Influence of drought or elephant on the dynamics of key woodland species in a semiarid African savanna

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Declaration

I hereby declare that the contents of this dissertation comprises my own original work, except where otherwise acknowledged or stated. This work has not been submitted for degree purposes to any other university.

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S. D. MacGregor

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Abstract

Extensive drought- and elephant-related dieback of *Colophospermum mopane* and *Acacia tortilis*, respectively, offered an opportunity for increasing understanding of the causes of drought-related patch dieback, the factors influencing elephant utilization of woody plants, and the response of woody plants to both aforementioned determinants of savanna structure and function. The dendrochronological analysis of both species was undertaken to estimate potential rates of replacement, following extensive mortality.

Areas of discrete dieback were compared with adjacent paired areas of 'healthy' vegetation, which revealed, on average, 87% and 13% loss of basal area by mortality, respectively. 'Live' and 'dead' plots did not differ in soil type, topography or mean slope, but differed in vegetation structure, soil surface condition, and soil chemistry. Although there was evidence of self-thinning, neither inter- nor intra-specific competition explained dieback. 'Dead', by comparison with 'live' plots, had changed from functioning as sinks of sediment and water to sources, were less likely to retain water because of a poor soil surface condition, and were predisposed to drought effects because of a greater proportion of fines, and Na concentration. Dieback resulted from insufficient soil water for survival during a drought owing to the development of a dysfunctional landscape during 50 years of livestock ranching.Spatial heterogeneity within a landscape was suggested to enhance woodland resilience to severe droughts by ensuring the survival of plants in run-on sinks or 'drought refuge' sites.

Stem sections were removed from 40 multi-stemmed *C. mopane* trees and prepared for examination under a dissecting microscope. It was impossible to age *C. mopane*, owing to a hollow and/or dark heartwood. Nevertheless, the distribution of stem diameters suggested a single recruitment event. Fire scars attributed to the last recorded fire in 1948 could explain the trees' multi-stemmed growth form and indicate that most trees of VLNR were > 50 years of age.

Growth rings were identified in 29 *A. tortilis* trees of unknown age, but were not correlated with annual rainfall records. Growth rates varied between trees; mean ring width ranged from 1.4 to 3.5 mm (overall mean 2.4 ± 0.1 mm). A technique was proposed for predicting growth rate from annual rainfall, using selected data, and several factors potentially influencing ring width in semi-arid environs were identified.

Permanent ground-based transects were located within riparian ($n = 16$) and *Acacia* ($n = 5$) woodlands to monitor elephant utilization. Elephant had not changed the population structure of the woodlands by 2000, but had reduced stem density from 215.6 stems ha^{-1} (1996) to 84.4 stems ha^{-1} (2000). *Acacia tortilis* trees in the woodlands had branches removed, were debarked, uprooted and broken. *Acacia tortilis* trees in the riverine had lower levels of utilization, whilst *Acacia nilotica* trees were mostly debarked. The method of elephant feeding varies within and between woody species, provided it is within the mechanical constraints of a certain size or species. Elephant behaviour is concluded to depend on spatiotemporal variation of forage abundance/quality, abundance of a preferred species, and species response (coppice or mortality). Elephant can cause a change of vegetation state, and increase spatial homogeneity of a plant population. The remnant population of woodland trees should provide the potential for recolonization, in which case the system would reflect the stable limit cycle. However, if browsing inhibits seedling recruitment, the system could reflect either a multiple stable state system or an artificial equilibrium imposed on a stable limit cycle.

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Chapter 1

Introduction

Range management is a discipline of applied ecology necessarily arranged around a model formulated by current perceptions of how particular ecological systems function (e.g. Westoby *et al.* 1989). Considering our interpretation of a system influences the manner in which we manipulate it, it is imperative that a thorough and objective accumulation of knowledge concerning the dynamics of these systems be collected. The traditional range succession concept (Clements 1916) failed to deal with African rangeland ecology on account of its shortcomings regarding systems not at equilibrium (Westoby *et al.* 1989). Arid and semi-arid ecosystems do not adhere to a monotonic gradient of states when subjected to variable conditions, but show discontinuous and irreversible transitions between discrete quasi-stable states (Wiegand *et al.* 1995). Changes in semi-arid systems, typically event-driven and episodic (e.g. Walker 1993), are an adaptation to a fluctuating environment (Wiegand *et al.* 1995), affected more by abiotic than biotic controls (Ellis & Swift 1988) which occur as rare or extreme events (Wiegand & Milton 1996). Climatic instability, manifested in low rainfall areas with high coefficients of variation, produces highly dynamic ecosystems (Caughley *et al.* 1987).

African savannas are highly dynamic systems with the potential of alternating between woodland and grassland states (Prins & Van Der Jeugd 1993). The dynamics of savannas and their woody species are affected by biological and physical controls, commonly termed determinants (Walker 1985). The inherent structure and function imposed on savannas by the primary determinants, plant-available water and plant-available nutrients, may be modified by the secondary determinants, fire and herbivory (Frost *et al.* 1986). Determinants of savanna dynamics may be identified as either natural events or management actions. Perhaps the single most important natural event affecting arid and semi-arid savannas is drought, whilst management actions, especially burning and the inclusion of herbivores, particularly elephant, are equally disruptive forces capable of halting, reversing and even trapping successional processes (Norton-Griffiths 1979). Drought and elephant are capable of implementing change at the community level because their effects range from local to regional or landscape scales and are therefore shared by the component species which comprise those communities. However, a few case studies on savanna woodland communities have revealed different population dynamics among the component species, owing to their different tolerances of drought (O'Connor 1999) and elephant impact (Barnes 1983).

The extent of drought-induced mortality, although influenced by soil type (Scholes 1985) and density (Smit 1994), differs among woody species. Some species, such as *Colophospermum mopane*, are more drought tolerant than others (O'Connor 1999). The intensity and spatial pattern of drought-induced mortality ranges from usually about 5% of the trees and uniform (Scholes 1985) to 100% mortality and patchy (Fensham & Holman 1999). Elephant are notorious for the changes they have caused in African savannas, specifically changes to vegetation structure (Ruess & Halter 1990), species composition (Anderson & Walker 1974), and density (Croze 1974b), which often do not coincide with management objectives (e.g. Pellew 1983a). Elephant utilize a wide range of species (Williamson 1975), although certain species are occasionally preferred (Tchamba 1995), such as *Acacia tortilis*, and spatial density gradients do result in different patterns of elephant-induced mortality (Barnes 1983). Spatial non-uniformities in patterns and processes of the environment and herbivores, such as drought-related patch dieback and density-dependent patterns of elephant-induced mortality, respectively, create spatial heterogeneity, thereby potentially enhancing the stability and resilience of populations or communities (Noy-Meir 1996) through the creation of drought- or herbivore-refuge sites.

The population dynamics of a single species can constitute major ecological perturbations at the community (savanna woodland) level, considering drought-related patch dieback is commonly associated with the dominant woody component (Heatwole & Lowman 1986; Fensham & Holman 1999) and preferred dominant species can be altered in their hierarchical order of abundance by elephant (Anderson & Walker 1974). The aforementioned is particularly relevant when the species concerned are of considerable economic and ecological value, maintaining community structure and functioning on account of their dominance. Elephant impact may reduce biodiversity (Cumming *et al.* 1997) and droughts possess at least the potential to reduce species-richness (O'Connor 1999). These agents of mortality may therefore modify ecosystem functioning (Solbrig *et al.* 1996), particularly in communities which contain few ecologically similar species capable of maintaining structure and function (Walker 1995). Species-rich systems are buffered against change on account of their biological diversity and redundancy (Walker 1995). Hence the reason for many conservation agencies adopting management policies that include the maintenance and in some instances increase of biotic diversity. Consequently, the integrity and long-term sustainability of species-poor systems warrant foremost conservation concern in the advent of possible species extinctions.

A monitoring approach was initiated in the Mopane Veld of the Northern Province in 1997 to allow assessment of the sustainability of woodland communities and provide warning of potentially deleterious change in vegetation composition and structure. Extensive drought-related dieback of *C. mopane* and utilization of *A. tortilis* woodlands by elephant offered an opportunity for increasing understanding of the causes of drought-related patch dieback, the factors influencing elephant utilization of, or response to, woody plants, and the response of woody plants to the aforementioned determinants. C*olophospermum mopane* is an ecologically and economically important plant species, considering it is a preferred firewood species (Tietema *et al.* 1991), has a high frequency of appearance in the woodcarving industry (Steenkamp 1999), and provides good quality browse for livestock and game (Bonsma 1942). It has a narrow distribution in South Africa (Mapaure 1994), a slow natural growth rate (Van Wyk 1972) and woodlands in which it occurs generally have a low species diversity (Mapaure 1994). *Acacia tortilis* is a drought-tolerant species (Coates Palgrave 1983) associated with encroachment (Dangerfield *et al.* 1996), popular as a source of shade, fodder (Coe & Coe 1987), fencing, housing (Coughenour *et al.* 1985), and fuelwood (Hayashi 1992), perhaps on account of its high density (Venter & Venter 1996). Thought needs to be given to the conservation of *C. mopane* and other species with which it occurs, such as *A. tortilis*, if the long term integrity of these species-poor systems are going to be sustained.

Models of population dynamics constitute an invaluable ancillary tool for the monitoring effort, considering questions about sustainability can not be judged from monitoring data alone. Dendrochronology enables one to estimate the age of long-lived woody species, calculate growth rates of trees, and forecast future populations. Although there has been scepticism concerning the demarcation of growth rings in tropical trees (Kigomo 1994), growth rings have been identified in *C. mopane* (Mushove *et al.* 1995) and *A. tortilis* (Gourlay & Grime 1994), and may therefore alllow for the estimation of potential rates of replacement in these two species, following extensive drought- or elephant-related dieback.

The following aims were undertaken to increase our understanding of the causes and effects of drought and elephant on the dynamics of two key woodland species, and so assist in the interpretation and management of semiarid African savannas.

(1) Estimate the growth rate of *C. mopane* and *A. tortilis* using dendrochronology.

(2) Describe quantitatively patch dieback of *C. mopane* and determine what factors were responsible for patch dieback, thereby providing a suitable hypothesis.

(3) Describe quantitatively the response of *A. tortilis* woodlands to elephant, the response of elephant to *A. tortilis* woodlands and compare the aforementioned with elephant response to *A. tortilis* within riverine vegetation and with *Acacia nilotica* woodlands.

Chapter 2

Literature review:
Drought and elephant as determinants of savanna structure and function, and Dendrochronology

Introduction

"Just as a mechanical engineer must learn the principles of physics to build a dam, a conservation biologist must learn the principles of ecology to save a species" (Gotelli 1995). Before we can forecast population trends, we need to gain an understanding of the relation between plant populations and the physical or biological factors that interact to bring about changes in those populations, specifically the fundamental demographic parameters which determine population growth; germination, mortality and dispersal (immigration and emigration) (Begon & Mortimer 1981). The dynamics of savannas and their woody species are influenced by the secondary determinants, fire and herbivory, which modify the inherent structure and function constrained by the primary determinants, rainfall and soil type (Walker 1985). Extensive drought-related dieback of *C. mopane* and utilization of *A. tortilis* woodlands by elephant offered an opportunity for increasing our understanding of the aforementioned determinants on population dynamics.

Drought

Although rainfall variability has been recognized as the primary determinant of short-term (years to decades) community dynamics (Wiegand & Milton 1996), controlling woodland structure and composition (Coughenour & Ellis 1993; Patten & Ellis 1995), knowledge on the impact of drought on the woody component of semi-arid savannas remains fragmentary. The herbaceous sward of semi-arid savannas is inherently unstable under drought conditions (O'Connor 1985) resulting in dramatic population crashes of perennial grasses (O'Connor & Everson 1998; O'Connor 1999), but display a high degree of resilience in the long-term (Kennan 1969; Donaldson *et al.* 1984) in contrast to the apparently less resilient long-term response of woody species to drought, for which there are only a few isolated accounts (e.g. O'Connor 1999). The extent of drought-induced mortality does, however, differ between woody species (Fensham 1998; Fensham & Holman 1999; O'Connor 1999) and is more pronounced for *Combretum apiculatum*, *Dichrostachys cinerea* and *Ximenia americana* (Van Wyk *et al.* 1969; O'Connor 1999). Mortality of the dominant species of the Mopani Veld, *C. mopane,* is adequately compensated for by recruitment, conforming with its regard as a drought-tolerant species (Coates Palgrave 1983). The increase in stem density of *C. mopane* on colluvial soils at the expense of other species showing no recruitment suggests a potential inclination for *C. mopane* dominated vegetation types to decrease in species richness (O'Connor 1999) over multi-drought years, contrary to the supposition that climatic variability promotes species diversity (Coughenour & Ellis 1993) on account of species differences across gradients in the physical environment (Patten & Ellis 1995).

Drought-induced mortality is associated with a soil water deficit below that which is required for the persistence of long-lived species (Tongway & Hindley 1995), usually visible as partial dieback of the crown (e.g. O'Connor 1999). Consequently, drought acts as a height-reducing agent in addition to a mortality agent. The intensity and spatial pattern of drought-induced dieback ranges from background and uniform, usually about 5% of trees in southern African savannas (Scholes 1985; O'Connor 1999), to catastrophic and patchy (up to 100% mortality - Fensham & Holman 1999). Uniform mortality is most pronounced for individuals < 3 m (Scholes 1985; O'Connor 1999), although growth is largely restricted to the same height class during a sequence of dry years (O'Connor 1999), whilst patch dieback appears to be independent of stem size (Fensham 1998; Fensham & Holman1999). Additional factors influencing drought dieback include: substrate type, soils with a high clay content reduce infiltration (Scholes 1985); and possibly pre-drought basal area (Fensham & Holman 1999).

Competition plays an important role in the spatial patterning and dynamics of woody vegetation in savannas (Smith & Goodman 1986). Woodlands influenced by competition may be more susceptible to drought-related mortality, considering tree mortality is affected by density (Smit 1994). The extent of perennial sward dieback may certainly be related to variation in woody cover (O'Connor 1999), especially in *C. mopane* dominated vegetation, given the species' ability to inhibit grass growth and its own (Smit 1994). Competition for resources is readily evident as self-thinning, a relationship between log mean plant weight and log density which generally has a slope of -3/2, for dense populations which show density-dependent mortality (Silvertown 1982), or a positive correlation between distance to nearest neighbour and combined canopy cover of the pair for comparisons (Smith & Goodman 1986). Death of individuals owing to competition or drought presumably allows neighbouring trees to extend their zone of influence (root system), or allows increased uptake due to decreased overlap of functional root zones, thereby increasing biomass production of neighbouring plants (Smith & Goodman 1986).

Herbivory, mainly by elephant

Spatial dimensions of plant-herbivore interactions

The spatial structure of rangeland vegetation is formed by non-uniformity in patterns and processes of the environment and herbivores (Noy-Meir 1996). Animals face the problem of meeting energy and nutritional requirements in an environment in which the quality and quantity of forage varies in space and time (Frank *et al.* 1998). Large herbivores overcome this dietary problem by making a series of hierarchical forage decisions at several levels of ecological resolution, spanning from micropatches (or feeding stations or plants) to plant communities, landscapes and regional systems. Herbivores may utilize momentary maximization to solve the quality-quantity problem at the patch and community scale. Momentary maximization dictates sequential acceptance of the most palatable items encountered at each feeding location until available palatability decreases to some threshold level (Staddon 1983) whereupon the herbivore moves to another patch or community. Consequently, patch and community residence times are proportional to the relative availability of preferred forage (Senft *et al.* 1987).Time and energy costs of travel relative to gain are important considerations when selecting for communities which have different nutrient contents (Senft *et al.* 1987). At the regional scale migrating grazers track spatiotemporal patterns in forage quality, produced by broad environmental (precipitation, soil type, altitude) gradients, to increase their diet quality and grazing efficiency (Frank *et al.* 1998). Furthermore, ungulates in grazing ecosystems may modify vegetation structure in a manner that increases their own foraging efficiency. Consequently, plant response to herbivory affects an animal's subsequent foraging decisions (Senft *et al.* 1987).

Key elements responsible for the sustainability of semi-arid grazing systems are the spatial and temporal variation in forage quality (Scoones 1995), the migratory behaviour of ungulates which track high quality forage, and the intercalary meristem of grasses which allows defoliated plants to grow (Frank *et al.* 1998). Similarly, the sustainability of woodlands may depend on the potential for its component species to replace lost biomass with regrowth. Spatial heterogeneity is further expected to enhance the stability and resilience of vegetation by the creation of refuge sites (Noy-Meir 1996). Topo-edaphic heterogeneity can create drought refuges in patches where infiltration is increased by run-on, whilst spatial heterogeneity in grazing pressure can create grazing refuges. These refuges may provide propagules for the recolonization of a landscape which has been decimated by a series of drought and/or grazing events.

Different foraging response patterns, specifically matching, overmatching and undermatching (Staddon 1983), are displayed at different scales. Matching occurs when an animal adjusts its foraging behaviour in proportion to changing dietary rewards, overmatching results from a disproportionately large foraging response to a change in reward, and undermatching from a disproportionately small response. Overmatching is the pattern most prominent when a large herbivore selects plants from a community because the generalist herbivore employs tactics in which preferences are nonlinearly related to forage abundance and quality, to maximize nutrient uptake (Senft *et al.* 1987). An animal's relative preference for plant communities is generally a linear function of the relative abundance and/or nutritive quality of the preferred plants in the communities. Consequently, matching is the prominent pattern when large herbivores select plant communities for feeding (Senft *et al.* 1987). Selection of feeding areas can be modified from a pure matching pattern by several factors, including topography, watering points and discomfort (Senft *et al.* 1987).

A stable limit cycle versus multiple stable states

Range management is a discipline of applied ecology necessarily arranged around a model formulated by current perceptions of how particular ecological systems function. The range succession model assumed a single state system. In a single state system, the position of the state will shift if an influencing factor is intensified, but will revert to its previous level when the factor does so. However, vegetation change in response to grazing has not always occurred as predicted along a single continuum (Westoby *et al.* 1989). The range succession model has since been replaced by the state-and-transition model in such systems (Westoby *et al.* 1989) which assumes a multiple stable state system. A multiple stable state system does not return to its previous state once the influencing factor has reverted to its previous level, the new state being held in place by a new factor (Dublin *et al.* 1990). Different stable states may be identified by different combinations of stably coexisting species in an ecosystem, or by different population levels of those species.

Caughley (1976) proposed a stable limit cycle which assumes a cyclical relationship between elephants and trees. The trend of elephants and of trees are similar to sine waves, that of trees being about 1/4 of a wavelength behind that of elephants. The trees decrease at the highest absolute rate when elephants are at peak density, whilst the absolute rate at which elephants decrease is greatest when tree density is at its lowest. The stable limit cycle implies no attainable natural equilibrium between elephants and forests, although an artificial equilibrium can be imposed. Both the single state hypothesis and Caughley's (1976) stable limit cycle assume the trend in vegetation change will reassert itself once external disturbances have been removed. However, Abel and Blaikie (1986) showed that human influence, particularly hunting of elephant for ivory, accounted for the decline in elephant numbers in the Luangwa valley, and not a food shortage (Caughley 1976). Although Abel and Blaikie (1986) do not preclude the existence of a cyclical relationship between trees and elephants, they provide evidence that human interference has long (since the 18th century) been associated with ecological systems. It would therefore be incorrect to assume that biological changes are intrinsic to biological processes alone. Consequently, forces of change, apart from elephant, would have to be absent if a cyclical relationship is to exist between elephant and trees.

The debate appears to be whether the two vegetation conditions of woodland and grassland are the extremes of a stable limit cycle (or a single stable state) or represent discontinuous conditions with two stable states. Considering a precondition for the stable limit cycle hypothesis of woodland recovery is the safe refuge of seedlings from elephants (Dublin *et al.* 1990), or other browsers, the system could be held in a new state if the recruitment or survival of seedlings is prevented. It would appear therefore that woodland dynamics following a reduced density of trees could follow either hypothesis, depending on the presence or absence of additional factors capable of holding the system in its new state. It is also arguable, however, whether a system held in a new state reflects the multiple stable state hypothesis, or an artificial equilibrium when the stable limit cycle is arrested.

Factors influencing elephant response

Elephant (*Loxodonta africana*) are notorious for the spectacular changes they have caused in southern and east African savannas. Elephant impact on woodland dynamics is multifarious, influencing vegetation structure, species composition, stem density and plant vigour. Vegetation changes can be related to their feeding ecology which takes many forms, including uprooting, breaking stems, debarking and stripping leaves and branches (Croze 1974a), and is influenced by vegetation structure, species composition, season and nutrition.

Vegetation structure

Population structure and species composition may be more powerful predictors of stand damage than either stand or species density (Ruess & Halter 1990), perhaps owing to the preference elephants have for particular size classes and species. Consequently, elephant feeding is not always deleterious to species abundance or diversity, affecting physiognomy more than density (Van De Vijver *et al.* 1999).

Size classes are generally utilized in proportion to their occurrence in the stand (Vesey-FitzGerald 1972; Croze 1974b; Kabigumila 1993), although elephants also concentrate disproportionately on the larger size classes (Pellew 1983a), often ignoring the youngest class (< 1 m - Vesey-FitzGerald 1972; Croze 1974b; Pellew 1983a; Ruess & Halter 1990). Elephant browsing has, however, been diverted to small trees < 1 m when available browse is less abundant (Dublin 1995) during the dry season (Kabigumila 1993). The preferred feeding height of elephants is such that damaged trees within the 1 to 5 m height class (Croze 1974b) have greater base diameters than undamaged trees (Van De Vijver *et al.* 1999), suggesting taller trees are either knocked down and reduced to thick, stunted stumps (Nott & Stander 1991) and shrubs (Anderson & Walker 1974) or trees are suppressed, prevented from growing into the next height class by repeated browsing (Pellew 1983a; Ruess & Halter 1990; Campbell *et al.* 1996), resulting in dense regeneration thickets in the absence of fire (Ruess & Halter 1990).

Damaged trees respond by coppicing (e.g. *C. mopane* - Anderson & Walker 1974; *Boscia albitrunca* - Nott & Stander 1991; *A. tortilis* - Van De Vijver *et al.* 1999), providing new regrowth which is preferred to adult plants (Anderson & Walker 1974; Lewis 1991) and hence promoted (Caughley 1976). The ability of *C. mopane* woodlands to coppice in response to elephant browsing is influenced by past levels of elephant browsing in association with soil characteristics, an impervious B horizon and nutrient rich A horizon promoting coppice (Lewis 1991).

Plant species and abundance

Elephants utilize a wide range of woody species, up to 87 browse species have been identified in Wankie National Park, Zimbabwe (Williamson 1975). Most woody species are fed upon at a rate proportional to their occurrence (Ruess & Halter 1990), especially in low and high-density woodlands (Kalemera 1989), with the exception of species that are preferred or deliberately avoided (Croze 1974b; Tchamba 1995). Often, the staple diet of the elephant corresponds with the dominant woody species (e.g. *C. mopane* - Pienaar *et al.* 1966; Ben-Shahar 1996; *Combretum* spp. - Jarman 1971; Thrash *et al.* 1991; *Acacia* spp. - Kalemera 1989; Ruess & Halter 1990).

Preferential selection may not be the sole contributing factor to a change in species abundance (Lewis 1991), but also the ability of the damaged tree to respond by coppicing (Van De Vijver *et al.* 1999), increasing the number of woody plant stems per unit area (Stuart-Hill 1992a). Species with a low tolerance to damage decrease in abundance (Anderson & Walker 1974). Consequently, the order of preferred species changes over time as over utilized woody species less tolerable to damage, such as *A. tortilis*, become less available and are replaced by the next favoured species (Anderson & Walker 1974). Species are selectively eliminated according to the ease with which they can be pushed over (Field 1971; Guy 1976). *A. tortilis* is uprooted more readily than *Balanites aegyptiaca* which has a strong root system resulting in attempts to push it over either failing or 30 cm stems being snapped (Croze 1974b). The physiognomic effects of elephant impact will therefore differ among species.

Increased elephant numbers do not necessarily result in a great decline in tree density (Van De Vijver *et al.* 1999), given their propensity to affect woodland physiognomy (Jachman & Bell 1985). Drought may be a key forcing function of transitions of the herbaceous component through dieback of the woody component (O'Connor 1999), and a reduced browsing pressure by ungulates may inhibit woody encroachment, the reduced population of grazing ungulates allowing an accumulation of fuel and hence fire (Norton-Griffiths 1979). Similarly, although a decline in elephant populations has coincided with bush encroachment and conversion of grassland to woodland (Leuthold 1996; Whateley & Wills 1996), encroachment of *Acacia* species may not necessarily result from reduced elephant impact, but rather a release from high browsing pressure by (epidemics amongst) small ungulates (Prins & Van Der Jeugd 1993).

Past concern surrounding the thinning of mature *A. tortilis* stands has had more to do with the aesthetic (e.g. Croze 1974a; Pellew 1983a) than the ecological implications. Opening up of woodland canopies allows regeneration and subsequent recruitment to replace senescing adults (Mwalyosi 1990), especially in *A. tortilis* woodlands, given the species' shade intolerance and inability to germinate under the parent canopy (Miller 1996). Woodland productivity is also improved through the establishment of other species, enhancing landscape diversity (Mwalyosi 1990), a function of fractionization (Noss 1987). Elephant can, however, also reduce biodiversity (Cumming *et al.* 1997).

Season and nutrition

The elephants' diet is seasonal (Croze 1974a), comprising mostly grass in the wet season (Thomson 1975) and browse in the dry season (Kabigumila 1993). Elephants show diversification in their diet during the late dry season, reducing dietary overlap with other herbivores (Jarman 1971). Different species are therefore favoured at different times of the year and for different food types (Williamson 1975). Season appears to influence which plant parts are eaten. Mostly leaves and shoots are taken during the wet season with the amount of woody tissue increasing in the diet during the dry season (Jarman 1971; Williamson 1975; Lewis 1991; Kabigumila 1993) corresponding to an increase in the frequency of damage to trees (Ruggiero 1992), particularly large succulents like *Adansonia digitata* and *Sterculia* spp. (Jarman 1971). Debarking has, however, been observed in the wet season (Lewis 1991; Kabigumila 1993).

The proportion of grass to browse consumed during each season depends on its nutritional status and availability (Jarman 1971; Kalamera 1989), to the extent that elephants may be either primarily grass eaters (Field 1971; Croze 1974a,b) or browsers (Williamson 1975). Elephants may switch to browse in the dry season on account of its higher crude protein content relative to grass (Williamson 1975) which rapidly declines in palatability (Field 1971).

Salts are an important constituent of elephants' diet, suggesting that calcium (Ca) content in the bark could be an important factor influencing utilization of some species (Williamson 1975). However, damage for different species has not always been successfully related to the chemical constituents of the plant or the soil (Anderson & Walker 1974; Thomson 1975). Despite similar Ca contents in the barks of *C. mopane* (4.12% - Anderson & Walker 1974), *A. tortilis* (4.15% - Anderson & Walker 1974) and *Brachystegia boehmii*, the latter two species have been more frequently debarked by elephants (Anderson & Walker 1974; Thomson 1975), whilst *Pterocarpus angolensis* is also frequently debarked, despite a relatively low Ca and high tannin content (Williamson1974). Factors other than chemical (nutrient or deterrent) are therefore likely to play a role in the selection of woody species by elephant.

Plant vigour

Tree vigour is determined to a large degree by the severity (Croze 1974b; Van De Vijver *et al.* 1999) and history of past browse damage (Lewis 1986), and tree age (Mwalyosi 1987) with the chance of survival and recovery decreasing with adolescence (Mwalyosi 1987).

Some tree species show a remarkable resilience to the removal of as much as 3/4 of their canopy foliage with almost certain survival the following year and nearly a 50 : 50 chance of surviving 3/4 to all of their canopy removed, whilst other trees, e.g. *A. tortilis* (Croze 1974b), do not. Species resilience is, however, likely to depend not only on the extent of feeding but the nature of the feeding, considering strip barking of *A. tortilis* has no immediate ill-effect (Guy *et al.* 1979).

Browsing stimulates shoot production thereby increasing the rate of browse production (Pellew 1983b), provided trees do not have a history of overexploitation, in which case browse production does not differ from browse removal (Lewis 1986). Consequently, trees with a history of past browse are less able to recover their losses by growth replacement. A past history of overutilization resulted in nearly 100 % mortality of coppiced *C. mopane* stands following a year of 14 % below average rainfall (Lewis 1991). Considering browse removal by elephants exerts a nutrient drain on individual trees and soil nutrients, the critical condition affecting the vigour and therefore response of coppiced individuals may be related to soil quality in the A horizon (Lewis 1991).

Dendrochronology

In addition to understanding the response of key woodland species to critical determinants such as drought or elephant, a knowledge of growth rates of trees offers the opportunity to estimate the potential rate of replacement of trees and therefore predict population trends in a system influenced by either drought or elephant. Dendrochronology is a technique that enables one to estimate the age of long-lived woody species.

Anatomical features that denote annual growth rings in temperate trees, such as changes in cell wall thickness and cell dimensions of earlywood and latewood in conifers, are uncommon in tropical species (Gourlay 1995). Despite much difficulty (Lilly 1977; Mariaux 1981) and scepticism (Kigomo 1994) concerning the demarcation of growth rings in tropical trees, growth rings have been identified in *C. mopane* (Mushove *et al.* 1995; Prior & Cutler 1996) and *A. tortilis* (Gourlay & Grime 1994; Gourlay 1995). According to Wyant & Reid (1992), however, tropical trees have never been cross-dated.

Marginal parenchyma bands, a form of axial parenchyma (Gourlay & Grime 1994), delimit annual growth zones in *A. karroo* (Gourlay & Barnes 1994). They are distinguished from the intra-seasonal banded parenchyma by their fineness (only a few cells wide) and evenness of appearance in contrast to the more irregular, wavy confluent bands (Gourlay 1995). The distinction of growth rings, however, is hampered by a few factors: false and discontinuous rings were discerned in both *A. karroo* and *A. tortilis* (Lilly 1977), whilst missing rings, approximating drought frequencies, were also detected in *A. tortilis* (Wyant & Reid 1992).

Calcium oxalate crystals, found in long chains along the marginal parenchyma or its periphery (Gourlay & Kanowski 1991), can be used to define growth rings in instances where marginal parenchyma bands are unclear. The crystalliferous chains are produced at the onset of the dry season when wood production ceases during the dry winter period from late March to early

September (Gourlay & Barnes 1994;Gourlay & Grime 1994; Gourlay 1995). Prior and Cutler (1996), however, could not relate crystalliferous chains to growth ring boundaries and found no correlation between the number of rings and the diameter of *A. karroo* and *A. tortilis* trunks, when they measured material of unknown age.

Robbertse *et al.* (1980) recorded 1 - 2 growth rings/mm in South African *A. tortilis* trees. The mean annual ring width across all African acacias and sites examined by Gourlay & Barnes (1994) and Gourlay (1995) was 6 - 7 mm. Mean ring widths for *A. tortilis* samples from Kenya and Zimbabwe were 5 and 9 mm, respectively (Gourlay & Grime 1994), whilst a separate study of two *A. tortilis* trees growing on sandy alluvium in Zimbabwe, measured 7 and 11 mm (Gourlay & Kanowski 1991). Hayashi (1992) reported a diameter increment at breast height (dbh) of *A. tortilis* over one year in Kenya (1 088 mm an^{-1}) equivalent to an annual radial increment of 3.5 mm.

Although ring widths of *Acacia* spp. have been related to precipitation (Gourlay & Barnes 1994; Gourlay 1995), Mushove *et al.* (1995) found no significant relationship between rainfall and the ring widths of *C. mopane* and *C. apiculatum*. Prior & Cutler (1996) also found no correlation between rainfall and the ring widths of *C. mopane* and *C. apiculatum*, despite attempting to match width with rainfall in the preceding year, and suggested the probability of a marked discrepancy between measured rainfall and the water accessible to trees. Although rainfall is recognized as having the greatest influence on tree growth, it is not necessarily an index to the amount of water available for tree growth, of which radial growth is a function (Gourlay & Barnes 1994). Rainfall interacts with local topography and the geology of the sites to affect plant-available soil water (Gourlay & Barnes 1994). Growth ring widths vary from site to site and are influenced by soil nutrient and water availability (Mushove *et al.* 1995).

Considerable variation in correlations between species at different sites and the various meteorological parameters (rainfall, evaporation and temperature) have also been attributed to the form of the rooting profile. Shallow rooting trees may be more sensitive to current rainfall (Gourlay 1995) and able to exploit rapidly small amounts of precipitation (Prior & Cutler 1996), whilst deeper rooted trees are able to reach a more permanent water table, and are therefore more drought tolerant.

Site selection is an important consideration when sampling trees. Trees growing on sites where growth limiting factors seldom limit growth, produce rings that are uniformly wide and do not reveal information on past climates (e.g. drought frequencies) (Fritts 1976). *Acacia tortilis* trees from riparian zones with year-round access to underground water were observed to contain only half as many rings as years in age (Wyant & Reid 1992). Only the ring widths of trees in the most extreme environments (or environments with distinct wet and dry seasons) are sufficiently limited by climatic factors to allow dendroclimatic analysis (Fritts 1976). Gourlay & Barnes (1994) noted that marginal parenchyma bands on wood taken from trees in the Richard's Bay area were not clearly defined, probably because its climate was less extreme than that from which the other samples were collected. Gourlay & Kanowski (1991) have shown that the number of rings in African *Acacia* spp., originating from climatic zones with a single wet season, approximate the age of the tree, whilst samples originating from bimodal climatic zones, have approximately twice the number of rings as the age of the tree.

The calculation of growth rates is confounded by poor correlations between stem diameter and age. Although Wyant & Reid (1992) achieved a good correlation between the basal stem diameter of *A. tortilis* and its known age, it was only significant for young (< 10 years) trees. Older trees of similar age showed a dramatic difference in basal stem diameters. Seedlings may also complicate correlations by being older than they appear, with factors such as animal impact and limited soil water contributing to slow growth rates (Phillips *et al.* 1996). Trees of varying age may be held at a similar size for an extended period by suppressing factors such as browsing, fire or shade. When released these trees mature together, forming stands of even size but dissimilar age (Young & Lindsay 1988). This inconsistency between diameter and age makes it difficult to date those trees for which no stem sections are available and emphasizes the variability of growth rates.

Chapter 3

Study area

Ecosystem: definition

Living organisms and their abiotic environment interact upon each other to form a continuum of cause-effect relationships. This entity of biological and physical processes is termed an ecosystem (Humphrey 1962) and is identified by the structure and function of its component parts. The major components of the study area, pertinent to the management and hence conservation of Venetia-Limpopo Nature Reserve, are the physical environment, vegetation, and animal populations.

Physical Environment

Location

Venetia-Limpopo Nature Reserve (VLNR) (29°12′ - 29°23′ E; 22°15′ - 22°30′ S) is situated in the Northen Province, South Africa, approximately 30 km south of the Limpopo River where Botswana, Zimbabwe and South Africa converge (Figure 3.1). The reserve, 34 500 ha in extent, is an amalgamation of 21 livestock farms acquired by De Beers Consolidated Mines Limited between 1981 and 1995.

Climate

The semi-arid environment is characterized by wet, hot summers, dry, mild winters (Figure 3.2). Mean monthly minimum and maximum temperatures at Messina (80 km E) are, respectively, 20.3°C and 32°C for summer (December) and 7.2°C and 24.7°C for winter (June). Frost does not generally occur (O'Connor 1992).

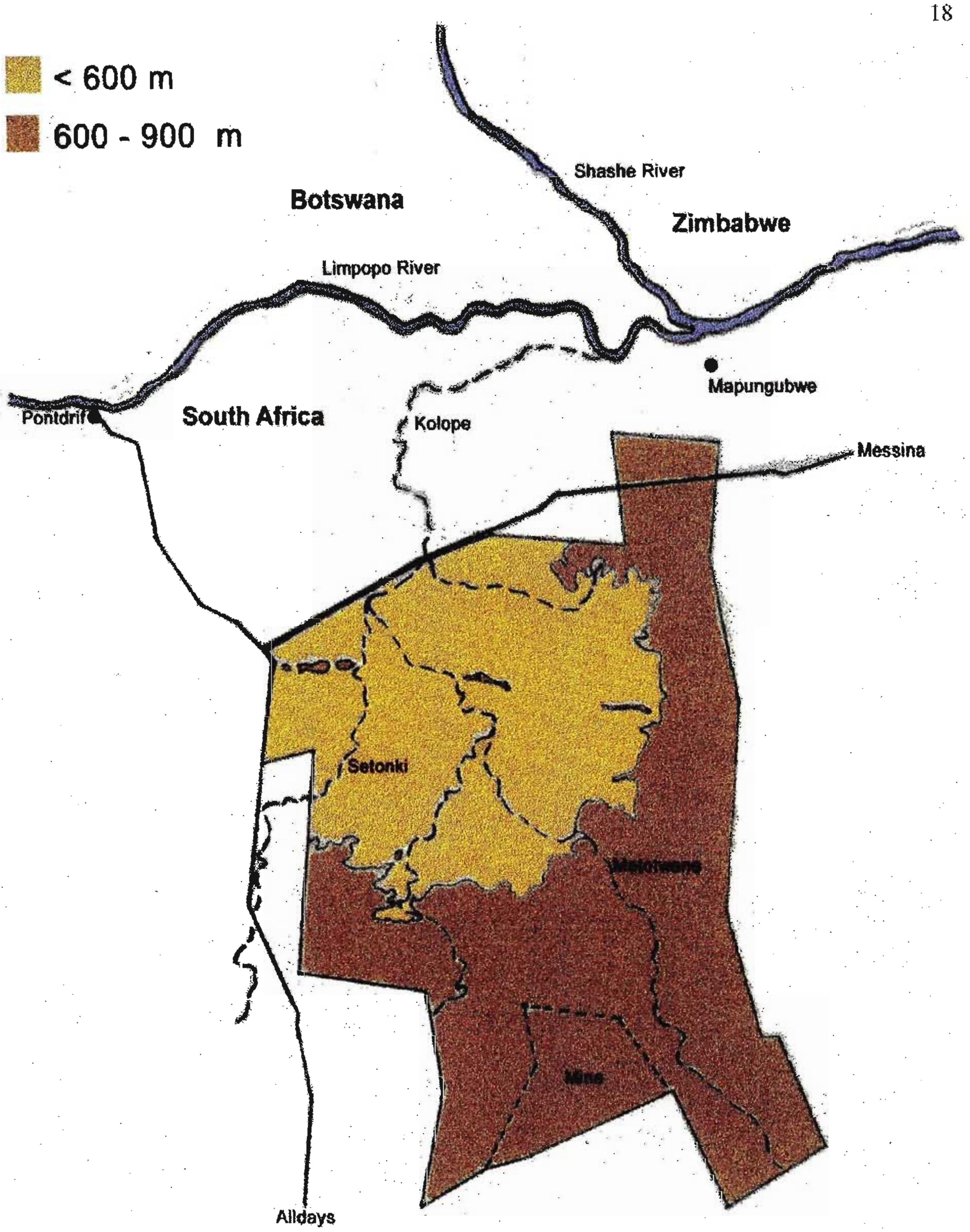


Figure 3.1 Schematic topographical and drainage features of Venetia-Limpopo Nature Reserve in relation to the Limpopo River. Produced by tracing the map of Chief Director of Surveys and Mapping (1986).

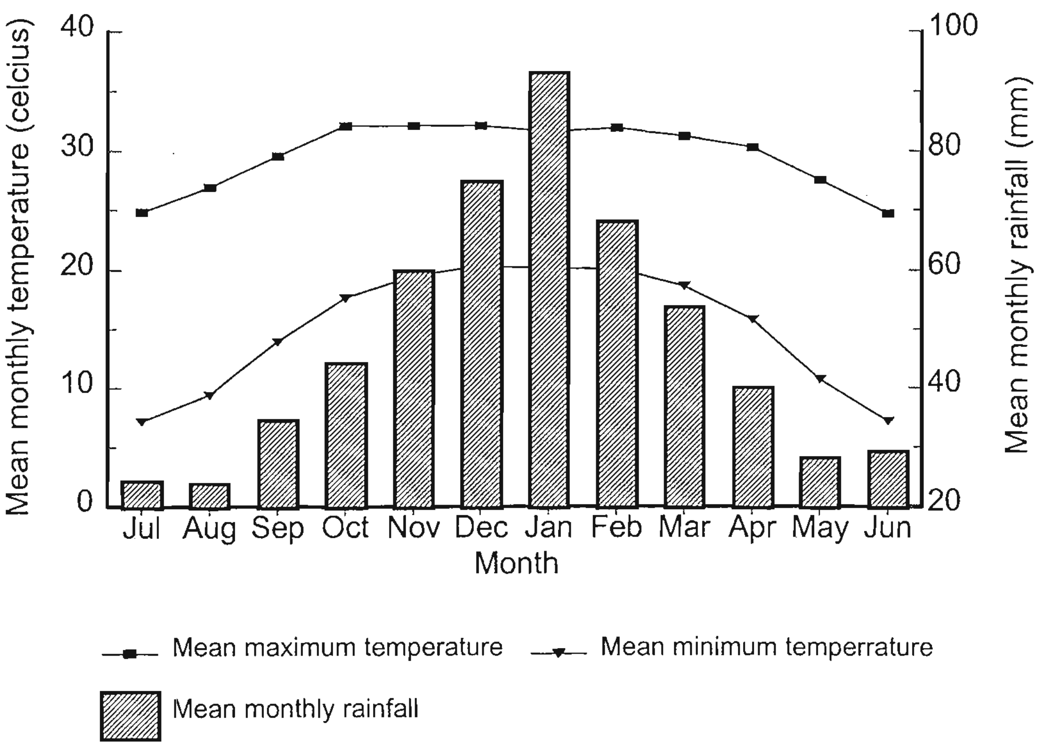


Figure 3.2 Mean monthly maximum and minimum temperatures for Messina in relation to mean monthly rainfall (1966/67 - 1994/95) for Pontdrif.

The mean annual (July-June) rainfall for Pontdrif is 366 mm (1966/7-1996/7) but has been erratic (38% coefficient of variation) over the past few decades with extended periods of above- and below-average rainfall (Figure 3.3). The mean annual (July-June) rainfall for VLNR was 297.5 mm between1995/6 and 1998/9 with the lowest recorded rainfall in 1997/98 (132.9 mm) (Figure 3.4). Severe droughts have occurred as recently as 1988/89 and 1991/92 (Figure 3.5). The almost cyclic pattern of rainfall from 1966/7 until now consists roughly of one extended period of above-average rainfall (1966/7-1981/2) and one extended period of below-average rainfall (1982/3-1996/7), with some years invariably out of phase (Figure 3.3). Rainfall, consisting mainly of thundershowers, falls primarily from October to March, peaking during December-February (Figure 3.2). Mean annual evaporation (2 000 to 2 200 mm) is six fold greater than mean annual rainfall (Midgley *et al.* 1994).

