A synthesis of the demography of African acacias

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ABSTRACT. Although acacias are ecologically and economically important, their demography is poorly known. In part this is because few field experiments have been undertaken. Also, a bewildering diversity of factors have been suggested to determine their demography. These factors include disease, fire, large and small browsers and grazers, climatic variation, competition with grass, seed predation and anthropogenic impacts. This synthesis concentrates on the life-history period from seed to adult plant and indicates that important hurdles have been demonstrated for some species in some habitats. Seed and seedling limitation have not been clearly demonstrated, nor has the value of dispersal been quantified. In contrast, the impacts of herbivores and fire in affecting the escape or release of resprouts has been repeatedly demonstrated. Whether fire and herbivory merely slow down the rate of promotion through size-classes or actually prevent it, needs further work. We note that very little comparative work amongst *Acacia* species has taken place. Most studies have concentrated on single aspects of their life history (especially seed predation), and have not been analysed in relation to population growth. Few field experiments, especially concerning seedling biology, have been performed. We conclude with some suggestions of a framework for interpreting acacia demography.

KEY WORDS: *Acacia*, Africa, demography, fire, herbivory, seedlings, seeds

INTRODUCTION

Acacias, the quintessential African trees, are important components of natural areas in tropical and subtropical savannas. They are also foci for birds, mistletoes and other plants (Dean *et al.* 1994, Milton & Dean 1995) and many are nitrogen fixers (Harrier *et al.* 2000). Acacias are also important outside of conservation areas, to local people and their domestic animals. Their use as fuel (wood and charcoal), agro-forestry, medicines, tannins, gums, building materials, rope, fibre and honey production has led to their decline in some places.

In some conservation areas acacias have declined (Mwaloysi 1988, Pellew 1983) and in other areas populations have invaded or are expanding (Sabiti & Wein 1988). Similarly, they are expanding (the phenomenon of 'bush-encroachment') (Donaldson 1969, Moleele & Perkins 1998, Skarpe 1990) or declining in pastoral areas. Because of their obvious ecological and economic

importance and the conspicuous fluctuations in their demographic status, there continues to be an interest and a proliferation of ideas and papers on acacias. Our aim is to synthesize these ideas so that further progress can be made in understanding the demography of acacias.

Three issues have dominated the literature. Firstly, the apparently cyclical nature of acacia population fluctuations in relation to the elephant population fluctuations in East Africa has attracted attention. High elephant populations were considered to be the cause of declining acacia populations, although now the situation is considered to also involve disease (anthrax and rinderpest), giraffe, small herbivores, climate and fire (Dublin *et al.* 1990, Prins & van der Jeug 1993). The evidence for the debate on the causes of *Acacia* population fluctuations has been centred on remotely collected data and modelling, rather than field manipulations. For example, there has been no experiment where seedling numbers have been manipulated to show whether herbivory is the key factor determining population decline, rather than for example climatic events. The second popular topic is the role of bruchids in the seed biology of acacias. No one has yet added seeds and seen whether seed predation makes any difference to the population growth of any acacia species, nor has the role of dispersal to safe microsites been quantified. The third popular topic is the phenomenon of bush encroachment (the invasion of trees, including acacias, into conservation and domestic rangelands) and it too, is poorly understood. It is believed to be due to over-grazing and associated loss of fuel leading to a disrupted fire regime, or to changed grass–tree competitive interactions, or even to the improved dispersal and establishment of propagules by domestic animals.

In this synthesis we have concentrated solely on African acacias (essentially the species in Ross (1979) which includes *Faidherbia albida* (= *Acacia albida*)) and we have listed what we consider as the relevant hypotheses affecting aspects of *Acacia* demography (numbered in the text and on Figure 1) and also suggested possible problems with information collected to date. We have focused on the different life-history stages from seed production to adult mortality. Although there are many (> 100 spp.) African *Acacia* species, it is clear that only a small group has had most of the attention (e.g. *A. tortilis* and *A. nilotica* in East and South Africa and *A. karroo* in South Africa). There is thus no basis for extrapolation (i.e. determination of guilds) from one species to another because almost nothing is known about life-history variation in the genus; for example how different species respond to the same fire regime. An experimental comparative approach to demographic issues would not only help with applied issues of invasion or decline but also evolutionary ecology of this important genus. A cautionary proviso is that there is enormous variation within and between species, within and between different areas and habitats and between years. In terms of acacia demography, we suggest that context (e.g. local climate, type, intensity and frequency of disturbance) is all important. Also, although acacia

species may respond differently to disturbance, they do appear to belong to guilds. We suggest that there are 'fire-acacias' (i.e. they tend to occur in tall grass areas and persist through most fires) as well as 'browsing-acacias' (i.e. those that occur in areas with high browser densities and which are able to persist through severe browsing). The successful classification of different species into guilds would be a significant advance for the understanding of *Acacia* demography.

