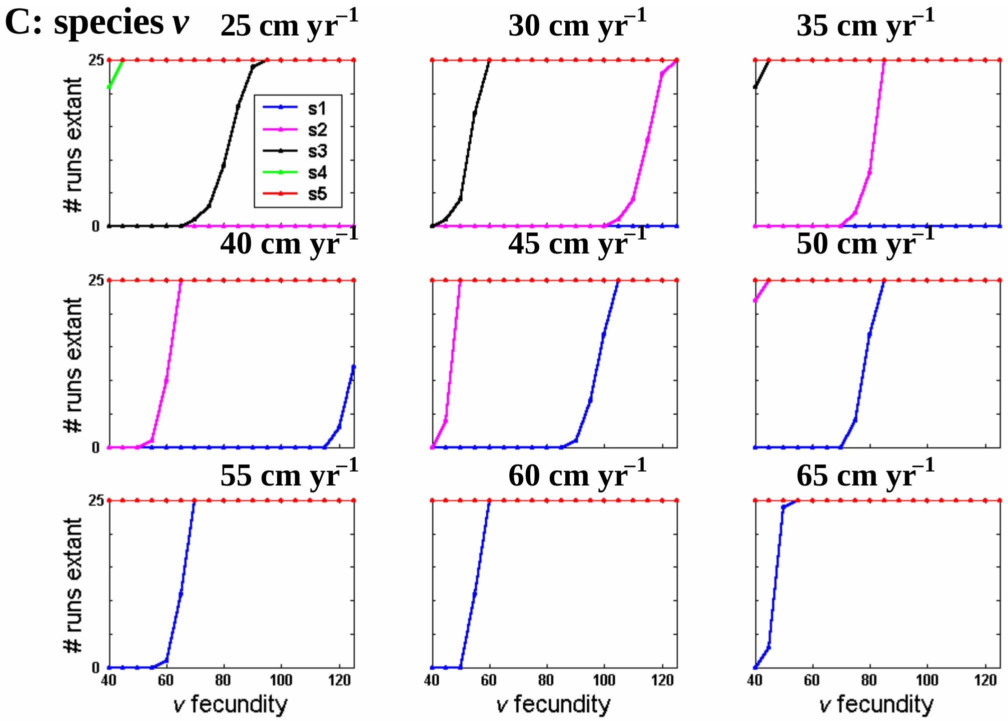
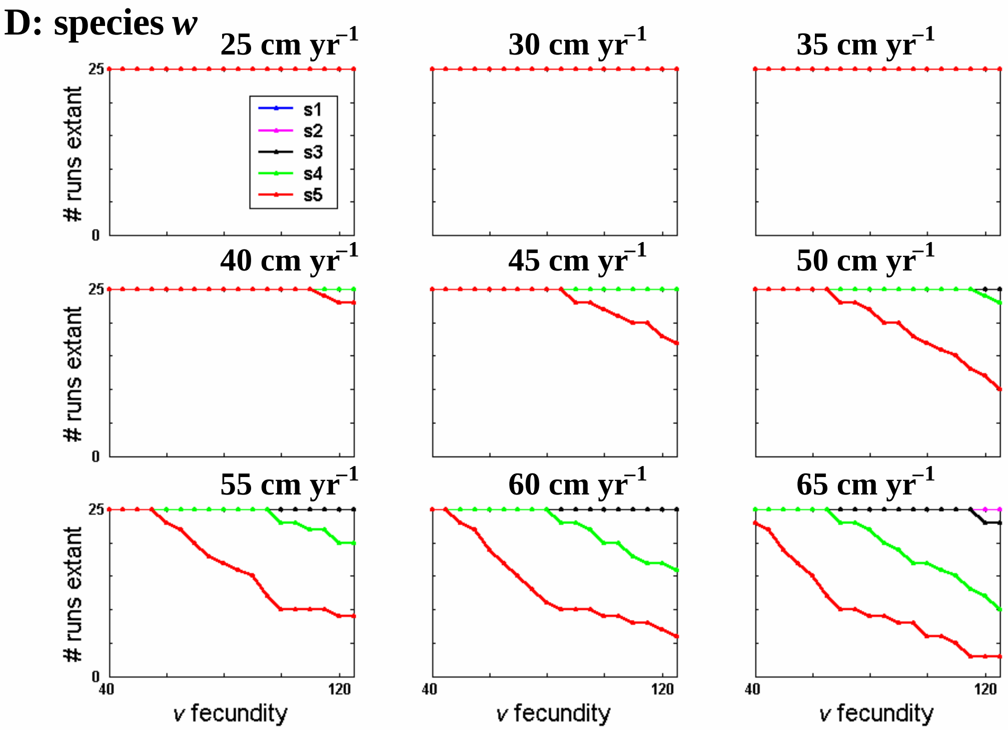


Figure 3. Effect of varying growth (25-65 cm y^{-1}), fecundity (40-125 seedlings $tree^{-1}$ y^{-1}) and survival ($\mathbf{s}_1$-$\mathbf{s}_5$) of species *v* on the persistence and cover of both woody species. A: mean cover at year 500 of species *v*; B: mean cover at year 500 of species *w*. (continued)



C: species *v*



D: species *w*

Figure 3 (continued). C, D: persistence to year 500 of species *v* and *w* respectively. Total or mean of 25 runs per parameter combination shown. Species *w* parameters are kept fixed throughout. Note that cover can sum to more than 100% (i.e. more than 10,000 m^2 per hectare cell) because saplings and grass can grow under tree canopies.

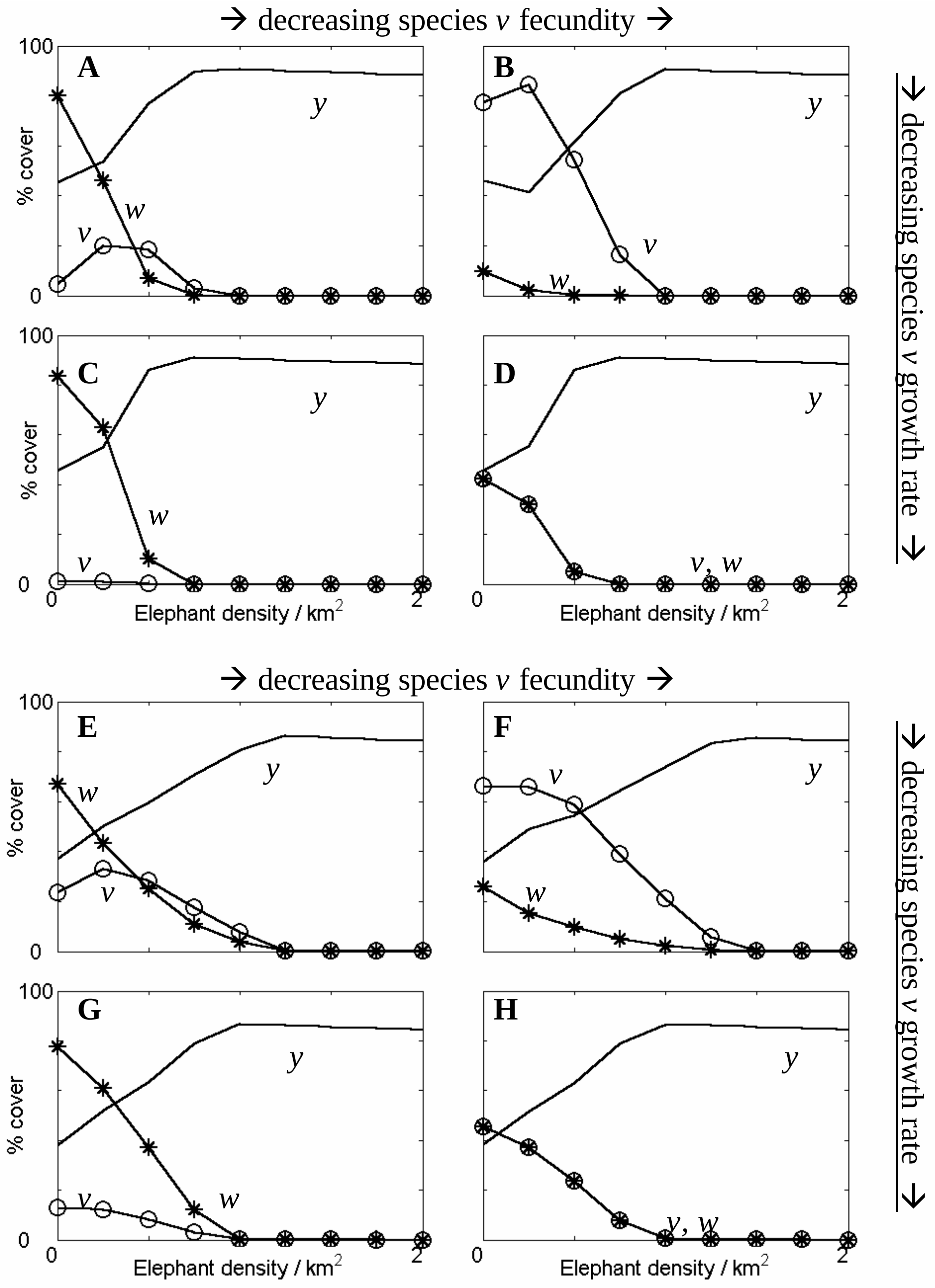


Figure 4. Vegetation state for four selected species *v* parameter combinations 400 years (A-D) and 100 years (E-H) after elephant introduction at the constant densities indicated (model is run for 100 years prior to elephant introduction). A, E: default species *v* parameters (60 cm y^{-1} growth, 100 seedlings $tree^{-1}$ y^{-1}, survival level $\mathbf{s}_1$); B, F: species *v* with lower fecundity, higher survival (60 cm y^{-1} growth, 50 seedlings $tree^{-1}$ y^{-1}, survival level $\mathbf{s}_3$); C, G: species *v* with lower growth, higher survival (30 cm y^{-1} growth, 100 seedlings $tree^{-1}$ y^{-1}, survival level $\mathbf{s}_3$); D, H: species *v* = species *w* (30 cm y^{-1} growth, 50 seedlings $tree^{-1}$ y^{-1}, survival level $\mathbf{s}_5$). See text for further details. Mean of 25 runs per elephant density/parameter combination shown. Species *w* parameters fixed throughout.

densities coupled with a higher growth rate, species *v* cover may increase. Figure 5 shows the changes in species composition with elephant density, as the difference in tree species composition (Figure 5A) and the ratios of each of the three species (two tree species and grass; Figure 5B). As woodland cover is decreased overall with increasing elephant densities, the dominance of species *w* over species *v* also decreases, the latter having greater cover at elephant densities >0.6 km^{-2}. The dominance of species *v* over species *w* decreases in turn as elephant densities increase further and both species are removed. Grass is always dominant to species *v*, but low elephant densities (≤0.5 km^{-2}) have little effect on the extent of dominance. Species *w* dominates grass at low elephant densities, its dominance subsiding with increasing elephant density, and grass dominates at elephant densities of ≥0.5 km^{-2}.

To explore additional plant strategies, we enhanced the resilience of either or both species to elephant impact by reducing the adult mortality rate given elephant utilization, $m^{e}_{q,i}$, from 0.8 to 0.4 ($q = v, w$; $i = 8, 9$; see Appendix). Elephant-enhanced germination (Lewis 1987a) was also modeled, based on an elephant density of 0.5 km^{-2}, by increasing the number of potential seedlings by 50% for those trees that had been utilized by elephant. We varied the elephant-preference weightings $e_{q,i}$ ($q = v, w$; $1 \leq i \leq 9$; see Appendix) to examine how these strategies interacted with elephant diet preference. We varied preference by species only, not by stage-class within species. Figure 6 shows the vegetation state after 100 years at an elephant density of 0.5 km^{-2} for different combinations of strategy for either species. Elephant preferences for species *v* are shown, as species *v*:species *w* utilization ratios ranging from 0.125 to 8 (given equal amounts of