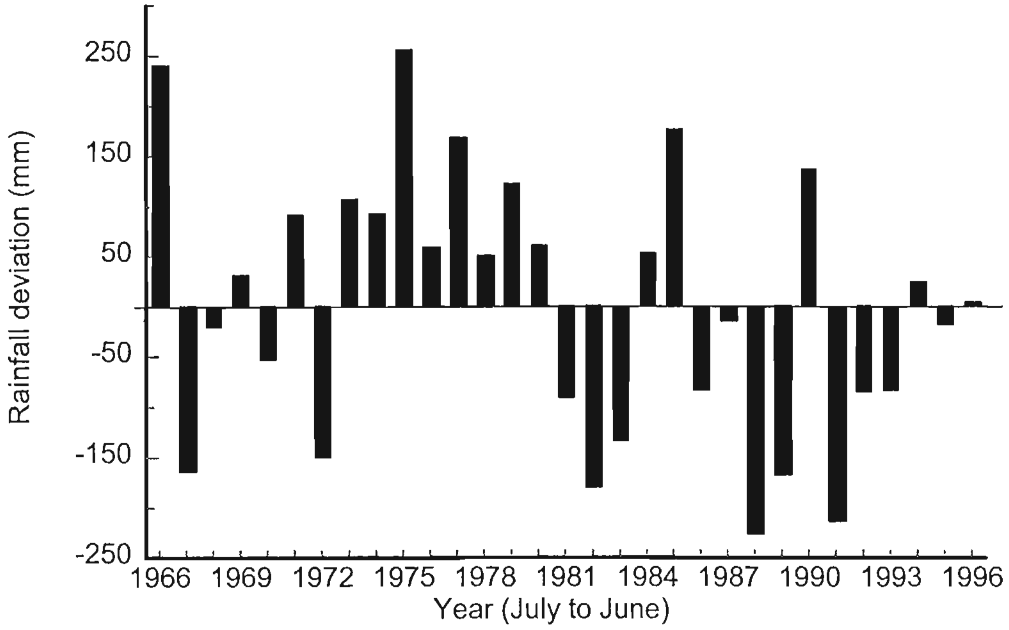


Figure 3.3 Annual deviation from the long-term (1966/67 - 1996/97) mean (366 mm) of rainfall at Pontdrif. Rainfall years are July to June inclusive.

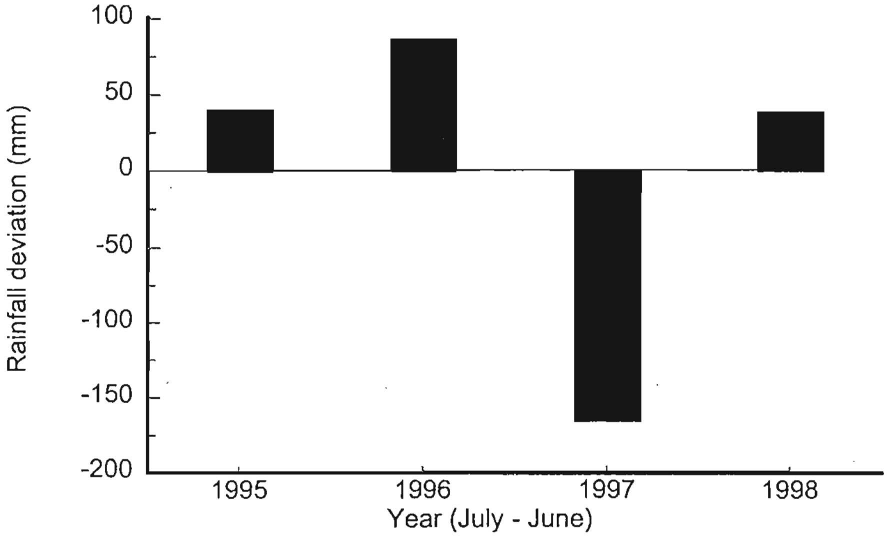
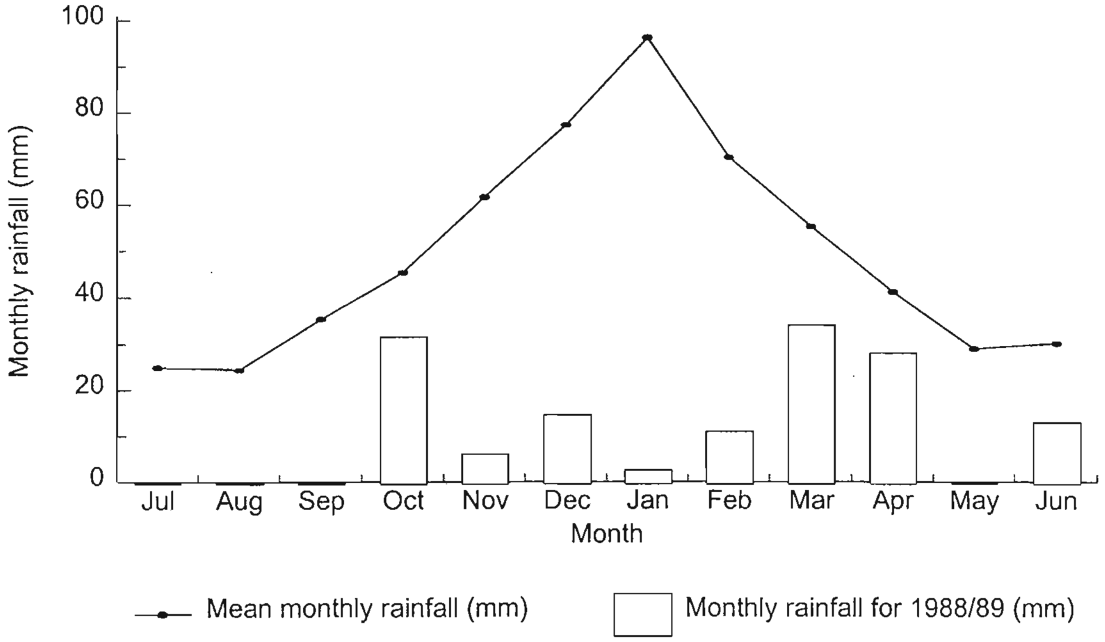


Figure 3.4 Annual deviation from the long-term (1995/96 -1998/99) mean (297.5 mm) of rainfall at Venetia-Limpopo Nature Reserve. Rainfall years are July to June inclusive.



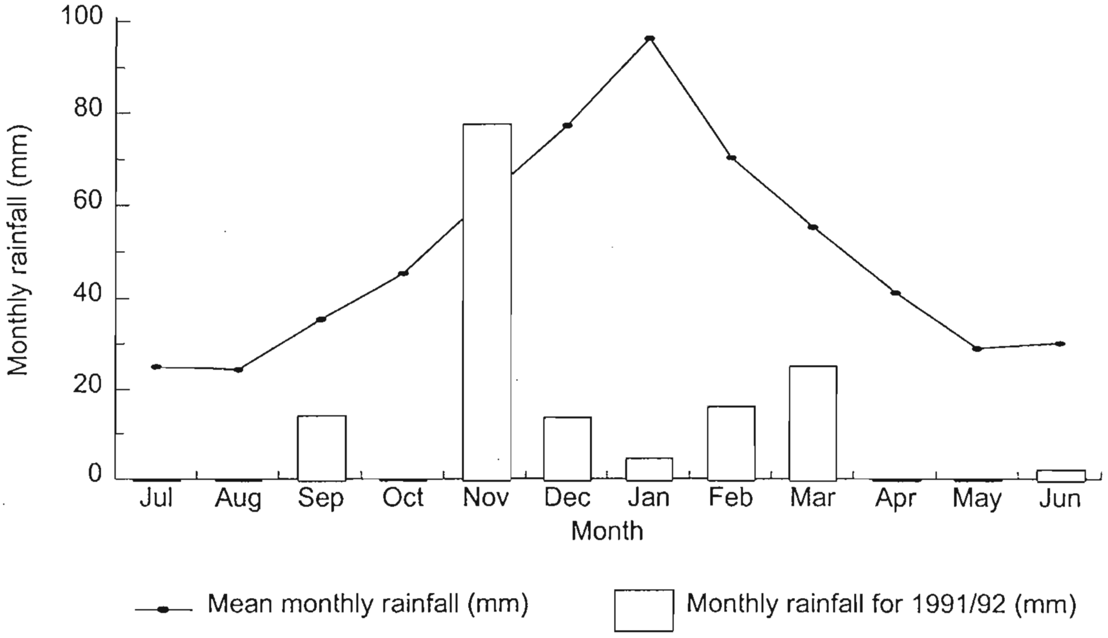


Figure 3.5 Mean monthly rainfall for the severe drought years of 1988/89 (141 mm an^{-1}) and 1991/92 (153 mm an^{-1}) in relation to the long-term (1966/67 - 1994/95) mean monthly rainfall at Pontdrif.

Geology

Geomorphologically, the study area falls within a dissected landscape resulting from cut back of the Limpopo's tributaries into a post-African 1 surface (Partridge 1997) (Figure 3.1), originally consisting mainly of marls, mudstones, siltstones and sandstones of the Karoo system (Truswell 1977). Although remnants of Karoo sediments and volcanics exist as flat-topped sandstone hills, the study area is mostly a large, relatively flat basin underlain by deep (>5 m) palaeo-alluvia derived from erosion and deposition of Karoo sediments with more recent alluvia occurring adjacent to currently active (non-perennial) water channels. The dominant soil forms and series encountered on the reserve were Oakleaf Buchuberg, Dundee Visrivier, Swartland Amandel and Valsrivier Goedemoed (Botha 1994), all having a sandy clay loam texture with relatively high clay (average 20%) and silt (average 19%) contents. Although Dundee soils were sandier than the Valsrivier soils, they were similar in that all were deep (> 900 mm) bottomland soils adjacent to drainage lines (O'Connor 1996). Oakleaf soils, usually situated on the crestal area of the catena, were not areas of significant runon, considering they served as sources of water for bottomlands, whilst Swartland, associated with the mudstones and siltstones of the Karoo sequence, extended from the pediment slope at the base of the sandstone hills to bottomlands (O'Connor 1996).

Hydrology

Venetia-Limpopo Nature Reserve is drained northwards by three ephemeral rivers, the Setonki, the Matotwane and the Kolope, before their confluence in the north western corner of the reserve (Figure 3.1), forming a tributary of the Limpopo River. There has been pronounced sheet and rill erosion by overland water flow (personal observation). Badly degraded areas were interpreted to be a result of their erosivity owing to a high clay and silt fraction, the almost complete elimination of a perennial grass cover (O'Connor 1999), intense rainfall events, and slopes (> 0.5 %) conducive to runoff (O'Connor 1996).

Vegetation

The study area falls within the Mopani Veld type (Acocks 1953), of which *C. mopane* is the dominant plant species, occurring in the riparian vegetation and the adjacent dryland vegetation types of VLNR (O'Connor 1991). O'Connor (1991) identified 71 woody species (nomenclature follows Arnold & De Wet 1993) and described 15 vegetation types within the Venetia-Limpopo Nature Reserve, of which five were relevant to this study; Riverine woodland, Grassland, *C. mopane* woodland, *C. mopane* shrub woodland and *C. mopane-Salvadora angustifolia* woodland. The main pattern of variation in composition of the woody vegetation is from species-poor woodlands dominated by *C. mopane* through to taller woodlands with a lower abundance of *C. mopane* and a greater equitability of other species, adjacent to the larger rivers.

Riverine woodland. The Kolope and the Setonki supported a tall (up to 15 m), relatively dense (median cover 51 - 75%) fringe of mostly hygrophilous species. Common canopy trees were *Combretum imberbe*, *Lonchocarpus capassa*, *Acacia nigrescens*, *Acacia tortilis*, *C. mopane* and *Faidherbia albida*, while *Ziziphus mucronata* and *Croton megalobotrys* were common sub-canopy individuals.

Grassland. Grasslands (0.3 - 12 ha in size; O'Connor 1996) were mostly associated with areas occasionally flooded, adjacent to the Kolope before its confluence with the Setonki. Water input is most likely provided by adjacent catchments (O'Connor1996) and by overflow from the Kolope or Setonki. Woody species, mainly *A. tortilis*, and *A. nilotica*, were restricted to the periphery of some grasslands, however mean woody cover on seven hydromorphic grassland sites has increased from 8% in 1955 to 39% in 1987 (O'Connor, submitted) following pronounced bush encroachment, particularly of *A. tortilis*. It appeared that trees showed distinct successional patterns in which patches of *A. tortilis* spread from core areas and converted previously open grasslands to densely vegetated woodlands (O'Connor, submitted). Herbaceous canopy cover was nearly complete. Principal grass species were *Urochloa brachyura* (annual), *U. mosambicensis* and *U. oligotricha* (perennials), with smaller amounts of *Panicum maximum* and *Cenchrus ciliaris*.

Colophospermum mopane-S. angustifolia **open woodland,** ***C. mopane*** **woodland and** ***C. mopane*** **shrub woodland**. *Colophospermum mopane-S. angustifolia* open woodland was found immediately adjacent to the Kolope and the Setonki on colluvial soils, merging into the dense *C. mopane* woodland further from the rivers, while *C. mopane* shrub woodland occurred on lithosols associated with areas of subdued relief. Woodlands had a median cover of 51 - 75%, except *C. mopane-S. angustifolia* open woodland which had a median cover of 26 - 50%, and supported a 5 m tall canopy, except *C. mopane* shrub woodland (3 m). Common species, besides *C. mopane*, included consistently occurring individuals of *Boscia foetida* and *S. angustifolia*. The herbaceous sward was sparse (< 20% median cover), the bulk of the sward comprising annual grasses *Tragus berteronianus* and *U. brachyura*, and short-lived perennial grass *Enneapogon cenchroides*.

Woody cover of *C. mopane* woodland has increased by > 20% over the period 1955 - 1977, resulting in woodland with high (> 70%) woody cover (O'Connor 1983).

Animal populations

Venetia-Limpopo Nature Reserve (345 km^2) comprises a reasonably diverse assemblage of herbivores (Table 3.1), despite the predominance of *C. mopane*.

Approximately 48 elephant have been introduced into VLNR since 1991, including the birth of five calves (one died at birth) in1999. A detailed report of the carrying capacity of VLNR is not possible, however, elephant density and mammalian biomass per unit area of VLNR can be compared with figures from the Kruger National Park (KNP). In most larger mammal species there is a considerable difference between the mass of adult bulls and females. It was not possible to obtain sex ratios for the respective species, so a mean value was taken to represent the mass of each species (Table 3.1). The elephant density of VLNR (0.15 elephant/km^2) does not exceed the critical density (0.5 elephants/km^2) beyond which savanna woodlands are generally converted to shrublands or grasslands (Cumming *et al.* 1997) and falls well below the theoretical carrying capacity (0.6 - 2.5 elephant/km^2) for the majority of elephant habitats in Africa (Pienaar *et al.* 1966). The elephant density in VLNR is lower than the elephant density (0.2 elephant/km^2) in the KNP (400 - 600 mm/an^{-1}), measured during the 1964 census (Pienaar *et al.* 1966), and three times less the number of elephants (0.48 elephant/km^2) in Tuli (200 - 400 mm/an^{-1}), Botswana (Viljoen 1988), although numbers do fluctuate according to migration patterns (pers. comm., B. Page, University of Natal, Durban). The KNP, predominantly *C. mopane*-, *Acacia*- and *Combretum*-woodland and savanna, was under no threat of overexploitation by elephant which had not yet (1964) reached their saturation point (Pienaar *et al.* 1966). Total herbivore biomass per unit area, of which elephants comprised 27% and 22% in VLNR and the KNP, respectively (Table 3.1), was higher in the KNP (± 3 t/km^2 - Pienaar *et al.* 1966) than VLNR (± 2.4 t/km^2). Although VLNR does appear to have a lower elephant density and biomass per unit area than the KNP, during a time when densities were acceptable, the

Limpopo basin is subjected to a high frequency of droughts, possibly one of the most important natural factors controlling elephant populations in Africa (Hanks 1979). The supportable woody biomass was exceeded during the two severe drought years (1988/89 and 1991/92) in VLNR, with a subsequent escalation in complete and partial mortality of *C. mopane* (O'Connor 1999).

Table 3.1 Population size and biomass of the major herbivore species in Venetia-Limpopo Nature Reserve between 1994 and 1999. Body masses were taken as the mean of male and female masses using Skinner & Smithers (1990). Biomass was calculated by multiplying the body mass of a species by its population size

Species		1994		1995		1997		1999		Mean	
	Bodymass (kg)	Count	Biomass (t)	Count	Biomass (t)	Count	Biomass (t)	Count	Biomass (t)	Count	Biomass (t)
blue wildebeest	215	430	92.5	300	64.5	523	112.4	460	98.9	428.3	92.1
eland	580	298	172.8	194	112.5	253	146.7	204	118.3	237.3	137.6
elephant	4750	42	199.5	45	213.8	42	199.5	48	228	44.3	210.2
gemsbok	225	158	35.6	171	38.5	198	44.6	211	47.5	184.5	41.5
giraffe	1010	10	10.1	21	21.2	30	30.3	28	28.3	22.3	22.5
hartebeest	135	18	2.4	12	1.6	39	5.3	38	5.1	26.8	3.6
impala	45	1421	63.9	1267	57	1356	61	1435	64.6	1370	61.6
kudu	225	989	222.5	705	158.6	526	118.4	707	159.1	731.8	164.6
white rhino	1800	-	-	-	-	-	-	3	5.4	3	5.4
warthog	85	150	12.8	109	9.3	220	18.7	128	10.9	151.8	12.9
waterbuck	250	67	16.8	50	12.5	101	25.3	19	4.8	59.3	14.8
zebra	320	47	15	42	13.4	87	27.8	121	38.7	74.3	23.8
Total			843.9		702.9		789.9		809.5		790.6

History

This area and its surrounding region is of national and international archaeological importance. Approximately 1000 AD a large concentration of Iron Age people settled on a prominent hill called Mapungubwe (Figure 3.1) and became immensely wealthy from trade, bartering in ivory and alluvial gold for glass beads, cowries, etc. (Voigt 1983). Apart from gold, ivory was one of the strongest motives for the development of Arab trade in the interior (Voigt 1983), and indicates the presence and exploitation of elephants as early as the 10th century. The community depended largely on herding (cattle, sheep and goats) rather than hunting and gathering for sustenance (Voigt 1983), indicating the additional presence of livestock since the 10th century. Mapungubwe and the entire Shashe/Limpopo basin was abandoned around 1 200 AD and may be attributed to either disease (Voigt 1983), or an end to their primary source of livelihood (herding) on account of drought or perhaps fluctuations in the tsetse fly belt.

In the mid-nineteenth century this area became the hunting ground of Voortrekker settlers and elephant herds, as large as one hundred animals (Cumming 1850), continued to be persecuted for the ivory trade in the 1840's. However, by the 1870's elephant hunters were already forced to trek as far north as the Zambezi valley (Selous 1881) to obtain ivory. The inhospitable Limpopo valley was generally avoided on account of stock (horses and oxen) losses incurred by the tsetse fly (Cumming 1850). Consequently, large tracts of crown land remained unoccupied well into the twentieth century.

In 1918, after the first World War, a vigorous white rural settlement policy saw farms in the valley being freely offered on extremely attractive terms. Drought, disease, competition from wildlife and theft across the Rhodesian and Bechuanaland borders hampered farmers, who subsequently campaigned to have their land values, and so too their loans, reduced. Persistent droughts (Figure 3.3) and inappropriate farming methods resulted in the degradation of the natural resources (O'Connor 1996) to the extent that the majority of the area was no longer able to support viable domestic livestock. Mean woody cover of *A. tortilis* (O'Connor, submitted) and *C. mopane* (O'Connor 1983) woodland increased by > 20% between 1955 and 1987, and coincided with the period of domestic livestock farming.

In 1980 kimberlite pipes were pinpointed on the farm Venetia. Construction work by De Beers Consolidated Mines Limited (an open cast diamond mine) began in 1990. Production started in 1991 and has a life expectancy of at least 20 years. Land adjacent to the mine was progressively acquired and in 1990 land-use practices changed dramatically when the area was destocked of livestock and established as Venetia-Limpopo Nature Reserve (VLNR). The population of indigenous herbivores, consisting predominantly of browsers and mixed feeders, has since increased. Drought has had a significant effect on the recent (< 20 yrs) ecology of the area (O'Connor 1999).

PART A: *Colophospermum mopane*

Chapter 4

Colophospermum mopane: a brief review of facts both general and specific to the study area

Distribution

Colophospermum mopane (Kirk ex Benth) Kirk ex J. Leonard occurs only in southern Africa, reaching its southernmost limit just below the Olifants River in the Kruger National Park, South Africa (Coates Palgrave 1983). Its distribution, principally influenced by moisture availability expressed through altitude, rainfall and soil texture (Mapaure 1994), often coincides with hot, arid conditions. The proportion of South Africa occupied by *C. mopane* vegetation is 2 % (4 % of the total *C. mopane* area) and is confined to two large belts; occurring along the Limpopo valley, which includes the study area, and in the Kruger National Park (Mapaure 1994). *Colophospermum mopane* is the dominant species of the Mopani Veld (Acocks 1953) and prominent in most of the plant communities described within its range south of the Limpopo River (O'Connor 1991; Dekker & Van Rooyen 1995), contributing up to 81 % of the leaf dry mass/ha^{-1} (Dekker & Smit 1996). The Limpopo valley supports single or multi-stemmed shrub or tree savanna on calcareous, alluvial soils (Mapaure 1994) with *C. mopane* trees attaining heights of up to 10 m in dryland situations in VLNR (O'Connor 1983).

Physiology

Colophospermum mopane is slow-growing (0.66 mm radial increment an^{-1} - O'Connor 1999) and adapted to drought conditions (Sharma *et al.* 1989): with (1) seeds capable of germinating at water potentials as strongly negative as -1.0 Mpa at 30 °C (Choinski & Tuohy 1991, Johnson *et al.* 1996); (2) adults extracting moisture at potentials of -1.5 Mpa (Smit 1994); and (3) significant stimulation of hypocotyl (Choinski & Tuohy 1991) and root (Johnson *et al.* 1996) elongation in response to water deficits. Temperature has little effect on percent germination unless seeds are subjected to negative water potentials, in which case the optimum temperature for germination is 25 °C (Choinski & Tuohy 1991). Successful germination under stressed conditions when previously imbibed in distilled water (Choinski & Tuohy 1991) correlates with the apparent lack of seed dormancy (Smit & Rethman 1998b).

Colophospermum mopane's high root biomass, shallow root system (66 % of fine roots, < 5 mm, occur within 400 mm of the soil surface) (Smit & Rethman 1998a) and ability to utilize soil water at a matric potential lower than herbaceous plants (Smit 1994) suggest a physiological adaptation to xeric conditions (Prior 1991) and heavier textured soils (Cole 1986; Fraser *et al.* 1987), and may explain the absence of herbaceous plants, the low species diversity (Mapaure 1994) and severe inter-tree competition for water and nutrients (Smit & Rethman 1998b) over vast areas of densely wooded Mopani Veld.

The availability of browse within the Mopani Veld is at its lowest from September to November, owing to the winter-deciduous nature of the dominant species, *C. mopane* (Dekker & Smit 1996). Trees lose their leaves earlier and flush later in densely wooded plots relative to low-density plots (Smit 1994).

Value

Colophospermum mopane is an ecologically and economically important plant species. Its timber is durable, hard and heavy (1 216 kg/m^3) (Van Wyk 1972), extensively used for mine props, railway sleepers (Coates Palgrave 1983), fencing posts (Mapaure 1994) and firewood (Prior & Cutler 1992). The bark is used medicinally and for tanning (5.9 - 8.7 % tannin) (Van Wyk 1972). *Colophospermum mopane* has a high phosphate and calcium content (crude protein = 13.6%, crude fibre = 21.1% and carbohydrate = 54.3% - Williamson 1975) and the ash can be used as fertilizer (Van Wyk 1972).

The long leaf-carriage period of *C. mopane* relative to other species in the Limpopo valley (Dekker & Smit 1996), underlies its importance as a fodder resource for livestock (Bonsma 1942), and wildlife, especially elephant, making up the greater portion of their diet where it is abundant (South Africa - Pienaar *et al.* 1966; Smallie & O'Connor 2000; Zambia - Lewis 1991; Zimbabwe - Jarman 1971; Guy 1976). Elephant feeding behaviour depends on tree size, influencing both the physiognomy and demography of *C. mopane* woodlands (Lewis 1991). A selection for pollarded or coppiced individuals rather than adult trees (Lewis 1991), perhaps owing to a larger portion of branches within the preferred browse size (Smallie & O'Connor 2000) and improved nutrient quality (Styles & Skinner 2000), prevents recruitment into the taller size classes (Caughley 1976) thereby promoting *C. mopane* scrubland and increasing browse availability for other herbivores. Although elephants encourage coppicing, the long-term survivorship of coppiced trees may depend on the soil nutrient reserves in the A horizon (Lewis 1991).

Caterpillars of *Imbrasia belina* are capable of defoliating vast stands of *C. mopane* trees, substantially reducing the dominant food source required by other browsers in the summer months (Styles & Skinner 1996). Commonly known as 'mopane worms', they live exclusively on the leaves and are a protein-rich delicacy, sought after by people (Styles & Skinner 1996) and baboons (personal observation).

Chapter 5

Patch dieback of *Colophospermum mopane* in a dysfunctional semi-arid African savanna

Introduction

Savanna, an extensive biome of Africa, covers a third of South Africa. Plant-available water and nutrients are primary determinants of savanna structure and function, whose influence may be modified by fire and herbivory (Frost *et al.* 1986). Whilst the influence of these determinants on the dynamics of herbaceous vegetation has been well researched because of economic considerations (e.g. O'Connor 1985), understanding of their effect on the dynamics of woody vegetation is relatively fragmentary. The increasing demand for goods and services offered by the woody component of savannas (Shackleton 1996) demands a detailed understanding of the mechanisms driving change in savanna woodlands.

Mortality is one of four fundamental demographic parameters (others are reproduction, immigration and emigration) driving community change (Watkinson 1997). Apart from affecting population dynamics, mortality of long-lived trees may modify biodiversity (Huston 1994) and ecosystem functioning (Solbrig *et al.* 1996). Consequently, the phenomenon of extensive dieback may constitute a major ecological perturbation, incurring substantial ecological and economic costs. Dieback of trees is a worldwide phenomenon, having increased in magnitude and extent since the turn of the century with unprecedented losses occurring in Australia, North America and industrialized Europe (Heatwole & Lowman 1986). Death of large stands is commonly associated with the dominant woody component, such as *Eucalypt* and *Acacia* in Australia (Fensham & Holman 1999). The causes vary in different geographic regions and are often speculated as synergistic combinations of more than one factor (e.g. Bunyard 1986). Suggested causes of dieback are: insect outbreaks (Haugen & Underdown 1990); fungal diseases (Crombie & Tippett 1990); climatic fluctuations (Watt 1987); shifts in geomorphologic or hydrologic gradients (Jimenez *et al.* 1985); air pollutants (Woodman 1987); salinity (Jolly *et al.* 1993); changes in land-use (Trenbath *et al.* 1990); and drought (Viljoen 1995; Fensham & Holman 1999). There are, however, few reports concerning dieback in African savannas: dieback of

Acacia xanthophloea has been attributed to both a raised ground water table and increased soil salinity following a period of higher rainfall (Western & van Praet 1973), and to senescence of even-aged stands (Young & Lindsay 1988).

A diverse array of mortality agents of African savanna trees has been identified: fire (Trollope 1982); debarking (e.g. porcupine, Thomson 1974) in conjunction with fire (Yeaton 1988); frost (Smit 1990); intensive herbivore browsing (e.g. Pellew 1983b; Stuart-Hill 1992b) in conjunction with fire (Trollope 1982); lightning (Spinage & Guiness 1971); and drought (Scholes 1985; O'Connor 1999). The extent of drought-induced mortality, of usually smaller individuals, depends on soil type (Scholes 1985; O'Connor 1999), density (Smit 1994), and species identity (O'Connor 1999). Mortality has not been shown, however, to occur as discrete patches admixed within healthy vegetation.

The continued availability of soil water is required for the persistence of long-lived species (Tongway & Hindley 1995). The effectiveness of rainfall in supplying plant-available water is influenced by soil texture (Brady & Weil 1996), evaporative demand, and topographic effects on landscape water redistribution (Coughenour & Ellis 1993). Vegetation cover, topography and slope determine the effectiveness of runoff at removing litter and eroding topsoil. On bare soils, runoff occurs as sheet flow on smooth slopes < 0.5%, but as high energy channelled flow when the gradient is steeper, which can cause rills and gullies (Ludwig & Tongway 1997). Rills redistribute surface flow resulting in greater plant production on run-on sinks compared with runoff-source zones (Hodgkinson & Freudenberger 1997). Landscapes incapable of efficiently capturing and retaining water and nutrients, often characterized by broad expanses of bare soil surfaces, a lack of perennial plant cover and severe soil erosion, are termed dysfunctional (Tongway & Ludwig 1997).

Colophospermum mopane is normally found in low altitude (400 - 700 m), low rainfall (200 - 800 mm an^{-1}) areas of southern Africa (Mapaure 1994) occurring usually as an almost monospecific woody component. Monitoring of *C. mopane* woodland in the Northern Province, South Africa, between 1982 and 1997 had revealed drought-induced mortality and extensive dieback (O'Connor 1999). This example offered an opportunity for increasing understanding of a poorly understood, infrequent and relatively recent biological phenomenon. The specific objectives were the following: (1) describe quantitatively this case of patch dieback, (2) establish if density effects influenced dieback, (3) test the hypothesis that patch dieback is a consequence of the senescence of a cohort (Young & Lindsay 1988), (4) assess whether soil type and drought were strong abiotic controls of dieback and, if so, what landscape-level factors had influenced that effect of drought such that patch dieback rather than another pattern of mortality had occurred, (5) test whether soil salinity was implicated in patch dieback (Western & van Praet 1973), and (6) test whether dieback was a consequence of localized reductions in soil water resulting from increased soil erosion, following the establishment of livestock ranches 50 years ago (O'Connor 1996). Erosion could influence soil water availability through its effect on runoff/run-on processes and by decreased water retention because of impaired soil surface condition (Tongway & Hindley 1995). In this study, patch dieback is differentiated from mortality by its localized distribution pattern within healthy vegetation and described as the synchronous mortality of neighbouring trees.

Methods

Data collection

A comparative approach was employed in 1998 in which areas of discrete dieback (all < 1 ha) were compared with adjacent paired plots of 'healthy' vegetation of apparently similar topography and soils. Forty sites of discrete patch dieback distributed over the full range of topographic units (crest to alluvial toeslope) (Figure 5.1) were selected. Plot size was 20 by 20 m. The distance between paired plots ranged from 23 m to 150 m with a median of 45 m. The general approach was to measure the vegetation of paired plots, specifically population size structure, stem and tree mortality, with associated measures of variables that may affect tree mortality, namely soil water availability and soil chemistry. An inherent problem of a retrospective study of an event such as dieback is to obtain measures of both vegetation and potential causal agents of tree mortality that reflect circumstances as they were at the time of dieback. It is possible that differences between paired plots for some variables could arise as a response to mortality.

Dieback took place following the 1988/89 and 1991/92 droughts because it was not evident following the 1982/3 drought, but was apparent by 1991 and was readily evident by 1996 (T. G. O'Connor, personal observation). The decay of standing dead trees (lack of bark shed, amount of fine branches lost) was consistent with mortality circa 1991/92 using criteria for ageing dead *C. mopane* trees (Appendix 1).

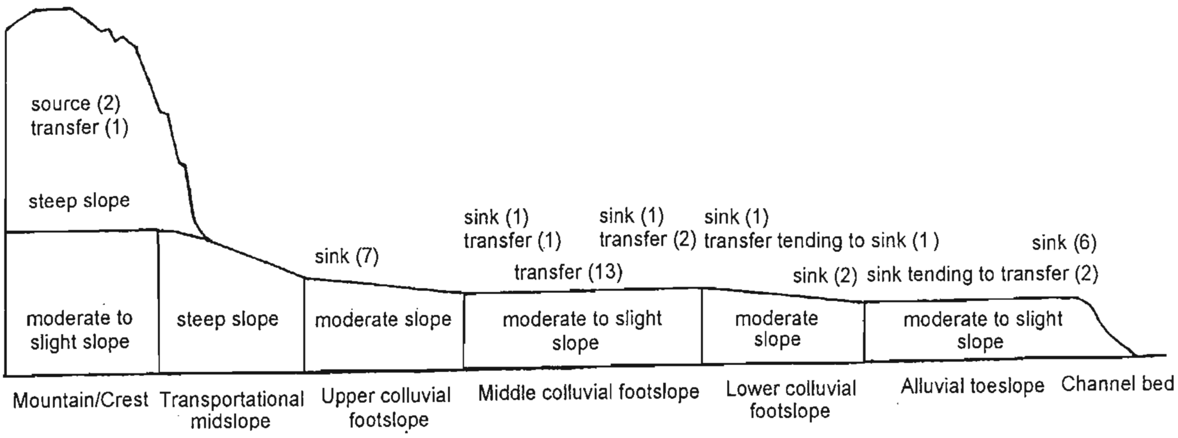


Figure 5.1 A generalized valley-side cross section (catena) showing most of the topographic units (defined by slope and relative location) encountered on the Venetia-Limpopo Nature Reserve. Terms relating to source, transfer and sink denote the functioning of a site in terms of surface redistribution of water and materials that would have prevailed prior to historical erosion (past ecological status). The numbers in parentheses indicate the number of sites assigned to each rank of past ecological status.

Measures of woody vegetation were species, height to the uppermost living and dead part of a tree, stem circumference (20 cm above ground level) and growth state (dead or alive) of each stem per tree. Dieback for each 'live' and 'dead' plot is the ratio of dead to total basal area, and for all 'live' or 'dead' plots is the number of trees with dead stems or the number of dead stems for each class of stem number per tree. Size, rather than age classes, are used to describe population structure because age can not be substituted for size in semi-arid systems owing to the effects of fire and herbivory (e.g. Pellew 1983), and the variable growth rates of similar-aged trees associated with the spatial and temporal heterogeneity of resources.

Slope was estimated using an electronic level (Leica Wild 3000). Each of the following abiotic variables were measured as the mean of four 10 by 10 m quadrants of a 20 by 20 m plot.

Surface water retention capacity (SWRC) was assessed using a 12 point ordinal scale adapted from Tongway and Hindley (1995) for this study (Table 5.1). Litter should affect SWRC (e.g. Kelly & Walker 1976), and was therefore included in the ranking procedure. 'Live' plots stood the risk of being assigned higher SWRC ranks owing to the occurrence of litter on those plots. Consequently, the ranking procedure was adjusted to reduce the bias by increasing the

Table 5.1 Surface water retention capacity (SWRC) rankings

Description	Class	Litter Cover (%)		Extent of Litter/Soil Incorporation
smooth surface, capping,	0.5	0-5% litter cover		loose litter, i.e. nil incorporation
very little sediment on soil surface	1.0	6-10% litter cover	if site >10% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
intermediate	1.5		if site >10% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
flakey surface, cracks present, hoof action, broken cap	2.0	11-25% litter cover	if site >25% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
intermediate	2.5		if site >25% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
uneven surface/relief, closed depressions (0-2.5 cm)	3.0	26-50% litter cover	if site >50% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
intermediate	3.5		if site >50% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
partially or fully sedimented rills (2.5-10 cm)	4.0	51-75% litter cover	if site >75% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
intermediate	4.5		if site >75% litter cover, then increase class ranking by 0.5	if the litter is moderately incorporated with the soil, increase ranking by 0.5
partially or fully sedimented rills (>10 cm)	5.0	76-90% litter cover		if the litter is moderately incorporated with the soil, increase ranking by 0.5
	5.5	91-100% litter cover		litter has a moderate contact with the soil
	6.0	100% litter cover		litter has an intimate contact with the soil

original SWRC ranking only if the observed litter cover exceeded the value already assigned to that class. It was assumed that rills, in which sand had subsequently been deposited, increased SWRC thereby improving plant-available water for adjacent trees by gaining runoff from up slope and promoting water transfer into the soil profile, unlike compacted surfaces which are more conducive to shedding of water.

Erosion severity (ES) was ranked using a seven-point ordinal scale adapted from Tongway and Hindley (1995) (Table 5.2).

Table 5.2 Erosion severity (ES) rankings

Class	Severity	Criteria
4.0	insignificant	a substantial herbaceous cover and/or litter accumulation, or no visible signs of surface flow
3.5		same characteristics as defined in class 4, but with additional pedestalling and weak sheeting
3.0	slight	sheeting, scalding and pedestalling is moderate
2.5		terracettes with rounded edges and shallow walls, sheeting, scalding and pedestalling is severe
2.0	moderate	same characteristics as defined in class 3, and/or terracettes with substantial walls, shallow rills
1.5		sedimented rills and gullies, weathered walls, sheeting half exposing gravel and revealing extensive pedestals
1.0	extensive	rills and gullies exposing roots, bedrock and/or steep walls, sheeting fully exposing a loose, stoney matrix

Ecological status (Est) describes whether a plot functions as a net source or sink of sediment and water taking into account the effect of geomorphic processes and topographic position. Each plot was assessed for past and current ecological status, using a seven-point ordinal scale (Table 5.3). The assessment of current status focussed on the 20 by 20 m plot and its immediate surrounds, whereas past ecological status assessed the flow of sediment and water across the plot that was likely to have occurred prior to the advent of extensive rill and gully erosion, depending on landscape position. Change in ecological status from erosion was the difference between past and current rankings. Aerial photography (1955 - 1987) revealed that gully erosion associated with the dieback sites preceded the death of trees but had occurred post 1955, that is, post the establishment of trees.

Table 5.3 Ecological status (Est) rankings

Class	Status	Description
3	sink	rills leading into and ending in a particular site signs of deposition only net gain of sediment, no loss
2	sink tending to transfer	slight loss of sediment, but overall a net gain
1	transfer tending to sink	slight gain of sediment, i.e. runon rills passing on the outskirts and/or through a site
0	transfer	signs of flow and deposition net gain of sediment = net loss
-1	transfer tending to source	slight loss of sediment, i.e. runoff
-2	source tending to transfer	slight gain of sediment rills originate from within a site and lead out of it
-3	source	signs of flow only net loss of sediment, no gain

The exposure of the surface of 'dead' plots since mortality may have resulted in exaggerated ranks, but this bias was consistent for change in ecological status.

Soil physical and chemical characteristics of both topsoil (0 - 200 mm) and subsoil (400 - 600 mm) were evaluated for each plot. Soil texture was analysed using the hydrometer method (Gee & Bauder 1986), pH (H_2O) was measured using a glass electrode pH meter (Crison micropH 2000), and the exchangeable cations (Na^+, Ca^{++}, Mg^{++}, and K^+) were determined by extraction with strontium (using 0.1 M strontium chloride) (Hughes & Girdlestone 1994) and expressed in meq/l. The sodium adsorption ratio (SAR) was calculated using the equation from United States Salinity Laboratory Staff (1954) (Na/sqrt(Ca/2+Mg/2)) and gives an indication of soil sodicity and thus the potential of a physiologically induced drought. Total exchangeable cations (TEC) was calculated as the sum of the concentrations of Na, Ca, Mg and K.

Data analysis

Differences between 'live' and 'dead' plots for biotic and abiotic variables were tested using paired *t*-tests; for tree height distribution using a Kolmogorov-Smirnov test; for independence of categories using χ^2. Classes containing fewer than five stems or trees were combined in the analyses using χ^2. Differences among soil types or topographic units were examined using Kruskal-Wallis or parametric ANOVA, depending on data properties. 'Live' and 'dead' plots were analyzed separately. A logistic regression was performed to test whether the probability of mortality on 'dead' plots depended on stem circumference, soil type, and their interaction.

To assess whether dieback had changed the nature of self-thinning (log of mean plant weight and the log of plant density) the relationship between individual plant size (volume) and stem density was examined. Density was expressed as the number of stems per unit area, owing to the multi-stemmed growth habit of *C. mopane*. Plant weight, because it is a cubic function of length, was indexed as the volume of a sphere using stem radius. It was considered acceptable to use the radius of trees that had died some years earlier because direct measures had shown radial growth to have been minimal over this period (O'Connor 1999). A weight correction was applied by multiplying by the wood density of *C. mopane* (1.25 g cm^{-3}) (Venter & Venter 1996).

The relationship between plot dieback, expressed as the percent loss of basal area (square-root transformed as indicated by a Box-Cox analysis), and those independent variables found to be significantly different between 'live' and 'dead' plots, was examined with multiple linear regression. The standardized variables were mean tree height, change in ecological status, SWRC, ES, pH (subsoil), texture (topsoil), SAR (subsoil), TEC (subsoil), number of stems, basal area of *C. mopane* and basal area of *Salvadora angustifolia*. On account of 66% of all fine (< 5 mm) *C. mopane* roots being found within 400 mm of the soil surface (Smit & Rethman 1998a) in this study area, cation concentrations implicated in dieback were likely to be encountered in this layer, and was the reason for including subsoil values in the regression. The order of entry of variables into the model was judged according to R^2 (adjusted) accounted for and reduction in s^2. Only significant main effects ($P < 0.05$), as there was no evidence of interactions, were included in the final regression. The only site located in riparian vegetation exerted undue leverage on the model and was therefore excluded.

Results

Patterns of dieback

The number of stems per tree ranged from 1 - 11 and 1 - 16 on 'live' and 'dead' plots, respectively. One third of the trees had single stems, two- and three-stemmed trees collectively accounted for half of the population of stems, and trees consisting of more than six stems contributed < 2% to the total population of trees. Across the classes of stem number per tree, the frequency of trees (Table 5.4) was independent of ($\chi^2 = 9.32$, df = 7, $0.25 > P > 0.10$), whilst the frequency of stems (Table 5.5) was dependent ($\chi^2 = 101.2$, df = 10, $P < 0.001$) on 'live' or 'dead' plots.

On 'live' plots, 27% of trees had dead stems, and 17% of stems were dead. In contrast on 'dead' plots, 89% of trees had dead stems and 86% of stems had died. Mostly entire trees died on 'dead' plots, whilst single-stem dieback prevailed on 'live' plots (Table 5.4). Dieback and tree mortality was related to the number of stems per tree. The frequency of trees with dead stems ('live': $\chi^2 = 320.56$, df =6, $P < 0.001$; 'dead': $\chi^2 = 19.81$, df = 5, $P < 0.005$) and the frequency of dead stems ('live': $\chi^2 = 29.34$, df = 8, $P < 0.001$; 'dead': $\chi^2 = 393.23$, df = 8, $P < 0.001$) were associated with stem number per tree. Although 69% of six-stemmed trees had dead stems on "live' plots, tree mortality was only 1.6% compared with 12.5% for single stems. Similarly on 'dead' plots, 10% fewer five- and six-stemmed trees died than single- or two-stemmed trees (Table 5.4). Consequently, dieback increased and tree mortality decreased with increasing stem number per tree on both 'live' and 'dead' plots. The frequency of trees with dead stems (Table 5.4) and of dead stems (Table 5.5) on 'live' and 'dead' plots were also proportional to the respective abundance (live plus dead) of trees and stems over the range in the number of stems per tree ('dead': $r = 0.99$, df = 11, $P < 0.001$; 'live': $r = 0.83$, df = 9, $P < 0.001$).