THE DEMOGRAPHIC HURDLES

Seed-set limitation

The influence of pollinator availability on seed-set does not seem to have been studied. Seed-set could also be affected by small population size via pollination failure in out-breeding species (1; the so-called Allee effect). Tybirk (1993) suggested that *A. tortilis* is an out-crosser. More information may be needed on seed-set in relation to population size/density, especially if further work confirms that populations are seed limited (see below).

Seed limitation due to predation

Are acacias seed limited (2)? Would the addition of seeds make any difference to the population structure/size, especially if the seeds are protected from
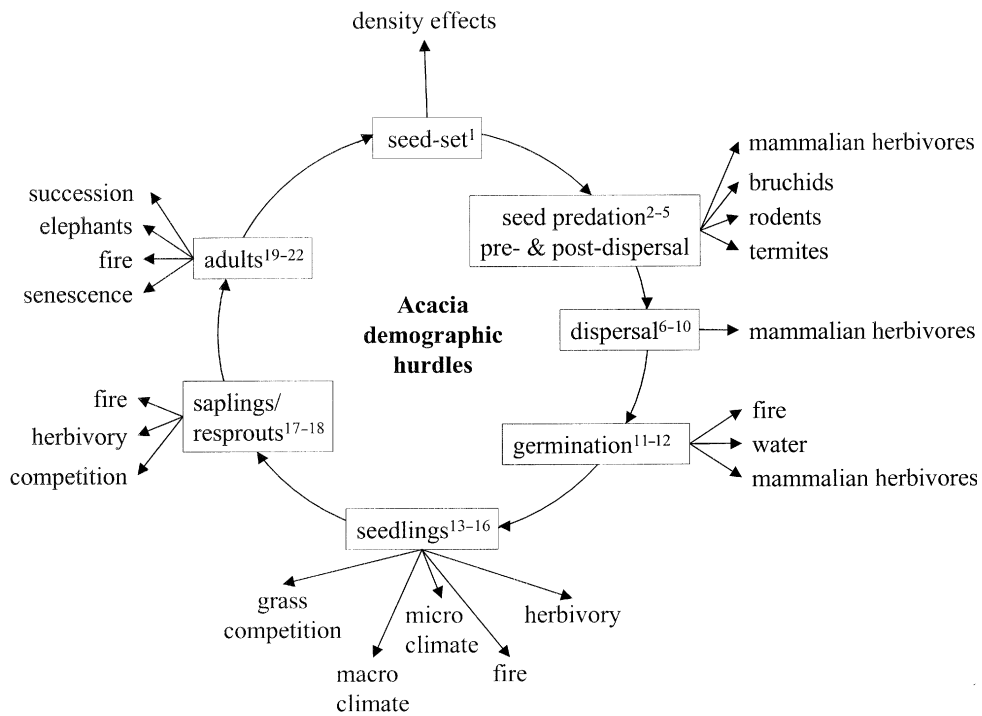

Figure 1.   The important hurdles of the Acacia life-cycle (see numbers in the text for details).

seed predators, notably bruchid beetles. Possibly the increased numbers of seedlings resulting from seed augmentation would merely all be consumed by fires and herbivores or die in the first drought? High levels of predation of seeds by bruchids has received much attention, starting from the observations of Lamprey *et al.* (1974). They noted high values of seed predation from 74–99.6% in parts of Serengeti in the early 1970s. In contrast, Pellew & Southgate (1984) noted values had dropped to about 5% by 1980, possibly in parallel to the decline in the density of the woodlands. They suggested that the degree of bruchid predation was positively related to seed crop size (3). To test this they also analysed levels of *A. tortilis* seed predation from the southern Serengeti, where elephant damage was low and the density of adult plants was high. They found high levels of predation (78%), supporting this hypothesis. However, this relationship has recently been questioned by Ernst *et al.* (1989). They found no link between seed output and degree of predation. They noted inter-annual variation in the degree of predation within individual trees and that it did not correlate with the size of the seed crop.

