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Die-back of kiat (*Pterocarpus angolensis*) in southern Africa: a cause for concern?

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Pterocarpus angolensis (kiat) is a well-known southern African tree species of commercial importance that occurs in several vegetation types in the Zambezi regional centre of endemism. The most prominent of these vegetation types are the Zambezi miombo woodland and undifferentiated woodland. A diverse range of ecosystems within these vegetation types necessitate adaptation by tree species to survive extremes of drought, temperature, altitude, soil nutrition and tolerate fire in order to compete with other plant species. There are several reports of a die-back disease of *P. angolensis* in Zambia, Zimbabwe and South Africa, but very little is known regarding the cause or significance of this problem. In this review, we provide details regarding the history of the disease and consider its possible causal agents. A pathology study conducted at three locations in South Africa on diseased and dying trees resulted in the collection of 199 fungal isolates; comprising saprophytic species such as *Candida*, *Penicillium* and *Humicola*, and potentially pathogenic species such as *Lasiodiplodia theobromae*, *Cytospora* spp. and *Fusarium* spp. Drought, during several years preceding disease, along with a lack of fire management may have contributed to both the present and past reports of tree die-back and death. Finally, an analysis is made of the importance of the problem and actions that might be taken to alleviate it.

Keywords: *Cytospora*, drought, fire management, *Fusarium*, *Fusarium oxysporum*, *Lasiodiplodia theobromae*, mukwa disease, stand-level die-back

Introduction

Pterocarpus angolensis (kiat) is a well-known southern African tree species valued for its timber (Lowore 1993) and use in several traditional medicinal applications (Coates Palgrave 1977). In South Africa, the species is protected by state law (Krynauw 1998) while in Tanzania a minimum stem diameter at breast height (DBH) is prescribed to limit harvesting of small trees (Caro et al. 2005). Despite these efforts, the species is under threat. Size prescriptions are ignored in some areas of Tanzania (Caro et al. 2005), past and present exploitation has raised concerns of the extinction of *P. angolensis* in Zimbabwe (Bradley and Dewees 1993, Clarke et al. 1996) and availability reported by woodcarvers in South Africa indicates that trees are becoming rare (Steenkamp 1999). These concerns are underscored by low seedling recruitment rates during both germination and the suffrutex stage (Boaler 1966, Schwartz et al. 2002, Caro et al. 2005) and by unsustainable rates of harvesting (Schwartz et al. 2002, Caro et al. 2005).

Pterocarpus angolensis occurs in several vegetation types in the Zambezi regional centre of endemism. The most prominent of these are the Zambezi miombo woodland, which includes both wetter and drier miombo, and the more species-rich north and south undifferentiated woodland (White 1983). These vegetation types span a range of

ecosystems that differ with respect to fire, frost and drought tolerance. *Pterocarpus angolensis* is, therefore, adapted to survive and tolerate extremes stemming from several environmental factors, including fire, drought and moisture availability. The species can tolerate an annual rainfall as low as 500 mm (van Wyk 1972) and as high as 1 250 mm (von Breitenbach 1973), average temperatures as low as 4 °C, and altitudes ranging from sea-level to 1 650 m above sea level (von Breitenbach 1973). The soils of both miombo woodland (Högberg 1992) and undifferentiated woodland (Scholes and Walker 1993) are poor in organic matter, nitrogen and phosphorus but *P. angolensis* possesses both vesicular-arbuscular (VA) mycorrhizae (Munyanziza and Oldeman 1995) and functional nitrogen-fixing root nodules (Boaler 1966, C Beukes FABI University of Pretoria, pers. comm.), ensuring that the species is able to efficiently utilise available nutrients. The species cannot tolerate competition with dense grass and dense stands of trees and regeneration is favoured by regular fire (Boaler 1966, Geldenhuys 1977).

Despite the adaptations of *P. angolensis* to relatively harsh environments, there are several reports dating back to the late 1950s of these trees becoming diseased and dying (Anonymous 1973, Pearce 1979, van Wyk et al. 1993, Mushove 1996, Krynauw 1998, 2000). These reports refer

to trees in the Livingstone district between Livingstone in Zambia and Bulawayo in Zimbabwe, as well as in several areas of South Africa. In this review, we discuss disease symptoms observed and the possible reasons for tree death, including ecological conditions that might predispose trees to diseases. Furthermore, advice is provided regarding management options for diseased *P. angolensis* trees and possible strategies that may help to alleviate the disease.

The situation in the Livingstone areas, Zambia and Zimbabwe

Disease of *P. angolensis* trees

In 1958, a disease resulting in the death of *P. angolensis* trees west of Livingstone, Zambia, was reported. Subsequently in 1964, additional affected trees were found in the Kalahari Sands/Zambezi Teak Forests (Anonymous 1973). By July 1964, the disease was reported close to the Victoria Falls village in Zimbabwe, and thereafter it was noted more widely (Geary 1972, Anonymous 1973). In March 1966, the disease was reported in the Bambezi Forest Reserve, about 100 km north-west of Bulawayo (Pearce 1979). Calvert (1972) produced evidence indicating that there had been earlier reports of the disease in Botswana in the early 1930s, in Zambia in the late 1940s and early 1950s, and in Zimbabwe in the early 1930s, late 1940s and early 1950s (Pearce 1979). Since then, the disease has become localised in the border area between Botswana, Zimbabwe and Zambia resulting in stand-level die-back in this area (van Wyk et al. 1993). The disease was named 'mukwa disease', referring to one of the common names (mukwa) given to *P. angolensis*.

Mukwa disease has a range of symptoms, the most prominent being blight and die-back of affected trees (Calvert 1972, Pearce 1979, 1986). Other symptoms include a generally unhealthy appearance of the crown foliage, wilt and chlorosis (Calvert 1972, Pearce 1979, 1986). Defoliation, desiccation, the occurrence of epicormic buds on the healthy parts of the tree trunks and branches, and premature development of new leaves are common symptoms. The bark discolours from brown to grey, cracks or flakes, and can be peeled off in large flaps, and xylem and sapwood become stained. Xylem/sapwood streaks are a dull blue-grey or orange-red in colour and appear as complete flecked rings or discontinuous arcs. In microtome sections, xylem vessels contain amorphous deposits, occlusions, and fungal hyphae (Pearce 1979). Vascular streaking appears to originate from several points in the root system or from a single rotten root (Pearce 1979). Van Wyk et al. (1993) noted that phloem streaking was often emphasised in affected trees and this appears to be a distinguishing factor on affected trees (Calvert 1972, Pearce 1979, 1986). The most intensive symptoms are observed at the height of the rainy season. Diseased trees typically occur in patches and usually die within two to three years (Calvert 1972, Pearce 1979, 1986).