Dieback of stem basal area ranged from 1 to 49% and 55 to 100% on 'live' and 'dead' plots, respectively. Overall mean canopy dieback was 88 ± 1.6% on 'dead' plots, whilst only 14 ± 1.9% on 'live' plots. The three woody species other than *C. mopane* encountered on the plots collectively accounted for, on average, 5% of woody basal area, confirming the almost monospecific nature of these woodlands.

Table 5.4 The frequency of live plus dead *Colophospermum mopane* trees and stems and the percent of trees with dead stems for each class of stem number per tree on 'live' and 'dead' plots. The combined area of 40 20 m by 20 m plots is 1.6 ha

'Live' plots
Number of stems per tree

		1	2	3	4	5	6	7	8	9	10	11	Total
Number of trees		1054	821	537	272	120	61	14	4	5	1	1	2890
Percent of trees		36.5	28.4	18.6	9.4	4.2	2.1	0.5	0.1	0.2	0.0	0.0	100
Number of stems		1054	1642	1611	1088	600	366	98	32	45	10	11	6557
Percent of stems		16.1	25.0	24.6	16.6	9.2	5.6	1.5	0.5	0.7	0.2	0.2	100
Number dead stems		Percent of trees with dead stems											
	1	12.5	14.1	26.6	31.3	26.7	32.8	21.4	25.0	40.0	100.0	0.0	
	2		9.6	2.8	11.0	10	29.5	21.4	0	20.0	0.0	100.0	
	3			8	1.8	7.5	4.9	7.1	25.0	40.0	0.0	0.0	
	4				5.5	0.8	0.0	0.0	25.0	0.0	0.0	0.0	
	5					1.7	0.0	7.1	0.0	0.0	0.0	0.0	
	6						1.6	0.0	0.0	0.0	0.0	0.0	
Total		12.5	23.8	37.4	49.6	46.7	68.9	57.1	75	100.0	100.0	100.0	
Percent of all trees		4.6	6.7	7.0	4.7	1.9	1.5	0.3	0.1	0.2	0	0	

'Dead' plots
Number of stems per tree

		1	2	3	4	5	6	7	8	9	10	11	13	16	Total
Number of trees		558	479	319	162	74	25	12	6	2	1	2	1	1	1642
Percent of trees		34.0	29.2	19.4	9.9	4.5	1.5	0.7	0.4	0.1	0.1	0.1	0.1	0.1	100
Number of stems		558	958	957	648	370	150	84	48	18	10	22	13	16	3852
Percent of stems		14.5	24.9	24.8	16.8	9.6	3.9	2.2	1.2	0.5	0.3	0.6	0.3	0.4	100
Number dead stems		Percent of trees with dead stems													
	1	85.7	3.5	1.3	3.7	5.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	2		85.8	2.8	4.9	4.1	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	3			88.7	1.2	5.4	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	4				85.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	5					74.3	4.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	
	6						76	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	7							83.3	16.7	0.0	0.0	0.0	0.0	0.0	
	8								66.7	0.0	0.0	0.0	0.0	0.0	
	9									0.0	0.0	0.0	0.0	0.0	
	10										0.0	0.0	100	0.0	
Total		85.7	89.4	92.8	95.1	89.2	96.0	83.3	100.0	0.0	0.0	0.0	100.0	0.0	
Percent of all trees		29.1	26.1	18.0	9.4	4.0	1.5	0.6	0.4	0.0	0.0	0.0	0.1	0	

Table 5.5 The number of *Colophospermum mopane* stems (live plus dead) for each class of stem number per tree, compared with the number of dead stems on ‘live’ and ‘dead’ plots. Stem mortality was expressed as a percent of the stems within each class and a percent of the total number of live plus dead stems

‘Live’ plots
Number of stems per tree

	1	2	3	4	5	6	7	8	9	10	11	Total
Number of stems	1054	1642	1611	1088	600	366	98	32	45	10	11	6557
Number of dead stems	132	274	302	220	97	71	17	8	10	1	2	1134
Percent of class	12.5	16.7	18.7	20.2	16.2	19.4	17.3	25.0	22.2	10.0	18.2	
Percent of all stems	2.0	4.2	4.6	3.4	1.5	1.1	0.3	0.1	0.2	0.0	0.0	17.3

‘Dead plots ’
Number of stems per tree

	1	2	3	4	5	6	7	8	9	10	11	13	16	Total
Number of stems	558	958	957	648	370	150	84	48	18	10	22	13	16	3852
Number of dead stems	478	839	871	580	297	129	70	40	0	0	0	10	0	3314
Percent of class	85.7	87.6	91.0	89.5	80.3	86.0	83.3	83.3	0	0	0	76.9	0	
Percent of all stems	12.4	21.8	22.6	15.1	7.7	3.3	1.8	1.0	0	0	0	0.3	0	86

Abiotic variables influencing dieback

Topography, soil type and slope did not explain dieback. Variation in mean dieback on the upper, mid and foot slopes was only 12 - 14% and 86 - 93% on 'live' and 'dead' plots, respectively. Although less dieback occurred on crests (7% and 83% on 'live' and 'dead' plots, respectively), dieback did not differ among topographic units on 'live' (F = 0.45, df = 39, P = 0.722), 'dead' (F = 0.9, df = 39, P = 0.449) or all plots (F = 0.05, df = 79, P = 0.986). Nor did dieback differ among soil types on 'live'(F = 0.93, df = 39, P = 0.438), 'dead' (F = 0.93, df = 39, P = 0.434) or all plots (F = 0.01, df = 79, P = 0.998) with mean dieback among soil types (across all plots) varying by only 2.5%. Slope, which varied by only 3.03% (< 3.07%), did not differ between 'live' and 'dead' plots (Table 5.6).

'Live' and 'dead' plots did not differ in past Est, in support of appropriate criteria having been used for pairing of sites, but they differed markedly in current Est (Table 5.6). Plots were originally functioning, on average, as transfer zones with a slight tendency to act as sinks of water and sediment. The current average Est for 'live' plots was similar to that described for average past Est, but that of 'dead' plots revealed they function as a transfer zone tending to a source. The change in Est reveals that both 'live' and 'dead' plots have, on average, become more dysfunctional, but the extent of change on the 'dead' plots is three fold that of the 'live' plots (Table 5.6), having altered 'dead' plots from receiving water and sediment to sources of these. If a greater than average change in Est had occurred on the 'dead' plots then the same could be expected of the 'live' plots (r = 0.74, df = 38, P < 0.001). The major cause of this change has been the interception of surface water by recently formed (< 45 years) rills, gullies and roads, located up slope and perpendicular to the flow of water. The transformation of a plot from receiving to losing water and sediment would reduce the amount of water retained for the persistence of long-lived trees.

Erosion severity and SWRC were, respectively, greater and lower on 'dead' than on 'live' plots (Table 5.6), and SWRC was negatively correlated with dieback (Figure 5.2), all evidence that a deficiency of soil water was an agent of dieback. The greater SWRC of 'live' plots, correlated with current Est (Table 5.7), underscores their functioning as sinks. The greater proportion of clay plus silt particles on 'dead' plots (Table 5.6) would have further reduced water availability during drought.

Table 5.6 Summary of the results from paired *t*-tests ($n = 40$) of variables describing vegetation structure and variables potentially responsible for dieback. Estimates of basal area include live plus dead stems

Variable		Live Plots Mean	*SE*	Dead Plots Mean	*SE*	*t* value	*P*
Vegetation Variables							
Stem Basal Area Dieback (%)		13.0	1.6	87.0	1.7	36.72	0.000
Tree Height (m)		3.7	0.19	3.2	0.14	3.4	0.001
Range for tree height (m)		5.3	0.29	4.3	0.25	4.1	0.000
Stem Circumference (cm)		23.0	1.1	25.0	1.0	1.4	0.162
Range in stem circumference (cm)		65.0	3.9	58.0	3.9	1.4	0.080
Total Number of Stems (per plot)		164	12	96.0	6.0	6.2	0.001
Stem Basal Area of *C. mopane* (m^2/ha)		19.0	0.7	13.0	0.7	8.4	0.001
Stem Basal Area of *S. angustifolia* (m^2/ha)		0.3	0.1	0.8	0.17	2.3	0.050
Stem Basal Area of *Boscia spp.* (m^2/ha)		0.5	0.15	0.4	0.1	0.7	0.520
Stem Basal Area of *L. austrinum* (m^2/ha)		0.08	0.029	0.02	0.008	1.9	0.060
Stem Basal Area of all species except *C. mopane* (m^2/ha)		1.2	0.21	1.3	0.21	0.4	0.678
Relief							
Slope (%)		1.2	0.09	1.2	0.10	0.31	0.750
Soil Condition							
Surface Water Retention		3.0	0.18	1.7	0.11	7.9	0.001
Erosion Feature/Severity		2.3	0.14	2.7	0.10	3.1	0.010
Past Ecological Status		1.3	0.28	1.3	0.28	0.0	1.000
Current Ecological Status		0.7	0.16	-1.2	0.16	8.0	0.001
Change in Ecological Status		-0.7	0.30	-2.5	0.32	8.0	0.001
Soil Chemisty							
pH	Topsoil	7.4	0.12	7.1	0.12	5.0	0.001
	Subsoil	7.3	0.11	7.0	0.1	5.2	0.001
Texture (sand:fines)	Topsoil	2.7	0.56	2.2	0.36	2.2	0.050
	Subsoil	3.2	1.19	2.0	0.5	1.8	0.070
Na (me/l)	Topsoil	0.05	0.005	0.09	0.018	2.8	0.010
	Subsoil	0.2	0.03	0.4	0.09	2.3	0.050
SAR	Topsoil	0.02	0.002	0.04	0.009	2.7	0.010
	Subsoil	0.06	0.011	0.13	0.03	2.3	0.030
TEC (me/l)	Topsoil	11	0.7	11	0.5	0.0	0.980

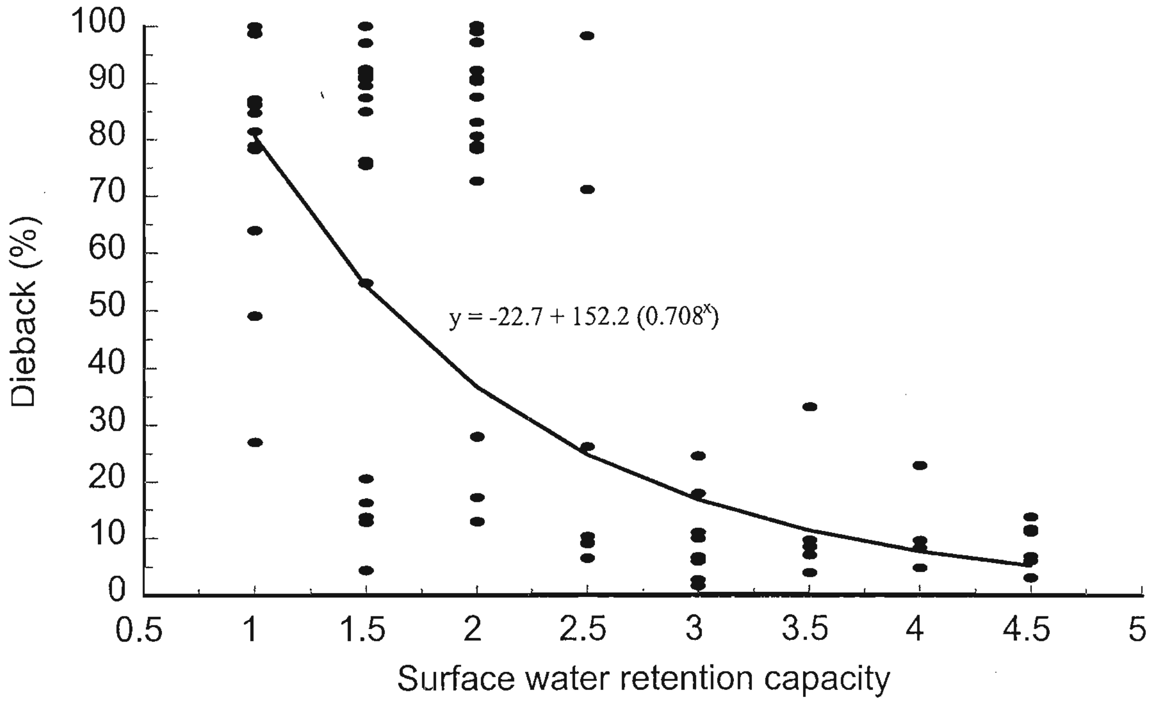


Figure 5.2 Percent dieback of *Colophospermum mopane* in relation to surface water retention capacity, including an exponential regression ($r^2 = 0.45$, $n = 78$, $P < 0.001$). The only site located within riparian vegetation was excluded from the analysis.

The differences in soil chemistry (pH, TEC, SAR) between 'live' and 'dead' plots (Table 5.6) are not large, possibly resulting from a change in nutrient cycling following mortality of *C. mopane* trees on 'dead' plots; they were not related to textural variation (Table 5.7). Individual cations (Ca, Mg and K) were not implicated in dieback. Although soils were not sodic, the two-fold difference of Na concentration between 'dead' and 'live' plots (Table 5.6) suggests the probability that Na exacerbated the reduced soil water availability on 'dead' plots by inducing a physiological drought. Subsoil TEC was a justifiable surrogate for individual cations (for inclusion in the regression model) considering it was correlated with all the subsoil cations (Table 5.7). Similarly, the SAR was highly correlated with Na levels (Table 5.7).

Table 5.7 Selected significant ($P < 0.001$) and non-significant (bold values, $P > 0.05$) correlations (Pearson's r) between site variables meaningful to dieback.. Column numbers represent site variables

Site Variable		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Dieback (%)	1	1.00																				
Mean stem circumference (cm)	2		1.00																			
Mean tree height (cm)	3		0.73	1.00																		
Basal area (*C. mopane*, m²/ha)	4	-0.51		0.68	1.00																	
Stem density (*C. mopane*, stems/plot)	5	-0.47	-0.72			1.00																
Past Ecological Status	6						1.00															
Current Ecological Status	7	-0.71			0.51			1.00														
Change in Ecological Status	8	-0.44					-0.78	0.60	1.00													
Surface Water Retention Capacity	9	-0.62		0.51	0.56	**0.17**		0.73		1.00												
pH (Topsoil)	10										1.00											
pH (Subsoil)	11											1.00										
Texture (Topsoil)	12			0.49						0.45	**-0.12**		1.00									
Texture (Subsoil)	13			0.58						0.45		**-0.11**	0.96	1.00								
Total Exchangeable Cations (Subsoil)	14		-0.44	-0.46										-0.36	1.00							
Sodium Adsorption Ratio (Subsoil)	15													**-0.09**	0.46	1.00						
Sodium Adsorption Ratio (Topsoil)	16											0.90	**-0.08**				1.00					
Na (Topsoil)	17															0.98		1.00				
Na (Subsoil)	18														0.50		1.00		1.00			
Ca (Subsoil)	19														0.62					1.00		
Mg (Subsoil)	20														0.79						1.00	
K (Subsoil)	21														0.46							1.00

Role of competition

Significant relationships between the log of mean stem 'weight' and the log of stem density on 'live' ($r^2 = 75.9$, $F = 124.02$, df = 39, $P < 0.001$) and 'dead' ($r^2 = 68.6$, $F = 86.15$, df = 39, $P < 0.001$) plots prior to dieback (Figure 5.3a) provide evidence of self-thinning, whose slopes did not differ ($t = 0.239$, df = 76, $P > 0.5$). Evidence, however, that intraspecific competition was not responsible for patch dieback was a negative correlation of percent dieback with total basal area and stem density of *C. mopane* (Table 5.7), and a greater stem density and total basal area on 'live' than on 'dead' plots (Table 5.6, Figure 5.4).

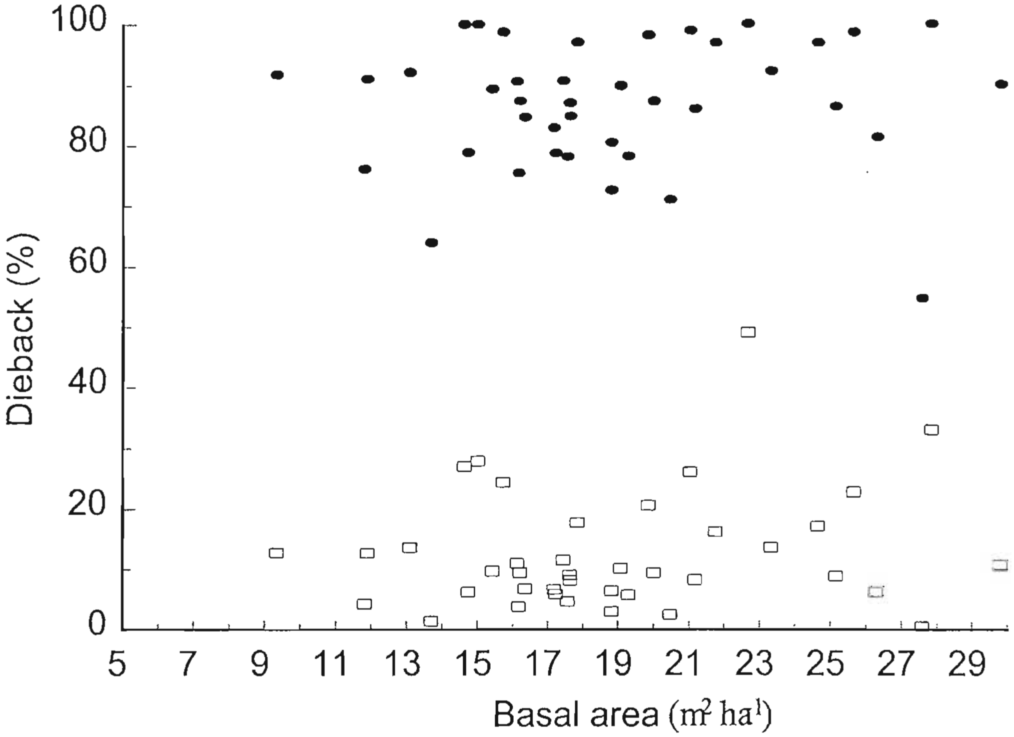


Figure 5.4 Relationship between percent dieback and the total basal area (live plus dead stems) of *Colophospermum mopane* stems on 'live' (squares) and 'dead' (circles) plots ($n = 80$).

The self-thinning relationship was still evident on live plots after dieback ($r^2 = 72.2$, $F = 102.14$, df = 39, $P < 0.001$) (Figure 5.3b) whose slope did not differ ($t = 0.038$, df = 76, $P > 0.5$) from that before mortality. In contrast, no self-thinning relationship was apparent on 'dead' plots after dieback ($r^2 = 5.9$, $F = 3.2$, df = 35, $P = 0.08$) (Figure 5.3b). Change in log of mean stem 'weight' on 'live' plots ('weight' of [live plus dead stems]-[live stems]) was negligible (Figure 5.3c),

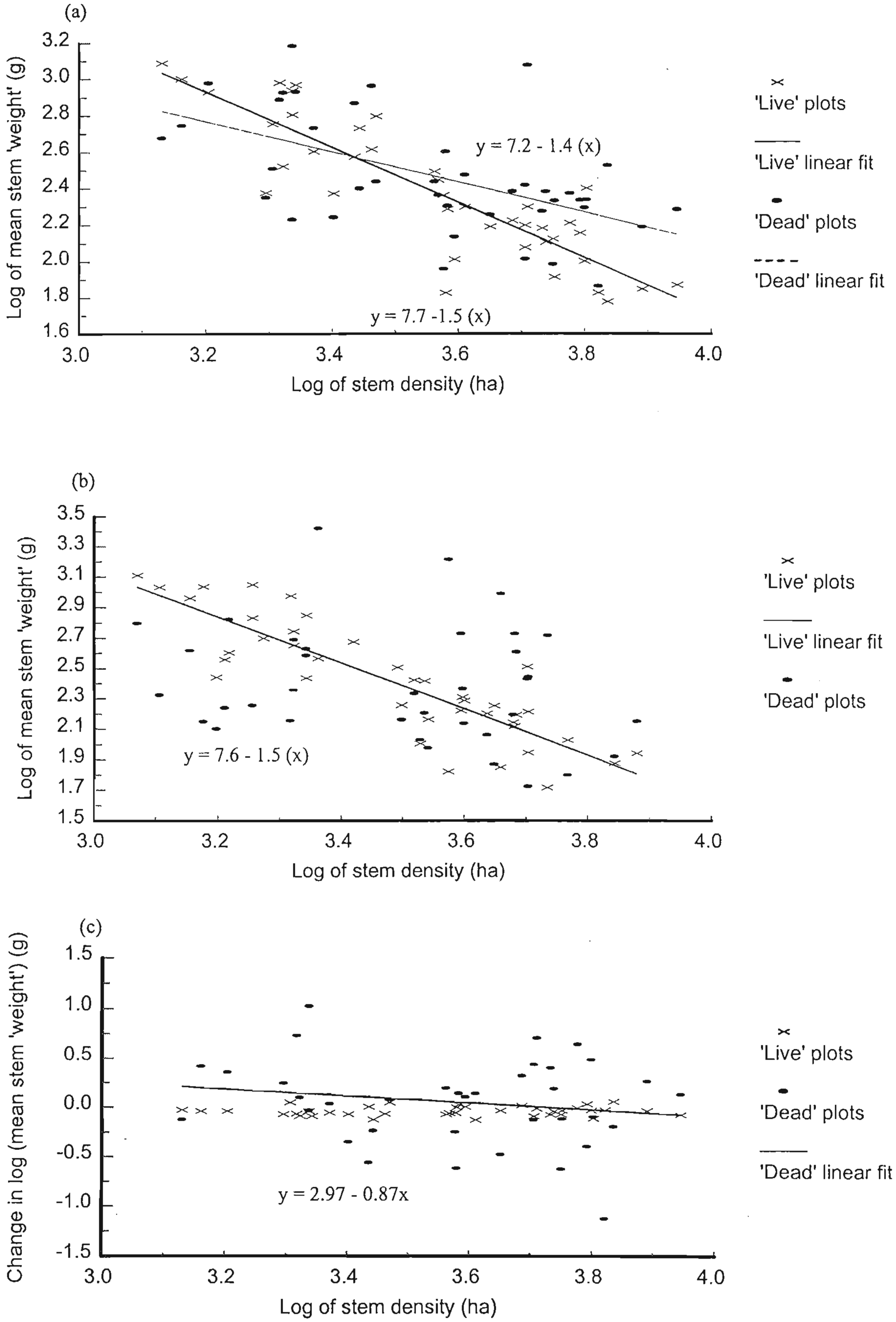


Figure 5.3 Relationship between log of mean stem 'weight' and log of stem density (ha) for *Colophospermum mopane* on 'live' ($n = 40$) and 'dead' plots ($n = 40$), prior to dieback (a), after dieback (b), and change in the log of mean stem 'weight' relative to the log of stem density (c).

and remained constant ($b_1 = 0.015$), irrespective of stem density ($F = 0.19$, df = 39, $P = 0.665$). This negligible change is attributable to the low stem mortality. On 'dead' plots, however, a significant negative ($b_1 = -0.868$) linear relationship between change in the log of mean stem 'weight' and the log of stem density ($r^2 = 11.0$, $F = 5.31$, df = 35, $P < 0.027$) occurred, indicating a greater mean individual size after dieback at lower stem densities.

There was no significant difference between 'live' and 'dead' plots in the stem basal area of other tree species combined (Table 5.6), refuting the possibility of inter-specific competition accounting for mortality. Although stem basal area of *S. angustifolia* was almost three times greater on 'dead' plots (Table 5.6), the species was absent on 38% of those plots, although there was a correlation ($r = 0.3$, df = 78, $P < 0.01$) between its stem basal area and percent dieback of *C. mopane*.

Population structure and dieback

'Live' and 'dead' plots had a similar mean stem circumference (live and dead trees) (Table 5.6). Although 'live' plots had a greater range in stem circumferences than 'dead' plots, neither consisted of even-sized stands, in contradiction of size-related senescence as a mortality factor. Trees were generally taller with a greater range in height on 'live' plots than on 'dead' plots (Table 5.6). The different ($P < 0.001$) tree height distributions of all trees (pre-drought) between 'live' and 'dead' plots (Figure 5.5) does not necessarily suggest that certain population structures were more predisposed to dieback than others considering there was only a 10% difference in the upper quartile of tree height between 'live' (4.1 m) and 'dead' (3.7 m) plots. The tree height distribution of dead trees on 'dead' plots was not different ($P > 0.10$) from the distribution of all trees on those plots prior to dieback (Figure 5.5).

Influence of soil type

Woodland structure and tree size depended on soil type. Differences among soil types on both 'live' ($\chi^2 = 143.0$, df = 3, $P < 0.001$) and 'dead' ($\chi^2 = 129.4$, df = 3, $P < 0.001$) plots and between 'live' and 'dead' plots on each ($n = 4$) soil type ($P < 0.05$, $n = 137$ to 1166) were evident for the distribution of tree height. On 'live' and 'dead' plots, Valsrivier soils had the tallest trees (10 m and 8.5 m, respectively) and greatest range in tree heights (9.8 m and 8.0 m, respectively), whilst Dundee soils had the shortest trees (6.5 m and 5.0 m, respectively) and smallest range in tree

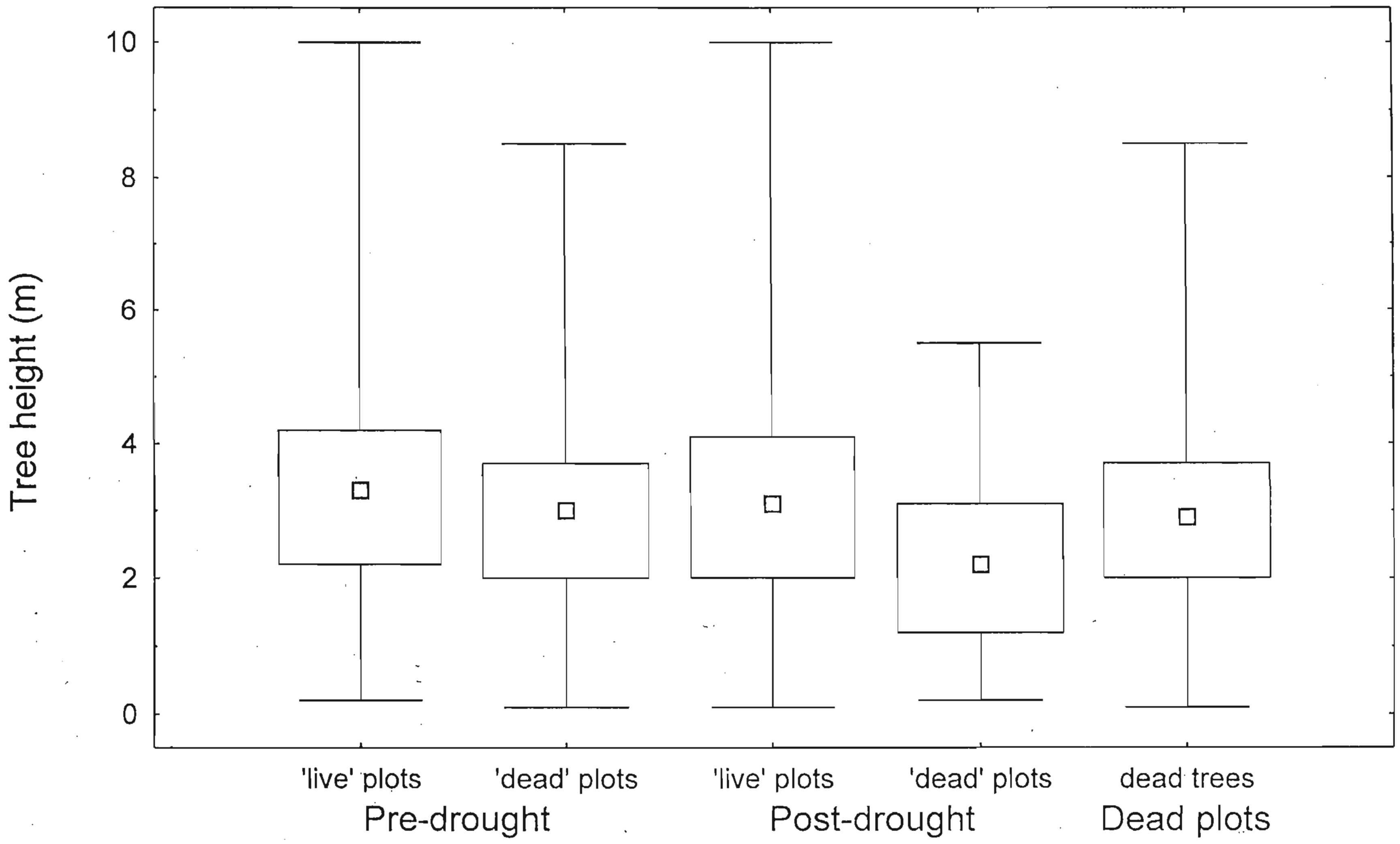


Figure 5.5 Box-and-Whisker plot of tree height of all *Colophospermum mopane* trees (pre-drought) on ‘live’ (*n* = 2712) and ‘dead’ (*n* = 1519) plots, of live trees (post-drought) on ‘live’ (*n* = 2481) and ‘dead’ (*n* = 236) plots, and of dead trees on ‘dead’ plots (*n* = 1283).

heights (6.2 m and 4.5 m, respectively).

Basal area differed (F = 4.85, df = 39, $P = 0.006$) among soil types on 'live' plots only. Basal area was highest (23.02 $cm^2 m^{-2}$) on Dundee soils and lowest (15.51 $cm^2 m^{-2}$) on Swartland soils. No differences were evident for stem density, mean tree height, and mean stem circumference.

Soil types differed in change in Est on 'live'(F = 4.92, df = 39, $P = 0.006$) and 'dead'(F = 11.03, df = 39, $P < 0.01$) plots, ES (F = 5.46, df = 39, $P = 0.003$) on 'live' plots, and SWRC on 'live'(F = 3.23, df = 39, $P = 0.034$) and 'dead'(F = 2.9, df = 39, $P = 0.048$) plots. Differences among soil types in change in Est, ES and SWRC may be attributed to differences in texture on 'live' (F = 3.56, df = 39, $P = 0.023$) and on 'dead'(F = 4.13, df = 39, $P = 0.013$) plots. In particular, Dundee and Oakleaf soils had a greater proportion of sand than Valsrivier and Swartland soils. The coarse-textured soils had a lower ES, a greater SWRC and underwent less change in Est, suggesting that fine-textured soils may be more susceptible to degradation and patch dieback. The probability of stem mortality on 'dead' plots (Table 5.8) was affected by soil type ($P < 0.001$), but not stem basal area ($P < 0.3$) or their interaction ($P < 0.5$). Trees growing on Oakleaf soils were less inclined to lose stems to dieback than trees growing on the other soil types.

Table 5.8 A summary of the effect of soil type, basal area and their interaction on the logistic regression of stem mortality

	Residual *df*	Residual Deviance	Approximate χ *P*
null model	3819	3054	
add soil type	3816	3026	
change	3	29	< 0.001
add basal area	3815	3023	
change	1	2	< 0.25
add soil*area	3812	3021	
change	4	5	< 0.5

	estimate	SE	*t* - critical	*P*	antilog of estimate
constant	-2.14	0.099	-21.74	< 0.001	0.12
Dundee	-0.21	0.177	-1.17	0.243	0.81
Oakleaf	0.38	0.115	3.26	0.001	1.46
Swartland	0.01	0.141	-0.1	0.922	0.99

Regression model of dieback

The final regression model of dieback explained 70% of the variation (Table 5.9). Dieback was affected most by SWRC (48.5% of the variance), stem density accounted for an additional 8.23%, whilst the remaining variables accounted each for 2-4% of the variance (Table 5.9). Dieback was less with a greater stem density, with greater SWRC (Figure 5.2), and with least change in Est. The poor correlation between stem density and SWRC (Table 5.7) was improved ($r = 0.53$, df $= 58$, $P < 0.001$) when 'live' plots containing rills were excluded from the analysis, suggesting that dieback may be related to an interaction between stem density and SWRC. Although dieback was associated with decreased erosion, it should be noted that an increase in erosion severity was associated with the occurrence of sedimented rills (Table 5.2) which were only found on 'live' plots (mean rill size: 25 cm deep by 115 cm wide). Although rills constitute a more severe type of erosion than sheeting, they may increase the availability of water to trees if sedimented, thereby reducing percent dieback. An increase in pH reduced dieback, whilst plots with taller trees experienced less dieback than plots with shorter trees (Table 5.9).

Table 5.9 Regression model of percent mortality (square-root transformed) of *Colophospermum mopane* ($r^2 = 70.4\%$, $n = 78$)

Added variable	Coefficient	Adjusted R^2	s^2
Water Retention Capacity	-0.9986	48.47	2.243
Stem Density	-0.0185	56.70	2.056
Erosion Severity	0.7278	61.08	1.949
Change in Ecological Status	-0.4246	63.10	1.898
Average Height	-0.8881	66.85	1.799
pH (subsoil)	-0.9549	70.43	1.699

Discussion

Preconditions and causes of patch dieback

Patch dieback of *C. mopane* was a distinct phenomenon in this region (Figure 3.3, Table 5.5), these patches having lost most of their woody biomass. Dieback has generally been associated with the synergistic combination of more than one factor. A combination of anthropogenic and natural factors were implicated in this study, which have in common a potential effect on the availability of soil water. The interpretation to be supported below is that patch dieback had occurred where the availability of soil water had been impaired to a level incapable of sustaining the growth of *C. mopane* trees during the severe drought period of 1988 to 1992.

Dieback from the top of the tree canopy down on all plots indicated a soil water deficit, exacerbated (up to 100% mortality) on 'dead' plots by local landscape-level factors identified using multiple regression: a lesser ability of the soil surface to retain water; a change in ecological status indicating areas receiving water and sediment changed to sources of these; and the absence of rills indicated by less severe erosion (or large erosion severity rankings [Table 5.2]) compared with 'live' plots (Table 5.9). These variables all reflect a degraded soil surface and subsequent shift in hydrologic gradients beyond *C. mopane*'s threshold of stress (*c.f.* Jimenez *et al.* 1985). A consistent characteristic of 'dead' plots was the development of rills adjacent to them that would have altered the previous pattern of surface water redistribution, resulting in rapid drainage (runoff) rather than ponding and infiltration of run-on. Patch dieback was therefore a symptom of a dysfunctional landscape (Tongway & Ludwig 1997) that became manifested during a drought period.

The evidence of self-thinning prior to dieback (Figure 5.3a) indicates intra-specific competition of *C. mopane* was operating. Although competition influences mortality through self-thinning (e.g. Lugo & Scatena 1996, Fensham & Holman 1999) and inter-tree competition was conspicuous during the drought in this study area (Smit 1994), it was judged not to be a cause of patch dieback because 'live' plots had a greater stem density and a greater stem basal area than 'dead' plots, and their self-thinning relationship was not different. The evidence of self-thinning suggests rather that inter-tree competition, most likely for soil water (Smit 1994), was a precondition for dieback. For 'dead' plots, the severe drought-induced dieback suggests intense competition during the drought, heightened by the dysfunctional nature of these patches by comparison with adjacent healthy patches. Inter-specific competition was not implicated in dieback, perhaps owing to the almost monospecific nature of the *C. mopane* woodlands.

Monospecific or species-poor communities, such as *C. mopane* woodlands (Mapaure 1994), have a less variable threshold to stress (Jimenez *et al.* 1985; Walker 1995) than species-rich communities, particularly if the dominant species has a narrow range of environmental tolerances and is arranged along specific geomorphic and hydrologic gradients, which, when altered, can trigger widespread dieback (Western & van Praet 1973). Consequently, monospecific communities are more vulnerable to patch dieback than species-rich communities.

The inverse relationship of dieback with stem density (Tables 5.7 & 5.9) is not easily explained. Tree stems may have a similar effect to grass tussocks by intercepting rainfall, impeding surface water flow, and channelling water into the soil (Freudenberger *et al.* 1997). The high litter cover of these *C. mopane* woodlands (up to 42%) (O'Connor 1999) is a critical control of infiltration and runoff (Kelly & Walker 1976), that may depend on woodland density. A lower woody density and therefore lesser litter cover (O'Connor 1999), would probably intercept less rainfall and have more bare soil exposed to compaction by rainfall (Finlayson & Statham 1980), thereby reducing infiltration and increasing runoff (Greene *et al.* 1994).

The hypothesis that patch dieback may be a consequence of the senescence of a cohort (Young & Lindsay 1988) was not supported as the distribution of dead trees on 'dead' plots covered the range of live tree heights prior to dieback (Figure 5.5). Tree survival on 'dead' plots appears, however, to have favoured smaller individuals (Figure 5.5) whereas smaller individuals had been the most likely to succumb to drought elsewhere in VLNR (O'Connor 1999). Synchronous dieback of different-sized trees suggests the infringement of a species-specific threshold, rather than a size-specific threshold.

The pattern of patch dieback of *C. mopane* illustrated that stands of heterogenous structure are no less vulnerable to patch dieback than homogenous stands. Structural homogeneity may render a woodland vulnerable to complete dieback by size-specific stressors (Young & Lindsay 1988), whilst senescence or size-related death in a heterogenous stand would be less noticeable. Mortality is often size-dependent (Huston 1994) because many ecological responses of trees, including those with drought (O'Connor 1999), herbivores and fire (Pellew 1983b), are dependent on size. The proportion of individuals within a vulnerable range of tree heights will therefore determine the extent or pattern of dieback. Plants of all sizes succumbed in this example of dieback.

The hypothesis that soil salinity (Western & van Praet 1973) or soil sodicity may be implicated in dieback was not upheld. The slightly higher sodium concentrations on some 'dead' plots may have predisposed them to dieback through physiological 'drought' compounding natural drought, but dieback occurred on sites across a range of Na concentrations.

Landscape variation in dieback

Although dieback did not differ among topography, slope or soil type, Dundee and Oakleaf soils, respectively, averaged the least dieback on 'live' and 'dead' plots. Similar findings were reported by Fensham & Holman (1999), viz. that least dieback occurred on alluvial soils and landscape position had no significant effect on dieback. Apart from affecting population structure, soil type had a greater effect on abiotic (change in Est, ES, and SWRC) than biotic variables (stem density, mean tree height and mean stem circumference). The most likely explanation for its influence on the abiotic variables, was the texture gradient that existed between the alluvial and palaeo-alluvial soil types. The significant effect Oakleaf soils had on reducing stem mortality, combined with the effect soil type had on the abiotic variables, suggests that percent dieback may be indirectly related to soil type. Sampling of this study was restricted to where dieback had occurred, but *C. mopane* was also the dominant species on sandy soils derived from gneisses or aeolian sandstones (O'Connor 1992), on which no patch dieback was found. Sandy soils are not prone to the formation of rills and maintain infiltration, even when cover is poor (Barnes & Franklin 1970). At a broader landscape level, therefore, soil type was a key control on patch dieback.

Studies on rills have been concerned with water flow and have neglected to take into account their potential influence on vegetation. The average slope of most sites exceeded 0.5% and was therefore conducive to a channelled flow of runoff (Ludwig & Tongway 1997), particularly as ground cover was sparse. Rills are usually considered to promote a loss of water, but one form of rill was observed to make water available to adjacent trees. Approximately 60% of the 33 sites associated with rills had rills passing through the 'live' plots. Rills converge water flow along concentrated routes and transport sediment from up slope (Finlayson & Statham 1980). Rills in 'live' plots were sedimented and characteristically had adjacent growing trees. It is proposed that, if sedimented, rills increase plant-available soil water in areas immediately adjacent to them, thereby influencing woodland dynamics in degraded systems. Roads placed perpendicular to the surface flow of water functioned as rills by intercepting and removing water to drainage lines. Consideration of the patterns of redistribution of overland flow need therefore to include (i) the placement of roads in drought prone areas and (ii) the influence of rills on woodland dynamics in dysfunctional landscapes.

Dieback: manifestation of a dysfunctional landscape

Concern regarding patch dieback lies not in the potential extinction of *C. mopane*, as it is prolific, but in that it signifies a dysfunctional system. Perhaps the single most important ecological implication of a dysfunctional system is the irretrievable loss of topsoil. Dieback areas will continue to be degraded unless erosion-control measures are implemented. Dead trees are persistent and can remain standing for at least 24 years in dryland areas with a low and erratic rainfall (Leuthold 1996) whereas they could be pushed over to obstruct overland flow and restrict sediment loss. Arid areas with a history of over-exploitation are potential candidates for dieback and should constitute an obvious conservation focus.

The degradation of this system is coincident with the 50 year period of commercial livestock ranching. Prior to ranching, the area formed part of a large, unfenced region occupied by wildlife. Aerial photography (O'Connor, submitted) from the early time (1955) of agricultural occupation provides diverse evidence of degradation including the initiation and rapid expansion of areas of bare soil, gullying, and desiccation of hydromorphic grassland, indicated by a five-fold increase in their woody cover. Much of the change was precipitated by the severe, extended drought of the 1960's (Figure 3.3). There had also been a 20% increase in the cover of *C. mopane* woodland over this period (O'Connor 1983) leading to extremely dense woodland by the late 1980's in which inter-tree competition, as revealed by thinning experiments, was intense (Smit 1994). Botanical composition and condition of the soil surface (O'Connor 1983, 1999) are consistent with a loss of perennial grasses and an increase in bare soil. The fine-textured soils of the study area are vulnerable to sealing and thereby shedding of water, as well as rill and gully formation, rendering them drought prone. Drought proneness is exacerbated in some spots by Na concentration.

The occurrence of patch dieback of *C. mopane* between 1988 and 1992 is therefore interpreted as a consequence of the preconditioning of the system by an increase in *C. mopane* and an increase in drought proneness through erosion on fine soils where texture and chemistry predispose them to drought effects. Water received during non-drought years was apparently sufficient for survival of these long-lived trees. Previous droughts (e.g. 1968, 1973 - Figure 3.3) did not result in patch dieback ostensibly because the dieback areas were still functioning as sinks of water and sediment (Table 5.6). Despite its drought tolerance (Prior 1991; Smit 1994) the demand of *C. mopane* for water could not eventually be met by supply on degraded patches as they deteriorated, but could on immediately adjacent patches still functioning as run-on sinks.

A widespread model of the degradation of rangeland is an increase in the woody component with an associated increase in soil erosion and decrease in water retained (Schlesinger *et al.* 1990). This study indicates degradation can proceed another step in which the drought-adapted woody species that had increased begin to decline.

Chapter 6

Coppicing (stem recruitment) of drought-stressed *Colophospermum mopane* trees

Introduction

Colophospermum mopane is a key species where it occurs because people (Whitlow 1979; Liengme 1983; Madzibane & Potgieter 1999) and browsers (Walker 1980) depend upon it for their sustenance. However, despite its abundance (Mapaure 1994) and hardiness (Kelly *et al.* 1976), it has become an endangered species in some parts (Chikuni *et al.* 1996) owing to its overexploitation by people. Widespread mortality is often a combination of factors which act synergistically to kill it (Lewis 1991; Chapter 5). Apart from removing the agents of mortality which may not always be possible, an alternative approach to conserve the species would be to gain an understanding of its longevity and ability to tolerate the removal of aboveground biomass compared with other woody species.