Ernst *et al.* (1990) noted a range of seed mortality within and amongst species from less than 10% (*A. mellifera*, *A. nilotica*) to greater than 60% (*A. erioloba*, *A. hebeclada*, *A. nilotica* and *A. tortilis*). They suggest that indehiscent species have greater levels of bruchid predation than dehiscent species (4). Mucunguzi (1995) also suggested that bruchid predation is higher in indehiscent species than dehiscent species. However this effect was balanced out by the seeds of indehiscent species being better able to tolerate seed damage by being larger and thus some of the endosperm may escape being eaten. It is thus possible that the percentage seed mortality by bruchids is negatively related to increasing seed size (5). Miller (1996) also noted high levels of bruchid predation (up to 68% in *A. tortilis*, 36% in *A. nilotica*, 41% in *A. robusta*, 40% in *A. karroo* and 21% in *A. caffra* and *A. luederitzii*) and some variation between years, e.g. 31–68% for *A. tortilis*. She argued against any differences in extent of predation between dehiscent and indehiscent species.

Miller (1994a,b) and Hauser (1994) suggested a limited role for already predated seeds in the population ecology of acacias in that most get destroyed in the stomach of the disperser. Miller (1995) also drew attention to the predatory role of termites and rodents on those seeds which managed to escape bruchid predation. In her observations, the combined effect of seed predators was almost 100% loss of seed crop.

There are problems with many of the studies concerning seed banks. For obvious reasons most studies have investigated predation under canopies of mature trees. However, these are unfavourable sites for seedlings of this typically shade-intolerant genus (Smith & Shackleton 1988).

Counting seeds in these sites is counting the countable but not necessarily giving useful information as to recruitment potential. There is still no information on predation of dispersed seeds, in sites away from canopies, to answer

questions concerning the importance of dispersal for predator escape and for escaping maternal shade. The next experiments should aim to add known numbers of seeds of various species. These seeds should be placed out in various sites (under-canopy versus open, tall grass versus short grass), in various years (wet, dry) and protected in various ways (insecticide, rodent exclosures etc.) to give further information on the impact of various seed predators. Seedlings produced by these experiments can then be followed, or protected, to determine their fate.

Do acacias have a persistent seed-bank (6)?

The high levels of seed predation by bruchids, termites and rodents noted above lends weight to the suggestion that seed banks should be transient in *Acacia*. Tybirk *et al.* (1992) looked at seed banks in under-canopy sites in a range of habitats. They noted no seed banks for some species in some habitats (*A. albida* (= *Faidherbia albida*), *A. seyal*, *A. senegal*), whereas other species had larger seed banks (up to a mean of 2439 seeds m^{-2} in *A. hockii*).

Again there are provisos with interpreting the above data. Sampling of seed-banks before and after rains and fire (their germination cues) will make a difference to numbers of remaining ungerminated seeds. For example Tybirk *et al.* (1992) noted high densities of *A. hockii* and *A. seyal* seeds in areas without regular fires. Also, sampling seed banks in under-canopy sites is problematic because, as has been mentioned above, these are poor sites for seedlings. Furthermore, it ignores the possibly important role of dispersal. Dispersed seeds may be more likely to germinate and produce seedlings which will grow up to adults, than undispersed seeds in under-canopy conditions. Garner & Witkowski (1997) suggested that some species do have a seed bank. However, they too did not give any information on where seeds were found (under-canopy or not) nor what the disturbance regime was (fire, herbivory) nor whether the seed-banks had accumulated over one or many years.

Seed dispersal limitation

Can recruitment levels (of the zoochorous *Acacia* species) be influenced by the levels of dispersal (7)? Dispersal may influence the numbers of seeds/seedlings that escape the maternal environment (high shade/predation) to safe sites. It may influence the numbers that (rapidly) receive their appropriate germination cue as a consequence of having been scarified in the disperser's stomach and thus escape predation by germinating. There is evidence that some seeds survive being ingested and eventually are expelled by ungulates (Coe & Coe 1987, Miller & Coe 1993), although pre-dispersal losses can be as high as 100% (Miller 1995). Miller & Coe (1993) and Miller (1995) suggest that the degree of seed damage during dispersal is possibly inversely related to the mass of disperser (8); with relatively less damage to seeds being associated with the relatively larger browsers such as elephants. The possibly positive interaction between ungulate dispersal and reduced levels of bruchid damage

(9) is now questionable, since the evidence is that most semi-predated seeds are in any event destroyed during ingestion. The idea was that bruchids would be destroyed in the stomachs of ungulates and this would then protect partially eaten seeds from total destruction. There is also no evidence that high levels of ungulate ingestion and seed dispersal negatively affect levels of bruchid predation in subsequent years (10).

