Demographic bottlenecks of three *Acacia* species in a South African savanna

Research in Ecology

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ABSTRACT

Savannas ecosystems consist of woody trees and grasses, and a dynamic relationship exists where areas fluctuate in the proportions of these two components. On the one hand grasslands are interspersed with few trees, and on the other hand woodlands are closed canopy areas where grass struggles to grow. Bush encroachment, where formerly open areas are increasingly occupied by trees, is occurring in many savannas. Changes in fire regime, herbivory intensity, climate and increases in atmospheric carbon dioxide have all been proposed as influences on bush encroachment, but the effects and relative impacts are still poorly understood. *Acacia* species are the dominant trees in African savannas, and are responsible for bush encroachment in some areas. Bottlenecks in the demography of these trees may have important implications on bush encroachment. However, few field experiments have been done on such bottlenecks, and in particular the seed-to-seedling and sapling-to-adult bottlenecks. This study used data from herbivore exclosure experiments in Hluhluwe-Umfolozi Game Reserve to elucidate the effects of herbivores, as well as rainfall on these two bottlenecks in the demographies of *Acacia nilotica*, *A.tortilis* and *A.nigrescens*, over a period of three years. Five sites in each of the parks (Hluhluwe – mesic savanna, and Umfolozi – arid savanna) along a grazing intensity gradient were used, with control (access to all animals), partial exclosure (rhino and buffalo excluded) and full exclosure (all animals larger than hares excluded) treatments at each site. Seedling emergence (the number of trees >100cm seen for the first time during the survey) was found to correspond closely to rainfall in all three species. Herbivory effects were small, mainly impacting seedling emergence indirectly by reducing grass cover and thus increasing water availability, which is required for imbibition of seeds. Herbivory had a greater impact on the subsequent fate of seedlings, especially if they are not well-defended against herbivores, although rainfall also affected the net increase in height over a growing season. Results indicate that *A.nilotica* (which is more abundant in the mesic savanna) emergence is dependant on a threshold rainfall, below which few seedlings emerge. However, it is not seed-to-seedling limited, as the threshold rainfall occurs sufficiently frequently to create a large seedling bank. The sapling-to-adult bottleneck is important, since few seedlings or saplings have the potential to escape the fire or herbivore trap in mesic savannas where fires are more frequent. *A.tortilis* is seed-to-seedling limited due to low water availability in arid savannas, but is well-defended against herbivores once it

is established, thus sapling-to-adult bottleneck is less important. *A.nigrescens* is also seed-to-seedling limited in the arid savannas, but less so than *A.tortilis*. It is poorly defended against herbivores, and grows best in grass swards where fire causes top-kill, and is thus also sapling-to-adult limited. Adult *A.nigrescens* are long-lived, and therefore don't require recruits progress to adulthood as often as the other species. Of these three species, *A.nilotica* is the only one with real potential to cause bush encroachment, since a large seedling/gulliver bank exists, and changes in fire frequency or herbivore intensity can easily allow these to become adults. In the arid savannas, water limitations and herbivory are probably sufficient to prevent bush encroachment by *A.tortilis* or *A.nigrescens*.

INTRODUCTION

Savanna ecosystems consist broadly of two interacting plant components, *viz.* the woody component on the one hand, and the grass component on the other (Scholes & Archer 1997; Bond *et al.* 2001; García-Núñez *et al.* 2001). Ecosystem processes result in oscillation between tree-dominated (bush encroached or woodland) or grass-dominated (grassland) savanna. These include varying disturbance regimes (such as herbivory or fire; Scholes & Archer 1997) as well as environmental conditions (e.g. rainfall variation, nutrients or temperature).

Bush encroachment, where trees and shrubs occupy open grasslands or congeal previously wooded areas (Trollope 1980), has been a worldwide phenomenon in many biomes, including African savannas (van Vegten 1983, O'Connor 1995). The factors that cause or prevent it are still poorly understood, in particular in savannas where tree demography is affected by numerous biotic and abiotic factors that are not well researched. Bush encroachment has been attributed to a reduction of fires in savanna systems due to fragmentation by anthropogenic structures has allowed the seedlings or gullivers to escape from the fire trap. Overgrazing leads to fuel loss for fires, and also results in a disrupted fire-regime that can benefit trees (Skarpe 1990). In non-reserve areas, a shift to domestic livestock, such as cattle, reduces the grass cover, and thus decreases inter-specific competition and fire effects. Bush encroachment may have been promoted by the increase in atmospheric carbon dioxide level, which allows woody plants to grow more vigorously.

Acacia species frequent African savannas, and are the main trees that constitute bush encroachment in savannas where this occurs. They form an integral part of the ecosystem functioning, and are themselves affected by many different influences in savannas. Despite large volumes of work being done on this genus, inadequate knowledge still exists on the demography of *Acacia* species due to few field experiments being undertaken (Midgley & Bond 2001). In an attempt to explain bush encroachment, much *Acacia* research has focused on been the unstable demographies of numerous populations in diverse geographical areas that contributes to the savanna dynamic of tree- or grass-dominance. Possible causes of variation in tree cover include fluctuations of climate (Mwalyosi 1990), fire (Danthu *et al.* 2003), elephant populations

(Ben-Shahar 1993), other herbivores, or tree diseases (Midgley & Bond 2001). While these factors have been shown to affect *Acacia* demographics to varying degrees in certain circumstances, the relative impacts are unknown, and we still lack a universal explanation, in particular regarding the mechanisms driving these fluctuations. Considering the diversity within the genus and the wide range of environments in which they occur, it is likely that different species have different dominant factors that determine their demography at a given time.

Midgley & Bond (2001) identified the main obstacles in Acacia life-history to be 1) seed set, 2) pre- and post dispersal seed predation, 3) seed dispersal, 4) seed germination, 5) seedling establishment, 6) sapling and resprout survival and 7) adult survival to sexual maturity. They also point out that, amongst other gaps in *Acacia* research, few field experiments focusing on seedling biology have been done, and thus very little information exists on this part of *Acacia* life history. It is therefore useful to examine this possibly crucial stage in the life-history (Goldberg 1990) to determine whether it represents a bottleneck in *Acacia* demography. There are many factors that may effect seedling emergence and their subsequent fate, such as water availability, fire, herbivory, competition or facilitation.

The impact of herbivory on seedlings can be direct or indirect. Browsers may target the softer shoots and leaves of seedlings because they are more easily digested. Grazers may also inadvertently feed on seedlings growing amongst grasses. Grazers also indirectly affect seedlings since they reduce the above-ground biomass of grass, which leads to a concomitant decrease in below-ground biomass (Chirara 2001). Above-ground, seedling are not shaded by the grass, and thus not light-limited. Below-ground, less water is used by the grass leaving more water in the soil for seedlings. Reduced above-ground biomass of grass also reduces the impact of fire on seedlings, to the extent that heavily grazed grasses do not allow a fire to spread at all, while intermediate grazing intensity may result in heterogeneous burning.

The negative effect of interspecific competition between seedlings and the grass sward is well documented (for examples see Harrington 1991; Davis et al. 1998; and Fetene 2003), and is probably because water is a limiting resource in the top layer of the soil. However, O'Connor (1995) found that *A.karroo* is not limited by grass competition in the

eastern Cape, South Africa, and since rapid root elongation has been reported for *A.nilotica* (40cm in 15 days; Wilson & Witkowski 1998), the effect of grass competition may be minor and only important for germination and the first few days of survival. Nonetheless, seedlings of *A.tortilis* have been observed to be more abundant in areas where grass has been removed (Knoop & Walker 1985), but *A.tortilis* (Smith & Shakleton 1988) and *A.karroo* (Chirara 2001) have been shown to be negatively affected by shading, thus providing an alternative explanation. Nonetheless, one would expect that competition with grasses is important to at least some species. The effect of shading may also be positive for seedlings growing in hot, arid conditions. Shading by tall grass may reduce evaporation from the soil, increasing water availability. Tall grass may also 'hide' seedlings from herbivores, thus 'facilitating' their growth and survival. It is expected that seeds that require longer imbibition times will be more affected by competition with grasses, while established seedlings may benefit from being shaded from the sun or hidden from herbivores, but pay for this with slower growth rates due to reduced photosynthesis rates.

The aim of this project was to investigate bottlenecks in *Acacia* demography that may shed light on bush encroachment. The first bottleneck is from seeds to seedlings, or from seedlings that have been damaged by fire or herbivores, to re-emerge (emergence bottleneck). The subsequent fate of saplings is another bottleneck, i.e. how many saplings become adults, and under what circumstances? Mega-herbivore exclusion experiments were used to determine the factors that influence seedlings in a South African savanna. Data from annual tree surveys spanning three years were used to compare seedling emergence in the presence and absence of herbivores, and how this differed in mesic and dry savannas. For three African Acacias, the effects of rain, herbivory and fire on seedling emergence and subsequent fate are investigated.

METHODS

Study sites

Ten existing study sites in Hluhluwe-Umfolozi Nature Reserve, Natal, South Africa were used (Figure 1). Each site has two exclosure treatments (total exclosure consisting of a mesh fence that excludes all animals larger than hares; and the partial exclosure consisting of a cable strung at a height of ca. 0.8m that excludes large herbivores like rhino and buffalo) and a control (allowing free access to all animals). Each treatment consists of a 40m x 40m plot, with half of each plot being divided into a 2m x 2m grid system. The exclosures were constructed in October-November 1999. Data was used from an annual survey of the trees within the grid area from 2000 to 2002, with species, height and location in the grid being recorded for all trees. These were records were mapped and compared from year to year to determine first emergence of seedlings, and net difference in height from year to year of seedlings that have survived. Grass species were recorded at each intersection of the grid. Additional data for rainfall, temperature and fire were also recorded.

