

**A COLLATION AND OVERVIEW OF RESEARCH INFORMATION
ON *ACACIA ERIOLOBA* (CAMELTHORN) AND IDENTIFICATION
OF RELEVANT RESEARCH GAPS TO INFORM PROTECTION OF
THE SPECIES**

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Executive Summary

Acacia erioloba is proposed for re-listing on the list of protected trees, such that it is protected in terms of Section 12 of the National Forests Act, 1998 (Act No. 84 of 1998). Under this act, "No person may (a) cut, disturb, damage, destroy or remove any protected tree; or (b) collect, remove, transport, export, purchase, sell, donate or in any other manner acquire or dispose of any protected tree, except under a licence granted by the Minister." The act does not distinguish between dead and live trees, and so removal of dead wood is also against the law.

A. erioloba is sometimes destroyed while clearing bush thickened areas or firebreaks, during mining and development of infrastructure. Wood from the tree also generates income, or is a source of domestic fuel wood or building materials for some. *A. erioloba* was proposed for re-listing because of its ecological importance, cultural value and because of the threat posed by uncontrolled (illegal) harvesting in some areas for commercial firewood and ostensibly to improve veld condition. Powell (2001, pg. 8) believes that the current rate of wood removal is so high that studies of the role of dead trees in the environment may be impossible "within a few years, or even months". At present, the tree is wide-ranging and abundant, however, and it is therefore difficult for landowners to support protection of this species. Landowners see only a "snapshot" in time, however, and for a long lived, slow growing species, uncontrolled harvesting may not only be unsustainable, but also exceptionally damaging.

Most benefits brought by *A. erioloba* are not immediately apparent, and it is only when they are large, years after establishment, that they begin to appreciably affect soil quality, produce large patches of shade, and produce pods, gum, and fuel wood (Barnes 2001c). Large trees also diminish nutrient leaching, increase nutrient levels beneath their canopies (owing to nutrient cycling and concentration of livestock dung) (Materechera and Materechera 2001), mitigate soil degradation, prevent soil erosion on steep slopes, sequester carbon and replenish organic matter (Barnes 2001c). Pod production is linearly related to tree size (Barnes et al. 1997), so as trees become older, they become more valuable as a source of forage, as livestock relish eating pods. They are also the main source of seed for future recruitment of this species. Other gains are further obscured in that they are indirect: increased yields from grain crops, stock weight gain or increased milk production invariably go unmeasured (Barnes 2001c).

The driving forces behind harvesting trees are only partially understood – financial need engendered as a result of environmental and economic conditions, combined with a demand for what is seen as "quality" *braai* (barbecue) wood in South Africa's major cities. *A. erioloba* does not appear to be significant as a bush encroaching species, and it is more likely merely part of the woody component in bush encroached areas. Recent research shows that *Acacia* recruitment is water (Ward 2002, Lloyd 2003) and seed (Joubert 2003) limited, and therefore, in order to prevent recruitment of this species, farmers should remove grazers in particularly *wet* years, if seed production was good in preceding years, rather than the accepted wisdom, which is to remove livestock in particularly dry years (Ward 2002). This would allow grass growth to compete with tree seedlings that germinate abundantly and have a high probability of surviving in above-average rainfall years. The long-term ecological implications of uncontrolled clearing (both in terms of future grazing and biodiversity) are unknown, yet crucially important, as they are fundamental to the future livelihoods of landowners, their dependants and their employees. As with many tree species, the value of *A. erioloba's* non-consumptive use is seldom fully acknowledged or known. Studies that encompass social and economic aspects of use of this species as well as its importance in the maintenance of biodiversity and ecological processes are therefore necessary to fully understand its economic and ecological importance. The South African Department of Water Affairs and Forestry (DWAF) has commissioned this study to collate all available information to inform decisions regarding harvesting of this species and identify gaps in our knowledge.

This species has had more research conducted around it than most other plant species in the region, but there are still considerable gaps in our knowledge, and more importantly, work that ties the findings together into a predictive, testable model, is still lacking.

While seed predation in various forms is considerable (Coe and Coe 1987, Barnes 1999, Dudley 1999), it appears not nearly as important as amount and pattern of rainfall for successful recruitment, as evidenced by the presence of cohorts (Ernst et al. 1990, Hoffman et al. 1994, Barnes 1999, 2001b). Although we know that timing of rain and a certain minimum, frequent amount is required for germination and establishment, we do not know the actual amounts or frequency necessary, which may be greater on sandy soils, which have a lower water holding capacity. It is likely that recruitment in the more arid extent of *A. erioloba*'s range is governed by 18-year oscillations (Tyson and Crimp 1998) in rainfall over the region. Therefore, the context in which trees occur is important for harvesting decisions. In drier areas, where rainfall is episodic, recruitment is likely to be low (Ernst et al. 1990, Barnes et al. 1997, Barnes 1999, 2001b). Therefore, any harvesting programme must consider rainfall and potential recruitment rates.

After successful establishment, seedlings are still vulnerable to drought, frost, herbivory and fire, although larger trees survive these. Large, old trees within populations are susceptible to fire (Van der Walt and Le Riche 1984) and storms (Wackernagel 1993, Barnes 1999), however. *A. erioloba* is able to resprout after fire (Skarpe 1980), felling (Henkel 1931) and herbivory (Barnes 1999), but appears unable to tolerate repeated herbivory or felling when already compromised (M. Sekhwela, *pers comm.*). The resprouting ability of this species likely varies with size, time and intensity or degree of harvesting, herbivory or fires, amount of rainfall and land use, and further research is recommended. Of particular importance are knowledge of both ability and subsequent growth rates for different size classes, to anticipate the consequences of harvesting. Subsequent responses of associated flora and fauna to concomitant changes in habitat structure are also needed. All of these factors need to inform harvesting decisions, if such decisions are to be made.

Harvesting of deadwood only, under *strict* criteria, may be sustainable, although the ecological consequences of deadwood removal can only be surmised. Therefore, the precautionary principle (i.e. no harvesting) should be applied until this gap in our knowledge has been addressed. The needs of hole nesting species, habitat characteristics important for maintenance of biodiversity, and importance of dead wood for nutrient cycling in particular, should be considered.

The comprehensive literature survey carried out in completion of this report reveals that large trees not only take decades to establish, but once established, improve grazing quality and provide other ecological services, such that when large, *A. erioloba* is a keystone species (Milton and Dean 1995). Therefore, harvesting of large trees should not be considered, particularly in the more arid extent of its range when it is often the only big tree growing on sand in areas that receive less than 400mm.year⁻¹ of rain (Acocks 1953).

Table one contains a summary of our current knowledge with particular reference to ecological factors, and important gaps therein. Among the most important questions relating to the ecology of this species are those surrounding recruitment, survival, and resprouting ability and how these are influenced by abiotic influences such as rainfall, drought, and expected increases of these with predicted anthropogenic climate change. The influence of tree size and density on grazing and biodiversity require urgent attention, as farmers list improved grazing among reasons for felling this species. A comprehensive evaluation of the current and potential value of this species is needed, to enable appreciation of the tree in all its roles. Finally, investigations of farming practices that minimise or avoid bush encroachment remain the Holy Grail for arid savanna researchers.

Species Description

COMMON NAMES:

Mpatsaka (Sotho), Mokala (Tswana), Kameeldoring (Afrikaans), Camelthorn (English), Umwhohlo (Ndebele), Mogohlo (Sependi)

Lichtenstein collected the original type specimen for this tree on his travels during 1803-06 (Ross 1975). It was named *Acacia giraffae*, an appellation which became generally applied to the Kalahari's camelthorn trees (Ross 1975). In the 1970s, however, it became apparent that the type specimen was in fact a hybrid of the camelthorn and *A. haematoxylon* (Ross 1975). Ross (1975) thus selected an alternative neotype, a specimen collected and described by E. Meyer, and proposed renaming the camelthorn *A. erioloba* (Ross 1975). The hybrid, which is restricted to the northern Cape of South Africa (Ross 1981) then became known as *A. erioloba* x *A. haematoxylon* (Ross 1975). It appears as if *A. erioloba* is a polyploid of *A. haematoxylon* (Coe 1998).

STATUS OF ACACIA ERIOLOBA

LEVEL OF PROTECTION

Acacia erioloba first gained protected status in South Africa in 1941, and again included on a revised list produced in 1976 that is still in effect. Recently, a new list was compiled to address weaknesses in the 1976 listing. *A. erioloba* has been included on this latest list, and hence the Minister of Water Affairs and Forestry intends to declare it a protected species, in terms of section 12 of the National Forests Act, 1998 (Act No. 84 of 1998).

The law under section 12 of Act No. 84 of 1998 states that if a tree species is declared protected, "No person may (a) cut, disturb, damage, destroy or remove any protected tree; or (b) collect, remove, transport, export, purchase, sell, donate or in any other manner acquire or dispose of any protected tree, except under a licence granted by the Minister."

The act does *not* distinguish between dead and live trees, so even removal of dead specimens is illegal without a permit.

GEOGRAPHIC DISTRIBUTION

Acacia erioloba is a southern African species, characteristic of Kalahari sandveld. Its range extends from southern Angola and Namibia, parts of Botswana, southwestern Zimbabwe, the north west of South Africa and just into south west Mozambique (Barnes et al. 1997). An isolated population of *A. erioloba* also occurs in Namaqualand near Kleinsee (R. Cowling *pers. comm.*). Over its range, rainfall varies from less than 40mm.year⁻¹ to 900mm.year⁻¹, and daily temperature ranges vary from less than 15°C to 45°C (Barnes et al. 1997). The Kalahari sands extend as far as Congo and Gabon, so this species may have been far more widespread in the past, during arid periods arising from successive glaciations (Coe 1998).

This species' ecology suggests that it is adapted to shallow to deep, infertile, sometimes alkaline sands, beneath which it uses its deep roots to access and use (even brackish) deep water containing dissolved nitrates (Barnes 2001c). Roots to 60m have been reported (Canadell et al. 1996). It may be restricted to sand owing to the competitive advantage it has on this substrate, in which it can rapidly expand its initial rooting system: it would not be able to achieve such rapid expansion on heavier soils (Barnes 2001c).

Even-aged stands may arise from previous clearing and subsequent cattle grazing (Timberlake et al. 1999). In the drier parts of its range, it seems to recruit during episodic good rainfall, when seedlings use transitory surface moisture to establish a taproot to permanently available ground water, after which it is independent of annual rainfall (Barnes et al. 1997, Timberlake et al. 1999, Barnes 2001b, Barnes 2001c). In the arid parts of its range, therefore, *A. erioloba* is often the only tree in its environment; whereas in the moister parts of its distribution, it is a component of savanna woodland communities (Barnes et al. 1997).