Miller (1994a, 1995) noted that the germination of seeds which survived ingestion by animals was greater than that of control seeds. Germination of her control seeds was very low, suggesting an additional important role for ingestion by animals is that it stimulates more rapid germination. This is traded-off with losses during ingestion. Ingestion losses taken together with losses due to seed predators are considerable, but dispersal benefits too may be considerable and need to be quantified. It has also been suggested that one of the reasons for the encroachment of *Acacia*s into pastoral areas is because of increased rates of dispersal and germination due to cattle (Donaldson 1969, Moleele & Perkins 1998). However, Hauser (1994) found that ingestion by cows did not improve germination of *A. albida* (= *F. albida*) seeds and Donaldson (1969) noted 97% seed mortality of *A. mellifera* after ingestion by cattle.

Seed germination limitation

Is acacia demography affected by the lack of appropriate germination cues (due either to scarification by animals and/or fire), in these essentially dormant species (11)? Sabiti & Wein (1987) suggested that acacia invasion of savannas occurs when intense fires stimulate germination. They showed that heat improves germination and argued that low grazing intensity would imply high fire intensity which would imply high germination levels and (presumably) establishment levels. Paradoxically, the 'hot-fires' which they suggest may initiate seed germination will also be the ones that cause high seedling/sapling damage. Thus for this hypothesis to be true it may need to be associated with a variable fire regime.

Mucunguzi & Oryem-Origa (1996) noted that larger-seeded species (*A. sieberiana*) tolerated heat better than the smaller-seeded species (*A. gerrardii*). The former germinated better after being heated, whereas *A. gerrardii* either had lower germination or was indifferent to heat. Do differences in seed size explain differences in germination rates (12)? Mbalo & Witkowski (1997) noted improved germination of seeds exposed to 150 °C for 3 mins in *A. karroo* (14.4–54%) and *A. nilotica* (0–4.8%). The larger-seeded species (*A. karroo*) was more tolerant than the smaller (*A. nilotica*), with lower germination rates in the latter species.

Wilson & Witkowski (1998) investigated *A. karroo*, *A. nilotica* and *A. tortilis* and found that the imbibition rate of scarified seeds was proportional to seed size. *A. karroo*, with the largest seeds, was quickest whereas the small-seeded *A. nilotica* was slowest to imbibe. They also suggested that frequent rainfall, not necessarily high rainfall, is needed over the first 7 wk after germination to

ensure establishment. Also germination itself, required constant moisture for about 16 d. They suggest that there should be variability in levels of seedling establishment in different years correlated with annual variability in climate.

Limits to seedling establishment

If drought is a significant factor limiting seedling establishment, then *Acacia* seeds should germinate and/or establish only rarely (i.e. display even-aged cohorts dating back to periods that were wet enough) (13). Walker *et al.* (1986) considered that acacia seedling germination was frequent, but that only a few actually established. In other words the hurdle is not at the level of numbers of seeds, or the lack of germination but of conditions that allow seedlings to establish. Their size-class distributions showed an inverse-J curve which suggested steady establishment rather than distinctly cohorted establishment.

Size class distributions reported by Shackleton (1993) also suggest steady recruitment and advance through size-classes rather than a cohorted demography (i.e. staggered size-class distributions). Kennenni & van der Maarel (1990) found that seedling recruitment was rare (populations were adult dominated and declined over the 3-y study period) and possibly linked to wet years. However, their study area seems to be extremely disturbed and so it is not clear whether this was due to excessive disturbance (e.g. herbivory by goats, trampling) or not.

O'Connor (1995) also found that sufficient moisture is needed for *A. karroo* seedlings to survive and suggested that in his study area only a fraction of the years would be suitable for seedling establishment. He found competition from grass to be unimportant in determining establishment success. Chirara *et al.* (1999) studied *A. karroo* seedling emergence and growth in relation to different degrees of grass biomass and defoliation. Their data indicate high dry season mortality throughout. They also concluded that bush encroachment by this species is probably not due to new seedlings benefiting from extra moisture in overgrazed areas. Since the above two studies were in semi-arid savannas, strong dry-season mortality may not be as important in moist savannas.

O'Connor (1995) found that *A. karroo* did not have a seed bank but did have a sapling bank of at least partially shade-tolerant individuals. Do some acacias have a seedling/sapling bank (14)?

Size-class distributions of acacias may be rather uninformative for discerning between the relative importance of recruitment (of new seedlings) versus release of established plants by escape of resprouts from the fire- or herbivore trap (zone < 1.5–2 m where there is intense fire or herbivory damage which limits individuals progressing to the taller size-classes). For example, the apparently even-sizedness (cohortedness) of adults in a stand may merely reflect rapid progress through size-classes of an essentially fast-growing shade-intolerant species with continuous recruitment. Even-agedness would normally be taken to reflect episodic recruitment or release. Similarly, short *Acacia* individuals may be young seedlings or they may be much older resprouts which

have yet to escape intense fire or herbivore damage. Is seedling establishment limited by herbivory; in that no matter how many seeds/seedlings are added to a population, they will all be eaten to death (15)? Prins & van der Jeug (1993) suggested that seedling recruitment was limited by impala and could thus only occur during periods when impala numbers were low such as during anthrax outbreaks. They had no observations on actual seedling establishment but used growth rate information to show that smaller plants may have established during the preceding anthrax outbreaks. However, dendrochronology of *Acacia*s based on ring-counts on stems cannot be used to distinguish between the importance of recruitment of new seedlings versus release of previously established individuals because above-ground age may be similar in both cases. Radiocarbon ageing of below-ground tissue may help determine whether regeneration or persistence is important.