Colophospermum mopane is a slow-growing tree on account of its hard wood density (Enquist *et al.* 1999). O'Connor (1999) reported a mean annual radial increment of 0.67 mm for the drought-stressed woody component of a *C. mopane* savanna. Although Prior and Cutler (1996) recognised growth rings in drought-stressed *C. mopane* (average radial increments ranged between 0.85 mm and 1.05 mm), they could not determine the age of trees because many stem discs were hollow and ring width could not be correlated with rainfall. Mushove *et al.* (1995) reported similar findings and identified inter-site differences (soil water and nutrient availability) in growth rates.

A number of agents have been shown to cause mortality of individual *C. mopane* trees: people (Chikuni *et al.* 1994), elephant (Ben-Shahar 1996) and drought (O'Connor 1999; Chapter 5). The ability of *C. mopane* to tolerate ringbarking (Kelly *et al.* 1976), stem breakage (Mapaure & Mhlanga 1998) and burning (Walters 2000) may be explained by its ability to coppice (Mapaure & Mhlanga 1998) and replace its former canopy with regrowth (Lewis 1986) following the removal of its aboveground biomass. Although soil condition affects the trees ability to coppice and therefore its tolerance to elephant feeding (Lewis 1991), elephant generally encourage a multi-stemmed scrub morph (Styles & Skinner 2000). Fire also changes the structure of woodland communities (Stuart-Hill 1992a). By killing the canopies of some woody plants fire causes them to coppice from their stem bases which leads to an increase in the number of woody plant stems per unit area (Pieterse & Boucher 1997; Walters 2000). Less is known, however, about the response of *C. mopane* trees to drought, following the dieback of aboveground biomass.

Colophospermum mopane exists as a single- and multi-stemmed tree in VLNR, with some individual trees comprising up to 16 stems (Chapter 5). The objective of this study was to determine the age of each stem of multi-stemmed trees using dendrochronological analysis and examine whether stem recruitment of *C. mopane* follows serious drought episodes or some other disturbance event during which there is extensive dieback of the existing canopy.

Methods

Data collection

Stem circumference at ± 20 cm above the ground was recorded for each stem of forty multi-stemmed trees on apparently similar topography (slope $< 3.07\%$) and soils (alluvial and colluvial deposits). Whole disc samples were taken approximately 20 cm from the base of the main stem using a bowsaw. The number of stems belonging to each tree was confirmed by exposing its root system by excavation. Stem discs were polished on a belt sander with four grades of progressively finer grit sizes (up to 1 200 grain size) to a high standard of clarity. Two radii were examined under a dissecting microscope with halogen bulb illumination at 15X magnification.

Data analysis

The stem size distributions of all trees were analyzed for approximate cohorts of stem recruitment (similar-sized stems). Some stems were joined at the base, but measured separately. Considering this particular growth form is likely to be the consequence of the original stem forking, the period since its recruitment would be underestimated from the diameters of the two separate stems. Consequently trees ($n = 3$) with the aforementioned growth form were excluded from the analysis of stem size distributions.

Three additional 'multi-stemmed' trees were excluded from the analysis of stem size distributions because the stems had been separated from one another on account of the fire in 1948, forming isolated individuals capable of sustaining themselves. Evidence which indicated that stems were once part of a larger individual included the relative placement of burnt appendages and the greater diameter of an individual stem's taproot relative to its own stem diameter and the roots of adjacent stems.

Expected stem diameters were calculated for a period of 50 years (1948 to 1998) using the estimated annual radial increments of *C. mopane* in drought prone areas from O'Connor (1999) and Prior and Cutler (1996).

Results

It was impossible to determine the age of *C. mopane* using dendrochronological analysis. Growth rings were difficult to discern and many stems were hollow and/or had a dark heartwood. A tiny creature (Family: Buprestidae) was observed in two of the stem sections sampled for dendrochronological analysis and was suspected to be responsible for the hollowing of the heartwood of *C. mopane* stems on which it feeds.

Although there was a large range in stem diameters and the number of stems per multi-stemmed tree, variation (SE) about the mean was relatively small (Table 6.1). The maximum distance between two stems of the same tree was 1 m. No single cohort of similar-sized stems existed (Figure 6.1). However, stem diameter followed a normal distribution (Figure 6.2). Fifty percent of all stem diameters ranged between 5.4 cm and 8.6 cm, suggesting they were recruited at approximately the same time following a specific event. Fire scars attributed to the last recorded fire in 1948 may account for the trees' multi-stemmed growth form and indicate that most of the individual trees of VLNR were greater than 50 years of age. Published figures of stem increment (mm an^{-1}) indicate that *C. mopane* stems can grow up to 8.5 - 10.5 cm in diameter, and 6.7 cm in diameter during below-average rainfall years, over a 50 year period, corresponding to the most abundant stem diameter classes (Figure 6.2).

Table 6.1 A summary of the stem diameters (*n* = 148) and the number of stems per multi-stemmed *Colophospermum mopane* tree (*n* = 34)

	Mean (SE)	Median	Mode	Minimum	Maximum
Stem diameter (cm)	7.2 ± 0.24	6.8	6.4	1.3	17.2
Number of stems per tree	4.4 ± 0.43	4.0	5.0	2.0	13.0

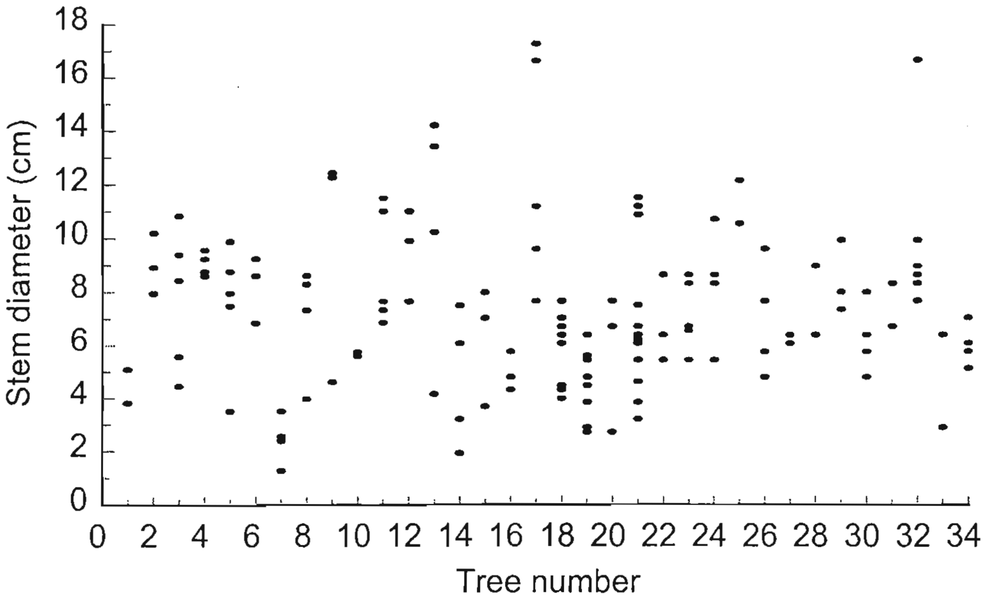


Figure 6.1 Stem diameter (cm) of each stem for each multi-stemmed *Colophospermum mopane* tree ($n = 34$).

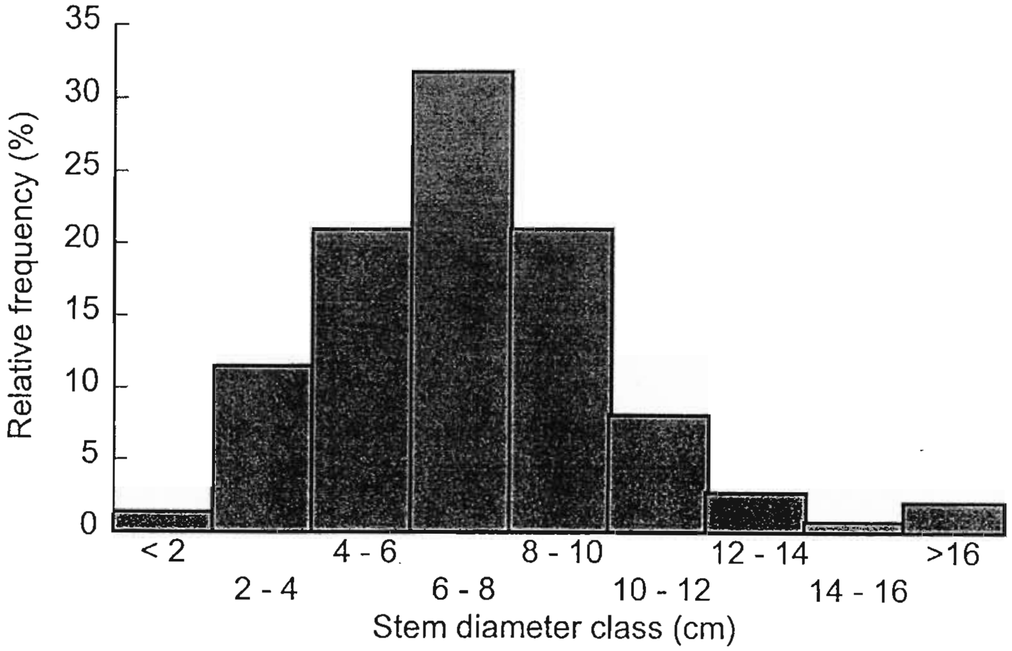


Figure 6.2 The relative frequency (25% = 5.4 cm, 75% = 8.6 cm) distribution of stem diameter classes (2 - 4 = 2 - < 4, 4 - 6 = 4 - < 6, etc.) for *Colophospermum mopane*.

Fire scars were observed below the soil surface in the 'bowl' of each multi-stemmed tree and often extended into the roots, suggesting the last recorded fire in 1948 was severe. Apart from a high tolerance to fire, the extent of the fire scars suggests severe topkill.

The normal distribution of stem diameters suggests either a period of recruitment in proportion to the longevity of a disturbance or more likely different growth rates of stems owing to variable micro-site conditions and stem densities per tree, following a single disturbance event. The frequency of stems with diameters > 16 cm (Figure 6.2) suggests topkill following the fire was not 100%. Although additional regrowth following the last recorded fire might have been attributed to dieback after drought episodes considering trees had not been browsed by elephant or burned since 1948, drought episodes as recent as 1988/89 and 1991/92 did not induce the simultaneous recruitment of regrowth (Figure 6.1).

A single-stemmed tree (diameter: 14.3 cm) had no fire scars, whilst two adjacent multi-stemmed trees did have fire scars, suggesting the single-stemmed tree recruited after the fire. Consequently, stems with a diameter < 14.3 cm may have been recruited after the severe fire of 1948. The diameters of those stems that were once joined ranged from 6.1 cm to 12.4 cm and each had fire scars.

Discussion

Although growth rates can be measured from the ring widths of *C. mopane*, (Mushove *et al.* 1995; Prior & Cutler 1996) the poor correlation between ring width and rainfall, and tendency for stems to be hollow, make it impossible to accurately age this species. Nevertheless, published figures of radial increment (Prior & Cutler 1996; O'Connor 1999) for *C. mopane* suggest that the majority of stems were recruited circa 1948, that is following the last recorded fire, corresponding to the findings of Walters (2000), viz. that fire increases stem density of *C. mopane*.

It appears from this study that the clarity of growth rings and therefore ability to determine mean radial increments varies between sites. The lack of a relationship between ring width and rainfall, and the ability to delineate clearly defined growth zones may be attributed to insufficient extremes in rainfall variation considering Scholes (1990) observed a significant increase in the annual stem increment of *C. mopane* only when rainfall increased by twofold. The effect of insufficient extremes in rainfall on tree growth may be more pertinent to hardwood species because they allocate more biomass to their stems than growth, compared with lighter woods (Enquist *et al.* 1999). Consequently hard woods such as *C. mopane* may be less responsive to rainfall variation than lighter woods.

Colophospermum mopane trees may be older than they appear, capable of persisting > 50 years by coppicing from the base of stems, thereby ensuring the longevity of an individual. Although *C. mopane* produces seed, no dormancy appears to exist in mopane seeds (Smit & Rethman 1998b) which seldom remain viable for more than one year (Jordaan & Wessels 1999). Although only three of 40 multi-stemmed trees split up to form independent individual stems as a consequence of fire in this study, coppicing from the base of stems may be an additional means whereby the species ensures its survival. *Colophospermum mopane* readily sprouts from belowground stock on abandoned roads in Mopani Veld (personal observation). Consequently, the longer longevity of viable belowground stock may serve to compensate for the absence of seed dormancy, thereby ensuring the persistence of the species in areas abandoned for more than one year.

Unlike fire, drought does not appear to induce the simultaneous coppicing of *C. mopane* trees. This may be due to the physiological response of trees to drought compared with the removal of a tree canopy by agents which induce coppicing of stems, such as elephant (Mapaure & Mhlanga 1998) or fire (Walters 2000). Drought results in the dieback of plant roots (Stasovski & Peterson 1993) on account of insufficient soil water which decreases the amount of water and nutrients transported upwards. Consequently, canopy dieback occurs because the existing root system is insufficient to support the aboveground biomass of the tree. Available resources to replace a canopy that was lost is therefore limited to a root system that is a fraction of what it was prior to the drought. In contrast, no restrictions are imposed on the resources available to replace a canopy following its removal by either elephant or fire, because the entire root system is still alive, although dieback of the root system is expected in the longer term on account of a reduced photosynthetic capacity. Drought is therefore a more severe agent of dieback than either fire or elephant, owing to a reduced root system and apparent inability to coppice and tolerate loss of aboveground biomass.

PART B: *Acacia tortilis*

Chapter 7

Acacia tortilis: life-history stages reviewed

Flowering

The timing and period of *A. tortilis* flowering is related to rainfall (Haro & Oba 1993; Tybirk 1993) and occurs from November to January (Coates Palgrave 1983), peaking in the mid-wet season (Du Toit 1990). Pod production follows in March until June (Coates Palgrave 1983).

Flowering is restricted to mature and over-mature trees (Pellew & Southgate 1984; Haro & Oba 1993), thereby limiting seed production to trees taller than 1 m (Miller 1994a). Large (> 10 m diameter) canopies produce significantly more (64 times more) seed than small (4 - 6 m diameter) canopies in Kenya (200 mm an^{-1}) (Haro & Oba 1993). There is significant variation in total pod production per tree and pod seed number between individual trees within local populations of the same species (Tybirk 1993). The mean seed production for *A. tortilis* trees (dbh: 6 - 20 cm, height: 3.4 - 8.0 m) in Senegal (400 - 600 mm an^{-1}) was 14 372 an^{-1} (Tybirk 1993), considerably less than larger *A. tortilis* trees (150 000 seeds an^{-1}) in Botswana (Tolsma 1989).

Acacia tortilis is largely self incompatible, depending almost exclusively on outcrossing (Tybirk 1993) rather than selfing. Pod set therefore depends on how efficient pollen transfer is. *Acacia* pollination is attributed mainly to insects, specifically wasps and bees, whilst butterflies, flies and beetles are secondary pollen vectors, although they may dominate locally. *Acacia tortilis* does not contain floral nectar, yet the diversity and frequency of insects visiting it does not differ from species with floral nectar (Tybirk 1993). Despite conspicuous aggregates of insects on the flowers of some species most African *Acacia* species have a remarkably low pod : flower ratio (Ross 1979), only 5.5 % of *A. tortilis* inflorescences (0.13 % of the flowers) develop fruit in Senegal (Tybirk 1993).

Browsers for which flowers constitute an important food resource during the dry winter months have also been speculated as potential pollen vectors. The predominant browser of flowers on *Acacia* trees appears to be giraffe and to a lesser extent kudu which feed on lowhanging branches, whilst smaller ungulates such as impala are unable to reach flowers on mature trees (Du Toit 1990). Giraffe feeding on *A. nigrescens* in the Kruger National Park (590 mm an^{-1}) was attributed to characteristics pertaining to the inflorescence; palatable, undefended, pale coloration, spicate structure and born in clusters on terminal shoots, suggesting that one group of African *Acacias* could be pollinated by ungulates (Du Toit 1990). Giraffe feeding on *A. tortilis* was comparatively low, belonging to the second *Acacia* group adapted for pollination by insects; bearing thorn-protected capitate inflorescences, many of which are a bright golden or orange-yellow colour with short peduncles clustered close to the stem (Du Toit 1990).

Dispersal

Several facts confirm the co-evolution of indehiscent African *Acacias* (e.g. *A. tortilis*) with ungulates, resulting in ungulate-adapted systems of seed dispersal (Coe & Coe 1987) compared with wind-dispersed species: pods contain more seeds (Tybirk 1993) with harder seed coats (Coe & Coe 1987) than wind dispersed species and do not split open on the tree, seeds remaining 'locked up' in nutritious and occasionally scented packages beneath the parent tree at a time when other food sources are rare. Pods are browsed on the tree (giraffe) and on the ground (kudu and impala) (Ben-Shahar 1991; Miller 1994a) potentially lowering soil seed banks under high grazing pressures (Tybirk *et al.* 1992). Other factors influencing the seed bank of African *Acacias*, apart from predation and dispersal, include annual seed production, germination, and the affect of fire on breaking seed dormancy (Tybirk *et al.* 1992). Soil seed banks vary significantly between and within species. Mean values reported for *A. tortilis* trees (0 - 81 seeds m^2) are low relative to *A. hockii* in Kenya (mean = 2 439 seeds m^2) (Tybirk *et al.* 1992).

The main negative effect of ungulate dispersal is the destruction of seeds during passage through the buccal cavity and alimentary canal. The proportion of *A. tortilis* seeds destroyed differs between species (Table 2.1). Despite substantial losses to mastication and digestion large numbers of seeds are dispersed per hectare per pod season (May to August): 1 636 ± 404, 2 952 ± 644 and 18 900 ± 5160 for kudu, giraffe and impala, respectively (Miller 1996). Browsing ungulates, specifically impala (Miller 1996), are the most important *A. tortilis* pod consumers, others being bruchid infestation, rodents and termites (Miller 1994a), however, any one of the aforementioned consumers may become locally dominant.

Table 7.1 Proportion of *Acacia tortilis* seeds destroyed following ingestion by different browse species

Proportion of seeds destroyed (%)	Browser	Source
100	duiker	Miller (1995)
19 - 95	goat	Tybirk et al. (1992)
72 - 90	goat	Miller (1995)
46	sheep	Tanner (1988)
92.3	impala	Miller (1995)
92.1	kudu	Miller (1995)
90	giraffe	Miller (1995)
59.7	elephant	Miller (1995)

In the absence of ungulate dispersal agents pods fall directly to the ground with fewer seeds potentially germinating than ingested seeds on account of losses incurred through bruchid infestation and rodent consumption (Miller 1994b). Approximately 3% of 1000 seeds germinated in the presence of ungulate dispersers (giraffe, kudu and impala) whilst only 0.3% germinated in their absence, in the Northern Province, South Africa (620 mm an^{-1}) (Miller 1994b). However, germination and seedling survival were calculated in a laboratory, and therefore represent optimal instead of natural conditions and only the fate of mature pods were recorded. The mean (±SD) daily population densities (no. ha^{-1}) of large herbivores within the study site were: giraffe 1.01 ± 2.31; kudu 0.39 ± 1.53; and impala 1.18 ± 2.60 (Miller 1994b). Benefits related to ungulate seed dispersal include: reduced bruchid infestation (Miller 1994b,c,1995); release of seed from their pods, which can remain dormant for as long as 2 - 5 years (Miller 1994a); scarification of the seed coat by digestive fluids (Miller 1995); dispersion of seeds into open rather than shaded sites (Miller 1996); and deposition of seeds in dung (Miller 1996).

The effective dispersal mechanism of *A. tortilis* coupled with its regular dispersion pattern (Ben-Shahar 1991) from core zones on mostly catchment areas (e.g. Ruess & Halter 1990; Ben-Shahar 1991) induces an early colonization and dominance of this species that conforms with the dispersion strategy of a pioneer species.

Germination

Acacia seed coats are water impermeable and require pretreatment to obtain maximum germination (Doran *et al.* 1983; Choinski & Tuohy 1991).Germination rates are positively correlated with scarification caused by passage through herbivore digestive tracts (Choinski & Tuohy 1991). Ingested and defecated seeds exhibit a greater potential germination than uneaten seeds (Table 2.2).

Table 7.2 Potential germination of ingested and defecated seeds compared with uneaten seeds

Germination potential (%)		Source
Eaten seeds	Uneaten seeds	
7	0.0	Lamprey (1963)
13	1.0	Halevy (1974)
11 - 28	1.3	Lamprey *et al.* (1974)
54	20.0	Ahmed (1986)
3	0.3	Miller (1994b)

Germination is controlled by the water potential and temperature of the imbibition medium, e.g. soil or dung, although optimum temperatures (25 - 30 °C) pertain only to water potentials more negative than - 0.14 MPa (Choinski & Tuohy 1991). Critical water potentials are between -0.51 MPa (Choinski & Tuohy 1991) and - 0.6 MPa (Coughenour & Delting 1986), no germination occurring at values more negative. Dung facilitates germination (Mwalyosi 1990) by retaining moisture (Miller 1996) at potentials sufficient for germination thereby reducing dehydration of imbibed seeds or seedlings (Coughenour & Delting 1986). However, *A. tortilis* seeds germinate successfully once given a brief (15-24 hrs) exposure to distilled water despite the onset of stressed (- 0.51 Mpa) conditions (Choinski & Tuohy 1991). This period of pre-imbibition might occur when the seed is circulated through the digestive tract of a herbivore (Ahmed 1986; Coughenour & Delting 1986), which may take several days (Miller 1995). Elevated nutrient (N and P) levels in dung are likely to be important during the early stages of growth rather than germination (Coughenour & Delting 1986), enhancing the survival and growth of first year seedlings to the extent that stands thin more rapidly due to overcrowding, relative to non-dung sites (Reid & Ellis 1995).

Germination during the first rainy season after seeds have passed through the digestive system intact (Reid & Ellis 1995) and successful germination without an extended germination lag, despite stressed conditions following a period of sufficient imbibition, may be an adaptive mechanism that conforms with the dispersion strategy of pioneer species (Choinski & Tuohy 1991). Seedling establishment is a rare event under conditions of high browsing pressure, bush encroachment usually coinciding with a decline in elephant (Leuthold 1996) or small ungulate (impala) populations (Prins & Van Der Jeugd 1993). Successful seedling establishment is further hampered by the species intolerance of shade (Pellew 1983b; Miller 1996) and dependence on extreme or rare recruitment events associated with the variable rainfall of semi-arid systems (Wiegand *et al.* 1995).

Growth and critical heights

Although generally slow growing (Coates Palgrave 1983), *A. tortilis* can reach ecological maturity (10 m canopy) in 15 to 35 years depending on local conditions, accruing an age of up to 100 years (Croze 1974b). Growth rates are, however, variable (height increment: 0.1 m an^{-1} Herlocker 1976 to 0.6 m an^{-1} ± 0.2 Mwalyosi 1990) between and within populations (Mwalyosi 1990; Grice *et al.* 1994), attributed mostly to variations in available soil moisture (Prior & Cutler 1996) and growth-retarding agents such as browsers (Pellew 1983a). Browsing, particularly by giraffe (Pellew 1983a), retards vertical and lateral development of *A. tortilis* shrubs (Dangerfield *et al.* 1996), increasing time to reach reproductive maturity (Bryant *et al.* 1983). It can take an *A. tortilis* seedling (< 1 m) up to 21 years and 36 years to exceed the maximum height of fire mortality (3 m) and browse reach of an adult bull giraffe (5.75 m) respectively, approximately 2.8 times longer than when not browsed by giraffe (Pellew 1983a). Browsing is therefore simulated as a time delay when modeling its effect on the population dynamics of *A. tortilis* (Pellew 1983a).

Characterization of the size and age class distributions of woody species is useful for the interpretation of population dynamics and alerting managers to declining recruitment and potential species compositional changes. However, previous studies have made the mistake of referring to size classes as age structures (e.g. Croze 1974b; Mwalyosi 1990; Lewis 1991) when dealing with semi-arid systems. Age and size can not be substituted for one another when referring to semi-arid systems. Age class data are less reliable in semi-arid systems because: (1) tropical trees are difficult to age, *A. tortilis* trees do produce growth rings, but rings are difficult to count (Lilly 1977; Prior & Cutler 1996) and are unreliable indicators of tree age beyond ten years (Wyant & Reid 1992); and (2) age is poorly correlated with stem diameter (Prior & Cutler 1996) most likely on account of variable growth rates associated with the spatial and temporal heterogeneity or disequilibrium nature of arid and semi-arid systems (Wiegand *et al.* 1995). Size would give a false estimate of age in instances where trees or seedlings are held at a similar size for an extended period, prevented from growing into larger size classes by suppressing factors such as browsing or fire (Pellew 1983a, Phillips *et al.* 1996).

The height of a tree is a more important determinant of function than age (inferred by stem diameter): reproduction of *C. mopane* trees in the Luangwa valley appear to be dependent on height (trees begin fruiting at 5 m; Caughley 1976), whilst height classes critical to the survival of *A. tortilis* in a system influenced by fire and large browsers (giraffe) are 3 m (Norton-Griffiths 1979) and 6 m (Pellew 1983a), respectively.

Browse value

Acacia tortilis is a hardy, drought-tolerant species (Coates Palgrave 1983) associated with encroachment (Dangerfield *et al.* 1996), and provides shade, fodder, fencing, housing (Coughenour *et al.* 1985) and fuelwood (Hayashi 1992). Valued mostly for their nutritious (26 % CP - Coppock & Reed 1992) pods, *A. tortilis* is used to supplement livestock diets (Coe & Coe 1987; Reid & Ellis 1995) and browse for wild herbivores (Pellew 1983b; Mwalyosi 1990) during the dry winter months when the quality of herbaceous forage drops dramatically (Williamson 1975). Defoliation of *A. tortilis* decreases N and P concentrations in the leaves, whilst simultaneously increasing the total phenol and condensed tannin concentrations the following year (Bryant *et al.* 1991). Highest phenolic concentrations occur at the onset of the growing season, thereafter decreasing with leaf senescence into the dry season, together with nutrients N, P and K (Ernst *et al.* 1991). Phenols may not be as much of a deterrent to ungulates as previously perceived (Cooper & Owen-Smith 1985), considering their preference for *C. mopane* leaves and *A. tortilis* pods (Cloudsley-Thompson 1990) despite their high phenolic concentrations (Lamprey *et al.* 1974). Elephants also feed on plant species and plant parts with a high tannin content (Williamson 1975).

Chapter 8

Determination of annual diameter and height increments for trees in a semi-arid African savanna

Introduction

Knowledge of age and growth rates of trees is necessary for an ecological understanding (Gourlay & Kanowski 1991) and modelling (Mushove *et al.* 1995) of woodland dynamics. Growth rings have been identified in tropical trees (Mushove *et al.* 1995; Prior & Cutler 1996) using anatomical features such as fine marginal parenchyma bands, a form of axial parenchyma (Gourlay & Grime 1994, but the majority of successful attempts at ageing acacia trees and relating rainfall to ring width have used material of known age (e.g. Gourlay & Kanowski 1991; Gourlay 1995). False, discontinuous and missing rings (Lilly 1977; Wyant & Reid 1992) hamper the distinction of growth rings and possible discrepancies between rainfall and plant-available soil water obscure relationships between rainfall and ring width (Mushove *et al.* 1995; Prior & Cutler 1996). Consequently, the dendrochronological study of tropical trees is not always successful. Although stem diameter has been used in predicting growth for tropical trees (Osmaston 1956; Kigomo 1994) it requires an extended time series. Growth rates of woody species within VLNR can be slow (O'Connor 1999) and the variability in diameter measurements obtained by repeated visits from different investigators would obscure growth measurements. Exploratory work by Gourlay (1995) has indicated the possibility of age determination for African acacias on the basis of fine marginal parenchyma bands and crystalliferous chains. The first objective of this investigation was to test the approach adopted by Gourlay (1995) using *A. tortilis* trees of unknown age and identifying annual ring boundaries in *A. tortilis* by relating ring width to annual rainfall. The second objective was to suggest a technique for predicting growth rates of woody plants from annual rainfall, using selected data. Previous studies have neglected to incorporate the influence of the phloem (or bark) on growth rates (e.g. Gourlay 1995), thereby producing figures of diameter increment that underestimate the true growth rates. The proposed technique was to therefore include the influence of bark on growth rates of *A. tortilis*, and express growth rate as an annual diameter and height increment.

Methods

Data collection

Thirty *A. tortilis* trees of unknown age were sampled from five 50 m transects situated in the *A. tortilis* woodlands in VLNR. Only trees killed by elephants within the last year were sampled. Although the samples were not in an advanced state of decay they were extracted from dead stems and stood the risk of being contaminated with the larvae of wood borers. One stem section was discarded on account of damage by wood boring beetles during storage, reducing the sample size to 29. Whole disc samples were taken approximately 20 cm from the base of the main stem using a bowsaw. The circumference (cm) of each sample was measured with and without the bark. Sample discs were polished on a belt sander with four grades of progressively finer grit sizes (up to 1 200 grain size) to a high standard of clarity. Two radii were examined under a dissecting microscope with halogen bulb illumination at 15X magnification. Narrow marginal parenchyma bands, identified by their fineness and evenness of appearance, were marked and counted. Ring widths were measured using a micrometer fitted to the microscope. Stem circumference and tree height measurements (to the nearest 1 and 10 cm, respectively) were taken from a second sample of *A. tortilis* trees located on 16 transects within riverine vegetation and four transects situated in the *A. tortilis* woodlands. The nearest rainfall records considered to represent accurately the pattern and annual variation in rainfall experienced at the site were taken from Pontdrif.

Data analysis

Annual diameter increment

Identification of marginal parenchyma bands allowed comparison with annual rainfall records, using Pearson's product-moment correlation coefficient. Annual deviations from the long-term mean rainfall (366 mm) at Pontdrif were compared with annual deviations from the mean ring width.

Linear regression was used to derive a relationship between stem diameter and the number of growth rings in order to estimate annual growth rates. The potential for two statistically different populations within the sample of stems warranted the inclusion of a dummy variable in a multiple regression of stem diameter and the number of growth rings.

Proposed technique for predicting annual diameter increment

Although entire ring width sequences were not correlated with the annual rainfall record from Pontdrif, parts of the sequence were in phase. Those parts of the ring width sequence that were correlated with annual rainfall for a period longer than 10 years on each stem, with not more than one year out of phase, were used to construct a composite sequence of ring widths that correlated with rainfall for the sole intention of demonstrating the technique. Three stem sections out of the original 29 met the aforementioned criterion and were used to construct the composite sequence of ring widths by placing the three separate sequences in chronological order and averaging ring width when rings overlapped. The criterion (a ring width sequence corresponding to at least 10 years of annual rainfall) for including stem sections into the sample was chosen arbitrarily to ensure that reasonably accurate data were used in explaining the technique for predicting annual diameter increment, using annual rainfall. Correlations between ring width and rainfall were improved by combining two ring widths only if (1) the following ring width sequence was in synchrony with rainfall, and (2) one of the rings were < 0.5 mm wide. Narrow rings that did not coincide with a low rainfall year are more likely to be false than wide rings on account of the climatic influences that produce false rings. Such climatic influences may include a mid growing season drought (Stokes & Smiley 1968) or out-of-season rainfall and are likely to produce narrow rings on account of their short duration.

An exponential relationship between annual ring width (mm) and annual rainfall (mm an^{-1}) was derived using regression analysis. The annual diameter increment (ADI, mm an^{-1}) was then estimated by predicting annual ring width from the long-term mean annual rainfall (31 year record: 366 mm an^{-1}). The ADI was assumed constant irrespective of the size of an individual.

Regression analysis was used to derive a function which explained the relationship between bark width and stem diameter without bark, so that the annual bark increment associated with an increase in stem diameter could be calculated from the ADI. Twice the annual bark increment plus the ADI would then collectively represent the annual growth rate of an *A. tortilis* stem. The sample, however, contained a limited range in stem diameters (10 cm to 24 cm).

Annual height increment

The approach undertaken to express the mean annual growth rate (ADI) as a height increment involved the derivation of an empirical relationship between stem diameter, excluding bark, and stem height. It was necessary to convert the measures of stem diameter from the second sample of *A. tortilis* trees to exclude the presence of bark because the estimated ADI excluded the influence of bark on growth. A linear regression between stem diameter with and without bark was therefore used to estimate the diameters of *A. tortilis* trees excluding bark. The sample size for the regression of stem diameter with and without bark was limited to 21 trees ranging in diameter from 10 cm to 24cm.

A regression of stem diameter (with bark) and tree height was also calculated. The sample of *A. tortilis* included trees measured on 20 transects placed within riparian and *A. tortilis* woodland. A normal plot of height (cm) and diameter with bark (cm) showed an exponential relationship. Nonlinear regression was performed to fit an exponential curve, but the residual plot was not random. A square-root-of-y (height) transformation, indicated by a Box-Cox analysis, improved the adequacy of the model. A second regression analysis of stem diameter (with bark) and tree height was performed using only the *A. tortilis* woodland transects. *A. tortilis* trees growing in riverine vegetation were excluded from the sample because they were expected to have higher growth rates on account of a higher water table adjacent to the rivers, relative to the drier conditions on the grasslands. The annual height increment of *A. tortilis* was calculated from the overall mean ring width.

Results

Annual diameter increment

Mean ring width across 29 stems ranged from 1.4 mm to 3.5 mm (overall mean ± SE: 2.4 ± 0.12 mm), whilst single ring widths ranged from 0.1 mm to 16.9 mm. If rings were formed annually, the mean ring width should approximate the mean annual growth rate. However, successive ring widths from the pith to the bark were poorly correlated with the annual rainfall records for each of the 29 stems (Table 8.1). Furthermore, stems were unable to be cross-dated. Plots of annual rainfall versus ring width for each stem were neither linear nor curvilinear. The poor correlation between ring width and annual rainfall suggests that the approach used to identify growth rings was unreliable, or alternatively, measured rainfall was an inaccurate estimate of water available to trees in this environment.

Table 8.1 Pearson's correlation coefficients (*r*) between annual rainfall (1967 - 1997) and ring width for 29 *Acacia tortilis* stems. Ring widths were matched with the annual rainfall corresponding to the same year

Sample number	*r*	*n*	*P*
1	-0.29	31	>0.1
2	0.12	31	>0.5
3	0.15	31	>0.2
4	0.12	31	>0.5
5	0.25	21	>0.2
6	-0.14	28	>0.2
7	-0.15	25	>0.2
8	0.31	31	>0.05
9	0.11	29	>0.5
10	0.10	31	>0.5
11	0.32	28	>0.05
12	0.16	31	>0.2
13	0.10	31	>0.5
14	0.32	24	>0.1
15	0.35	31	>0.05
16	0.25	26	>0.2
17	-0.02	31	>0.5
18	0.13	31	>0.2
19	0.07	31	>0.5
20	0.09	31	>0.5
21	0.08	31	>0.5
22	-0.19	31	>0.2
23	-0.04	31	>0.5
24	0.00	31	>0.5
25	-0.22	31	>0.2
26	-0.10	27	>0.5
27	-0.18	31	>0.2
28	0.04	31	>0.5
29	0.27	26	>0.2

There was a poor linear relationship between the number of growth rings and stem diameter (Figure 8.1). The overall inconsistency in stem diameters for similar aged trees may be an indication of the sensitivity of *A. tortilis* to differences in site conditions, particularly soil water. A linear regression of stem diameter and the number of rings ($n = 29$) explained only 1% of the variance. However, the residuals of the stems at the top (squares) of the graph (Figure 8.1) were all positive, whilst most (72%) at the bottom (circles) of the graph were negative suggesting that the ages of stems located at the top and bottom of the plot were underestimated and overestimated, respectively. This suggests the existence of two distinct statistical populations owing possibly to different micro-site conditions.

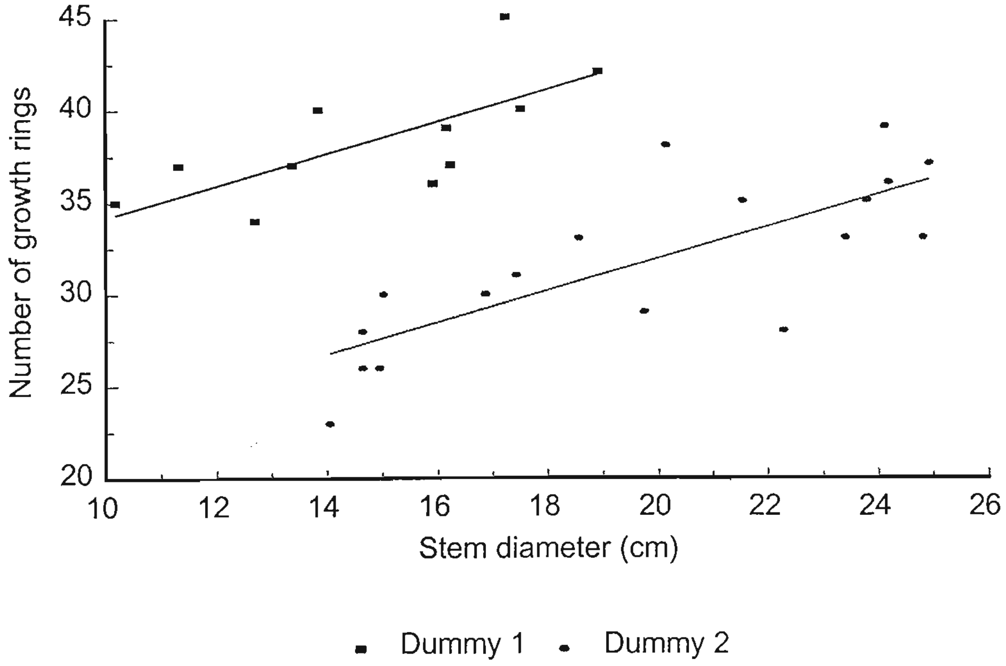


Figure 8.1 Relationship between the number of growth rings and stem diameter (cm) of *Acacia tortilis* including the fitted lines (Dummy 1and Dummy 2) for two potentially different populations represented by squares and circles.

The two statistical populations represented by dummy variables (Figure 8.1) had significantly different intercepts ($t = -8.16$, $df = 26$, $P < 0.001$), but not slopes ($t = -0.17$, $df = 25$, $P = 0.869$), suggesting a similar growth rate. The regression including the dummy variables was significant ($F = 37.89$, $df = 28$, $P < 0.001$, $R^2 = 72.5$ %). Unfortunately, the two distinct populations were not identified in the field, highlighting the need for additional information regarding site characteristics when sampling trees. The annual diameter increment (ADI = 12 mm) was six times the growth rate estimated by calculating mean ring width (Table 8.2). Missing (or indiscriminate) rings close to the pith of *A. tortilis* trees prevented accurate ring counts and therefore age determination. Consequently mean ring width is the more accurate measure of annual growth rate, assuming rings are formed annually, compared with estimating growth rate from the relation between stem diameter and the number of growth rings.

Table 8.2 Mean annual diameter increments (ADI) of *Acacia tortilis* using three different procedures. *n* is the number of stems

ADI estimate (mm an^{-1})	*n*	procedure
2.4	29	overall mean ring width
12.0	11, 18	regression function of stem diameter and number of rings
2.9	3	regression function of ring width and annual rainfall

Proposed technique for predicting annual diameter increment

Despite the poor correlation between ring width and annual rainfall, a technique for predicting the annual diameter increment of trees was described using a composite sequence of ring widths from three selected stems. Trees could not be dated accurately on account of missing rings at the pith, but the remaining sequence of ring widths were related to rainfall by matching the last ring with the year of the last growing season (1997) before trees were felled by elephant. Three stem sections; 10 cm, 22 cm and 24 cm diameter, had a ring width sequence in phase with annual rainfall for 22, 12 and 14 years, respectively. Collectively, they formed the composite sequence of ring widths which ranged from 1969 to 1994 (Figure 8.2). The composite sequence of ring widths was adequate for using as an example to demonstrate a technique for predicting growth rate using annual rainfall, considering ring width was strongly correlated with annual rainfall ($r = 0.7$, $df = 24$, $P < 0.001$).

The relationship between ring width and annual rainfall was exponential ($R^2 = 69\%$, $F = 29.15$, $df = 25$, $P < 0.001$) (Figure 8.3). An influential point (Figure 8.3) may have caused the fitted line to shift on account of its high leverage (0.92). There is no evidence, however, to suggest that it was an outlier. The rate of ring width increased slowly relative to increasing rainfall until approximately 400 mm an^{-1} whereupon radial growth showed a dramatic increase. Mean annual radial growth (1.4 mm), corresponding to an ADI of 2.9 mm, was estimated by substituting mean rainfall (366 mm an^{-1}) into the regression equation.

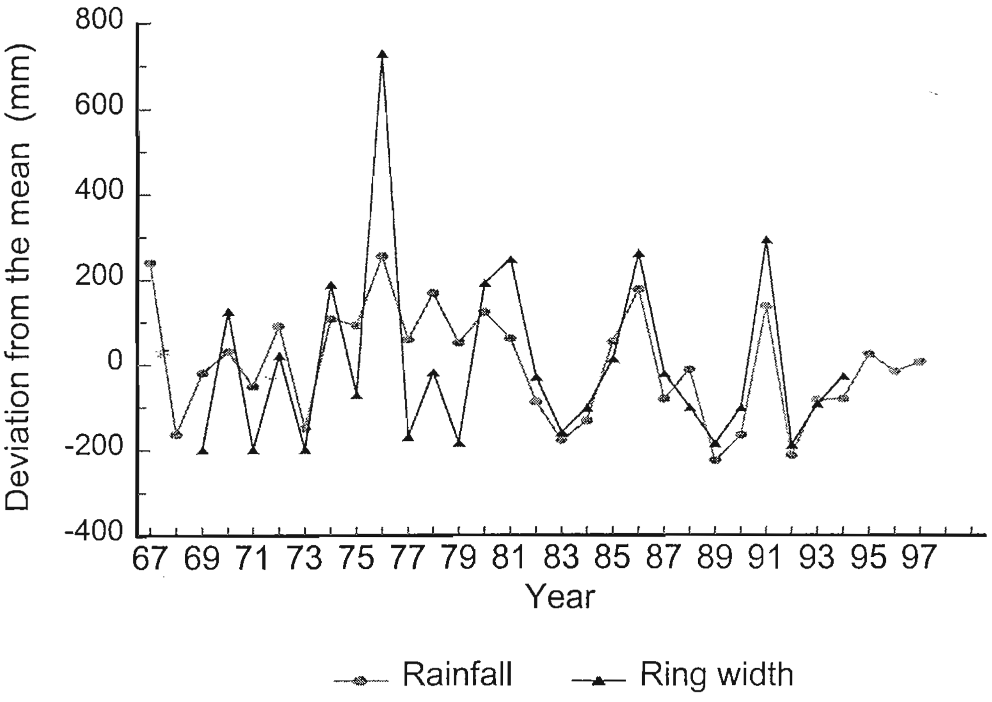


Figure 8.2 Correlation between the annual deviation from the long-term mean rainfall (366 mm an^{-1}) and the annual deviation (x100) of the composite ring width sequence from the mean ring width (2.1 mm) between 1969 and 1994.