Five of these experimental sites were selected along a grazing intensity gradient for each park, Hluhluwe representing a mesic savanna (mean rainfall = 990mm / year), and Umfolozi representing an arid savanna (mean rainfall = 720mm / year; Whateley & Porter 1983). Ranks of sites are as follows, with 1 representing low grazing intensity and 5 high grazing intensity: Hluhluwe – 1 Ledube, 2 Maqanda, 3 Nombali, 4 Seme, 5 Klazana; and Umfolozi – 1 Sokhwezela, 2 Gqoyeni, 3 Mbuzane, 4 Thobothi, 5 Mona. For all graphs, sites are arranged from low grazing intensity (on the left) to high grazing intensity (on the right).

Sites also vary in their rainfall. For the three years of this study, the rainfall gradient for each park is as follows (Figure 2): Hluhluwe – 1 Nombali, 2 Maquanda, 3 Klazana, 4 Ledube 5 Seme; and Umfolozi – 1 Mona, 2 Mbuzane, 3 Gqoyeni, 4 Thobothi, 5 Sokhwezela (with 1 being the wettest site and 5 the driest). However, the reliability of this rainfall data is questionable, since the manual rain gauges were monitored irregularly (especially in the first year), and those that were visited less frequently (e.g. Sokhwezela) were often full of water, thus under-measuring rainfall at those sites.

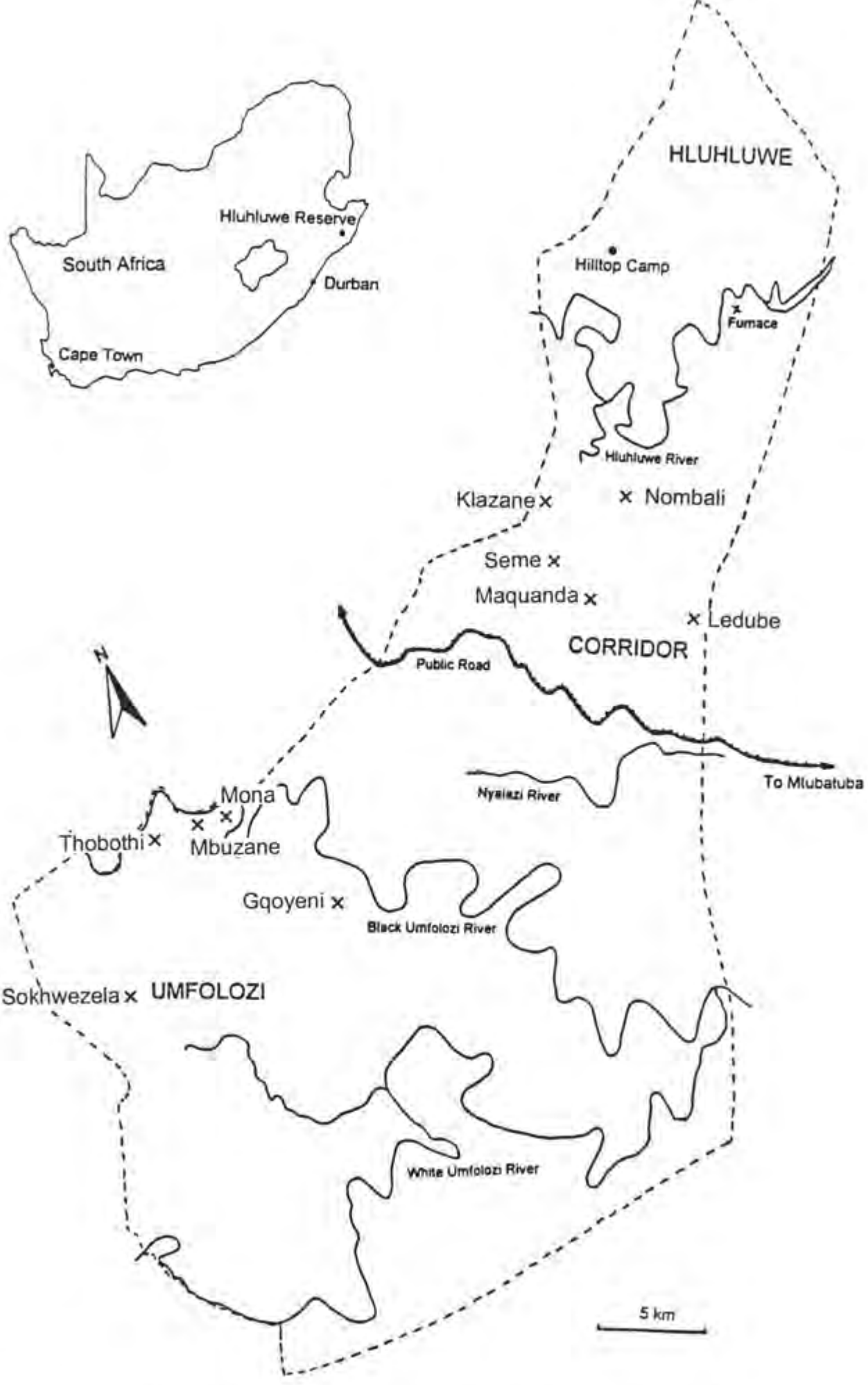

Figure 1. Map of Hluhluwe-Umfolozi indicating the locations of the sites.

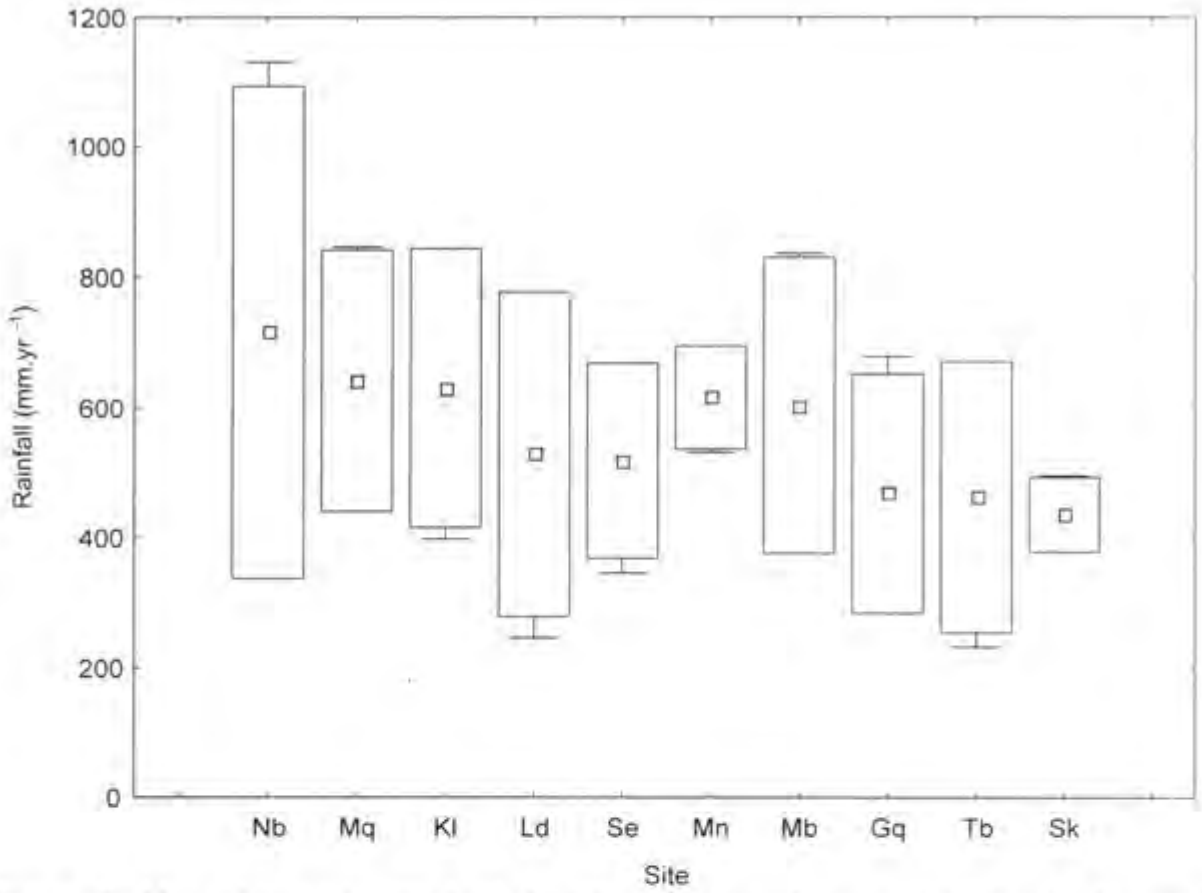

Figure 2. Mean (square), standard deviation (box) and range (whiskers) of annual rainfall for the period of 2000 to 2002 at each site.