Van de Koppel & Prins (1998) suggested that interactions between smaller herbivores such as impala and buffalo and larger herbivores such as giraffe and elephant, due to competition and facilitation, will result in transitions and cycles of the different herbivores. This in turn may explain transitions and cycles between grassland and woodland. They envisage that transitions from coarse-grass feeders (buffalo, zebra) to selective feeders (e.g. impala, gazelles) would cause a change from woodlands to grasslands by preventing regeneration of acacias. When grass is freely available there will be low utilization of acacias by elephants (i.e. high adult survival) but there will also be higher fire intensities. Conversely, when graze is limited there will be higher utilization of acacias by elephants but also fires of low intensity. Data are now needed to test these ideas. For example, information on the effect of impalas on recruitment and release is apparently critical.

Belsky (1984), by excluding large herbivores, found that browsing by small herbivores kept plant individuals short and that the effect of browsing and fire on plant height was no different to browsing alone. She noted growth of up to 153 cm y^{-1} in protected *A. senegal*, but growth of at least 10 cm y^{-1} even in the face of herbivory and fire. This suggests a relentless journey to escape height (i.e. mixed size-classes rather than cohorts) and that escaping herbivores was more important than escaping fire. In their model, Dublin *et al.* (1990) assume seedling regeneration of 17 ha^{-1} and steady height growth of seedlings even in the presence of fire and herbivory. Although they did not indicate how they determined this number of seedlings, it is a rather low input suggesting seedling limitation. Further contextual information is needed; are these levels of herbivory and fire exceptions or medians?

Few studies have focused on actual seedlings in the field; short individuals are often considered to be seedlings, not resprouts. A crucial experiment would be to place seedlings out in the field and to protect some with exclosures. The responses of seedlings of different species and different ages/sizes to different types of herbivory would enable the answering of questions such as 'how old/

large must a seedling be to survive herbivory and how does this vary amongst species?'. Does (repeated) herbivory cause death, intense suppression or does it merely delay the inevitable escape? A demography determined by continual, albeit slow, growth in the face of chronic disturbance is different to one where these disturbances reset damaged individuals (i.e. the resprouts) to ground level. The 'continual growth model' suggests size-class distributions that do not show distinct cohorts and should thus include intermediate size-classes. Under this scenario, numbers of new recruits would be the strongest limitation on increasing population size because any new individuals will eventually be added to the population.

The 'reset model' suggests that size-classes should be strongly bi-modal; a few large escaped individuals and many stunted resprouts. The lack of small and intermediate size-classes noted in many savannas would, under this model, probably be due to a chronic lack of escape opportunities rather than seed/seedling limitation. Bush encroachment may be due to increased levels of seedling recruitment or due to increased frequency of release of resprouts. Released individuals may increase in size and this may lead to an increase in seed output and recruitment.

Competition with grass

Is seedling establishment limited by negative interactions with grass (16)? Skarpe (1990) noted an increase in plant size of woody plants, including *Acacia mellifera*, in over-grazed areas. She explained this as being due to increased water availability due to the decline in grasses brought on by over-grazing. In contrast, this could be due to a decline in fire; as Skarpe (1980) previously noted *A. mellifera* can experience mortality in intense fires.

Mwalyosi (1990) focused on the decline of *A. tortilis* in relation to elephants and the compression hypothesis. According to this hypothesis, elephants have been compressed into increasingly smaller areas, which has led to them drastically over-utilizing the vegetation until negative feedback caused the decline of the elephants. This arose because elephant habitats have been reduced over the years and their migration routes too were closed.

In contrast to the compression hypothesis, Mwalyosi (1990) suggested that climatic fluctuations explain population cycling in acacias. He suggested that elephants are not the reason for lack of acacia recruits because they only target larger individuals. Wet years were considered to favour acacia germination and subsequent dry years, with a reduction in grass cover and an increase in soil disturbance, would allow these seedlings to establish. He estimated that the growth rate of small acacia individuals was about 50 cm y^{-1} despite disturbance (compare with Dublin *et al.* 1990), and was thus enough to replace lost adults. Thus the problem of declining acacia stands was due to hurdles at the seedling stage, in particular due to interactions with grass and climate. Mwalyosi (1990) provided no field information on seedling numbers in relation to germination and establishment. His argument would fall into the 'continual growth model'.