SPECIES DESCRIPTION

Acacia erioloba is variable in form over its range, from a small spiny shrub approximately 2m high, to a tall tree up to 16m (Coates Palgrave 1983). Its growth form is dictated by rainfall and availability of water at depth (Barnes et al. 1997), and presumably also by soil depth. It has drooping, often contorted, branches and a rounded or umbrella-shaped crown (van Wyk and van Wyk 1997). Tree architecture varies with tree age and abiotic factors (e.g. depth of soil and water) (C. Seymour, *pers. obs.*). Some trees form small groves of about 5 to 15 trees, which when excavated, prove to be interconnected (Grobbelaar 1996) O. Huyser, *pers. comm.*).

The bark is rough, grey to blackish-brown and highly fissured (Coates Palgrave 1983). Most larger trees have trunk diameters in the region of 60 – 80 cm, although some individuals reach up to 100 cm in diameter (Timberlake et al. 1999). Young twigs are characteristically zigzag-shaped with a purple twinge owing to a translucent epidermis (Timberlake et al. 1999).

The straight stout thorns are between 2 – 5 cm long, whitish in colour, and often inflated and fused together at the base (van Wyk and van Wyk 1997, Timberlake et al. 1999). Each pair points in the opposite direction to the previous pair, and young thorns are usually thin and sharp (Timberlake et al. 1999). During years of good rain, nearly all thorns on trees exhibit some form of swelling, whereas in dry years, perhaps as few as 5% of thorns manifest such swellings (Gubb 1988).

Leaves are broader than long, with 2-5 pairs of pinnae, with blue-green leaflets (Timberlake et al. 1999). Petiolar glands are absent, but there are glands at the base of each pair of pinna (van Wyk and van Wyk 1997). The tree remains green throughout the dry season. At times, outbreaks of invertebrate herbivores (e.g. *Gonometa postica*) can strip trees of their leaves (C. Seymour, *pers. obs.*).

Flowering usually begins in July, ending in November, with a sharp flowering “peak” in September (Barnes et al. 1997). The tree produces bright golden-yellow balls of flowers, singly or in pairs, along twigs of growth from the previous season (Timberlake et al. 1999). Insects pollinate this species, although a list of pollinating agents has not been compiled (Barnes et al. 1997). At time of flowering, frosts are infrequent, thunderstorms rare and temperatures high (Barnes et al. 1997). Thus, insect activity is invariably high, pollination generally uninterrupted, and likelihood of damage to young pods by violent thunderstorms or strong winds, low (Barnes et al. 1997). The tree’s ability to access water deep in the soil effectively immunises it to fluctuations in annual rainfall (Barnes et al. 1997), but access to ground water influences pod production (Seely et al. 1979-81). Pod production is neither annually cyclic nor predictable (Seely et al. 1979-81). Occasional late severe frosts can damage the flower initials and unseasonably early severe thunderstorm with accompanying strong winds can break off developing pods, reducing production for that year (Barnes et al. 1997). As flowering times within populations are short (sometimes within 6 weeks), these occasional destructive events can severely reduce pod production (Barnes et al. 1997).

A. erioloba has the largest indehiscent pods recorded for any African *Acacia* (Coe 1998). They are kidney-shaped, large and woody (hence the name “*erioloba*” (= woody lobe)), and appear to be covered in light-grey velvet. Individual trees exhibit visible differences in pod shape, size, phenology and yield (Barnes et al. 1997). Across its range, single populations can have trees with small (5 x 20mm) and almost cylindrical pods alongside trees bearing large (130 x 170 mm), flat, almost semi-circular pods (Barnes et al. 1997). Pods are spongy within and seeds are irregularly distributed within the pod (Barnes et al. 1997).

Seeds are lenticular to elliptic, between 8-14mm x 7-10mm (Barnes et al. 1997). There are typically between 8 – 25 seeds per pod (Leistner 1961, Dudley 1999); with an average of about 16 seeds per pod (Hoffman et al. 1989). Seeds are only released as the pod decays on the ground, or is eaten by animals (Timberlake et al. 1999). Pods have been found to fall between May to August in the Kuiseb River, (van Wyk et al. 1985), although in Hwange National Park the effective fruiting season is over 10 months (January to October), with pods that fall early in the season being either sterile or heavily parasitised by insects (Dudley 1999).

CONSERVATION

Historically, many of the large *A. erioloba* around Kimberley were felled for fuel for the diamond mines (Carr 1974). The dense wood of this slow-growing species produces coals that last longer

than many other fuel woods (Venter and Venter 1996). It has now become popular as a quality *braaiwood*, although the rate at which it cools is not significantly different to other *Acacia* species, including the exotic invasives *A. cyclops* and *A. mearnsii* (Raliselo 2002). Commercial felling and/or collection for firewood is widespread throughout South Africa, and as much as 60 tons per month are being bundled on some properties (Anderson and Anderson 2001, Liversidge 2001). Areas in which this activity has been observed include the Kathu area (Liversidge 2001), Debeng along Gamagara, around Tswalu (S. Milton *pers. obs.*) and Van Zyls Rus area (C. Seymour, *pers. obs.*), although this will never be easily quantified, owing to its illegality. Demand by consumers in South Africa's large cities (e.g. Cape Town and Johannesburg) are likely driving exploitation of camelthorn wood (Anderson and Anderson 2001).

Ongoing harvesting indicates that the legislation and/or its implementation are inadequate in protecting these trees. Likely, a number of socio-economic and ecological factors need to be addressed. A commonly cited justification for clearing camelthorn is its value as a form of job-creation, but closer analysis reveals that farmers and employees *together* earn only a third of the selling price (Milton et al. 2002). In spite of this, farmers and employees bear the greatest risk of all involved, carrying the potential of a degraded environment (and therefore livelihood) because of injudicious and unsustainable removal of *A. erioloba*. Among other reasons for felling are for use as fencing poles, or clearing lands in an attempt to improve pasture (Powell 2001). Removal of *A. erioloba* with the aim of improving pasture is linked to perceptions that this species is implicated in bush densification or encroachment. Farmers also believe that trees reduce the carrying capacity of the veld (Powell 2001). Bush densification is the phenomenon whereby woody species suppress growth of palatable grasses and herbs. While certainly part of the woody component that becomes dominant in bush encroached areas, this species lacks the characteristics of a bush encroaching species, and so is unlikely to be the primary encroaching species. Efforts to clear bush encroached areas found initially that application of tebuthiuron was effective in removing target species (*A. mellifera*, *A. reficiens* and *Grewia flava*), but that *A. erioloba* was also sensitive, although less so than target species (Moore et al. 1985). The study did not state whether further mortality of *A. erioloba* occurred after the study, or whether mortality was restricted to certain size classes.

The driving forces behind harvesting are only partially understood – economic need engendered as a result of environmental and economic conditions and demand for wood in the major cities. The long term ecological implications of clearing (in terms of future grazing, biodiversity and socio-economics) are also only partially understood, but perhaps most important, as they represent the livelihoods of farmers and their employees.

BIOLOGY

DISPERSAL

A. erioloba is mammal dispersed. A number of game species feed on its pods, including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), black rhino (*Diceros bicornis*), gemsbok (*Oryx gazella*), eland (*Taurotragus oryx*), greater kudu (*Tragelaphus strepsiceros*) (Leistner 1961), and livestock also feed on pods (Timberlake et al. 1999). Often, large quantities are consumed: as many as 170 seeds have been found within a single set of eland droppings (Leistner 1961). Seeds are thick and hardy, enabling them to withstand the shearing forces of herbivores' molar teeth (Coe and Coe 1987), and the tough seed coat protects the seed as it passes through the digestive system (Leistner 1961). Seeds often germinate in dung (Henkel 1931, Dudley 1999, Milton and Dean 2001). Thus, large herbivores are likely the primary means of seed dispersal (Timberlake et al. 1999), confirmed by the concentration of *A. erioloba* seeds in areas near watering points in Botswana (Ernst and Tolsma 1990).

There are a number of advantages to large herbivore dispersal. Among these are dispersal away from the parent tree, with implications for both gene flow and escape from the parent tree's seed parasites (although this may only reduce bruchid larval infestation in the year in question (Miller 1994a, b)). The possibility that passage through the gut eliminates olfactory cues used by beetles and other seed parasites to locate seeds may also be beneficial (Coe and Coe 1987).

Changes in land use may have implications for gene flow, although the significance of this for overall population viability is unknown: Presence of fences and herbivores different to the original

inhabitants of areas has likely reduced dispersal distances. In areas containing megaherbivores (e.g. elephants), potential dispersal distances are far greater (about 20 – 50km) (Dudley 1999) than within livestock areas, where dispersal distances by cattle are estimated to be about 2 – 3km (Ernst and Tolsma 1990).

GERMINATION

Although dispersal away from the parent tree by large herbivores carries clear advantages, the influence of vertebrate dispersal on *total number* of germinating seeds remains equivocal. Among studies conducted on *Acacia* species, some have found that digestion improves germination rates by softening the seed testa (Leistner 1961, Lamprey 1967, Lamprey et al. 1974, Hoffman et al. 1989, Materechera and Materechera 2001), and perhaps also killing bruchid larvae that parasitise seeds (Coe and Coe 1987, Miller 1994b). Other studies have found no difference (Barnes 1999, 2001b), and still others have found *lower* germination rates of both *Acacia tortilis heteracantha* and *A. erioloba* seeds collected from greater kudu and eland dung than those collected directly from trees (Coe and Coe 1987, Coe 1998). Germination of seed from elephant dung and cattle dung were 78% and 52% respectively, while germination rates for seeds from ripe pods was 92% (Walter 1954). Greater germination rates for undigested seeds might be attributed to undetectable bruchid beetle holes increasing germination in the non-dung seed group (Coe and Coe 1987).

Field studies conducted on *A. erioloba* germination rates may be more valuable than laboratory studies, as low water holding capacities of Kalahari sands likely influence observed outcome. Just such a study was conducted in Chobe (Barnes 1999, 2001b). Total number of seeds germinating did not differ significantly between those from dung and those removed from pods, but seeds from dung germinated far faster - after three days, while those directly from pods only germinated after 10 days (Barnes 1999, 2001b). This could be significant for a semi-arid savanna species such as *A. erioloba*, where sufficient rainfall for germination and establishment are rare, along with sandy soils that do not hold water for long (Barnes 2001b). Fire may also make seeds more permeable to water, so facilitating germination (Coe and Coe 1987).

Acacia seeds may remain viable in the soil for as long as 50 years, such that natural seed scarification processes may be greatly delayed (Coe and Coe 1987). Small batches may become available for germination at irregular intervals, which may be beneficial in arid and semi-arid environments, where unpredictability of rainfall means mass germination may be undesirable (Coe and Coe 1987).