Possible causes of mukwa disease

Mukwa disease has been attributed to *Fusarium oxysporum* Schldl. based on the consistent isolation of this fungus from discoloured wood (Pearce 1979, 1983, 1986, van Wyk et

al. 1993). *Fusarium oxysporum* is a well-known pathogen, causing wilt diseases, damping off, and crown and root rots of a wide variety of plants (Leslie and Summerell 2006). It has also been recorded as a wilt and die-back pathogen of several leguminous tree species, including *Acacia koa* and *Albizia julibrissin* (Anderson et al. 2002), and was recently associated with cankers on *Cedrelinga cateniformis* in the Amazon basin (Lombard et al. 2008). The fungus is typically associated with plant roots, and Gordon and Martyn (1997) suggest that either the fungus grows beyond the cortex into the xylem to initiate plant disease or that it already exists as an endophyte within affected plants. Strains of the fungus are often non-pathogenic in nature and it is more likely that some change, either physiological or biological, in the host or the fungus allows disease to develop (Gordon and Martyn 1997).

Drought has been mentioned in every report of mukwa disease and stress might be an important factor in its development (Calvert 1972, Geary 1972, Anonymous 1973, Pearce 1979, 1986). For example, affected trees in Matabeleland in Zimbabwe experienced 12 consecutive seasons of poor rainfall up to 1973 (Anonymous 1973). Rainfall data from the South African Weather Bureau for the area (Figure 1), from the two closest weather stations (Bulawayo in Zimbabwe and Livingstone in Zambia), based on *World Weather Records, vol. 5: Africa* for 1951 to 1980 (Anonymous 1967, 1979, 1987) show a correlation between annual rainfall in the area and mukwa disease. From 1958 to 1959, there was a drop in rainfall at Livingstone from 1 410 mm to 620 mm, which is considerably lower than the average of c. 800 mm in preceding years. In general, rainfall remained at this level at both weather stations until 1965, other than in 1962 when 1 078 mm of rainfall was recorded in Livingstone. From 1972, rainfall improved at Livingstone. Outbreaks of mukwa disease were reported in Zimbabwe in 1958/59, 1964, 1966, 1967 and 1968 (Calvert 1972, Pearce 1979) and this is supported by the low rainfall reported (Figure 1) in Bulawayo. From 1973 to 1977, the disease was studied at Livingstone by Pearce (1979) and it is likely that his observations centred on trees that were dying from the sustained drought period of previous years.

Fire is a critical factor in the ecology of *P. angolensis* that has frequently been overlooked or ignored in studies on mukwa disease. It positively influences individuals of *P. angolensis* by suppressing competition for nutrients and water in the soil and demand and competition for sunlight and space. The species is a pioneer in areas where fire has occurred (von Breitenbach 1973). Seed germination is dependent on the removal of the underlying grassy layer and the wings and bristles of the fruit by a 'cold' fire enabling seed to come into contact with the ground (von Breitenbach 1973, van Daalen 1991), and subsequent exposure to rain (Boaler 1966). Seedlings of the species produce an extensive, although shallow (Geldenhuys 1977), underground root system in several successive years of annual die-back (the so-called suffrutex stage) to collect sufficient water and nutrients for stem production (Boaler 1966, von Breitenbach 1973, Vermeulen 1990, Lowore 1993) and to survive subsequent fires (Vermeulen 1990). Fire also benefits *P. angolensis* by suppressing competing