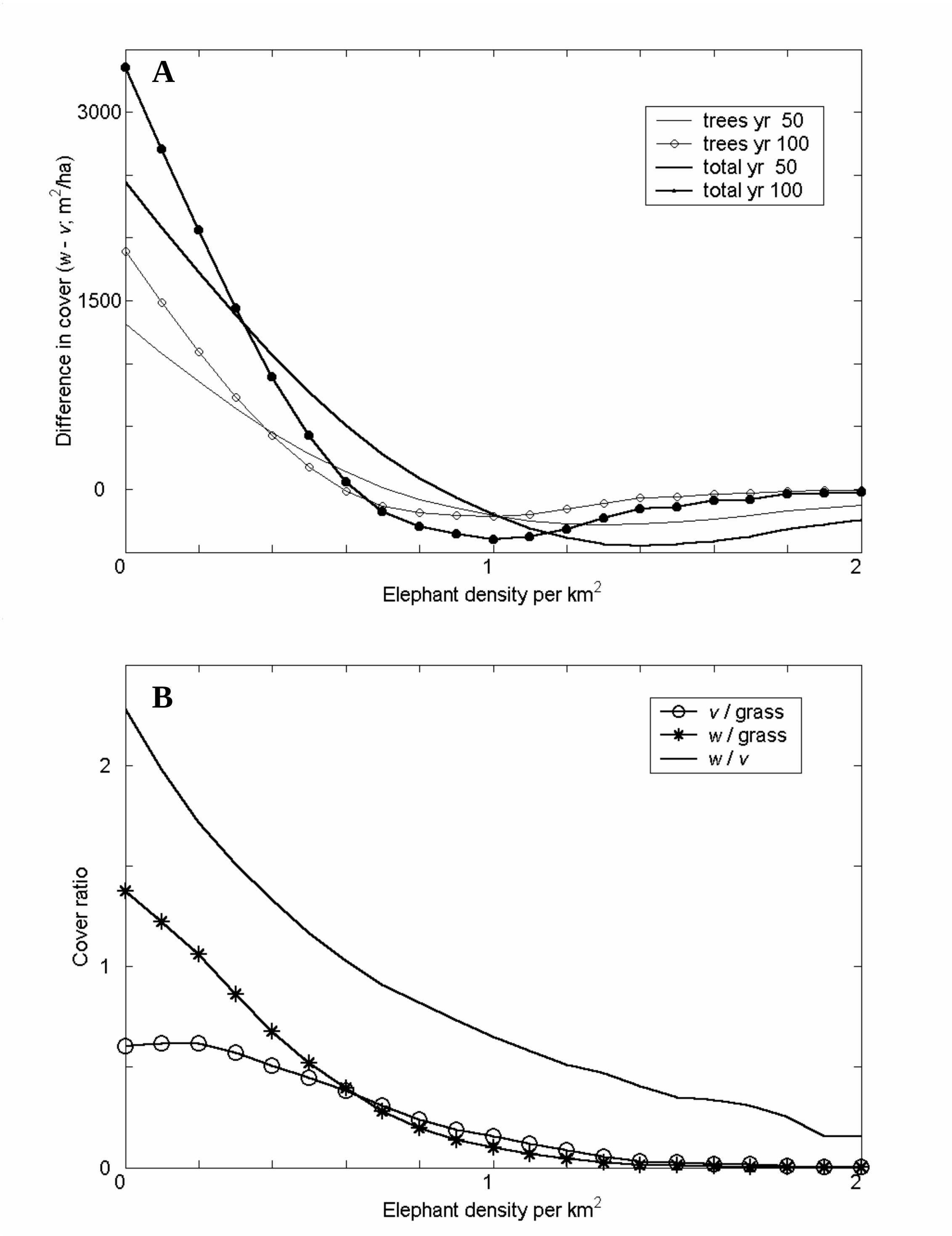


Figure 5. Species shifts following elephant introduction at the constant densities indicated (model is run for 100 years prior to elephant introduction). A: difference between mean cover of species *w* and species *v*, for trees and total cover, 50 and 100 years after elephant introduction; B: ratios of species cover 100 years after elephant introduction. Mean values of 250 runs per elephant density shown. Default species *v* and *w* parameters used throughout.

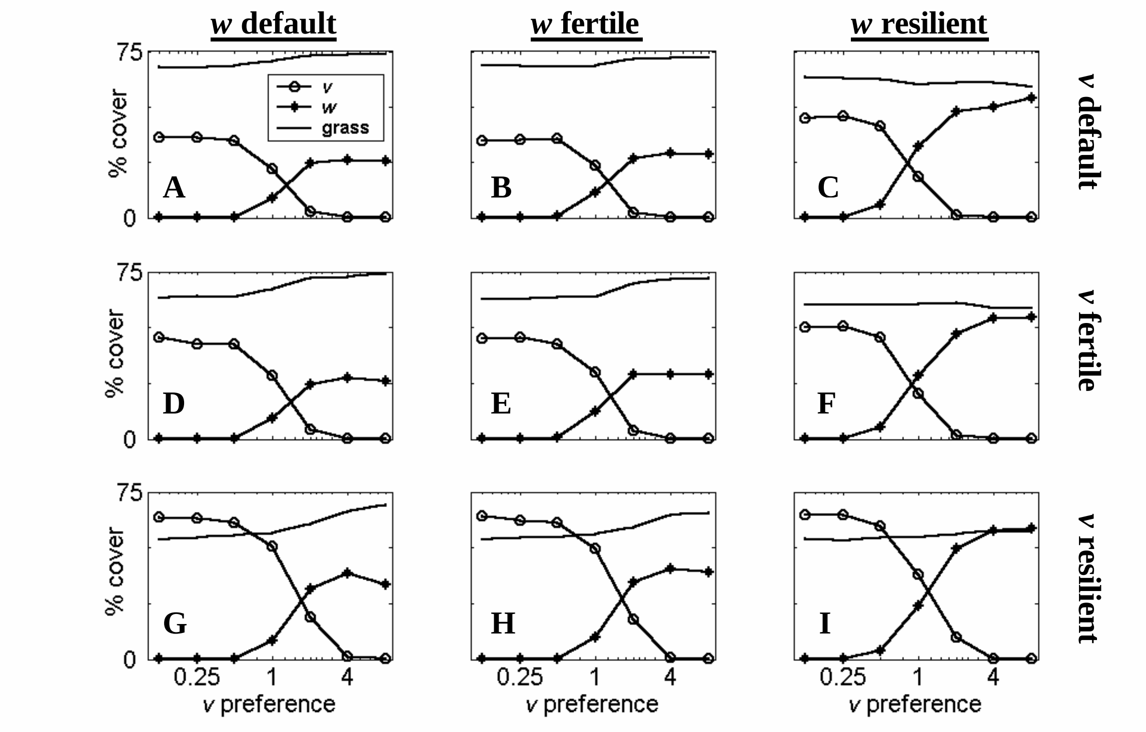
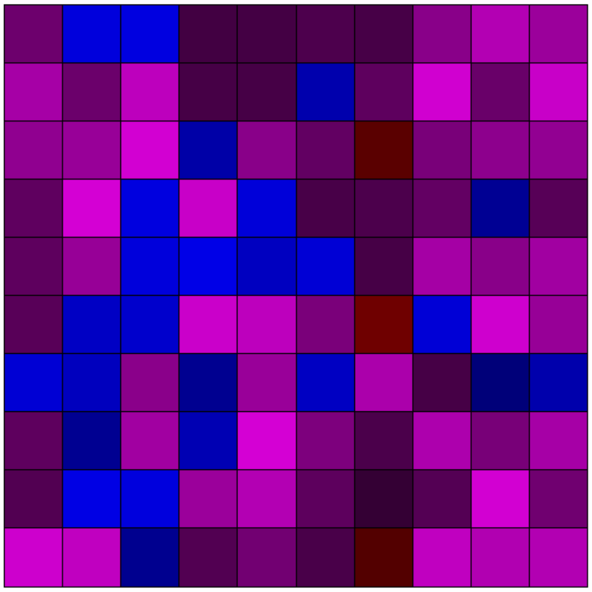


Figure 6. Effect of elephant preferences and plant responses on vegetation state 100 years after introduction of 0.5 eles km^{-2}. Relative preference for species *v* over species *w* is plotted on a $\log_2$ scale. Plant responses are default conditions, "fertile" (elephant-assisted germination) and "resilient" (40% mortality of impacted adult trees vs 80%). Mean values of 25 runs shown.

each species, elephant use of species *v*:species *w* is in the ratio 1:8 and 8:1 respectively). Grass tends to dominate after 100 years of elephant utilization in almost all strategy combinations (cf. Figure 4), and cover of either tree species decreases as elephant preference for that species increases. Resilience to impact (decreased mortality) has a greater mitigating effect than elephant-enhanced germination.

Examples of the spatial output of the model are shown in Figure 7, which represents two snapshots in time for two runs with 0.25 or 0.50 elephants km^{-2} introduced at year 100. The same random seed was used for each run so that rainfall patterns are identical throughout and the fire regime was identical up until elephant introduction at year 100, (which altered vegetation cover between the two runs, thus changing the fire experience). We calculated the coefficient of variation of each stratum across grid cells to examine the variation in spatial heterogeneity with different elephant densities over time. Figure 8 shows the mean coefficients of variation for 100 runs, as a function of elephant density and time. The woody cover results shown (aggregated stratum cover (Figures 8A-C) or aggregated species cover (Figures 8D-E)) all demonstrate an increase in spatial heterogeneity with elephant density and time, indicating clumping of woodland patches as overall woody cover decreases under prolonged elephant impact. This pattern is also repeated by each stratum within either species (not shown; e.g. species *v* adult trees). Grass cover on the other hand demonstrates less spatial heterogeneity as exposure to elephant pressure increases either by time or elephant density, as the woodland tends toward a uniform grassland. The signal of the 20-year wet-dry rainfall cycle can also be detected in grass spatial pattern, with more homogeneity (lower CV) at the end of dry periods (years 20, 40, …, 100).

A: 0.25 elephants per km^2, end of wet cycle (year 130)



B: 0.25 elephants per km^2, end of dry cycle (year 140)

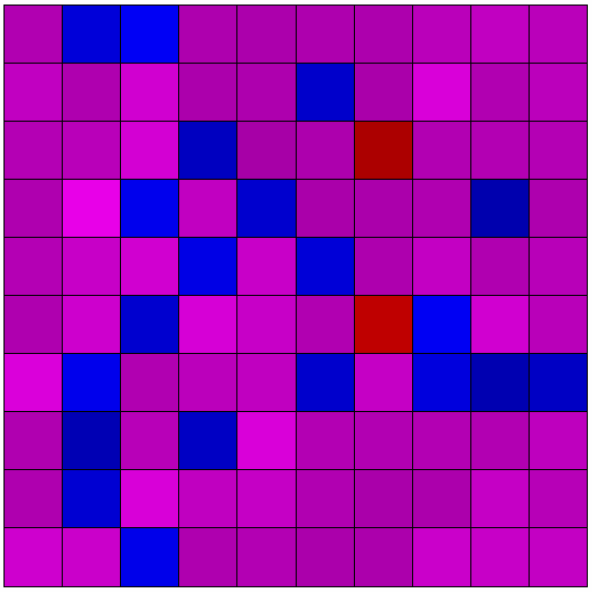
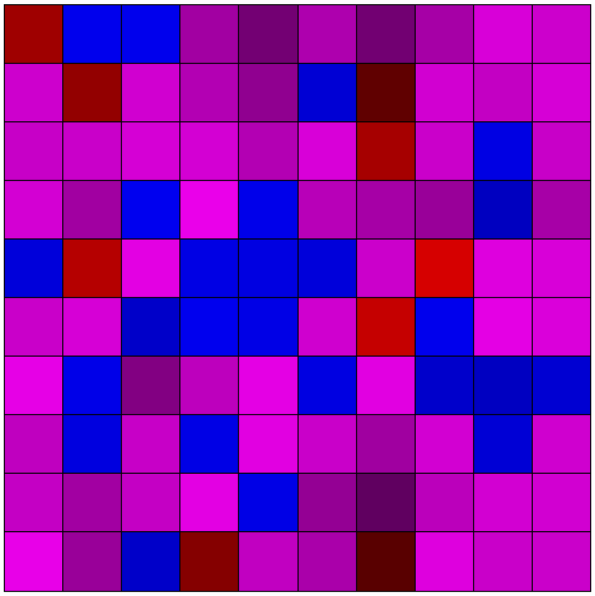


Figure 7. Typical output from the model, for two points in time along trajectories of two levels of elephant density. Degree of dominance of the woody component is depicted, where "dominance" of a species entails 25% more cover area than the other species (red, blue cells for species *v*, *w* dominating respectively). "Co-dominance" of the woody component (purple cells) occurs when the ratio of *v* to *w* cover lies between 0.8 and 1.25. Cells get lighter as grass cover increases. A: Vegetation 30 years after the introduction of 0.25 elephants km^{-2}, at the end of a 10-year wet period; B: Vegetation 40 years after the introduction of 0.25 elephants km^{-2}, at the end of a 10-year dry period; (continued)

C: 0.50 elephants per km^2, end of wet cycle (year 130)



D: 0.50 elephants per km^2, end of dry cycle (year 140)

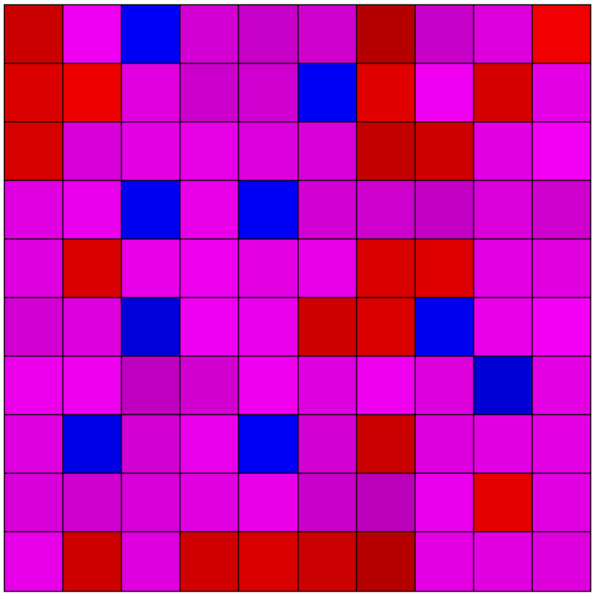


Figure 7 (continued). C: Vegetation 30 years after the introduction of 0.50 elephants km^{-2}, at the end of a 10-year wet period; D: Vegetation 40 years after the introduction of 0.50 elephants km^{-2}, at the end of a 10-year dry period. The same random seed was used for both runs so that the fire regime was identical up until elephant introduction at year 100, and rainfall pattern is identical throughout.