A study of four African savanna tree species, three of which were *Acacias*, found that larger scarified seeds took longer to absorb, and subsequently lose, water (Wilson and Witkowski 1998). *A. erioloba*, with large seeds, thus also likely takes some time to absorb water and by implication is also slow to lose it again. The species used in the study were all still viable after having been soaked and subsequently dried (Wilson and Witkowski 1998), and it is likely that *A. erioloba* has the same ability to withstand cycles of soaking and dehydration. It is not known how many cycles of imbibition and drying can be withstood without loss of viability, however (Wilson and Witkowski 1998). This study also found that frequent rainfall, rather than large amounts, is more important for germination and establishment (Wilson and Witkowski 1998).

A. erioloba seeds had no light requirement for germination, likely because they often need to be below ground to access sufficient water for this process (Briers 1988).

That large herbivores are important for dispersal of this species is unequivocal. Importance of game to germination success rate is unresolved, but appears to revolve around relative speed of germination, with seeds that have been digested germinating far faster than those that have not (Barnes 1999, 2001b).

SEED PARASITES AND PREDATORS

As with many *Acacia* species, various species of bruchid beetle parasitise seeds of *A. erioloba*. The large pods of this species are easier for bruchids to locate, but also rattle more loudly when falling, thus attracting their mammal dispersers (Coe 1998). In addition, large seeds, while better able to withstand shearing forces of herbivore molars, and fluctuations in water availability, are susceptible to infestations by beetles of a greater size range than small seeds (Coe and Coe 1987).

There appears to be substantial variation between trees in extent of bruchid damage (Barnes et al. 1997). This could be due to differences in flowering time, or to inherent chemical differences influencing attractiveness to beetles (Barnes et al. 1997). Alternatively, protection from bruchids could arise from the trees' residents: many *A. erioloba* trees have colonies of *Crematogaster* ants living within them. A study conducted in Spain found that *Crematogaster brevispinosa* prey on bruchid eggs laid on *A. farnesiana* pods, thus lowering infestation rates (Traveset 1990). Trees with *Crematogaster* colonies may therefore also experience lower bruchid infestation rates in the Kalahari.

Bruchid larval infestation begins early in seed development, before maturation and dispersal (Mucunguzi 1995a). Larvae develop inside seeds, pupating and emerging as adults, unless seeds are destroyed or consumed by mammals (Mucunguzi 1995a). Bruchid infestation can vary strongly between years (Ernst et al. 1989), and in years with large seed crops, percentage bruchid infestation is lower (Ernst et al. 1990). Time of year also affects observed infestation rates, with lower rates of infestation recorded early in the season. Different bruchid species may have different life histories, such that composition of bruchid species assemblage also influences infestation rates. Thus, the literature reports a range of infestation rates, of between 47-52% (Barnes 2001b), 71-90% (van Wyk et al. 1985) and 54-96% of seeds (Ernst et al. 1990).

Influence of bruchid infestation on germination remains uncertain: some studies report increased rates, some decreased. The effect on germination is governed by how far bruchid larval development has progressed, a factor which no doubt also interacts with timing of rains (Miller 1994b). As long as the seed embryo is not damaged, bruchid-infested seeds can still be viable, with the bruchid entry hole perhaps even increasing germination rate, by elevating rate of water uptake in the seed (Lamprey et al. 1974). In *A. tortilis heterocantha*, germination of bruchid infested seeds was twice that of seeds from dung (Coe and Coe 1987). Studies on other large-seeded *Acacia* species have also found accelerated germination when infested with bruchid beetles (e.g. *A. sieberiana*, (Mucunguzi 1995b)). Hoffman et al. (1989) found, however, that germination success rate was lower in bruchid infested *A. erioloba* seeds, although the sample size in this study was small (Hoffman et al. 1989).

There appears to be a delicate balance in which degree of progress of bruchid development is pivotal in the switch from viable to non-viable seeds (Miller 1994b), and ungulate ingestion of seeds influences this balance. Ungulates do not discern between bruchid-infested and non-infested pods (Miller 1994b), and it appears that the sooner ripe seeds are consumed by herbivores, the better, as infestation rates increase with time (Coe and Coe 1987). Large herbivores may therefore be important in eating seeds before they are infested by bruchids, and Coe & Coe (1987) assert that this factor may be more important to seed survival and subsequent germination than seed scarification. Germination of *A. erioloba* seeds from goat dung showed no seeds with damage, however, suggesting that damaged seeds had been digested (van Wyk et al. 1985). Similarly, in cattle droppings only 3% of seeds were bruchid infested, compared with 64.5% from trees (Ernst and Tolsma 1990). Amongst seeds collected from elephant dung, only 2.9% (cf. 47-52% of non-digested seeds) had bruchid exit holes, again suggesting that seeds with bruchid damage are usually digested (Barnes 2001b). Of the few bruchid-infested seeds that survived digestion, only 5% germinated, so although some bruchid-infested and digested seeds remain viable, the majority are not (Barnes 1999, 2001b).

Infestation rates by bruchid beetles averages about half or more seeds, but Barnes (1999, 2001b) found that within Chobe (Botswana), at sites where primate populations were large, monkeys and baboons exerted greatest predation pressure on *A. erioloba*. These primates tend to eat unripe pods, the seeds of which failed to germinate (Barnes 2001b). Large ungulates that eat unripe pods no doubt also decrease the pool of available seeds.

Birds, primates and smaller mammals (e.g. tree squirrels *Paraxerus cepapi*) (Dudley 1999) and ground squirrels (*Xerus inauris*) (S. Milton, pers. obs.) have been seen to seek out and consume *A. erioloba* seeds present within dung. Millipedes (Myriapoda: Diplopoda) have also been found to feed on the emerging cotyledon of germinating seeds within cattle dung (C. Seymour pers. obs.). Rodents may also consume seeds (Miller, 1994c), although some seeds do survive and become incorporated into the seedbank (Miller 1994a). Rodents of the genus *Rhabdomys* and *Thallomys* also play a role in pod damage. They may actually release seeds from pods such that

they are more readily available for germination (van Wyk et al. 1985). No study has been carried out to quantify importance of rodent predation on *A. erioloba*, however. Since it is often the only *Acacia* species occurring within the harsh Kalahari environment, it may well feature in rodent diets. Rodent assemblages vary in both species composition and number with vegetation cover (Joubert and Ryan 1999, Keesing 2000). If bruchid predation is already high (as it appears to be for *A. erioloba*), it may be important to quantify effect of rodent predation on seed availability for this species for different forms of land use (and consequently different vegetation cover). Although *Acacia* produce large seed crops, their shade intolerance means that they have few suitable germination sites, so few seedlings survive (Miller 1994a). We do not yet know enough to say whether *Acacia* recruitment is seed limited (Miller 1994a).

SEEDLING ESTABLISHMENT AND SURVIVAL

The presence of cohorts of *A. erioloba*, particularly in the drier parts of its range, suggest that even if various sources of seed predation are high, they are not as influential as abiotic factors (e.g. amount and pattern of rainfall) (Ernst et al. 1990, Barnes 1999, 2001b). In a four year (1994-1997) study in Chobe, seedling emergence was low and survival zero, in drought years (Barnes 1999, 2001b). In an average rainfall year, new seedlings emerged after more than 100mm rain over several days, but within two months, 85% had died, and none survived to the next wet season (Barnes 1999). In addition to good rains, favourable conditions are needed for a considerable period. Investigation of percentage establishment found that for untreated seeds under favourable moisture and temperature conditions, nearly 64% of seeds established (Briers 1988). This process was slow, however, between 50 and 280 days of favourable conditions needed for establishment rates of 30% and 64% respectively (Briers 1988). Further evidence arises in studies in the south west of the species' range, where rainfall is particularly variable. In these areas, recruitment is episodic, with seedlings and saplings suffering high mortality rates in dry years (Theron et al. 1985). Good rains in preceding years increased seedling establishment in the Kuiseb River valley, such that many seedlings had established by 1978 (Theron et al. 1985). Seedling abundance had declined substantially by 1981, however, likely as a consequence of low rainfall in intervening years, with mortality occurring in the 0 – 16 cm diameter size class (Theron et al. 1985).

Studies on *Acacia karroo*, have revealed that there is no, or poor, survival for rainfall lower than 500 ml (O' Connor 1995). Although we know that timing of rain and a certain minimum, frequent, amount is required for germination and establishment, we do not know actual amounts or frequency required, which can be assumed to be greater on sandy soils, which have a lower water holding capacity.

In addition to being temporally variable, recruitment is spatially variable (Skarpe 1991). In years of higher than average rainfall, seedlings establish near mature trees or in clumps, where there are more tree seeds, so young *A. erioloba* trees tend to be closely spaced, with older trees more widely and randomly spaced (Skarpe 1991, Barnes et al. 1997, Jeltsch et al. 1999). With good rains, concomitant build up of fuel in the grass component of savannas increases fire frequency, which controls spread of trees, imposing a clumped distribution (Jeltsch et al. 1999). In times of low rainfall, intraspecific competition for moisture may decrease chances of seedling establishment near mature trees, and additional "establishment patches" are needed away from mature trees (e.g. tree seeds dispersed in herbivore dung) (Jeltsch et al. 1999).

Newly germinated *Acacia tortilis* were more common under canopies than away from them, but biomass production decreased significantly with decreasing photon flux density (PFD) (Smith and Shackleton 1988). Trees grown in low light levels (equivalent to under canopies) had less well developed root systems, which would be important for survival through the dry season, or for coppicing following fire or herbivory (Smith and Shackleton 1988). Also, plants grown in shade also have lower water use efficiencies, owing to leaf structure that results from growing in shaded conditions (Smith and Shackleton 1988). We therefore expect lower survival rates for seedlings under tree canopies.

Trampling can also kill trees that have yet to establish. Modelling exercises suggest that small-scale heterogeneities and disturbances (e.g. dung, water washes) cause differential probabilities of tree establishment and survival (Jeltsch et al. 1996), and are probably highly influential in vegetation dynamics in semi-arid savannas (Jeltsch et al. 1999).

In conclusion, the primary determinant of seedling recruitment therefore appears to be rainfall. We do not know, however, if recruitment is restricted to good years, or if average years with some rain in the dry season can suffice. Small scale habitat heterogeneities appear to be important for spatial recruitment patterns (Jeltsch et al. 1996), and location of recruitment sites means that small trees tend to have clumped distributions, with intra- and inter-specific competition resulting in greater spacing between larger trees (Skarpe 1991, Barnes et al. 1997, Jeltsch et al. 1999). Areas of heavy trampling experience low recruitment as seedlings are killed before they become established.

GROWTH RATES

Over the first three or four years, *A. erioloba* grows slowly, but thereafter comparatively fast for a long lived tree (Timberlake et al. 1999). Average annual increase in tree radius is calculated to be in the region of 1.5 mm a year (roughly 9 mm/year increase in circumference), although this is variable (I. Gourlay, *unpubl. data*). Similarly, van Rooyen et al. (1994) found trunk circumference to increase by 10 mm/year for trees along the Nossob River bed in Kalahari Gemsbok National Park, with growth rates being lower in drier years.

