TOWARDS IMPROVED LIVESTOCK PRODUCTION OFF SWEET GRASSVELD

VOLUME 1

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DECLARATION

This thesis is the result of the author's original work, unless specifically stated to the contrary in the text.

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"To obtain a constant supply of fresh grass, let us suppose that a farmer who has a large extent of pasture ground, should have it divided into fifteen or twenty divisions, nearly of equal value; and that instead of allowing his beasts to roam indiscriminately through the whole at once, he should collect the whole number of beasts that he intends to feed, into one flock, and turn them all at once, into one of these divisions; in this case, the grass being quite fresh, and of a sufficient length for a full bite, it would please their palate so much, as to induce them to eat it greedily, and fill their bellies before they thought of roaming about, and thus destroying it with their feet" (James Anderson, 1797 - a Scottish pastoralist).

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CHAPTER 1

INTRODUCTION

Rangeland deterioration in South Africa has been well documented. As early as 1775 Sparrman wrote of the spread of "renosterbos" in the veld (cited by Meredith & Rose, 1955), and Holden Bowker, who in 1828 travelled through the area that today comprises Transkei, found that the "country was rather overstocked as the grass was very much eaten down" (cited by Mitford - Barberton, 1970). More recently, this degradation has been documented by numerous authors including Acocks (1953) who assessed and anticipated changes in South Africa's vegetation, and Roux, (1983) who reviewed the current state of veld deterioration in the country as reported by other authors.

Much of the range deterioration in South Africa has taken place at the expense of semi-arid grassveld. Acocks (1953) stated that the spread of karoo at the expense of sweet grassveld was probably the most striking change in South Africa's vegetation in recent centuries.

It is difficult to assess precisely the pristine extent of grassland in South Africa. There is evidence from early nineteenth century reports cited by Meredith & Rose (1955) that much of the land to the west of the Escarpment was originally open grassveld. Added to this is the mere fact that it was possible to travel by ox wagon through the Great Karoo with sufficient certainty of finding both grazing and water for oxen (Kokot, 1950: in an investigation of evidence bearing on climatic changes in Southern Africa). Acocks (1953) estimated the extent of South African grassland as it would have been in 1400 (Figure 1.1), and indicated that the western boundary coincided with a transition in climate from tropical to temperate. It is of note that Acocks (1953) was of the opinion that much of what is today grassland to the east of the Drakensberg was originally forest or scrub forest. Despite this, historical evidence suggests that this area has been grassland at least since it has been known to Europeans: Vasco da Gama observed a multitude of fires from the sea off the east coast of South Africa in the fifteenth century (Acocks, 1953); the eastern parts of the country had been settled as far as the Great Fish river by the Xhosa, a nation of pastoralists with vast cattle herds, by 1703 (Soga, 1931), and these people fired veld on an extensive scale to provide nutritious grazing for their animals (Alberti, 1807); and Fleming (1854) reported that open grass plains were intersected by densely wooded valleys in British Kaffraria. In all probability, the pristine vegetation to the east of the Escarpment consisted of dense bush in the valleys, forest on the mountain slopes (particularly southern aspects), and for the rest the vegetation would have been open grassland or wooded savanna, with woody species kept in check by fire and utilisation by wild ungulates.

Regardless of its pristine or biotic climax condition, it is convenient for pastoral production purposes to classify potential grassland as veld, the most useful manageable form of which is grassveld or at most, open wooded savanna. For practical purposes, this can be regarded as that area of grassland that can be achieved and/or maintained by scientific management as described by Acocks (1953) (Figure 1.2). This covers some 44 220 000 ha, or 37% of South Africa.

The actual area of grassland to be found in South Africa today is considerably smaller than the potential extent quoted above (Acocks, 1953) (Figure 1.3). Acocks (1953) believed that changes in climate alone could not be held responsible for the degradation of South African vegetation, and identified mismanagement as the overriding cause. With continued mismanagement, Acocks (1953) suggested that very little grassland is likely to remain by the year 2050 (Figure 1.4).

The potential grassland illustrated in Figure 1.1 can be classified as sweet or sour according to its acceptability to livestock. Precise differentiation between these two types of grassveld is difficult because of the existence of "mixed" veld between the two. However, a rough classification of South Africa's potential grassveld (Figure 1.2), using the maps of Acocks (1953), reveals that approximately 45% of the veld is sweet, and 55% sour, mixed veld being regarded as representing varying degrees of sourness.

The sweet grassveld areas are rapidly being degraded. According to the maps of Acocks (1953), as little as 35% of the potential sweet grassveld remains in this form today, the majority having been replaced by false karoo. In addition much of the sweet grassveld that does remain is seriously degraded, and the current production considerably below its potential. In contrast, 90% of potential sour grassveld still remains in this form.