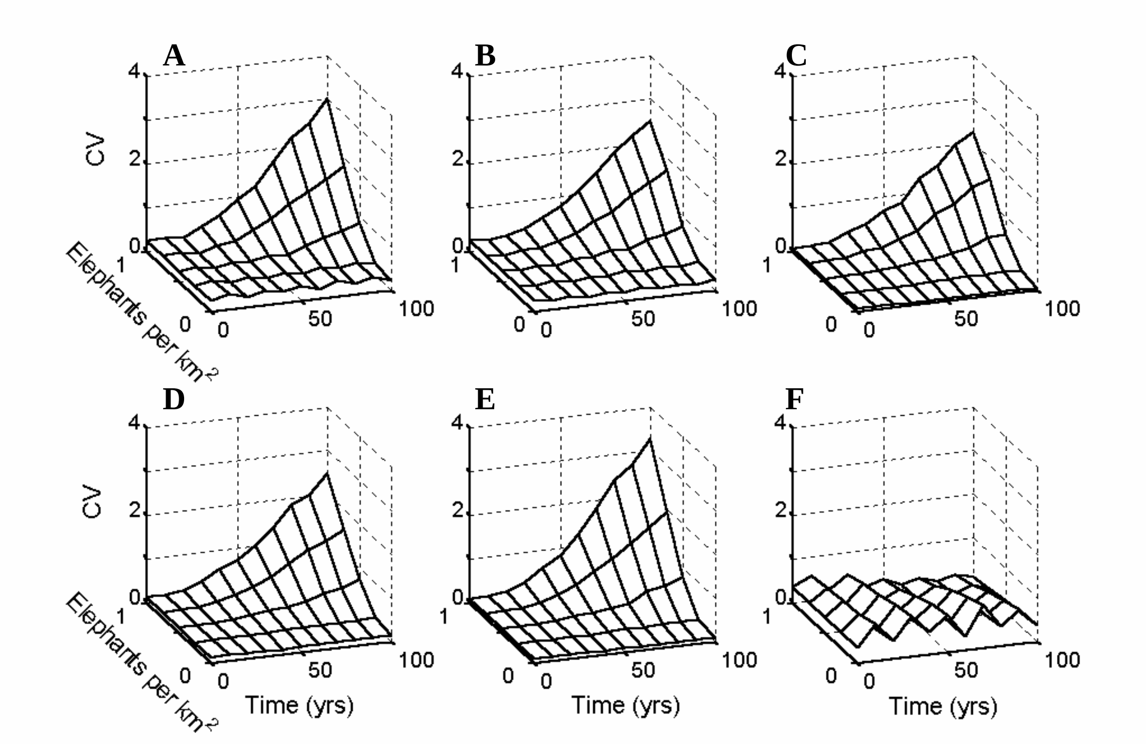
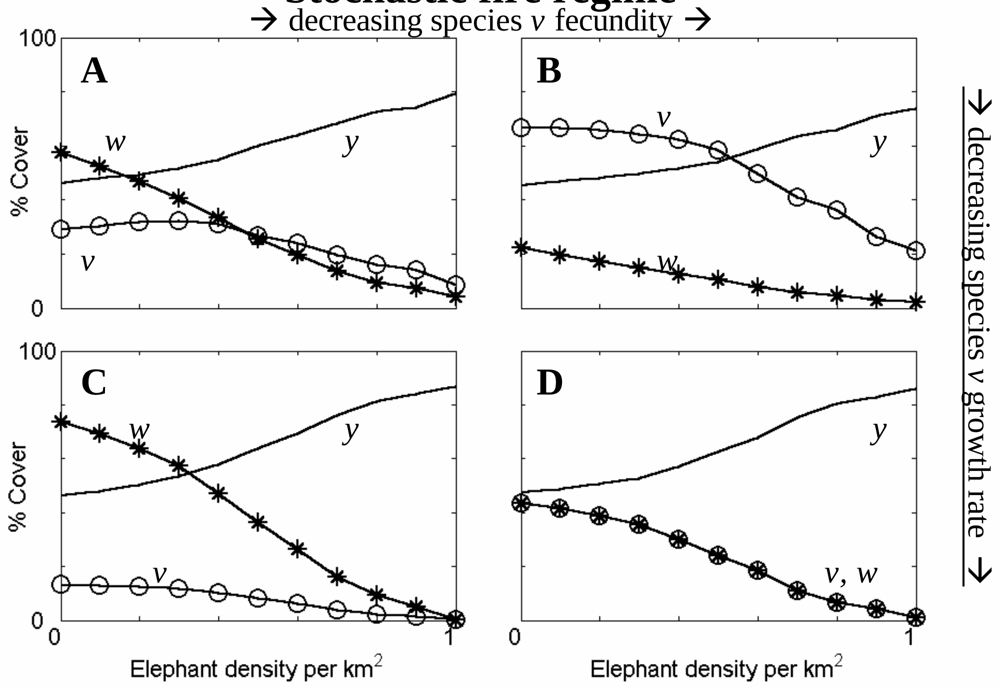


Figure 8. Mean values of coefficient of variation of cover over the 100 grid cells for various species and strata, following elephant introduction at the constant densities indicated (model is run for 100 years prior to elephant introduction). A: All juvenile (<1m) cover; B: all shrub (1–3m) cover; C: all tree (>3m) cover; D: all species *v* cover; E: all species *w* cover; F: grass cover. Mean values of 100 runs shown.

Finally, we briefly explored the effect of complete fire suppression as a possible management strategy. Figure 9 shows the vegetation state, for the four species types depicted as species *v* in Figure 4, 100 years after elephant introduction under (a) normal fire conditions (stochastically dependent on grass biomass: P(fire occurring) = grass biomass $\times 10^{-4}$; see Appendix) and (b) complete fire suppression (P(fire occurring) = 0). For all elephant densities, cover of both tree species is increased by fire suppression (at the expense of grass cover), the increase in cover generally increasing with elephant density.

Stochastic fire regime



Complete fire suppression

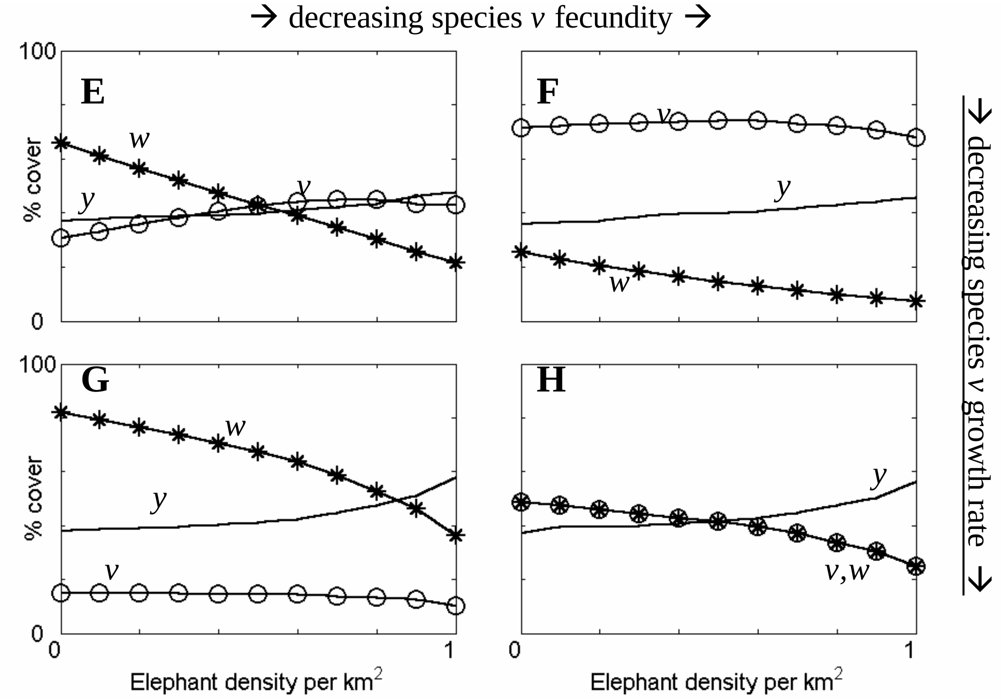


Figure 9. Effect of fire control measures on vegetation state following elephant introduction at the constant densities indicated (model is run for 100 years prior to elephant introduction). A-D: default stochastic fire regime; E-H: complete fire suppression, for four species-*v* strategists (cf. Fig 4). Mean values of 25 runs shown.

Discussion

Our savanna model is the first model designed to include a realistic vegetation component, incorporating the main stochastic disturbances experienced by savannas (fire and drought), on a scale suitable for exploration of elephant impacts. The vegetation component displays tree-grass coexistence and responds to environmental variation in a reasonable manner (Chapter 2). The inclusion of the second tree species in this paper allows for further novel insights into savanna composition and dynamics with and without elephant influence.

For two model tree species, with similar dominant eigenvalues of their Lefkovitch matrices, similar dynamics result when the model is run with only one species at a time (Figure 1), especially in the trajectories of grass and adult tree cover. Between-species differences in vertical structure are more pronounced with respect to the juvenile (<1 m) and shrub (1-3 m) layer, and are attributable to greater reproductive output and quicker growth. Species *v* (more "r-selected") has greater coverage than species *w* (more "K-selected") of plants in the <1m and >3m strata, due to its higher reproductive output and faster growth. Conversely, shrub (1-3 m) cover is lower in species *v* due to quicker passage through the subadult phase (quicker growth) and grass cover is suppressed by the higher number of juveniles.

The inclusion of both species together in the model produces the familiar ecological process of succession (Clements 1936), the earlier successional species *v* with stronger germination and growth being eventually out-competed by the later successional species with stronger survival (species *w*). O'Connor (1991) describes a process whereby a palatable savanna grass species with low seed output may be replaced by invasive and unpalatable species in the presence of variable rainfall and heavy grazing. Similarly in the case of our two savanna tree species, introduction of extra herbivory (elephants) can interrupt or reverse the succession seen in the absence of elephants, and low elephant densities (e.g. 0.25 elephants km^{-2} in our model) can actually increase tree cover of the more disturbance-tolerant species (Guy 1989). (When elephants are introduced at year 100, species *w* is already slightly more abundant (mean overall cover of 4800 m^2 ha^{-1}) than species *v* (3757 m^2 ha^{-1}), see Figure 2B.) Over a time-scale of decades, biodiversity can thus be maintained or even enhanced by elephants.

Tree-grass coexistence is maintained at reasonably steady mean levels throughout the double-tree-species model, allowing for the effect of the rainfall cycles, with tree and shrub densities consistent with southern African savannas (van Wyk and Fairall 1969, Witkowski and O'Connor 1996). Grass cover changes little as tree species dominance shifts, reflecting the similarity of grass cover output in the two single-species scenarios; for other parameter combinations (other model tree species), a shift in tree species produces more pronounced changes in grass cover (simulations not shown).

Figure 3 illustrates sensitivity of either tree species to growth, fecundity and survival of species *v*. As expected, persistence and cover of species *v* increase as these attributes are increased, whereas species *w* persistence and cover decrease. The sensitivity of species *v* persistence to its fecundity is quite pronounced (Figure 3C), suggesting a threshold effect (compare the gradual reduction in species *w* persistence with increased species *v* fecundity, Figure 3D). Note that our definition of persistence (>0.5 m^2 cover ha^{-1}) is quite lax, and does not necessarily imply viability, so that graphs with apparently zero cover may still be deemed to persist (e.g. compare Figures 3B and

3D). Cover (mean of all runs, including those that have gone extinct) exhibits sigmoidal patterns of increase (species *v*) and decrease (species *w*) with increasing species *v* fecundity. Faster growth and higher survival rates move the sigmoid curves to the left for species *v* and to the right for species *w*. This follows logically from the relative vigor of species *v* and *w* and the competitive play-off between the two species.

Introduction of constant elephant densities from year 101 onwards generally leads to a decreasing woody cover with increasing elephant densities. Persistently high elephant densities induce a drop in woody cover 100 years after introduction (Figure 4B) and no woody plants survive 400 years of 1 elephant km^{-2} density (cf. Anderson and Walker 1974, Tafangenyasha 1997 and Birkett 2002 who found annual rates of tree loss between 1.5% and 9% for elephant densities around 1 km^{-2}). These declines in woodland, while striking, are well within the reported range; e.g. Lamprey *et al*. (1967) found a 6% p.a. decline in large trees as elephant density in the Serengeti National Park, Tanzania increased from 0 to 0.135 km^{-2}. Nevertheless, elephants are parameterized as male elephants (largely from Croze 1974b – whose results refer to sites selected for obvious elephant impact; see Chapter Two) which may have heavier impact on trees than breeding herds. Stokke and du Toit (2000), for example, found that tree-felling rates were five times higher for bulls than for breeding herds. Thus the predicted effects at any given elephant density may be somewhat exaggerated. The decrease in species *w* cover with increasing elephant densities is more pronounced than that of species *v*. This reflects an elephant-induced species shift in the community with the faster-growing species benefiting from increased disturbances (Buechner and Dawkins 1961, Simpson 1978).

The change in species composition is emphasized in Figure 5, which shows decreasing dominance of species *w* over species *v* with increasing (constant) elephant density and time. As the constant elephant density is increased, dominance of the woody component switches from species *w* to species *v*, first in terms of adult tree cover and then in terms of total cover (e.g. between 0.7 and 0.9 elephants km^{-2} for 50 years, Figure 5A) – suggesting that loss of adult trees can signal imminent changes in species composition. Figure 5B includes grass in considering elephant-induced changes in the vegetation community: grass is always dominant to species *v* and becomes more abundant than species *w* at elephant densities of >0.5 km^{-2}, its overall dominance increasing with elephant density. Species *w* is more than twice as abundant as species *v* in the absence of elephants but declines more quickly with increasing elephant density (compare Figure 4E) so that species *v* is more abundant at elephant densities >0.6 km^{-2}, albeit in the context of a declining woodland.