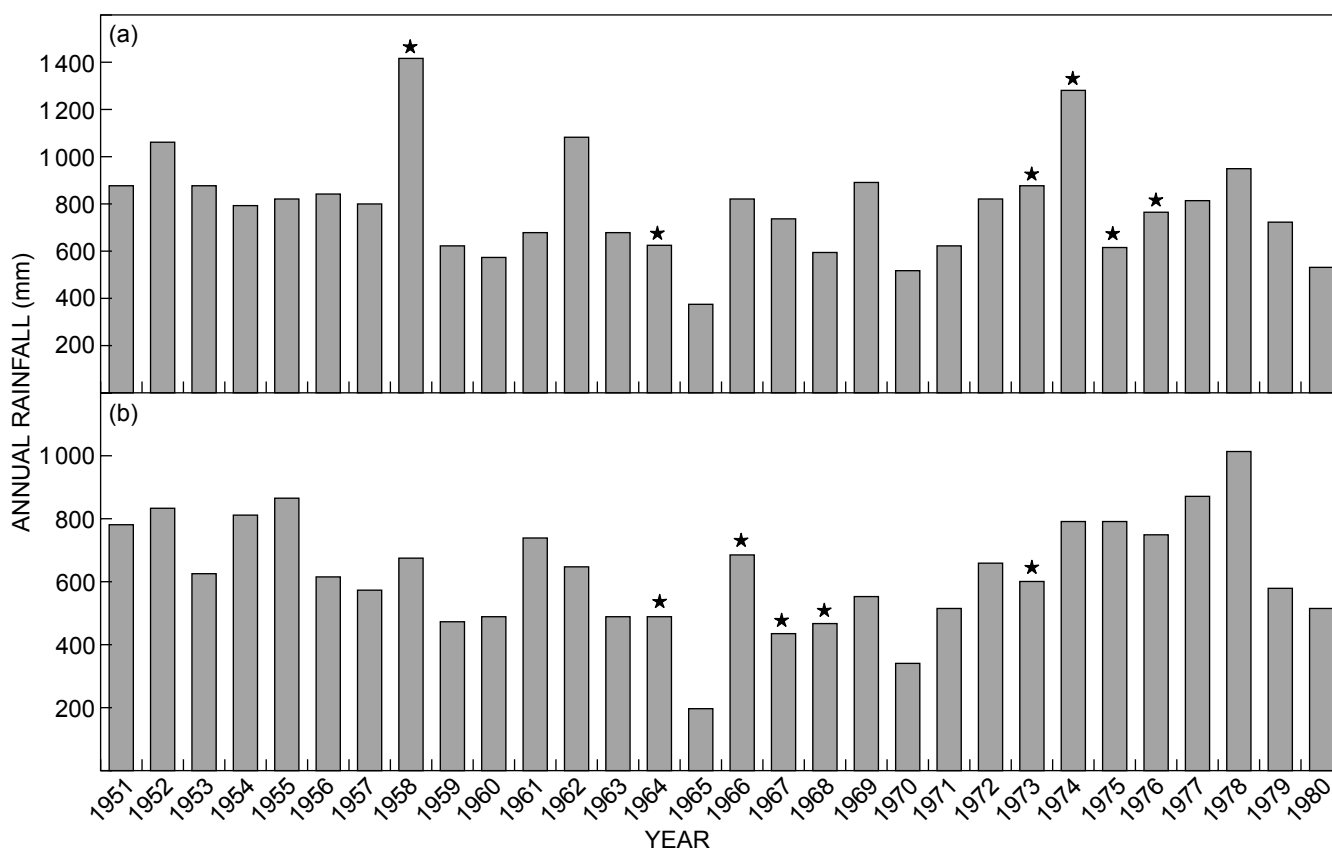


Figure 1: Charts of rainfall data from the Livingstone and Bulawayo areas. Mukwa disease reports are denoted by stars above bars

plant species and by eliminating root competition for soil water and nutrients from neighbours (which is probably exacerbated by the shallow root system of the species), helping to prune side-branches and secondary stems and releasing nutrients in the form of ash (Boaler 1966, Orpen 1982, Vermeulen 1990). In fact, both Boaler (1966) and von Breitenbach (1973) noted positive growth effects from fire. Boaler (1966) reported an increase of 20% in sapling shoot length after burning of the herbaceous layer and von Breitenbach (1973) noted a rapid increase in trunk diameter and crown size following removal of competing dense grass and scrub. Saplings are also light-demanding, developing a zig-zag appearance to maximise absorption, and fire eliminates competition for sunlight from neighbouring plants (Boaler 1966, Orpen 1982, Vermeulen 1990). A lack of sunlight results in shorter shoot length, a greater proportion of annual shoot die-back (Boaler 1966, Vermeulen 1990) and eventual death (Groome et al. 1957, Vermeulen 1990). Consequently, many reports of mukwa disease may easily be explained by a lack of fire and/or fire management in areas where *P. angolensis* occurs.

Several other tree species in the same stands, including *Burkea africana*, *Erythrophleum africanum*, *Lannea schweinfurthii* var. *stuhlmanni*, *Strychnos cocculoides* and *Terminalia sericea* (the most severely affected), have also been reported to be suffering from die-back and death (Anonymous 1973, Pearce 1979). Of these, *B. africana* (Burke 2006, Holdo

and Timberlake 2008), *E. africanum* (Holdo and Timberlake 2008) and *T. sericea* (Geldenhuys 1977, Rutherford 1983, Yeaton 1988, Holdo and Timberlake 2008) are known to have shallow root systems. In contrast, *S. cocculoides* has a deep rooting system but is physiologically limited in that there are almost no fine or adventitious roots in the first 20 cm of soil and this low root surface area density continues at lower soil levels (Oppelt et al. 2005). Several of these species are known to be tolerant to fire, including *B. africana* (Burke 2006), *E. africanum* (Lawton 1978), *L. schweinfurthii* var. *stuhlmanni* (Simute et al. 1998) and *T. sericea* (Strang 1974, Yeaton 1988). Like *P. angolensis*, some species are ecological pioneers, including *E. africanum* (also light-demanding) (Lawton 1978), *L. schweinfurthii* var. *stuhlmanni* (Welch 1960), *S. cocculoides* (light-demanding) (Hines and Eckman 1993) and *T. sericea* (light-demanding) (Strang 1974, Yeaton 1988). Consequently, all of these species share many physiological requirements with *P. angolensis* and reports of symptoms similar to those of mukwa on these trees are not surprising.

Based on the observation that trees follow a cyclic pattern in response to the disease, Calvert (1986) proposed that mukwa disease is a form of stand-level die-back that encourages regeneration. Indeed, Pearce (1983) noted that mukwa disease was beginning to wane, based on a decrease in the rate of new infections and the recovery of some affected trees. This was confirmed by Mushove (1996)

who concluded that mukwa disease is episodic. Also, van Wyk et al. (1993) noted an increase in saplings as mukwa disease progressed, indicating species regeneration, and that the disease affected older trees (with larger diameters) rather than young trees.

The stand-level die-back of *P. angolensis* in the Kalahari Sands/Zambezi Teak Forests has been compared to stand-level die-back of *Metrosideros polymorpha* (Myrtaceae) trees in Hawaii (Ohia disease) (van Wyk et al. 1993). In the case of *M. polymorpha*, it has been suggested that die-back is related to primary succession and that the establishment of seedlings and sapling maturation is strongly related to the degree of opening in the forest canopy (Jacobi et al. 1983). This is consistent with the cohort senescence theory where many large cohorts/groups of individuals of the same (woody) plant species are established non-uniformly (a patchy distribution) in an area after a catastrophe or a decrease in the forest canopy (Mueller-Dombois 1983, 1986). These cohorts eventually begin to senesce/age from the effect of one or more environmental stresses that are either abiotic or biotic. Similarly, cohorts occurring in areas exposed to the same environmental stress/stresses can begin to senesce at the same time. At this stage a fluctuating/variable environmental site factor begins to contribute to stand-level die-back as its intensity increases over time. The resulting stress predisposes trees to attack by other biotic agents that begin to cause rapid decline or die-back. If trees manage to temporarily recover following the environmental site factor, these biotic agents can cause a lingering decline or die-back (Mueller-Dombois 1983, 1986). Drought, a lack of fire and *F. oxysporum* are considered possible contributors to stand-level die-back of *P. angolensis* (van Wyk et al. 1993).

The situation in South Africa

Reports of die-back of *P. angolensis*

In South Africa, *P. angolensis* trees were first reported dying by Krynauw (1998, 2000) in the Mawewe Nature Reserve/Cattle Game Project, close to Malelane, in the east of the country. Recruitment of tree seedlings was low (Krynauw 1998, 2000), indicating that the species was not sustaining itself and raising further alarm regarding its conservation. Although the reserve has a number of giraffe, nyala, kudu and impala, livestock husbandry with cattle is also practised on the reserve (Krynauw 1998). Coppice regrowth of trees is likely inhibited by grazing of cattle (Desmet et al. 1996). Fire management is not practised on the reserve due to the risk it poses to cattle and the potential effects it may have on their grazing (P Khosa, Mawewe Nature Reserve and Cattle Game Project reserve manager, Mpumalanga Parks Board, pers. comm.). When fires do occur, typically every five to six years, they are extremely intense.

