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The prediction of woody productivity in the savanna biome, South Africa

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2012-01-20
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Table 16.1. Attributes of woody community structure relative to fire frequency.

Attribute	Height stratum	BURN FREQUENCY (Years)					
		1	2	3	4	6	Exclus.
Biomass (t/ha)	< 4.5 m	0.34 (0.11)	0.27 (0.07)	0.35 (0.08)	1.12 (0.26)	1.09 (0.45)	3.14 (0.49)
	> 4.5 m	4.67 (1.63)	4.25 (1.47)	3.22 (1.72)	1.47 (0.52)	2.89 (1.12)	10.9 (3.55)
Basal area (m^2/ha)	< 4.5 m	0.52 (0.12)	0.91 (0.17)	1.07 (0.19)	1.44 (0.20)	0.98 (0.22)	2.73 (0.36)
	> 4.5 m	0.62 (0.18)	0.57 (0.16)	0.45 (0.22)	0.25 (0.14)	0.41 (0.10)	2.82 (0.83)
Density (stems/ha)	< 4.5 m	2712 (329)	3480 (582)	3544 (567)	3883 (493)	1960 (294)	2645 (266)
	> 4.5 m	3.0 (0.79)	3.6 (0.73)	3.1 (0.81)	3.3 (0.71)	6.7 (1.29)	138.7 (53.53)
Height (cm)	< 4.5 m	77.2 (5.58)	85.2 (4.79)	83.2 (4.88)	100.3 (6.72)	92.4 (9.78)	115.0 (5.63)
Circumf. (cm)	< 4.5 m	4.04 (0.37)	4.63 (0.28)	4.85 (0.25)	5.63 (0.36)	5.97 (0.60)	8.13 (0.79)
No. stems/ plant	< 4.5 m	5.3 (0.87)	4.0 (0.62)	3.5 (0.23)	4.0 (0.31)	2.8 (0.28)	2.7 (0.22)
No. species /transect	< 4.5 m	4.9 (0.51)	5.6 (0.38)	6.8 (0.50)	6.3 (0.41)	5.0 (0.47)	6.7 (0.40)

16.4.2 Basal area

Since biomass was calculated from the basal area, the trends in basal area per fire treatment mirrored

those for biomass (Table 16.1). The fire exclusion treatment had a significantly greater basal area than any of the treatments in the low ($F=11.96$; d.f.=5; $p<0.0001$) and high ($F=8.71$; d.f. = 5; $p<0.005$) strata. Basal area increased in the low stratum with decreasing fire frequency except for the 6 year burn. The reverse applied for the high stratum where basal area increased with increasing fire frequency, except for the 6 year burn.

16.4.3 Density

There were significant differences in density of stems in both height strata; less than 4.5 m ($F=2.66$; d.f.=5; $p<0.05$) and greater than 4.5 m ($F=6.38$; d.f. = 5; $p<0.005$) (Table 16.1). In the lower stratum density increased with decreasing fire frequency until dropping off with the two lowest frequencies, i.e. the 6 year burn and fire exclusion. For larger stems there was a slight trend for increasing density with decreasing fire frequency, although not consistent. Analysis of LSDs indicated that for the larger stems the fire exclusion treatment had a significantly greater density than any of the burned treatments, between which there were no significant differences.

16.4.4 Height

There was a slight trend of increasing mean height with decreasing fire frequency that provided an overall significant result ($F=4.5$; d.f.=5; $p<0.001$) (Table 16.1). The annual burn had the shortest stems on average (77.2 ± 5.6 cm), whilst the fire exclusion had the tallest (115.0 ± 5.6 cm).

16.4.5 Number of stems/plant

The greatest number of stems per plant was evident in the annual burn treatment (Table 16.1), and the least in the fire exclusion treatment, which had almost half the stems per plant relative to those burnt annually. Overall there was a significant decrease in stems per plant with decreasing fire frequency ($F=3.72$; d.f.=5; $p<0.005$).

16.4.6 Number of species per transect

Although there were significant differences in the number of species per transect ($F=3.57$; d.f.=5; $p<0.01$) there was no clear relationship relative to fire frequency (Table 16.1). The fire exclusion treatment, 4 year, 3 year and 2 year burns had significantly more species than either the 6 year and 1 year burns which were not significantly different from one another.

16.4.7 Proportion of regenerative stems

A significantly higher proportion of regenerative stems was recorded in the annual burn treatment (31.4 $\pm$ 4.1 %) than any of the other treatments or fire exclusion ($F=5.29$; d.f.=5; $p< 0.001$). There was a marked decrease in the proportion of regenerative stems with decreasing fire frequency, except for the fire exclusion treatment, which was higher than the four and six year burn frequency (Fig 16.1).

16.4.8 Soils

There were no significant differences attributable to fire frequency for any of the soil variables except organic matter ($F=3.31$; d.f.=2; $p<0.05$) and magnesium ($F=4.15$, d.f.=2; $p<0.05$). Organic matter was highest in the fire exclusion treatment (2.2 $\pm$ 0.14 %) and least in soils from the triennial burn frequency (1.9 $\pm$ 0.15 %). Magnesium was greatest in the annually burnt soils (776 $\pm$ 91 mg/kg), and least in the triennial plots (597 $\pm$ 60 mg/kg). The fire exclusion was intermediate between these two.

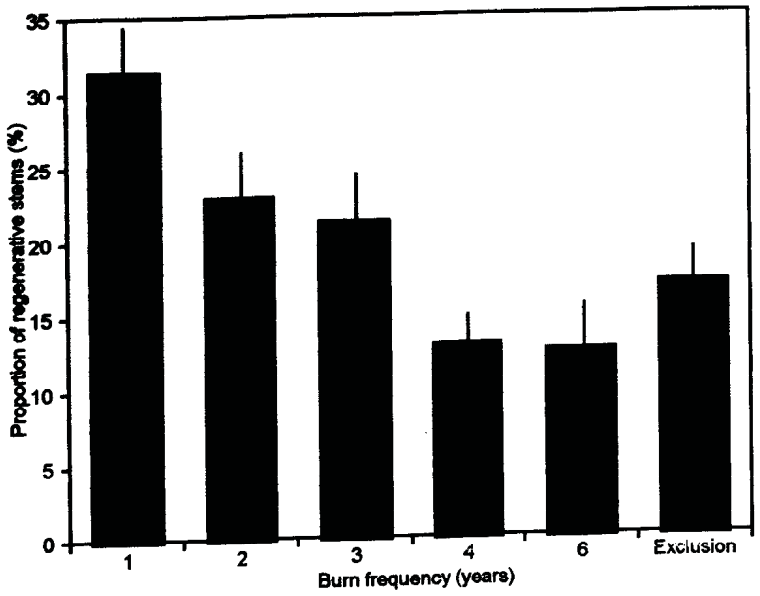

Figure 16.1. Proportion of regenerative stems across a range of fire frequencies.