Vis-à-vis the trade-off in *v*'s growth/fecundity/survival rates, improved fecundity is insufficient to compensate for increased mortality (compare Figures 4F and 4G). Increased fecundity is likely to be of reduced benefit as seedling establishment is impeded by the greater grass cover resulting from higher elephant densities. Increased growth rate on the other hand improves cover even when offset by increased mortality (e.g. compare Figures 4G and 4E). For default values for *v* (Figure 4E), introduction of up to 0.5 elephants km^{-2} increases area covered by *v* (while decreasing area covered by *w*), and decreasing either fecundity or growth of *v* while increasing its survival rates (Figures 4F and 4G) result in no decreases in cover following introduction of 0.25 elephants km^{-2} (again, species *w* cover decreases).

Comparing Figures 4A-D with 4E-H (the only difference being 300 extra years' elephant impact in Figure 4A-D) demonstrates differences in elephant impact over time. Overall, tree populations that persist for 100 years under a given elephant density tend have decreased by year 500. However, more interesting unanticipated dynamics emerge at low elephant densities: in the absence of elephants, species *v* is dominant in terms of cover if it has fast growth (60 cm year^{-1}), low fecundity (50 seedlings tree^{-1}) and intermediate survival ($\mathbf{s}_3$). Following introduction of 0.25 elephants km^{-2} from year 100, species *v* cover actually increases between years 200 and 500, at the expense of grass and species *w*. A similar effect, though much less pronounced, is seen for *w* if species *v* fecundity is lower: in the absence of elephants, *w* is dominant in terms of cover for higher levels of species *v* fecundity (when either survival or growth of *v* is at lower levels than *w*). Following introduction of 0.25 elephants km^{-2} from year 100, area covered by *w* increases slightly between years 200 and 500, at the expense of species *v* (grass cover slightly increases also). The fast-growth, low-fecundity, intermediate survival species *v* parameter combination is the only one of the four for which increasing cover (of either species, in this case species *v*) between years 200 and 500 is actually augmented by the introduction of elephants.

In the only other elephant-vegetation model to include two interacting tree species, Duffy *et al.* (2000) found that a faster-growing species may facilitate persistence of a more K-selected species by diverting utilization pressure away from it, and here we see that while *w* on its own cannot sustain elephant densities of 1 km^{-2} for 100 years (species *v* and *w* parameters identical, Figure 4H), both *w* and a faster growing species (Figures 4E and 4F) can persist for over a century at 1 elephant km^{-2}. Hence, while low elephant densities may enhance biodiversity, biodiversity itself imparts a degree of ecosystem resilience to continued utilization.

For plants experiencing prolonged elephant utilization, resilience to impact (reduced mortality given the impact, usually entailing strong resprouting ability) is a more successful strategy than elephant-enhanced germination (Figure 6) – which is understandable as a resprouting plant has less stage classes to work back up through to become reproductive again than a newly emerging seedling. This helps to explain why resprouting is such a common strategy for savanna plants to survive disturbance by fire or elephants (Jachmann and Bell 1985, Smallie and O'Connor 2000; see also Chapter Two), whereas elephant-enhanced germination has been less commonly reported (Lewis 1987a). Elephant-enhanced germination produces little improvement for species *w* (compare Figures 6A and B). Nevertheless elephant-enhanced germination can be an effective strategy, especially for model species *v*, which invests more than *w* in reproduction and growth in any case.

There is also evidence for a synergistic effects from vegetation strategies, particularly the resilience strategy: when a species experiences lower elephant-induced mortality, their increased vigor provides more abundant browse for elephants, and reduced grass cover, so that the other species is also "rescued" to some degree (compare Figures 6G, 6C with Figure 6A). This again resonates with the result of Duffy *et al.* (2000), whereby faster-growing species deflect elephant pressure from slow growers. When the two tree species share the same strategy (Figures 6A, 6E, 6I), *v* benefits more by adapting the strategy than *w*, as the main difference between the species reverts to the relatively higher tolerance for disturbance of species *v*.

Our model demonstrates that relative elephant preference for a tree species can have a pronounced affect on the resulting savanna vegetation composition, with palatable species being selectively reduced (Guy 1989, Jachmann and Croes 1991, Leuthold 1996). Bowland and Yeaton (1997) found that domesticated elephants introduced to a savanna preferred later successional trees (*Acacia caffra* and broadleaves) to earlier successional trees such as *A. nilotica*, and that 80% of felled trees were late successional, equivalent to a species *v* preference of 0.25 (Figure 6). Grass cover increases slightly with increasing elephant preference for *v*, for all strategies except *w* resilience coupled with *v*'s default or elephant-enhanced germination strategies (Figures 6C, 6F). These are the only two strategy combinations where overall woody cover increases with elephant preference for *v*, and the only scenarios whereby equal elephant preference for either species leads to greater abundance of *w* than *v*. With this strong resilience of *w*, overall woody cover (species *v* + species *w*, not shown) increases slightly as elephant diet becomes more concentrated on species *v* (left-to-right, Figures 6C, 6F), entailing the concomitant drop in grass cover. When both species experience lower elephant-induced mortality, combined woody cover is higher throughout, but increases with elephant preference for *w* (right-to-left, Figure 6I), and grass cover increases with elephant preference for *v*.

Although the optimal foraging algorithm we employ, whereby elephants utilize grid-cells in proportion to their woody cover (see Appendix), would be expected to even out the effects of elephant impact over the grid, spatial heterogeneity, as measured by the coefficient of variation, increases strikingly over time and with elephant density (Figure 8). The formation of residual tree clumps under persistent elephant pressure has been noted in the past and is typically associated with patchy elephant utilization of woodland

and linked to other environmental features, particularly water sources in the dry season (van Wyk and Fairall 1969, Laws 1970, Swanepoel and Swanepoel 1986, Tchamba 1995) or nutrient hotspots (Nellemann *et al.* 2002). The extent of clumping of elephant damage can also vary by species (Calenge *et al.* 2002), and our model shows slightly higher levels of heterogeneity for species *w* (Figure 8E). As the model employs stochastic fire occurrence and spread, and elephants can browse in any or all cells each year, the model does not readily provide useful positional information (although the palatability coefficients could be varied in a cell-specific manner to reflect preferential browsing locations, e.g. near a water-source).

The role of fire in exacerbating elephant impacts has been emphasized (Pellew 1983, Dublin *et al.* 1990). Jacobs and Biggs (2002a) attribute decline of the marula *Sclerocarya birrea* in Kruger National Park, South Africa to a fixed-frequency burning policy combined with high localized elephant concentrations (up to 5.7 km^{-2}) although Ben-Shahar (1998) argues that woodland decline in Botswana was caused mainly by fire, despite elephant densities of 2.5-3.0 km^{-2}. Fire management, with or without other measures, is often advocated as a means of mitigating elephant damage (Thomson 1975, Barnes 1983b, Pellew 1983). Although 100 years of complete fire suppression is unlikely to be achieved in practice (as is 100 years of constant elephant density), the hypothetical model scenario nevertheless provides useful insights (and see Pellew 1983, Dublin *et al.* 1990, Ben-Shahar 1996b). In particular, our model shows that complete fire suppression preserves the woodland and prevents shifts in species composition of the community. With elephant impacts, complete fire suppression will still yield savanna (not forest), with adequate grass fuel for fires, so that prolonged management effort may be needed to continue fire suppression. However, maintaining high densities of grazers such as white rhino (Owen-Smith 1988; pp. 235-238), wildebeest (Dublin *et al*. 1990) or African buffalo (Prins and Douglas-Hamilton 1990) may reduce grass fuel load and thus assist managers in reducing fire frequency and/or intensity and allow regeneration of impacted woodland (Mwalyosi 1990).

In summary, our model develops understanding of interspecific interactions and relative life history trade-offs of competing savanna tree species. While most of the dynamics were predictable, with higher growth, fecundity or survival favoring one species over another, more interesting patterns also emerged. Consideration of a second species showed that elephant impacts can be mitigated to some extent if the additional species is faster-growing. Tree species adaptive strategies can act synergistically to improve resilience of the woody vegetation component, by increasing regeneration and providing increased food supply while delaying the transition to grassland. Fire management can also relieve savanna vegetation of the perceived negative consequences of elephant impact.

A few points on the limitations of this model are in order. While we have seen that two contrasting tree species provide greater insight into elephant-induced vegetation changes, we have limited the grass component to one generic grass "species." Grass species are also prone to local extinction depending on environmental and herbivory conditions (O'Connor, 1991) and elephant-induced changes in grass species composition have been implicated in subsequent effects on the herbivore community (Field 1971). Other herbivores are not modeled (plant growth rates assumed instead to be net of general, unspecified "herbivory"), whereas browsers may affect the outcome of elephant herbivory by having similar effects to fire in preventing reestablishment of trees (Lewis 1987a, Ruess and Halter 1990) and grazers may suppress fire. Model predictions can be evaluated against field experience, and divergence from expected results can point to the possible importance of excluded factors. Notwithstanding these limitations and assumptions, we have demonstrated that under certain conditions elephants can enhance spatial heterogeneity and maintain biodiversity in terms of species richness. While simplicity in models is desirable for transparency, knowledge of how different species types interact with themselves and agents of disturbance is critical to astute management for biodiversity.

Acknowledgements

The authors wish to thank Cherie Briggs, James Lloyd-Smith, Dale McCullough, Chris Wilmers and George Wittemyer for helpful ideas and comments on an earlier draft of this manuscript. We would also like to thank South African National Parks and the Scientific Services Division of the Kruger National Park for facilitating parts of this study. The work was supported in part by NSF grant DEB-0090323 to W. M. Getz.

REFERENCES

Addy, J. E. 1993. *Impact of elephant induced vegetation change on the status of the Chobe bushbuck along the Chobe River, northern Botswana.* M.Sc. thesis, University of the Witwatersrand, Johannesburg, South Africa.

Agnew, A. D. Q. 1968. Observations on the changing vegetation of Tsavo National Park (East). *East African Wildlife Journal* **6**:75–80.

Anderson, G. D., and B. H. Walker. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the southern African Wildlife Management Association* **4**:1–14.

Anderson, J. M., and M. J. Coe. 1974. Decomposition of elephant dung in an arid, tropical environment. *Oecologia* **14**:111–125.

Barnes, R. F. W. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology* **20**:123–136.

Barnes, R. F. W. 1983a. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology* **20**:521–540.

Barnes, R. F. W. 1983b. The elephant problem in Ruaha National Park, Tanzania. *Biological Conservation* **26**:127–148.

Barnes, R. F. W. 1985. Woodland changes in Ruaha National Park (Tanzania) between 1976 and 1982. *African Journal of Ecology* **23**:215–221.

Barnes, R. F. W. 1994. The long-term impact of elephant browsing on baobab trees at Msembe, Ruaha National Park, Tanzania. *African Journal of Ecology* **32**:177–184.

Behnke, R. H. Jr., and I. Scoones. 1993. Rethinking Range Ecology. Pages 1–30 *in* R. H. Behnke Jr., I. Scoones, and C. Kerven, editors. *Range Ecology at Disequilibrium: new models of natural variability and pastoral adaptation in African savannas.* Overseas Development Institute, London, England, UK.

Belsky, A. J. 1990. Tree/grass ratios in East African savannas: a comparison of existing models. *Journal of Biogeography* **17**:483–489.

Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients and tree-grass competition. *Ecology* **75**:922–932.

Ben-Shahar, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* **65**:249–256.

Ben-Shahar, R. 1996a. Do elephants over-utilize mopane woodlands in northern Botswana? *Journal of Tropical Ecology* **12**:505–515.

Ben-Shahar, R. 1996b. Woodlands dynamics under the influence of elephants and fire in northern Botswana. *Vegetatio* **123**:153–163.

Ben-Shahar, R. 1998. Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology* **136**:189–194.

Ben-Shahar, R., and D. W. Macdonald. 2002. The role of soil factors and leaf protein in the utilization of mopane plants by elephants in northern Botswana. *BMC Ecology* **2**:3. url: [http://www.biomedcentral.com/bmcecol/]

Birkett, A. 2002. The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology* **40**:276–282.

Bond, W. J., and B. W. van Wilgen. 1996. *Fire and Plants.* Chapman and Hall, London, England, UK.

Bond, W. J., and D. Loffell. 2001. Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology* **39**:286–294.

Bond, W. J., and J. J. Midgeley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* **16**:45–51.

Bowland, J. M., and R. I. Yeaton. 1997. Impact of domesticated African elephants *Loxodonta africana* on Natal bushveld. *South African Journal of Wildlife Research* **27**:31–36.

Buechner, H. K., and H. C. Dawkins. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* **42**:752–766.

Buss, I. O. 1961. Some observations on food habits and behavior of the African elephant. *Journal of Wildlife Management* **25**:131–148.

Calef, G. W. 1988. Maximum rate of increase in the African elephant. *African Journal of Ecology* **26**:323–327.

Calenge, C., D. Maillard, J.-M. Gaillard, L. Merlot, and R. Peltier 2002. Elephant damage to trees of wooded savanna in Zakouma National Park, Chad. *Journal of Tropical Ecology* **18**:599–614.

Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts, USA.

Caughley, G. 1976. The elephant problem – an alternative hypothesis. *East African Wildlife Journal* **14**:265–283.

Caughley, G., H. Dublin, and I. Parker. 1990. Projected decline of the African elephant. *Biological Conservation* **54**:157–164.

Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* **24**:252–284.

Coetzee, B. J., A. H. Engelbrecht, S. C. J. Joubert, and P. F. Retief. 1979. Elephant impact on *Sclerocarya caffra* trees in *Acacia nigrescens* tropical plains thornveld of the Kruger National Park. *Koedoe* **22**:39–60.

Croze, H. 1974a. The Seronera bull problem. I. The elephants. *East African Wildlife Journal* **12**:1–27.