Vertical growth rates of seedlings have been reported to be between 300 and 500 mm/year (Venter and Venter 1996), and work in Chobe suggests that growth is independent of rainfall, with small trees growing 500 mm per year in both dry and average rainfall years (Barnes 1999). Herbivory can reduce this growth rate considerably (Barnes 1999), however. An average vertical growth rate of *A. erioloba* of 170 mm a year over 93 years was recorded at Savuti (Sommerlatte 1976) in Wackernagel (1993), and 65 mm a year between 1978 and 1994 was measured by van Rooyen et al. (1994) in the Kalahari Gemsbok National Park.

In a study of seeds from various provenances, height growth was strongly negatively correlated with latitude (Barnes et al. 1997). Comparison of germination and establishment of seeds showed that those from the northern-most site (Makatoolo, Zambia) grew to the greatest height (Barnes et al. 1997). It may be that these seeds do indeed have faster growth rates, but conditions in which maternal plants grow when seeds are produced can also influence seed quality (Guterman 2000). These latitudinal effects may therefore be partly explained by local conditions of maternal plants. Seedlings from the northern-most provenance also survived frost far better than more southerly sites (Barnes et al. 1997). This result is at first counterintuitive, as minimum temperatures in Zambia are the highest, but this effect may not be associated with frost resistance at all, and may merely be an artefact of greater size than to physiological differences (Barnes et al. 1997).

AGE TO MATURITY

At about 10 years of age, *Acacia erioloba* can begin flowering, and by age 20, can produce regular large pod crops (Barnes et al. 1997). In the Kuiseb River valley, they do not start to produce pods until over 3m in height (van Wyk et al. 1985).

The tree's longevity is unknown, although a study of trees of the Kalahari Gemsbok National Park revealed the oldest specimens to be about 250 years old (Steenkamp 2000). Other studies estimate that these trees live to 300 years of age, a long lifespan for an *Acacia* (Barnes 2001c).

DEMOGRAPHY AND MORTALITY WITH DISTURBANCE

Demography is dictated by potential longevity, the effects of drought and above average rainfall on recruitment as well as disturbance regimes.

We have seen that evidence suggests that *A. erioloba* recruits in years of good rainfall (Hoffman et al. 1994, Barnes 1999, 2001b). We therefore predict that in the dry extent of its range, recruitment of *A. erioloba* is pulsed. Between 1974-1976, the Kalahari Gemsbok National Park experienced above average rainfall, followed by eight years of average or below-average rainfall (van Rooyen et al. 1994, Milton et al. 1999). Large *A. erioloba* were unaffected by these weather patterns, but sapling recruitment was low (van Rooyen et al. 1994). Similarly, *A. erioloba* populations sampled in the south west of its distribution during the 1980s and early 1990s had few saplings (Theron et al. 1985, Hoffman et al. 1994), possibly indicative of low to average rainfall experienced throughout southern Africa between 1977 and 1994 (Milton et al. 1999). *A. erioloba* forms stands of even

sized individuals over areas of 100 ha on flat ground or between sand dunes, in western Botswana (Skarpe 1991). In northern Botswana, however, Ben-Shahar (1998) found that *A. erioloba* were regularly dispersed and most size classes were represented. Areas with cohorts appear to be on the dry end of the scale (e.g. 18.7 mm Mean Annual Precipitation (MAP) (Theron et al. 1985), 300mm MAP (co-efficient of variation 50-60%) (Skarpe 1991), whereas Ben-Shahar's (1998) site, where most size classes were represented, had rainfall between 400 to 600mm.year⁻¹. Many authors believe that even aged stands are genuine cohorts, their presence governed by episodic rainfall events (Theron et al. 1985, Ernst et al. 1990, Barnes et al. 1997, Barnes 2001b).

Disturbances also appear to influence recruitment patterns and subsequent demography. Cohorts of even-sized individuals were recorded within a cattle pen that had been abandoned for 20 years at Riemvasmaak (Richtersveld, South Africa) (Hoffman et al. 1994), and on disused agricultural land along the Molopo River, North West Province, South Africa (Milton and Dean 1995). Fires and herbivory may exaggerate the apparent presence of cohorts, as both effectively "reset" (above-ground) tree size within certain size classes (C. Seymour *pers obs.*), such that trees of varying age could appear equal-aged. The importance of this hinges on this species' ability to tolerate repeated herbivory or fire: if it is not tolerant, cohorts seen in the field are likely even-aged.

A study on the age of *A. erioloba* in the KGNP showed that there is a strong linear relationship between stem circumference and carbon date age (Steenkamp 2000). It appears, however, that tree diameter, although useful as an indicator of tree age within populations, cannot be universally applied to ascertain age. For example, trees within the Askam region of the Kalahari in South Africa, with relatively small diameters (15 - 20 cm) have been found to be about 100 years old, whereas trees in the Koichab area, near Sossusvlei (Namibia) with large diameters (over 100cm) are only about 250 years of age (S. Woodborne, *pers comm.*). The availability of ground water appears to dictate tree size relative to age (S. Woodborne, *pers. comm.*).

Longevity and rare, episodic recruitment makes it difficult to assess the status of tree populations in arid southern Africa (Milton et al. 1999). We know little of the causes of mortality of arid zone trees and shrubs (Milton et al. 1999), although a review of the literature sheds some light on the effects of herbivory, fire, harvesting, drought, frost, storms, land uses, outlined below. Monitoring tree demography is important also in that managers can anticipate problems arising as a result of changes in land use or climate. In Amboseli National Park (Kenya), the *Acacia xanthoploea* populations appear to belong to the same cohort, and at present, seem to be senescing simultaneously (Young and Lindsay 1988). If one of our aims is to conserve biodiversity, then both vertical and horizontal heterogeneity must be maintained (Pianka and Huey 1971, Milton and Dean 1995, Dean et al. 1999).

EFFECTS OF HERBIVORY

A. erioloba woodlands are usually home to an abundance of herbivores that inhibit growth through feeding, or outright destruction through trampling (Ben-Shahar 1998, Barnes 1999). Even if rains are good, recruitment can still be thwarted by herbivory and/or fire. Thus, while ingestion by livestock may increase germination, subsequent seedling defoliation can eliminate new recruits (Hoffman et al. 1989). In spite of good rains between 1976 - 1978, recruitment of *A. erioloba* in the Kuiseb River valley was low, possibly owing to the large numbers of livestock kept in the area (Theron et al. 1980). Similarly, elephants and fire have been recorded to reduce seedling height and number, and small browsers tend to suppress growth, keeping seedlings vulnerable to fire, and delaying growth to reproductive maturity (Barnes 2001a).

In situations of high herbivory and trampling (e.g. Chobe, Botswana, where elephants occur in high densities), it appears as if the smaller size classes of *A. erioloba* are most adversely affected (Wackernagel 1993). High elephant densities appear to be behind steep declines in *A. erioloba* representation within tree assemblages along the Linyanti river, where representation dropped from 54% to 26% of the tree layer between 1974 and 1992 (Wackernagel 1993). Similarly, its representation within the shrub layer also declined, from 8% to 1%, although it was not possible to say whether competitive release (i.e. an increase in density of a species not favoured by elephant) had occurred (Wackernagel 1993). Elephants have also been recorded to ringbark *A. erioloba* in Chobe (Barnes 1999), although in Hwange, Zimbabwe, the most damage they appear

to do is occasional damage while shaking the tree to access pods (Dudley 1999). It may be that within Chobe, elephants are nutritionally stressed and therefore ringbark trees to meet their needs. Porcupines may also cause mortality in younger trees by stripping the bark (van der Walt 1992).

Larger trees are likely better able to endure herbivory, but this species also coppices well and therefore, once beyond a certain threshold size, is likely to be able to resprout and survive, although they appear unable to tolerate repeated assault (see "Effects of harvesting and clearing").

Insect herbivores (e.g. *Gonometa postica*) remove a much higher volume per mass of plant material than do ungulates, for this tree, and in some summers, caterpillar outbreaks totally strip some trees of their foliage (Gubb 1988). Trees survive to the next season (C. Seymour, *pers. obs.*), however, although the effect of loss of total foliage on pod and flower production has not been recorded.

EFFECTS OF FIRE

The very fissured bark of *A. erioloba* decreases outside surface temperatures of fire (Uhl and Kauffman 1990), which might suggest some adaptation to fire. Ecological effects of fires depend on their frequency, intensity (influenced by amount of dry fuel load, weather conditions), season of burn (with consequences for plants at different stages of their growing cycles) and type of fire (along the ground or in canopies, with or against the wind).

For conflagrations for which data has been collected and/or published it appears that *A. erioloba* can resprout (O. Huyser, *pers. comm.*, C. Seymour, *unpubl. data*). In south-western Botswana, after a fire with a large amount of dry grass, *Acacia erioloba* were seen to re-sprout from the base, even though some of the canopy was still alive (Skarpe 1980). One third of *A. erioloba* trees died, however (Skarpe 1980). Similar mortality rates were recorded after a fire in the Kalahari Gemsbok National Park (Van der Walt and Le Riche 1984). Under similar conditions in Vaalbos National Park, South Africa, a fire killed above ground growth on smaller trees, eliciting resprouting from the bases of small trees, and in the canopies of larger specimens (C. Seymour, *unpublished data*). Six months after the fire, 12.6 % of trees had been killed, with large trees (>8m high) suffering the highest mortality rates (40%) (C. Seymour & O. Huyser, *unpublished data*), although it is not yet known whether all trees resprouting after the wet season will survive the dry season. Fires in Chobe National Park (Botswana) killed above ground vegetation, but established *A. erioloba* seedlings survived, coppicing from the roots (Barnes 2001a).

Thus fire appears to be a major cause of mortality for seedlings that have yet to establish (Skarpe 1980, 1991), and for large trees (Van der Walt and Le Riche 1984). Fires are usually more common and intense after good rains, because of higher grass fuel loads. This coincides with the time at which seedlings germinate and are becoming established, implying that over much of its range, seedling survival is not ensured by good rains –fire risk associated with good rains may hinder their establishment.

Fire also has effects on the spatial distribution of trees. Fire damage amongst clumped trees is lower, owing to lower grass fuel loads (Skarpe 1991). With burning, the clumping effect increases, as trees respond to fire by producing multiple sprouts (Skarpe 1991), and also because trees in clumps have a higher chance of survival. As tree size increases, however, distributions become random to regular, presumably driven by a balance between competition for soil moisture and fire sensitivity, which shifts when canopies are high enough to escape fires (Skarpe 1991).

Demographically speaking, then, fire can be expected to exert the greatest influence on the youngest and the oldest trees within an *A. erioloba* population. Spatially, fire is likely to lead to clumped distributions, owing to both patterns arising as a result of low vulnerability to fire and the patterns induced by fire (e.g. resprouting).