16.5 DISCUSSION

Increasing fire frequency had a clear effect on several attributes of woody community structure. In general, basal area, biomass, density, height, and mean stem circumference all decreased with increasing fire frequency, and overall woodiness was highest in areas protected from fire, as found by other workers (Trapnell 1959, Spence & Angus 1971, Trollope 1982). The number of stems per plant and proportion of regenerative stems increased with increasing fire frequency. This is in agreement with other work (San Jose & Farinas 1983, Scholes & Walker 1993). Not only do the number of regenerative stems increase with fire frequency, but survival of seedlings is greater in recently burnt areas relative to unburnt sites (Khan & Tripathi 1989). However, trends in the number of stems per plant is species specific (Tchie & Gakahu 1989), and for the period immediately after the fire is related to fire intensity (Canadell *et al.* 1991). However, the effects of fire intensity with respect to the number of shoots per plant decreases in time.

Trollope (1982), summarising other studies, concluded that fire frequency had little effect on density of stems over a long period (15 years). Strang (1974) also found woody density to be unaffected by regular burning after comparison of two paired sites (fire break versus fire protected area). Results here

tend to contradict that finding. In the lower height category (< 4.5 m) density decreased with increasing fire frequency, although density of all treatments was of the same order, except for the 6 year burn frequency. In the taller height category (> 4.5 m) the density of stems was approximately 40 times greater in the exclusion plots than the fire treatments. Conversion of these data through to plant basal area or biomass multiplies this difference considerably because of the greater role of large trees in ecosystem processes. Additionally, although the density of stems in the different treatments was of the same order of magnitude, the size of stems (circumference and height) in the fire exclusion plots was significantly larger. Thus, perhaps density of stems is an inadequate index of fire impact, and 15 years is too short a period to contrast fire treatments.

Increasing fire frequency results in a conversion of woody communities to ones dominated by thinner and shorter stems, at the same or higher densities (this study) or lower densities (Strang 1974). If stem densities do not decrease, or only marginally, it can be anticipated that relative woody productivity will increase with increasing fire intensity because small stems are characterised by higher growth rates. Net production per unit area will be lowered because of the greatly reduced total woody biomass. Additionally, this study indicated an increasing biomass of large stems with increasing fire frequency, other than the exclusion treatment. This suggests that those few trees that succeed in growing sufficiently tall to be relatively immune to fire, benefit from reduced competition from the reduced understory layers.

Investigations of the effect of fire frequency on soil chemistry have yielded variable results (Scholes & Walker 1993). This study found little effect except for organic matter and magnesium. Organic matter was not significantly different between differing fire frequencies, but was significantly higher in the exclusion treatment. The absolute difference between the exclusion areas and the fire frequency with the lowest organic matter was small (0.3 %), representing a relative decrease of 14 % over more than four decades. Scholes and Walker (1993) suggested that whether or not organic matter increased or decreased under contrasting fire frequencies was dependent on fire intensity, soil type and changes in primary production resulting from the effects of fire, and required more attention to provide some predictive capacity in this regard. Magnesium was highest under annual burning, but there was no clear trend with respect to fire frequency. Previous work suggest that soil cations are rarely effected by fire frequency (Scholes & Walker 1993). The absence of differences recorded here support this conclusion. Where effects have been recorded, trends are inconsistent, depending upon vegetation type, soil type, climate and fire behaviour (Cass *et al.* 1984), and may be a result of differential ash deposition.

This study found no differences in soil nitrogen. Jones *et al.* (1990) analysed soil from one of the three sites (Nwanetsi) sampled in this study. They found a trend of decreasing total nitrogen with increasing fire frequency, but without replication were unable to determine statistical significance. Their results for organic carbon were similar to those of this study. Given that that C:N ratio of soils falls within a narrow range (Scholes & Scholes 1997) it is anomolous that the change in soil carbon was not associated with a change in total nitrogen.

PLANT LEVEL IMPACTS OF FIRE ON WOODY PRODUCTIVITY
TREE AND SEED MORTALITY AND SURVIVAL

17.1 INTRODUCTION

Fire research is relatively well-developed in southern Africa because of the controversial nature of fire as a management tool. A large proportion of the research effort has been orientated at the herbaceous layer (Schrige & Penderis 1978). Less than 20 % of published papers (up to 1983) dealing with fire in South Africa are based on work in the savanna biome (Scott 1984). Of research including the woody component, the most frequent consideration has been the role of fire in tree mortality, and the use of fire to maintain a particular balance between the woody and herbaceous components, especially with respect to bush encroachment. A broader spectrum of fire topics in African savannas , theoretical and applied, has been conducted in Zimbabwe and East Africa (e.g. Spence & Angus 1971, Kennan 1972, Strang 1974, Dublin *et al.* 1990).

Fire plays a dualistic role in plant population dynamics in that it is responsible for the death of established stems, but it also promotes vigorous coppice growth. Whether or not it influences seedling recruitment is uncertain, although there are several reports that increased temperatures increase germination of some species, although not all (Sabiiti & Wein 1987, Jeffery *et al.* 1988, Mucunguzi & Oryem-Origa 1996). Given that mortality of stems has a significant impact on community productivity (Chap. 3) the impact of fire on recruitment needs to be examined further towards the development of predictive capacity. Such a predictive knowledge must go beyond determination of the number of stems killed. It must also develop appropriate models regarding coppice regrowth. Regeneration dynamics are key to the role of fire in community productivity since (1) new shoots and recruits replace the death of other productive individuals (from a fire or otherwise), and (2) small stems have a high relative growth rate.

At a finer scale, fire alters the ratio of production between different plant organs. This is dependent upon plant size. The greater the degree of aerial dieback, the greater will be shift towards production of leaf material (Scholes & Walker 1993). The influence of fire on root production remains unknown.

17.2 OBJECTIVES

To determine (1) the role of fire as an agent of stem mortality and coppice regrowth, and (2) the influence of fire on seed germination of selected woody species.

17.3 METHODS

17.3.1 Mortality of individual stems

Between 1990 and 1993 (inclusive) the mortality of individual stems was recorded in two separate fires per year at at the semi-arid locality (Wits Rural Facility). Prior to burning, a line transect was established with a tape measure and all woody stems mapped to a set distance on either side of the tape (3 - 5 m). The length of the transect was variable, until 100 - 150 stems had been mapped. The species, height and circumference (at 35 cm) of each stem were recorded. Ten quadrats (50 cm x 50 cm) were clipped 10 m away from both sides of each transect (20 in total) to determine fuel-load. This material was air or oven dried to constant mass and weighed. Air temperature and estimated rate of spread was recorded at the time of burning. The characteristics of each fire are given in Table 17.1.

Table 17.1. Characteristics of each experimental burn.

FIRE NO.	DATE	FUEL LOAD (t/ha)	AIR TEMP. (°C)	ESTIM. RATE OF SPREAD (m/s)	ESTIM. FIRE INTENSITY (kJ/m/s)
1	06.09.90	8.2	24	1.8	2 214
2	06.09.90	5.2	28	1.2	936
3	23.09.91	7.1	26	1.6	1 704
4	12.09.91	4.9	22	0.8	588
5	06.10.92	6.4	24	1.1	1 056
6	06.10.92	6.2	27	1.6	1 488
7	12.10.93	9.1	21	1.3	1 775
8	12.10.93	3.2	24	0.7	336

Three to four months after each fire the line transect was re-established and each of the mapped stems categorised as either (1) unaffected by the fire, (2) total kill with no regrowth, (3) top kill with regrowth from the aerial portions, (4) top kill with regrowth from root buds, and (5) top kill with resprouting from both aerial and subterranean organs.