Croze, H. 1974b. The Seronera bull problem. II. The trees. *East African Wildlife Journal* **12**:29–47.

Cumming, D. H. M. 1981. The management of elephant and other large mammals in Zimbabwe. Pages 91–118 *in* P. A. Jewell and S. Holt, editors. *Problems in management of locally abundant wild mammals*. Academic Press, New York, USA.

Cumming, D. H. M., M. B. Fenton, I. L. Rautenbach, R. D. Taylor, G. S. Cumming, M. S. Cumming, J. M. Dunlop, A. G. Ford, M. D. Hovorka, D. S. Johnston, M. Kalcounis, Z. Mahlangu, and C. V. R. Portfors. 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* **93**:231–236.

de Boer, W. F., C. P. Ntumi, A. U. Correia, and J. M. Mafuca. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology* **38**:188–201.

Desmet, P. G., C. M. Shackleton, and E. R. Robinson. 1996. The population dynamics and life-history attributes of a *Pterocarpus angolensis* DC. population in the Northern Province, South Africa. *South African Journal of Botany* **62**:160–166.

Douglas-Hamilton, I. 1987. African elephants: population trends and their causes. *Oryx* **21**:11–24.

Du Toit, J. T., J. P. Bryant, and K. Frisby. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology* 71:149–154.

Dublin, H. T. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. Pages 71–90 *in* A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management and conservation of an ecosystem.* University of Chicago Press, Chicago, Illinois, USA.

Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**:1147–1164.

Duffy, K. J., V. B. Bajic, and B. R. Page. 2000. Analysis and dynamics of an elephant-tree ecosystem having abundant and rare tree species. *Systems Analysis Modelling Simulation* **38**:663–676.

Duffy, K. J., B. R. Page, J. H. Swart, and V. B. Bajic. 1999. Realistic parameter assessment for a well known elephant-tree ecosystem model reveals that limit cycles are unlikely. *Ecological Modelling* **121**:115–125.

Duffy, K. J., R. van Os, S. Vos, J. van Aarde, G. Ellish, and A.-M. B. Stretch. 2002. Estimating impact of reintroduced elephant on trees in a small reserve. *South African Journal of Wildlife Research* 32:23–29.

Eckhardt, H. C., B. W. van Wilgen, and H. C. Biggs. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1988. *African Journal of Ecology* **38**:108–115.

Engelbrecht, A. H. 1979. Olifantinvloed op *Acacia nigrescens*-bome in ’n gedeelte van die Punda Milia-Sandveld van die Nasionale Krugerwildtuin. *Koedoe* **22**:29–37.

Enslin, B. W., A. L. F. Potgieter, H. C. Biggs, and R. Biggs. 2000. Long term effects of fire frequency and season on the woody vegetation dynamics of the *Sclerocarya birrea/Acacia nigrescens* savanna of the Kruger National Park. *Koedoe* **43**:27–37.

Field, C. R. 1971. Elephant ecology in the Queen Elizabeth National Park, Uganda. *East African Wildlife Journal* **9**:99–123.

Field, C. R., and I. C. Ross. 1976. The savanna ecology of Kidepo Valley National Park. II. Feeding ecology of elephant and giraffe. *East African Wildlife Journal* **14**:1–15.

Fowler, C. W., and T. Smith. 1973. Characterizing stable populations: an application to the African elephant population. *Journal of Wildlife Management* **37**:513–523.

Fritz, H., P. Duncan, I. J. Gordon, and A. W. Illius. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* **131**:620–625.

Frost, P. G. H., and P. Robertson. 1987. The ecological effects of fire in savannas. Pages 93–140 *in* B. H. Walker, editor. *Determinants of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

Gadd, M. E., T. P. Young, and T. M. Palmer. 2001. Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. *Oikos* **92**:515–521.

Gertenbach, W. P. D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* **23**:35–43.

Getz, W. M. 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology* **77**:2014–2026.

Getz, W. M., and R. G. Haight. 1989. *Population harvesting: demographic models of fish, forest, and animal resources.* Princeton University Press, Princeton, New Jersey, USA.

Gignoux, J., J. Clobert, and J. C. Menaut. 1997. Alternative fire resistance strategies in savanna trees. Oecologia **110**:576–583.

Glover, J. 1963. The elephant problem at Tsavo. *East African Wildlife Journal* **1**:30–39.

Guy, P. R. 1976. The feeding behaviour of elephant (*Loxodonta africana*) in the Sengwa area, Rhodesia. *South African Journal of Wildlife Research* **6**:55–63.

Guy, P. R. 1981. Changes in the biomass and productivity of woodlands in the Sengwa Wildlife Research Area, Zimbabwe. *Journal of Applied Ecology* **18**:507–519.

Guy, P. R. 1989. The influence of elephants and fire on a *Brachystegia-Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology* **5**:215–226.

Herremans, M. 1995. Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. *Ecography* **18**:440–454.

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* **88**:213–229.

Hiscocks, K. 1999. The impact of an increasing elephant population on the woody vegetation in southern Sabi Sand Wildtuin, South Africa. *Koedoe* **42**:47–55.

Hoare, R. E. 1999. Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology* **36**:689–700.

Hochberg, M. E., J. C. Menaut, and J. Gignoux. 1994. The influences of tree biology and fire in the spatial structure of the West African savannah. *Journal of Ecology* **82**:217–226.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**:385–398.

Illius, A. W., and T. G. O'Connor. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* **89**:283–294.

Jachmann, H., and R. H. V. Bell. 1985. Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology* **23**:245–258.

Jachmann, H., and T. Croes. 1991. Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation* **57**:13–24.

Jacobs, O. S. 2001. *An autecological study of the marula* (Sclerocarya birrea) *in the Kruger National Park with specific reference to the relative impact from elephants and fire*. M. Sc. thesis, University of Pretoria, Pretoria, South Africa.

Jacobs, O. S., and R. Biggs. 2001. The effect of different fire treatments on the population structure and density of the marula, *Sclerocarya birrea* (A. Rich.) subsp. *caffra* (Sond.) *kokwaro* (Kokwaro and Gillet 1980) in the Kruger National Park. *African Journal of Range and Forage Science*. **18**:13–23.

Jacobs, O. S., and R. Biggs. 2002a. The status and population structure of the marula in the Kruger National Park. *South African Journal of Wildlife Research* **32**:1–12.

Jacobs, O. S., and R. Biggs. 2002b. The impact of the African elephant on marula trees in the Kruger National Park. *South African Journal of Wildlife Research* **32**:13–22.

Jarman, P. J. 1971. Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia* **8**:157–178.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. van Rooyen. 1996. Tree spacing and coexistence in semiarid savannas. *Journal of Ecology* **84**:583–595.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. van Rooyen. 1997a. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* **8**:177–188.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. van Rooyen. 1997b. Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *Journal of Applied Ecology* **34**:1497–1508.

Jeltsch, F., S. J. Milton, W. R. J. Dean, N. van Rooyen, and K. A. Moloney. 1998. Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. *Journal of Ecology* **86**:780–793.

Jeltsch, F., G. E. Weber, and V. Grimm. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* **161**:161–171.

Johnson, C. F., R. M. Cowling, and P. B. Phillipson. 1999. The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? *Biodiversity and Conservation* **8**:1447–1456.

Kalemera, M. C. 1989. Observations on feeding preference of elephants in the *Acacia tortilis* woodland of Lake Manyara National Park, Tanzania. *African Journal of Ecology* **27**:325–333

Kennedy, A. D. 2000. Wildfire reduces elephant herbivory on *Colophospermum mopane* (Fabaceae). *African Journal of Ecology* **38**:175–177.

Kiker, G. A. 1998. *Development and comparison of savanna ecosystem models to explore the concept of carrying capacity.* Ph.D. thesis, Cornell University, Ithaca, New York, USA.

Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* **73**:235–253.

Lamprey, H. F., P. E. Glover, M. I. Turner, and R. H. V. Bell. 1967. Invasion of the Serengeti National Park by elephants. *East African Wildlife Journal* **5**:151–166.

Laws, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* **21**:1–15.

Laws, R. M., I. S. C. Parker, and R. C. B. Johnstone. 1975. *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda*. Clarendon Press, Oxford, England, UK.

Lawton, R. M., and M. Gough. 1970. Elephants or fire – which is to blame? *Oryx* **10**:244–248.

Leuthold, W. 1977. Changes in tree populations of Tsavo East National Park, Kenya. *East African Wildlife Journal* **15**:61–69.

Leuthold, W. 1996. Recovery of woody vegetation in Tsavo National Park, Kenya, 1970-94. *African Journal of Ecology* **34**:101–112.

Leuthold, W., and J. B. Sale 1973. Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya. *East African Wildlife Journal* **11**:369–384.

Lewis, D. M. 1986. Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. *African Journal of Ecology* **24**:227–241.

Lewis, D. M. 1987a. Fruiting patterns, seed germination, and distribution of *Sclerocarya caffra* in an elephant-inhabited woodland. *Biotropica* **19**:50–56.

Lewis, D. M. 1987b. Elephant response to early burning in mopane woodland, Zambia. *South African Journal of Wildlife Research* **17**:33–40.

Lewis, D. M. 1991. Observations of tree growth, woodland structure and elephant damage on *Colophospermum mopane* in Luangwa Valley, Zambia. *African Journal of Ecology* **29**:207–221.

Lock, J. M. 1993. Vegetation change in Queen Elizabeth National Park, Uganda: 1970-1988. *African Journal of Ecology* **31**:106–117.

Mapaure, I. N., and B. M. Campbell. 2002. Changes in miombo woodland cover in and around Sengwa Wildlife Research Area, Zimbabwe, in relation to elephants and fire. *African Journal of Ecology* **40**:212–219.

Mapaure, I., and L. Mhlanga. 2000. Patterns of elephant damage to *Colophospermum mopane* on selected islands in Lake Kariba, Zimbabwe. *Kirkia* **17**:189–198.

McShane, T. O. 1989. Some preliminary results of the relationship between soils and tree response to elephant damage. *Pachyderm* **11**:29–31.

Meissner, H. H., E. B. Spreeth, P. A. de Villiers, E. W. Pietersen, T. A. Hugo, and B. F. Terblanché. 1990. Quality of food and voluntary intake by elephant as measured by lignin index. *South African Journal of Wildlife Research* **20**:104–110.

Menaut, J. C., J. Gignoux, C. Prado, and J. Clobert. 1990. Tree community dynamics in a humid savanna of the Côte-d'Ivoire: modelling the effects of fire and competition with grass and neighbors. *Journal of Biogeography* **17**:471–481.

Midgeley, J. J., P. McLean, M. Botha, and D. Balfour. 2001. Why do some African thorn trees (*Acacia* spp.) have a flat-top: a grazer-plant mutualism hypothesis? *African Journal of Ecology* **39**:226–228.

Mosugelo, D. K., S. R. Moe, S. Ringrose, and C. Nellemann. 2002. Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* **40**:232–240.

Musgrave, M. K., and S. G. Compton. 1997. Effects of elephant damage to vegetation on the abundance of phytophagous insects. *African Journal of Ecology* **35**:370–373.

Mushove, P. T. 1993. Shoot/root growth relations as determinants of nursery rotation in *Colophospermum mopane* seedlings raised in containers. Pages 221–225 *in* G. D. Piearce and D. J. Gumbo, editors. *The ecology and management of indigenous forests in southern Africa*. Forestry Commission, Harare, Zimbabwe.

Mushove, P. T., and J. T. Makoni. 1993. Coppicing ability of *Colophospermum mopane*. Pages 226–230 *in* G. D. Piearce and D. J. Gumbo, editors. *The ecology and management of indigenous forests in southern Africa*. Forestry Commission, Harare, Zimbabwe.

Mwalyosi, R. B. B. 1987. Decline of *Acacia tortilis* in Lake Manyara National Park, Tanzania. *African Journal of Ecology* **25**:51–53.

Mwalyosi, R. B. B. 1990. The dynamics ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. *African Journal of Ecology* **28**:189–199.

Napier Bax, P., and D. L. W. Sheldrick. 1963. Some preliminary observations on the food of elephant in the Tsavo Royal National Park (East) of Kenya. *East African Wildlife Journal* **1**:40–53.

Nåsell, I. 2001. Extinction and quasi-stationarity in the Verhulst logistic model. *Journal of Theoretical Biology* **211**:11–27.

Nellemann, C., S. R. Moe, and L. P. Rutina. 2002. Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology* **18**:835–844.

Nicholson, S. E. 1993. An overview of African rainfall fluctuations of the last decade. *Journal of Climate* **6**:1463–1466.

Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 310–352 *in* A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.

Noy-Meir, I. 1982. Stability of plant-herbivore models and possible applications to savanna. Pages 591–609 *in* B. J. Huntley and B. H. Walker, editors. *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

O'Connor, T. G. 1991. Local extinction in perennial grasslands: a life-history approach. *American Naturalist* **137**:753–773.

O'Connor, T. G. 1995. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* **103**:214–223.

O'Connor, T. G. 1998. Impact of sustained drought on a semi-arid *Colophospermum mopane* savanna. *African Journal of Range and Forage Science* **15**:83–91.

Okula, J. P., and W. R. Sise. 1986. Effects of elephant browsing on *Acacia seyal* in Waza National Park, Cameroon. *African Journal of Ecology* **24**:1–6.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. Pages 359–404 *in* B. J. Huntley and B. H. Walker, editors. *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

Owen-Smith, N., and J. E. Danckwerts. 1997. Herbivory. Pages 397–420 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of southern Africa*. Cambridge University Press, Cambridge, England, UK.

Owen-Smith, R. N. 1988. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge, England, UK.