It is generally considered that *Acacia* invasion into pastoral lands is due to the grazers removing the competitive interaction with grass, which allows the woody plants in (Moleele & Perkins 1998, Scholes & Archer 1997, Skarpe 1990). There is little unambiguous support from field observations in Africa for the importance of grass competition in suppressing the seedlings of acacia species. Knoop & Walker (1985) showed experimentally that herbaceous vegetation below acacia adults negatively influenced the growth of the adults. They commented that seedling numbers of *A. tortilis* increased where grasses had been removed. However, O'Connor (1995) showed that grass competition did not limit seedling establishment in *A. karroo* in the eastern Cape of South Africa. More experiments need to be repeated for acacia seedlings.

Fire mortality and fire damage limitation

Is seedling establishment limited by fires and how does this differ amongst species and fires (16)? Pellew (1983) and Dublin *et al.* (1990) have argued that fire, especially when associated with large herbivores, is important in determining the state (grassland or mixed) of a savanna. Higgins *et al.* (2000) developed a model for tree-grass coexistence based on fire response alone using equations partly derived from extensive measures of *Acacia* response to fires of different frequency and intensity in South African savannas. Pellew's (1983) classic modelling paper incorporated a diversity of impacts (elephants, giraffe and fire) on *A. tortilis*. In general, savanna fires are considered to cause top-kill in taller individuals (Trollope 1984) rather than mortality. Fires induce resprouting from the base or even in the canopy. Most woody savanna species, including probably most (all?) acacias, are able to resist fire and to resprout to a certain degree. More comparative information is crucially needed on fire-sensitivity and fire response in relation to fire intensity and plant size/age. There is some evidence that fires can cause mortality, not just top-kill. Pellew (1983) suggested that fire caused mortality of *A. tortilis*. Van der Walt & Le Riche (1984) noted considerable mortality (75% of all burned individuals) of *A. erioloba* in a desert ecosystem. Ruess & Haller (1990) suggest *A. xanthophloea* is fire sensitive and Skarpe (1980) noted fire sensitivity in *A. mellifera*. In contrast, Sabiti & Wein (1988) showed that *A. sieberiana* seedlings acquire resistance against intense fires by 2 y of age and Story (1952) showed *A. karroo* acquired resistance in 12 mo. There is clearly a range of fire responses amongst *Acacia* species and different responses for different size classes.

Pellew (1983) noted that herbivores exacerbate the effects of fire by keeping a large percentage of the population in the fire-trap. He noted that regeneration, even in the putatively fire-sensitive species *A. tortilis*, is mainly from rootstock. He had limited information on patterns/determinants of seedling recruitment (assumed to be 1.7 seedlings per mature tree in his model). His suggestion that the greatest need is for more studies of regeneration rather than mortality of adults, has not yet been taken up. There have been few experimental analyses of *Acacia* seedlings in East Africa.

Other studies have questioned the role of fire as a general explanation for the structure of acacia populations. For example, Prins & Van der Jeug (1993) studied an area where fire had been absent for 60 y and where they suspected small herbivores were the main limiting factor for acacia recruitment.

Future experiments should determine the relative importance of seedlings, as opposed to resprouts (see later), and should be considered in relation to various disturbance regimes. Responses of seedlings of different species/sizes/ ages to different fires should be determined so as to be able to answer questions such as: how old/large must a seedling be to survive fires of various intensities and how does this vary amongst species? Does fire cause death, suppression or merely extend the period in the fire-trap (i.e. continual growth versus resetting). What is the interaction between fire frequency and intensity, degree of browsing and seedling establishment?

Resprout release limitation

Most (all?) acacias can resprout, at least after a single mild fire and/or incidence of herbivore damage. Does their demography depend on the release of resprouts (rather than on the input of seeds or seedlings). There may be enough resprouts persisting in the grass layer to replace adult densities, when they are given a window of opportunity. How does fire (17) and herbivory (18) affect the release of resprouts (see above papers on establishment of seedlings)? How does it vary between species and different environments (e.g. arid vs. mesic)? Is release of sprouts sporadic (leading to cohorts and missing size-classes) or steady (leading to more even spread of size-classes)? Martin & Moss (1997) noted that individuals spend several years in the herbivory-trap – at heights < 2.5 m within reach of most mammal herbivores. They suggested that ageing of acacias will thus give information not on their age but on the period since release.