17.3.2 Seed germination

Seeds were collected from seven species common in the Mpumalanga lowveld (*Acacia swazica*, *Combretum apiculatum*, *C. hereroense*, *Dichrostachys cinerea*, *Diospyros mespiliformis*, *Euclea natalensis* and *Terminalia sericea*). Fifteen seeds of each species were placed in petri-dishes according to two treatments and a control, following the design of Zacharias *et al.* (1988) for grass seeds. For *C. apiculatum*, *C. hereroense*, and *T. sericea* the size of the attached winged fruit was reduced by rubbing several fruits together so that sufficient seeds could be put in the petri-dish. This removed most of the wings, but the hard protective centre remained.

For the 'surface' treatment the petri-dish was filled with soil until level with the sides of the dish. The seeds were then placed on top of the soil in the petri-dish. Twelve replicate petri-dishes, for each of three separate fires (therefore 36 replicates per species), were then placed in a randomised grid in the field. The surface of the petri-dish was flush with the surface of the soil *in situ*. For the 'buried' treatment a 2 - 3 mm layer of soil was put in the bottom of each petri-dish, followed by fifteen seeds per species, followed by more soil to fill the petri-dish as described for the 'surface' treatment. Each petri-dish was then placed in the field so that the depth of the seeds under the soil surface was approximately 1.0 - 1.5 cm. This treatment was also replicated in terms of petri-dishes (12 per species) and fires (3). The control dishes were set up in the same manner, for buried and surface seeds, but were not subjected to fire. A shortage of seeds reduced the number of replicates for the control for three of the species, with a minimum number of seven.

The fire treatments were applied on 15 September 1995. There was a difference in ambient temperatures and fuel loads for each of the fires. Fire 1 was a medium to hot head fire (air temperature was $\pm$ 18°C; fuel load = 5.2 t/ha). Fire 2 was a patchy head fire (air temperature $\pm$ 21°C; fuel load = 3.1 t/ha). Fire 3 was a hot head fire (air temperature $\pm$ 27°C; fuel load = 4.6 t/ha).

All the petri-dishes were recovered the day following burning, and transported to a nursery for

monitoring of germination. Seeds of the surface treatment were covered with a light layer of sand. All dishes were covered with 70 % shade-cloth and watered liberally to ensure that inadequate moisture was not a factor limiting germination. The number of germinated seeds per dish was recorded every 4-6 days for a period of 56 days. Some rodent predation occurred in the field the night following the burn, and from the nursery. Seed numbers per dish were adjusted accordingly in calculation of percentages.

During recovery of dishes the morning after burning, it was evident that some seeds had been completely ashed during the course of the fire. Consequently, at the end of the monitoring period the soil in each petri-dish was sieved to remove any ungerminated seeds. If the summation of the number of germinated and ungerminated seeds was less than number for the dish it was assumed that the difference was due to complete ashing of those seeds during the fire.

All data were tested for normality and appropriate transformations made where necessary. Basic analysis was via ANOVA with subsequent analysis of residuals. For significant ANOVAs treatment means were compared further using the Least Significant Difference (LSD).

17.4 RESULTS

17.4.1 Mortality of individual stems

Most stems survived burning, largely through regrowth after death of the aboveground organs of the plant. The proportion of stems killed during a fire ranged from 1.7 % to over 12 %, but was relatively consistent across the eight experimental fires (Table 17.2).

There was a strong positive relationship between fuel-load and mortality of stems during a fire

% mortality = 0.992 (fuel-load) (t/ha) (r^2=0.83; p< 0.001; n = 8)) (Fig. 17.1).

Table 17.2. Fate of marked stems after eight experimental burns.

FIRE	% OF STEMS				
	Unaffected	Coppice growth from stems	Coppice growth from roots	Coppice growth from stems & roots	Killed
1	22.9	10.5	52.4	6.7	7.6
2	18.3	12.7	54.0	10.3	4.8
3	30.1	4.1	58.5	3.3	4.1
4	19.3	9.3	46.7	17.3	7.3
5	13.8	44.0	30.3	3.7	8.3
6	1.3	9.2	67.3	9.8	12.4
7	41.7	7.4	41.7	3.7	5.6
8	37.0	11.8	45.4	4.2	1.7
MEAN (± SE)	23.0 (4.60)	13.6 (4.45)	49.5 (3.97)	7.4 (1.73)	6.5 (1.14)

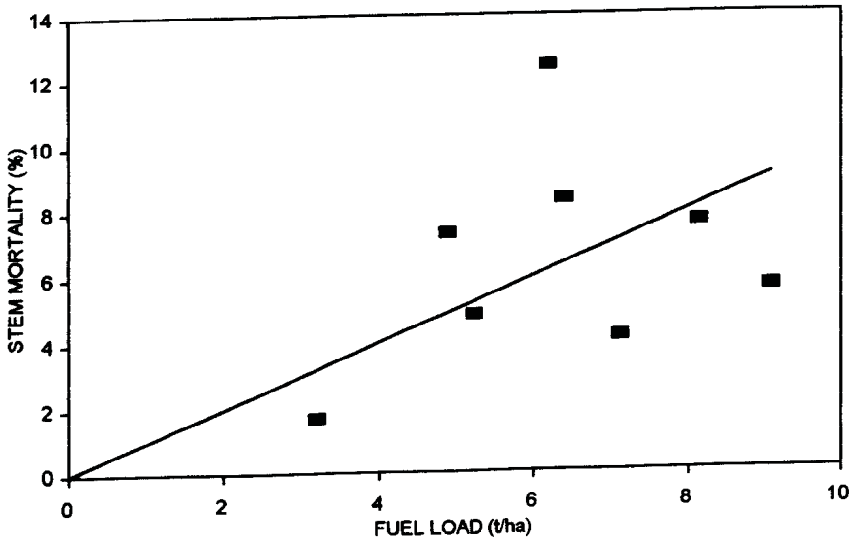

Figure 17.1. Woody stem mortality relative to fuel-load.

Mortality was significantly greater amongst stems in the smallest size classes (S=0.25; $p<0.001$). In general, stem circumference had an important bearing on the fate of a stem during burning (Fig. 17.2).

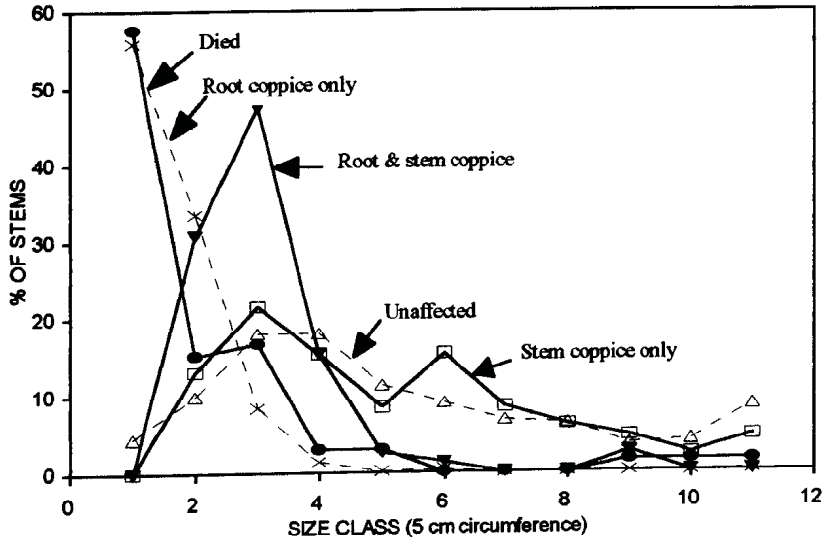

Figure 17.2. Fate of woody stems after burning.