EFFECTS OF HARVESTING AND CLEAR-FELLING

A. erioloba has been found to be able to coppice even from cut stumps and fallen over, partly dead trees (M. Sekhwela, *pers. comm.*). It also multiplies by root suckers, if felled (Henkel 1931). In spite of this apparent resilience, coppices out of cut stumps were highly sensitive to browsing by

goats and presumably other browsers, which substantially reduced biomass and totally killed regeneration from old tree stumps (M. Sekhwela, *pers. comm.*). Unless resprouting shoots can grow beyond the goat browsing line, the trees are eventually killed through constant goat browsing (M. Sekhwela, *pers. comm.*). In communal lands in Botswana, these dead stumps are also uprooted in times of serious shortage. If trees do escape browsing, re-growth can be impressive, however, particularly in years of good rainfall (M. Sekhwela, *pers. comm.*).

We therefore conclude that, although able to resprout after fire, felling and herbivory (Skarpe 1980, Van der Walt and Le Riche 1984), *A. erioloba* do not survive repeated herbivory (M. Sekhwela, *pers comm.*). The extent to which this species can tolerate repeated herbivory, harvesting and fire, and the interaction between these three factors, is not known. Further research is likely required into the resprouting ability of this species, as this ability likely varies with size, time of harvesting, herbivory or fire, amount of rainfall and land use. The findings would have implications for land uses, grazing regimes and harvesting.

If harvesting is limited to dead wood, and governed by strict criteria, it may be sustainable, but bears further investigation. In a study carried out in the semi-arid savannas of Mpumalanga/Limpopo, in which wood collection was limited to dead wood up to a height of 2.5m that could be broken off by hand, and small enough to be carried, yet large enough to be worth collecting, it was found that harvesting about 1.7% of the standing live biomass was sustainable (Shackleton 1998). In contrast to live biomass, deadwood production appears relatively constant from year to year, and across rainfall amounts, suggesting that deadwood production is controlled by factors other than those responsible for living system productivity (e.g. fungal attack, insect infestation, wind and browser damage) (Shackleton 1998). Humans have lived in savanna systems for millennia, and it would not be surprising if these systems have evolved to have some low level of deadwood harvesting (such that some deadwood removal is actually beneficial to trees, with removal of parasites, etc.). If wood removal were restricted as in Shackleton's (1998) study, about 70% of dead wood remains in the environment. The ecological consequences of deadwood removal require further investigation, however.

It is vital to determine precisely which habitat characteristics are most crucial to biodiversity maintenance (e.g. vertical or horizontal heterogeneity, ground cover, etc.), to ascertain acceptable levels of dead wood harvesting. A major implication of consistency of deadwood supply is that there is a certain amount of predictability for management, which may help managers set removal levels (Shackleton 1998). These levels may be too low to make deadwood removal financially viable, however.

Research in Botswana has shown a reliable relationship between stem basal area at ankle height, and tree fresh weight (Tietama 1993). A positive relationship was demonstrated for 14 species of tree, with *Acacia erioloba* as:

$$B = 0.1376 \times BA^{1.2562} \quad (n=27, R^2=0.96),$$

where B = above ground biomass, and BA = basal area calculated at ankle height (Tietama 1993).

This relationship between stem basal area and above-ground biomass was remarkably constant across locations (Tietama 1993). This information is useful for surveying standing tree biomass, establishing tree stocks and mean annual increments and in assisting the interpretation of remote sensing data (Tietama 1993). If basal areas are used by managers to ascertain biomass, the data inherently carries information about the population structure and demographics (Tietama 1993). Demographic data is a far better early warning system than biomass alone, and the data therefore is more valuable for management (Tietama 1993).

EFFECTS OF DROUGHT

Both historical and geological records indicate that droughts are common in all parts of the Southern African sub-region (Darkoh 2003). Sandy soils have a low capacity for storing water, and exceptionally severe droughts are expected to result in some mortality.

Between 1981-1987, Botswana experienced a continuous drought - none of the years was exceptionally dry, but the cumulative effect of drought years was effectively an episodic event (Parry 1989). Mortality rates were likely exacerbated by the unusually wet period of the late

1970s, which would have enabled establishment of woody plants in ordinarily unsuitable areas (Parry 1989). *Terminalia sericea*, *Dichrostachys cinerea*, and *Acacia mellifera* succumbed to the drought, but *A. erioloba* only succumbed in one area, which had compacted calcareous soils (Parry 1989). In other areas, where the drought was extreme, this species survived (Parry 1989).

Drought has also been reported to result in total mortality or death of above ground growth (with subsequent resprouting) of trees less than 50 cm high (Leistner 1967) and amongst saplings (Van Rooyen et al. 1984). A seedling only 25 cm high can have roots longer than 320 cm (Leistner 1967), and even tiny seedlings (about 5cm high and estimated to be about two months old) had a root of nearly 140 cm (C. Seymour, O. Huyser *pers.obs.*).

Therefore, although saplings are likely vulnerable to drought owing to rooting systems unable to reach far moister soils, their rooting systems are deep enough to perhaps enable them to escape moderately dry periods. Depth of sands therefore influence rooting depth and likelihood of surviving drought. Therefore, we conclude that once trees are over a certain threshold height (or more likely, root depth), *A. erioloba* are principally immune to drought (Parry 1989). Seedlings, however, appear unable to survive severe droughts (Leistner 1967).

EFFECTS OF FROST

This species is frost tolerant, if above a certain height (Barnes et al. 1997), although late frost can result in acute reduction in flowering (Timberlake et al. 1999). Frost occurs about 30 days per year in the South African portion of *A. erioloba*'s range (Tyson and Crimp 1998), and since significant for seedling survival, should be included in models predicting demography.

EFFECTS OF STORMS

Winds associated with violent storms, common in the Kalahari, were found to damage 0.85 trees per ha in 1992 (primarily trees over 6m high) (Wackernagel 1993), and killed more than half the mature trees in a study area in Chobe (Botswana) in 1995 (Barnes 1999). Storms in the Kalahari are often accompanied by lightning, which may cause fires and which will influence demographics through mortality.

A review of the literature therefore reveals that *A. erioloba* is able to coppice in response to fire (e.g. (Skarpe 1980)), harvesting (M. Sekhwela *pers comm.*) and herbivory (Barnes 1999). The ability to coppice is dictated by intensity of the disturbance, however, as well as tree age or size. These considerations require some investigation and consideration in management plans for this species.

EFFECTS OF LANDUSE

BUSH ENCROACHMENT

Grazing is the most extensive form of land use in Southern Africa (Darkoh 2003). Bush encroachment is thought to arise primarily because heavy grazing reduces the herbaceous layer, thereby conferring a competitive advantage to woody plants. An increase in woody plant density beyond a certain threshold leads to suppression of herbaceous plants, resulting in lower yields of herbaceous plants and therefore lower grazing capacity (Donaldson and Kelk 1970, Richter et al. 2001).

A. mellifera is widely considered the main encroaching species in heavily grazed arid savanna in southern Africa (Donaldson and Kelk 1970, Skarpe 1980, van Vegten 1983, van Vetgen 1983, Tolsma et al. 1987, Richter et al. 2001). Skarpe (1990) found that *A. mellifera* and *Grewia flava* increased significantly within 5 years, in areas subjected to heavy grazing. Briers (1988) and Joubert (2003) found that *A. mellifera* seedlings germinate relatively quickly, but survive only one or two seasons in the soil, whereas *A. erioloba* seeds germinate slowly, but remain viable in the soil seed banks for longer. We therefore expect that *A. mellifera* may be able to germinate more readily with lower amounts of rainfall than *A. erioloba*, but that it may have limited seed banks. Thus, rainfall (Ward 2001; Lloyd 2003) and seeds (Joubert 2003) limit *A. mellifera* recruitment. As seed production in *A. mellifera* is influenced by rainfall, farmers are advised to reduce stocking

numbers in situations where there have been successive wet years, rather than the accepted wisdom of removing stock in dry years. Further research is needed, however, to ascertain which thresholds of rainfall and seed production cause a transition between states.

Although some farmers claim that *A. erioloba* is a bush-encroaching species, *A. erioloba* is not listed as a primary encroaching species in the literature (Smit 2000, Barnes 2001c), and is also not included on the National Department of Agriculture's list of "Declared indicators of Bush Encroachment" (Table 4, Regulation 16) (NDA 2003). It seems unlikely that it is a major encroaching species, but rather a component of the shrub and tree element. *A. erioloba's* growth form also does not lend itself to successful bush encroachment: usually, it has one or few stems, and its upright form and narrow canopy when young also often allows grass and other herbaceous growth beneath it (M. Sekhwela, *pers. comm.*, C. Seymour, *pers. obs.*). In spite of this, some farmers have been reported to clear significant amounts of *A. erioloba* from their farms (Anderson and Anderson 2001, Liversidge 2001). Powell (2001) interviewed a number of farmers in the Northern Cape, and most cited improved grazing as the reason for clearing *A. erioloba*. The short-term financial gains (as much as R 10 000 a month for some farms) are difficult to discount as motivation for harvesting, however.

Areas with larger single or few stemmed trees generally have higher grass production than areas with many small multi-stemmed bushes, regardless of cover (Joubert and Zimmermann 2002). Almost total woody plant removal may result in increased production in the short term, but chances of degradation by erosion increase with tree removal, particularly immediately after clearing (Joubert and Zimmermann 2002). Other studies have found that whereas removal of woody plants at some sites improved grass density, it had no significant effect in others, implying that soil type, along with rainfall regime are also influential at these sites (Richter et al. 2001).

Interestingly, the quality of grass forage also varies with tree cover (Richter et al. 2001, Joubert and Zimmermann 2002). In some instances, the proportion of desirable grass species increases with woody cover (Joubert and Zimmermann 2002), although phytomass production and bush density have been found to be negatively exponentially related (Richter et al. 2001). This relationship is also governed by rainfall, such that in average rainfall years, bush encroachment can significantly suppress phytomass production (Richter et al. 2001).

Removal of *large* trees may exacerbate bush encroachment. Findings from Botswana suggest that main-stem coverage per hectare remains constant such that when large trees are removed, the gaps between them become filled with smaller, shrubby, multi-stemmed species (Barnes 1999). The difference is that most of these smaller, shrubby, species are leafless during the dry season, providing forage only until the mid dry season and little shade (Barnes 1999). The influence of trees on grazing quality is only partially understood – large, well-spaced trees not only provide shade for livestock, but influence nutrients and water in the soil so that species assemblage, and therefore quality of grass production are improved. A predominance of small, shrubby trees leads to reduced grass production and less palatable species (although this may also be a response to grazing itself). The actual ideal tree density for optimal grazing is still to be determined.