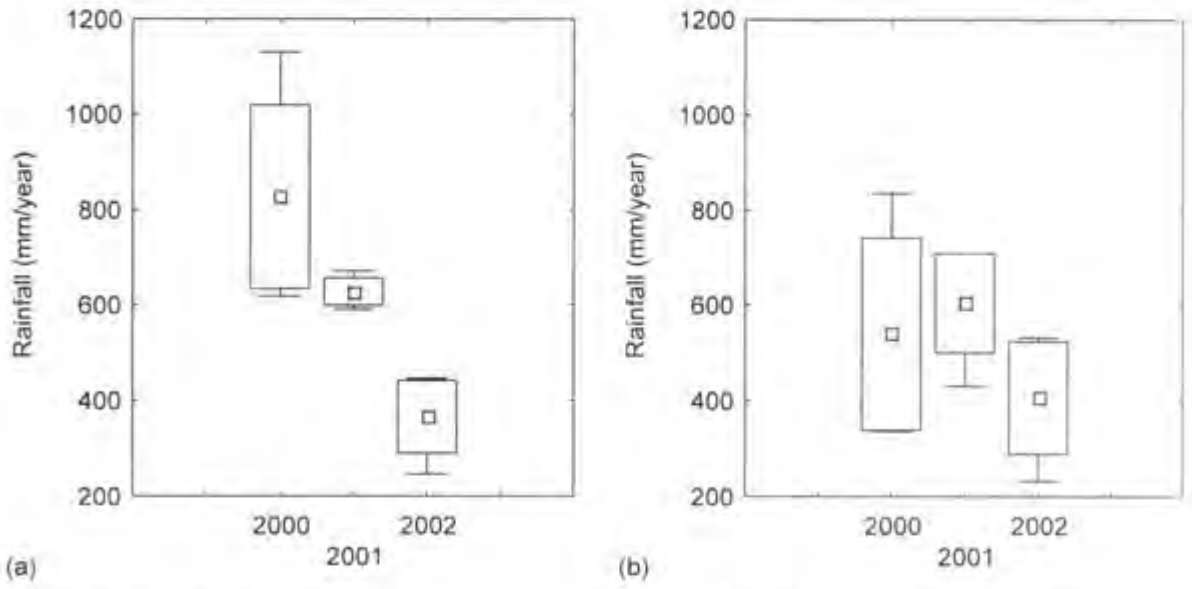

Figure 3. Rainfall for Hluhluwe (a) and Umfolozi (b) sites for the years indicated (for five sites in each park: square = mean, box = standard deviation, whiskers = min-max).

The tree survey database was managed in Microsoft® Access, manipulated in Microsoft® Excel, while analyses and graphs were done in STATISTICA.

1) Seedling emergence

The frequency of *A.nilotica*, *A.tortilis* and *A.nigrescens* 'seedlings' (trees < 100cm) emerging for the first time during the survey was extracted from the data. Since *Acacias* are resprouters and seedling age cannot be determined by above-ground measurements, this count consists of newly germinated seedlings and seedlings that had previously germinated and established, but had since been knocked back to ground height by fire or herbivory. To determine the effect of the amount of rain on seedling emergence, the total (from all sites and plots) number of seedlings per species was calculated for each growing season during the survey (1999-2000; 2000-2001; 2001-2002; and 2002-2003; Figure 3). For a qualitative evaluation, these frequencies were plotted with the concurrent rainfall for each season (annual rainfall calculated from June to July). The same data was used to determine the effect of fire on emergence, since plots were burnt after the 2000 survey, and again after the 2002 survey.

The effect of herbivory on seedling emergence was determined by qualitative and quantitative comparison of frequencies in control and exclosure plots of each site. Quantitatively, the effect of herbivory on each species was examined by comparing the expected frequencies with observed frequencies. Expected frequencies for the control and partial plots were calculated by multiplying the total emergence at all sites of each respective plot with the proportion of seedlings at each site in the exclosure plots (where there is no direct effect of herbivory), and residuals were calculated by subtracting the expected from the observed frequencies. (E.g. for species *A*, the control and exclosure had a total of 110 and 190 new seedlings respectively, at all sites. At site *1*, the control and exclosure plots had 20 and 30 new seedlings respectively, thus the expected frequency for species *A* at site *1* in the control plot = [30 / 190] x 110 = 17, and the residual is 20 – 17 = 3.) Residuals were analyzed by Chi-squared tests (Zar 1999) to determine significant differences.

2) Seedling fate

The effective growth rates (i.e. difference in height between one year and the next) for seedlings (trees < 100cm) were calculated for two successive growing seasons (2000 to 2001 – fire effect and above average rainfall; 2001-2002 – no fire effect and below average rainfall; see Figure 4 and Figure 5 for departures from mean, and Figure 6 for long-term context of the study period). Effective growth rate is equal to the real growth of the seedling minus the damage caused by fire or hebivory. For all seedlings of both seasons, the difference in height between species as well as between control and exclosure plots were tested for significance using the Kruskal-Wallis ANOVA test for non-parametric data (distribution was normal, but variances were significantly different; $p<0.05$, Levene's test for homogeneity of variances). The proportion of seedlings that showed a positive increase in height, as well as the proportion of seedlings that increased in height by 40cm or more, was calculated. It is reasoned that seedlings that increase 40cm or more in height over a growing season have a greater chance of escaping the fire or herbivore trap. Given a fire frequency of between 2 and 5 years, these seedlings can potentially increase 80 to 200 cm between fires, which may be sufficient to escape the fire or herbivore trap. Two-by-two Chi-squared tests (Zar 1999) were used to determine significant effects between growing seasons (and hence fire and rainfall effects). The heights of seedlings in each growing season that grew 40cm or more were determined for each species, and independent t-tests were used to determine differences in height between the growing seasons (for those seedlings that grew 40cm or more). The rationale is that larger seedlings have a greater chance of escaping the fire or herbivore trap, especially if they increase in height by 40cm or more per year.

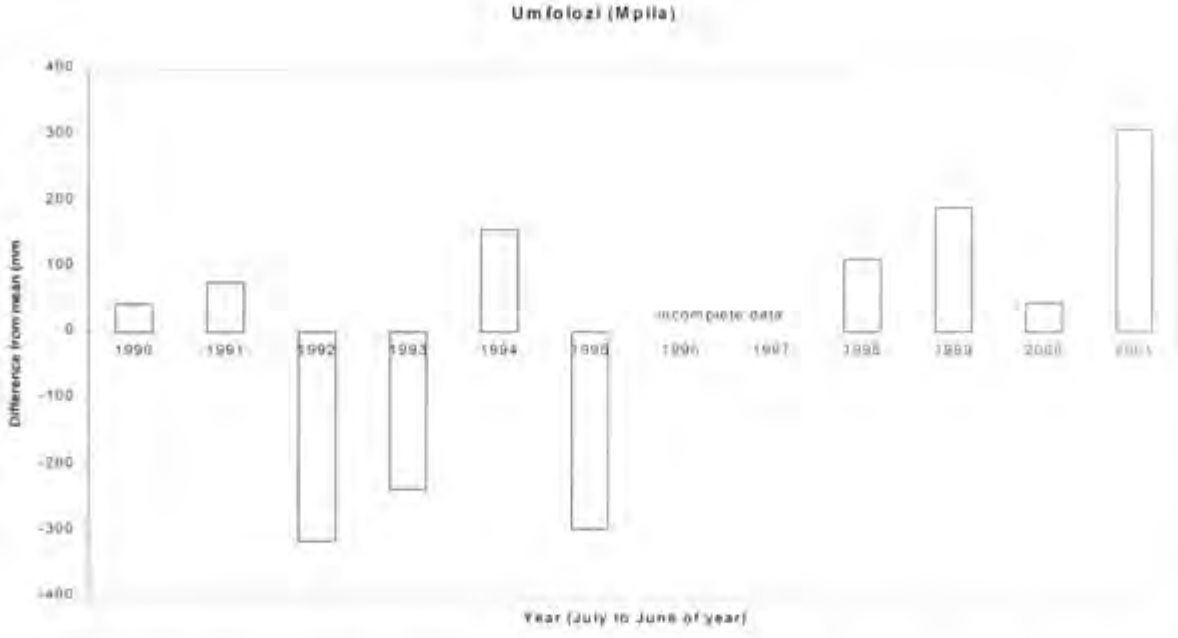

Figure 4. Annual rainfall in Umfolozi from 1990 to 2001. Bars indicate departures from the mean annual rainfall (1960 to 2001). Rainfall is summed from July to June with the year given for June. The mean rainfall at Mpila was 707 mm for the period 1960 to 2001 (excluding incomplete records for 1996 and 1997).

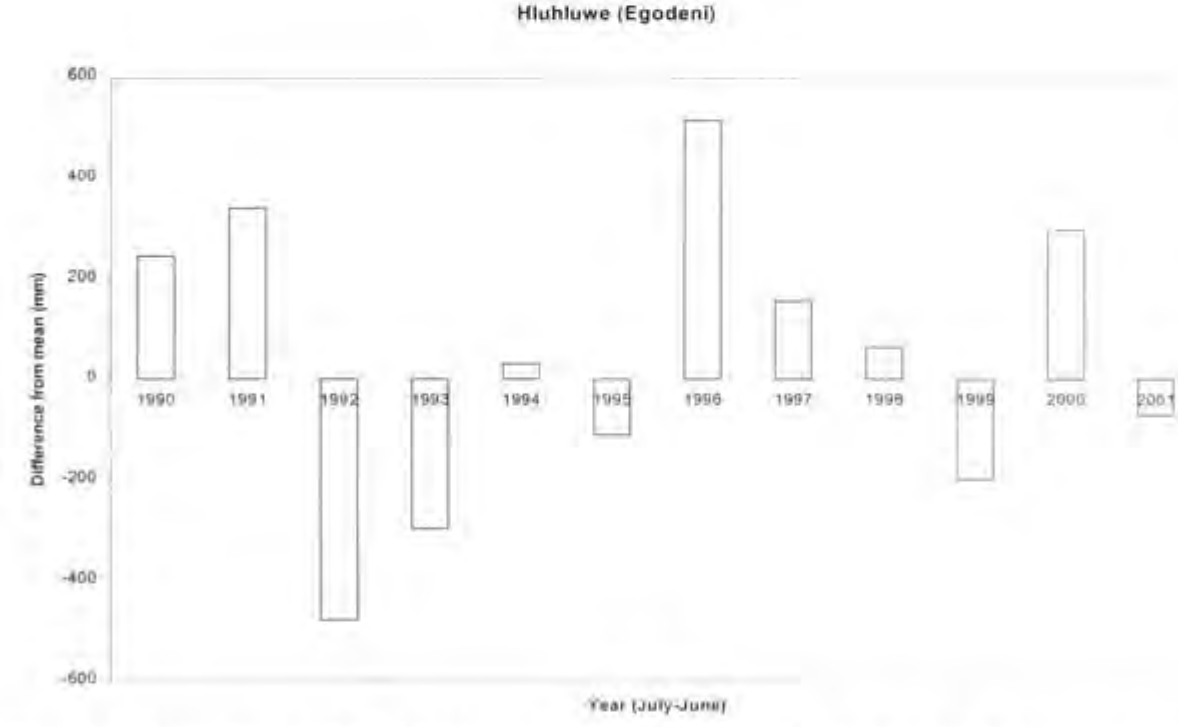

Figure 5. Annual rainfall for Hluhluwe from 1990 to 2001. Bars indicate departures from the mean annual rainfall (1934 to 2001). Rainfall is summed from July to June with the year given for June. The mean rainfall at Egodeni (Hilltop) was 990 mm for the period 1960 to 2001.