Krynauw (1998), mentioned that *P. angolensis* trees had been reported dying near Bushbuckridge due to the 1991/92 drought in the area (CM Shackleton, University of the Witwatersrand, 1998, pers. comm.). The effects of this drought had also been noticed on trees in the nearby Kruger National Park (Viljoen 1995, Krynauw 1998). In particular, Viljoen (1995) found that although only 16% of trees greater

than 8 m in height were dead at the Napi area in the Kruger National Park, 80% of the total tree population had less than 10% growth, based on assessments of coppice, a single living branch, or a stem or shoot sprouting from the roots, although even coppicing was poor. In the Pretoriuskop area, Viljoen (1995) noted that survival was considerably better and only 21% of the trees sampled had drought-induced damage of more than 50%. In addition to the reports from the Kruger National Park and Mawewe, John Burrows (Buffelskloof Nature Reserve reserve manager, Lydenburg, pers. comm.) reported that *P. angolensis* trees on that reserve appeared unhealthy.

Observations from a pathology study in 2005

To determine whether the reports of disease and death of *P. angolensis* in South Africa were similar to mukwa disease, samples from trees in three locations in the Mpumalanga Province of South Africa (Figure 2) were collected during November and December 2005. Samples of diseased material were collected from trees at Mawewe Nature Reserve (near Malelane) (seven trees) and Buffelskloof Nature Reserve (near Lydenburg) (three trees) and fungi were isolated from symptomatic tissue. Samples were also collected from stem wounds on trees in the Sudwala Caves area (10 trees) and Mawewe Nature Reserve (eight trees) and isolations made onto standard artificial media for the culturing of a broad range of fungi. To investigate the possible connection between the observed tree mortality and drought, rainfall data for each area were obtained from the South African Weather Bureau.

Diseased and dying *P. angolensis* trees (Figure 3) had a range of disease symptoms. These included crown and branch die-back, wood stain and rot (Figure 3), production of epicormic shoots (Figure 3a), lack of fruit and oozing of sap. Basidiomycete fruiting bodies were present on some trees (Figure 3b). Many trees, especially those in the Mawewe Nature Reserve, had signs of fire damage. In many cases these fire scars were most severe at the bases of the trees and associated with internal wood rot (Figures 3c and d).

A total of 199 fungal isolates were obtained from samples collected from diseased and dying trees (Table 1). Isolates were identified based on morphological characters (size, shape and colour of spores, conidiophores and conidiogenous cells) as observed using a Zeiss Axioskop microscope (Carl Zeiss, Germany). Most isolates were of common saprophytes such as species of *Candida*, *Penicillium* and *Humicola*. A number of isolates did not sporulate in culture and are probably basidiomycetes. Common genera and species isolated that could contribute to disease included *Lasiodiplodia theobromae*, *Cytospora* spp. and *Fusarium* spp.

Species of *Cytospora* and *Fusarium* and *L. theobromae* are commonly associated with stress-induced decline of trees globally. *Lasiodiplodia theobromae* is known to cause a variety of tree diseases, including die-back and bluestain (Punithalingam 1980). Inoculation trials in the field on *P. angolensis* trees (Mehl et al. in press), however, did not demonstrate pathogenicity. However, disease expression following infection by species of the Botryosphaeriaceae, including *L. theobromae*, has been linked to drought

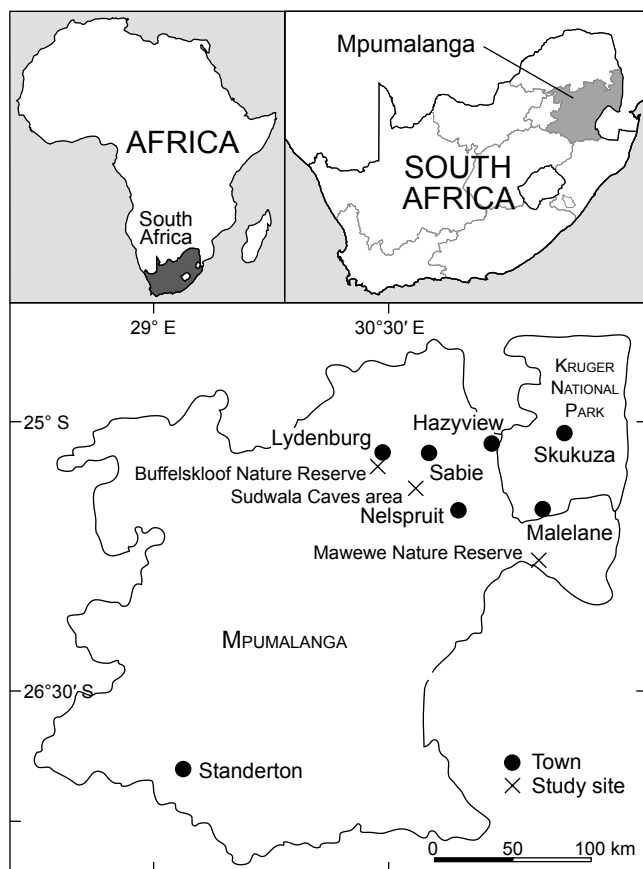


Figure 2: Map of the sites sampled. The boxed area on the South African map indicates the Mpumalanga Province from where samples were collected. The three sampling sites (Mawewe Nature Reserve, Buffelskloof Nature Reserve and Sudwala Caves area) on the larger map of Mpumalanga Province are denoted by X [South Africa map source: http://upload.wikimedia.org/wikipedia/commons/thumb/b/bc/Map_of_South_Africa_with_Mpumalanga_highlighted.svg, accessed on 27 September 2009; Mpumalanga Province map source: http://www.stayinsa.co.za/southafrica/mpumalanga_hotels.html, accessed on 27 September 2009]

stress (Schoeneweiss 1975, Lewis and van Arsdel 1978, Mullen et al. 1991, Ma et al. 2001, Desprez-Loustau et al. 2006). The genus *Cytospora* includes species that cause cankers and die-back on infected trees (Adams et al. 2006). Disease expression associated with these species has also been linked to numerous forms of predisposition, including drought stress (see Adams et al. 2005 and cited references). Likewise, species of *Fusarium* cause a variety of plant diseases, including vascular wilts, root rots and damping-off (Bloomberg 1981, Leslie and Summerell 2006).