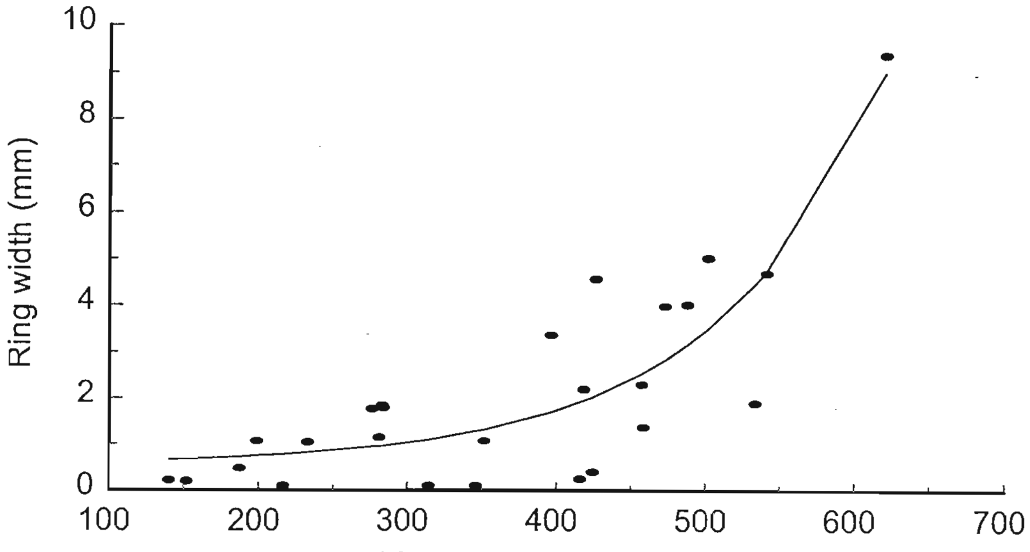


Figure 8.3 Relationship between annual rainfall (mm) for Pontdrif station and mean ring width (mm) of *Acacia tortilis*.

The regression of bark width and stem diameter without bark (Table 8.3) was weakly significant (*F* = 4.77, *df* = 20, *P* = 0.022) and accounted for 27.4% of the variation. The accuracy and hence applicability of the model was restricted to trees with diameters between 10 cm and 24 cm, on account of the limited range of stem diameters sampled. Annual diameter increments < 1 cm could therefore not be used to establish the associated increment in bark width. The relationship between bark width and stem diameter without bark (Figure 8.4) indicated a weak quadratic tendency with small diameters supporting narrower bark widths than moderate and large diameters.

Table 8.3 Summary of the regression functions

Variables	Equation	Parameter	estimate	SE	*P*
y = number of growth rings	$y = D + bx$	b	0.85	0.146	< 0.001
x = stem diameter (cm)		D0	25.6	2.31	< 0.001
		D1	14.7	2.94	< 0.001
y = bark width (cm)	$y = a + bx + rx^2$	a	-1.8	1.53	0.25
x = diameter without bark (cm)		b	0.45	0.195	0.03
		r	-0.012	0.0059	0.06
y = ring width (mm)	$y = a + br^x$	a	1.0089	0.00223	
x = annual rainfall (mm)		b	0.034	0.0459	
		r	0.55	0.515	
y = stem diameter with bark (cm)	$y = a + bx$	a	1.2	0.38	0.005
x = stem diameter without bark (cm)		b	1.0598	0.02298	< 0.001
y = square root of stem height (cm)	$\text{sqrt } y = a + br^x$	a	30.9	1.09	
x = stem diameter with bark (cm)		b	-26.4	1.1	
		r	0.9296	0.00739	
y = tree height (cm)	$y = a + bx$	a	16.4	46.5	0.7
x = stem diameter with bark (cm)		b	21.2	2.24	< 0.001

Bark width reached a maximum corresponding to stem diameters between 18 cm and 21 cm before tailing off to a relatively constant bark width between 2 cm and 2.5 cm for larger trees. Once a tree matures, the bark begins to split and slough off thereby maintaining a relatively constant width irrespective of stem diameter or tree age. Increase in radial growth beyond a particular stem diameter (± 20 cm) is therefore unlikely to be accompanied by further increases in bark width, e.g. annual radial growth rate would approximate the true annual growth rate.

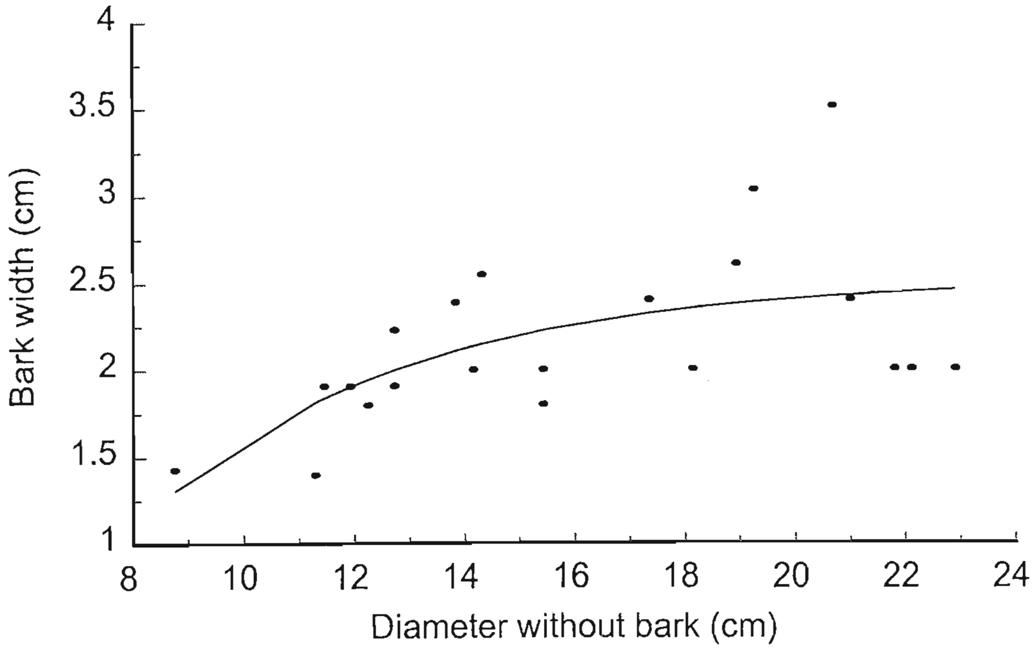


Figure 8.4 Relationship between bark width (cm) and stem diameter without bark (cm) of *Acacia tortilis.*

Annual height increment

The linear relationship (Figure 8.5) between stem diameter with bark and stem diameter without bark was significant (*F* = 2127.97, *df* = 20, $P < 0.001$, $R^2 = 99\%$) (Table 8.3). Stem diameter without bark was significantly related to tree height (*F* = 16.25, *df* = 100, $P < 0.001$), but only accounted for 13.2% of the variance and the gradient of the fitted line, expressing the relationship between diameter without bark and stem height, applied only to a limited range in tree sizes (9 cm - 24 cm). The estimated annual height increment would be inaccurate for more than three quarters of the population of *A. tortilis* trees, applying only to trees with stem diameters between 9 cm and 24 cm, and was therefore considered insufficient. Future samples should therefore include the full range of stem diameters within a community. The regression of tree height and stem diameter with bark was significant (*F* = 276.39, *df* = 202, $P < 0.001$, $R^2 = 73.2\%$). However, the square-root-of-height transformation reduced potential correlation between the residuals and fitted values, and improved the model (Table 8.3) ($F = 454.78$, $df = 202$, $P < 0.001$, $R^2 = 81.8\%$). Tree height increased linearly with stem diameter until stem diameter was approximately 25 cm, thereafter the rate of increase in tree height declined until about 45 cm stem diameter, when maximum height was attained (Figure 8.6). A conspicuous gradual change with accruing maturity is the decline in growth rate, particularly height increment.

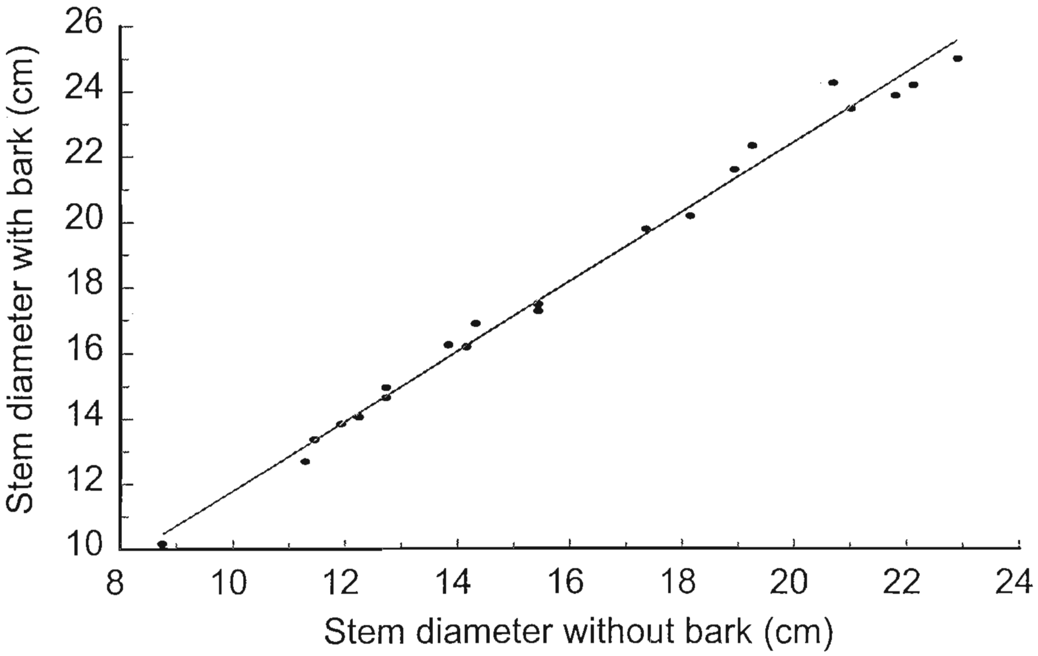


Figure 8.5 Relationship between stem diameter with bark (cm) and stem diameter without bark (cm) for *Acacia tortilis*.

The second regression ($F = 89.22$, $df = 33$, $P < 0.001$, $R^2 = 72.8\%$) of tree height and stem diameter with bark excluded the riverine population of *A. tortilis* trees (Figure 8.7). It was the preferred model because *A. tortilis* trees growing within riverine areas are likely to have different growth rates compared with trees growing in the *A. tortilis* woodlands.

The gradient of the linear plot (Table 8.3) showed a 21.2 cm increase in tree height for every 1 cm increase in stem diameter. The mean annual height increment for *A. tortilis* was therefore 10 cm.

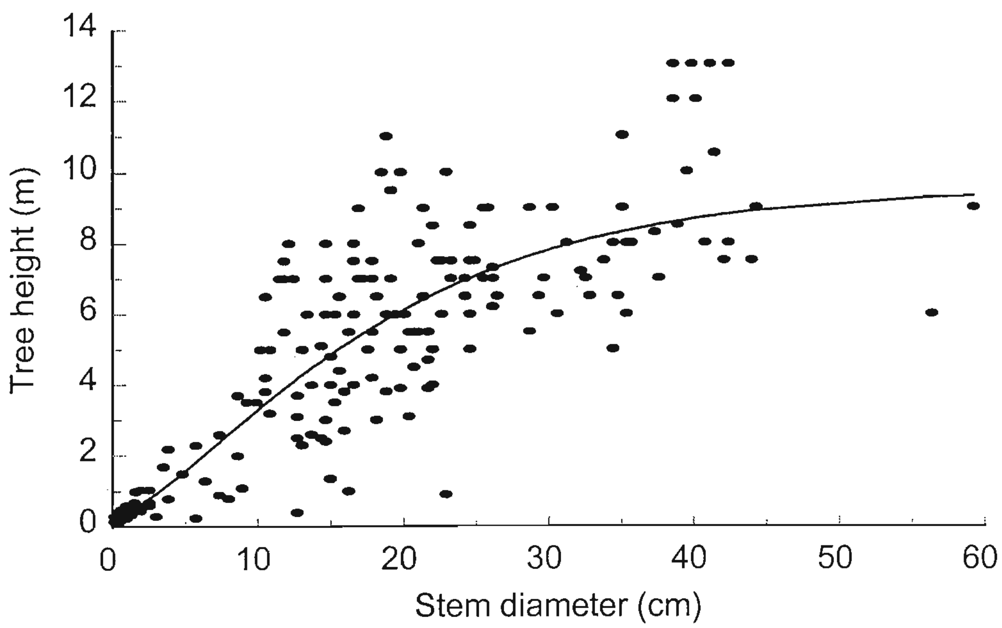


Figure 8.6 Relationship between tree height (m) and stem diameter with bark (cm) for *Acacia tortilis* trees growing in riverine and *Acacia tortilis* woodlands.

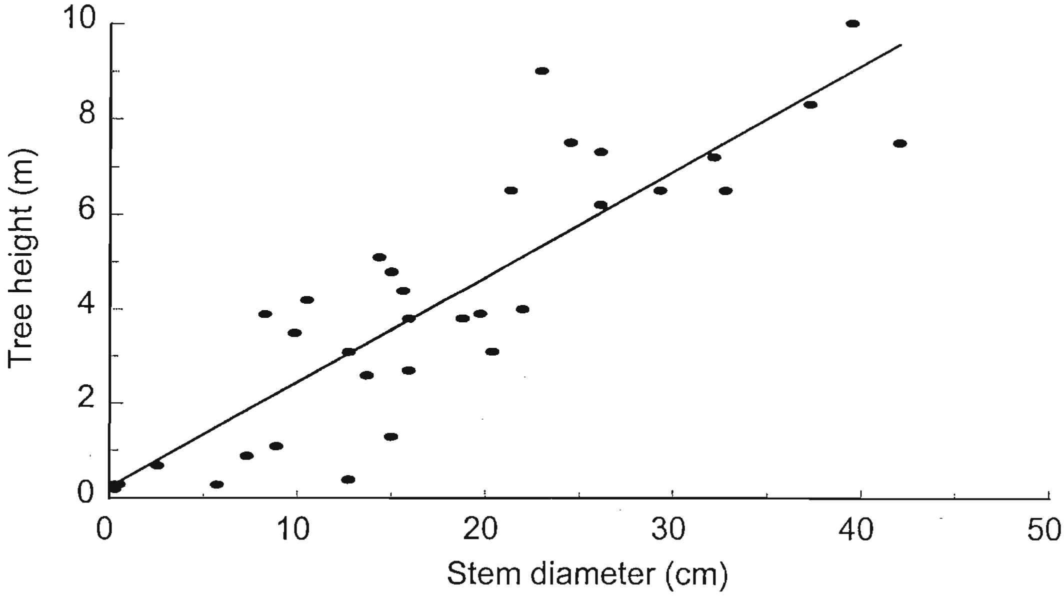


Figure 8.7 Relationship between tree height (m) and stem diameter with bark (cm) for *Acacia tortilis* trees growing in *Acacia tortilis* woodlands.

Discussion

Annual diameter increment

Although the approach adopted by Gourlay (1995) does not indicate that rings are formed annually when using material of unknown age (Prior & Cutler 1996), the method is not entirely unsuccessful considering mean ring width gave an estimate of annual growth rate, assuming rings are formed annually. The predicted mean ADI for *A. tortilis*, given an average rainfall of 366 mm an^{-1} was similar to the overall mean ring width calculated by averaging the mean ring widths from all 29 stems. The aforementioned method of estimating mean growth rate was preferred to the regression of stem diameter with the number of rings because it does not depend on an accurate count of the number of growth rings which was proved impossible in this study, and is not affected by variable stem diameters.

The estimated growth rate (2.4 mm an^{-1}) of *A. tortilis* was similar to growth rates previously recorded in VLNR (O'Connor 1999), but lower than elsewhere on the continent. Although the recorded diameter at breast height for an *A. tortilis* tree in Kenya was more than two fold (7 mm) the estimated diameter increment in this study, the mean annual rainfall was also considerably higher (1 088 mm an^{-1}) (Hayashi 1992). The mean ADI of African *Acacia* spp., including *A. tortilis,* ranges from 12 mm to 14 mm (Gourlay & Barnes 1994; Gourlay 1995). Prins & Van Der Jeugd (1993) calculated the mean rate of diameter increase for *A. tortilis* to be 5 mm an^{-1} (irrespective of tree size) by taking the average of five similar estimates from sources within Tanzania and included work of their own as well as work done by Mwalyosi (1977), Herlocker (1976) and Weyerhaeuser (1982). Overall mean ADIs for *C. mopane* and *Combretum apiculatum* from four sites in Zimbabwe (average rainfall across all sites ± 663 - 730 mm an^{-1}) were 18 and 22 mm, respectively (Mushove *et al.* 1995; Prior & Cutler 1996). The higher growth rates of *C. mopane* and *C. apiculatum*, relative to *A. tortilis* in the Northern Province, South Africa, may be attributed to the two-fold difference in annual rainfall. Enquist *et al.* (1999) found that differences in wood density resulted in substantial differences in growth rates as measured as change in basal diameter. There is a trade-off in the growth rate of stem diameter with the allocation of resources to wood density: species that allocate less biomass to their stems (light woods) increase in basal diameter faster than species that allocate more to stems (dense woods). However, considering *C. mopane* (air-dry 1 250 kg m^3), *C. apiculatum* (air-dry 1 230 kg m^3) and

A. tortilis (air-dry 990 kg m^3) are hard and heavy woods (Venter & Venter 1996), the negligible differences in wood densities are unlikely to explain any differences in growth rates. The mean rate of diameter growth for *Brachylaena huillensis*, from the semi-deciduous dry forests of Kenya (mean annual rainfall; ± 1000 mm), was 3.2 mm an^{-1} (Kigomo 1994). Although density-dependent processes such as competition may reduce growth rates, it appears the estimated rate of growth for *A. tortilis* in the Northern Province, South Africa, may be reasonably high considering the low annual rainfall (366 mm) and the fact that samples were of acacias growing under natural conditions. Tree samples sought from material of known age have been taken from areas for which the management history is known and include areas seeded by man or previously cultivated farmland (e.g. Gourlay & Barnes 1994), and may explain the high growth rates of those samples.

Annual height increment

The estimated height increment (0.1 m an^{-1}) of *A. tortilis* in VLNR was either lower or equal to growth rates from north of the equator. Although the mean annual growth rate of *A. tortilis* in Lake Manyara National Park, Tanzania (n = 37) was 0.597 m, there was a large variation between individual trees (Mwalyosi 1990). Croze (1974b) and Pellew (1983a) used a height growth estimate of 0.3 m an^{-1} for *A. tortilis* trees in Tanzania, whilst Herlocker (1976) estimated the annual height increment for mature *A. tortilis* trees to be 0.1 m. Growth rates are highly variable both between and within the same species, particularly in semi-arid environments (e.g. Grice *et al.* 1994) and may be the consequence of different environments, microhabitats, browsing pressure and edaphic conditions (Pellew 1983a).

Senescence of trees is evident as a decline in height and girth increments (Leopold 1980). Gourlay & Barnes (1994) plotted the cumulative diameter increments of seven *A. karroo* trees against age and showed a curvilinear relationship (exponential). It was apparent that there was a fairly uniform increase in diameter increment in young trees, but growth started to decline when individuals attained 20 years. Metabolism produces the energy and materials used for all biological processes, thereby limiting production or growth (Enquist *et al.* 1999). It is known that relative growth rate decreases with increasing plant size/maturity (Enquist *et al.* 1999) because respiration costs are continually increasing on account of the increased biomass that has to be supported. Consequently, growth rates are likely to depend on the physiognomy of the population sampled.

Proposed technique for predicting annual diameter increment

In order to predict growth rates for different rainfall seasons the technique proposed in this study requires an accurate count of rings and measure of ring widths. The technique is workable given a good correlation between annual rainfall and ring width and may therefore be applied in less arid environments or species that are more responsive to rainfall, e.g. species that allocate fewer resources to stem density.

The advantage of using this technique for calculating mean ADIs is the ability to estimate growth rates for successive years of below- and above-average rainfall. The regression model uses rainfall as the explanatory variable and therefore assumes (1) growth rate is constant irrespective of a tree's life-history stage and (2) rainfall has a greater influence on growth rate than a tree's life-history stage. Most, if not all estimates of radial increments have been calculated by taking the average ring width from pith to bark and are therefore also guilty of assuming a constant growth rate, irrespective of a tree's life-history stage. However, considering a decreased rate of growth is largely associated with accruing maturity and senescence, the assumption of a constant diameter increment remains valid for the most part of a tree's life. The assumption that rainfall was more important than life-history stage when influencing growth rate was justified by the variable and erratic nature of ring width from pith to bark e.g. ring width did not progressively decrease from the pith to the bark of a stem.

Growth rates are provided by a number of authors but they have neglected to include the additional influence bark has on stem diameter. Although attempted in this study, restricted sampling limited the applicability of the technique to a small range of stem diameters. The procedure is simple and may improve the accuracy of predicted diameter increments for trees < 20 cm in diameter if the sample size for formulating a predictive function includes a sufficient range in stem diameters.

Anomalies associated with ring identification

Fine bands of marginal parenchyma were obscured by broad bands of confluent aliform parenchyma, often masking narrow rings and making them difficult to detect. The same problem was experienced by Gourlay & Kanowski (1991) and Gourlay & Barnes (1994). Obscured rings close to the pith of *A. tortilis* for the first few years of growth (Schnabel 1994) were also noted in this study, making it impossible to estimate age accurately. However, considering stem sections were sampled at a height of 20 cm, it is probable that rings representing the first few years of growth would be absent, despite any obscurity at the pith of the stem. Further complications included merging rings, wood-borer beetles and a fungus. Merging rings are not uncommon to acacias (e.g. Gourlay & Kanowski 1991), and may be explained by the unevenness of stem growth under certain climatic and topographic conditions. Wood-borer beetles were present because samples were taken from dead trees.

Potential factors influencing ring width

Although annual ring formation could not be verified in this study previous attempts have shown marginal parenchyma bands to be annual, particularly in ecosystems with a seasonal unimodal rainfall pattern (Wyant & Reid 1992). Growth in the arid tropics is closely related to a short rainy season (Gourlay 1995) with the abrupt transition from wet to dry season producing the necessary dormancy that is likely to result in a detectable anatomical change. The poor correlation between ring width and rainfall and hence failure to verify that growth increments were formed annually can be attributed to several factors: site location, and its influence on plant available soil water through topographic (Coughenour & Ellis 1993) and edaphic (Scholes 1985) effects; rainfall data taken from Pontdrif may not have been an adequate indicator of plant available soil water; problems of imprecise ageing, associated with the aforementioned anomalies of ring identification; and climatic influence may be masked by other growth factors such as browsing, particularly since the arrival of elephant. Although the time of death of the *A. tortilis* trees could be dated to the previous year with reasonable accuracy, trees can take up to three years to die following elephant utilization (Chapter 9). Consequently, ring growth may have been abnormal during the last few years of a tree's life, suggesting that trees which have died from elephant utilization may not be an appropriate source for dendrochronological analysis. The poor correlation between annual rainfall and ring width could also be attributed to insufficient extremes in rainfall variation. Scholes (1990) only observed a significant increase in the annual stem increment of *C. mopane* when annual rainfall increased by two fold to 800 mm, suggesting that small variations in rainfall about the long-term mean do not necessarily produce equivalent deviations about the mean ring width. Mean ring width may respond erratically and unpredictably to small variations in rainfall, but increase significantly in response to large rainfall years.

Future sampling of trees in arid environments for dendrochronological studies need to incorporate the site characteristics of individual trees that reflect plant-available soil water, e.g. stem density, soil texture, soil depth, and runon versus runoff zones. The annual rainfall and population structure should also be noted and accompany estimates of growth rates when they are mentioned in scientific literature. These additional explanatory variables may assist in the interpretation of (1) correlations between rainfall and ring width, and (2) variable sizes (or radial growth rates) of similar aged trees (e.g. the relationship between number of rings and stem diameter).

Chapter 9

The functional response of elephant to *Acacia tortilis* in the Northern Province, South Africa

Introduction

The evolution of the large body size of the African elephant (*Loxodonta africana*) has had two important consequences for its feeding behaviour. Firstly, males eat about 170 kg (fresh weight) per day (Guy 1975), and secondly, their size enables them to uproot entire trees. Elephant have consequently caused spectacular changes in vegetation physiognomy, reverting woodlands to grasslands (Laws 1970). They are an obvious concern when placed in closed ecological systems, particularly when selecting for certain species of woody plants (Ruess & Halter 1990). Considering the response of an individual tree or a population will depend on the manner in which it is fed upon, it is imperative that a quantitative understanding of elephant response to woody species be gained, specifically for woody species that are favoured by elephant. Elephant response refers to either the method of feeding, e.g. removing branches, debarking, stem breakage or uprooting, or the pattern of utilization, e.g. the frequency distribution of tree heights fed upon or the number of trees utilized associated with different tree densities. Whilst woodland response to elephant feeding has been well researched, critical studies of the complexity of the manner in which elephant impact upon a specific species is relatively fragmentary.

Elephant response is determined most often by woodland structure; feeding occurs predominantly on larger size-classes (Pellew 1983a; Mwalyosi 1987; Tchamba 1995) whilst trees less than one metre tall are ignored (Vesey-Fitzgerald 1972; Croze 1974b; Pellew 1983a; Ruess & Halter 1990), although exceptions do occur (Mwalyosi 1990; Kabigumila 1993; Dublin 1995). Previous studies have indicated a preferred feeding level of 1 - 2 m (Guy 1976; Jachman & Bell 1985) and in some instances pollarded trees are repeatedly cropped to maintain them at a preferred browse height (Jachman & Bell 1985; Smallie & O'Connor 2000; Styles & Skinner 2000). Trees > 2 m are more frequently broken and reduced to a feeding level of 1 - 2 m (Jachman & Bell 1985), trees > 4 m are more frequently debarked (Smallie & O'Connor 2000), and trees which exceed the upper limit of an adult bull (6 m) are more frequently uprooted (Croze

1974a), indicating an association between the type of utilization and tree height.

Elephant response is also determined by species composition and tree density. The staple diet of the elephant often corresponds with the dominant woody species (*C. mopane* -,Pienaar *et al.* 1966; Ben-Shahar 1996; Smallie & O'Connor 2000; *Combretum* spp. - Jarman 1971; Thrash *et al.* 1991; *Acacia* spp. - Kalemera 1989; Ruess & Halter 1990). Species are occasionally fed upon at a rate proportional to their occurrence (Ruess & Halter 1990), and deliberately avoided or selected (Croze 1974b; Tchamba 1995; Smallie & O'Connor 2000). *Acacia tortilis* is a favourite woody browse species of elephant (Douglas-Hamilton 1972; Anderson & Walker 1974; Mwalyosi 1987; Kalemera 1989; Ruess & Halter 1990), although not all mature *A. tortilis* trees are able to be pushed over by elephant (Croze 1974a) and therefore utilized. Elephant impact on, or response to, *A. tortilis* includes debarking (Anderson & Walker 1974), breaking off large branches (Kalemera 1989) and uprooting (Croze 1974a). Utilization of *A. tortilis* woodlands and riverine vegetation dominated by *A. tortilis* causes changes in woodland structure (Ruess & Halter 1990) and relative species abundance (Anderson & Walker 1974), respectively. *Acacia tortilis* is generally utilized in direct proportion to its occurrence (Croze 1974b; Ruess & Halter 1990), forming a large proportion of the diet in high density woodlands and less at lower densities where other woody species are available (Kalemera 1989). Barnes (1983) identified four patterns of tree mortality in response to elephant browsing, specifically (1) density-independent mortality (a fixed mortality rate), (2) density-dependent mortality, (3) inverse density-dependent mortality and (4) a fixed number mortality.

The spatial variability of elephant herbivory associated with different densities of sub-populations within a population of a certain species can affect the spatial structure of a population already manipulated by the spatial non-uniformity in patterns and processes of the environment and the plant populations themselves (Noy-Meir 1996). The outcome of spatial herbivory upon a population is of some value, considering spatial heterogeneity generally enhances the stability and resilience of rangeland vegetation to climatic variability in time, principally because drought- or herbivore-refuge sites maintain sufficient genetic resources for the restoration of a decimated population, following a severe drought or overutilization (Noy-Meir 1996).

Forty-eight elephant have been re-introduced into Venetia-Limpopo Nature Reserve (VLNR) since 1991, restricting themselves to the northern portion of the reserve, primarily in close proximity to rivers, thus existing at relatively high local densities (Macfarlane 1998). Their distribution within the reserve has meant that certain habitats have received substantial impact, including the riparian and *A. tortilis* woodlands (De Beer 1998; Macfarlane 1998). Anticipated selection for these two woodland types (TG O'Connor, pers. comm.) and concern over losing floristic and habitat diversity led to the annual assessment of individual plants from 1997 to 2000, offering estimates of important population processes within these two vegetation types. At VLNR a poor grass cover prevents it from being a major component of the elephant's diet. Consequently, a predominantly woody diet persists throughout the year. The *A. tortilis* woodlands were largely ignored during the wet season (Smallie & O'Connor 2000), suggesting they were most probably utilized towards the end of the dry season when *C. mopane* trees, which form the bulk of the elephant's diet (O'Connor & Page 1997; Smallie & O'Connor 2000), lose their leaves. Tree damage was therefore likely to be at its most intense in the late dry season (Barnes 1982).

Considering our perception of ecological systems determines the approaches we advocate in attempting to manage them, it is imperative that we gain a thorough knowledge and understanding of the processes that define them. The general objective of this study was to describe quantitatively the response of *A. tortilis* woodlands to elephant, the functional response of elephant to *A. tortilis* woodlands and compare the aforementioned with elephant response to *A. tortilis* within riverine vegetation and with *Acacia nilotica* woodlands. Before one can consider solving complex environmental problems concerning the population dynamics of woody plants and generate predictions, we need to understand the basics by answering a few fundamental questions. The following key questions were addressed:

(1) What has been the population structure and mortality rate of *A. tortilis* each year since they were first recorded in 1997?
(2) What has been the pattern of mortality and what does it infer about the woodlands' tolerance to elephant browsing?
(3) Has the frequency of each method of utilization differed annually and, if so, was it related to annual rainfall or stem density?
(4) Is there an association between tree height and the method of utilization?
(5) Does each method of utilization reduce tree height?
(6) What was the primary response of individual stems to each method of utilization?

(7) Does each method of utilization induce mortality?

(8) Does canopy browsing influence the probability of stems being broken, debarked or uprooted?

(9) Did the history of past canopy browse damage influence the ability of *A. tortilis* to survive being uprooted or broken?

(10) How did elephant feeding of *A. tortilis* within riverine vegetation compare with the *A. tortilis* woodlands and what are the implications of the spatial variability of plant-herbivore interactions?

(11) Was *A. nilotica* subjected to similar or different feeding methods than *A. tortilis*?

Methods

Data collection

A monitoring programme of elephant utilization of the woody vegetation was implemented in February 1997. After stratification according to vegetation type, transects for each vegetation type were randomly selected ensuring a comprehensive spatial coverage of the reserve. Twenty-one permanent ground-based transects were located within riparian ($n = 16$) and *Acacia* ($n = 5$) woodlands.

Four 50 by 20 m transects and one 50 by 10 m transect located within the *A. tortilis* woodlands and 16 50 by 5 m to 85 by 35 m transects located in riverine vegetation were revisited each year from 1997 to 2000 and 1997 to 1999, respectively. Transects were measured during the mid rainy season (January to March) and reflect change incurred during the previous dry season. The 50 by 10 m transect located within the *A. tortilis* woodlands was not found in 1999, despite use of a Global Positioning System (GPS), on account of a tall grass sward which concealed the rock cairns that demarcate the boundaries of the transects. An additional transect (150 by 15 m) was measured in the approximate region of the 'missing' transect which was relocated the following year when all five *Acacia* woodland transects were revisited.

Transect size was increased for uncommon species until sufficient individuals were accounted for. Elephant impact was measured for each stem of sometimes multi-stemmed trees. Each tree was measured for the following variables:

(1) species identity;

(2) basal diameter (cm) of each live and dead stem, approximately 20 cm above ground level;

(3) height (cm) to the uppermost living entity of the tree (only one height per multi-stemmed tree was measured);

(4) percent volume of canopy removed according to an eight-point scale (Walker 1976) and the agent of utilization. The percent volume of canopy lost was estimated from the original canopy volume for each incident of canopy removal and would confound the different causal agents of loss;

(5) percent circumference and percent height of bark removed from the main stem using an eight-point scale (Appendix 1);

(6) age of canopy utilization and debarking according to an eight-point scale (Appendix 1);

(7) the biological (dead or alive) and physical state of the individual tree, dependent upon the nature of the damage (e.g. uprooted or broken stems);

(8) growth response to stress and utilization. Apart from a reduction in height associated with uprooted or broken stems, *A. tortilis* trees responded to elephant utilization in a number of different ways: (1) unaffected, (2) coppice, (3) reduced vigour, or (4) death. Reduced vigour was a subjective assessment of whether a tree appeared to be dying based on the amount of new growth relative to adjacent, unaffected trees.

An *A. nilotica* woodland (0.5 ha) was sampled in 1999. The total amount of bark and canopy removed by elephant since 1991 was recorded using the same criteria for the *A. tortilis* transects. The volume of canopy removed by browsing was distinguished from dieback following debarking. Canopy dieback associated with debarking was identified by the location of dead (and isolated) branches on the side of the stem that was debarked. The mean percent of stem circumference and stem height that was debarked was calculated by averaging the midpoints of each utilization class. Although utilization was recorded for each stem in the *A. nilotica* woodland, only one height per multi-stemmed tree was measured.

Data analysis

Population structure of *Acacia tortilis*

Size is preferred to age when describing population structure and dynamics because (1) spatial and temporal heterogeneity of growth rates produces cohorts of dissimilar sized trees, and morphological changes occur during growth (Begon & Mortimer 1981) not necessarily ageing (Smit 1990), and (2) survival depends on size (Young & Lindsay 1988) when disturbances, such as fire (Norton-Griffiths 1979) and browsers (Pellew 1983b), are height specific.

The *A. tortilis* population was divided into eight equal height-classes: < 1 m, 1 - 1.9 m, 2 - 2.9 m, 3 - 3.9 m, 4 - 4.9 m, 5 - 5.9 m, 6 - 6.9 m, and > 7 m. The population structure of the *A. tortilis* woodlands was described using all five woodland transects, whilst the population structure of the *A. tortilis* trees within riverine vegetation was described using all 16 riverine transects (combined area = 1.4 ha). The population structure prior to the height-reducing influences of elephant in 1997 was reconstructed for 1996. The original heights of trees with broken or uprooted stems in 1997 were calculated for the *A. tortilis* woodlands using the regression of tree height on stem diameter for trees growing in *A. tortilis* woodlands (Table 8.3), and for *A. tortilis* trees within riverine vegetation using the regression of tree height (square-root-transformed) on stem diameter for *A. tortilis* trees growing in riverine vegetation (Table 8.3). One height was recorded for multi-stemmed trees. The remaining heights of stems of a multi-stemmed tree were predicted using the relevant regression equations (Table 8.3), despite potential differences in height between the stem of a multi-stemmed tree and the stem of a similar-sized (diameter) single-stemmed tree. The Kolmogorov-Smirnov two-sample analysis was used to test for annual differences in the frequency distribution of tree height.

Stem density and frequency (%) per height class were estimated for each year from all five woodland transects (0.45 ha in 1996, 1997, 1998 and 2000; 0.625 ha in 1999). Year-by-year differences in stem density for each height class (ha) were tested using paired *t*-tests (n = 8). Stem densities recorded one year represent the number of trees available for utilization by elephant the following year. Mortality rate (% an^{-1}) therefore expressed the number of stems that died each year relative to the total number of live stems recorded at the end of the previous year, and was calculated from the four 50 by 20 m transects that were monitored each year from 1997 to 2000.

Elephant response to *Acacia tortilis*

The following is a descriptive analysis of elephant response, specifically canopy removal, stem breakage or uprooting, and debarking, to *A. tortilis* woodlands, unless otherwise indicated. Only those four 50 by 20 m woodland transects measured each year between 1997 and 2000 (Table 9.2) were analyzed. The 50 by 10 m transect that was not located or measured in 1999, was excluded from the analyses, except when otherwise indicated.

Canopy removal

Although browsing by elephant has previously referred to all methods of feeding, its usage in this study has specific reference to the removal of canopy by breaking off branches. The amount of canopy removed by browsing was confounded by additional types of elephant utilization that induce canopy dieback, specifically debarking, uprooting and breaking stems. It was not possible to ascertain from the data sheets whether canopy removal, following the aforementioned methods of utilization, was the result of browsing or the consequence of debarking, uprooting or broken stems. Consequently, measures of canopy browsing by elephant include the frequency and volume (%) of canopy removed prior to the other methods of utilization. Canopy loss associated with debarking incidents which removed > 50% of the stem circumference was assumed to be the consequence of dieback due to debarking.

The percent volume of canopy browsed by elephant was represented by the midpoint of classes used to rank the percent volume of canopy browsed and was calculated from the original canopy volume and from the available canopy volume. The mean percent volume of canopy removed by elephant was calculated for 1st and subsequent (2nd, 3rd and 4th) browsing incidents by averaging the midpoints of each canopy removal class. Differences in the percent volume of canopy removed from the original canopy volume, and from the available canopy volume between initial ($n = 54$) and subsequent ($n = 30$) browsing incidents were examined using t-tests. Pearson's correlation coefficient (r) was used to test for a relation between initial and subsequent browsing incidents in the percent volume of canopy removed from the original canopy volume, and from the available canopy volume.

Tree height was compared with canopy volume browsed, and browse frequencies per tree between 1996 and 1999.The frequency of browse incidents ($n = 84$) was calculated for each height class and for each year between 1996 and 1999. Tree heights represented the heights of trees when first browsed. Preference ratios (PR) were calculated for each height class per annum, using a formula adapted from Viljoen (1989):

$$\text{Preference ratio} = \frac{\text{percent utilization}}{\text{percent availability}}$$

$$\text{where percent utilization} = \frac{\text{No. of trees browsed in a height class}}{\text{total No. of trees browsed across all height classes}} \times \frac{100}{1}$$

$$\text{and percent availability} = \frac{\text{No. of available trees in a height class}}{\text{total No. of trees across all height classes}} \times \frac{100}{1}$$

Preference ratios were calculated for tree height using the number of trees that were browsed by elephant in each height class for each year. Preference ratios calculated for 1996 ($n = 43$) and 1997 ($n = 6$) used the stem densities of the *A. tortilis* woodlands in 1996, whilst PR calculated for 1998/99 ($n = 5$) were estimated using stem densities recorded in 1997. Preference ratios were also calculated for the *A. tortilis* trees in the riverine vegetation, using the height distribution of stems in 1997, and the total browse frequency of each height class between 1996 and 1999.

Differences in tree heights before and after *A. tortilis* trees were browsed were examined using paired *t*-tests (1996 was excluded). Heights recorded for a particular year represent the heights of stems after their canopies were browsed that same year. Consequently, heights of stems before browsing took place in 1997 were estimated using the heights calculated for 1996. Canopies browsed for the first, second, third or fourth time between 1997 and 1999 were included in the analysis ($n = 31$).

The response (unaffected, coppice, reduced vigour or dead) of *A. tortilis* canopies to browsing by elephant was described by calculating the time (years) taken and volume (%) of canopy removed for a tree to respond. The sample of trees that were only browsed ($n = 16$) was expanded ($n = 48$ trees) to include trees that were browsed before they were broken, uprooted or had > 50% of their circumference debarked. Consequently, a response to browsing had to be at least one year before a stem was uprooted, broken or had > 50% of its circumference debarked. The time taken for trees to respond to browsing (and other methods of utilization) was calculated by subtracting the last recorded year a tree was browsed prior to the response, from the year of the particular response. The time taken to respond was zero (years) if trees were browsed and responded in the same year. The percent volume of canopy removed which led to a response was calculated by summing the midpoints of each canopy removal class. If a particular response occurred more than once on the same tree, the time taken and volume browsed leading to the first response was recorded. Trees not affected by browsing one year after the incident were assumed unaffected during the same year as the browsing incident.

Broken and uprooted stems

It is likely that elephants, seeking to improve browse availability or display social dominance, do not consciously decide on whether to break the stem of a tree or uproot it, unless perhaps purposefully seeking out roots, a feeding habit not apparently associated with *A. tortilis* in VLNR (personal observation). When an elephant pushes against a tree it is either uprooted or the stem snaps. Irrespective of whether the tree is uprooted or whether the stem snaps, the role of the elephant is equally two-fold, acting as either a mortality or a height reducing agent. The small sample of uprooted stems ($n = 6$) and hence skeptical statistical inferences regarding uprooted stems, was sufficient justification for combining the two samples (uprooted plus broken stems). The combined sample of uprooted and broken stems is referred to as recumbent stems.

Potential differences in stem height and diameter between partially ($n = 7$) and completely ($n = 30$) broken stems, and uprooted ($n = 6$) and broken (partially plus completely broken, $n = 37$) stems, were tested using *t*-tests. Tree-height distributions of partially and completely broken stems was compared with a Kolmogorov-Smirnov two-sample test. The samples of partially and completely broken stems were increased to 15 and 37, respectively, by including those stems utilized on the 50 by 10 m transect which was not recorded in 1999, but measured in 1997 and 1998.

Preference ratios were calculated for each height class per annum, using the aforementioned formula (substitute 'recumbent stems' for 'trees browsed'). Preference ratios were calculated for height classes of uprooted, of partially broken, of completely broken, and of recumbent stems, using the previous year's frequency distribution of stem density across height classes and were not calculated for 2000 because no trees were uprooted or broken that year.

Pearson's correlation coefficient was used to test for a relation between stem height prior to utilization and percent height lost, and between survival (years) and height lost.

The response of *A. tortilis* trees to being either broken or uprooted was described by calculating the time taken for a tree to respond (refer to *Canopy removal*).

The dependence of trees surviving one, two or three years on the methods of utilization, and the dependence of recumbent stems surviving one year on the year of utilization were examined using χ^2 or G - tests, depending on data properties. Potential differences in stem diameter and height between individuals that died one year after utilization and individuals that survived at least one year after utilization, and between stems that survived one year after utilization and stems that survived two or three years after utilization were examined using t-tests.

A logistic regression tested the probability of stems surviving at least one year after being utilized (uprooted, broken and recumbent). Explanatory variables included the total canopy removed before utilization, canopy removed during utilization, and total canopy removed after utilization. Total canopy removed, either before or during utilization, was calculated by adding the midpoints of each canopy removal class. Total canopy removed after utilization was the sum of total canopy removed before utilization and canopy removed during utilization. Factors included in the regression of recumbent stems were the presence of debarking, and the type of utilization (uprooted and partially or completely broken stems).