Mortality was greatest for the smallest stems and tailed-off rapidly with increasing size class, but was evident at low levels even for the largest size-classes. Above 30 cm circumference mortality was very low. The same pattern applied with respect to stems resprouting via root coppice. This strategy was largely confined to the smaller size classes. Resprouting from both root and shoot buds was characteristic of stems in the small and intermediate size classes, with the distribution curve being shifted to the right relative to the previous two. Coppicing from the aerial portions alone was evident for nearly all the size classes, but peaked at intermediate size classes. Similarly, there were some stems in each size class that were unaffected by burning, but were generally the intermediate and large size class, with the distribution curve to the right of all the others.

17.4.2 Seed germination

The effect of fire on seed germination differed between species, and whether they were buried or on the surface (Table 17.3). Two of the seven species (*E. natalensis* and *C. hereroense*) failed to germinate

Table 17.3. Influence of burning on percentage seed germination (± SE) of surface and buried seeds.

SPECIES	RESULT	SURFACE SEEDS		BURIED SEEDS	
		BURNT	CONTROL	BURNT	CONTROL
Acacia swazica	Germinated	96.2 (2.0)	34.0 (1.1)	11.6 (1.6)	4.9 (5.0)
	Ungerm.	0	66.0 (2.2)	88.4 (3.7)	95.1 (5.7)
	Ashed	3.8 (0.2)	-	0	-
Combretum apiculatum	Germinated	3.0 (1.2)	73.3 (5.2)	68.7 (2.5)	66.3 (8.7)
	Ungerm.	58.7 (4.0)	26.7 (4.3)	31.3 (2.6)	33.7 (5.5)
	Ashed	38.3 (3.5)	-	0	-
Combretum hereroense	Germinated	0	0	0.3 (0.3)	0
	Ungerm.	78.9 (4.8)	100.0	98.6 (1.4)	100.0
	Ashed	21.1 (2.3)	-	1.1 (0.2)	-
Dichrostachys cinerea	Germinated	6.6 (5.0)	100.0	12.7 (3.6)	18.9 (13.9)
	Ungerm.	93.4 (27.9)	0	87.3 (10.8)	81.1 (34.3)
	Ashed	0	-	0	-
Diospyros mespiliformis	Germinated	1.4 (1.1)	21.9 (10.7)	76.2 (6.8)	59.2 (12.3)
	Ungerm.	98.4 (14.5)	78.1 (18.5)	23.8 (3.3)	40.8 (8.0)
	Ashed	0	-	0	-
Euclea natalensis	Germinated	0	0	0	0
	Ungerm.	100.0	100.0	89.1 (8.0)	100.0
	Ashed	0	-	10.9 (0.7)	-
Terminalia sericea	Germinated	0	13.5 (3.2)	19.2 (3.2)	22.7 (4.5)
	Ungerm.	95.9 (5.4)	86.5 (10.2)	79.9 (4.1)	77.3 (5.4)
	Ashed	4.1 (0.5)	-	0.9 (0.3)	-

irrespective of treatment. Of the remaining five species, burning significantly reduced the percentage germination of seeds on the soil surface in all species except *A. swazica*, where the opposite occurred. With respect to buried seeds, burning increased germination in two species (*A. swazica* and *D. mespiliformis*), decreased it in one (*D. cinerea*), and had no effect on two others (*C. apiculatum* and *T. sericea*).

In the burn treatments germination was always greater for buried seeds than surface seeds, except for *A. swazica*. The same applied for the controls, except for no difference for *C. apiculatum* and *D. cinerea*.

For *C. apiculatum* and *C. hereroense* more than 20 % of the seeds were ashed by fire. Ashing was significantly greater amongst surface seeds than buried seeds in all species, except for *E. natalensis*.

17.5 DISCUSSION

17.5.1 Mortality of individual stems

Mortality of stems in a fire is directly related to the fire intensity and stem size (Trollope & Tainton 1986, Tchie & Gakahu 1989, Glitzenstein *et al.* 1995). Greater fire intensities result in a higher mortality of stems of a given size. Smaller stems are affected the most, and larger stems the least for a given fire intensity. Trollope and Tainton (1986) indicated that few stems taller than 2 m were killed during a fire, irrespective of fire intensity. Tchie & Gakahu (1986) indicated that the percentage mortality relative to plant height was species specific. Generally, for a given fire intensity, mortality will be greatest amongst the smallest stems. Those small stems that are not killed, experience extreme disturbance manifest as the death of the aerial portions of the plant. Regrowth is from root buds. Slightly larger stems also lose leaves and active buds during a fire, but the aerial organs retain their capacity to regenerate. Thus, sprouting is from root and stem or branch buds. Larger stems still experience less aerial bud mortality, but not as severe, which results in coppicing from the above-ground organs. The largest stems are relatively unaffected with little loss of biomass, and hence no compensatory resprouting response is triggered. The finding of Scholes and Walker (1983), summarising other work, that fire

induced mortality was generally less than 5 % of all stems, and was most pronounced for the smallest size-classes, is in general agreement with the results of this study, where mean mortality was 6.5 ± 1.1 % throughout, and was size dependent.

In terms of productivity, the loss of individual stems and plants is at least partially compensated by vigorous coppicing of remaining plants in the immediate post-fire period. Coppice shoots have a high productivity typical of smaller stems (Chap. 3), although leaf biomass is usually reduced relative to the pre-fire situation (Scholes & Walker 1993). However, frequent burning reduces total density of large and small stems (Chap. 16) to level where overall community production is diminished, although relative productivity may be high.

17.5.2 Seed germination

The effect of fire on seed germination differed between species, and between seed location, in or on the soil. Fire intensity also plays a role and is largely responsible for inconsistencies between species and depth effects (Hodgkinson & Oxley 1990, Mucunguzi & Oryem-Origa 1996), as found in this study.

Generally, burning decreased the percentage of surface seeds germinating, in common with the findings of Mucunguzi & Oryem-Origa (1996). This is also the case with herbaceous species Zacharias *et al.* (1988). The exception was *A. swazica*. This species was also anomalous in another respect, in that seed germination was lower for buried seeds, burnt or unburnt, than for surface seeds. These two features may be related to its being a relatively small, and invasive species.