To ascertain the identity of isolates of *Fusarium* species obtained in this study and to determine whether any isolates represented *F. oxysporum*, we obtained DNA sequence data for the translation elongation factor 1 α gene region for 29 isolates. Standard phylogenetic analysis, including parsimony analysis, was done as described for the Botryosphaeriaceae by Mehl et al. (in press). *Fusarium* isolates grouped into five clades (total isolates collected in

brackets), namely the *F. oxysporum* (five), *F. equiseti* (13), *F. solani* (five), *F. graminearum* (three), and *Gibberella fujikuroi* (three) clades (data not shown). Most of the isolates grouping in the *F. oxysporum* clade were obtained from stem wounds while most of the isolates obtained from diseased plant tissue grouped into the *F. equiseti* clade. *Fusarium equiseti* is known to colonise damaged or senescent plant tissues (Leslie and Summerell 2006) and has been associated with wilt and decline of date palm in Iraq (Abbas et al. 1991). However, *F. equiseti* is primarily a saprophyte or secondary invader of diseased plant tissues (Leslie and Summerell 2006), arguing against a role in facilitating disease of *P. angolensis*.

Possible contributing factors

A review of the rainfall data for the sampled areas showed that rainfall was probably a principal factor in decline of *P. angolensis*. Die-back and death of trees was not immediate, but occurred several years after drought, which is typical for stress-related diseases (McDowell et al. 2008 and references cited therein). Stress resulting from drought predisposes trees to attack from other biotic agents, including insects and fungi, and weakens them, increasing their vulnerability to subsequent periods of drought (Bréda et al. 2006, McDowell et al. 2008). Other biotic agents such as mistletoes (*Loranthus* spp.) have been noted in the crowns of *P. angolensis* trees dying from mukwa disease (Boaler 1966, Orpen 1982, Vermeulen 1990) and other symptoms such as black spots on the leaves, fungal fruiting bodies and lichens were frequently seen in Krynauw's (2000) study area.

The shallow root system of *P. angolensis* (Geldenhuys 1977), particularly when in competition with a dense grass or shrub layer, undoubtedly contributes to susceptibility to drought and disease development, when annual rainfall is lower than 500 mm. A deep, dense and ramified root system, absent in *P. angolensis*, is known to confer drought tolerance in trees by providing access to both larger reserves of water already present between soil particles, as well as to the water table, which may be several layers deep (Bréda et al. 2006). A lack of soil water in the upper soil horizon and the resultant unfavourable dry soil conditions explain the production of epicormic shoots by *P. angolensis* trees suffering from mukwa disease (Pearce 1979). Epicormic shoot production also indicates degeneration of feeder roots and mycorrhizae (Manion 1991, Jurskis 2005) and was also observed in our field studies. Drought-like conditions in Mawewe Nature Reserve, Pretoriuskop and Bushbuckridge (Figure 4) in 1993/94 could thus have influenced the disease noted by Krynauw (1998) in South Africa. Several subsequent periods of drought in the years 2002–2005 could similarly have contributed to the disease problem we observed during 2005 and 2006 in Mawewe Nature Reserve, Pretoriuskop, Bushbuckridge and Buffelskloof Nature Reserve (Figure 4).

In most areas where sampling occurred, fire management was not practised. Burning in these areas would suppress competition that *P. angolensis* trees face from neighbouring vegetation (Boaler 1966, von Breitenbach 1973, Vermeulen 1990). Fire also suppresses bush encroachment, a