An example where deterioration of sweet grassveld is taking place is in the False Thornveld of the Eastern Cape (Acocks, 1953; veld type no.21). Danckwerts (1982*a*) developed a model to estimate the stocking rate that should be applied in the veld type in order to achieve maximised sustained livestock production accompanied by veld improvement in the case of degraded veld. According to this model, the recommended stocking rate for veld in its current condition (Score 50 by the method of Foran, Tainton and Booysen (1978) adapted for use in the veld type by Danckwerts (1981)) with a mean annual rainfall of 450 mm, is 0,13 mature livestock units (MLU) per ha (7,7 ha per MLU). The recommended stocking rate for veld in good condition (Score 80) is 0,25 MLU per ha (4 ha per MLU). In terms of the model of Danckwerts (1982), the capacity of the veld to support animals for commercial pastoralism is thus only 52% of its potential. Meanwhile the stocking rate of animals actually applied is 0,19 MLU per ha (5,4 ha per MLU) (Bradfield, 1981), or 46% higher than the recommended stocking rate. On the basis of expected trends in animal production/stocking rate models, these data suggest that farmers may be operating in the range of stocking rates where both production per ha and production per animal drop with increasing stocking rate.

It can thus be concluded that livestock production in the False Thornveld of the Eastern Cape is being considerably depressed through both: (i) grazing capacities being lower than their potential as a result of degraded veld, and (ii) stocking rates being set considerably in excess of the recommended stocking rates for maximised sustained production. The latter practice is likely to cause further veld deterioration, accompanied by a further decrease in the potential of the veld to support livestock. Similar trends are probably occurring throughout the sweet grassveld areas of South Africa. The situation could be exacerbated where grassveld has been replaced by karoo.

The current livestock production situation in the False Thornveld exists despite considerable veld research in South Africa. Pioneer investigations, including those by Scott (1948), Botha (1957) and Tidmarsh (1957) led to recommendation and application of conventional two, three and four camp systems. Subsequent publications by Acocks (1966), Pienaar (1968), Booysen (1969), Venter & Drewes (1969), Booysen, Klug & York (1974), Howell (1976) and Tainton, Booysen & Nash (1977) have highlighted the necessity for more than four camps per group of animals. Today, the principles of "controlled selective grazing" are widely advocated in sweet grassveld areas. Despite this, controversy still exists regarding the optimum stocking rate and management system that should be applied on veld, evidence of this being the recent explosion of so called "short duration grazing" systems in the Eastern Cape.

The preceding argument provides the rationale for the current investigation: ***to provide quantitatively the means towards improved livestock production off sweet grassveld.*** The study was undertaken in the False Thornveld of the Eastern Cape but the intention is that results and guidelines should be extrapolated to other sweetveld areas where applicable.

There can be many approaches towards realisation of this objective. One such approach was proposed by Aucamp (1981) (Figure 1.5). This network diagram proposes a logical direction and sequence of research in order to attain the goal of maximised sustained livestock production per unit area off veld. The network diagram is used to identify those areas where the greatest research input is required.

Relatively little information is available regarding the growth and utilisation responses of the most important sweetveld grasses (Steps 6 - 15 in Figure 1.5). Without this knowledge, veld management systems (Steps 15 - 19) are based on untested assumptions. This was also the opinion of Tidmarsh (1966) who indicated that while early work on veld in South Africa was directed primarily at establishing broad management principles, the modern trend in pasture research should be towards isolating the physiological, morphological and utilisation requirements of plants being grazed. Also, Barnes (1972) stated that while knowledge of growth patterns and defoliation effects in grasses is a prerequisite for rational use of veld, current knowledge of this subject was far from adequate. In this context, Booysen (1966) emphasised the importance of physiological research in order to utilise pasture for maximum yield within the varietal and environmental limitations of the particular situation.

In conclusion therefore, the current investigation will approach the problem of improved veld management in the False Thornveld of the Eastern Cape along the lines set out in Figure 1.5. The False Thornveld today is comprised of both woody and herbaceous plants. The herbaceous component of the vegetation is, however, potentially more productive on a sustained basis than the woody component. Moreover, management requirements of the woody component are currently being researched by Teague (in prep.). The investigation is thus confined to the herbaceous component of the vegetation. Particular emphasis will be given to the growth and utilisation requirements of veld (Steps 6 - 15 in Figure 1.5) since it is here that the greatest vacuum of information is considered to exist. In this context the first research action is to identify key grass species for management purposes (Step 6 - 7 in Figure 1.5).

CHAPTER 2

IDENTIFICATION OF KEY GRASS SPECIES

2.1 Introduction

In order to achieve the objective of improved livestock production off rangeland, it is necessary that those plants that make the greatest contribution to this production be maintained in both presence and vigour. Stoddard & Smith (1955) indicated that on most ranges, correct use of the two to four most important pasture species resulted in correct grazing for the entire range. There has, to date, been no objective assessment of the relative importance of the various grass species toward livestock production in the False Thornveld of Eastern Cape. It is thus logical that identification of the most important grass species should be the first step towards improved grassveld management in the veld type.