Fire effects on buried seed were inconsistent; germination of some species increased, whilst other species remained unaffected, or experienced a decrease in germination. This is possibly related to the magnitude of temperature change at depth (Portlock *et al.* 1990). Thus, deeper seeds experience lower peak temperatures than seeds closer to or on the soil surface. However, given that in this experiment all the seeds were buried at the same depth, differences between species cannot be attributed to depth effects, and may simply be a reflection of the inherent species differences to heat tolerance (Jeffery *et al.* 1988, Mucunguzi & Oryem-Origa 1996). This, coupled with the importance of depth results in a poor predictability for fire effects on buried seed.

The proportion of seeds ashed during a fire may have a significant impact on the size of the seed bank, and consequent recruitment following a fire. Up to one-third of surface seeds of *C. apiculatum* were destroyed during burning. Mucunguzi & Oryem-Origa (1996) report charring of *Acacia sieberiana* seeds on the soil surface at a range of fire intensities, and a consequent reduction in germination. In the same experiment, no seeds of *A. gerrardii* placed on the soil surface germinated since the seed coat and embryos were destroyed. Clearly, burial of seeds serves to reduce the negative impact of fires, as well as predation (e.g. Miller 1994)

The proportion of seeds ashed is possibly related to the size of the fruit structure around the seed. Of the species investigated, the largest fruit structures are found in *C. apiculatum*, *C. hereroense* and *T. sericea* (in order of decreasing fruit size). Seeds of the remaining species had been extracted from their fruiting structure. The proportion of seeds ashed followed the same order. Thus, in effect, it appears that the fruit structure provides a concentration of fuel load around the seed, and also prevents them from being buried.

At the micro-scale, fire results in mortality of individual seeds, stems and plants. The magnitude of mortality is dependent upon a multitude of factors including fire intensity, post-fire soil moisture, fruit size, stem size, and species involved. On the other hand, surviving seeds may be stimulated to germinate after a fire (e.g. Sabiiti & Wein 1987), and plants produce a multitude of shoots to replace those lost or damaged through fire. The gaps created by total mortality of individual plants are prime sites for colonisation by a new cohort of the same or competing species.

The net result of the interplay between increased mortality after a fire, and subsequent compensatory responses, is dependent upon localised fire frequency. If fires are relatively infrequent, then community structure and productivity will be little affected. With increasing fire frequency, compensatory responses become overshadowed by the increased mortality at all scales, and community structure and woody plant productivity decline (Chap. 16).

SUMMARY AND SYNTHESIS

Savannas are considered to have the third highest primary productivity per unit area of all terrestrial biomes. The contribution of woody plants to the total savanna primary production is variable, but can be up to 70 %. Above this level, the savanna would be classified as a woodland or dry forest. Herbaceous productivity, which is relatively well studied in savannas, is primarily determined by soil moisture, soil nutrients and the degree of woody cover, modified by fire, herbivory and humans (Scholes & Walker 1993). In contrast, woody productivity has been studied relatively little. It has been variously hypothesised or implied that the interplay between soil moisture, soil nutrients and competition are the primary determinants of woody productivity at any site, modulated by fire, herbivory and human impact (Frost *et al.* 1986, Skarpe 1992, Teague & Smit 1992, Scholes & Walker 1993).

This study has attempted to address some of the major gaps in current knowledge on woody productivity in South African and world savannas. In particular, it focused on providing empirical measurements of woody productivity from a large range of sites. These sites have been mapped, and it is feasible that annual data collection could continue for many more years, enhancing the existing data set on aboveground stand and individual species productivity. Overall, this study set four objectives (Sect 1.7.2):

1. To determine aboveground woody productivity across a range of environments within the South African savanna biome.
2. To seek relationships between woody productivity and structural and site characteristics.
3. To determine the productivity of the different components of aboveground woody biomass.
4. To explore the effects of management practices on woody plant productivity.

This chapter aims to summarise and synthesise the main findings in answer to these objectives.

18.1 WOODY PRODUCTIVITY

This study has shown that from 1992/93 to 1994/95 the mean woody plant basal area increment in 51 plots distributed throughout the South African savanna biome was relatively consistent, ranging from 0.20 ±

0.052 m^2/ha to 0.29 $\pm$ 0.034 m^2/ha. In 1995/96, a particularly wet year, it was 0.65 $\pm$ 0.051 m^2/ha (Chap. 3). The mean for all four years was 0.35 $\pm$ 0.028 m^2/ha. Given the wide range in site characteristics in the sample, there was a high degree of variance around these mean values, and several sites had negative changes in basal area for a given year, even after correction for stem death. The basal area increment equated to an annual biomass change of 0.66 - 0.97 t/ha for the first three years and 2.19 t/ha for 1995/96. Densitometry analysis failed as a tool to determine annual growth rates over a longer duration through analysis of growth rings (Chap. 4), mainly because (1) on many traces it was impossible to define distinct growth events, and (2) it was not possible to establish a correlation between ring width and the annual basal area increment of individual stems measured in each of the three years prior to felling of the stem.

There was a high degree of variance around the relative increase in stand basal area (expressed as a percentage). The mean relative increase in stand basal area ranged from 2.0 $\pm$ 0.5 % to 6.9 $\pm$ 2.9 % during the four years of study at 51 sites (Chap. 3). On an individual site basis, basal area increment ranged from -1.7 % to 15.4 % (corrected for death). On an individual stem basis the range was greater, from -35 % to greater than 140 %. These values are comparable to relative increments measured in other vegetation types, such a dry and moist forests. This large variance and range about the mean (reflecting the large degree of heterogeneity in savanna systems) demands that future extrapolations and models use the regression equations for growth, rather than the mean values reported here. Modelling woody plant production for specific areas of the biome should include MAR and stand basal area as minimum input variables.

The values of mean annual increment from this study will be slight underestimates for several reasons. (1) Stems less than 75 cm tall were not included. However, although smaller stems demonstrate higher growth rates, their contribution to the total basal area is low, and therefore so too is their effect on the plot growth rate, unless it is an atypically shrubby plot. (2) Recruitment of new stems were not included. The values reported represent growth of existing stems. The omission of new recruits should not be too significant for the few seasons immediately after establishment of a permanent plot because their overall contribution to the basal area is negligible while they are small. The impact of their omission will increase with time. (3) Most of the 51 study sites experienced below average rainfall for the first three years of the study.

Given the variability in woody productivity in response to site and structural attributes, mean values are of little value except for large spatial areas, such as at the biome level. Since most components of woody production were related to stand woodiness (basal area, density or biomass), it is possible to provide some

summary figures as a guideline for management at smaller spatial scales. Specific regression equations are provided in the relevant chapters of this thesis (wood - Chap. 3; deadwood - Chap. 10; litter - Chap 11; fruit - Chap. 12). The higher the rainfall at a site with a given biomass, the greater will be the woody productivity. The moist sites fall within the higher end of the range provided here, and drier sites towards the lower end of the range (Table 18.1). The values are applicable to relatively undisturbed stands in protected areas, characterised by a range of species and size classes per site. Given that woody plant productivity is a function of stand basal area, and individual stem size (Chap. 3), it is expected that any management actions that alter these to any significant degree (such as bush clearing, or intensive fuelwood harvesting) will have an effect on the relative and absolute woody productivity. The nature and degree of change would be dependent upon the degree of alteration of the stand basal area and size class profile. For example, a stand dominated by coppice regrowth will have an increased relative productivity because of the dominance by small stems, but a lowered absolute increment because of the lowered basal area. Expressing productivity as a function of stand woodiness (basal area or biomass) allows the values derived in this study to be applied across the full range of savanna environments and management situations after determination of stand basal area or biomass.