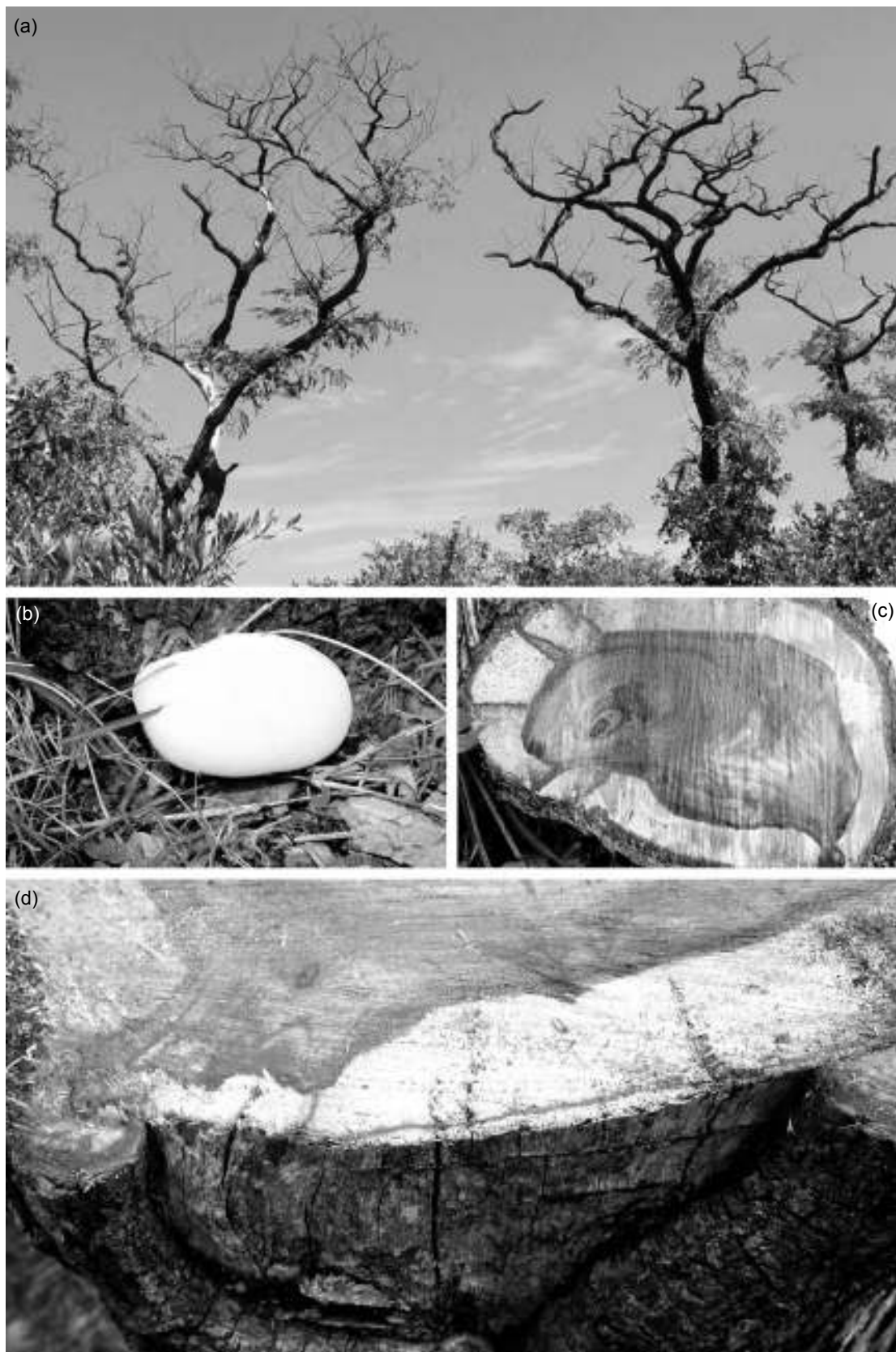


Figure 3: Disease symptoms observed on *P. angolensis* trees in South Africa. (a) Diseased trees in the field. (b) *Ganoderma* fruiting body at the base of a fire-damaged tree. (c) Heart rot with evidence of zone lines present. (d) Heart rot initiated due to fire damage of the stem

Table 1: Overview of fungi isolated from *P. angolensis* trees in South Africa with locations noted

Fungus	Location ¹
<i>Acremonium</i> sp.	BNR, MNR, SCA
<i>Alternaria</i> sp.	MNR
<i>Aspergillus</i> sp.	MNR, SCA
<i>Candida</i> sp.	BNR, MNR, SCA
<i>Chrysosporium</i> sp.	BNR, MNR, SCA
<i>Cylindrocarpon</i> sp.	BNR, MNR, SCA
<i>Cytospora</i> sp.	MNR, SCA
<i>Diplodia alatafructa</i>	BNR, SCA
<i>Fusarium</i> sp.	MNR, SCA
<i>Geotrichum</i> sp.	BNR
<i>Gliocladium</i> sp.	BNR, MNR, SCA
<i>Humicola</i> sp.	BNR, MNR, SCA
<i>Lasiodiplodia crassisporea</i>	MNR
<i>L. pseudotheobromae</i>	MNR, SCA
<i>L. theobromae</i>	BNR, MNR
<i>Mycelia sterilia</i>	BNR, MNR, SCA
<i>Myriodontium</i> sp.	MNR
<i>Penicillium</i> sp.	BNR, MNR, SCA
<i>Rhizopus</i> sp.	MNR
<i>Staphylotrichum</i> sp.	BNR, MNR, SCA
<i>Trichoderma</i> sp.	BNR, MNR, SCA
<i>Trichosporon</i> sp.	MNR

¹ BNR = Buffelskloof Nature Reserve, MNR = Mawewe Nature Reserve, SCA = Sudwala Caves area

phenomenon where the density of woody plants present, in the form of a thicket of fire-sensitive species (Geldenhuys 1977), progressively increases (Scholes and Archer 1997 and references cited therein). Both the crowns and roots of neighbouring trees and grasses compete with *P. angolensis* for resources including sunlight, soil moisture, soil nutrients and space (Boaler 1966, Orpen 1982, Vermeulen 1990). Both soil nutrients and moisture are concentrated in the upper soil horizon or topsoil (Scholes and Archer 1997). It is, therefore, not surprising that most of the root biomass of both trees and grasses is confined here (Jackson et al. 1996). It is also known that grass roots predominate and outnumber tree roots at these shallow levels (Scholes and Walker 1993). Consequently, competition for these resources is exacerbated by the shallow root system in both mature trees and developing seedlings of *P. angolensis* (Geldenhuys 1977). This competition can influence tree seedling recruitment and regeneration and is heightened in times of drought, probably contributing to the development of disease.

Fire management impacts positively on tree seedling recruitment and regeneration of *P. angolensis* (Boaler 1966, Geldenhuys 1977). Recruitment of seedlings is necessary to sustain populations of *P. angolensis* (Desmet et al. 1996). Low recruitment rates were noted by Krynauw (1998, 2000). It is known that developing tree seedlings initially obtain moisture at shallower depths than grasses but at later stages of development they co-occur at the same levels and compete with grass roots (Weltzin and McPherson 1997). Root nodulation of *P. angolensis* seedlings enables nitrogen fixation (Boaler 1966) but is energy-demanding and can be limited by the availability of carbon (Vitousek and Howarth

1991, Sprent 1999, Cramer et al. 2010). Consequently, the introduction of fire can enable and promote nodulation by suppressing and removing neighbouring vegetation competing for energy and carbon. Fire also releases nutrients such as phosphorus and nitrogen so that they are readily available to persisting vegetation, including seedlings and mature trees of *P. angolensis*, thereby promoting nitrogen fixation (Reiners 1981, Vitousek and Howarth 1991). In this regard, very little phosphorus is lost through volatilisation or leaching from soil (Certini 2005), both during and after a fire. Instead, organic phosphorus is converted to orthophosphates (Cade-Menun et al. 2000, Certini 2005), increasing the levels of phosphorus available to plants (Serrasolsas and Khanna 1995, Certini 2005). In contrast, nitrogen-containing compounds are transformed during fire via two steps: initially free amino acids and amino groups (NH₂) are removed, subsequently amide-N is converted to heterocyclic aromatic compounds such as pyrimidine, pyrroles, imidazoles, indoles and carbazoles (Knicker et al. 1996, Certini 2005). Additionally, inorganic ammonium (NH₄⁺-N) and nitrate (NO₃⁻-N) are generated during a fire, with some of the ammonium converted to nitrate some time after the fire (a process known as nitrification) (Covington and Sackett 1992, Certini 2005). The two forms have different destinies: nitrate is leached down while ammonium is retained by the soil, being adsorbed by minerals and organic matter (Mroz et al. 1980, Certini 2005).