Adult mortality: limited life span and senescence

Young & Lindsay (1988) suggested that acacias may show cohorted senescence. They provided no demographic information to show whether acacias are in fact cohorted, nor whether the species they concentrated on (*A. xanthophloea*) is representative of the genus. What is the natural lifespan of acacias and how does it vary amongst acacia species and in different environments (19)? Are acacia individuals within a stand predominantly single-aged and if so does this date back to cohorted regeneration or release of sprouts from fire and herbivore damage? Will an absence of disturbance lead to the decline of acacias through rapid senescence?

Herbivory

What is the impact of elephant, and other grazers on the mortality of adult trees (20)? It has long been observed that elephants can damage the intermediate-to-large size-classes of Acacias either by ring-barking or by pushing them

over. Ruess & Haller (1990) investigated *A. xanthophloea*, *A. tortilis* and *A. senegal* in relation to elephant damage of large trees and giraffe damage of smaller trees. In 1971 most species appeared to have bimodal size-class distribution and 10 y later more of an inverse-J size-class distribution occurred with fewer larger trees. They took this to indicate high impacts of large herbivores on the larger size classes.

Competition and succession

Smith & Goodman (1986) used an experimental approach to show strong competition amongst the woody components of a savanna. Increased growth when neighbours were removed and regular spatial patterns indicated competitive effects. These results suggest that some mortality of adults may be due to intrageneric competition, resulting in a carrying capacity of adult acacias in an area that may be relatively low. Thus sparse stands are not necessarily maintained by damage due to fire or herbivores. Furthermore, replacement of these low adult densities can readily be achieved by the release of stunted resprouts which often occur at replacement densities, but are inconspicuous because they are restricted to the grass layer. Similarly, low levels of recruitment may be sufficient to ensure adult replacement at carrying capacity.

Smith & Goodman (1987) suggested that in some situations, acacias may be prone to being out-competed by shade-tolerant broadleaf species which establish in their shade, gradually over-top and kill them (21). They suggested that continual disturbance of acacia stands by elephants was necessary to prevent this phenomenon; either by directly reducing the establishment of these woody species or indirectly, by keeping the system open and allowing fire in.

Fire

As has been mentioned above, some species appear to be fire sensitive. Generally adults escape fire damage by their taller size but they may suffer higher mortality than smaller individuals because of an age-dependent loss of buds whence to resprout. To what degree does fire impact demography of adult acacias (22)? This especially applies to intense fires (which may themselves be associated with wet years and high fuel loads from dense long grass as well as relatively low grazing levels).

A DEMOGRAPHIC FRAMEWORK FOR *ACACIA*

An understanding of acacia demography is needed for conservationists, pastoralists and those involved with economic utilization of acacias. So too, is a general framework needed so that extrapolation is possible between species and sites. For example, bush encroachment, although a serious problem in Africa is still not well understood. Acacias may invade because overgrazing releases more resources for woody plants or because it is associated with a reduced

incidence of fire (e.g. Hoffman & O'Connor 2001). However, significant changes in fire regimes are more likely in mesic areas and changes in access to water more important in arid areas. Below is a speculative framework which suggests how different factors may vary in importance in different sites.

We suggest that in productive areas grass is able to grow tall and provide enough fuel for fire to be the dominant demographic hurdle (Figure 2a). Under high rainfall conditions, seedling establishment may be adequate each year but conditions for release of seedlings and resprouts from the fire-trap, will not (Figure 2b). In arid areas, drought is likely to be a major factor limiting seedling establishment. In most years, grass height and density is generally too low to support intense fires, and thus herbivory is likely to be a second major demographic hurdle (Figure 2a). Here conditions for seedling establishment will vary with annual rainfall conditions (i.e. low in dry years) and the demographic hurdle preventing established seedlings from moving up in size class will be herbivory and rainfall (Figure 2b). Acacias in intermediate areas will be exposed to both fire and herbivory or, if animal numbers are high, only to herbivory as a major demographic hurdle.

This framework may also provide a landscape perspective for interpreting the extent of the evolution of defences against fire and herbivory. For example, we predict that bark thickness should be relatively greater in long grass areas and mechanical defences (thorns) relatively greater in short grass areas. Fire resprouters should be more common in productive areas. Finally, we suggest that landscape changes/reversals in the occurrence of these dominant disturbance regimes could cause major changes in *Acacia* populations. For example, the occurrence of fire in an unproductive area may cause higher mortality than in a productive long-grass area. Similarly increased herbivory in long-grass areas should have relatively larger impacts because species may not have evolved the capacity to sustain intense herbivory.