Debarking

Preference ratios were calculated for each height class per annum, using the number of new trees debarked each year. Preference ratios compared the frequency distribution of newly debarked trees across all height classes with the previous year's frequency distribution of stem densities (1996 and 2000 was excluded). The PRs for 1997 were estimated using the stem densities for each height class in 1996. Preference ratios were also calculated for each height class for the period between 1991 and 1999 by comparing the frequency of debarked stems over this period with the frequency distribution of stems in 1996.

The response of *A. tortilis* to debarking was described by calculating the time taken to respond, and the associated stem circumference (%) that was debarked (refer to *Canopy removal*). Canopy loss owing to browsing could not be excluded from the analysis and may have confounded tree response to debarking. A few debarked stems were uprooted and had their stems broken. Tree response to debarking was analyzed up until the particular stems were uprooted or broken. One of the debarked stems ($n = 13$) was excluded from the analysis ($n = 12$) because it was debarked after it had been broken.

Potential differences between *A. nilotica* and *A. tortilis* trees in the percent volume of canopy dieback associated with debarking during the period 1991 to 2000 and the percent height of bark removed from the stem during each debarking incident were examined using *t*-tests.

Factors influencing the different methods of utilization

A logistic regression tested the effects that browse frequency, browse volume (%), and tree height had on the probability of a stem being uprooted, debarked or broken. Browse frequency was the number of browse incidents before a tree was uprooted ($n = 6$), debarked ($n = 13$) or broken ($n = 37$), and tree height was the height of a tree when first browsed. The percent volume of canopy browsed was estimated from the original canopy volume for each browse incident. Consequently, the percent volume of canopy browsed until a stem was broken, uprooted or debarked was calculated by summing the midpoints of classes used to rank percent volume of canopy browsed. The probability of trees being only browsed ($n = 16$) was also analyzed. Trees that had > 50% of their stem circumference debarked before 1997 and completely broken stems recorded dead in 1997 were excluded from the analysis ($n = 5$) because browse frequencies, volumes and tree heights were unknown. An additional 14 trees were excluded from the analysis because they were either dead in 1997 ($n = 9$) or were seedlings ($n = 5$) which recruited during 1997 and 1998. The probability of being subjected to one type of utilization was tested relative to a combined sample of the remaining stems, irrespective of their method of utilization. An analysis of variance tested for differences in browse frequency, browse volume (%), and tree height between trees that had been uprooted, debarked, broken, and browsed.

Results

Population structure of *Acacia tortilis* woodlands

Apart from an under-representation of trees below 2 m in height, each height class constituted > 10% of the *A. tortilis* population in 1996 (Table 9.1). The increase in the number of trees below 2 m in 1997 coincided with the height-reducing influences of elephant. Thereafter, the frequency distribution within height classes was erratic, until 2000 when elephant activity was absent.

The distribution of tree heights changed significantly from 1996 ($n = 97$) to 1997 ($n = 89$, $P < 0.05$) and 1998 ($n = 80$, $P < 0.005$) (Figure 9.1). In 1997 the frequency of trees < 2 m had increased over two fold at the expense of the mid (2 - 6 m) size classes and continued to do so in 1998, reducing mean (± SD) tree height from 4.6 m (± 1.97 m) in 1996 to 3.7 m (± 2.68 m) in 1998, whilst the proportion of trees > 6 m remained relatively constant. In 1999 and 2000 the population of trees < 1 m decreased to ± 10%, whilst trees between 1 and 2 m were eliminated, indicating no recruitment from trees < 1 m. The proportion of trees > 5 m showed a steady increase, accounting for about two thirds of the *A. tortilis* population, at the expense of the mid (2 - 5 m) size classes which decreased. The increase in mean (±SD) height from 3.7 m (± 2.68 m) in 1998 to 4.4 m (± 2.44 m) and 5.0 m (± 2.28 m) in 1999 and 2000, respectively, resulted from greater reduced stem densities below 6 m relative to the more prominent height classes > 6 m (Figure 9.1). Consequently, the frequency distribution of tree heights in 1996 was not significantly different from 1999 ($n = 70$, $P > 0.1$) and 2000 ($n = 38$, $P > 0.1$).

The mean stem density per height class in 1996 was 27 stems ha^{-1} (Figure 9.1). Although mean stem density per height class decreased in 1997 and 1998 to 25 and 22 stems ha^{-1}, respectively, significant reductions only occurred in 1999 (mean: 14 stems height $class^{-1}$ ha^{-1}, $t = 4.14$, df = 7, $P = 0.004$) and 2000 (mean: 11 stems height $class^{-1}$ ha^{-1}, $t = 4.14$, df = 7, $P = 0.002$). The overall stem density (ha) of the *Acacia* woodlands decreased by 61% between 1996 and 2000 (Table 9.1).

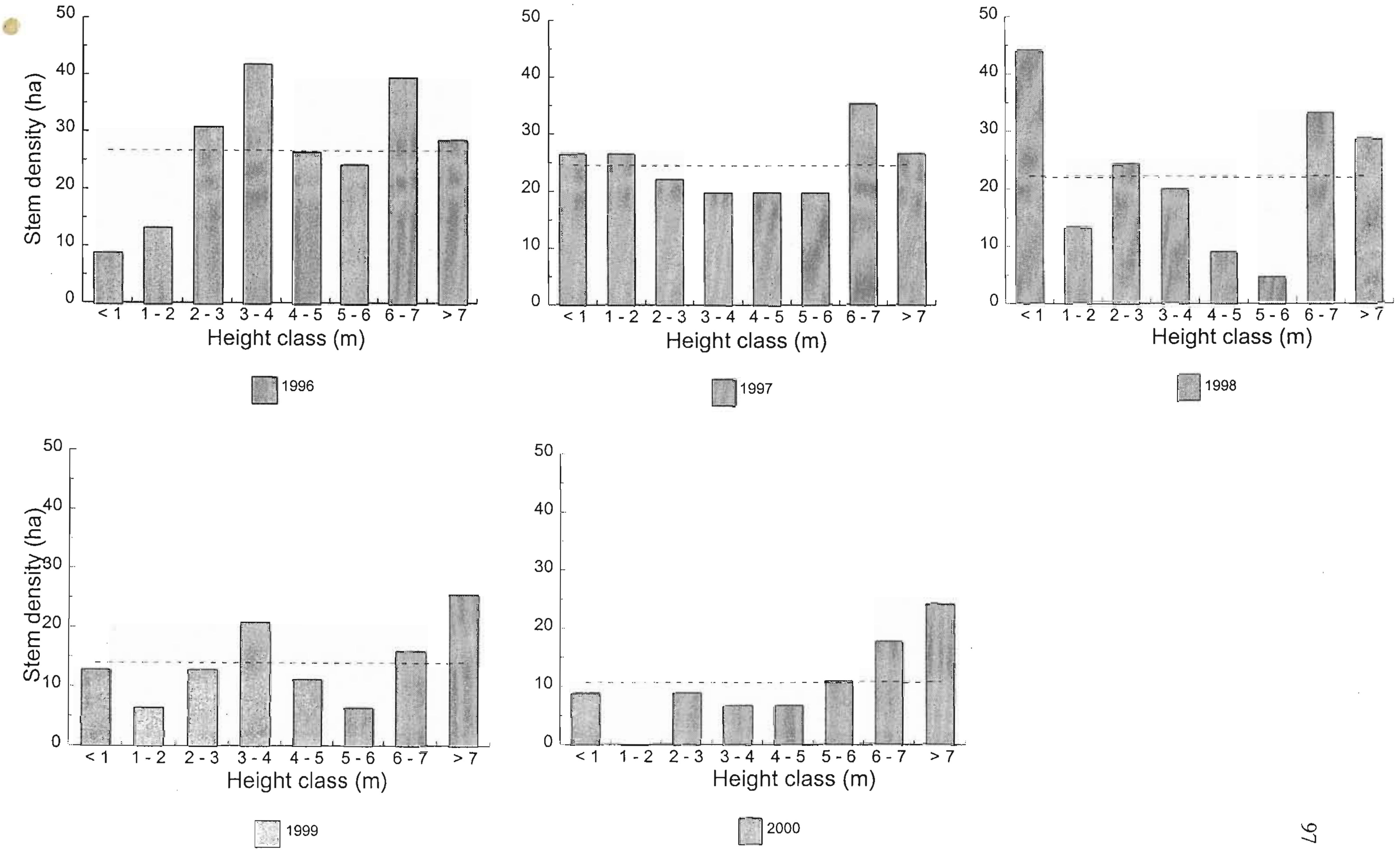


Figure 9.1 Height-class density (ha^{-1}) distributions of *Acacia tortilis* woodlands during 1996 (n = 97), 1997 (n = 89), 1998 (n = 80), 1999 (n = 70) and 2000 (n = 38). Population structures were calculated from a combined sample of five *Acacia* woodland transects. (----) represents mean stem density/height class.

Table 9.1 Height-class frequency (%) distributions of live *Acacia tortilis* stems for each year between 1996 and 2000 in the *Acacia tortilis* woodlands. Stems (n) were sampled from 0.45 ha in 1996, 1997, 1998 and 2000, and 0.625 ha in 1999

Height classes (m)	Relativ ey (%) frequenc				
	1996 (n = 97)	1997 (n = 89)	1998 (n = 80)	1999 (n = 70)	2000 (n = 38)
< 1	4.1	13.5	25.0	11.4	10.5
1 - 2	6.2	13.5	7.5	5.7	0
2 - 3	14.4	11.2	13.8	11.4	10.5
3 - 4	19.6	10.1	11.3	18.6	7.9
4 - 5	12.4	10.1	5.0	10.0	7.9
5 - 6	11.3	10.1	2.5	5.7	13.2
6 - 7	18.6	18.0	18.8	14.3	21.1
> 7	13.4	13.5	16.3	22.9	28.9
Total stem density (ha^{-1})	215.6	197.8	177.8	112.0	84.4

Elephant response to *Acacia tortilis* woodlands

Population structure

The increase in stem density below 1 m in 1997 (Table 9.2) was due to the height-reducing influences of elephants (80%) and seedling recruitment (20%). Further increase in stem density below 1 m in 1998 was attributed to a four-fold increase in seedling (mean height: 0.1 m, mean diameter: 0.3 cm) recruitment (40%) compared with 1997, and stems broken (60%) by elephant. The poor rainfall of the 1997/98 season (Table 9.2) may account for the absence of seedlings in 2000. Annual mortality increased each year until 1999. The decreased annual mortality in 2000 coincided with no elephant utilization, confirming a 'lag' period between utilization and death, and reduced elephant activity, perhaps associated with the decline in stem density. Although the height-reducing influence of elephant takes immediate effect upon woodland structure, elephant-induced mortality does not.

Table 9.2 Stem density (ha^{-1}) of *Acacia tortilis* for each year between 1997 and 2000 in the *Acacia tortilis* woodlands, and annual rainfall (July to June inclusive). The population structure for 1996 was reconstructed from the 1997 data sheets

Height class (m)	Year				
	1996	1997	1998	1999	2000
< 1	0	13	35	20	8
1 - 2	15	18	8	5	0
2 - 3	20	23	23	13	10
3 - 4	38	23	18	18	8
4 - 5	15	15	8	10	8
5 - 6	23	18	5	3	8
6 - 7	40	35	28	10	13
> 7	23	18	20	13	15
Total stem density	173	160	143	90	68
Mortality rate (% an^{-1})		8.7	17.2	36.8	25
Season	1994/95	1995/96	1996/97	1997/98	1998/99
Rainfall (mm an^{-1})	389.7	337.5	383.7	132.9	335.8

Canopy removal

Approximately two thirds of the *A. tortilis* population was browsed in 1996 (Table 9.3). Browse frequency decreased each year from 1996, coinciding with a decrease in stem density and an increase in the number of recumbent stems ($r = -0.98$, df = 2, $P < 0.05$). No browse incidents were recorded in 2000 when available stem density had decreased to 36 stems per 0.4 ha. However, the significant decline in stem density occurred in 1999, whilst browse frequency decreased most in 1997 when additional methods of utilization were recorded.

Elephant most frequently browsed 6%, 18% and 95% of the canopy volume (Table 9.3). The mean percent volume of canopy removed from the original canopy volume and from the available canopy volume were both less ($t = 6.96$, df = 74, $P < 0.001$) during repeated visits to the same tree (Table 9.4). However, elephant tended to remove proportions of the existing canopy that correlated ($r = 0.56$, df = 25, $P < 0.001$) with the percent volume that was first browsed. *Acacia tortilis* trees may therefore have differed in palatability, assuming the percent volume browsed by elephant corresponds to a tree's nutritional value.

Table 9.3 The number of browse incidents by elephant on *Acacia tortilis* woodlands (combined transects = 0.4 ha) between 1996 and 2000 before trees were uprooted, broken or had > 50% bark removed from their stem circumference. Canopy removal classes express the percent volume of canopy removed and are represented by the midpoint of each class

Canopy removal class (%)	1996	1997	1998	1999	2000	Total
6	9	6	3	8	0	27
18	7	6	5	1	0	19
38	7	1	2	0	0	10
63	5	1	2	0	0	8
83	1	1	0	0	0	2
95	13	2	2	0	0	17
100	1	0	0	1	0	2
Total browse frequency	43	17	14	10	0	84
Stem density (0.4 ha)	69	64	57	36	27	
Number of trees browsed	43	6	4	1	0	54

Table 9.4 The percent volume of canopy removed from the original canopy volume and from the available canopy volume of *Acacia tortilis* trees during initial (1st) and subsequent (2nd, 3rd & 4th) browsing incidents in the *Acacia tortilis* woodlands

Statistics		Original canopy		Available canopy	
(%)	1st incident	2nd incident	3rd & 4th incident	2nd incident	3rd & 4th incident
mean ± SE	53.9 ± 5.00	15.5 ± 2.51	16.2 ± 1.63	29.0 ± 5.03	26.0 ± 3.78
median	63	6	18	16	17
mode	95	6	18	6	8
range	0 - 100	6 - 63	6 - 38	6 - 100	8 - 68
n	54	19	9	19	8

Browse frequency per tree between 1996 and 1999 inclusive ranged from one to four and was independent of tree height (Figure 9.2). An exponential regression of tree height and browse frequency per tree ($F = 5.31$, df = 53, $P = 0.008$), indicated a tendency for larger trees to be browsed more frequently, but only 14% of the variation was accounted for by the model and browse frequency is not a continuous variable. The percent volume of canopy removed by elephant during the first browsing incident also appears to be independent of tree height (Figure 9.3). Only first-browse incidents were analyzed because the volume of canopy removed during subsequent visits, particularly following browse incidents which removed 91 - 99% of the canopy

The number of trees browsed per height class in 1996 was positively correlated ($r = 0.8$, df = 6, $P < 0.05$) with stem density per height class in 1996. Although trees were browsed in proportion to their abundance in each height class, elephant preferred to browse trees taller than 4 m in 1996 (Table 9.5). It is difficult to generalize which specific height classes were browsed in preference to others, given the fine scale (1 m intervals) of the height classes used and the tendency for elephant to prefer different sized trees during different years (Table 9.5).

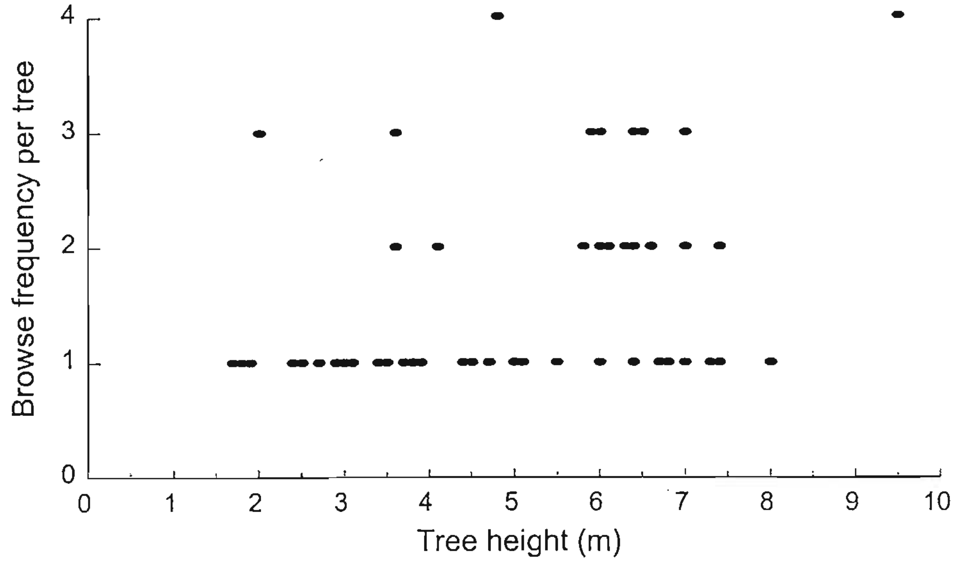


Figure 9.2 The relationship between stem height (m) of *Acacia tortilis* when first browsed, and browse frequency between 1996 and 1999 ($n = 54$) in the *Acacia tortilis* woodlands.

Table 9.5 Preferred height classes for browsing in the *Acacia tortilis* woodlands. Stems that were absent are indicated by an asterix, whilst 0 indicates stems that were not browsed, 1 indicates height classes which comprised the same percent of the elephants' diet as it comprised total stem density, > 1 represents height classes which constituted a greater percent of the elephants' diet than their relative abundance

Height class (m)	PR 1996	 1997	 1998/99
< 1	*	*	0.0
1-2	0.8	1.9	0.0
2-3	0.8	1.4	3.1
3-4	0.6	0.8	4.6
4-5	1.1	1.9	0.0
5-6	1.2	0.0	0.0
6-7	1.2	0.7	0.0
> 7	1.2	1.3	0.0

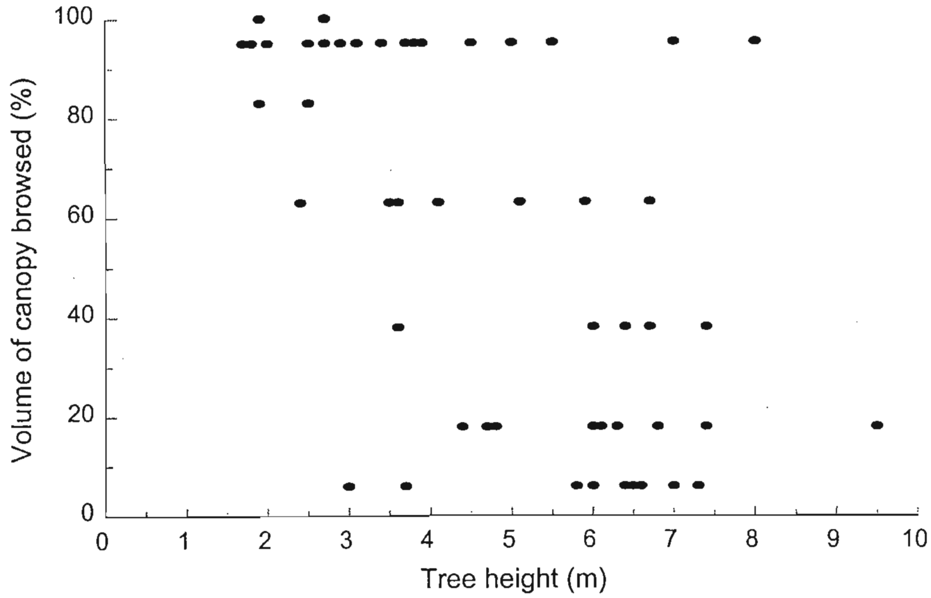


Figure 9.3 Relationship between the stem height (m) of *Acacia tortilis* and the percent volume of canopy browsed by elephant when first browsed ($n = 43$) in the *Acacia tortilis* woodlands. Canopy removal is represented by the midpoint of classes used to rank percent volume of canopy browsed.

The low preference for trees < 1 m in1998/99 (Table 9.5) was on account of the absence of trees growing in that particular height class. Sixty percent of the trees < 1 m in 1998 were there because their stems had been broken, whilst the remaining 40% were seedlings.

The strong correlation ($r = 0.98$, df = 6, $P < 0.001$) between the number of trees browsed in each height class during 1996 and the frequency of browse incidents within each height class between 1996 and 1999 (Figure 9.4), and the fact that browse frequency per height class (> 2 m) had doubled by 1999, meant that trees were consistently browsed in proportion to their abundance in each height class (Table 9.3). The three years taken for browse frequency per height class (> 2 m) to double is an indication of the reduced browsing activity.

Although *A. tortilis* trees did not differ ($t = 0.46$, df = 30, $P = 0.323$) in height after being browsed, the results regarding potential differences in tree height before and after canopies were browsed are questionable on account of the procedures (refer to **Data analysis**, Population structure) used to estimate the heights of stems in 1996 and of stems not recorded in subsequent years.

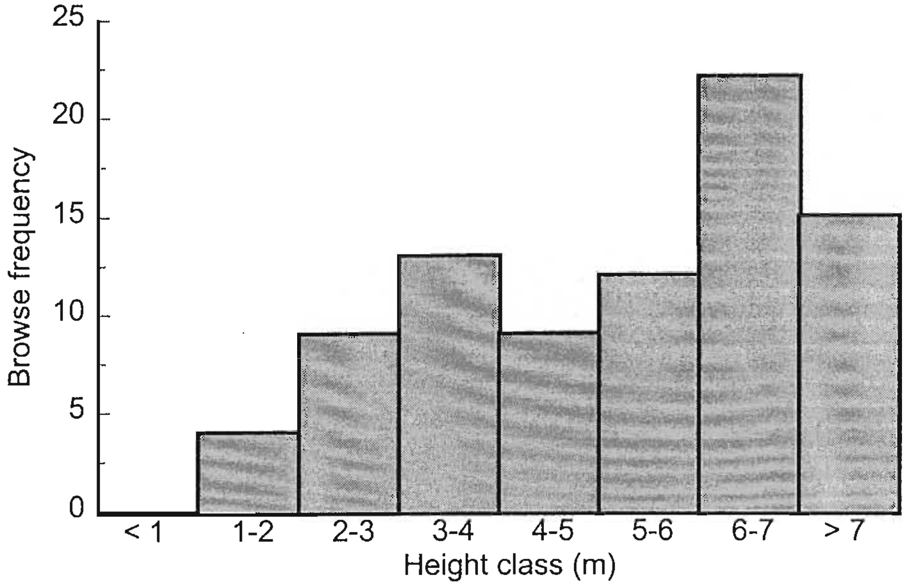


Figure 9.4 Number of trees browsed in each height class (1 - 2 = 1 - < 2, etc.) between 1996 and 1999 in *Acacia tortilis* woodlands. Eighty-four incidents of browse were recorded on 54 stems.

Table 9.6 The response (unaffected, coppice, reduced vigour or dead) of *Acacia tortilis* trees (*n* = 48) to different percent volumes of canopy removed by elephant in the *Acacia tortilis* woodlands, including the time taken (years) to respond and tree heights specific to each response. Height represents the heights (m) of trees when they were first browsed and *n* is the number of stems

Response	*n*	Canopy volume removed (%)	Time (years)	Height (m) mean	range
coppice	14	91 - 100	0 - 1	3.7	1.7 - 7.0
	9	26 - 90	0 - 2	3.9	1.9 - 6.4
	5	1 - 25	2 - 4	5.4	3.8 - 7.0
Total	28			4.1	1.7 - 7.0
Reduced vigour	2	76 - 100	2	3.9	1.9 - 5.9
	2	51 - 75	1 - 4	3.4	3.2 - 3.5
	3	11 - 50	1	5.8	4.3 - 7.0
Total	7			3.9	1.9 - 7.0
dead	1	100	1	2.7	
	3	91 - 99	2	3.4	2.5 - 4.5
	1	76 - 90	3	1.9	
Total	5			2.9	1.9 - 4.5
unaffected	24	1 - 90	0 - 1	5.9	2.5 - 9.5

Stems which had 91 - 99% of their canopy volume removed had a mean (± SE) difference in height of 1.5 m ± (0.84 m) (range: 0.0 - 3.1 m, *n* = 4), whilst trees which had 1 - 90% of their canopy volume removed had a mean (± SE) difference in height of 0.1 m (± 0 .08 m) (range: 1.5 m - 0.6 m, *n* = 27). The negative mean difference in the height of trees which had < 91% of their canopy volume removed is attributed to either growth following browsing or to estimation error.

Half the number of browsed trees were unaffected the following year, whilst more than half coppiced and approximately two thirds of the trees that were only browsed (*n* = 16) survived between 1996 and 2000 (Table 9.6). Mortality was attributed to excessive (> 76% volume of canopy removed) defoliation. The time taken for *A. tortilis* trees to coppice or die after being browsed decreased with the severity of the defoliation (Table 9.6). Although canopy removal by browsing has the potential to induce > 31.3% mortality over four years, given the amount of trees that had > 76% of their canopy removed (Table 9.3), most trees were uprooted or broken after they were browsed and died as a result of the aforementioned methods of utilization rendering browse-related mortality relatively small.

Broken and uprooted stems

Although elephants were re-introduced into the reserve in 1991, *A. tortilis* stems on these sites were only broken or uprooted between 1997 and 1999.

Table 9.7 The number of uprooted, partially and completely broken *Acacia tortilis* stems between 1997 and 1999 in the *Acacia tortilis* woodlands. Stems were not uprooted or broken in 2000

Height class (m)	Partially broken stems			Completely broken stems			Uprooted stems			Total		
	Year			Year			Year			Year		
	97	98	99	97	98	99	97	98	99	97	98	99
< 1	0	0	0	0	0	0	0	0	0	0	0	0
1 - 2	1	1	0	1	2	0	0	0	0	2	3	0
2 - 3	0	1	0	0	1	1	0	0	0	0	2	1
3 - 4	0	0	0	1	4	3	0	0	0	1	4	3
4 - 5	0	0	0	1	1	0	0	1	0	1	2	0
5 - 6	0	0	0	2	2	1	1	0	0	3	2	1
6 - 7	1	0	1	0	1	5	2	1	0	3	2	6
> 7	1	0	1	1	1	2	0	0	1	2	1	4
Total	3	2	2	6	12	12	3	2	1	12	16	15

The total number of recumbent stems after 1997 did not differ by more than 4 stems despite a two-fold increase in the number of completely broken stems in 1998 and 1999 because fewer stems were partially broken or uprooted (Table 9.7). By 1999, elephant had pushed over (uprooted or broken) stems in proportion to their abundance within each height class during 1996 ($r = 0.93$, df = 6, $P < 0.001$). No additional stems were pushed over in 2000 when the available stem density had been reduced to 90 stems ha^{-1}. The number of recumbent stems each year between 1997 and 2000 did not correlate with annual rainfall (Figure 3.3) or stem density (Figure 9.2).

Although no stems were broken or uprooted in 2000, previously broken or uprooted trees continued to die (Table 9.8), indicating that the mortality rate for 2000 does not reflect elephant utilization that year. The severity of the outcome of broken stems appeared to have increased considering 11 of the 14 trees that were either partially or completely broken in 1999 died that year. The large immediate mortality in 1999 could possibly be related to the low rainfall season of 1997/98 (Figure 3.3).

Table 9.8 The number of *Acacia tortilis* stems that were uprooted, partially and completely broken each year (combined woodland transects = 0.4 ha) compared with the number of trees recorded dead from each method of utilization in that year. Recumbent stems include uprooted plus broken stems

	Year					Total
	1996	1997	1998	1999	2000	
Partially broken stems	0	3	2	2	0	7
Dead	0	0	1	0	1	2
Completely broken stems	0	6	12	12	0	30
Dead	0	3	6	15	3	27
Uprooted stems	0	3	2	1	0	6
Dead	0	0	3	1	1	5
Recumbent stems	0	12	16	15	0	43
Dead	0	3	10	16	5	34

Only stems > 1 m were either broken or uprooted, because there were no trees less than 1 m in height (Table 9.7). Elephant preferred to push over (uproot, partially or completely break) stems of all heights during one year or another (Table 9.9) between 1997 and 1999, with the exception of those < 1 m, and between 2 and 3 m in height. Mean preference ratios for the period between 1997 and 1999 suggested a tendency for elephants to push over stems between 5 and 6 m proportionally more than their relative availability (Table 9.9). Preferred height classes varied from year to year for each method of utilization and between the methods of utilization. Between 1997 and 1999 elephants preferred to partially break stems in the 1 - 3 m and > 6 m height classes, to completely break stems across all height classes with the exception of trees < 1 m and between 2 to 3 m in height, and to uproot trees > 4 m.

Table 9.9 Preferred height classes in the *Acacia tortilis* woodlands, and a comparison of stem density (0.4 ha) with the number of *Acacia tortilis* stems that were uprooted, or partially and completely broken each year between 1997 and 1999. Stems were not broken or uprooted in 2000

Height class (m)	Year 1996	1997		1997	1998		1998	1999		Mean 97 - 99
	Density	Utilized	PR	Density	Utilized	PR	Density	Utilized	PR	PR
< 1	0	0		5	0	0.0	13	0	0.0	0.0
1 - 2	6	2	1.9	7	3	1.7	3	0	0.0	1.2
2 - 3	8	0	0.0	9	2	0.9	9	1	0.4	0.4
3 - 4	15	1	0.4	9	4	1.8	8	3	1.4	1.2
4 - 5	6	1	1.0	6	2	1.3	3	0	0.0	0.8
5 - 6	9	3	1.9	7	2	1.1	2	1	1.9	1.7
6 - 7	16	3	1.1	14	2	0.6	11	6	2.1	1.2
> 7	9	2	1.3	7	1	0.6	8	4	1.9	1.2
Total	69	12		64	16		57	15		

Acacia tortilis stems were either partially ($n = 7$) or completely ($n = 30$) broken. Although there was no significant difference in stem diameter ($t = 0.12$, df = 8, $P = 0.906$) or height ($t = 0.15$, df = 7, $P = 0.887$) between partially and completely broken stems, a Kolmogorov-Smirnov two sample test revealed that partially ($n = 15$) and completely ($n = 37$) broken stems differed significantly ($P < 0.05$) in their tree height distributions; partially broken stems contained a greater portion of smaller trees (Table 9.10). Half the number of partially broken stems were < 3.0 m in height, whilst less than one quarter of completely broken stems were < 3.0 m.

Uprooted stems (mean height: 5.9 m, $n = 6$) were taller ($t = 2.39$, df = 14, $P = 0.016$) than broken stems (mean height: 4.7 m, $n = 37$) because elephant broke stems across the full range of height classes, with the exception of trees below 1 m, whilst only uprooting trees taller than 4 m. It would be misleading, however, to conclude that elephants uproot taller trees considering they broke more stems ($n = 21$) > 4 m than they uprooted ($n = 6$). The height of uprooted stems was not different ($t = 0.59$, df = 9, $P = 0.285$) from the height of broken stems that were taller than 4 m (mean: 6.1 m, $n = 21$). There was no difference in stem diameter ($t = 0.36$, df = 6, $P = 0.364$) between uprooted and broken stems. Nor was the diameter of uprooted stems (Table 9.10) different ($t = 0.55$, df = 7, $P = 0.299$) from the diameter (20.1 cm) of broken stems > 4 m in height.

Table 9.10 The diameters and heights of uprooted ($n = 6$), partially ($n = 7$) and completely ($n = 30$) broken *Acacia tortilis* trees between 1997 and 1999 in the *Acacia tortilis* woodlands. Height is the height of stems prior to utilization. Total broken stems includes partially and completely broken stems

	Diameter (cm)			Height (m)		
	mean ± SE	median	range	mean ± SE	median	range
Partially broken stems	17.3 ± 3.29	14.0	7.0 - 31.6	4.8 ± 1.00	6	1.8 - 8.0
Completely broken stems	16.9 ± 1.09	16.3	2.3 - 31.4	4.7 ± 0.31	4.6	1.0 - 7.4
Total broken stems	16.7 ± 1.11	16.2	2.3 - 31.6	4.7 ± 0.32	5.0	1.0 - 8.0
Uprooted stems	18.2 ± 3.09	19.7	7.3 - 28.7	5.9 ± 0.37	6.0	4.7 - 7.3

Acacia tortilis stems that survived being broken or uprooted were reduced in height ($t = 4.40$, df = 14, $P < 0.001$), affecting woodland structure. Although the height to which *A. tortilis* trees were reduced varied considerably, trees were generally reduced to approximately half their original height (Table 9.11). Forty percent of stems that survived being pushed over (broken or uprooted) were reduced to 2 - 5 m in height, whilst the remaining 60% were reduced to < 2 m. This accounted for the marked increase in the density of stems < 2 m in 1997 and 1998, followed by the high mortality rate of recumbent stems in 1999 which reduced the density of stems below 2 m.

Trees of all heights survived being pushed over by elephant (Table 9.12). There was a positive correlation ($r = 0.45$, df = 13, $P = 0.05$) between the height of a tree before it was pushed over and the percent height lost; taller trees lost a greater proportion of their height.

Table 9.11 Percent height lost owing to partially broken, completely broken and uprooted stems in the *Acacia tortilis* woodlands. *n* is the number of trees that survived more than one year after being pushed over between 1997 and 1999

Statistics	Partially broken stem ($n = 5$)	Completely broken stem ($n = 8$)	Uprooted stem ($n = 2$)	Total ($n = 15$)
mean ± SE	48 ± 15.4	48 ± 11.6	55 ± 5.0	49 ± 7.7
median	50	49	55	50
range	0 - 87	5 - 94	50 - 60	0 - 94

Table 9.12 Percent height lost of *Acacia tortilis* trees that survived the different methods of utilization (uprooted: U, partially broken stems: P, or completely broken stems: C) for at least one year, survival (years) of trees in their new height classes, and the number of stems utilized (uprooted or broken) in the *Acacia tortilis* woodlands. Bold values indicate trees that were alive in 2000

Height (m)	1997			1998			1999		
	Utilized	Height lost (%)	Survival (years)	Utilized	Height lost (%)	Survival (years)	Utilized	Height lost (%)	Survival (years)
< 1	0			0			0		
1 - 2	2	10 (C)	2	3	30 (C)	1	0		
		74 (P)	1		50 (P)	2			
2 - 3	0			2	***0 (P)***	2	1		
3 - 4	1	67 (C)	1	4			3		
4 - 5	1	70 (C)	1	2	**32 (C)**	2	0		
5 - 6	3			2			1	**5 (C)**	1
6 - 7	3	50 (U)	2	2	**60 (U)**	2	6	77 (C)	1
		32 (P)	3		94 (C)	1			
> 7	2			1			4	**87 (P)**	1
Total	12	6		16	6		15	3	

Trees survived for one to three years (Table 9.12) in their new height classes. Survival (years) following utilization decreased with the intensity of utilization ($r = -0.5$, df = 13, $P = 0.05$) measured in terms of height lost (%). Trees that survived only one year ($n = 8$) lost a greater ($t = 2.07$, df = 12, $P = 0.03$) percent of tree height (mean: 63%) than trees which survived two or three years ($n = 7$), and lost, on average, 33% of their height.

The primary response of *A. tortilis* to completely broken and uprooted stems was mortality (Table 9.13). Less than half of the completely broken and uprooted trees (1997 - 2000) coppiced, whilst even fewer (17%) individuals survived. In contrast more partially broken stems coppiced than died (Table 9.13). Overall mortality (43%) of partially broken stems between 1997 and 2000 was less than completely broken (83%) and uprooted (83%) stems, inferring that partially broken stems had a greater probability of survival than completely broken and uprooted stems (Table 9.13). It is unlikely that the single uprooted tree which survived (for two years), will be an exception to the observation that uprooted trees eventually die, given (1) the 'survivor's' reduced vigor (e.g. dying) and reduced canopy volume (to ± 1/4) in 2000, and (2) the time taken for uprooted trees to die (up to three years). Consequently, it is concluded that uprooting ultimately results in death. The probability of a tree surviving one ($G = 4.81$, df = 2, $0.1 < P > 0.05$), two ($G = 5.47$, df = 2, $0.1 < P > 0.05$) or three ($\chi^2 = 3.27$, df = 2, $0.25 < P > 0.10$) years after being uprooted or partially and completely broken was independent of the method of utilization.

Although the probability of recumbent stems surviving one year decreased with a corresponding decrease in the previous season's rainfall (Table 9.14), suggesting that survival may depend on the availability of soil water following the rainfall season that preceded utilization, the survival of recumbent stems for one year after being uprooted or partially and completely broken was independent of the year (1997, 1998 or 1999) of utilization ($G = 2.80$, df = 2, $0.25 < P > 0.10$). Nevertheless, partially broken stems appeared to have a greater chance of surviving than uprooted or completely broken stems (Table 9.14).

The range in heights that survived partially broken (Figure 9.5) and completely broken (Figure 9.6) stems relative to the heights of trees that died one and two years after they were broken suggests that the probability of survival (years) was independent of tree height.

Mortalities (stems that died during or one year following utilization, $n = 28$) did not differ ($t = 1.63$, df = 24, $P = 0.117$) from survivors (stems that survived at least one year following utilization, $n = 15$) in tree height (Figure 9.7), although there was a significant ($t = 2.23$, df = 35, $P < 0.016$) difference in stem diameter (mortalities: 18.7 cm, survivors: 14.3 cm). Prolonged survival following utilization was independent of tree height ($t = 0.44$, df = 13, $P = 0.66$) and stem diameter ($t = 0.15$, df = 13, $P = 0.88$). Mean height and diameter of stems that survived one year ($n = 8$) was 4.4 m and 14.1 cm, whilst the mean height and diameter of stems that survived two and three years ($n = 7$) was 3.9 m and 14.6 cm, respectively. Consequently, the ability of *A. tortilis* to recover from uprooting or a broken stem was independent of the size of a tree.

Table 9.13 The time (years) taken for *Acacia tortilis* to respond (unaffected, coppice, reduced vigour or dead) to uprooting, completely and partially broken stems in the *Acacia tortilis* woodlands, and tree heights specific to each response. Height represents the heights (m) of trees when they were pushed over, whilst *n* is the number of trees

Completely broken stems		($n = 30$)		
Response	Time (years)	*n*	Height (m)	
			mean	range
coppice	0	10	4.2	1.0 - 7.0
	1	1	4.1	
Total		11	4.2	
reduced vigour	1	1	5.1	
unaffected	0	1	4.1	
	1	1	1.0	
Total		2	2.3	
dead	0	19	4.8	1.7 - 7.0
	1	3	4.8	3.5 - 7.0
	2	2	4.0	3.9 - 4.0
	3	1	1.0	
Total		25	3.7	
Partially broken stems ($n = 7$)				
coppice	0	4	3.6	1.8 - 8.0
	1	1	6.0	
Total		5	3.4	
reduced vigour	0	2	7.8	6.5 - 7.0
unaffected	0	1	6.0	
dead	1	2	7.3	6.5 - 8.0
	2	1	1.9	
Total		3	5.5	
Uprooted stems ($n = 6$)				
coppice	0	3	5.7	5.0 - 6.2
reduced vigour	2	2	6.0	6.0 - 6.0
unaffected	0	1	6.0	
dead	0	2	6	4.7 - 7.3
	1	2	5.9	5.0 - 6.7
	3	1	6	
Total		5	5.9	

Table 9.14 The probability of *Acacia tortilis* surviving after being uprooted or partially and completely broken in the *Acacia tortilis* woodlands for 1997, 1998 and 1999, in relation to (1) mean annual rainfall for 1995/1996, 1996/97, and 1997/98 and (2) mean stem density (ha) per height class for those height classes utilized (1 - > 7 m). Mean stem density represents the density of trees at the end of the previous season (e.g. 1996, 1997 and 1998)

	Partially Broken		Completely Broken		Uprooted		Recumbent		Rainfall (mm/an)	Mean Stem Density (ha)
	Frequency	(%)	Frequency	(%)	Frequency	(%)	Frequency	(%)		
1997									337.5	29.2 (1996)
Probability of surviving 1 year	2 out of 3	(67)	3 out of 6	(50)	1 out of 3	(33)	6 out of 12	(50)		
Probability of surviving 2 year	1 out of 3	(33)	1 out of 6	(17)	1 out of 3	(33)	3 out of 12	(25)		
Probability of surviving 3 year	1 out of 3	(33)	0 out of 6	(0)	0 out of 3	(0)	1 out of 12	(8)		
1998									383.7	24.2 (1997)
Probability of surviving 1 year	2 out of 2	(100)	3 out of 12	(25)	1 out of 2	(50)	6 out of 16	(38)		
Probability of surviving 2 year	2 out of 2	(100)	1 out of 12	(8)	1 out of 2	(50)	4 out of 16	(25)		
1999									132.9	18.9 (1998)
Probability of surviving 1 year	1 out of 2	(50)	2 out of 12	(17)	0 out of 1	(0)	3 out of 15	(20)		
Total										
Probability of surviving 1 year	5 out of 7	(71)	8 out of 30	(27)	2 out of 6	(33)	15 out of 43	(35)		
Probability of surviving 2 year	3 out of 5	(60)	2 out of 18	(11)	2 out of 5	(40)	7 out of 28	(25)		
Probability of surviving 3 year	1 out of 3	(33)	0 out of 6	(0)	0 out of 3	(0)	1 out of 12	(8)		

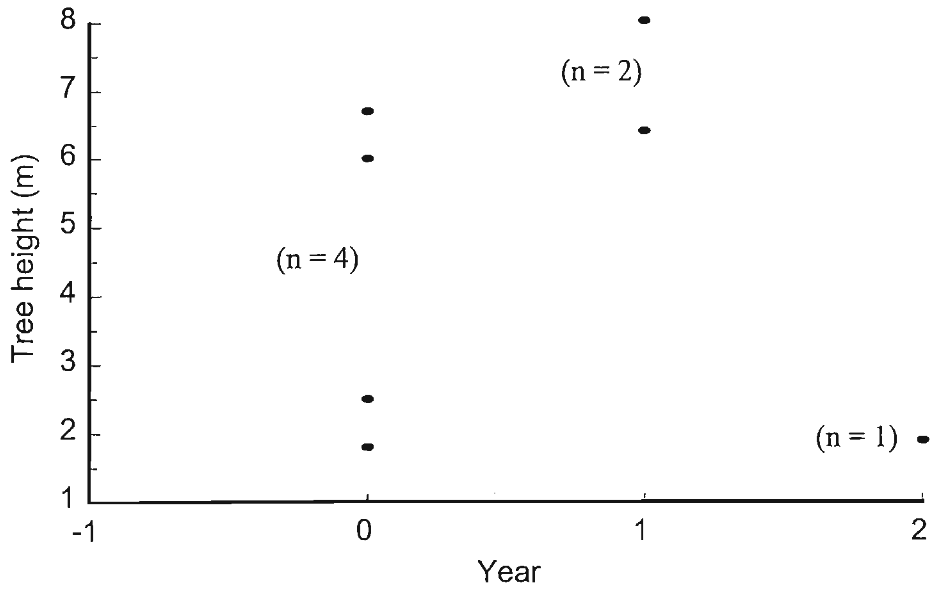


Figure 9.5 Heights of the seven *Acacia tortilis* stems that were partially broken, and were either alive in 2000 (0) or died one (1) and two (2) years after their stems were partially broken in the *Acacia tortilis* woodlands.