APPLICATION OF HERBICIDE

In a quest to rid the Molopo of blackthorn (*Acacia mellifera*) infestation, application of hormone-type chemicals in the Molopo area achieved root kills of at least 80% (Donaldson 1966). Tebuthiuron was applied aurally to bush encroached areas in the Molopo. Although it appeared to have partial selectivity for target species (i.e. *A. mellifera*, *A. reficiens* and *Grewia flava*), it also adversely affected *A. erioloba*, although this study does not specify if sensitivity varied with tree size (Moore et al. 1985).

ECONOMIC VALUE

CONSUMPTIVE

FUEL

One of the greatest demands on *Acacia erioloba* is through harvesting of wood for fuel. At present, this harvesting is illegal in South Africa, but economic unsustainability of dryland ranching, removal of agricultural subsidies, and demand for firewood, primarily by middle and upper class consumers for *braaiwood* (barbecue wood), are all driving clearing.

Braaiwood consumers in the Western Cape rated long lasting coals as important in determining their choice (Raliselo 2002). When compared with other fuel woods available at retailers in that province, *A. erioloba* has the greatest density, lowest moisture content and highest heat capacity, all characteristics of a "good" fuel wood (Raliselo 2002). It also has the highest ash content, however, thus its Fuelwood Value Index (a measure of "goodness" as a fuelwood) was not as high as *A. mearnsii*, an invasive species in the Western Cape (Raliselo 2002).

A calculation of farm off-take and income for *A. mellifera* and *A. erioloba* found that farms clear on average 23 tonnes per month, at R 450 a tonne (Milton et al. 2002), giving a total of R 10 350 per month. Powell (2001) calculated that about 3 380 tonnes of wood are cleared from an area of about 11 000 km² in the Northern Cape. The removal is so complete, that often only twigs remain (Powell 2001). Farmers also contract to other farms, thus moving around an area systematically clearing, sharing a proportion of the income with the landowner (Powell 2001). Such clearing is unlikely to be ecologically sustainable. The farming community's representatives cite unemployment and financial need as reasons for harvesting this species. The financial case is not entirely convincing, however: employees earn R 0.80 per bundle, farmers R 1.90 a bundle (Milton et al. 2002). Those who transport the wood earn R 2.90, and end point retailers earn R 2.55 per bundle (Milton et al. 2002). In other words, on average, labourers earn less than 10% of the final price, with farmers doing not much better, at 23%. The risks in this arrangement are borne by the farmer and his/her employees, as it is their environment (and future income) at stake. Thus, the situation seems inequitable, as the farmer and his/her labour force receive the lowest return for the highest risk. The total long-term cost of this removal has not been considered fully against the short-term gains. More research is thus needed into the long-term effects of tree removal. For instance, reduced grazing quality, and veld in a poor state will sell at lower prices, thus overall, the exercise of wood removal may be economically unsound.

Farmers sometimes remove dead trees from the veld, as they constitute a fire hazard, and can burn for days.

In Namibia, some charcoal producing companies have acquired certification from the Forestry Stewardship Council, a non-profit organisation established to support "environmentally appropriate, socially beneficial, and economically viable management of the world's forests" (FSC 2003). These companies provide charcoal made from bush encroaching species, primarily *A. mellifera*, *Dichrostachys cinerea* and *Terminalia sericia* to overseas (primarily British) markets (FSC 2003).

Pods are also used as domestic "firewood" in North West Province, as they burn slowly producing little ash and smoke and produce high quality charcoal (Materechera and Materechera 2001).

BUILDING MATERIALS

The heartwood of *A. erioloba* is uniformly deep red to purple-red, the sapwood wide and pale (Timberlake et al. 1999). The wood is impressively dense and heavy (1230 kg/m³), with a medium to fine texture (Timberlake et al. 1999). The heartwood is durable and immune to attack by fungus, borer and termite, and although prone to splitting, if cut with sharp blades and oiled and waxed, has a fine finish (Timberlake et al. 1999). In the past, the wood was used for making mine props and in wagon building (Coates Palgrave 1983). The wood is also used for fence posts and hut poles, but usually too twisted to be used for furniture or turning (Timberlake et al. 1999).

No economic evaluation of the value of *A. erioloba* as a building material has been carried out.

FEED FOR LIVESTOCK / GAME

FLOWERS, PODS AND SEEDS

A wide variety of herbivores, from cattle to eland, kudu and elephant, eat the pods (Timberlake et al. 1999). The nutritive value of pods compares well with lucerne (Leistner 1961). A study in Hwange National Park (Zimbabwe) found pods to be higher in protein and acid soluble mineral than the veld grasses with which it was compared (Henkel 1931). Indehiscent pods, in particular, have lower tannin and high protein levels such that they are considered a valuable food source (Coe 1998). Thus, pods provide a nutritious browse supplement, and when crushed with the seeds, can contain between 10-20% protein (Timberlake et al. 1999). Some ranchers collect the pods and mill them with sulphur (to neutralise prussic acid contained within the pods) to supplement their cattle in times of drought (Timberlake et al. 1999). This enables herds to survive in times when they would otherwise have suffered great losses (Timberlake et al. 1999, Barnes 2001c). Pod production is linearly related to tree size, but variation in value of pods and seeds as well as pod size is high between individual trees (Barnes et al. 1997). This variation seems genetically based (Barnes et al. 1997). Rough estimates place the yield for parkland with 15 *A. erioloba* per hectare at a crude protein equivalent of 372 kg/ha, higher than the maximum expected from small-holder grain crops in the same area. Input costs, apart from a minimal amount for pod collection, are zero, yet the trees provide shade and browse, and have a beneficial effect on grass production beneath their canopies (Timberlake et al. 1999).

In spite of this knowledge, we lack quantitative data on how pods relate to animal weight gains or increases in milk production (Barnes 2001c). We do know that pods fed to sheep at a rate of 0.5kg/day adequately met their macro and micro nutrient requirements (Ngwa et al. 2000), but further research may be needed to convince farmers of the value of pod crops.

LEAVES AND SHOOTS

In a comparison with other veld forage plants within communal rangelands in Botswana (e.g. *Acacia fleckii*, *Diospyros lycioides*, *Ziziphus mucronata*), availability of crude protein from leaves and twigs of browse plants showed *A. erioloba* to be among the lowest scoring in terms of crude protein (Aganga et al. 2000). In spite of this, its foliage can contain as much as 17% protein (Skarpe and Bergström 1986). It has only average amounts of phosphorous, but is one of the highest sources of calcium (Aganga et al. 2000). These amounts change with wet and dry season, with peaks in calcium in March/April, Protein in November/December and phosphorous in September/October (Aganga et al. 2000). In the Olifants Drift area, south-east Botswana, cattle preferred to eat other woody plants, instead of *A. erioloba*, and when they did feed on this species, were seen to eat leaf litter, perhaps because of the presence of thorns (Moleele 1998). Therefore, although pods are valuable as forage to herbivores, the leaves and twigs of this species are less so.

MEDICINAL USES

The bark, leaves and pods are used medicinally in Botswana (Coe 1998). Tree gum dissolved in water is used to treat influenza (Van der Walt and Le Riche 1999). An extract of the bark can be a remedy for diarrhoea (Van der Walt and Le Riche 1999), and if burnt can be ground to produce a remedy for headaches (Coates Palgrave 1983). Extract of the root can be used as cough mixture, and if finely ground, as a preventative for nose-bleeds (Van der Walt and Le Riche 1999). A powder made from dried and crushed pods is used to treat ear infections (Coates Palgrave 1983). Economic possibilities presented by these uses have yet to be explored.

FOOD FOR HUMAN CONSUMPTION

Finely-ground pods can be eaten as porridge, the burnt seeds used as coffee (Van der Walt and Le Riche 1999). In addition, the white droppings of Sociable weavers (*Philetairus socius*) are collected by the San as a catalyst for *n!Harries* beer (Van der Walt and Le Riche 1999).

The foliage is often eaten by larvae of the emperor moth *Gynanisa maja*, and these are occasionally harvested and eaten by humans (Timberlake et al. 1999).

OTHER

Roots are stripped of their outer layers by Bushmen and used to make arrow quivers (Coe 1998).

The potential use of this tree species for agroforestry bears further investigation. Potentially, it can provide fuel, medicines, and livestock feed, as well as improving soil quality (Materechera and Materechera 2001).

NON-CONSUMPTIVE

ECOLOGICAL SERVICES

Most benefits that acacias bring are not immediately apparent (Barnes 2001c). Only when trees are large, years after establishment, do they begin to have appreciable effects on soil quality, produce large enough patches of shade, and produce pods, gum, and fuel wood (Barnes 2001c). Some gains are further obscured in that they are indirect: increased yields from grain crops or stock weight gain (Barnes 2001c) invariably go unmeasured. It is also difficult to quantify the complexity of the effects of acacias on grass and soil fertility in the range (Barnes 2001c).

We do know, however, that large trees reduce nutrient leaching, increase nutrient levels beneath large trees (owing to nutrient cycling and concentration of livestock dung) (Materechera and Materechera 2001), mitigate soil degradation, prevent soil erosion on steep slopes, sequester carbon and replenishes organic matter (Barnes 2001c).

CULTURAL VALUE

It is considered a royal tree in Botswana (Palmer and Pitman 1972).

TOURISM AND AESTHETICS

It is difficult to quantify the economic value of *A. erioloba* trees from an aesthetic point of view. Tourism is currently the largest industry in the world (Roe and Urquhart 2001), and in Africa, competition for tourist dollars is high, with Kenya even doing away with its USD 50 visa fee in 1998 in response to a decline in visitors, presumably to other African destinations. This competition is also reflected in the management of parks in the region, which has focussed on high quality tourism (Barnes 1999). *A. erioloba* is an icon of the Kalahari, with great aesthetic appeal, and open savannas with well-spaced trees likely present better game viewing and photographic opportunities than closed wood thickets, or grassy plains. Thus, healthy savannas have great aesthetic value.

SILK INDUSTRY

A. erioloba is one of the hosts of the lepidopteran *Gonometa postica* that occasionally outbreaks in the Kalahari. This species pupates in a silk cocoon that can be used to produce high quality silk. The industry has considerable economic potential, with naturally golden, quality silk having a market value of about USD 30.kg⁻¹ (Veldtman 2003).

Collection of the cocoons is taking place around Ganyesa, North West Province, under supervision by the textile division of the CSIR, TEXTEC (Veldtman 2001). About 4 tonnes of cocoons are harvested per year, ultimately producing 1.9 tonnes of raw silk (Veldtman 2001). Possibilities also exist for employment from this silk industry for value added activities, e.g. craft or clothing production. At present, the industry is reliant on natural outbreaks, but there is potential for artificial rearing and seeding of individuals in suitable habitats to boost numbers (Veldtman 2001).