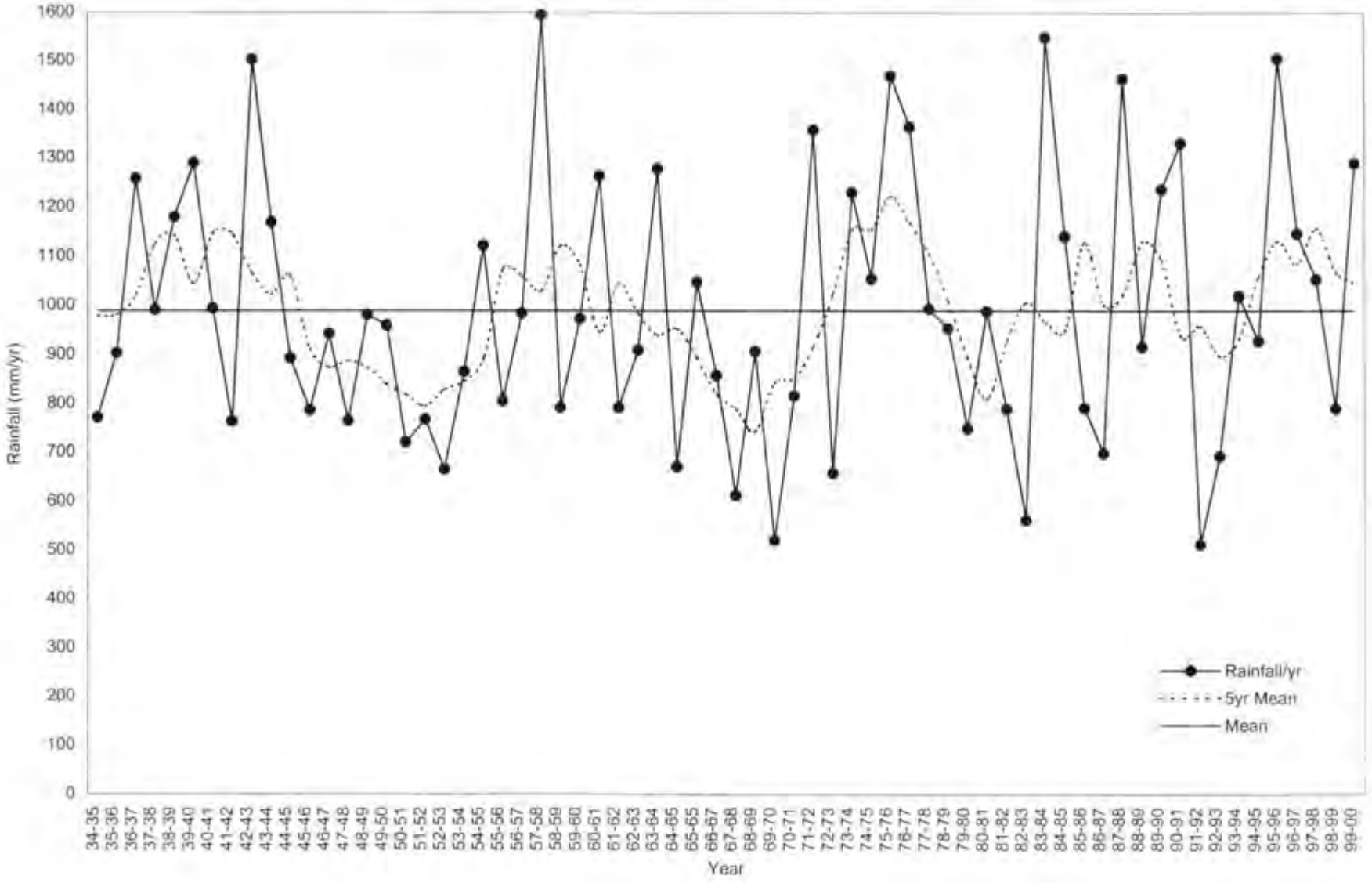

Figure 6. Long-term rainfall record for Egodeni (in Hluhluwe) from 1934-2000. Annual rainfall in mm (solid line with dots) is calculated to span the growing season (July – June). Mean rainfall for this period (990mm/year; solid line) and 5-year mean (dashed line) are also shown.

RESULTS

1) Seedling emergence

A.nilotica showed the greatest seedling emergence of all species in each year, while the fewest seedlings of the three species in this study were A.tortilis seedlings (Figure 7), although there were other species that were much fewer. Partial plots had a greater seedling emergence for all species in all years, and this effect was most evident in 2000. Seedling emergence strongly paralleled the total annual rainfall for all species (Figure 8). Only for the 2000-2001 season did A.nigrescens not follow this pattern, with fewer seedlings emerging. This may be due to the effect of fire prior to this season.

For *A.nilotica* and *A.nigrescens*, there was no trend in number of seedlings emerging in control plots along the grazing intensity gradient (Figure 10). However, more seedlings emerged at high grazing intensity sites in the exclosure plots, and both species had greater emergence in the control than exclosure plots (Figure 10), although this is probably skewed by the high 2000 numbers (Figure 7). Despite significant differences between observed and expected frequencies ($p<0.05$, Chi-squared; Table 1) for these species, residuals indicate that there is little pattern. Greater than expected emergence occurred at a low grazing intensity site for *A.nilotica*, and at a high grazing intensity site for *A.nigrescens* (Figure 9)

The highest total emergence (from all years) of *A.tortilis* seedlings occurred at a low grazing intensity site (Sokhwezela; Figure 10) and the greatest annual emergence in a season occurred in the exclosure plots (of 2001; Figure 7). Thus herbivores impact this species negatively. However, the total number of seedlings emerging in control and exclosure plots at each site was approximately the same for *A.tortilis* (Figure 10), indicating that herbivores have a minor effect on emergence. There was no significant difference between expected and observed frequencies in control plots ($p=0.076390$, Chi-squared=8.450980, d.f.=4; Table 1), but partial plots had had significant departures from the expected ($p<0.000000$, Chi-squared=39.78571, d.f.=4; Table 1). Residuals indicated that seedlings in the partial exclosures do best at heavily grazed sites, while emergence was greater than expected at low intensity sites in the control (Figure 9).

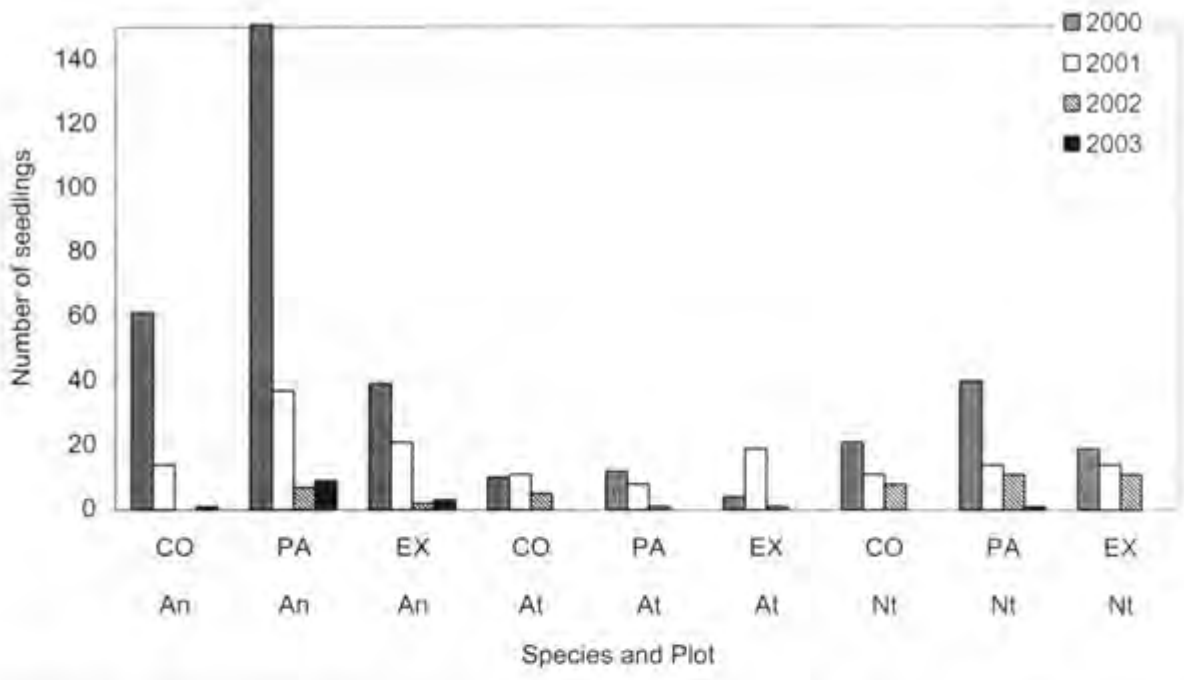

Figure 7. Total number of seedlings that emerged during the survey at all sites in control (CO), partial (PA) and exclosure (EX) plots for *A.nilotica* (An), *A.tortilis* (At) and *A.nigrescens* (Nt).