Table 18.1. Mean production per tree component per year.

COMPONENT	PRODUCTION (kg/t biomass/ha/yr)	% OF TOTAL ABOVE-GROUND BIOMASS
Wood	20 - 60	2.0 - 6.0
Deadwood	16 - 18	1.6 - 1.8
Litter	60 - 120	6.0 - 12.0
Fruit	14 - 20	1.4 - 2.0

18.2 WOODY PRODUCTIVITY AND ENVIRONMENTAL CORRELATES

This study has shown that there is a considerable range in productivity of each of the components of woody production, namely wood, leaves, and fruits. The ratios between these are not constant (Chap. 9); thus,

determination of one does not necessarily allow estimation of the other. Basal area increment, as an index of aboveground woody productivity, was found to be correlated with several variables, including current seasons's rainfall, soil texture, soil nutrients, stand basal area and mortality rates. Individual stem productivity is largely a function of stem size.

18.2.1 Rainfall

Stand structure and growth were strongly influenced by plant available water as indexed by rainfall. Stand basal area and biomass were positively related to MAR, but density was not (Chap.3). Similar results were found by Frost (1996) for miombo woodlands. The proportional size class profile changed in favour of smaller stems at higher rainfall, whereas the proportion of spinescent species declines (Chap. 2). Although there is a greater proportion of small stems at moist sites, the overall biomass per unit area was greater because the large trees are bigger than at arid sites, with the mean canopy height being 20 - 60 % taller.

There was a linear relationship between absolute basal area increment and rainfall (either rainfall or the negative deviation from MAR, in the season immediately prior to measurement) for two of the three years analysed. The relative growth rate for individual years was significantly related to variables associated with rainfall and soil type, but the same did not apply with respect to mean relative growth rate over the three year period (Chap. 3).

The relationship between MAR and mean relative basal area increment indicates that stand productivity begins to level off at intermediate MAR, from approximately 600 - 700 mm p.a. (Chap. 3), and even decreases at higher MAR (Chap. 3). The tapering of the slope at high rainfall at a level greater than that at low rainfall suggests that growth at high rainfall is limited by a different factor to that which limits growth at low rainfall. I propose that limited moisture is the key factor at low MAR, and either limited nutrients (because of leaching) and/or increased competition (because of higher basal areas) is responsible for reduced relative growth at high MAR. It is noteworthy, that the intermediate range of MAR is also that at which least mortality was suggested (Chap. 3). Additionally, measured growth in a fertiliser experiment (Chap. 5), and litterfall per unit biomass, were highest at the site of intermediate MAR relative to the arid and mesic sites.

Seedling recruitment and survival during 1995/96 were less than in 1994/95 (Chap. 8). This was unanticipated, since all but one site experienced better rainfall during 1995/96 than 1994/95. Nevertheless, in absolute numbers, recruitment was still greater than mortality of seedlings and mature stems, leading to a net increase in the density of seedlings. Recruitment and survival during 1994/95 were a function of rainfall, but no relationship was evident for 1995/96. Herbaceous layer cover and vigour probably play a role, which requires further experimentation to be elucidated (see Chap. 8).

Increasing aridity resulted in a concentration of phenological activity into a shorter period (Chap. 7), parallelling the findings of Hoffman (1989) for karroid scrub. This is possibly a response to a greater carryover of soil-moisture between wet seasons in higher rainfall regions than occurs at more arid sites (Scholes & Walker 1993). Generally, the moist locality demonstrated earlier leaf expansion than the semi-arid or arid localities. Emergent and mature leaves were recorded earlier, and in the case of mature leaves, retained longer. Overall there was a lower proportion of leafless trees during winter at the moist locality, followed by the semi-arid, and then the arid localities. The finding with respect to the earlier onset and longer duration of mature leaves at the moist locality is particularly pertinent in that it suggests that the often greater productivity of sites in higher rainfall areas may relate to the longer growing season, rather than the greater rainfall *per se*, as commented by Murphy & Lugo (1986).

Although the amount of litterfall was strongly related to stand biomass, irrespective of rainfall, the greatest litter production per unit standing biomass was at intermediate rainfall (Chap. 11). Collins (1977) found a strong positive linear correlation between rainfall and absolute litterfall, but did not assess production relative to stand basal area or biomass. Madge (1965) failed to detect any relationship with total annual rainfall, and Whigham *et al.* (1990) reported a significant decrease in leaf-fall with increasing rainfall over several years at a single site. In light of these contradictory findings between studies, it is probable that seasonal distribution of the rainfall may be a critical factor in determining the strength of any relationship between litterfall and mean annual rainfall (Collins 1977). The greater litterfall per unit biomass at the intermediate locality parallels the greater relative basal area increment recorded at these sites (Chap. 3). The lower litterfall per unit biomass at the mesic site could be a reflection of the lower amount of total annual production that is assigned to leaves, relative to wood, because of the larger mean tree size at the mesic site (Chap. 9). The increasing seasonality of litterfall with increasing aridity has been recorded previously (Collins 1977), as has been the early onset of the peak period of litterfall following a rainy season with less than normal rainfall (Whigham *et al.* 1990).

Rainfall had a strong impact on fruit production (Chap. 12). For a given species, the tree size at which fruiting first begins is larger for arid than moist sites, as was the size at which 100 % frequency was attained. Total production of fruit per unit area also increased with increasing aridity. This requires further study, and given the above, it may simply be a reflection of the greater densities of large trees per unit area at the arid locality under study.

Production of deadwood (stems and branches) was independent of rainfall (Chap. 10), corroborating the finding that stem mortality in the biome plots was not a function of rainfall (Chap. 3).

18.2.2 Edaphic factors

Soil nutrients were not identified as important predictors of woody productivity during this study from the 51 sites around the savanna biome (Chap. 3). Nevertheless, direct empirical investigation through the addition of fertiliser induced a significant increase in woody plant growth rate, whereas the addition of extra water did not, albeit the magnitude of the additions relative to background levels was greater for fertiliser than for water (Chap. 5). If production was not nutrient limited, fertiliser addition would not have produced a significant increase in growth, irrespective of the amount of fertiliser added. There was no interaction between these two experimental treatments, indicating that the growth enhancement resulting from fertiliser addition was independent of the need for additional water, i.e. rainfall alone was adequate for manifestation of the fertiliser effects. Thus, it seems that production is nutrient limited, but requires adequate moisture as the switch, as argued by Scholes & Walker (1993). It is not possible to conclude from this study whether the proximate cause of the relationship between soil texture and basal area increment (Chap. 3) is soil moisture or soil nutrient status, since soil texture is related to both. There was no consistent difference in annual or mean growth for the paired productivity plots on toplands relative to bottomlands. Woody plant abundance, as indexed by basal area, density and biomass, were not related to any of the soil nutrient variables.