Pamo, E. T., and M. N. Tchamba. 2001. Elephants and vegetation change in the Sahelo-Soudanian region of Cameroon. *Journal of Arid Environments* **48**:243–253.

Pellew, R. A. P. 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. *African Journal of Ecology* **21**:41–74.

Prins, H. H. T., and I. Douglas-Hamilton. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* **83**:392–400.

Prins, H. H. T., and H. P. van der Jeugd. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* **81**:305–314.

Ruess, R. W., and F. L. Halter. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. *African Journal of Ecology* **28**:259–275.

Rutherford, M. C. 1981. Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana-Ochna pulchra* savanna. *Bothalia* **13**:531–552.

Rutherford, M. C. 1997. Categorization of biomes. Pages 91–98 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of southern Africa*. Cambridge University Press, Cambridge, England, UK.

Scholes, R. J. 1985. Drought related grass, tree and herbivore mortality in a southern African savanna. Pages 350–353 *in* J. C. Tothill and J. J. Mott, editors. *Ecology and management of the world's savannas.* Commonwealth Agricultural Bureaux, Canberra, Australia.

Scholes, R. J. 1997. Savanna. Pages 258–277 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. *Vegetation of southern Africa.* Cambridge University Press, Cambridge, England, UK.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517–544.

Scholes, R. J., and B. H. Walker. 1993. *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge, England, UK.

Shackleton, C. M. 1997. *The prediction of woody productivity in the savanna biome, South Africa*. Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.

Shackleton, C. M., and R. J. Scholes. 2000. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. *Koedoe* **43**:75–81.

Silva, J. F. 1987. Responses of savannas to stress and disturbance: species dynamics. Pages 141–156 *in* B. H. Walker, editor. *Determinants of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

Simioni, G., X. Le Roux, J. Gignoux, and H. Sinoquet. 2000. Treegrass: a 3D, process-based model for simulating plant interactions in tree-grass ecosystems. *Ecological Modelling* **131**:47–63.

Simpson, C. D. 1978. *Effects of elephant and other wildlife on vegetation along the Chobe River, Botswana*. Occasional Papers, The Museum, Texas Tech University. No. 48.

Smallie, J. J., and T. G. O'Connor. 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *African Journal of Ecology* **38**:1–9.

Smit, G. N., and N. F. G. Rethman. 1998. The influence of tree thinning on the reproduction dynamics of *Colophospermum mopane*. *South African Journal of Botany* **64**:25–29.

Smith, T. M., and P. S. Goodman. 1986. The effect of competition on the structure and dynamics of *Acacia* savannas in southern Africa. *Journal of Ecology* **74**:1031–1044.

Smith, T. M., and S. E. Shackleton. 1988. The effects of shading on the establishment and growth of *Acacia tortilis* seedlings. *South African Journal of Botany* **54**:375–379.

Solbrig, O. T., E. Medina, and J. F. Silva. 1996. Determinants of tropical savannas. Pages 31–41 *in* O. T. Solbrig, E. Medina, and J. F. Silva, editors. *Biodiversity and Savanna Ecosystem Processes*. Springer-Verlag, Berlin, Germany.

Spinage, C. A., and F. E. Guinness. 1971. Tree survival in the absence of elephants in the Akagera National Park, Rwanda. *Journal of Applied Ecology* **8**:723–728.

Starfield, A. M., and A. L. Bleloch. 1986. *Building models for conservation and wildlife management*. Macmillan, New York, New York, USA.

Starfield, A. M., D. H. M. Cumming, R. D. Taylor, and M. S. Quadling. 1993. A frame-based paradigm for dynamic ecosystem models. *AI Applications* **7**:1–13.

Steyn, A., and M. Stalmans. 2001. Selective habitat utilisation and impact on vegetation by African elephant within a heterogeneous landscape. *Koedoe* **44**:95–103.

Stokke, S. 1999. Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* **77**:1723–1732.

Stokke, S., and J. T. du Toit. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* **23**:70–80.

Styles, C. V., and J. D. Skinner. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, *Colophospermum mopane*, in Botswana's Northern Tuli Game Reserve. *African Journal of Ecology* **38**:95–101.

Swanepoel, C. M., and S. M. Swanepoel. 1986. Baobab damage by elephants in the middle Zambezi Valley, Zimbabwe. *African Journal of Ecology* **24**:129–132.

Tafengenyasha, C. 1997. Tree loss in the Gonarezhou National Park (Zimbabwe) between 1970 and 1983. *Journal of Environmental Management* **49**:355–366.

Tchamba, M. N. 1995. The impact of elephant browsing on the vegetation in Waza National Park, Cameroon. *African Journal of Ecology* **33**:184–193.

Thomson, P. J. 1975. The role of elephants, fire and other agents in the decline of a *Brachystegia boehmii* woodland. *Journal of the Southern African Wildlife Management Association* **5**:11–18.

Trollope, W. S. W. 1974. Role of fire in preventing bush encroachment in the eastern Cape. *Proceedings of the Grassland Society of SouthernAfrica* **9**:67–92.

Trollope, W. S. W. 1982. Ecological effects of fire in South African savannas. Pages 292–306 *in* B. J. Huntley and B. H. Walker, editors. *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

Trollope, W. S. W. 1984a. Fire in savanna. Pages 149–175 *in* P. de V. Booysen and N. M. Tainton, editors. *Ecological effects of fire in South African ecosystems.* Springer-Verlag, Berlin, Germany.

Trollope, W. S. W. 1984b. Fire behaviour. Pages 199–218 *in* P. de V. Booysen and N. M. Tainton, editors. *Ecological effects of fire in South African ecosystems.* Springer-Verlag, Berlin, Germany.

Trollope, W. S. W. 1993. Fire regime of the Kruger National Park for the period 1980–1992. *Koedoe* **36**:45–52.

Trollope, W. S. W. 1999. Veld burning: savanna. Pages 236–242 *in* N. Tainton, editor. *Veld Management in South Africa*. University of Natal Press, Pietermaritzburg, South Africa.

Trollope, W. S. W., and N. M. Tainton. 1986. Effect of fire intensity on the grass and bush components of the Eastern Cape thornveld. *Journal of the Grassland Society of Southern Africa* **3**:37–42.

Trollope, W. S. W., L. A. Trollope, H. C. Biggs, D. Pienaar, and A. L. F. Potgieter. 1998. Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. *Koedoe* **41**:103–112.

Tyson, P. D., and T. G. J. Dyer. 1978. The predicted above-normal rainfall of the seventies and the likelihood of droughts in the eighties in South Africa. *South African Journal of Science* **74**:372–377.

van de Koppel, J., and H. H. T. Prins. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. *Journal of Tropical Ecology* **14**:565–576.

van Langevelde, F., C. A. D. M. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**:337–350.

van Wijngaarden, W. 1985. *Elephants – trees – grass – grazers: relationships between climate, soil, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya)*. ITC Publication number 4. International Institute for Aerospace Survey and Earth Sciences, Enschede, Netherlands.

van Wilgen, B. W., H. C. Biggs, S. P. O'Regan, and N. Marè. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science* **96**:167–178.

van Wyk, P., and N. Fairall. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* **12**:57–89.

Viljoen, A. J. 1988. Long term changes in the tree component of the vegetation in the Kruger National Park. Pages 310–315 *in* I. A. W. MacDonald and R. J. M. Crawford, editors. *Long-term data series relating to southern Africa's renewable natural resources*. South African National Scientific Programmes Report no. 157, CSIR, Pretoria, South Africa.

Wackernagel, A. 1993. *Elephants and vegetation: severity, scale and patchiness of impacts along the Linyanti River, Chobe district, Botswana*. M.Sc. thesis, University of the Witwatersrand, Johannesburg, South Africa.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556–590 *in* B. J. Huntley and B. H. Walker, editors. *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh, Scotland, UK.

Weber, G. E., F. Jeltsch, N. van Rooyen, and S. J. Milton. 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. *Journal of Applied Ecology* **35**:687–699.

Weyerhaeuser, F. J. 1995. Survey of elephant damage to baobabs in Tanzania's Lake Manyara National Park. *African Journal of Ecology* **23**:235–243.

Whyte, I. J., H. C. Biggs, A. Gaylard, and L. E. O. Braack. 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe* **42**:111–132.

Wiegand, K., D. Ward, H. H. Thulke, and F. Jeltsch. 2000. From snapshot information to long-term population dynamics of Acacias by a simulation model. *Plant Ecology* **150**:97–114.

Wiegand, T., R. J. W. Dean, and S. J. Milton. 1997. Simulated plant population responses to small-scale disturbances in semi-arid shrublands. *Journal of Vegetation Science* **8**:163–176.

Williamson, B. R. 1975. The condition and nutrition of elephant in Wankie National Park. *Arnoldia* **7**:1–20.

Witkowski, E. T. F., and R. D. Garner. 2000. Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites. *Plant Ecology* **149**:91–106.

Witkowski, E. T. F., and T. G. O'Connor. 1996. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland. *Vegetatio* **124**:9–23.

Yeaton, R. I. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. *Journal of Ecology* **76**:1017–1029.

APPENDIX

Model equations for two-tree-species model.

The model equations given below follow those of Chapter 2 closely, the main difference between the two models being the presence of two woody species instead of one, and so the introduction of extra subscripts, denoting species *v* or *w*, into the woody plant notation. Also, we use *y* instead of w_{10} for grass biomass, and $e_{v/w,i}$ instead of v_i for elephant preference values.

Rainfall

The southern African lowveld region experiences two seasons, wet and dry. We incorporate this seasonality by iterating our model using 6-month time steps and we assume that each year's rainfall falls entirely in the wet season. In southern Africa, rainfall also follows a pronounced "quasi 20-year oscillation" of relatively wet and dry periods (Tyson and Dyer 1978, Gertenbach 1980). Thus 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 (i.e., changes in biological rates as a function of relative rainfall levels are scaled to long term average rates). Specifically, we set relative rainfall $r(t)$ to be:

$$r(t) = \max\left(0, 1 + h \sin \frac{p\,(t+1)}{2w} + z(t)\right), \qquad t \text{ even (start of wet season)},$$

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

where h is the amplitude (relative to the long-term mean) of wet-dry cycles of period w years (doubled above to take our 6-monthly seasonal time step into account), and $z(t)$ is a stochastic variable accounting for interannual variation around these underlying cycles. We assume that for each even t the value of $z(t)$ is drawn from the same distribution (i.e., $z(t)$ is i.i.d). The rainfall is applied evenly over the entire grid, a reasonable assumption given the size of our representative plot (Du Toit *et al*. 1990).

Wet season dynamics.

Wet season woody plant dynamics.

All growth and reproduction is assumed to occur in the rainy season (see Box 1, Chapter 2). The change in the woody population during a wet season starting from time t is given by:

$$q_{x,i}(t+1) = \left(g_{x,q,i-1} q_{x,i-1}(t) + \left(1 - g_{x,q,i}\right) q_{x,i}(t)\right)\left(1 - h_{x,i}(t)\right), \qquad i = 2, 3, \ldots, 9$$

where $q_{x,i}(t)$ represents the number of individuals in cell x, of species $q = v$ or w, in woody class i at the beginning of the wet season, $h_{x,i}(t)$ is loss of individuals due to encroachment by the growing and expansion of larger individuals, and $g_{x,q,i-1}$ is the transition rate from class i–1 to class i for that species, cell and season. In general, $g_{x,q,i-1}$ will depend not only on t, but also on the current vegetation ($\mathbf{v}_x(t)$, $\mathbf{w}_x(t)$ and $y_x(t)$) as well as on rainfall: i.e., $g_{x,i-1} = g_{x,i-1}(t, \mathbf{v}_x, \mathbf{w}_x, y_x, r)$. The seedling classes ($i$ = 1) are given by

$$q_{x,1}(t+1) = \left(g_{x,q,0}c_{x,q}(t) + \left(1-g_{x,q,1}\right)q_{x,1}(t)\right)\left(1-h_{x,1}(t)\right),$$

where $c_{x,q}(t)$ is the expected number of new seedlings of species q emerging in cell x at time t, and $g_{x,q,0}$ is the proportion of these which successfully recruit (see below; the zero-subscript refers to a notional class of presumptive seedlings). The seed bank is not explicitly modeled (Menaut *et al*. 1990), rather the expected number of emerging seedlings depends on the adult tree population at the end of the previous wet season (i.e., which ran from t–2 to t–1) and is given by

$$c_{x,q}(t) = m_q\left[\left(1-d\right)\left(q_{x,8}(t-1) + q_{x,9}(t-1)\right) + \frac{d}{4}\sum_{z=\text{neighbourof } x}\left(q_{z,8}(t-1) + q_{z,9}(t-1)\right)\right],$$

where m_q is the fecundity of mature trees of species q. The dispersal parameter d represents the proportion of seedlings parented by individual trees from the four neighboring cells. We assume no difference between dispersal abilities of either species (although such difference could easily be incorporated by choosing $d_v \neq \delta_w$).