Another obvious continuum along which *Acacia* species are spread is that from tall single-stemmed reseeders to short multi-stemmed resprouters. We expect that the multi-stemmed species are good persisters in the face of disturbance but poor recruiters (Figure 2c). Multi-stemmed fire-resisters will not necessarily be herbivory tolerant and vice-versa. The demographic hurdle limiting population expansion for the multi-stemmed species will be conditions that favour recruitment. Conversely, single-stemmed species should be less recruitment limited but will be release limited. Opportunities for release from the fire-trap may limit their population growth.

In unproductive areas, population age-structures should be cohorted and reflect limited opportunities for seedling establishment (Figure 2d). In productive areas populations should be bimodal (those that have escaped and those still suffering in the fire-trap). In intermediate areas size-class distributions should contain all size-classes because the fire/herbivory/climate interactions are less intense.
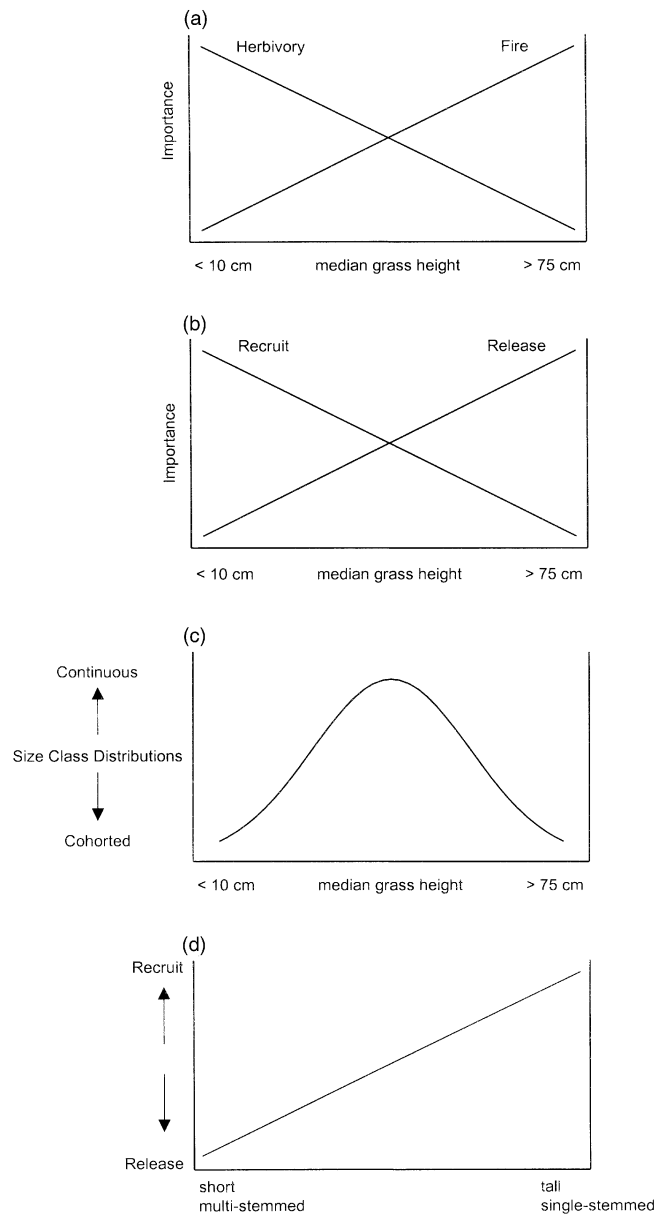
Figure 2. (a) The hypothesized relationship between amount of grass (fuel), habitat, fire and herbivory. Fire is the dominant demographic hurdle in mesic long-grass areas whereas moisture availability for establishment and herbivory dominate in short-grass areas. (b) The hypothesized relationship between grass height and the importance of release of resprouts or recruitment of new individuals. *Acacia* spp. in tall grass areas are dependent on periods where release occurs whereas short grass areas require favourable climatic conditions to allow recruitment. (c) The hypothesized relationship between size-class distribution type and habitat. Size-class distributions indicate cohorts in more mesic and arid areas whereas size-class distribution indicate an even distribution of sizes in intermediate areas. (d) The hypothesized relationship between recruitment or release and single-stemmedness or multi-stemmedness. Recruitment is rare in multi-stemmed species whereas release is rare in single-stemmed species.

SUMMARY

We suggest that the major questions concerning *Acacia* demography are: (1) are populations seed limited, seedling limited or release limited? (2) what is the importance of dispersal? (3) does progression from life-cycle/size stage to the next occur steadily or abruptly? and (4) what are the patterns of variation between species, areas and disturbance regime?

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