Analysis of clayey and sandy sites separately highlighted different variables as influencing annual increment (Chap. 3). Absolute basal area increment at clay sites was generally a function of the woody plant basal area of the site. In contrast, stand basal area was not a significant variable related to basal area increment for sandy sites, except in 1994/95, but even then only as a secondary variable. On these sites

moisture regime appeared to be the key variable influencing growth.

Soil type was interactive with the degree of competition in influencing growth (see below), sites with a high competition index tended to be more clayey than those with a low competition index, but not exclusively so.

Bottomlands had a greater proportion of trees with leaves during winter, and a lower proportion of trees recorded with senescent leaves, relative to toplands (Chap. 7). Both of these are a result of the greater proportion of evergreen species in bottomlands, as well as increased leaf retention by the deciduous species. Murphy & Lugo (1986) concluded that soil type was an important determinant of the degree of evergreenness of a community, whereas Pierce and Cowling (1984) concluded that soil type had no influence on species phenology for fynbos species occurring across several soil types. However, the contrast of catenal position here does not relate solely to contrasting soil texture and nutrients, but also to soil water status. Bottomlands have a greater soil moisture status but reduced availability due to their higher clay content. At low rainfall regimes, available soil-moisture is greater in sands than clays during the limiting periods, i.e. at the start and cessation of the rainy season, which are key transitional periods for woody phenology.

The only difference in the amount and timing of litterfall between toplands and bottomlands was the shorter duration of litterfall at toplands (Chap. 11). This phenomenon also occurs with increasing aridity, parallelling the findings on community phenology (Chap. 7). John (1973) found no differences in litterfall dynamics on two different soils along a catena, one well drained and one not.

18.2.3 Competition

The tendency towards a saturating relationship between basal area increment and stand basal area suggests that plant competition is an important limiting factor in aboveground woody productivity above approximately 5 m^2/ha (lower on clays) (Chap. 3), although the asymptote of the relationship was not identifiable within the range of stand basal areas measured in this study. The nearest-neighbour analysis did not reveal a strong competitive effect (Chap. 6), with less than 25 % of broadleaved sites demonstrating evidence of inter- or intra-specific competition, and only 55 % and 18 % of *Acacia* sites indicated intra-

and inter-specific competition, respectively. However, methodological problems were identified with nearest-neighbour analysis which may mask evidence of competition (Chap. 6). Corroborating those results, no significant relationship was revealed between basal area increment and the competition index used in the stepwise regression (Chap. 3), although this was also derived from the nearest-neighbour analysis. On the other hand, a thinning study (Chap. 15) indicated that growth rates of individual trees increases after removal of neighbours. However, the growth enhancement was not in proportion to the relative increase in space, but rather the absolute space available. This suggests some limitation on growth imposed by neighbours, but a limited ability to exploit newly-opened spaces. The growth enhancement after thinning supports the negative hyperbolic relationship between stand basal area and basal area increment (Chap. 3). On the basis of the nearest-neighbour analysis, soil texture served to differentiate sites with significant inter-specific competition from those without, i.e. more intense competitive effects were manifest on more clayey sites, although the classes were not mutually exclusive. This corresponds with the finding that growth on clays is more of function of basal area of the stand (see above), whereas on sands it is more function of moisture.

The absolute production of deadwood, fruit and litter increased with increasing stand biomass or basal area. No asymptote was evident, suggesting that competition was not a key factor in limiting production of these components across the range of stand biomass measured in this study.

18.2.4 Stem mortality

On an annual basis mortality rate appeared to be independent of site characteristics, but was always greater than 3 % on a density basis, or 1.4 % of basal area. The relatively constant mortality rate in the 51 plots from around the biome (Chap. 3) is corroborated by the low interannual variation in production of deadwood from the intensive monitoring sites (Chap. 10), even though the latter included production of dead branches by otherwise healthy trees, and the biome plots did not. At a stand level, mortality is a key factor in determining aboveground woody productivity, exemplified by the observation that approximately one-third of the productivity plots experienced a net decrease in basal area over the four year period due to mortality and stem shrinkage (Chap. 3). The greater the degree of shrinkage in a given year, the greater was the probability of stem death in the subsequent year. A calculated individual stem half-life of 15 years indicates that woody communities in savannas are very dynamic systems.

There was a suggestion of a weak bimodal relationship between mean mortality and MAR, with a minor peak at 450 - 550 mm and a major peak at 680 - 880 mm, and reducing again at higher MAR. There was a trough with a cluster of sites between these two peaks. This rerquires further investigation.

The effect of constant high mortality rates is that maintenance of stand productivity requires sufficient recruitment of new stems through vegetative or seedling recruitment. Mean recruitment of seedlings was found to more than compensate for death of mature stems (Chap. 8); however, it was highly spatially variable. Thus, a small stand may conceivably experience several successive years with a net decline in basal area, until sufficient seedling recruitment occurs to replace the dead stems. During the first year of this study seedling recruitment was dependent upon adequate rainfall in the season of recruitment or the preceding season. There was no relationship with rainfall in the second year. Survival and growth were positively related to seedling height.

18.2.5 Stem size

The primary focus of this study was on aboveground productivity of a plot/stand of woody plants. However, certain components were examined at the plant level, which allows examination of the role of plant size in productivity studies. It is implicit, although untested, that a stand dominated by small stems would differ from one with a range of size class in a variety of ways pertaining to growth dynamics.

Relative growth rate decreased hyperbolically with increasing stem size (Chap. 3). For example, stems with a circumference of less than 5 cm experienced relative basal area increases of greater than 20 %, whereas stems with a circumference of greater than 100 cm increased at less than 2 % p.a.. This is countered by the significantly higher mortality of small stems. Mean mortality of stems less than 5 cm circumference was greater than 10 % p.a., with a corresponding value of approximately 1 % p.a. for stems greater than 100 cm circumference. However, larger cohorts still remain susceptible to pulsed mortality events as do smaller stems. This pattern is replicated in terms of seedling survival. Taller seedlings had a better chance of surviving to the following year than did shorter seedlings (Chap. 8).

Prolonged retention of leaves at moister sites relative to arid sites has been implicated in contributing to the higher community productivity with increasing rainfall. Previous literature suggests a similar pattern for

smaller stems relative to bigger stems, i.e. small stems retain leaves longer, and fewer are totally leafless during the winter (Milton 1987, Novellie 1989). This may also be a contributory factor in explanation of the higher growth rates of smaller stems.

Stem size is a key attribute determining the productivity of harvestable components, as well as the balance of productivity between the individual plant organs, or harvestable components (Chap. 9). No fruit is produced by small trees. This study (Chap. 12) found that fruiting commenced on some individuals of a given species once they had grown to approximately 20 % of their maximum size (in the field). All stems produced fruit once larger than 67 % of the potential maximum size for that species. For most species there was a linear transition between these two extremes, although a few species demonstrated other patterns.

The absolute ratio of leaf mass to wood mass decreased with increasing stem size, although the annual mass of leaves produced generally exceeds the annual production of wood across all but the very largest stem sizes (Chap. 9). The relative contribution of leaf production to total productivity also decreased with increasing stem size. This higher leaf to wood ratio is also a contributory factor to the increased growth rates of small stems, as it represents a higher photosynthetic area per unit of wood tissue.