Spatio-temporal variation in *Gonometa postica*'s abundance and density is poorly understood, as is the importance of enemies and the distribution and quality of host plants (Veldtman et al. 2002). One way to obviate the need for further research in terms of sustainability, is to collect only cocoons from which the adults have already emerged (Veldtman et al. 2002). Unfortunately, this also yields a product of lower quality as the cocoon surface is ruptured with emergence holes, made either by the moth itself or parasitoids (Veldtman et al. 2002). Thus, there is pressure to harvest occupied cocoons, and additional information is therefore required to support a sustainable harvesting programme (Veldtman et al. 2002).

BIODIVERSITY VALUE

Often, *Acacia erioloba* is the only large tree in its environment. It hence increases habitat heterogeneity in the Kalahari, increasing species richness by providing habitats and services for a variety of plants, reptiles, birds and mammals (Dean et al. 1999, Milton and Dean 1995, Murn et al. 2002).

Shade under *Boscia albitrunca* can reduce sand temperatures by 21 degrees C (Eloff 1984), and it is not unreasonable to expect almost as great temperature differentials between the subcanopy and matrix environment for *A. erioloba*. The trees' canopies reduce solar radiation and therefore temperatures and evaporation rates beneath their canopies (Gubb 1988). Thus, in the heat of the day, mammals tend to concentrate their activities around large trees, with resultant accumulation of nutrients beneath their canopies, through deposition of faeces and carcasses (Milton and Dean 1995, Dean et al. 1999). Soil samples from beneath trees significantly higher levels of nitrogen, carbon and phosphorous than soils from the matrix, which appear to decrease following the death of a tree (Milton and Dean 1995). Sodium and potassium appear to be less influenced by presence of trees, however (Milton and Dean 1995). Although Gwaze et al. (1998) found *A. erioloba* exhibited low nodulation in seedlings, the conditions of the experiment may be responsible for the observed low rate of nodulation. Evidence also suggests that it obtains nitrogen from deep ground water (Barnes et al. 1997, Barnes 2001c). It thus cycles nutrients from great depths, making them available above ground (Barnes et al. 1997), probably of particular significance in the oligotrophic Kalahari.

High nutrient levels and shade of the subcanopy microhabitat increase survivorship of shade-tolerant fleshy fruited plants (Milton and Dean 1995, Dean et al. 1999). This microhabitat enables a suite of species, not adapted to conditions in the matrix, to exist in this environment, thus enriching overall biodiversity (Leistner 1996). The most common species found beneath large trees are virtually exclusively zoochorous (Leistner 1996). These plants provide a valuable food resource for a number of bird and mammal species (Milton and Dean 1995, Dean et al. 1999). Establishment of these assemblages is slow, and may take decades, so large trees, rather than small are needed to facilitate their existence (Milton and Dean 1995). Larger trees are important as nesting and as perching sites (Dean et al. 1999). White-browed sparrow weavers (*Plocepasser mahali*) tended only to nest in trees taller than 3m (Ferguson and Siegfried 1989). Sociable weaver nests built in trailing *Acacia* branches or short *Boscia* trees tend to be small and not continuously occupied, but some large nests in the Kalahari and Namibia are known to have been maintained for more than a century (Milton and Dean 1995). Tree rats (*Thallomys paeuducus*), sociable weavers (*Philetarius socius*) and many species of raptors and vultures have been found to nest preferentially in large trees (Dean et al. 1999, Murn et al. 2002). Other data collected in the southeastern Kalahari suggests that most other cup-nesting bird species also preferentially select larger trees as nest sites (C. Seymour, *unpubl. data*). Holes within large, dead or dying trees are crucial for hole nesting species (e.g. African Hoopoe *Upupa epops*, Scimitar-billed woodhoopoe *Rhinopomastus cyanomelas*) (Milton and Dean 1995), and the densities of these species appear to be governed by the densities of camelthorns (Maclean 1970). In addition, the highly fissured bark of large trees in particular (Cooper and Whiting 2000) is important for a number of lizard and rodent species (Van der Walt and Le Riche 1999). Tree rats preferred large dead trees and as nesting sites (Eccard et al. 2001).

The tree's growth habit, swollen spines, extra-floral nectaries and rough bark enable the existence of a diverse invertebrate community within the trees (Gubb 1988). Large, hollowed out spines are used by caterpillars, spiders, solifugids, cockroaches and ticks to hide and to escape the harshness of the external environment (Gubb 1988). Past or present occupation of thorns is high, particularly for swollen spines (60-95%) (Gubb 1988).

This tree's foliage, shoots and pods are consumed by a variety of game species, and are likely important within their diets, particularly in the harsher parts of *A. erioloba*'s range. New leaf and shoot growth provides a relatively high protein forage resource during the late dry season period when elephants and other large herbivores are subsisting on diets with a negative protein-nutrient-energy balance (Dudley 1999). Examination of seed abundance in elephant dung collected in Hwange National Park (Zimbabwe) suggests that distribution and availability of fruiting *A. erioloba* trees influences observed shifts in their foraging ranges (Dudley 1999). Kori bustards (*Ardeotis kori*) have also been seen to feed on the nutritious gum of this species (Van der Walt and Le Riche

1999). Leopards (*Panthera pardus*) have been found to use *A. erioloba* preferentially as scratching posts in the Kalahari Gemsbok Park (Bothma and le Riche 1995).

When *A. erioloba* is large, it facilitates processes which also maintain habitat heterogeneity (seed dispersal, site modification), suggesting that it is a keystone species in this environment (Milton and Dean 1995). Changes in tree demography, however, could impair these processes, thus invalidating its role as a keystone species. The influence of these trees on their surrounding habitat and biodiversity is dictated by their size and spacing (Dean et al. 1999). Saplings tend to have clumped distributions with densities of 5000 trees.ha⁻¹ (Skarpe 1991), so land uses that result in a landscape of predominantly small, closely spaced trees are likely to adversely affect biodiversity pattern and process in the Kalahari (Dean et al. 1999). Recognition of this context dependency is vital if managing for maintenance of biodiversity patterns and processes.

Clearly, disturbance that fundamentally changes the population or size structure of this species is likely to have detrimental effects on both biodiversity pattern and process. In situations of intense herbivory, a combination of browsing and trampling keeps unprotected (fruiting) species down, such that old trees have no undergrowth (Milton and Dean 1995). Bush encroachment leads to dense stands of small, shrubby plants, and animals that ordinarily would have rested (and therefore deposited dung) beneath large trees do not focus their activities around relatively isolated large trees in such situations (Milton and Dean 1995). Similarly, dung beetles have been found to avoid dense thickets of *Prosopis* which impeded their movement (Steenkamp 1993 in (Milton and Dean 1995). How these changes affect mineralisation processes can only be surmised (Milton and Dean 1995).

Thus an understanding of *A. erioloba*'s functions are necessary before conservation of the species can contribute to conservation of ecosystems (Mills et al. 1993). When merely a component of a savanna woodland (as in the mesic parts of its range), or where it is only a small tree in association with other small trees (as in the Kalahari dunes) its role could likely be filled by another species (Milton and Dean 1995). Across much of its range, however, it is the only large tree species to grow on sand in regions that receive less than 400mm.year⁻¹ of rain (Acocks 1953), and in these situations, it is likely vital to maintenance of biodiversity patterns and processes.

HARVESTING CRITERIA & THRESHOLDS: INFORMATION OF RELEVANCE

This comprehensive literature survey has shown that large trees not only take decades to establish, but once established, improve grazing quality and provide other ecological services. They are also the source of much of the seed bank required for future generations. Therefore, harvesting of large trees should not be considered.

The context in which trees occur is also important. In drier areas, where rainfall is episodic, recruitment is likely to be low (Ernst et al. 1990, Barnes et al. 1997, Barnes 1999, 2001b). Therefore, any harvesting programme must consider rainfall and potential recruitment rates. These rates will also be influenced by stock numbers (Theron et al. 1980, Hoffman et al. 1989, Barnes 2001a), droughts, fire and frost. All of these factors must be included in harvesting decisions, if they are to be made.

The population structure of *A. erioloba* in the area in question is also important. If there are no seedlings and saplings, then resource capital is being used (J. Timberlake *pers. comm.*). Other anomalies in expected demography can reveal instances in which the population is experiencing problems (e.g. intense herbivory, barriers to recruitment, etc.).

Once trees escape herbivory, fire, frost and drought, they are reliant on adequate ground water, so levels of extraction of ground water may also need to be monitored. Thus, land use is an important consideration. Although these trees can resprout and sucker, they seem unable to tolerate felling, followed by heavy herbivory (M. Sekhwela *pers. comm.*). Further research is likely required into the resprouting ability of this species, and how this ability varies with size, time of harvesting, herbivory or fire, amount of rainfall and land use.

Small, shrubby tree species are more important as causes of bush encroachment, and perhaps incentives to conserve could be combined with an environmentally-certified charcoal industry similar to that in Namibia (FSC 2003).

Limited harvesting of dead wood only may be sustainable, but the Precautionary Principle demands further research, as the effects of removal on ecological processes is not known. It is possible that, if there are limits and criteria on how wood is harvested, the amount of wood removed may be effectively limited. Shackleton (1998) found that harvesting about 1.7% of standing biomass was acceptable.

The potential economic value of non-consumptive use of this species is a clearly apparent from this report. The wild-silk industry, possibilities for agroforestry, use as a source of livestock feed, as well as the less tangible aspects, such as ecological services, maintenance of biodiversity, as well as aesthetic value all suggest a greater value than the R 450 per tonne that farmers receive for clearing their land. Thus, the economic value of this tree in all its roles bears further investigation.

CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

The conclusions and recommendations for further research that arise from this report fall into two main categories. These are:

- (a) Ecological factors that are vital for ensuring harvesting decisions are sustainable, and
- (b) Socio-economic factors, driving demand for harvesting to take place.

ECOLOGICAL FACTORS

What do we know about the ecology of *A. erioloba*? We know that it is a slow growing species, thought to live to about 300 years of age (Barnes et al. 1997). The primary determinant of recruitment seems to be rainfall (Ernst et al. 1990, Hoffman et al. 1994, Barnes 1999, 2001b), which follows oscillations of roughly 18-year cycles, with 9 dry, followed by 9 wet years (Tyson and Crimp 1998). Effects of the El Niño Southern Oscillation, that behave on average cycles of 3-4 years (although this can vary between 3-8 years), also influence inter-annual rainfall variability (Tyson and Crimp 1998). Any attempt to calculate sustainable harvesting rates would need to model recruitment and demography, by including these cycles. Assuming rainfall is sufficient to enable survival of seedlings to establishment, seedlings must also withstand herbivory, trampling, fire and frost. Once established, this species is able to coppice if burnt (Skarpe 1980), browsed (C. Seymour, *pers. obs.*) or felled (Henkel 1931), but appears unable to withstand repeated insult (M. Sekhwela, *pers. comm.*). Large trees do not seem to be able to coppice as vigorously as younger specimens (C. Seymour, *unpubl. data*), and are crucial to maintenance of biodiversity patterns and processes. They are also likely important in out-competing smaller, shrubby trees and may therefore be very important in limiting bush encroachment. Large trees have positive effects on available grazing quality (Barnes 2001c), and also provide shade and other products (e.g. pods, etc.), vital in times of drought (Barnes et al. 1997, Timberlake et al. 1999). The density of dead trees needed for maintenance of biodiversity is also not known, not every tree is appropriate for nesting, so dead wood removal would likely need to follow strict guidelines ((Shackleton 1998), to ensure sustainable harvesting. It is crucial that we have a thorough understanding of the demographic patterns of this species, and the factors that help and impede recruitment and subsequent survival. The relative importance of these factors likely varies between size classes. This information can then be used to ascertain levels and periods for sustainable harvesting, if the decision to allow harvesting is made.