2) Seedling fate

The effective growth of seedlings did not differ significantly between control and exclosure plots for any of the species ($p>0.05$; Kruskal-Wallis ANOVA; Table 2). In the control plots, effective growth rates of *A.tortilis* seedlings differed significantly ($p<0.05$, Kruskal-Wallis ANOVA; Table 2) from those of *A.nilotica* and *A.nigrescens*, being higher in both cases (Figure 11). The range of effective growth rates was always larger in the exclosure than control plots for all species, while of the three species *A.nilotica* showed the greatest range and *A.nigrescens* the smallest (Figure 11).

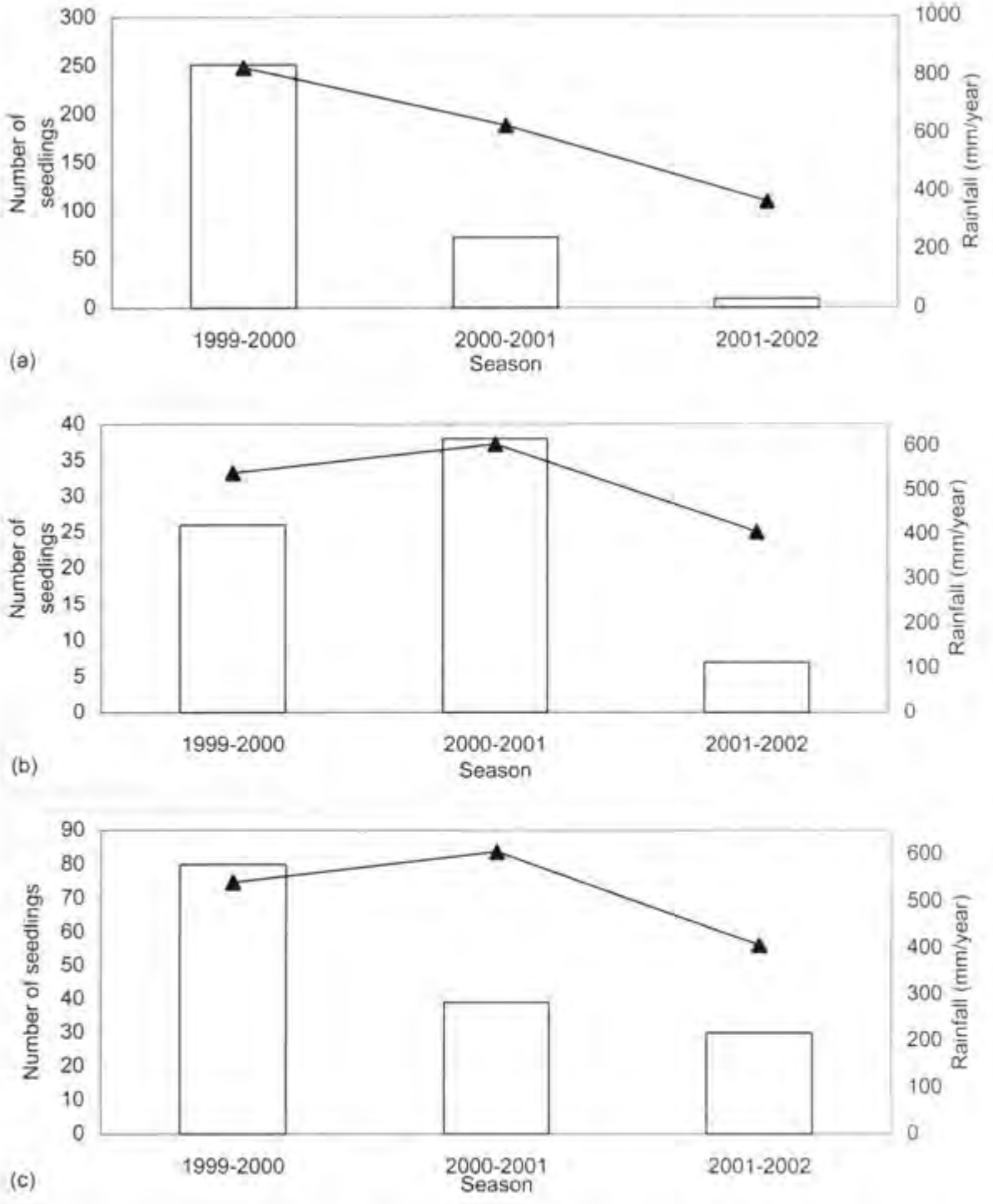

Figure 8. Number of *A.nilotica* (a), *A.tortilis* (b) and *A.nigrescens* (c) seedlings emerging in a growing season (columns), and the mean rainfall of sites where seedlings were found (triangles).

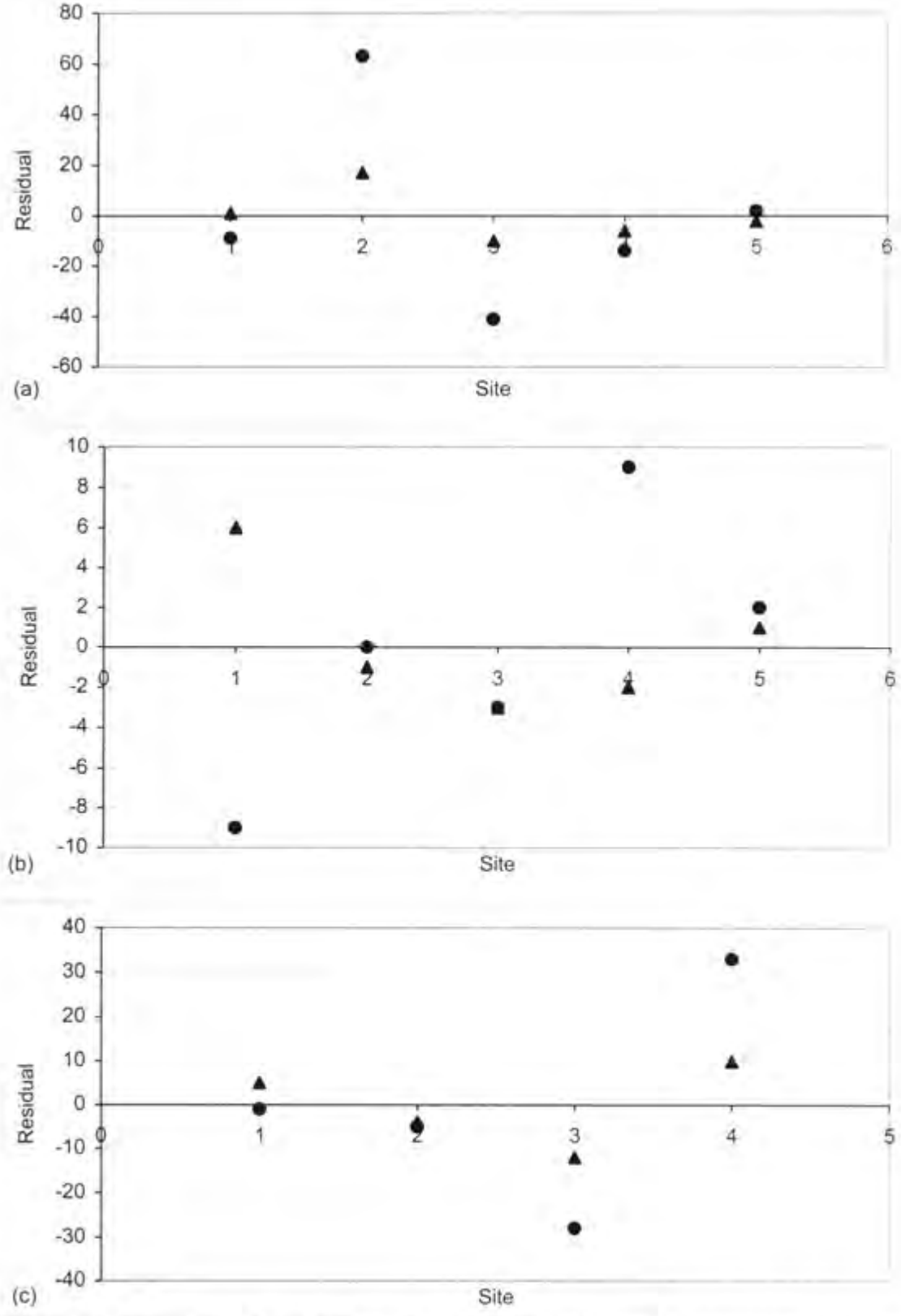

Figure 9. Residuals of *A.nilotica* (a), *A.tortilis* (b) and *A.nigrescens* (c) seedling emergence in control (triangles) and partial (dots) plots of each site along a grazing intensity (1 – low grazing intensity, 5 – high grazing intensity)

Table 1. Expected and observed frequencies of seedlings in control and partial plots (see **METHODS** for explanation on how expected frequencies were calculated).