Fire damage and fire scars represent possible contributing factors in *P. angolensis* decline and death. Fire is particularly important for *P. angolensis*. Both fire and the clearing of vegetation for cultivation remove competing plant species that adversely affect the growth and development of *P. angolensis* (Boaler 1966, von Breitenbach 1973). 'Cold fires' (450 °C lasting 30 s or less), as already mentioned, enable and promote germination of seedlings by burning off wings and bristles of fruit and removing the grassy layer, allowing the enclosed seed to encounter water during an ensuing rainfall (von Breitenbach 1973, van Daalen 1991). Fire damage to the boles of trees can occur, possibly due to an accumulation of litter, grass and thicket (fuel) at the base of trees (Geldenhuys 1977), resulting in attack by woodborers and fungi (Schoeman 1982, Vermeulen 1990). After a 'hot' fire (450 °C lasting 90 s or more) (van Daalen 1991), the debris smolder and the sustained heat can contribute to, if not cause, the observed damage of the stem (Braam van Wyk, pers. comm.). Hot fires, as a result of fuel load, can also influence the nutrient composition of soil. During hot fires, soil pH increases firstly as a result of ash deposition (Arocena and Opio 2003, Certini 2005), and secondly due to the denaturation of organic acids (Certini 2005). This results in phosphorus binding to calcium minerals or precipitating as calcium phosphate (Certini 2005).

Some of the trees observed in this study were ring-barked, probably by porcupines that gnawed the base, exposing the underlying wood to damage by fire as well as providing entry sites for pathogens such as *Ganoderma* spp. (Yeaton 1988, Shackleton 2002). Although ring-barking by porcupines during periods of drought has been noted (Shackleton 2002), a number of single points of fire-damaged wood were observed in this study (data not shown). These single

points suggest a fire intense enough to penetrate through to the underlying wood, scarring and damaging it, regardless of size or diameter. The lack of fire management would contribute to the buildup of fuel for such a fire, although the effects of porcupines could ultimately contribute to the damage and mortality observed.

It is recommended that fire be applied biannually just before the annual rainfall season (Geldenhuys 1977) to maintain populations of *P. angolensis* and to enhance recruitment (Geldenhuys 2005) as annual burning adversely affects developing seedlings until the suffrutex

root system has fully developed (Groome 1955, Boaler 1966, Högberg 1986). Field observations indicate that fires that occur in areas where biannual burning is not practised, are inordinately hot for the sustainable growth of mature trees and can inhibit recruitment of seedlings and saplings. Previous studies support these findings. In areas where biannual burning was not practised, a thicket of woody species developed that inhibited *P. angolensis* recruitment and fires that subsequently occurred were so intense that they damaged trees severely by burning the phloem and xylem (van Wyk et al. 1993). In addition,

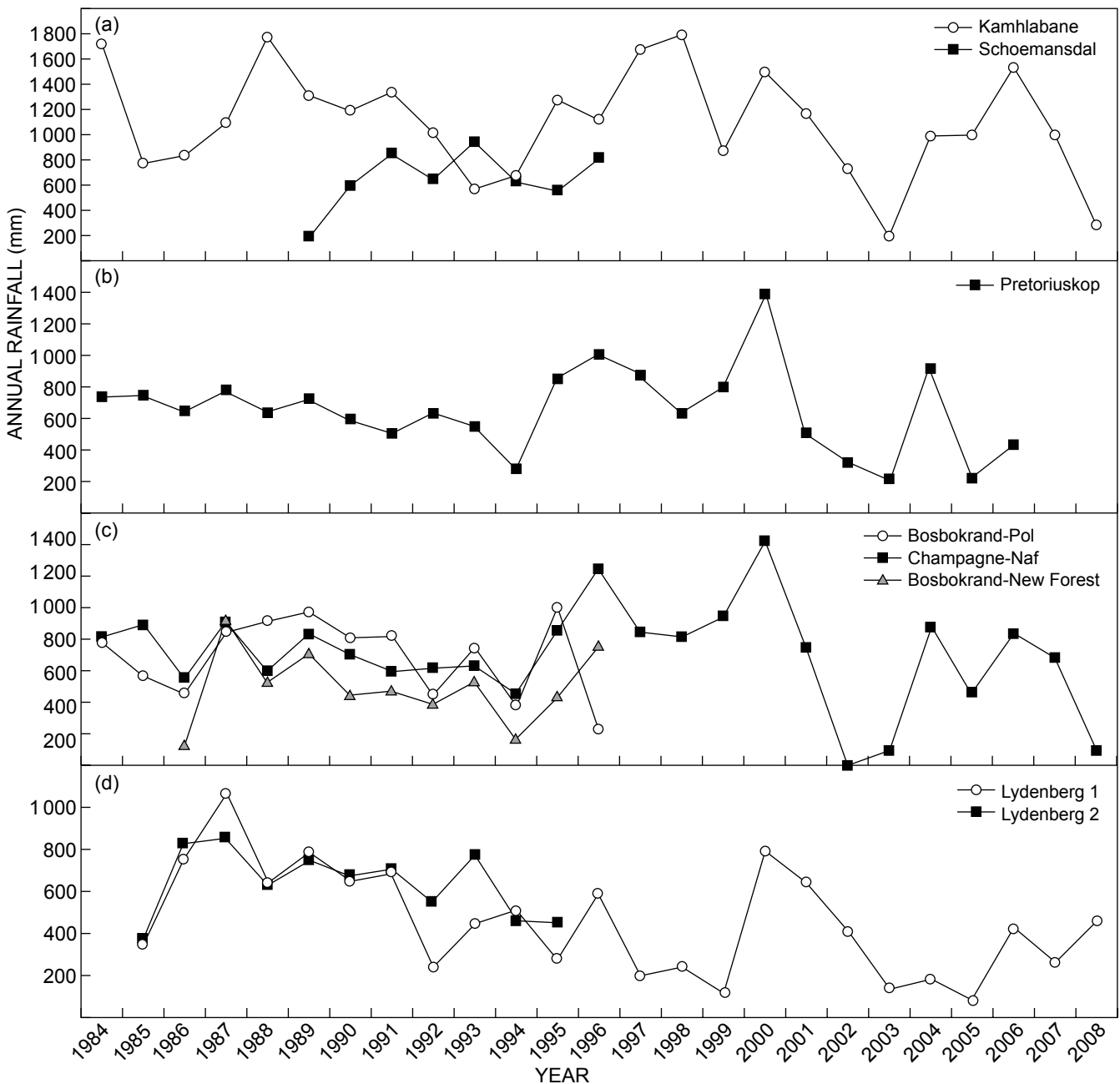


Figure 4: Rainfall data (mm) for the various areas considered in this study. Weather stations noted are closest to the sites from where we sampled. (a) Mawewe Nature Reserve area, (b) Pretoriuskop, (c) Bushbuckridge area and (d) Buffelskloof Nature Reserve area

these 'hot fires' can destroy both seedlings and saplings (van Daalen 1991, Banda et al. 2006) and the damage to stems and roots of mature trees, especially shallow-rooted trees, can easily enable rot fungi to invade burnt tissues and commence heart rot. Wounds created by fires are further exacerbated by drought conditions (Desprez-Loustau et al. 2006) and provide entry points for fungi responsible for heart rot and disease (Roux et al. 2004, 2005, Chungu et al. 2007).