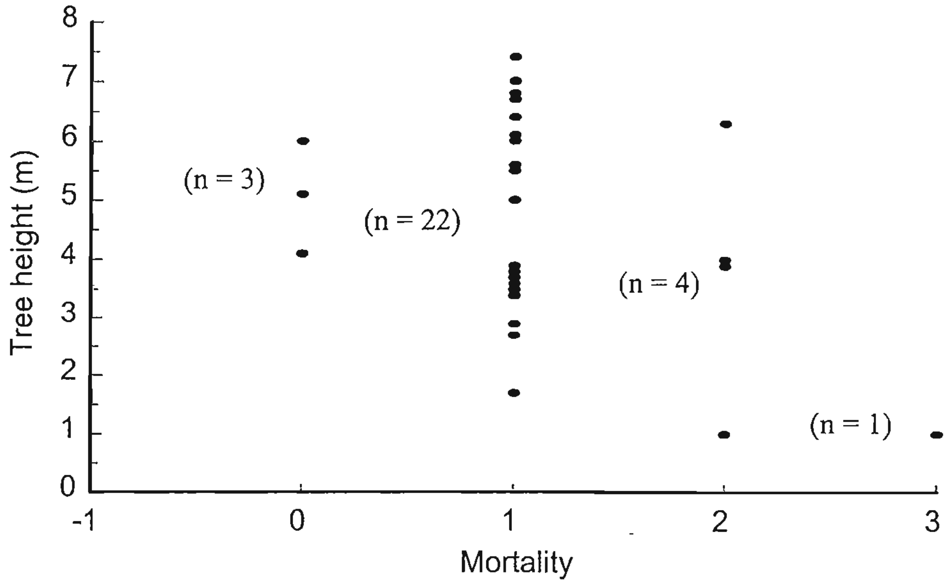


Figure 9.6 Heights of *Acacia tortilis* stems that were completely broken ($n = 30$) in the *Acacia tortilis* woodlands. 0 represents stems that were alive in 2000, whilst 1, 2 and 3 represent stems that died one, two and three years after they were completely broken, respectively.

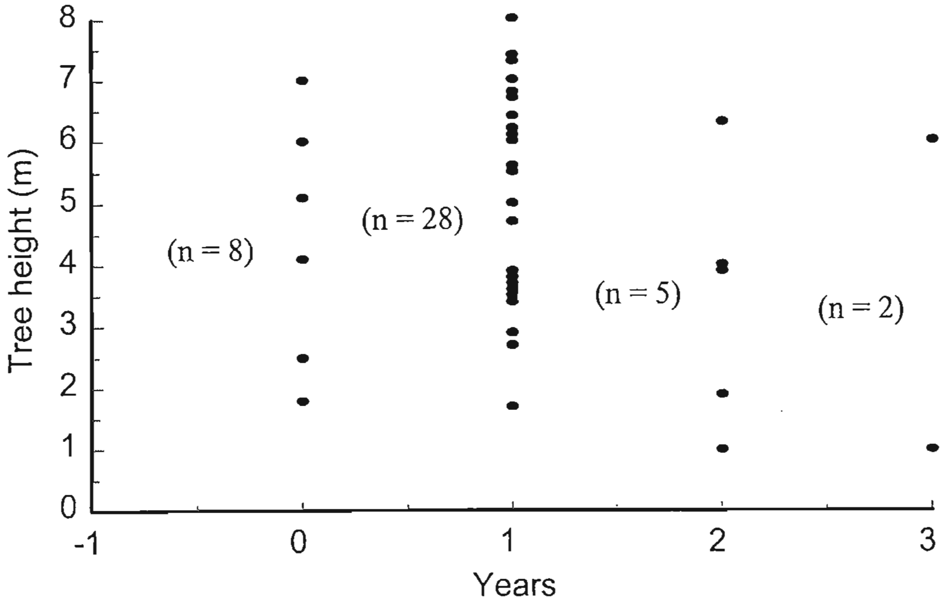


Figure 9.7 Heights of uprooted and broken *Acacia tortilis* stems which either survived (0), died the same or following year (1; mean: 5.2 ± 0.31 m, median: 5.5 m, range: 1.7 - 8.0 m), or died two (2) and three (3) years after they were pushed over (mean: 4.2 ± 0.54 m, median: 4.1 m, range: 1.0 - 7.0 m) in the *Acacia tortilis* woodlands.

The canopies of trees were browsed (0 - 99% of canopy volume) before they were uprooted and one individual had its entire circumference debarked. The total volume of canopy removed before ($F = 0.5$, df = 5, $P = 0.480$) or volume lost during the same year a tree was uprooted ($F = 1.19$, df = 5, $P = 0.276$) did not affect the probability of survival. Although total canopy loss immediately after utilization did not affect the probability of a tree surviving at least one year ($F = 2.39$, df = 5, $P = 0.122$), the four trees that died the same or following year they were uprooted lost 100% of their canopy after being uprooted and the trees that survived at least one year lost only 6% and 63% of their canopy. It would appear, therefore, that survival (for one to two years) may depend on a portion of the canopy remaining intact after utilization. The inevitable death of uprooted trees (Table 9.13) irrespective of past canopy browse damage reflects the poor ability of *A. tortilis* to recover from uprooting. Canopy loss from those two trees that survived more than one year progressively increased.

Unfortunately it is unknown whether the increased loss was the result of dieback or elephant browsing after being uprooted. Nevertheless, canopy loss owing to either dieback or browsing did not exceed 25% after a tree had been uprooted.

Acacia tortilis stems that were broken were also subjected to debarking and canopy removal before they were broken. Four stems were debarked (one tree had its entire circumference debarked) prior to their death, whilst two trees were alive in 2000 despite being debarked and having completely and partially broken stems in 1999. The incidence of debarking on stems, either before or after they were broken, did not affect their probability of survival ($F = 0.41$, df $= 36$, $P = 0.523$). Only nine stems were not browsed prior to being broken ($n = 37$), but they were broken in 1997 and 1998; trees broken in 1997 and 1998 had only one and two years, respectively, during which they could be browsed, considering canopies were browsed since only 1996. Although trees were browsed (1 - 99% of canopy volume) up to three years before their stems were broken, accumulated canopy removal (calculated by adding the midpoints of each class) before breakage did not affect the probability of survival ($F = 0.8$, df $= 36$, $P = 0.371$). Similarly, the volume of the canopy lost when the stem was broken did not affect the probability of survival ($F = 0.01$, df $= 36$, $P = 0.905$). The total accumulated percent of canopy lost subsequent to the stem being broken, however, did affect the probability of survival ($F = 7.1$, df $= 36$, $P = 0.008$).

Trees that died either the same or following year their stems were broken ($n = 24$) had a mean canopy removal of 100% (range: 95 - 100%), whilst trees that survived one or more years after their stems were broken ($n = 13$) had a mean canopy loss of 84% (range: 56 - 99%). Survivors consisted of both partially ($n = 5$) and completely ($n = 8$) broken stems (Table 9.13). The probability of survival was not affected ($F = 2.68$, df $= 36$, $P = 0.101$) by the nature (partial or complete) of the broken stem. Theoretically, completely broken stems should have no canopy remaining because the canopy would be completely separated from the roots. Coppice is the likely explanation for the presence of some canopy after stems were completely broken, whilst partly broken stems were able to support a reduced canopy through that part of the stem that was intact. A broken stem may therefore lose its entire canopy and survive (1 to 3 years) on coppice growth alone.

Debarking

Debarking frequency reached a maximum in 1998 and subsequently decreased (Table 9.15). The high incidence of debarking recorded in 1998 followed an above average rainfall season (1996/97) and coincided with a period of below average rainfall (Figure 3.5). Considering changes in stem density per height class were only significant in 1999 and 2000, the decrease in the frequency of debarking incidents after 1998 might be associated with the reduced availability of trees in 1999, particularly in the 6 - 7 m height class.

Table 9.15 Annual debarking frequency distributions and the number of new trees debarked each year in the *Acacia tortilis* woodlands. The debarking classes are defined as the percent circumference of bark removed from the stem

Debarking class (%)	Year					Total
	< 1996, 1996	1997	1998	1999	2000	
1 - 10	2	1	3	3	0	9
11 - 25	0	2	3	1	0	6
26 - 50	0	0	1	1	1	3
51 - 75	1	2	0	0	0	3
76 - 90	0	0	0	0	0	0
91 - 99	0	0	0	0	0	0
100	0	0	2	0	0	2
Total	3	5	9	5	1	23
New trees	3	5	3	2	0	13

Debarking never affected more than 7% of the total stem density (Table 9.15) during any given year. Thirteen *A. tortilis* stems were subjected to 23 debarking incidents (Table 9.16) until 2000, although most ($n = 11$) stems were debarked between 1996 and 1999. Elephant most frequently debarked < 25% of the stem circumference. The first two debarking classes accounted for more than two thirds of the debarking incidents until 2000 (Figure 9.8).

Approximately half ($n = 7$) of the 13 debarked *A. tortilis* trees were revisited, although never more than three times. Three stems were revisited for a third time in 1999 when < 25% of their circumference was removed.

Table 6.16 Diameter and height statistics of *Acacia tortilis* stems ($n = 13$) that were debarked by elephant in the *Acacia tortilis* woodlands

	Diameter (cm)	Height (m)
Mean (± SD)	24.5 (± 9.4)	6.3 (± 1.6)
Median	24.5	6.7
Range	2.3 - 42.6	1.0 - 7.4

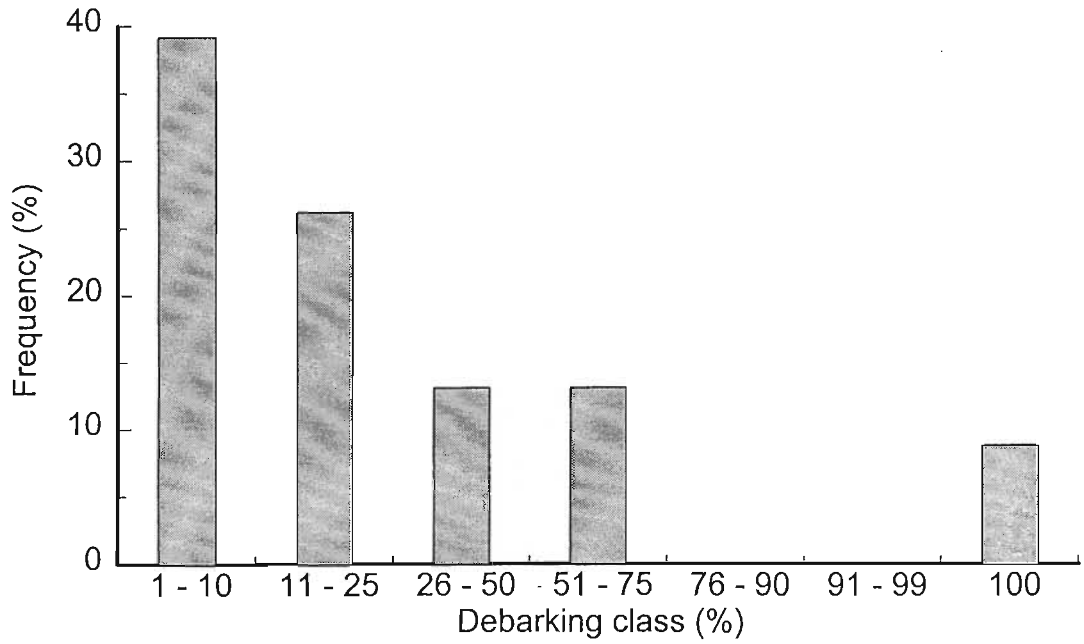


Figure 9.8 The utilization frequency (%) of debarking classes ($n = 23$) until 2000 in the *Acacia tortilis* woodlands. Debarking classes were defined as the percent circumference of bark removed from the stem.

Time between revisits ranged from < 1 to 3 years (mean: 1.3 years). Only stems with diameters > 20 cm and taller than 6 m were revisited. Although there was a weak correlation ($r = -0.2$, df $= 5$, $P > 0.05$) between the percent circumference of bark removed during the first and second debarking incidents, the negative correlation confirmed that severe initial debarking incidents were most likely to be followed by less severe debarking incidents and *vice versa*. Three trees had almost 100% of their stem circumference debarked after the second time they were debarked in 1998 (1997: 51 - 75%, 1998: 11 - 25%), but this was not fatal; one tree was still alive in 2000, whilst the remaining two died after their stems were broken the following year. The frequency of utilization (Figure 9.9) was correlated with stem diameter ($r = 0.6$, df = 11, $P > 0.05$) and to a lesser extent, tree height ($r = 0.4$, df = 11, $P > 0.05$).

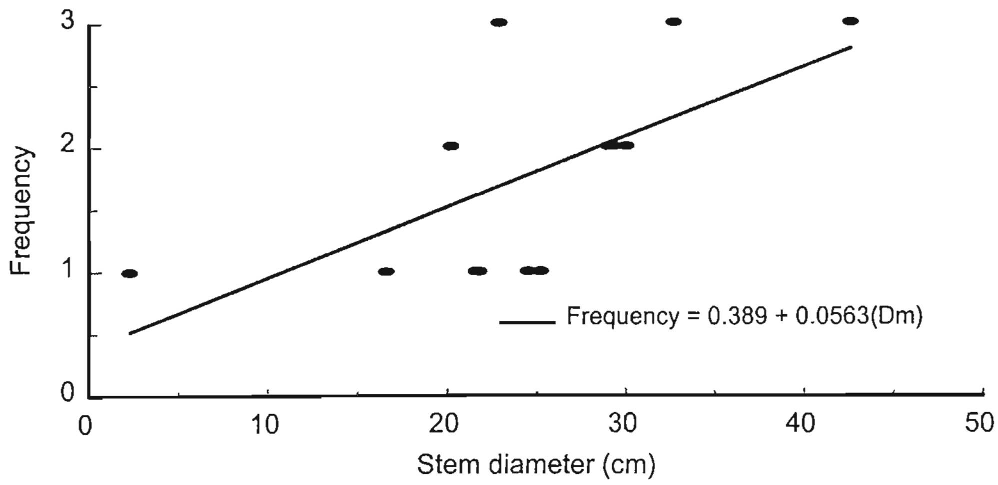


Figure 9.9 Scatter plot and linear regression ($n = 13$, $R^2 = 35.1$, $P = 0.02$) of stem diameter (cm) and debarking frequency per tree in the *Acacia tortilis* woodlands.

The one-year lag between the frequency of first and later (2nd and 3rd) debarking incidents (Figure 9.10) suggests a close association between the frequency of 'follow-up' debarking incidents and the number of new trees debarked the previous year. Only two of the seven trees that were debarked more than one year ago were revisited.

Debarking incidents which removed < 50% of the stem circumference occurred over a large range of stem diameters and tree heights, relative to severe debarking incidents (> 50% - 100%) which were restricted to trees either greater than 20 cm diameter or 6 m in height (Figure 9.11).

There was no correlation between stem diameter, tree height and the percent circumference of stem that was debarked (measured as the midpoint of each debarking class). Considering that 85% of the debarked trees were > 6 m, it is concluded that trees < 6 m in height were generally avoided.

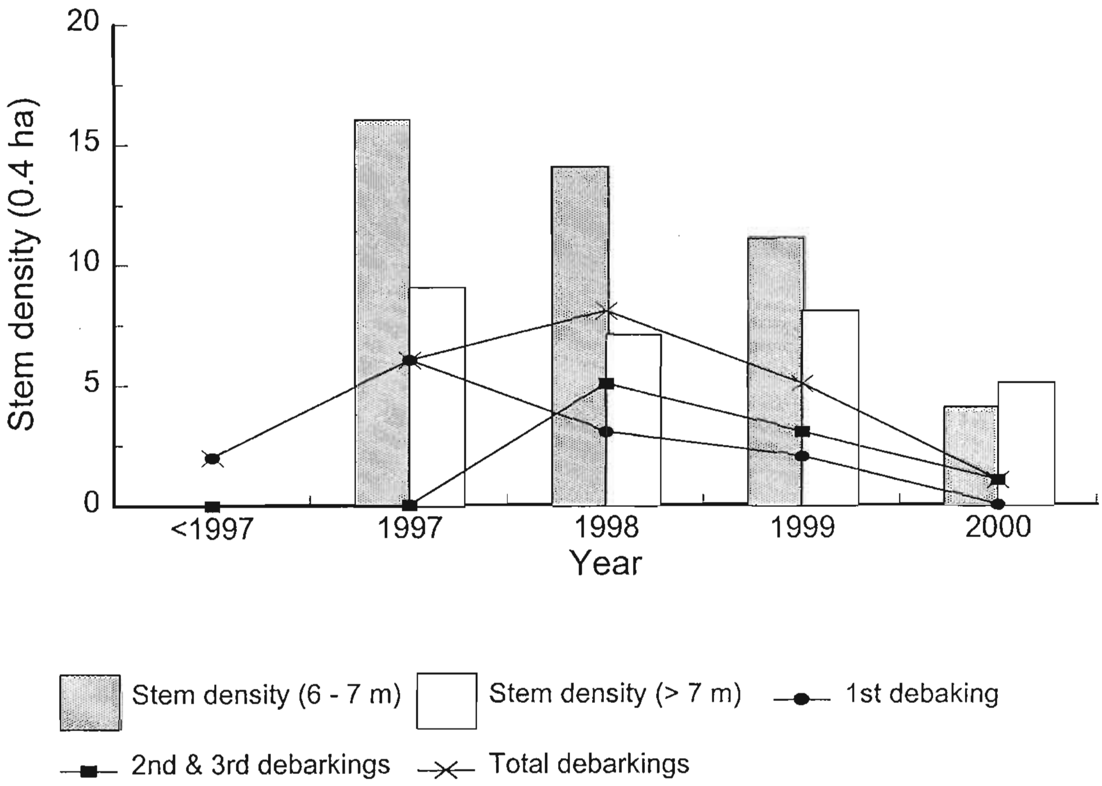
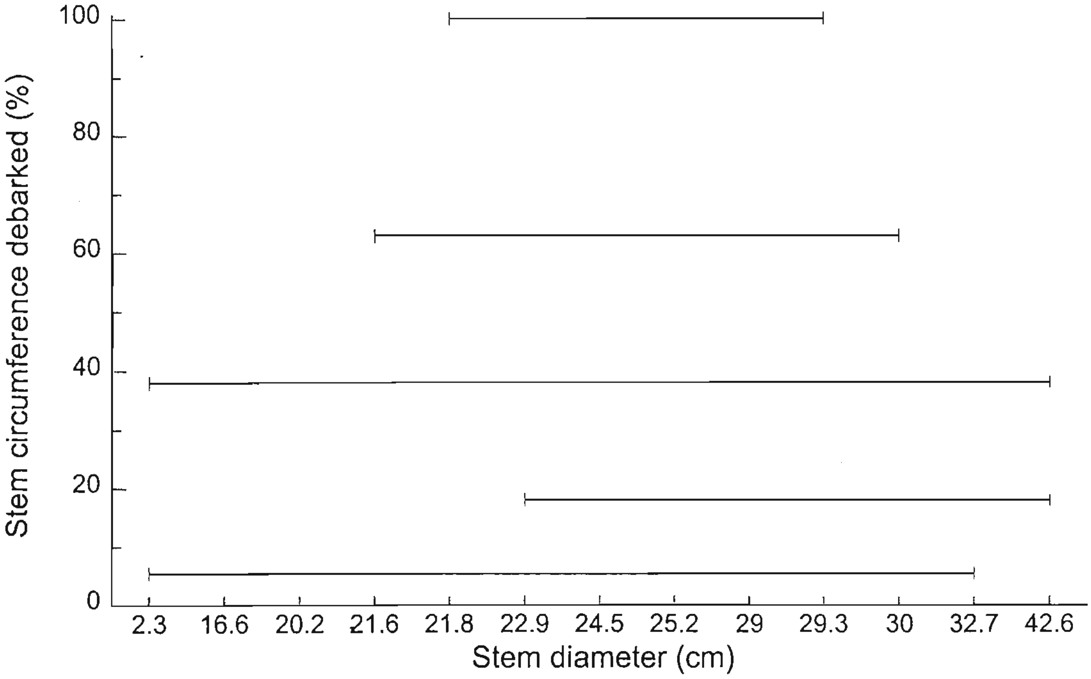


Figure 9.10 The number of *Acacia tortilis* trees debarked each year in the *Acacia tortilis* woodlands compared with annual stem density per height class. Stem density is the number of trees in the preferred height classes (> 6 m) at the end of the previous year and therefore the number of trees available for the current year.

One tree < 1 m had up to 50% of its stem circumference removed, but was the consequence of a canopy browsing incident rather than a deliberate debarking. It is therefore unlikely that this height class was sought after for debarking. The second debarked tree less than 6 m had only 1 - 10% of its stem circumference and stem height removed. It would appear that trees < 6 m in height were too small to be debarked. This does not, however, exclude the possibility of smaller trees being debarked, considering branches removed from the canopy can strip bark from the stem.



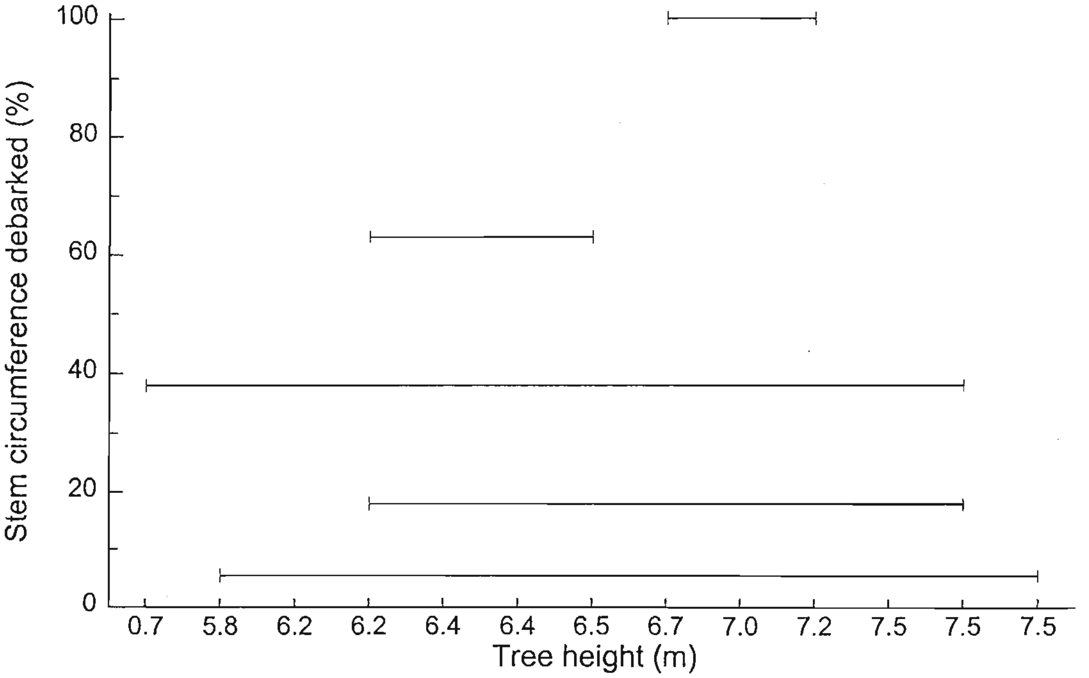


Figure 9.11 Range in stem diameters (cm) and tree heights (m) utilized by elephant for the different debarking classes in the *Acacia tortilis* woodlands. Debarking classes are defined as the percent circumference of bark removed from the stem, and represented by the midpoint of each class.

Debarking was restricted mostly to trees in the 6 - 7 m ($n = 6$) and > 7 m ($n = 5$) height classes (Table 9.17). Overall utilization since the re-introduction of elephant (Table 9.17) indicated that elephants preferred to debark trees greater than 6 m in height. Consequently, elephants did not debark *A. tortilis* stems in proportion to their abundance, avoiding trees < 5 m.

Table 9.17 The number of *Acacia tortilis* stems per height class with 1 - 75% or 100% of their stem circumference debarked in the *Acacia tortilis* woodlands and preferred height classes for each year and the period 1991 to 1999. Trees that were absent are indicated by an asterix. Preference ratios estimated for 1997 and the period 1991 - 1999 used the reconstructed population structure of 1996, whilst 1998 and 1999 preference ratios were estimated using the previous year's stem densities for each height class

Height class	Debarking class (%)		Preference ratios			
(m)	1 - 75	100	1997	1998	1999	1991 - 1999
< 1	1	0	*	0	2.2	*
1 - 2	0	0	0	0	0	0
2 - 3	0	0	0	0	0	0
3 - 4	0	0	0	0	0	0
4 - 5	0	0	0	0	0	0
5 - 6	1	0	0	0	0	0.6
6 - 7	5	1	2.9	0	2.6	2.2
> 7	4	1	2.6	9.1	0	3.2
Total	11	2				

Debarking will only reduce tree height if it results in dieback at the top of the canopy from the death of a prominent branch. The mean increase in tree height one year after the first debarking (0.09 m) was not significant ($t = 0.88$, df = 10, $P = 0.4$), indicating that debarking, which ranged from 1 - 75%, does not result in large (> 0.1 m) changes in tree height. However, errors associated with estimating height by different field workers each year means that small changes in tree height resulting from growth or canopy dieback can not be accounted for, with any degree of precision or accuracy, particularly over a three year period (1997 - 2000) in a semi-arid environment.

Half of the debarked stems coppiced and one quarter of them showed signs of reduced vigour (dying), but there were no fatalities. The total percent volume of canopy removed until the last debarking incident ranged from 6% - 63% and may have confounded individual tree response to debarking. The three debarked trees with reduced vigour (dying) (Table 9.18) in 2000 had only 12 - 30% of their canopies removed.

Table 9.18 The response (unaffected, coppice, reduced vigour or dead) of *Acacia tortilis* stems (n = 12) to debarking by elephant in the *Acacia tortilis* woodlands, including the time taken (years) to respond and tree heights specific to each response. Height represents the heights (m) of trees when they were first debarked, whilst n is the number of trees

Response	n	Circumference debarked (%)	Time (years)	Height (m) mean	range
coppice	2	100	0	7.0	6.7 - 7.2
	2	51 - 75	1	7.0	6.4 - 7.5
	2	1 - 10	1 - 2	6.4	5.8 - 7.0
Total	6			6.7	5.8 - 7.5
reduced vigour	1	76 - 90	2	6.5	
	1	11 - 25	1	7.5	
	1	1 - 10	1	6.2	
Total	3			6.7	
unaffected	12	1 - 90	0 - 1	6.7	5.8 - 7.5

Five debarked *A. tortilis* stems died. Death was not, however, the result of debarking, but rather uprooting ($n = 1$) and broken stems ($n = 4$), which occurred one year after the last debarking. Two trees had their entire circumference (100%) debarked in 1998 and died the following year; the one tree was uprooted, whilst the other had its stem completely broken in 1999. Consequently, the time taken to die after a stem has been 100% debarked is unknown.

Three stems had more than 50% of their stem circumference removed in 1996 (n = 1) and 1997 (n = 2). The one tree debarked (50 - 75%) in 1996 was still alive in 2000, despite additional debarking in 1998 (11 - 25%) and canopy removal twice in 1999 (1 - 10% on each occasion). Both trees debarked (50 - 75%) in 1997 had their stems partially broken in 1999; one was alive in 2000. The tree that died in 2000 had 100% (1997: 51 - 75%; 1998: 11 - 25%; 1999:1 - 10%) of its stem circumference removed from accumulated debarking incidents, apart from a broken stem. Trees with more than 50% of their circumference debarked are therefore capable of surviving up to four years, despite additional debarking, canopy removal and broken stems. Debarking can not be established as a mortality agent, especially given the confounding influences of uprooting and broken stems.

All except three debarked trees were browsed 1 - 2 years before they were debarked. On average, approximately 25% of the *Acacia tortilis* canopies were removed by browsing (range: 1 - 75%) before trees were debarked. Mean canopy loss associated with debarking (due to either browsing or dieback) was low, relative to the stem circumference that was debarked (Table 9.19).

Table 9.19 The amount of canopy lost (to either browsing or dieback) after debarking (n = 12) in the *Acacia tortilis* woodlands. Debarking is the total percent of stem circumference debarked until 2000 or until the tree was uprooted or broken. The percent volume of canopy lost is the total volume of canopy lost from the first debarking until 2000 or until the tree was uprooted or broken. Accumulated amounts of canopy and bark removal were calculated by adding the midpoints of each class used to rank canopy removal and debarking, respectively

	Debarking (%)	Canopy lost (%)
	6	6
	36	6
	63	0
	100	0
	63	6
	18	24
	44	38
	81	24
	81	56
	6	44
	100	0
	6	6
mean	50.3	17.5
median	53.5	6
range	6 - 100	0 - 56

Stems that had their entire stem circumference debarked did not experience canopy dieback that same year (Table 9.19). Unfortunately their stems were broken the following year. Debarking should not result in canopy dieback unless prominent branches are isolated from the main stem by debarking which extends from the stem into the canopy (personal observation). The debarking of *A. tortilis* trees rarely (43% of browsing incidents) extended into the canopy. The mean (± SE) percent height of bark stripped from the stem per debarking incident was 63.7% (± 8.77%) (median: 95%, range: 6 - 100%, $n = 23$). Canopy removal either prior to or during debarking did not affect the probability of mortality, considering six of the 13 debarked stems, that were not uprooted or broken, were alive in 2000.

There was a weak correlation ($r = 0.45$, df = 21, $P < 0.05$) between percent circumference of stem debarked and percent height of stem debarked. The percent height of stem that was debarked when debarking incidents removed < 10% of the stem circumference (mean ± SE: 30.4 ± 13.60, median: 6, $n = 9$) was significantly less ($t = 3.56$, df = 12, $P = 0.004$) than the percent height removed from stems which had > 10% of their circumference debarked (mean ± SE: 85.1 ± 7.10, median: 100, $n = 14$).

Factors influencing the different methods of feeding

Browse frequency, browse volume, tree height or their interactions did not influence the probability of *A. tortilis* stems being broken. However, half the number of broken stems had lost almost 80% of their canopy volume on account of browsing prior to them being broken (Table 9.20). Nor did browse frequency, browse volume, tree height or their interactions influence the probability of trees being browsed only (e.g. not uprooted, debarked or broken). The probability of stems being debarked was significantly dependent, however, on tree height ($F = 10.55$, df = 66, $P = 0.001$) and browse volume ($F = 5.29$, df = 66, $P = 0.021$); debarked trees were taller than 5 m, with one exception, and never had more than two thirds of their canopy browsed before they were debarked (Table 9.20). The probability of being uprooted was significantly dependent on browse frequency ($F = 6.98$, df = 66, $P = 0.008$); uprooted trees ($n = 6$) were browsed only once before they were uprooted.

Significant differences existed in browse frequency ($F = 4.06$, df = 66, $P = 0.01$), browse volume ($F = 4.78$, df = 66, $P = 0.005$) and tree height ($F = 5.62$, df = 66, $P = 0.002$) among the different types of utilization (Table 9.20), including trees that were only browsed. Debarked stems were taller than stems that were broken or only browsed, whilst uprooted stems were taller than stems that were only browsed (Table 9.20; LSD = 1.59, df = 63, $P < 0.05$). Debarked and uprooted trees were, on average, taller than trees that were only browsed because the aforementioned trees were taller than 4 m, whilst browsed trees occurred across the full range of height classes, with the exception of trees < 1 m.

Table 9.20 The browse frequency, browse volume (%), and height (m) of trees that were debarked (n = 11), uprooted (n = 6), broken (n = 34) or only browsed (n = 16) in the *Acacia tortilis* woodlands. Browse frequency is the number of browsing incidents per tree before the stem was debarked, uprooted or broken, browse volume is the sum of the midpoints of each class used to rank percent volume of canopy browsed before a tree was debarked, uprooted or broken, and tree height is the height of a tree when it was first browsed

Statistics	Browse frequency			
	Debarked	Uprooted	Broken	Browsed
mean	1.7	0.5	1.2	1.8
median	2	0.5	1	1
range	1 - 3	0 - 1	0 - 3	1 - 4
	Browse volume (%)			
	Debarked	Uprooted	Broken	Browsed
mean ± SE	27.5 ± 5.58	21.8 ± 15.07	62.4 ± 6.25	60.6 ± 9.12
median	30	9	77.5	66
range	6 - 63	0 - 95	0 - 100	6 - 100
	Height (m)			
	Debarked	Uprooted	Broken	Browsed
mean ± SE	6.7 ± 0.17	5.9 ± 0.38	4.5 ± 0.35	4.3 ± 0.51
median	6.7	6	4.1	3.6
range	5.8 - 7.4	4.7 - 7.3	1 - 8	1.9 - 9.5

Broken (and recumbent stems: $t = 0.80$, df = 27, $P = 0.216$) were not taller than trees that were only browsed and had the greatest mean percent volume of canopy removed by browsing (Table 9.20), indicating that trees were within the limit of the upper reach of an adult elephant before they were pushed over. It is concluded that the feeding response of elephant to *A. tortilis*, specifically the distinction between pushing trees over and browsing the canopies of trees, was independent of tree size.

Elephant utilization of riverine *Acacia tortilis*

Population structure

The recruitment of *A. tortilis* seedlings in 1998 accounted for the large increase in stem density that year (Table 9.21) and coincided with the increased seedling recruitment on *A. tortilis* woodlands (Table 9.2). The high mortality rate in 1999 was attributed to the mortality of seedlings, most likely on account of insufficient soil water during a season of below-average rainfall (Table 9.21).

Table 9.21 Stem density (ha) of *Acacia tortilis* per height class in riverine vegetation between 1997 and 1999, and annual rainfall (July to June inclusive).

Height class (m)	Year		
	1997	1998	1999
< 1	33	48	27
1 - 2	3	3	3
2 - 3	5	4	4
3 - 4	6	2	1
4 - 5	5	6	3
5 - 6	14	12	11
6 - 7	14	15	11
> 7	31	33	38
Total stem density	111	123	99
Mortality rate (% an^{-1}):		3	17
Season	1996/97	1997/98	1998/99
Rainfall (mm an^{-1}):	383.7	132.9	335.8

Apart from fluctuations in stem density owing to episodic recruitment of seedlings, stem density remained below 112 stems ha^{-1} corresponding to the stem density of *A. tortilis* woodlands in 1999 (Table 9.2), after which time elephant activity was absent. Although approximately 50% of *A. tortilis* stems were > 5 m (Figure 9.11) in both the woodlands (mean height ± SD: 4.8 m ± 1.90 m) and riverine vegetation (mean height ± SD: 4.7 m ± 3.61 m), the distribution of *A. tortilis* stems in the riverine vegetation (n = 155) was significantly (P < 0.001) different from the woodlands (n = 69). Apart from the greater proportion of trees < 1 m in the riverine vegetation, approximately 25% of the trees were between 7 and 13 m compared with 6 and 10 m in the woodlands. Twenty percent of the trees in the riverine vegetation were taller than 8 m, whilst only 1% of the trees in the woodlands were taller than 8 m.

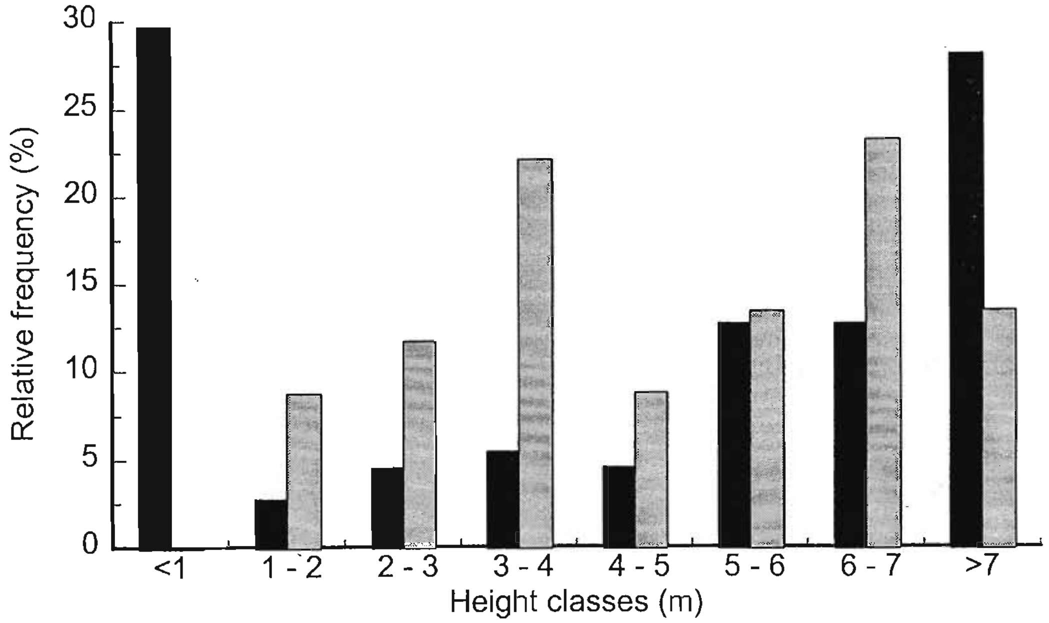


Figure 9.11 The height frequency distribution (1 - 2 = 1 - < 2, etc.) of *Acacia tortilis* stems in riverine vegetation (black) during 1997 compared with *Acacia tortilis* woodlands (grey) before stem breakage or uprooting by elephant (1996).

Canopy removal

Elephant first browsed *A. tortilis* trees within riverine vegetation circa 1996 (Table 9.22), and coincided with the onset of canopy browsing in the *A. tortilis* woodlands (Table 9.3). Browse frequency decreased after 1996 and remained relatively constant each year, corresponding to the browse frequency observed in the *A. tortilis* woodlands when stem density had decreased in 1999 (Table 9.2). Elephant rarely removed as much as 26 to 50% of the canopy during a browsing incident (Table 9.22) and accumulated canopy volume removed between 1996 and 1999 never exceeded 56%. Consequently, canopy removal by elephant within the riverine vegetation did not induce mortality, compared with the *A. tortilis* woodlands (Table 9.6).

The number of trees browsed decreased each year between 1996 and 1999. First browse incidents occurred in 1996 and 1997. Thereafter elephant browsed mostly trees which had been previously browsed (Table 9.22), most likely on account of the reduced availability of unbrowsed trees in the larger (> 3 m) height classes which were favoured (PR: 3 - 4 m = 2.5, 4 - 5 m = 1.8, 5 - 6 m = 1.7, > 7 m = 1.6) by elephant for browsing (Figure 9.12). Trees < 2 m were not browsed, despite an abundance of trees below 2 m relative to the *A. tortilis* woodlands (Table 9.2).

Table 9.22 The number of *Acacia tortilis* trees browsed by elephant within riverine vegetation (combined transects = 1.4 ha) for each year between 1996 and 1999. Browse frequencies are recorded for each canopy removal class. Canopy removal classes express the percent volume of canopy removed and are represented by the midpoint of each class

Canopy removal (%)	Year 1996	1997	1998	1999	Total
6	26	6	6	5	43
18	6	3	4	3	16
38	1	0	0	1	2
63	0	0	0	0	0
83	0	0	0	0	0
95	0	0	0	0	0
100	0	0	0	0	0
Total	33	9	10	9	61
Number of trees first browsed	33	9	1	3	46

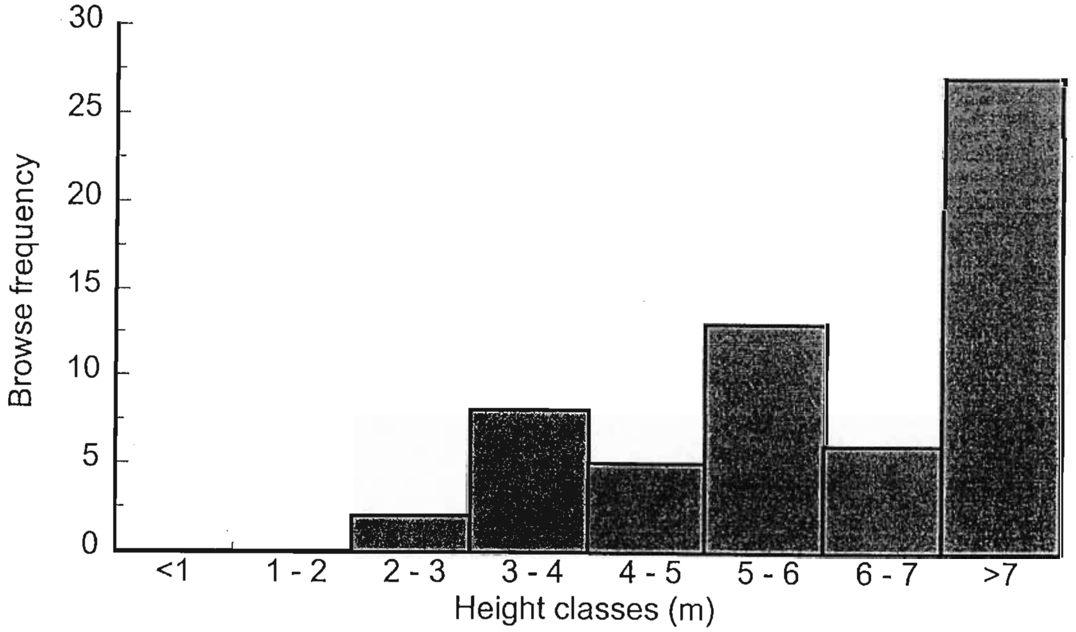


Figure 9.12 Browse frequency of *Acacia tortilis* trees within riverine vegetation for each height class (1 - 2 = 1 - < 2, etc.) between 1996 and 2000. Sixty-one incidents of browse were recorded on 46 trees.

Broken and uprooted stems

No trees < 1 m or > 7 m were uprooted or broken. Two stems (2.6 and 3.5 m tall) were uprooted between 1996 and 1999 and died the same year they were uprooted (1998), in accordance with the low probability of survival associated with uprooted stems in the *A. tortilis* woodlands (Table 9.14).

Five stems were either partially or completely broken in 1999. Two trees died that same year and were 4.4 and 6.8 m tall, whilst those trees which survived ranged in height from 1.3 to 6 m before they were broken. Only one tree that survived being broken was reduced in height and lost 54% of its original (1.3 m) height. It was not possible to calculate the probability of survival for one year considering transects were not revisited in 2000. Nevertheless, the seven stems which were pushed over (uprooted or broken) between 1996 and 1999 represent only 4.5% of the population of *A. tortilis* stems measured in the riverine vegetation in 1997. Although utilization was low relative to the number of uprooted and broken stems in the *A. tortilis* woodlands (Table 9.9), the mortality of middle-age (1 - 5 m) stems in the riverine vegetation potentially could affect the rate of replacement of the larger trees in those plant communities considering there was a low abundance of stems in those height classes (Figure 9.11).

Debarking

Four stems were debarked between 1996 and 1999. One debarking incident removed 100% of the bark from the stem circumference in 1996 and the tree died three years later in 1999, suggesting a high tolerance to debarking. Debarking does therefore function as a mortality factor, albeit negligible. The remaining three debarking incidents which occurred in 1996 (*n* = 2) and 1998 (*n* = 1) removed < 50% of the bark from the stem circumference. Stems were not revisited and were taller than 4 m, corresponding to the heights of debarked stems in the *A. tortilis* woodlands (Table 9.18).