Absolute and relative production of dead wood is also a function of tree size (Mudekwe 1997), more specifically, in terms of relative production, crown biomass. No harvestable deadwood is produced by stems less than 20 - 25 cm circumference.

Stem size effects the response to certain management factors such as the survival and regrowth following fire or cutting. Smaller stems are more prone to fire and have a higher mortality rate than large stems (Chap. 17). Immediately after harvesting small stems regrow faster than larger stems, and produce more coppice shoots. This initial burst of regrowth is not maintained, and larger stems eventually have more and longer regrowth shoots than smaller stems.

18.3 BROAD-LEAVED AND MICROPHYLLOUS SAVANNAS

Much of the previous literature on the structure and function of southern African savannas recognises a distinction between broad-leaved and microphyllous savannas (e.g. Huntly 1982, Frost *et al.* 1986, Scholes

and Walker 1993). Typically, broad-leaved savannas are at the more mesic end of the rainfall continuum of savannas, they occur on dystrophic soils (with exceptions), and the role of herbivory is low, whilst the role of fire is significant. On the other hand, microphyllous savannas are typically dominated by spinescent species, particularly members of the Mimosaceae, and they occur in more arid sites, and on more eutrophic soils. A greater proportion of herbaceous and woody productivity is consumed by herbivores than in broad-leaved savannas, but the role of fire is small, due to low fuel-loads.

Although not an explicit objective of this study, the findings tend to support this structural and functional division of savannas (albeit the boundaries are not discrete) largely on the basis of the effects of rainfall. Most of the sites receiving less than 650 mm per annum were microphyllous savannas, and most receiving more than 750 mm per annum were broad-leaved communities, although there were exceptions in both instances. Results in Chapter 3 indicate that absolute basal area increment is highest in high rainfall sites, which are typically broad-leaved communities, and least at arid sites, namely microphyllous communities. The effects of rainfall on community phenology (Chap. 7), litter fall (Chap. 11) and fruit production (Chap. 12) highlighted in this study also indicates differences between arid and moist sites, corresponding largely to differences between microphyllous and broad-leaved communities. The opposite applies in terms of competitive effects, where inter- and intra-specific competition was more prevalent in microphyllous communities (Chap. 6). However, in all instances, it is not a distinct dichotomy, but rather a continuum from one to the other, reflecting the large and continuous variability in savanna determinants (Chap. 1).

On the other hand, at a finer scale, there were no differences in overall productivity on contrasting soil types of toplands and bottomlands (Chap. 3), even though species composition was usually markedly different. Thus, the eutrophic - dystrophic divide between microphyllous and broad-leaved savannas, was not apparent that this scale. Phenological differences according to catenal position (Chap. 7) conformed to existing models relating to soil moisture differences resulting from contrasting soil texture.

18.4 MANAGEMENT OF WOODY PRODUCTIVITY

Standard management actions employed throughout savannas to meet site-specific objectives that impact woody productivity include fire, browsing, and clearing or thinning. Most of these effect woody

productivity through their impact on stand structure, mainly stand density and size class profile, the net result being a change in stand biomass (Chap. 13). Given previous acceptance of the role of competition in woody community dynamics, the opening up of a stand through the use of fire or clearing, should increase the growth rate of the remaining stems, although absolute stand production may be lowered if the degree of thinning is severe. The thinning study (Chap. 15) supported this understanding. However, the results of the nearest-neighbour analysis suggested that competition is not a frequent occurrence in savanna dynamics (Chap. 6). Given the methodological short-comings of nearest-neighbour analysis, greater credence is placed on the results of the thinning study, whereby competition clearly is a factor in regulating woody productivity.

Removal of biomass through fire or cutting stimulates vigorous coppice regrowth. Mortality from cutting seems negligible (Chap. 13), and possibly only occurs if there is significant browsing of regrowth material (Trollope 1974). Mortality from fire is dependent upon a number of factors; the key ones being fuel-load and stem size. Mean mortality from eight fires in this study was 6.5 % (Chap. 17), which is within the upper range of values reported in previous work. Mean mortality for stems less than 5 cm circumference was almost 58 %, and for stems 5 - 10 cm circumference it was 35 %. Mortality was less than 10 % for stems greater than 10 cm circumference. This demonstrates the significant potential fire has in restricting recruitment into larger size classes. The influence of fire on seed germination was species-specific, with most experiencing a decline in germination success after burning of seeds situated on the soil surface (Chap. 17). Up to 20 % of seeds on the soil surface were totally destroyed by fire.

The nature of regrowth from stems burnt, but not killed by fire, is also dependent upon stem size (Chap. 17). Small stems that experience a total death of the aerial organs of the plant regrow from the root stock. Somewhat larger stems regrow from the root stock as well as resprouting of apical buds under the bark of the charred stems. Stems least affected by fire regrow by means of a flush of coppice from singed stems, and not from the root stock.

The net effect of these plant-level responses to fire is an altered stand structure in areas where fire is frequent. Results from this study showed that there is a polarisation of the community profile. Comparison of areas with a fire interval of one, two, three, four or six years, indicated that the biomass of large trees per hectare increased with increasing fire frequency, but the biomass of small stems decreased, although the total density, and number of stems per plant increased (Chap. 16). The higher unit area biomass of large

stems was not due to increased density, but due to increased size per tree. Complete exclusion of fire resulted in markedly higher stand biomass, largely due to a higher density of large trees relative to areas where fire occurs at least once in six years.

In contrast to fire, the effects of thinning or cutting are generally greatest in intermediate size classes. Harvesters gathering wood for energy purposes select for particular sizes, ignoring very small and very large stems. Conservation areas practising bush thinning usually retain all stems above a certain size (determined by the manager's primary reasons for the thinning), as well as a small proportion of smaller stems to prevent a totally uniform size class profile.

The amount of regrowth from cut stems is a function of species, original stem size and cutting height - all attributes that can be relatively easily controlled by the harvester (Chap. 14). Density of coppice regrowth is species specific, being negatively related to the maximum potential height of the species; taller species have less dense coppice growth than shorter, shrubby species. Larger trees yield more coppice regrowth (number of shoots, mean shoot length and mass per stump) than smaller ones, although this may not be the situation immediately after cutting. Smaller stumps appear to initiate coppice growth sooner after cutting than do larger stumps. Increasing cutting height results in a greater number of coppice shoots per stump, and greater biomass of coppice. Whilst a relatively labour-intensive management option, pruning of coppice shoots can have a marked effect on regrowth rates of coppice. Pruning reduces the number of shoots thereby facilitating the re-establishment of apical dominance sooner than through inter shoot competition and thinning. Whether or not to prune, would depend upon local circumstances and needs that would demand an accelerated rotation period between harvests or not. Where labour is readily available coupled with a need for shorter periods between harvests, it could be a beneficial return.

In conclusion, this study has for the first time established an objective guideline for sustainable wood harvest from South African savannas. It should not exceed 3 % of preharvesting site specific biomass annually. If harvesting is limited to deadwood, a sustainable offtake of 1.7 % of preharvesting biomass is automatically achieved. Fruit production is more spatially variable, but if limited to harvesting from trees taller than 50 % of the maximum potential height of that species, would ensure that a necessary proportion of fruit enters the seed bank to allow for recruitment of new individuals.

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