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

$$g_{x,q,i}(t) = \min\left(c_{x,v,i}(t),\ l_{x,q,i}(t)\right), \qquad 0 \leq i \leq 8$$

where $c_{x,q,i}(t)$ represents the underlying growth rates for species q, adjusted for competition and rainfall, and $l_{x,i}$(t) is the maximum proportion of class i that can grow to class i+1 without causing the cell x to overfill. (The growth algorithm is schematically depicted in Box 2, Chapter 2.) For seedling establishment, the proportion recruited is given by

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

and for plants already established ($i \geq 1$), the adjusted growth rate is given by

$$c_{x,q,i}(t) = r(t)g_{q,i}\, f_{x,i}(\mathbf{v}_x(t), \mathbf{w}_x(t), y_x(t)),$$

where $g_{q,i}$ is the underlying growth rate from class i to i+1 of species q and $f_{x,i}()$ is the proportion of those overcoming competition for space and resources. Within the sapling classes, growth is assumed to be automatic, so that $f_{x,i}(t) = 1$ for i = 2, 3, 4. For other classes ($i \leq 9$), the $f_{x,q,i}(t)$ are defined below. First, recall that we define "resource areas," a_i, in terms of the area (in hectares) occupied by one individual of class i. Then let $a_{x,q,i}(t)$ represent the total proportion of area (in cell x at time t) controlled by all individuals in class i of species q, i.e.,

$$a_{x,q,i}(t) = a_i q_{x,i}(t), \qquad 1 \leq i \leq 9.$$

Calculation of $a_{x,y}(t)$, the area covered by grass, is elaborated in the subsection on wet season grass dynamics below. Next we consider competition for light, nutrients and water, and calculate $f_{x,i}(t)$, the "competition coefficient" (*sensu* Getz and Haight 1989). We approximate competitive effects by aggregating on a per-area basis:

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

$$f_{x,i}(t) = 1 - \sum_{j=i}^{9} a_{x,v,j}(t) - \sum_{j=i}^{9} a_{x,w,j}(t), \qquad \text{i} = 5, 6, 7, 8.$$

Effectively, we assert that recruitment of seed (again employing the notional class $i = 0$) into seedlings, and of seedlings into saplings, will be limited by competition from existing seedlings, saplings, shrubs and grass. Interspecific competition is modeled as differential growth ability, using only differences in the growth rates $g_{v,i}$ and $g_{w,i}$. Growth of individuals in classes $i = 5, \ldots, 8$ (i.e., growth of saplings to shrubs, and so on up to mature trees) is assumed to be limited by competition from individuals in equal or higher stage classes (Menaut *et al*. 1990; also see Getz and Haight (1989) for tree classes with competition treated by canopy cover).

The expansion limiting coefficients, $l_{x,i}$, come into play in situations of strong woody dominance coupled with excellent growth conditions. Because we allow the more mature individuals to dominate, and thus grow in preference to smaller individuals, the coefficients $l_{x,i}$ involve projecting total possible recruitment and then reducing that recruitment, in order of trees, …, seedlings, in case of overflow (see Box 2, Chapter 2). To derive the recruitment equations presented below, we have assumed that seedlings and saplings can grow under tree-canopies but that shrubs cannot. Thus, to grow into seedlings, seeds can use bare ground or space under trees but not under existing seedlings, saplings, shrubs or grass. Similarly, seedlings can only expand under trees or over bare ground to grow into saplings, saplings can only expand over seedlings or grass to grow into shrubs, and the expansion space available for the shrub class $i = 7$ to grow into trees equals all but the existing trees. In the case of growth of shrubs to trees, $l_{x,7}$ is simply the available area for new trees divided by $a_8(v_{x,7}(t)+w_{x,7}(t))$, the area which would be taken up by shrubs currently in class $i = 7$, were they all to become trees (i.e., if the growth rate equaled 1). As we assume mature trees can dominate over all other classes, the available area for recruitment is given by total area, less area already occupied by adult trees, giving

$$l_{x,7}(t) = \frac{1 - a_{x,v,8}(t) - a_{x,v,9}(t) - a_{x,w,8}(t) - a_{x,w,9}(t)}{a_8\left(w_{x,v,7}(t) + w_{x,w,7}(t)\right)}.$$

This allows us to calculate $g_{x,v,7}(t)$ and $g_{x,w,7}(t)$, and thus determine the actual number of recruits to the tree stage and then proceed to calculate the available space for sapling recruitment to shrubs and so on (dropping the x and t arguments for convenience):

$$l_5 = \frac{1 - a_{v,6} - a_7(1 - g_{v,7})v_7 - a_8 g_{v,7} v_7 - a_{v,8} - a_{v,9} - a_{w,6} - a_7(1 - g_{w,7})w_7 - a_8 g_{w,7} w_7 - a_{w,8} - a_{w,9}}{a_6(v_5 + w_5)},$$

$$l_1 = \frac{1 - f_{l_1}(\mathbf{v}) - f_{l_1}(\mathbf{w})}{a_2(v_1 + w_1)},$$

where

$$f_{l_1}(\mathbf{q}) = a_{q,2} + a_{q,3} + a_{q,4} + a_5(1 - g_{q,5})q_5 + a_6 g_{q,5} q_5 + a_{q,6} + a_7(1 - g_{q,7})q_7,$$

$$l_0 = \frac{1 - f_{l_0}(\mathbf{v}) - f_{l_0}(\mathbf{w}) - a_y}{a_1(c_v + c_w)},$$

where

$$f_{l_0}(\mathbf{q}) = a_1(1 - g_{q,1})q_1 + a_2 g_{q,1} q_1 + f_{l_1}(\mathbf{q}).$$

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

Any given level of growth, $g_{q,i}$, may also entail shading out other plants in the same or lower height class and so we introduce h_i as a "crowding coefficient," representing the proportion of plants overcrowded by the individuals growing from class i to $i+1$ (see Box 2). Again using per-area aggregation, we set h_i as the ratio of the extra area now occupied by the grown individuals (i.e., area encroached over), to the total area occupied by those plants which can be crowded out by their growth, i.e., the area which had been available for the expansion of the growing individuals (the numerator of the l_i above). Since we assume that crowding of shrubs is experienced equally by both shrub classes, and likewise for the sapling classes, this gives us (again space subscripts and time arguments are understood):

$$h_6 = h_7 = \frac{(a_8 - a_7)(g_{v,7} v_7 + g_{w,7} w_7)}{1 - a_{v,8} - a_{v,9} - a_{w,8} - a_{w,9}},$$

$$h_2 = h_3 = h_4 = h_5 = \frac{(a_6 - a_5)(g_{v,5} v_5 + g_{w,5} w_5)}{1 - f_{h_{2-5}}(\mathbf{v}) - f_{h_{2-5}}(\mathbf{w})},$$

where

$$f_{h_{2-5}}(\mathbf{q}) = a_{q,6} + a_7(1 - g_{q,7})q_7 + a_8 g_{q,7} q_7 + a_{q,8} + a_{q,9},$$

$$h_1 = \frac{(a_2 - a_1)(g_{v,1}v_1 + g_{w,1}w_1)}{1 - f_{h_1}(\mathbf{v}) - f_{h_1}(\mathbf{w})},$$

where

$$f_{h_1}(\mathbf{q}) = a_{q,2} + a_{q,3} + a_{q,4} + a_5(1 - g_{q,5})q_5 + a_6 g_{q,5} q_5 + a_{q,6} + a_7(1 - g_{q,7})q_7 .$$

Note that the crowding coefficients, being proportions, are applied equally to both woody species, and that we don't need any crowding coefficient for recruitment to the seedling class as this growth just "encroaches" over bare ground. Also note that h_1 and h_5 are applied to crowding out the grass layer too (see below).

Wet season grass dynamics.

We also model wet season grass growth in terms of area covered and biomass. The area covered by grass is updated to account for changes in the woody vegetation cover (including woody growth during the wet season), reduced by the level of elephant grazing (it is assumed that elephants uproot whole grass tufts when grazing; Owen-Smith 1988, Kalemera 1989) and adjusted for rainfall amount:

$$a_{x,y}(t+1) = r(t)\left(1 - \sum_{i=1}^{7} a_{x,v,i}(t) - \sum_{i=1}^{7} a_{x,w,i}(t)\right)(1 - u_{x,y}(t))(1 - h_{x,1}(t) - h_{x,5}(t)), \qquad t \text{ even},$$

where $u_{x,y}(t)$ represents the proportion of the grass in cell x grazed by elephant. As discussed above we reduce the grass area by the proportion of extra ground shaded out by individuals growing into the first sapling and shrub classes (i.e., entering classes $i = 2$, 6). The area occupied by grass is rainfall-dependent as it is assumed that grass tufts expand or shrink in higher or lower rainfall conditions, which may be important in seedling recruitment dynamics.

The grass biomass then increases by the productivity of the area $a_{x,y}(t+1)$, adjusted for wet season senescence (Illius and O'Connor 2000) and for elephant grazing:

$$y_x(t+1) = s_y^W r(t)\big(1 - u_{x,y}(t)\big)\big(y_x(t) + g_y a_{x,y}(t+1)\big),$$

where g_y is annual grass productivity in kg/ha and s_y^W is wet-season persistence ("survival") of grass biomass.

Elephant grazing

Elephants are assumed to visit each cell in proportion to the relative amount of grass biomass present. Let $l(t)$ be the elephant density (numbers per hectare) at time t and I_y be the elephant intake rate of grass in units of kg/elephant/wet-season. Then the elephant utilization of cell x is given by:

$$u_{x,y}(t) = l(t) I_y \frac{y_x(t) + g_y r(t)\left(1 - \sum_{i=1}^{7} a_{x,v,i}(t) - \sum_{i=1}^{7} a_{x,w,i}(t)\right)}{\sum_{z=1}^{100}\left(y_z(t) + g_y r(t)\left(1 - \sum_{i=1}^{7} a_{z,v,i}(t) - \sum_{i=1}^{7} a_{z,w,i}(t)\right)\right)}.$$

Note that we project grass biomass forward in time in the calculation of $u_{x,y}(t)$ to allow initial grass recovery from dry season burns, senescence etc.

Dry season dynamics.

In our model, woody plant mortality, elephant browsing and fire are limited to the dry season (see Box 1, Chapter 2) giving overall woody plant dynamics for species q (= v or w) of

$$q_{x,i}(t+1) = F_{q,i}\left(\mathbf{v}_x(t), \mathbf{w}_x(t), s_{q,i}, r(t-1), l(t)\right), \qquad t \text{ odd},$$

where $s_{q,i}$ represents the mean survival rate of stage class i in species q, and recalling that $r(t-1)$ is the rainfall from the previous wet season and $l(t)$ is the density of elephants (number per hectare) at time t. Here $F_{q,i}$ is a concatenation of the functions $f_{\text{surv},q,i}$, $f_{\text{ele},q,i}$ and $f_{\text{fire},q,i}$, that incorporate the effects of mortality, elephant browsing and fire respectively: i.e.,

$$f_{\text{surv},q,i} \equiv f_{\text{surv},q,i}\left(q_{x,i}(t), r(t-1), s_{q,i}\right),$$

$$f_{\text{ele},q,i} \equiv f_{\text{ele},q,i}\left(\mathbf{v}_x(t), \mathbf{w}_x(t), l(t), f_{\text{surv},q,i}, f_{\text{surv},q,i}\right),$$

$$F_{q,i} = f_{\text{fire},\, q,i} \equiv f_{\text{fire},\, q,i}\left(\mathbf{q}_x(t), f_{\text{ele},q,i}\right).$$

We now consider the functions $f_{\text{surv},q,i}$, $f_{\text{ele},q,i}$ and $f_{\text{fire},q,i}$ in turn.

Woody plant survival.

A certain proportion of subadult woody plants die, depending on the rainfall for that year. We also assume that mature trees are fairly resilient to short-term fluctuations in rainfall, but will experience increased mortality in droughts lasting more than two years (Scholes 1985):

$$f_{\text{surv},q,i}(r(t-1), s_{q,i}, q_{x,i}) = s_{q,i} r(t-1) q_{x,i}\ , \qquad i = 1,\ldots,7$$

$$f_{\text{surv},q,i}(r(t-1), s_{q,i}, q_{x,i}) = (s_{q,i} - m^{r}_{q,8-9} x(t)) q_{x,i}\ , \qquad \mathrm{i} = 8, 9\,,$$

where $m^{r}_{q,8-9}$ represents additional mortality experienced by mature species q trees in drought conditions, weighted for drought severity (calculated from a three-year running mean, i.e., through wet seasons at t–5, t–3 and t–1) using the function $x(t)$:

$$?(t) = \frac{k^{z}}{\left(\sum_{j=t-5}^{t} \frac{r(j)}{3} \right)^{z} + k^{z}}.$$

Given this form, we see that the function x maps the three-year mean relative rainfall to points on the interval [0, 1], where the parameter z describes the steepness of the drought response (cf. density response in Getz 1996), and the constant k is the value of the three-year mean which causes 50% of the additional drought-related mortality. Recall that $r(t)$ = 0 for odd values of t (dry seasons) so that in the above summations $r(j)$ = 0 for y = t, t–2, t–4.

Elephant browsing.

Elephants are assumed to browse in each cell, with the total browsing pressure in a cell depending on that cell's "attractiveness" (a preference-weighted sum of its woody plant availability) relative to the others'. Within each cell elephants browse on the different species and size-classes in proportion to each class's availability, with the exception of the tallest and shortest sizes (Croze 1974b, Lewis 1987a). Using the vector notation $\mathbf{q}_x(t)$ for the structure of species q (= v, w) in each cell, $\mathbf{f}_{\text{ele},\mathbf{q}}$ for the column vector ($f_{\text{ele},q,1}$, $f_{\text{ele},q,2}$, …, $f_{\text{ele},q,9}$)′, and employing $\mathbf{u}_{x,q}(t)$, the elephant-utilization vector for species q in cell x (see below), we can express the effect of elephant browsing on the woody vegetation as:

$$\mathbf{f}_{\text{ele},\mathbf{q}}(l(t),\mathbf{v}_x,\mathbf{w}_x) = \left(\mathbf{I} - \mathbf{E}_q \cdot \mathbf{U}_{x,q}(t)\right)\mathbf{q}_x ,$$

where $\mathbf{U}_{x,q}(t)$ is a 9×9 diagonal matrix with the elements of the utilization vector $\mathbf{u}_{x,q}(t)$ on the diagonal, $\mathbf{I}$ is the (9×9) identity matrix and $\mathbf{E}_q$ is an elephant-effect matrix mapping for species q the rates of death and stunting resulting from elephant utilization.