Elephant utilization of *Acacia nilotica* woodlands

Elephant responded differently to the *Acacia nilotica* woodlands which consisted mostly of mature trees (Table 9.23) compared with the *A. tortilis* woodlands. *Acacia nilotica* was primarily debarked. Elephant had utilized 60 of the 69 stems (47 live and 22 dead stems) on 0.5 ha by

1999; six stems died from moisture stress and unknown causes, whilst the remaining 16 stems (23.2%) were killed from elephant-related influences. Six stems died from being severely (91 - 100%) debarked. Eighty percent of those stems utilized by elephant were debarked, 30% of the stems were browsed (mean volume ± SE: 43.2 ± 9.22%, median: 28%, range: 6 - 100%, $n = 18$) and 7% were pushed over. Half the number of debarked trees lost parts of their canopy on account of dieback (mean volume lost ± SE: 32.4 ± 5.94%, median: 18%, range: 6 - 100%, $n = 28$). The volume of canopy lost to dieback on *A. nilotica* trees ($n = 25$) was significantly greater ($t = 1.83$, df = 31, $P = 0.038$) than the volume of canopy lost due to either browse or dieback after debarking on *A. tortilis* stems ($n = 12$). The mean (± SE) percent circumference and height of *A. nilotica* stems ($n = 48$) removed by debarking was 56.5 ± 4.77% and 95.3 ± 2.82%, respectively (median: 63% and 100%, respectively). Debarking extended into the branches of 94% of debarked *A. nilotica* stems. The percent height of bark removed from the stem was significantly greater ($t = 3.43$, df = 27, $P = 0.001$) on *A. nilotica* than on *A. tortilis* stems.

Table 9.23 Tree density (ha) of live and dead *Acacia nilotica* (multi-stemmed) trees per height class in 1999

Height class (m)	Tree density
< 1	0
1 - 2	0
2 - 3	0
3 - 4	2
4 - 5	4
5 - 6	16
6 - 7	14
> 7	40
Total	76

Discussion

The functional response of elephant to *Acacia tortilis*

The favoured method of feeding differs between and within woody species. Elephant respond to different species of woody plants by removing branches from the canopy, stripping bark from the stem and/or uprooting (and breaking) entire trees. *Acacia tortilis* in the Northern Province, South

Africa, had branches removed, was pushed over (uprooted or broken) and occasionally debarked. Elsewhere, *A. tortilis* has been debarked (Anderson & Walker 1974; Barnes 1982; Mwalyosi 1987, 1990) or had branches removed, uprooted and occasionally debarked (Croze 1974b; Kalemera 1989; Ruess & Halter 1990). In contrast, *Acacia nilotica* (woodlands) in the Northern Province was debarked and occasionally pushed over or have branches removed, whilst *Colophospermum mopane* has had branches removed (Lewis 1986) or stems broken and occasionally uprooted (Anderson & Walker 1974). It would appear, given the variability of feeding methods used by elephant both within and between species, that each ecosystem is unique and will need to be managed accordingly.

Nevertheless, factors influencing elephant response are usually relate to the size of a tree and therefore the height distribution of the tree population. The method of feeding on *A. tortilis* woodland trees in the Northern Province was independent of tree height, apart from trees < 4 m not being uprooted or debarked, considering the canopies of most trees were browsed before they were pushed over. However, fewer *A. tortilis* trees were pushed over or debarked in the riverine vegetation and is attributed to the greater proportion of smaller (< 1 m) and larger (> 8 m) trees than in the woodlands. The population structure of riverine *A. tortilis* trees could have induced less response from the elephant considering *A. tortilis* trees < 1 m are usually avoided (Vesey-Fitzgerald 1972; Croze 1974b; Pellew 1983a; Ruess & Halter 1990), and many large *A. tortilis* trees are unable to be uprooted by elephant (Croze 1974b). Elephant damage to *Pterocarpus angolensis* in Zimbabwe was characterized by the uprooting of many small trees, whilst larger trees were mainly debarked (Campbell *et al.* 1996). In East Africa, where the canopy of mature *A. tortilis* trees exceeds 10 m, Croze (1974b) suggested a mechanical reason related to feeding for which to push over trees. The greater frequency of uprooted trees above 6 m than trees with broken branches above 6 m was attributed to the limit of the upper reach of an adult elephant (± 6 m). It is concluded that elephant respond to a tree in any manner befitting within the mechanical constraints of a certain size or species.

The relatively low abundance of *A. tortilis* trees in the riverine vegetation, compared with the woodlands, is also expected to have influenced elephant response considering total stem area of *A. tortilis* in riverine vegetation has been reduced by > 80% (Anderson & Walker 1974) when it was the dominant tree and the method of feeding was predominantly debarking.

Elephant first browsed the canopies of *A. tortilis* trees in the Northern Province before adopting additional methods of feeding when the availability of unbrowsed trees decreased after one to two years. Initial browse frequency may be determined by elephant density considering a similar number of trees were first browsed in the riverine vegetation and *A. tortilis* woodlands (33 and 43 trees, respectively). Subsequent browse frequency under the same elephant population may then depend on stem density. The annual browse frequency decreased each year in the *A. tortilis* woodlands, corresponding to a decrease in stem density, until 10 and zero browse incidents were recorded in 1999 and 2000 when stem density was reduced to 143 stems ha^{-1} and 90 stems ha^{-1}, respectively, compared with the nine to 10 browse incidents each year within the riverine vegetation which contained 99 to 123 stems ha^{-1}, depending on seedling recruitment. Mwalyosi (1990) observed a decline in the frequency of trees killed by elephant to 11% when stem density was reduced to 75 trees ha^{-1}, whilst Ruess & Halter (1990) recorded 8.4% dead trees when the population of *A. tortilis* trees had been reduced to 53.2 trees ha^{-1}. Considering the percent of trees either utilized or killed decreases with the stem density or the relative abundance of a species, the aforementioned factors together with woodland structure appear to be relevant determinants of elephant response to this species.

Elephant may prefer to browse trees not previously browsed on account of the ability of *A. tortilis* to increase total phenol and tannin contents upon being defoliated (Bryant *et. al.* 1991). Although elephant uprooted or broke stems after they browsed their canopies, there was little evidence (personal observation) to suggest they browsed the canopies of trees they had pushed over. Canopy loss after trees had been pushed over was more often the result of dieback owing to stress.

The elephant population in VLNR had no mature bulls. Elephant bulls, which congregate in small groups of ever-changing composition, are usually responsible for the destruction of woodlands (Croze 1974a) compared with family units comprising mostly adult and sub-adult females. The population dynamics of the *A. tortilis* woodlands may therefore have differed, had the elephant population in VLNR contained mature bulls.

The biological response of *Acacia tortilis* to elephant feeding

Acacia tortilis responded differently to each method of elephant feeding in the Northern Province. Tree response also varied considerably among individuals, suggesting additional influences.

In the Northern Province and East Africa (Croze 1974b) *A. tortilis* has a low ability to recover from being pushed over (uprooted or broken). Mwalyosi (1987) found that younger *A. tortilis* trees had a greater chance of survival after being debarked than older trees. Although uprooting or stem breakage may be a more severe form of feeding, the ability of trees to survive being uprooted or broken did not depend on their size (or age) in the Northern Province, although the period of survival did depend on the percent of height lost. The ability of a species to recover from elephant use is most likely dependent on its ability to coppice and replace lost canopy with regrowth (Lewis 1986), considering relatively few uprooted or broken trees had coppiced. Multi-stemmed coppicing of *Brachystegia* (Jachman & Bell 1985) and *C. mopane* (Styles & Skinner 2000) woodlands results in a scrub morph with a large biomass at an accessible height to elephant. *Colophospermum mopane* is capable of sustaining relatively low rates of mortality (Lewis 1991) and continue to produce seeds and nutritious leaves (Styles & Skinner 2000) despite high levels of herbivory.

It appears that trees in the woodlands had a greater chance of surviving canopy removal than trees that were pushed over on account of the greater proportion of browsed trees which coppiced. Survival may be related to the severity of the defoliation in which case canopy removal had the potential to induce substantial mortality owing to the number of woodland trees with > 75% of their canopy removed. Similar findings were reported by Croze (1974b), viz. that *A. tortilis* had a low probability ($P = 0.2$) of surviving one year if more than 3/4 of its canopy was removed by elephant. The removal of canopy in the riverine vegetation was not a mortality agent because elephant removed less from those canopies, suggesting that the severity of browse incidents and hence survival was related to the size of a tree, and perhaps stem density. Canopy removal did not induce substantial mortality in the woodlands because browsed trees were often uprooted or broken and the aforementioned methods of feeding had a more sudden and severe effect on tree survival.

Although debarking (and associated attack by wood-boring insects) has induced mortality of *A. tortilis* (Anderson & Walker 1974), it was not a mortality or height-reducing agent in the *A. tortilis* woodlands on account of its low frequency relative to the other more severe methods of elephant feeding and the extent of each debarking incident, compared with *A. nilotica*. Debarking was a mortality agent in the riverine vegetation because fewer stems were pushed over. The response of trees to debarking is therefore influenced by the frequency of uprooted or broken stems. Whether debarking kills trees will also depend on the species concerned and its ability to coppice. An *A. tortilis* stem that has been ringbarked and then broken above the area that was debarked, is likely to die as a result of the broken stem considering death from broken stems generally preceded death from debarking, whereas a *C. mopane* tree that has been debarked and then broken might still survive, given its tolerance of ringbarking (Kelly *et al.* 1976). The volume of canopy dieback associated with debarking is most likely related to the interaction between the percent height and the percent circumference of stem that is debarked. *Acacia nilotica* trees experienced greater canopy dieback and tree mortality on account of debarking, than *A. tortilis* trees, because the former species was more severely debarked; debarking on nearly all the *A. nilotica* trees extended into their canopies, thereby isolating branches in the canopy from the roots.

The functional response of *Acacia tortilis* to elephant feeding

The mature *A. tortilis* woodlands reverted to a more open woodland/grassland, following the re-introduction of 48 elephant since 1991. Bush encroachment was effectively halted and reversed. Population structure changed immediately in 1997 and 1998 after the first signs of elephant utilization in 1996. However, by 1999 and 2000 the negatively skewed population structure was not significantly different from the structure of the benchmark population in 1996, despite three years of persistent utilization and a considerable reduction in stem density. These findings do not coincide with the observed shifts in relative abundance of various size classes in Tanzania (Mwalyosi 1990; Ruess & Halter 1990). This particular population trend is explained by the utilization of trees in proportion to their abundance by 1999 and the high mortality rate of utilized trees in 1999, compared with the utilization of specific height classes in Tanzania (Mwalyosi 1990; Ruess & Halter 1990). *Acacia tortilis* trees were collectively pushed over in proportion to their abundance by 1999 in the Northern Province. Although *A. tortilis* responded to each method of feeding, population trend was almost exclusively determined by either uprooting or stem breakage considering they resulted in the greatest mortality and reduced tree height. Secondly, the greatest mortality of recumbent stems occurred in 1999. Population structure changed significantly in 1997 and 1998 because elephants had reduced tree height but mortality remained below half that which occurred in 1999. Temporary survival of uprooted and broken stems and a below-average rainfall (1997/98, Figure 3.5) season resulted in a four-fold increase in the mortality rate in 1999 compared with1996, despite a relatively consistent number of stems pushed over each year. Despite the height reducing influence of elephant upon trees, Jachman and Croes (1991) suggested that long-term use by elephant might result in a decreasing woody-stem density without significant changes in size class distribution. This study has shown that this woodland response is possible, although not for all species given the ability of some woody species to withstand heavy elephant browsing pressure. In such areas, the size distribution of a tolerable species is affected more than tree density (Van De Vijver *et al.* 1999). Woodland structure is therefore determined by two factors, namely species-specific response or tolerance and elephant response e.g. whether or not elephant feed upon each height class in proportion or disproportion to its occurrence.

Barnes (1983) identified four patterns of tree mortality based on the relationship between percent mortality and tree density. These patterns were determined by a cross-sectional study of each tree population, e.g. at one point in time, and applied longitudinally as tree density changed with time. In contrast, this study related percent mortality to tree density as it changed with time. Barnes's (1983) method of estimating the percent mortality associated with a particular tree density over a period of five years (1971 - 1976) might be considered inaccurate because annual elephant damage after 1971 would not have been representative of the initial tree density considering density changes each year. Nevertheless, the procedure adopted for estimating the pattern of mortality in this study showed that mortality patterns do not accurately reflect elephant activity on account of the lag period between utilization and death and the potential effect of rainfall (and perhaps site conditions) on the period of survival following utilization. Elephant activity was relatively consistent from year to year irrespective of stem density (excluding 2000), particularly concerning the number of stems pushed over and broken. Mortality rate, however, increased until stem density was reduced to 90 stems ha^{-1} at the end of the 1999 season. Although elephant feeding was absent in 2000, the mortality of trees persisted albeit at a lower rate. Annual mortality rate did not reflect current utilization, but rather previous years' damage in addition to some current utilization.

If an annual mortality rate was to be calculated by averaging the difference in stem density by the number of years between the initial and subsequent densities, the estimate of mortality would depend on the period between initial and subsequent density counts because annual mortality changes each year. The aforementioned method of calculating mean annual mortality is misleading because it gives the impression that annual mortality is constant from year to year.

Spatial heterogeneity of herbivory and its implications

Although the *A. tortilis* woodlands and the *A. tortilis* trees within the riverine vegetation belong to the same *A. tortilis* population considering there were no topographic or other boundaries separating the two vegetation types within VLNR, they are referred to as sub-populations because they were influenced either more or less by similar processes of vegetation change. Spatial structure refers to the variable patterning or distribution of individuals within a population of a certain species, e.g. among its sub-populations.

The *A. tortilis* woodlands have been decimated by elephant to a relatively small remnant population of trees, whereas fewer *A. tortilis* trees in the riverine vegetation were pushed-over or debarked. Non-uniformities in browsing pressure is one element (others are heterogeneities of the environment and plant populations themselves) which usually creates spatial structure within a population of a species (Noy-Meir 1996). However, this study has shown that spatial variability of herbivory can reduce spatial structure within a population, owing to the dependance of elephant herbivory upon tree density of *A. tortilis* in VLNR. Consequently, elephant reduced spatial heterogeneity of the *A. tortilis* population, specifically differences in the distribution or density of *A. tortilis* trees between the two sub-populations. It is unlikely, however, that this type of reduced heterogeneity will affect the future resilience of the population to climatic variability, as mentioned by Noy-Meir (1996).

The above finding contradicts drastic changes in species composition and soil condition (Lange 1969) of rangelands in the vicinity of water, owing to the spatial variability of grazing pressure associated with distance from watering points. Thrash *et al.* (1991) found that *Combretum apiculatum* trees were disproportionately selected for by elephants when pushing over trees and that the occurrence of this activity was inversely proportional to distance from water. The aforementioned, compared with elephant utilization of *A. tortilis* in VLNR, emphasizes that spatial variability of elephant herbivory has different consequences for the spatial structure of different species, owing perhaps to a number of factors, including patterns of mortality which are dependent upon tree density (Barnes 1983) and the availability of permanent water.

Communities furthest away from a permanent supply of drinking water serve as refuges for conserving biodiversity and genetic resources. They are consequently potentially valuable as foci for the regeneration and restoration of vegetation closer to water (Noy-Meir 1996). In contrast, the remnant population of *A. tortilis* trees in the woodlands, owing to an absence of elephant utilization when tree density approached the density of trees within the riverine vegetation, is capable of regenerating itself and therefore need not rely on the sub-population within the riverine vegetation as a source of genetic material (or refuge). The proportion of the area recolonized and overall rate of recolonization is usually determined by the spatial pattern of refuges (Noy-Meir 1996): the size of the refuge; the distance between refuges relative to the dispersal distance of the species; the density of plants within refuges and; subsequent seed production of each refuge. However, considering the greater portion of 68 stems ha^{-1} for 2000 were reproductively mature and *A. tortilis* is ungulate-dispersed, the recolonization of the area is less likely to depend on the aforementioned variables, which are most likely intended for areas in which there has been an almost complete decimation of plants, resulting in isolated pockets of refuges and hence source material.

A speculative interpretation of the past and future population processes of the *Acacia tortilis* woodlands

Although the spatial structure of the remnant *A. tortilis* population in 2000 was determined largely by non-uniformities in browsing pressure by elephant, the spatial structure of the *A. tortilis* population prior to elephant impact was most likely determined by a combination of heterogeneities in the environment and non-uniformities in browsing pressure. Seedling establishment is a rare event under conditions of high browsing pressure, with bush encroachment usually coinciding with a decline in small ungulate (impala) populations (Prins & Van Der Jeugd 1993). Successful seedling establishment is further hampered by the species intolerance of shade (Pellew 1983b; Miller 1996) and dependance on extreme or rare recruitment events (Wiegand *et al.* 1995) given germination is controlled by both water potential (-0.14 to -0.6 MPa) and temperature (25 to 30 °C) (Choinsky & Tuohy 1991). Nevertheless, *A. tortilis* has the attributes of a pioneer species, capable of germinating without an extended germination lag, despite stressed conditions following a period of sufficient imbibition (Choinsky & Tuohy 1991), and an effective ungulate-dispersal mechanism (Coe & Coe 1987), thereby ensuring early colonization and dominance of a site (Ben-Shahar 1991). The period (1955 - 1987, O'Connor, submitted) of bush encroachment which led up to the *A. tortilis* woodlands preceded the acquisition of VLNR (1990), after which time the population of indigenous browsers increased (Table 3.1). Considering impala are important pod consumers and therefore dispersal agents (Miller 1996), the density of ungulates (including livestock) at the time of bush encroachment would have been sufficient for the dispersal of seed into areas with less shade, but sufficiently low to ensure a low browsing pressure. The greater density of *A. tortilis* trees below 1 m in height in the riverine vegetation suggests better conditions for germination, compared with the woodlands, but the greater density of trees in the 1 - 2 m height class in the woodlands suggest better recruitment conditions.

The woodlands are tolerant of elephant feeding because elephant appear to considerably lessen their utilization of *A. tortilis* trees once they have been reduced to a stem density below 100 stems ha^{-1}. Considering seed production is limited to mature (> 1 m) trees (Miller 1994a), the remaining source population of woodland trees should provide the potential for regeneration. A frequency distribution strongly skewed towards larger trees in 1996 suggests that recruitment was episodic, with subsequent conditions under a canopy of taller plants not conducive to the establishment of *A. tortilis* seedlings (Miller 1996). The gaps created by trees being pushed over may therefore create conditions more conducive to the establishment of seedlings that do not tolerate shade. However, recolonization does not occur continuously in time, but rather in discrete events facilitated by favorable combinations of weather and grazing conditions (Westoby *et al.* 1989). Poor seedling recruitment (n = 5 from 1997 to 2000) and survival (indicated by the absence of seedlings in 2000), combined with the paucity of middle-aged (1 - 5 m) trees could affect the future rate of replacement of the larger height classes. Poor seedling recruitment could be attributed to the rarity of ideal recruitment conditions, considering the absence of trees < 1 m in height in 1996 indicated the absence of ideal recruitment conditions since 1986, given a growth rate of 0.1 m an^{-1} (Chapter 8), whereas poor seedling survival could be a result of the high density of indigenous browsers compared with the period of bush encroachment.

Chapter 10

General Discussion

Is patch dieback and woodland destruction cause for immediate concern regarding loss of biodiversity, with possible implications on the structure and functioning of the *Colophospermum mopane* and *Acacia tortilis* populations, respectively?

Changes in biological diversity have profound ecological and societal consequences on account of the services that humans derive from ecosystems, particularly woodlands in Africa. Indigenous woodland communities are of significant economic value owing to the dependance of rural populations on their natural resources for an assortment of commodities, including: firewood (Loh 1999), kraalwood and fencing (Gandar 1990), woodcarvings (Steenkamp 1999) and traditional medicine (Mander 1998). Consequently, wood resources in South Africa are under pressure. The AIDS pandemic and anticipated increase in tourism are expected to increase the demand for indigenous medicinal products (Mander 1998) and indigenous tree species for carving (Steenkamp 1999), respectively. The provision of tangible ecosystem goods and services by natural systems depends not only on species presence or absence, but also on their abundance. Biodiversity is a multidimensional concept (Purvis & Hector 2000) incapable of being fully explained by a single number. Indices of biodiversity should quantify those facets that assist in the interpretation of the effects reduced biodiversity have on system function. The most commonly considered facet of biodiversity is species richness. However, the relative abundance of component species (species evenness) influences the chance of two randomly chosen individuals being of the same species (Purvis & Hector 2000). Species evenness is influenced more frequently by and respond more rapidly to human activities than the presence or absence of a species (species richness) (Chapin *et al.* 2000). Scientists subsequently adopted management policies based on the relative abundance of indicator species, allowing managers to act before a species goes extinct. Consequently, species evenness is as important as species richness as a measure of biodiversity.

Conserving biodiversity is essential because we rarely know *a priori* which species are critical to current functioning or provide resilience and resistance to environmental changes (Chapin *et al.* 2000). However, considering *C. mopane* and *A. tortilis* dominated their respective vegetation types in VLNR, they are likely to be key species, maintaining structure and function of *C. mopane* and *A. tortilis* woodlands, respectively.

Drought-induced patch dieback did not change the height structure of *C. mopane,* because mortality was not height-specific and 'live' and 'dead' plots did not differ in tree height structure. Although dieback was severe (up to 100%) and reduced the abundance of trees, it was localized and did not occur throughout the entire population within VLNR. *Colophospermum mopane* is also prolific in the area and is therefore unlikely to become locally extinct. Similarly, elephant did not change the population structure of the *A. tortilis* woodlands, but significantly reduced the density of trees by 2000. Although *A. tortilis* trees are not as prolific as *C. mopane* in VLNR and the destruction of the woodlands represents the loss of a habitat type, it is erroneous to perceive and manage semi-arid savannas as static systems, especially considering the effective dispersal mechanisms of pioneer species, such as *A. tortilis*. The remnant population of mature *A. tortilis* trees in the woodlands combined with the trees within the riverine vegetation should provide sufficient material for recolonization. Consequently, although drought and elephant reduced local abundance, and hence biodiversity, of the *C. mopane* and *A. tortilis* woodlands, respectively, there is sufficient spatial heterogeneity of resources and temporal heterogeneity of processes within the VLNR ecosystem to counteract the loss of habitat in time. Besides, the re-expansion of the grasslands may benefit the system, particularly the carrying capacity for grazers, considering there is a poor cover of perennial grasses (O'Connor 1983). Less severe drought episodes are likely to influence population structure in addition to the density of trees in VLNR owing to the height-specific (< 3 m) nature of mortality, and partial dieback of the tree canopy (O'Connor 1999), compared with the mortality of entire trees of all sizes associated with patch dieback. Elsewhere, elephant have also influenced both woodland structure and density (Ruess & Halter 1990). Change in woodland structure by elephant may be influenced by the original population structure, and tree survival. Most trees in the *A. tortilis* woodlands were available to elephant (1 - 7 m). Consequently, height classes were utilized in proportion to their abundance. The preference of certain-sized trees may also result in changes in woodland structure (Croze 1974b; Pellew 1983a).

Patch dieback of *Colophospermum mopane* woodlands

The occurrence of patch dieback of *C. mopane* between 1988 and 1992 is the consequence of the preconditioning of the system by an increase in density of trees, and an increase in drought proneness through erosion. Nevertheless, the monospecific nature of *C. mopane* woodlands is suspected to have made the system vulnerable to large-scale dieback on account of a single threshold to stress.

It is proposed that species diversity is capable of influencing the pattern of mortality, considering patch dieback is commonly associated with monospecific communities (Fensham & Holman 1999). Monospecific or species-poor communities characteristically have a less variable threshold to stress (Jimenez *et al.* 1985) than species-rich communities, particularly if the dominant species has a narrow range of resource tolerances and is arranged along specific geomorphic or hydrologic gradients, which, when altered, trigger widespread mortality. Apart from species richness, the size structure of a population has also been implicated in large-scale dieback (Young & Lindsay 1988). Mortality is often size-dependent (Huston 1994), considering many ecological interactions, including interactions with drought (O'Connor 1999), herbivores and fire (Pellew 1983), are influenced by size. The proportion of individuals in the vulnerable size range will therefore determine the extent or pattern of dieback. Structural homogeneity therefore enhances a woodland's vulnerability to widespread dieback by size-specific stressors (Young & Lindsay 1988), whilst size-related death or senescence in a heterogenous stand would be less noticeable. Despite these findings, this study showed that a heterogenous size structure is just as vulnerable to patch dieback as a homogenous stand.

Species composition and size structure are important community attributes affecting population dynamics. Consequently, woodlands are described most often by their component species and/or size structure. It is proposed that the interaction between a species- or size-specific mortality agent and the characteristic of a community, defined by the nature (homogenous or heterogenous) of its size structure and species composition, will influence the pattern of mortality, specifically patch dieback (Table 7.1). The homogeneity of species and heterogeneity of tree heights associated with the *C. mopane* woodlands in VLNR, suggests patch dieback was the consequence of a breached threshold relating to species tolerances, rather than size.

Table 10.1 A proposed model for predicting the pattern of mortality (patch or other) given the nature of the mortality agent (size- or species-specific) and different combinations of community characteristics (homogenous: hom, or heterogenous: het) relating to size structure and species composition

	mortality agent: size-specific			
size structure	hom	het	hom	het
species composition	hom	het	het	hom
outcome	patch	other	patch	other

	mortality agent: species-specific			
size structure	hom	het	hom	het
species composition	hom	het	het	hom
outcome	patch	other	other	patch

Foraging behaviour of elephant

The methods of feeding, including removing branches from the canopy, stripping bark from the stem and/or uprooting (and breaking) entire trees, differ between and within woody species. Elephant respond to a tree in any manner befitting within the mechanical constraints of a certain size or species.

Elephants experience the least overlap upon their diet with the diets of other large herbivores, relative to other animals, most probably because they increase their number of browse species into the late dry season (Jarman 1971). Elephants also utilize a wide spectrum of browse species, 61 browse species were recorded in Wankie National Park (Williamson 1975). However, *C. mopane* appears to be the predominant browse species where it occurs (Pienaar *et al.* 1966; Jarman 1971; Williamson 1975) and is a preferred species in VLNR, despite its prolific abundance (Smallie & O'Connor 2000), most probably owing to its high fat content (Williamson 1975). Ecological separation of large mammalian herbivores in Africa is mainly a consequence of their differential occupation of habitat types and the selection of distinct diets (Van Zyl 1965; Gwynne & Bell 1968). Despite a restricted range of habitats, ecological separation between the diets of herbivores including elephant, rhino, buffalo, impala and kudu, can be achieved through dependance on different staple foods (Jarman 1971). Consequently, browsers which share a common staple food on account of its prolific abundance (low diversification), such as *C. mopane*, could compete with one another. One animal with which the elephant's diet was found to correlate most with (Jarman 1971) was the kudu, however, mixed feeders, including eland and impala, could also compete with elephant for browse in areas where *C. mopane* dominates and grass is sparse, considering a sparseness of grasslands in plant communities encourages herbivores to browse (Jarman 1971). Despite its sparseness and rankness, however, grass was observed in the impala's diet on VLNR, during the dry winter months (personal observation). However, *C. mopane* was present in the stomach of every species examined, including kudu, impala, and eland (personal observation). Dietary overlap and interspecific competition among browsers for *C. mopane* late into the dry season could explain the expansion of the elephant's diet to include *A. tortilis*.

Utilization of the *A. tortilis* woodlands appears to have occurred mainly in the late dry season when *C. mopane* drops its leaves, suggesting utilization was in response to a spatiotemporal variation in forage abundance (or quality). Elephant response to spatiotemporal variation in forage quality is more pronounced in systems in which grass is replaced by more palatable browse in the dry season (Kabigumila 1993). Elephant response is similar to the response of large grazers which migrate to increase their diet quality and grazing efficiency (Frank *et al.* 1998).

Furthermore, ungulates in grazing ecosystems increase their own grazing efficiency by modifying vegetation structure. When forage biomass concentration (per bite) is below critical levels, herbivores may be unable to acquire sufficient energy and nutrients to maintain themselves (Chacon *et al.* 1978). Grazers make forage more concentrated by reducing canopy height more than aboveground biomass (McNaughton 1984). Elephants may have the same foraging goals, to manipulate vegetation structure and improve future foraging efficiency, although they may not always get the desired response, considering different species of woody plants respond differently to elephant feeding. The elephant of VLNR select for pollarded *C. mopane* trees 1 - 2 m in height which have, on average, more branches than similar-sized non-pollarded trees (Smallie & O'Connor 2000), owing to coppice growth from previous damage. The same growth response was not attainable with *A. tortilis* on account of its poor ability to coppice. Species response to elephant utilization therefore determines subsequent foraging behaviour. *Colophospermum mopane* can withstand high browsing pressure by elephant (Lewis 1991) and predominates in the elephant's diet in VLNR (Smallie & O'Connor 2000), whereas *A. tortilis* was unable to sustain the foraging pressure imposed upon it by elephant. Consequently, the elephant are forced to seek alternative forage species (Anderson & Walker 1974).

Herbivores must balance time invested in energy and nutrient intake with nonfeeding activities, such as travel (McNaughton 1984). This may account for the absence of elephant utilization in the *A. tortilis* woodlands when density of trees was reduced to below 100 stems ha^{-1}. It may no longer be worthwhile for elephants to feed in these woodlands.

It is concluded that the foraging behaviour of elephant is associated with plant species response to herbivory, the abundance of preferred forage species, and possibly dietary overlap among browsers and spatiotemporal variation of forage abundance and/or quality.

Spatial heterogeneity

Drought-induced dieback was localized and patchy on account of non-uniformities in the patterns and processes of the environment. Landscape heterogeneity, although exacerbated by a history of overexploitation, created runoff zones and run-on sinks. Although woodland resilience was not measured directly, it is suggested that spatial heterogeneity within a landscape enhance's a woodland's resilience to severe drought episodes by ensuring the survival of some plants in runon sinks or 'drought refuge' sites.

Non-uniformities in the patterns and processes of the environment and herbivores, e.g. suitable growth and browse conditions for *A. tortilis* recruitment in grasslands, compared with the riverine vegetation, created spatial heterogeneity within the *A. tortilis* population of VLNR. Furthermore, *Acacia* woodlands have the potential of being replaced by forest trees (Whateley & Wills 1996), although perhaps not in this environment. The seedlings of deciduous broadleaf or evergreen species are usually 'canopy tolerants' (Smith & Goodman 1986), which can grow to maturity under *Acacia* canopies, resulting in a transition from a community of microphyllus species, such as *A. tortilis*, to a stand dominated by evergreen and broadleaf species (Smith & Goodman 1987), by means of a nucleation process from under-canopy environments (Whateley & Wills 1996).

Nevertheless, plant succession was effectively halted and reversed by elephant. The spatial variation of herbivory by elephant resulted in a more homogenous distribution of *A. tortilis* trees within the reserve, considering the woodlands and riverine now have a similar density of trees. This study provides evidence that herbivores can create spatial homogeneity through their spatial feeding patterns, in addition to creating spatial structure (Noy-Meir 1996). Furthermore, it is unlikely that this type of reduced heterogeneity will affect the future resilience of the population to climatic variability, as mentioned by Noy-Meir (1996).

Future implications of current trends

Recolonization does not occur continuously in time, but rather in discrete events facilitated by favorable combinations of weather and grazing conditions (Westoby *et al.* 1989). Considering seed production is limited to mature trees (Miller 1994a), the remaining source population of woodland trees, and trees within the riverine vegetation, should provide the potential for regeneration. Despite extreme or rare recruitment events (Wiegand *et al.* 1995) in semi-arid systems, *A. tortilis* has the attributes of a pioneer species: capable of germinating without an extended germination lag, despite stressed conditions following a period of sufficient imbibition (Choinsky & Tuohy 1991); intolerance of shaded environments (Smith and Goodman 1986); and an effective ungulate-dispersal mechanism (Coe & Coe 1987), thereby ensuring early colonization and dominance of a site (Ben-Shahar 1991). The gaps created by trees being pushed over may create conditions more conducive to the establishment of seedlings, on account of their intolerance of shade, and allow the increased growth of neighbouring individuals (Smith & Goodman 1986). Furthermore, the diversifying effect of disturbances (structural heterogeneity) (Huston 1994) created in gaps can alleviate widespread mortality by reducing the impact on previously dominant species (e.g. Mwalyosi 1990).

However, seedling establishment is a rare event under conditions of high browsing pressure. Consequently, the recolonization of the woodlands will depend on the current levels of browsing pressure by small ungulates, such as impala. If browsing pressure is too high, the current open woodland condition will hold, in which case woodland dynamics reflects both the stable limit cycle hypothesis and the multiple stable state hypothesis. Although the stable limit cycle has recently been criticized (Duffy *et al.* 1999), this study shows that a similar pattern is possible. The stable limit cycle requires that the elephant are dependent primarily on one dominant vegetation type (Duffy *et al.* 1999). *Colophospermum mopane* comprises the majority of the elephants' diet in VLNR. Consequently, the destruction of the *A. tortilis* woodlands will not result in a population crash of elephants. Nevertheless, *A. tortilis* woodlands may show a pattern similar to the stable limit cycle hypothesis because the elephant population has removed itself from the woodlands, potentially allowing them to recover. If they do not recover immediately owing to a high browsing pressure on seedlings, the system could reflect a stable limit cycle that has been arrested at an artificial equilibrium, with a subsequent reduction in browsing pressure leading to recolonization of the woodlands (Prins & Van Der Jeugd 1993). Alternatively, population dynamics under conditions of a high browsing pressure could be interpreted as the multiple stable state hypothesis, considering the evidence would be consistent with the two criteria required to demonstrate a boundary between stable states: a factor capable of causing a change of state, which when reduced does not result in regeneration of the woodlands, and a new factor, browsing by small ungulates, to hold the system in a new state. The results, that elephant are responsible for causing a change of state, are contrary to the findings of Dublin *et al.* (1990), viz. that elephant are not capable of moving a system from one state to another.

Severe drought episodes are also capable of causing a change of state from woodland to grassland. The complete drought-related mortality of *C. mopane* in discrete patches should provide an opportunity for the recruitment of annual and possibly perennial herbaceous plants, owing to the absence of severe competition for soil water with *C. mopane* (Smit 1994). Recolonization of perennial grasses will depend on the availability of seed, post-drought rainfall, browsing pressure, and woody recruitment on the bare areas (O'Connor 1999). Nevertheless, complete drought mortality and elephant impact have created a window of opportunity for the recovery of perennial grasses in *C. mopane* and *A. tortilis* woodlands, respectively, following a period of extensive livestock ranching (O'Connor 1983) which led to the increased density of both woodland types.

The mopane veld within VLNR is susceptible to irreparable degradation in view of the patch dieback phenomenon and potential threat of elephant. Venetia-Limpopo Nature Reserve is largely a dysfunctional landscape. Soil and organic resources are being lost from the system along drainage lines that feed the Limpopo River. Litter, comprising mostly *C. mopane* leaves, has failed to accumulate over a period of 15 years (O'Connor 1999) because of surface wash, despite substantial annual inputs (Smit 1994), thereby reducing the system's nutrient capital. Lewis (1991) suggested that years of below annual rainfall combined with a history of continuous browse removal by elephant can exert patch dieback of coppiced *C. mopane* trees owing to a nutrient drain on individual trees. The continued removal of nutrient (browse and litter) reserves and topsoil therefore poses a threat to VLNR, especially given the mopane woodlands' current vulnerability to soil moisture deficits. Current trends implicate the potential for an interaction between elephant, drought and a dysfunctional landscape, resulting in more frequent incidents of patch dieback within the *C. mopane* woodlands, particularly woodlands upon an eroded substrate, and subjected to high local elephant densities (coppiced trees).

If large-scale die-offs of *C. mopane* and loss of vegetation types persists, it will have implications on the carrying capacity of the reserve. Competition between herbivores is a function of (1) overlap, (2) population density, and (3) resource abundance (French 1985):

(1) Overlap. Dekker (1997) calculated indices of overlap for diet composition between ungulate species using estimates of the grass:browse ratio (impala: 50:50, kudu: 0:100, respectively) in the mopane veld, Northern Province. A lack of grass cover induces the preponderance of browsers in the spectrum of herbivores (impala [grass:browse]: 4.6:95.4, kudu [grass:browse]: 1.5:98.5) (Jarman 1971). Despite a preponderance of browsers, Jarman (1971) attributed the ecological separation of herbivores to their dependance on different staple plants (elephant: *C. mopane*, impala: *Disperma* spp., kudu: *Croton* spp., buffalo: grass). Nevertheless there was still an overlap in the diets of elephant and impala (all year: 12%) and, elephant and kudu (all year: 22%). Consequently, there is likely to be dietary overlap among the herbivores of VLNR given its lack of grass cover and predominance of *C. mopane*. If *C. mopane* is a common staple diet among herbivores, dietary overlap among herbivores in VLNR could increase on account of patch dieback of *C. mopane* and loss of *A. tortilis* woodlands, even if temporarily, before the replacement of the aforementioned woodlands by other species.

(2) Population density. Elephant are the one species most likely to have an impact on the abundance of all other browsers or intermediate feeders, on account of the substantial contribution they make to the total herbivore biomass (Table 3.1), the future implications of their successful breeding, and

the absence of restrictions imposed on the population growth of other herbivores (hunting, culling and natural predators, including lion). If the reserve's carrying capacity is kept constant, an increase in elephant biomass will lead to the displacement of other species.

(3) Resource abundance. Patch dieback of *C. mopane* and loss of *A. tortilis* woodlands will reduce the abundance of browse and alternative vegetation types for foraging or other non-feeding activities, such as rest associated with shade, assuming no immediate replacement of woodlands. Potential consequences include animal population crashes or overexploitation of the existing vegetation.

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Appendix 1

A definition of the criteria used to quantitatively describe elephant utilization of woody plants

Table 1 Codes and their description for assessing the volume of canopy and the circumference of stem removed

Utilisation Index (Ut. Ind.)

Code	Description
	Canopy
0	0 %
1	1 % - 10 % of The Volume of The Canopy Removed
2	11 % - 25 %
3	26 % - 50 %
4	51 % - 75 %
5	76 % - 90 %
6	90 % - 99 %
7	100 %
	Debarking
11	1 % - 10 % Of The Circumference Of The Stem Removed
12	11 % - 25 %
13	26 % - 50 %
14	51 % - 75 %
15	76 % - 90 %
16	91 % - 99 %
17	100 %
.1	1 % - 10 % of height of stem
.2	11 % - 25 % of height of stem
.3	26 % - 50 % of height of stem
.4	51 % - 75 % of height of stem
.5	76 % - 90 % of height of stem
.6	91 % - 100 % of height of stem
.7	Whole stem plus branches

Table 2 Codes and their description for assessing the agent of utilization

Agent (Agt.)

Code	Description
1	Elephant
2	Giraffe
3	Black Rhinoceros
4	Other Browsers
5	Human
6	Moisture Stress
7	Flooding
8	Shading
9	High Light
10	Fire
11	Unknown

Table 3 Codes and their description for the age of utilization

Age of Utilization (Age)

Code	Description	Removed Portions	Breaks on Tree	Bark Around Edges of Wound
1	< 1 month	Leaves drying, still present; petioles, spines and smallest twigs (1 - 2 mm diam) drying; still present on all species;	Splinters on Breaks still sharp; colour of wood still yellow; wood still wettish	Edges of attached strips still very fibrous; exposed wood bright yellow colour
2	1 mth - 2 mth	Leaves all or nearly all lost (depending on time of year and prevailing weather - compound leaves last longer than simple); spines and 1-2 mm diam. twigs still present; 1 - 2 mm diam twigs and spines becoming brittle; twigs > 2 mm drying	Points of finest splinters beginning to turn grey, especially in direct sunlight; break dry; splinters not yet brittle;	Fibres on tips of bark strips remaining on tree beginning to curl; exposed wood fading yellow;
3	2 mth - 4 mth	Leaves all lost ;1- 2 mm diam twigs brittle, larger twigs still relatively supple	Points of all splinters grey finest splinters all grey, except where break may be in deep shade. rest still faded yellow to grey;.	Fibres lost; exposed wood turning light grey
4	4 mth - 6 mth	1 - 2 mm diam twigs lost in softer textured species, still present on hardwoods; 5 mm diam twigs brittle larger twigs all dry; bark at breaks beginning to curl back.	Splinters all grey on outside, yellow on interior of break	Sharp edges of attached bark becoming rounded; exposed wood nearly all light grey

Table 3 (continued) Codes and their description for the age of utilization

5	6 mth - 12 mth	1 - 2 mm diam twigs lost; 1 cm diam twigs becoming brittle; bark curling back	Sharp points on splinters weathering, break becoming smoother; break dark grey in colour	Beginning of callus growth beneath edges of bark around wound, depending on the time of year of sampling and of the damage; exposed wood light grey
6	1 yr - 2 yrs	1 cm twigs lost in softer textured species; some still present on hard woods; most bark lifted	No sharp points; break smooth; dark grey	Callus growth on edges of wound; exposed wood turning darker grey
7	> 2 yrs	Most branches less than 5cm lost; most bark lost	Break smooth; dark grey; mottled	More than 1 season callus growth on edges of wound
	Total >6 mnths	Leaves lost; 1- 2mm diam twigs lost	Breaks not yet grey	No callus growth
	Total <6 mnths	1 - 2 mm twigs still present	Breaks all grey	Callus growth (other than wounds close to six months

Table 4 Codes and their description for assessing the biological state, physical state, and growth response of a tree, following branch removal, stem breaking and debarking

State (St.)

Code	Description
0	No Utilisation
1	Branches Removed - Tree Living
2	Main Stem Partially Broken - Tree Still Living
3	Main Stem Completely Broken (Pollarded) - Tree Still Living
4	Main Stem Pushed Over (Partially Uprooted) - Tree Still Living
5	Coppice Growth from Larger (Older) Dead Stem
6	Coppice Growth from Accumulated Browsing of Young Plant
7	Coppice Growth from Repeated Fire
8	Coppice Growth from Repeated Moisture Stress
9	Senescing
10	Main Stem Partially Broken - Tree Dead
11	Main Stem Completely Broken (Pollarded) - Tree Dead
12	Main Stem Pushed Over (Partially Uprooted) - Tree Dead
13	Tree Totally Uprooted
14	Main Stem Intact. Tree Killed From Accumulated Elephant Damage
15	Main Stem Intact. Tree Killed By Moisture Stress
16	Main Stem Intact. Tree Killed from Combination Of Moisture Stress And Accumulated Elephant Damage
17	Dead From Shading
18	Dead From High Light
19	Dead From Unknown Causes (Not Elephant)
20	Multi-Stemmed Tree - 1+ Stems removed
30	Only Leaves Removed. No Branches Broken
31	Debarking Only (No Change in Vigour)
50	Die-Back From Moisture Stress
51	Top-Kill From Frost
60	Die-Back From Debarking

Growth Responses (G.R.) Branch Removal, Stem Breaking and Debarking

Code	Description
1	Coppice Growth
2	No Coppice Growth - Vigour Appears Unaffected
3	No Coppice Growth - Vigour Appears Reduced (Tree Dying)
4	Tree Dead