Regular biannual application of fire also likely promotes the health of *P. angolensis*. Heat resulting from fire is known to inhibit and suppress weed plants and seeds, and is antimicrobial against fungi, bacteria, nematodes and insects (Hardison 1976). Smoke emanating from a fire and from smoldering material is also antimicrobial; inhibiting spore germination, mycelial growth and plant infection (Parmeter and Uhrenholdt 1975). Neighbouring vegetation such as grasses, weeds and other trees, can act as alternate hosts for pathogens of *P. angolensis*, and so their removal by fire impacts positively on the species. Regular application also minimises the risk of fuel buildup, which can lead to runaway fires hazardous to humans. In addition, application of fire can promote and safeguard the health of livestock, particularly in Mawewe Nature Reserve, by eliminating dead and senescent leaves and plant material that can accommodate mycotoxic fungi (Hardison 1976).

Fire aids pruning of side branches and multiple, secondary stems of *P. angolensis* trees (Boaler 1966, Orpen 1982, Vermeulen 1990). A lack of fire can result in poor growth form, a common field observation (Figure 5a and b). In fact, the umbrella-like form of mature, healthy *P. angolensis* trees (Figure 5c) was virtually absent in all the areas where diseased trees occurred. As the species is light-demanding (Boaler 1966, Orpen 1982, Vermeulen 1990), lower branches shaded by newer branches higher up progressively die (Boaler 1966, Vermeulen 1990). As the branches break off, they can provide entry points for rot

fungi. If the branch partially breaks off, the remainder can become encased in the bark, serving as a residual entry point for rot fungi. Consequently, if side branches and multiple stems are not pruned or burnt off when branches are small enough to enable active bark recovery, then their presence can contribute to die-back and death of trees. In *Acacia mangium*, the presence of multiple stems results in 'intrastem competition' and a reduced height and diameter of the main stem (Beadle et al. 2007). Thus, multiple stems in *P. angolensis* could result in premature death due to other neighbouring trees overshadowing the light-demanding individuals of the species. Apart from these obvious health benefits to *P. angolensis* trees, pruning also has commercial importance: it can be used to correct stem defects (Boaler 1966, Vermeulen 1990, Geldenhuys 2005) and can result in an increased length of planks and logs (Boaler 1966, Vermeulen 1990) as well as a trunk increase of 20–25% (Groome et al. 1957, Vermeulen 1990).

Conclusions

A number of factors noted in this review most likely impact on the health of *P. angolensis* trees. Drought has been implicated in the disease of these trees in both Zambia and South Africa. Rainfall data sets gathered from these areas indicate that reports of die-back and death of trees can be correlated with several years of drought, either intermittent or sustained over several years. The effect of these drought periods is observed in subsequent years, when trees begin to die back and decline. Along with *P. angolensis*, other tree species in the same area are affected by disease. The symptoms of mukwa disease noted in this review, along with these facts, argue that the primary cause of the disease is most likely not biotic.

Together with rainfall, fire is a crucial factor impacting on the health and sustainability of *P. angolensis*. Fires enable germination, regeneration, nitrogen fixation, and nodule



Figure 5: Incorrect growth forms of *P. angolensis* due to side branches and secondary stems during field observations (a, b) and correct growth form (c). Correct growth form can be obtained through fire management and by manual pruning. Note competing plants at the base of the tree in (a). (c) copyright Geldenhuys (2005)

formation in *P. angolensis*, ensuring that seedlings and saplings are not impeded during growth. Fires also suppress neighbouring plant and tree species that compete with *P. angolensis* for soil nutrients, moisture, space and sunlight. Competition for these is likely elevated during times of drought and predisposes *P. angolensis* individuals to stress. Both heat and smoke resulting from fires can promote health of *P. angolensis*. Consequently, the interaction between adverse environmental conditions or improper management, in combination with the biology of *P. angolensis*, likely predisposes individuals of the species to disease.

The timing of application of fire is critical. An annual fire inhibits regeneration of *P. angolensis* by negatively affecting recruitment of seedlings. A fire applied too infrequently has a similar effect, but can also damage mature trees, contributing to subsequent die-back and disease of stressed *P. angolensis* trees.

Both mukwa disease and the symptoms on *P. angolensis* trees noted in South Africa are probably the result of fire exclusion and improper fire management, but data from the field will be needed to either confirm or refute this. Indeed, field observations in the course of this study would have benefited from further information regarding the ecology of affected diseased trees to determine whether trends exist and if they are consistent. These observations would add weight to findings or introduce new data to be considered. Data with regard to the age of trees, the vegetation surrounding affected trees, grass cover and tree interaction as well as whether these are due to fire frequency and/or grazing, the degree of competition from neighbouring vegetation, data regarding rainfall including frequency and timing are all factors that would have to be considered in future studies. This review, consequently, is superficial in investigating the cause and reasons for the observed decline of *P. angolensis*, relying mainly on a review of the literature and drawing upon previous data to support observations. However, it is the first to consider the broader problem and should be seen as motivation for future studies.

In the light of global climate change, die-back and death of *P. angolensis* is indeed a cause for concern. It is likely that droughts in areas where the species occurs will continue to increase in frequency and intensity, adding to conservation concerns. At present, reserve managers and nature conservation agencies are advised to practise biannual burning, just prior to the annual rainfall season in areas where *P. angolensis* occurs. Fuel load is an important factor to consider in fire management and can be affected by grazing and clearing of litter, grass and thicket. An optimal fuel load will result in a cold fire that will encourage regeneration of the species, rather than one of high intensity resulting in damage to stems and fire scars, prompting rot to develop. Natural side-branch pruning should also be done at an early age on small branches and secondary stems where necessary and wounding of trees should be prevented and prosecuted where possible.

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