The utilization profile of the vegetation within each cell is measured with the 9-element column vectors $\mathbf{u}_{x,q}(t)$, which are composed of the elements $u_{x,q,i}(t)$, representing the proportions of each stage-class used. These are calculated from a weighted sum of all woody vegetation, with $e_{q,i}$, the perceived "preference-value" of each stage-class and species, providing the weights. As utilization of adult trees differs from that of size-classes <3m, we consider adult utilization separately from that of saplings and shrubs. We assume that within our square kilometer of interest, elephants allocate their foraging effort between cells in proportion $p_x(t)$ to the cells' perceived attractiveness, and that within each cell they then forage on each species and stage-class in proportion $p'_{x,q,i}(t)$ to each stage class's presence (also weighted by the preference value), where

$$p_x(t)=\frac{\sum_{k=1}^{7}\left(e_{v,k}v_{x,k}(t)+e_{w,k}w_{x,k}(t)\right)}{\frac{1}{n}\sum_{z=1}^{n}\sum_{k=1}^{7}\left(e_{v,k}v_{z,k}(t)+e_{w,k}w_{z,k}(t)\right)},$$

$$p'_{x,q,i}(t)=\frac{e_{q,i}q_{x,i}(t)}{\sum_{k=1}^{7}\left(e_{v,k}v_{x,k}(t)+e_{w,k}w_{x,k}(t)\right)},\qquad 1\le i\le 7$$

and n is the number of cells in the grid (n = 100). (Note that $e_{q,1}=0$ as we assume seedlings are not utilized.) Thus the proportion of individuals utilized in each cell, of each stage class <3m (for each species q) is:

$$u_{x,q,i}(t)=l(t)I_{1-7}p_x(t)p'_{x,q,i}(t)\frac{1}{q_{x,i}(t)},\qquad q_{x,i}(t)>0,\ 1\le i\le 7,$$

which simplifies to

$$u_{x,q,i}(t)=l(t)I_{1-7}\frac{ne_{q,i}}{\sum_{x=1}^{n}\sum_{k=1}^{7}\left(e_{v,k}v_{x,k}(t)+e_{w,k}w_{x,k}(t)\right)},\qquad q_{x,i}(t)>0,\quad 1\le i\le 7,$$

where $I_{1\text{-}7}$ is the elephant intake rate of sub-adult woody vegetation, in units of plants per elephant per dry season. Similarly, we calculate the proportions of adult trees utilized as:

$$u_{x,q,i}(t)=l(t)I_{8-9}\frac{ne_{q,i}}{\sum_{x=1}^{n}\sum_{k=8}^{9}\left(e_{v,k}v_{x,k}(t)+e_{w,k}w_{x,k}(t)\right)},\qquad q_{x,i}(t)>0,\quad i=8,9,$$

where $I_{8\text{-}9}$ is the elephant intake rate of adult trees (again in units of plants per elephant per dry season). If $q_{x,i}(t) = 0$ then we also set $u_{x,q,i}(t) = 0$. We then compose $\mathbf{u}_{x,q}(t)$ as the vector corresponding to the $u_{x,q,i}(t)$'s:

$$\mathbf{u}_{x,q}(t) = \left(u_{x,q,1}(t), u_{x,q,2}(t), \ldots, u_{x,q,9}(t)\right)' .$$

The species-specific elephant-effect matrices $\mathbf{E}_v$ and $\mathbf{E}_w$ are 9×9 matrices which adjust the woody vegetation for the impact of elephant browsing, incorporating both mortality and sub-lethal effects. Broken stems may either die or resprout. Resprouting saplings are assumed to re-enter the seedling height class, similarly shrubs are reduced to sapling height and trees may be reduced to sapling or shrub height. To reflect accelerated growth of coppiced individuals due to below-ground stored tissue, plants re-entering the sapling or shrub metaclasses are assigned to the highest cohort ($i = 5$ or $i = 7$) within those strata, giving

$$\mathbf{E}_q = \begin{pmatrix} \mu^e_{q,1} & -r_{q,21} & -r_{q,31} & -r_{q,41} & -r_{q,51} & 0 & 0 & 0 & 0 \\ 0 & \mu^e_{q,2}+r_{q,21} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mu^e_{q,3}+r_{q,31} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mu^e_{q,4}+r_{q,41} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mu^e_{q,5}+r_{q,51} & -r_{q,65} & -r_{q,75} & -r_{q,85} & 0 \\ 0 & 0 & 0 & 0 & 0 & \mu^e_{q,6}+r_{q,65} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mu^e_{q,7}+r_{q,75} & -r_{q,87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu^e_{q,8}+r_{q,85}+r_{q,87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu^e_{q,9} \end{pmatrix},$$

where $m^{e}_{q,i}$ is the proportion of individuals (of species q in class i) utilized by elephants, which die, and $r_{q,ik}$ is the proportion of species q in class i which are reduced in height to class k following utilization. Note that not all browsing results in death or stunting (if $m + r < 1$).

Fire.

Burning is assumed to take place only in the dry season. Grass biomass provides fuel for fires and in our model the probability of fire occurring is linearly related to grass biomass. This is a close approximation to the logistic regression formula produced by van Wilgen *et al*. (2000) from Kruger National Park fire history data. 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

$$\begin{aligned} b_x(t) &= 1 \qquad \text{if} \qquad R_x < y\, y_x(t) \\ b_x(t) &= 0 \qquad \text{if} \qquad R_x \geq y\, y_x(t), \end{aligned}$$

where R_x is a uniform random variable drawn on [0, 1] for each cell x, and y is a constant which scales biomass to a fire probability. The spread of fire is modeled by repeating this procedure (drawing another random number for comparison) for every non-burning cell with a burning neighbor, for each burning neighbor. For example, if a non-burning cell x has two burning neighbors, then two further values of R_x are drawn and compared with $y\, w_{x,10}(t)$. The procedure is further repeated until no additional cells burn.

Fire intensity is also assumed to be linearly related to grass biomass (Trollope 1984b, Higgins *et al*. 2000), and is modeled relative to the biomass yielding maximum intensity:

$$b_x(t) = \frac{b_x(t)y_x(t)}{y_{\max}},$$

where $b_x(t)$ is the fire intensity relative to that yielded by a grass biomass of $y_{\max}$. Other variables such as heat yield, rate of spread, relative humidity, fuel moisture and wind speed (Trollope 1984b, Higgins *et al*. 2000) can also affect fire intensity but we ignore these factors in this model.

Woody plants have their above-ground stems burned which may cause death or resprouting. We assume here that both woody species experience identical responses to fire. The proportion, $t_{x,i}(t)$, of those in class i experiencing topkill is calculated as follows:

$$t_{x,1}(t) = b_x(t),$$

$$t_{x,i}(t) = \min\left(1, \frac{b_x(t)y_x(t)}{y^*}\right), \qquad 2 \le i \le 5$$

$$t_{x,i}(t) = m^b_{6-7} b_x(t), \qquad i = 6,\ 7$$

$$t_{x,i}(t) = m^b_{8-9} b_x(t), \qquad i = 8,\ 9,$$

where $w*$ is the grass fuel required to kill 100% of saplings, and m^b_{6-7} and m^b_{8-9} are the topkill rates of shrubs and mature trees, respectively, under maximum intensity fires. These equations assume that all seedlings are killed by fire (Jeltsch *et al.* 1996) and that above-ground tissue death is proportional to fire intensity for all other stage-classes. Although our tree class has been defined based on the fire-escape height (≥3m; Pellew 1983), we allow for some mortality from fires which may be linked to, for example, scarring of bark by porcupine (Yeaton 1988). The woody vegetation is adjusted for topkill from fires as follows:

$$f_{\text{fire},q,i}(q_{x,i}(t)) = \left(1 - t_{x,i}(t)\right)q_{x,i}(t) + k_{i+1}t_{x,i+1}(t)q_{x,i+1}(t)\ ,$$

where k_i is the proportion of top-killed plants in stage-class i that resprout following fire; these are assumed to enter the next lowest stage-class due to strong regrowth enabled by below-ground biomass reserves.

Dry season grass dynamics.

Dry season grass dynamics are comparatively simple. We assume that grass burns entirely in fires, and senesces (again depending on annual rainfall) in the absence of fire:

$$a_{x,y}(t+1) = \left(1 - b_x(t)\right)a_{x,y}(t), \qquad t \text{ odd},$$

$$y_x(t+1) = r(t-1)s^D_y\left(1 - b_x(t)\right)y_x(t)\ ,$$

where s_y^D is the dry-season persistence (“survival”) of grass biomass.

Table A1. Parameters and variables used (in alphabetical order) for the two-tree-species model. Symbols including subscript q refer to woody species v and w. See Chapter 2 for details of parameter estimation.

Symbol	**Description**	**Units**
$a_{x,q,i}(t)$	area controlled by woody species q in class i in cell x at time t	ha
$a_{x,y}(t)$	grass coverage in cell x at time t	ha
b_x	fire indicator for cell x	binary
$c_{x,q}$	potential species q seedlings emerging in cell x	plants
$\mathbf{E}_{\boldsymbol{q}}$	elephant browsing effect matrix for species q	–
$e_{q,i}$	elephant preference weighting for stage-class i in species q	–
$F_q()$	dry-season woody plant function for species q, comprised of $f_{\text{ele},q}$, $f_{\text{fire},q}$, $f_{\text{mort},q}$.	–
$f_{\text{ele},q}()$	dry-season elephant impact function for species q	–
$f_{\text{fire},q}()$	dry-season fire-impact function for species q	–
$f_{\text{surv},q}()$	dry-season survival function for species q	–
$g_{x,q,i}$	realized transition rate from species q class i to i+1 for cell x	–
$h_{x,i}$	crowding coefficient resulting from all woody plant growth to class i+1 in cell x	–
i	woody plant stage-class index ($1 \leq i \leq 9$)	–
I_y	intake rate of grass by elephants, wet season only	kg/ele /season
$I_{1\text{-}7}$	elephant utilization of sub-adult woody plants, dry season only	plants/ele /season
$I_{8\text{-}9}$	elephant dry season utilization of adult trees	plants/ele /season
k	value of mean relative rainfall inducing 50% of maximum drought-related tree mortality (m_m^r)	–
$l(t)$	elephant density at time t	individuals /ha
m_q	fecundity of mature trees of species q	seedlings /tree/yr
n	number of hectare cells in grid	–
q	woody species indicator ($q = v$ or w).	–
$\mathbf{q}_x(t)$	vector of woody structure of species q in cell x at time t	individuals
R_x	uniform random variable drawn from U(0, 1)	–
$r(t)$	rainfall relative to the long-term mean (=0 for dry seasons)	–
$s_{q,i}$	survival of stage class i in species q	–
s_y^D	dry season survival (non-senescence) of grass	–
s_y^W	wet season survival (non-senescence) of grass	–
t	time index	half-year
$\mathbf{U}_{x,q}$	diagonal matrix with $\mathbf{u}_{x,q}$ on the diagonal	–
$\mathbf{u}_{x,q}$	elephant woody plant utilization vector for species q in cell x	–
$u_{x,q,i}$	elephant browsing intensity on class i of species q in cell x (dry seasons)	–

Table A1 (continued).

Symbol	Description	Units
$u_{x,y}$	elephant grazing intensity in cell x (wet seasons)	–
$v_{x,i}(t)$	number of plants in woody species v of class i, in cell x at time t	individuals
$w_{x,i}(t)$	number of plants in woody species w of class i, in cell x at time t	individuals
x	cell index ($1 \le x \le 100$)	–
$y_x(t)$	biomass of grass in cell x at time t	kg
$y_{\max}$	grass biomass yielding maximum intensity fire	kg
y^*	grass fuel required for a fire to kill 100% saplings	kg
$z(t)$	stochastic variable accounting for interannual variation around underlying rainfall cycles, drawn from $N(0,\ s_r^2)$.	–
a_i	area controlled by one individual of class i	ha
b_x	relative fire intensity in cell x	–
$g_{q,i}$	expected transition rate (under mean, uncrowded conditions) from species q class i to i+1	–
g_y	net annual grass productivity under mean rainfall	kg/ha
d	proportion of seedlings dispersing to neighboring cells	–
z	drought severity steepness control (shape parameter)	–
h	amplitude of wet-dry rainfall cycles, relative to long-term mean	–
k_i	resprouting rate of woody class i following fire	–
$l_{x,i}$	expansion-limiting coefficient for woody class i in cell x	–
$m_{6\text{-}7}^{b}$	shrub topkill under maximum intensity fire	–
$m_{8\text{-}9}^{b}$	mature tree mortality under maximum intensity fire	–
$m_{q,i}^{e}$	mortality of species q class i plants utilized by elephant	–
$m_{q,8\text{-}9}^{r}$	additional drought mortality for species q adults	–
x	drought severity coefficient	–
p_x	proportion of elephant foraging allocated to cell x	–
$p'_{x,q,i}$	proportion of elephant foraging allocated to species q class i in cell x	–
$r_{q,ik}$	proportion of species q class i reduced to class k after elephant utilization	–
s_r	standard deviation in annual rainfall relative to long-term mean	mm
t_i	topkill rate of woody class i due to fire	–
$f_{x,i}$	competition coefficient applied to growth rate of woody class i	–
$c_{x,q,i}$	net growth rate of species q class i given sufficient area for expansion	–
y	scaling constant converting grass biomass to fire probability	kg^{-1}
w	period of wet-dry rainfall cycles	years