A.nilotica CONTROL: Chi-Square = 19.96515, d.f. = 4, p < .000508				
Site	Observed	Expected	O-E	(O-E)**2/E
Ledube	9	8	1	0.12500
Maqanda	45	28	17	10.3214*
Nombali	7	17	-10	5.8823*
Seme	5	11	-6	3.27273
Klazane	9	11	-2	0.36364
Total	75	75	0	19.96515
A.nilotica PARTIAL: Chi-Square = 100.1178, d.f. = 4, p < 0.000000				
Site	Observed	Expected	O-E	(O-E)**2/E
Ledube	11	20	-9	4.05000
Maqanda	137	74	63	53.6351*
Nombali	6	47	-41	35.7659*
Seme	16	30	-14	6.53333
Klazane	32	30	2	0.13333
Total	202	201	1	100.11776
A.tortilis CONTROL: Chi-Square = 8.450980, d.f. = 4, p < .076390				
Site	Observed	Expected	O-E	(O-E)**2/E
Sokhwezela	23	17	6	2.1176*
Gqoyeni	0	1	-1	1.00000
Mbuzane	0	3	-3	3.0000*
Thoboti	1	3	-2	1.33333
Mona	2	1	1	1.00000
Total	26	25	1	8.45090
A.tortilis PARTIAL: Chi-Square = 39.78571, d.f. = 4, p < .000000				
Site	Observed	Expected	O-E	(O-E)**2/E
Sokhwezela	5	14	-9	5.78571
Gqoyeni	1	1	0	0.00000
Mbuzane	0	3	-3	3.00000
Thoboti	12	3	9	27.0000*
Mona	3	1	2	4.00000
Total	21	22	-1	39.78570
A.nigrescens CONTROL: Chi-Square = 43.85091, d.f. = 3, p < .000000				
Site	Observed	Expected	O-E	(O-E)**2/E
Sokhwezela	6	1	5	25.0000*
Gqoyeni	0	4	-4	4.00000
Mbuzane	13	25	-12	5.76000
Thoboti	21	11	10	9.09091
Total	40	41	-1	43.85090
A.nigrescens PARTIAL: Chi-Square = 84.28862, d.f. = 3, p < .000000				
Site	Observed	Expected	O-E	(O-E)**2/E
Sokhwezela	1	2	-1	0.50000
Gqoyeni	1	6	-5	4.16667
Mbuzane	13	41	-28	19.1219*
Thoboti	51	18	33	60.5000*
Total	66	67	-1	84.28862

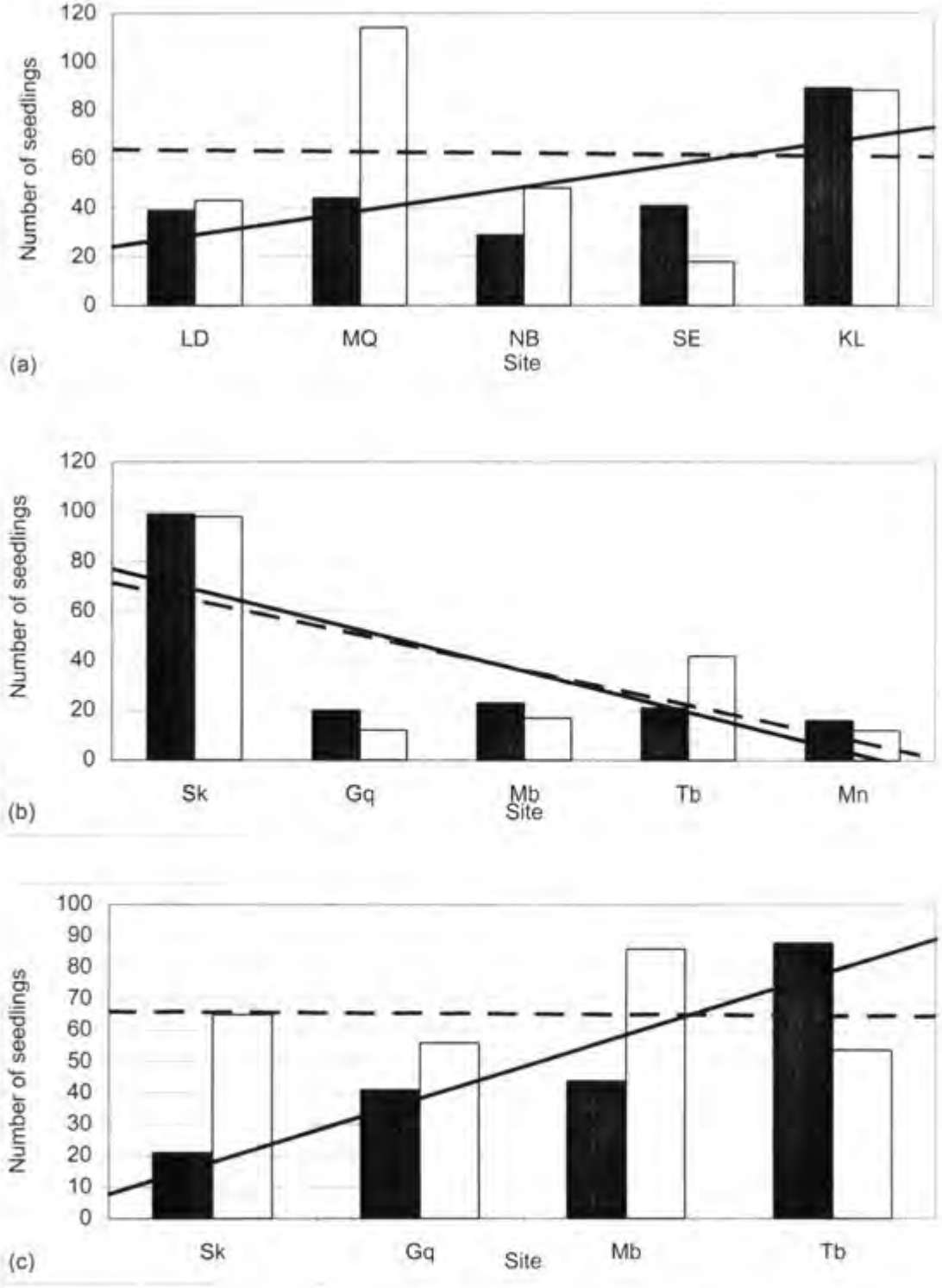

Figure 10. Seedling emergence of *A.nilotica* (a), *A.tortilis* (b) and *A.nigrescens* (c) in the exclosure (black; solid line) and control (white; dashed line).

Table 2. Significant p-values (two-tailed) of multiple comparisons using a Kruskal-Wallis test (p=0.0000, H=65.17339, N= 1501), comparing the annual difference in height for all seedlings (for both seasons) of the four species in the control (CO) and exclosure (EX) plots (n.s.=not significant; control vs. exclosure results for the same species are underlined).

Species		*A.nilotica*		*A.tortilis*		*A.nigrescens*	
	Plot	CO	EX	CO	EX	CO	EX
A.nilotica	CO	/	n.s.	0.0332	n.s.	n.s.	n.s.
	EX	n.s.	/	0.0020	n.s.	n.s.	n.s.
A.tortilis	CO	0.0332	0.0020	/	n.s.	n.s.	0.0019
	EX	n.s.	n.s.	n.s.	/	n.s.	n.s.
A.nigrescens	CO	n.s.	n.s.	n.s.	n.s.	/	n.s.
	EX	n.s.	n.s.	0.0019	n.s.	n.s.	/

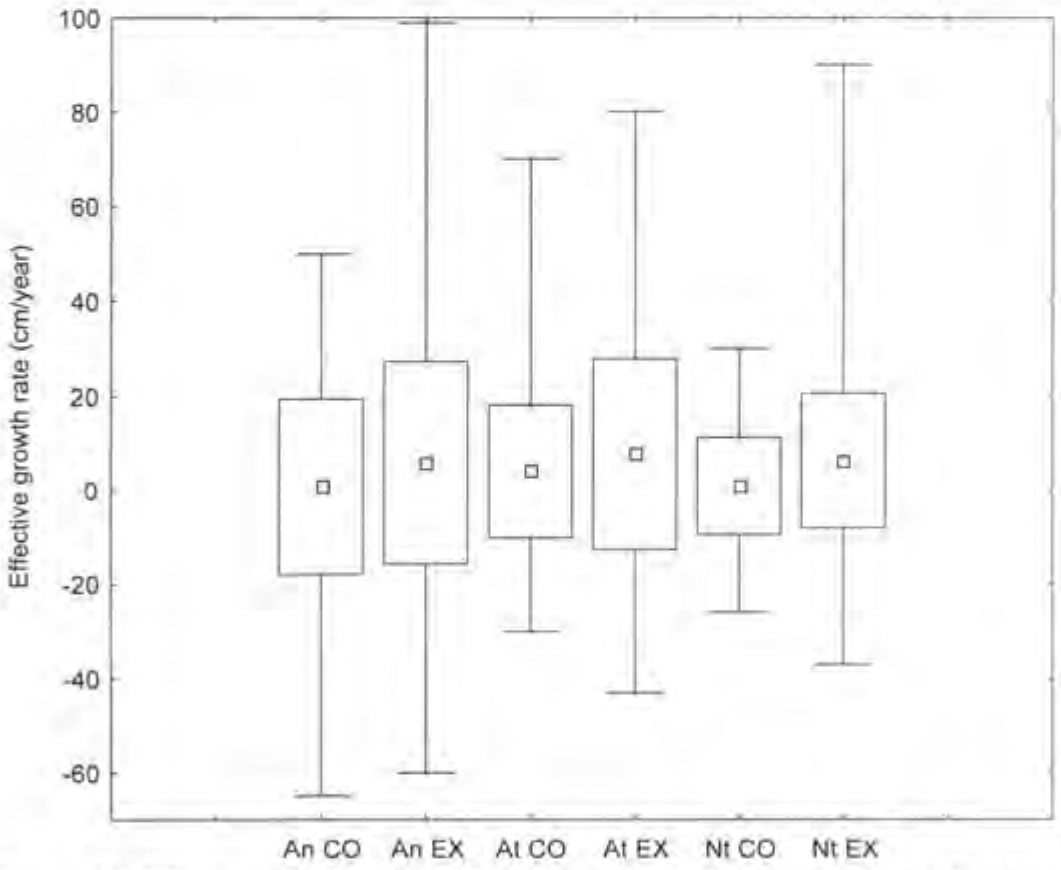

Figure 11. Effective growth rates of *A.nilotica* (An), *A.tortilis* (At), and *A.nigrescens* (Nt) in the control (CO), partial (PA) and exclosure (EX) plots. Square – mean, box – standard deviation, whiskers – min-max.