Table 1 summarises our knowledge and gaps therein regarding the ecology of this species.

SOCIO-ECONOMIC FACTORS

The issue of harvesting and demand for it cannot be viewed in isolation to the socio-economic context in which it occurs. Degradation of South African savannas are no doubt linked to increasing costs of production, loss of subsidies, misconception about grazing strategies, as well as changes in fire regimes, perverse incentives and subdivision of farms into units that are not

economically viable. Thus, harvesting cannot be addressed without its socio-economic context. If we assume that *A. erioloba* must “pay for itself”, then likely, we need to explore non-consumptive use of this slow growing species.

At present, farmers and their employees bear the greatest risk for the smallest returns, in harvesting this species. This may indicate that farmers and their employees are unaware of the potential damage that uncontrolled harvesting is visiting upon the ecology of their farms, or that short-term financial concerns govern decisions. Environmental policy making routinely ignores economic considerations, yet environmental conservation cannot take place in a vacuum of these considerations (Mogaka et al. 2001). Potential of African *Acacias* to improve agricultural productivity is unequivocal (Barnes 2001c), but must be demonstrated with proof of economic return and development of appropriate practice (Barnes 2001c).

RESEARCH GAPS OF RELEVANCE FOR CONSERVATION AND SUSTAINABLE USE POLICY

Among the questions we need to address are:

- (a) What is the economic value of products already used (both consumptive and non-consumptive), for example, pods to livestock farmers, ecological services provided by trees (which will no doubt vary with tree size, density and degree of aridity), etc. It is also important to ask and answer the question of “What is the contribution of these woodlands to the country’s economy as a whole?” (Mogaka et al. 2001). This evaluation should be complete and comprehensive.
- (b) What is the economic value of potential products: e.g. the silk industry, coffee from beans, agroforestry, etc.
- (c) What are the primary reasons for felling wood? Powell (2001) found that the main reason for clearing cited by farmers was to improve grazing. Interestingly, more than 75% of the wood that leaves the area is *A. erioloba* (with the remainder being *A. mellifera*) (Powell 2001). This implies that clearing bush encroached areas is perhaps not the primary reason for this wood removal, as bush encroached areas would likely yield proportionately far more *A. mellifera*. Alternatively, *A. mellifera* may be kept for domestic use, but it remains unlikely that demand for domestic fuel is as high as these numbers suggest. If there is a perceived advantage to clearing lands to improve grazing, education programmes regarding the value of these trees to the ecosystem are vital.
- (d) Are consumers and landowners aware of the full value of the species to future grazing and ecological services? Do farmers see all thorn trees as bush encroaching species, or do they differentiate when dealing with the problem? Free advice and subsequent awareness may reduce pressure to harvest these trees. If communities are to be willing and able to conserve *A. erioloba*, then the rewards for conserving this species must be greater than the benefits of destroying it. The benefits of sustainably managing this species must be evident to the communities involved.
- (e) What are the disincentives, if any, for conserving this species?
- (f) Geographically, where is *A. erioloba* under greatest harvesting pressure, and where does it occur in greatest densities? Why are these areas particularly problematic?
- (g) In the arid systems of the Kalahari, livestock farming is only profitable on large scales. Subsidies in the past allowed and perhaps even encouraged unsustainable land use practices, such that farmers are now dealing with environmental degradation that started long before present, and often not of their own making. Unsustainable farming practices therefore also need to be evaluated in these arid zones, bearing in mind that the situation is unlikely to improve, with anthropogenic climate change expected to cause a slight decrease in rainfall and an increase in the incidence of droughts and floods (Tyson and Crimp 1998). What is the best strategy for dealing with unsustainable farming practices?

- (h) What criteria should be used to define over use, sustainable use and invasion?
- (i) If sustainable use is to be allowed, under what circumstances should a strategy for replacement of removed trees be non-negotiable, and what should these strategies be? For example, reseedling, which might be expected to succeed only once every 18 years under current rainfall regimes, or planting programmes, likely to have a greater chance of success.

MONITORING GUIDELINES

- If permits are approved for harvesting, they should *clearly* outline the conditions that must be satisfied and penalties for non-compliance. These penalties must be enforced, however.
- If harvesting is allowed, it should not proceed without a detailed monitoring programme. This programme must be dictated by the management objectives, but as a rule, simple systems are more likely to succeed. If Geographic Information Systems are available, they are useful for mapping fires or grazing regimes. If unavailable, however, hard copy maps can be very informative. Such monitoring will likely need to be carried out by the regulating body (Department of Water Affairs and Forestry), although if landowners see the value in such monitoring, it may be possible for them to carry it out themselves. If self-monitoring is opted for, then there must be clear guidelines on what information needs to be gathered. Data would need to be submitted to a central database (again, likely administered by the regulating body) for analysis to ascertain if current harvesting rates and practices are sustainable.
- Monitoring must include rainfall (daily or monthly), at least one station per 5000 ha, animal stocking rate, type and duration, as well as mapped extent and intensity of fires. Tree demography and density, as well as herbaceous species composition and cover, state of soil surface (bare/vegetated, leaf litter, compacted, etc.), once every 3-5 years can also be used to inform the importance of trees for grazing and soil. Records of quantity, type, date and location of removals for harvesting must be conscientiously maintained.

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APPENDIX 1: TERMS OF REFERENCE

Tender to collate, synthesise and identify research priorities in order to inform and guide protection of Acacia erioloba, Boscia albitrunca and Combretum imberbe in South Africa.

Objectives

We undertake to catalogue and provide a comprehensive collection of all research completed and available information on *Acacia erioloba*, *Boscia albitrunca* and *Combretum imberbe*. This will include research reports that are not ordinarily easy to obtain (e.g. Thesis dissertations, unpublished reports, as well as expert opinion and other information gathered from consultations with relevant researchers). We will summarise current knowledge and include a conceptual model highlighting aspects requiring further research.

We also undertake to provide a searchable spreadsheet that will contain information on relevant research, as well as contact details of researchers and brief details regarding their areas of expertise, if they indicate their willingness to be included on such a list. This spreadsheet may be made available over the DWAF website to increase its accessibility to researchers, so minimising duplication and guiding further research.

BACKGROUND

Acacia erioloba, *Boscia albitrunca* and *Combretum imberbe* are all considered keystone species within their respective habitats. Evidence to date suggests that the loss of these species will result in the concomitant loss of species that rely on these trees for resources, and so lead to the deterioration of ecological processes. These species are, however, also of economic importance to rural communities, used both consumptively (e.g. as firewood and building materials) and non-consumptively (e.g. for the emerging silk industry and tourism). The opportunities and constraints for consumptive use are not well understood – all three species are slow-growing, and in arid environments in particular (i.e. *A. erioloba* and *B. albitrunca*), recruitment events tend to be rare. Certain forms of land use may also lead to bush encroachment, with a subsequent loss of habitat heterogeneity and thus biodiversity. Loss of biodiversity and sound ecosystem functioning within these habitats is also not well understood, but it is likely that they carry economic implications through the loss of grazing, disrupted water regimes and the loss of products from the trees themselves. Measures to control bush encroachment (i.e. the indiscriminate application of arboricides), however, often kill protected species (although *Boscia albitrunca* appears to be immune to some arboricides). Consumptive use of these species is thought to be unsustainable (both in terms of economics and biodiversity), because of these species' slow growth and low recruitment rates. It is difficult to determine appropriate rates and conditions for consumptive use without access to crucial information about ecological, economic and cultural factors associated with wood removal.

The Department of Water Affairs and Forestry is called upon to grant permission to harvest these species, and must balance socio-economic needs of communities with environmental considerations. We hereby tender to catalogue and synthesise available information on the state of all three species, and the nature and seriousness of the threats they face. This will facilitate informed decision-making based on available information and sound scientific principles. Our consultations and literature surveys will also highlight gaps in research and will inform further research investment, while helping to minimise duplication of research efforts.

METHODS

We will meet with relevant authorities/officials within the Department of Water Affairs and Forestry to refine the project plan.

We will perform an extensive survey of relevant library literature. We will also access sources of information not conventionally easily available, including sources of information from neighbouring countries (i.e. Namibia, Botswana, Zimbabwe, Mozambique). We will also consult with local and international professional experts and others (Appendix A) who have conducted research into these species, and will incorporate a summary of these interview findings into the report.

We will contact our reference group (Appendix A) to interview them to access current expert knowledge that may not be available in print. We will also obtain permission from each person within this reference group to be included in a database of contacts.

Our search for information for each species will focus on primary references and sources of information. Issues related to habitat, seed production and dispersal, germination and recruitment, optimal environmental conditions for germination and recruitment, age to maturity, adult survival rates, growth rates, assessment of population structure and health, effects of land use and disturbance (e.g. fire, grazing, felling) on tree demography, drivers of bush encroachment, economic importance (for both consumptive and non-consumptive use), cultural value, aesthetics value, importance to biodiversity and proper ecosystem functioning, historical information regarding use in the past and success of subsequent recovery (or not) of population(s) and associated biota. We will highlight any information that may inform development of criteria and thresholds at which trees may be harvested or killed, and under what conditions. Interviews with our reference group (Appendix A) will seek to reveal current extent and sources of threat to each of the three species.

PRODUCTS

We undertake to produce:

- 1) Copies of research reports in hard copy and/or electronic format;
- 2) A catalogue of research reports, including authors, title, date of publication, publisher, place of publication, as well as information as to where each report can be found. We will make this list available as a searchable database or spreadsheet in MicroSoft Excel or MicroSoft Access, depending on DWAF's requirements. We envisage that this spreadsheet will be useful both within DWAF and also to researchers and decision-makers, reducing duplication of effort and facilitating the flow of information.
- 3) Depending on permissions, we undertake to provide a searchable spreadsheet of details of relevant contacts of researchers, experts and other interested and affected parties for each species.
- 4) We will provide a report that gives a synopsis of research conducted to date, which will also identify priorities for future research in sustainable use and conservation of each species.
- 5) We undertake to inform all interested and affected parties with whom we consult during this project the objective for gathering the information, and that this is to be used by DWAF to enable informed decisions (i.e. based on both published research and professional opinions of all interested experts), regarding the exploitation of these tree species.