Fewer than half the seedlings of *A.nilotica* and *A.nigrescens* showed a positive increase in height in the first growing season (2000-2001 – fire effect and above average rainfall), while for the second season more than half the seedlings of all three species showed a positive increase. However, no species showed a significant difference between seasons for the number of seedlings with a positive increase in height ($p>0.05$, d.f.=1, Chi-squared). Similarly, no species showed a significant difference between seasons for the number of seedlings that increased by 40cm or more per year ($p>0.05$, d.f.=1, Chi-squared). Of the three species, *A.nilotica* seedlings that increased by more than 40cm were the most abundant for both years, while the greatest percentage of seedlings growing 40cm or more per year was found in *A.tortilis*. *A.nigrescens* had the fewest absolute numbers and percentages for both seedlings with a positive increase, and seedlings increasing by 40cm or more per year (Table 3).

Of all the seedlings that increased in height by 40cm or more in a growing season, only for seedlings of *A.nilotica* was there a significant difference in the heights of these seedlings ($p=0.007076$, $t=-2.90613$, d.f.=28; t-test for independent samples), with 2001 seedlings being higher (Figure 12). The heights of *A.tortilis* ($p=0.161081$, $t=-1.45031$, d.f.=22; t-test for independent samples) and *A.nigrescens* ($p=0.212296$, $t=-2.88675$, d.f.=1; t-test for independent samples) were not significantly different, but 2001 seedlings were taller (Figure 12).

Table 3. Frequencies of *A.nilotica* (An), *A.tortilis* (At), and *A.nigrescens* (Nt) seedlings that showed a positive increase in height (>0) and a positive increase of 40cm or more (>40). Percentage of total seedlings that were recorded for that growing season is shown.

		Growth Season			
		2000-2001		2001-2002	
Speices	An	Frequency	%	Frequency	%
Height	>40	15	3.8	20	4.4
increase	>0	193	49.4	256	56.9
	Tot	391		450	
Speices	At	Frequency	%	Frequency	%
Height	>40	7	2.7	17	5.6
increase	>0	158	59.8	167	55.3
	Tot	264		302	
Speices	Nt	Frequency	%	Frequency	%
Height	>40	2	0.6	1	0.3
increase	>0	158	48.5	217	54.7
	Tot	326		397	

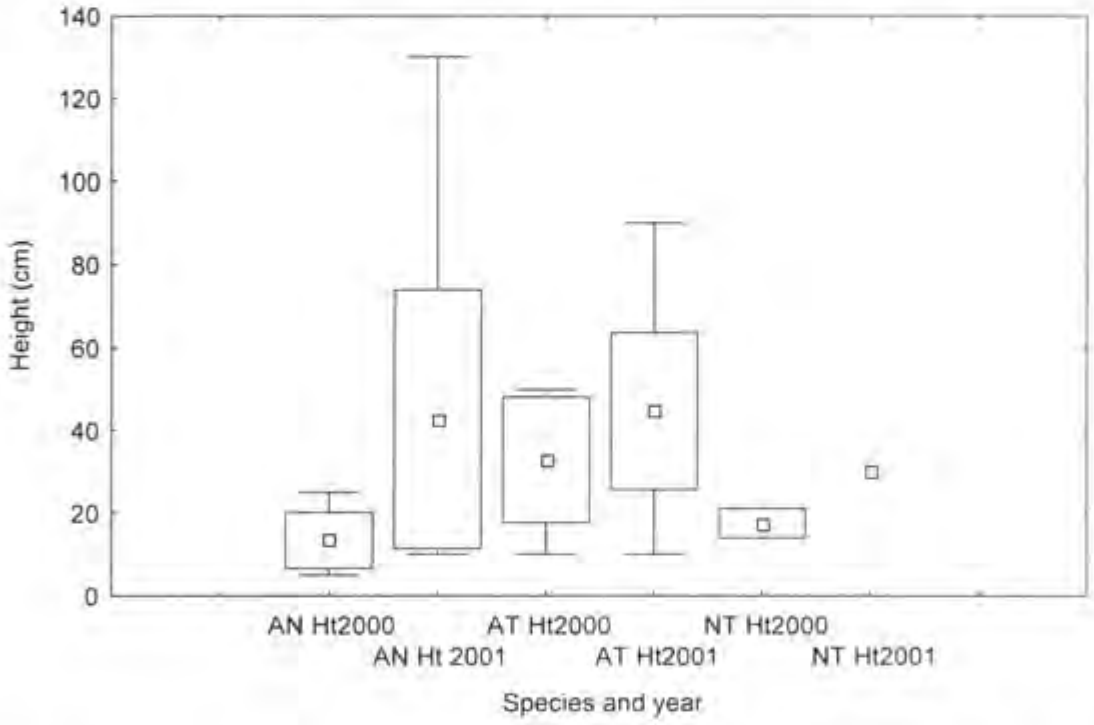

Figure 12. Heights of seedlings that grew more than 40cm in a year. (Square – mean, box – standard deviation, whiskers – min-max).

DISCUSSION

Acacia nilotica

The three- to four-fold higher seedling emergence of this species compared to the other two (Figure 7) is most likely due to the fact that it occurs mainly in the mesic savanna (Hluhluwe), where water is not as limiting as it is in the arid savanna (Umfolozi) where *A.tortilis* and *A.nigrescens* occur. Although high adult numbers may be primarily responsible for the high emergence of *A.nilotica*, it is still surprising since they produce relatively fewer seeds (by inference, since they have the largest seeds of the three species, and seed size is traded-off with seed number; Coomes & Grubb 2003). However, seed size could have a direct effect on seedling emergence, since large seeds produce seedlings that are superior competitors. Nonetheless, an apparent disadvantage of large seed size is that water requirements for germination are higher, since seed size and imbibition times are inversely correlated (Wilson & Witkowski 1998). Thus, germination of these seeds requires frequent rain over a sustained period, rather than high once-off rain events. This may seem like a disadvantage, but may in fact be regarded as beneficial. By limiting germination events to periods when there is sustained rainfall over a period, the chances of those seedlings surviving are increased, because they will only germinate in good rainfall years. If germination were triggered by any amount of water, then seeds would germinate in dry years after the first rainfall event, but die due to subsequent lack of water. Another advantage of large seeds is that seedling growth rates are higher (Westoby *et al.* 2002), due to the food stored in the endosperm of the seed. This is of particular importance for the roots, since it is imperative that they grow down quickly to retrieve water for the plant, and thereby avoid competition for water and nutrients with the roots of grasses. Indications are that *A.nilotica* does this well, considering that root elongation of 40cm in the first 15 days have been recorded in field simulating laboratory experiments (Wilson & Witkowski 1998).

The high water requirement for germination is likely the key to explaining the correlation between seedling emergence and rainfall (Figure 8). Due to the much slower rate of imbibition of *A.nilotica* seeds (28hr for complete imbibition compared to 8hrs for *A.tortilis*; Wilson & Witkowski 1998), a high rainfall threshold probably exists for *A.nilotica*, below which no or very few seeds germinate. The high seedling emergence in 2000 was most likely because the previous growth season received well

below average rainfall (Figure 5 and Figure 6) and thus few of the seeds produced in that year germinated, resulting in a seed bank. The above average rainfall of the 1999-2000 season thus saw the emergence of seedlings from two years worth of seeds. Unfortunately, the data may be misleading, since 2000 was the first year of the survey, and many of the seedlings recorded as 'new' may have established previously. However, in subsequent years this error is minimized, since previous records were used to validate the first appearance of a particular seedling. In addition, the trend of positive correlation between annual rainfall and seedling emergence continues for the other years of the survey. The fact that 2000-2001 has much fewer seedlings emerging may be because only one year's worth of seeds are available to germinate, since most seeds in the seedbank probably germinated in the preceding year. Low numbers in 2000-2001 may also be due to the lower rainfall, although if there is some threshold rainfall, seedling emergence numbers should not correlate with rainfall, but should rather be very high or very low, depending on whether the threshold rainfall was attained. This is supported by the extremely low seedling emergence in 2001-2002 and 2002-2003, where rainfall was well below average. It is proposed that dependence of seedling emergence in *A.nilotica* is two-fold. Firstly, there is a critical amount of rainfall required to trigger germination, which determines whether any new seedlings emerge in a season. Data from this study is insufficient to determine this threshold level of rainfall, but it is likely to be above average. Secondly, the number of seedlings emerging is a function of the number of seasons since the threshold rainfall amount was last attained. It is predicted that long drought periods will be followed by a high emergence of *A.nilotica* seedlings once the drought is broken, and long periods of above average rainfall will see a similar number of seedlings emerging from year to year, which is lower than the number of the first year after the drought.

As with the other species, trends from the impact of herbivory on seedling emergence were weak. This is to be expected, since herbivores can only really affect seedlings once they have emerged. However, the lower emergence in exclosure plots at most of the sites (Figure 10) is probably due to competition with grasses, which is an indirect positive effect of herbivores. The fact that partial exclosures had the highest emergence by far may be indicative of the trade-off between competing with grasses and coping with fire in low herbivory areas (exclosure plots), and coping with herbivory

in high herbivory areas (control plots). The partial plots allow smaller herbivores (impala and zebra) to reduce grass cover, thus minimizing competition and fire intensity, while excluding large herbivores (white rhino and buffalo) that are more indiscriminant when grazing and may cause damage to seedlings in the process. The greatest impact of herbivory however, is on the subsequent fate of seedlings.

While there was no statistical difference in net growth over a season between control and exclosure plots (Table 2), the exclosure plots did have a higher mean effective growth rate, and also had the highest maximum growth rates (Figure 11). This shows that absence of herbivory creates circumstances that maximize effective seedling growth rates. This is not to say that these seedlings necessarily grow faster, but it indicates that where herbivores are present, they do damage seedlings. However, where herbivores are excluded, grass competition may be a factor (although this is unlikely given the rapid growth of seedling root). The biggest effect of reduced herbivory is most likely the accumulation of fuel for fires. Tall grass burns easily, and a seedling within a tall grass patch will most certainly be top-killed. This is shown by the data for the first season when fewer than half the *A.nilotica* seedlings had a positive increase in height (Table 3), probably due to the effect of fire overriding any benefit that may have come from the above-average rainfall in that year. However, the lack of statistical support for differences in frequencies of seedling showing a net positive increase or a net increase of 40cm or more in height, between the fire and no-fire seasons shows that disturbance caused by fire and herbivores are approximately equivalent in their short-term effect. However, the fact that the heights of seedlings that grew more than 40cm in a season were much higher in the no-fire season (2001) indicates that frequent fires may prevent seedlings from escaping at all. This may mean that net height-gain for *A.nilotica* is greater in the absence of fire (despite herbivory or competition with grass).

Acacia tortilis

Emergence of *A.nigrescens* and *A.tortilis* seedlings was much lower than that of *A.nilotica* (Figure 7), which reflects their occurrence in the arid savanna (Umfolozi), where water limitations likely reduce germination events and subsequent survival. Of the two arid savanna species, emergence of *A.tortilis* seedlings was the lowest, but

still closely followed the total rainfall in a season (Figure 8). In contrast to *A.nilotica*, much less rainfall is required for germination (8hrs for complete imbibition compared to 28hrs for *A.nilotica*; Wilson & Witkowski 1998). This means that germination is triggered by any substantial rainfall event, but subsequent survival depends on the occurrence of subsequent rainfall events. The reason low numbers of emerging seedlings were recorded, despite a relatively higher number of seeds (they have smaller seeds than *A.nilotica*, and seed size is traded-off with seed number; Coomes & Grubb 2003), is probably because the majority of germinated seeds die before the end of the season due to lack of water availability.

There was no difference in emergence of *A.tortilis* seedlings between the control and exclosure plots of the sites (Table 2), and the higher emergence at the low grazing intensity site (Sokhwezela; Figure 10) is probably merely a product of the higher numbers of adults in that area. This is substantiated by the lack of pattern shown by the residuals, although it is noteworthy that higher than expected emergence occurred in the partial plot of a high grazing intensity site (4; Figure 9). This may once again be due to the exclosure of indiscriminant large grazers (white rhino and buffalo), but the lack of pattern among sites makes this difficult to verify. The effect of herbivores on net growth rates was also small (Table 2), but the fact that *A.tortilis* had the highest mean and maximum net increase in height in control plots, indicates that it is the most resistant to herbivory of the three species. The higher minimum increase in height of the arid savanna species is indicative that fire (in mesic savannas) has a greater knock-back effect than herbivory (in arid savannas). While *A.nilotica* may remain in the fire trap for a long time while it is stem-killed repeatedly by fire, requiring a fireless window of three to five years to escape the fire trap, *A.tortilis* steadily progresses out of the herbivore trap despite the attention of herbivores. It does this by building a heavily defended cage around the main stems, thus allowing herbivores to browse the leaves on the outside while limiting damage to the main stems. This is supported by the findings that more than half of the *A.tortilis* seedlings had a positive net increase (Table 3), which was higher than the other two species. The heights of seedlings that had a net increase in height of 40cm or more was also the greatest for *A.tortilis*, indicating that of the three species, they are probably least limited by the seedling-to-adult bottleneck.

Acacia nigrescens

Of the two arid savanna species, *A.nigrescens* had greater seedling emergence (Figure 7). The decrease in seedling emergence in each successive year was not as marked for *A.nigrescens* seedlings in the exclosure as it was for the other two species in the exclosure plots (Figure 7). This is probably because *A.nilotica* and *A.tortilis* are animal dispersed, thus not many new seeds were brought into the exclosure plots. However, *A.nigrescens* is wind-dispersed, thus the exclosure would have no effect on seed-dispersal.

A.nigrescens seedling emergence followed annual rainfall for two of the three seasons in the study period, but was lower than would be predicted by the rainfall in the 2000-2001 season (Figure 8). It is uncertain what caused this departure. Overall, seedling emergence is probably still highly dependant on high rainfall. However, more data is needed to support this claim for this species. As with *A.nilotica*, direct impacts of herbivory on *A.nigrescens* seedling emergence were low, since herbivores can only affect seedlings once they have emerged. Indirectly, however, herbivores decrease competition with grasses by reducing the grass cover, thus increasing water availability for germination and establishment. This explains the lower emergence in exclosure plots at most of the sites (Figure 10). However, the fact that higher than expected emergence occurred in the control plots of the high grazing intensity site (Figure 9) confounds the grass-competition theory. However, this data may be misleading, since the seedlings in the exclosure plots are much easier to see because they are taller, while the seedlings in the control are much smaller, and thus very difficult to see. This may skew the data towards the exclosure plots. On the other hand, if the data is accurate, then it could be that where herbivory is very high, seedlings may be killed by browsing before they have a chance to establish.

Seedlings of *A.nigrescens* showed no difference in net height change between the control and exclosure plots (Table 2), but as with the other species, the range of this effective growth rate was greatest in the exclosure plots (Figure 11). The exclosure plots all had very tall grass, which was burnt twice during the survey, and this may explain the large range. Seedlings can grow more in the absence of herbivores, but then have a greater potential height is lost by burning. In the control plots, herbivores

reduced the effective growth rates of *A.nigrescens* substantially. This species is not well defended against herbivores, since they only have small hooks (compared to the very long spines of *A.tortilis*). Hence they do not form a cage like *A.tortilis*. Of the three species, *A.nigrescens* had the lowest proportion of seedlings that had an effective growth rate of greater than 40cm per season (Table 3), and these seedlings were much shorter than those of *A.tortilis* (Figure 12).

Therefore, in the absence of herbivores, *A.nigrescens* competes well with grasses, and is not limited in terms of establishment or growth rates. However, they are stem-killed with every fire (which is less frequent in the arid savanna, but probably still frequent enough to prevent any such seedlings from escaping). Where herbivores reduce the grass cover, thus relieving the seedlings from the effect of fire, they are heavily browsed (since they are poorly defended against them). Thus *A.nigrescens* is less limited by the seed-to-seedling bottleneck than *A.tortilis*, but seems unlikely to easily escape the fire (in absence of herbivory) or herbivore (in absence of fire) trap, and is limited more by the sapling-to-adult bottleneck.

Conclusions

Evidence from this study suggests that *A.nilotica* is not seed-to-seedling limited, since high rainfall years are frequent enough in the mesic savanna to allow sufficient germination and establishment of seedlings (which also explains the low number of *A.nilotica* in the arid savanna). However, a major demographic bottleneck occurs at the seedling-to-adult stage of the life cycle. Very few seedlings have the potential to escape the fire or herbivore trap, and it is suggested that circumstances which allow cohorts of seedlings to escape are specific and fairly rare. The mean age of adult stands in Hluhluwe is 32.3 years (based on dendrochronology, n=6, range=7; Mader *pers. comm.*), which means that they escaped the fire trap in the early 1970's. Prior to this, from 1962 to 1970 there was a drought (Figure 6), which probably resulted in most of the adult trees dying. The drought probably also reduced the grass cover, and fire intensity and frequency was reduced. When the drought ended, grasses probably took a few years to recover fully, but by this time the established seedling could have escaped the fire trap, thus allowing the current adults to come through as a cohort. Thus, what may appear as sudden bush encroachment may be due to a singular

event, although the effect may be exacerbated by a decrease in fires due to landscape fragmentation by roads and fire-breaks, or a decrease of mega-herbivores. Longer-term observations are needed to establish whether bush encroachment is actually increasing, or whether is forms part of the inter-decadal and inter-centenary cycles that are prevalent in savannas.

In contrast to *A.nilotica*, indications are that *A.tortilis* is seed-to-seedling limited, with this bottleneck being a function of water limitations in the arid savanna. However, of the three species, *A.tortilis* is least affected by the seedling-to-adult bottleneck. Thus, despite the low number of seedlings germinating and establishing, the population is maintained by the steady progression of seedlings to adults. However, a reduction in herbivore pressure may increase the rate at which seedlings escape the herbivore trap, and could result in bush encroachment, although in arid areas water will always be limiting, so bush encroachment is unlikely.

In the arid savanna, *A.nigrescens* emergence was higher than that of *A.tortilis*, but still represents a major bottleneck in the demography of *A.nigrescens*, since numbers were fairly low. It also seems to be affected to a greater extent by herbivory than *A.tortilis*, and thus the seedling-to-adult bottleneck is also limiting the number of adults. Thus it seems that this species should be less common because it has two major bottlenecks in it's demography. However, large monotypic stands (mean age=54.5 years, n=6, range=37, dendrochronology; Mader *pers. comm.*) occur in the arid savanna, indicating that adulthood can be attained regularly. However, the range in adult ages is much more than for *A.nilotica*, indicating events leading to sapling escape are sporadic and infrequent.

The most important hurdle for *A.nigrescens* seedlings is herbivory (since fire is less frequent and less intense in the arid savanna, due to lower fuel loads). However, since it has weak structural defenses as a seedling (as does *A.tortilis* with it's long spines and cage-like structure), there has to be another way of coping with herbivory. It was noted that where adult trees (conspecific or inter-specific) had been pushed over by elephants, they created a 'cage' that excluded herbivores, where *A.nigresens* seedlings were thriving (personal observation). While these patches also had high grass biomass, the likelihood of fire reaching them is very small. Thus, facilitation by

adult trees and elephants may be crucial to overcoming the seedling-to-adult bottleneck in *A.nigrescens*. However, more research is required to strengthen this argument.

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