For practical purposes the relative importance of individual species at any particular site can be considered to be in proportion to their contribution by mass to the diets of animals. If animals grazed plants at random, then the contribution made by individual species to the diets of animals would be directly proportional to the contribution these species make to total herbage on offer. However, the fact that animals graze range plants selectively has been well documented (includes work by Tribe, 1952; Theron & Booysen, 1966; Heady, 1975; Daines, 1976; Van der Westhuizen, 1976; and Bester, 1977). In practice, two forms of selective grazing occur; species selective grazing and area selective grazing (Theron & Booysen, 1966). In the context of identifying key grass species, it is species selective grazing that is of interest. Since animals graze species selectively, the species composition of animals' diets is a function of both the acceptability of the species on offer and the availability of these species.

Acceptability in the above context is defined as the sum of those factors which operate to determine whether and to what degree items are taken by animals (Mentis, 1981). Acceptability of a grass species is thus a relative characteristic, and the preference shown for any given species will depend on the characteristics of that species and of the associated species. These characteristics include physical properties and chemical properties, both of which vary between species, but can also change within a particular species depending on its maturity. Animals themselves can also affect acceptability. Age, stage of pregnancy, general physical condition as well as type of animal affect the preference shown for species (Anon, 1962). However, a plant species that is preferred by one type of animal is generally preferred by other types of animals as well (Mentis, 1981). The characteristics of animals are thus likely to have relatively small effect on the acceptability of herbage when compared with the properties of grass, particularly when dealing with one species of animal.

In contrast, the availability of a species, as opposed to its acceptability, will be determined by the abundance of that species in the sward, its spatial distribution and the forage production of that species per unit basal area.

In view of the above arguments, in order to identify key grass species in the False Thornveld of the Eastern Cape an investigation was undertaken to determine both the acceptability (in terms of the preference exhibited by cattle) and the production of available material per unit basal area of commonly occurring grasses on two sites of contrasting condition within the veld type. The grazing animals under consideration were beef cattle since they are generally recommended as the livestock production base in sweet grassveld.

2.2 Herbaceous species preference by cattle

The preference an animal may show for a particular feed is defined as the extent to which the animal will take that feed in a larger proportion than that in which it occurs with other types of feed (Mentis, 1981). The objective of this study was to test whether:

i. cattle exhibit preference for different herbaceous species in the False Thornveld of the Eastern Cape;

ii. such preference changes with time of year;

iii. preference for species changes with a decline in overall availability of feed;

iv. changes in the abundance of different species affect the preference exhibited by cattle; and

v. cattle prefer to graze taller grass species relative to shorter species.

2.2.1 Procedure

The investigation was carried out at the Adelaide Experimental Station and on a farm situated at Kroomie, approximately 20 km east of Adelaide.

2.2.1.1 Adelaide Experimental Station

Four plots (each 4 ha in size) of reasonably uniform veld in moderate to poor condition were subjected to severe grazing by cattle during winter 1979. Each plot was grazed at a different time of the year during the subsequent season. Periods of occupation were during spring (22 to 29 October, 1979) (Plot 1); summer (8 to 15 February, 1980) (Plot 2); autumn (17 April to 25 April, 1980) (Plot 3); and winter (22 to 31 July 1980) (Plot 4). Plots were grazed by Bonsmara steers, and animal numbers were adjusted so that most of the available forage was removed by the end of periods of occupation.

A stratified wheel point survey of 500 points was conducted on each plot before grazing, and each day thereafter during periods of occupation. Species of rooted living grasses were recorded when struck. In the absence of a strike, the species of the nearest grass plant to the strike was recorded. All plants recorded were classified into utilisation classes according to the classification of Kruger & Edwards (1972): Class 4: ungrazed; Class 3: less than 50% of leaf material removed; Class 2: more than 50% leaf material removed, and Class 1: total removal of all leaf material. The relative utilisation percentage (RUP) of each species was calculated on a daily basis using the formula:

$$\mathrm{RUP} = 33{,}33\ \frac{(3 \times AT) + (2 \times BT) + (1 \times CT)}{T}$$

(Kruger & Edwards, 1972) where AT is the number of individuals of a species occuring in Class 1; BT is the number of individuals of a species occurring in Class 2; CT is the number of individuals of a species occurring in Class 3, and T is the total number of individuals of a species. The mean height of the tallest leaves of each plant encountered was also recorded.

The overall availability of forage was estimated each day during periods of occupation by means of 100 standard disc pasture meter readings. The disc meter was calibrated before and after each period of occupation by the method described by Danckwerts & Trollope (1980).

2.2.1.2 Kroomie

A 4 ha plot of veld in good condition was subjected to severe defoliation by cattle during winter 1981. The site was characterised in terms of botanical composition by means of a wheel point survey of 500 points. Strikes and nearest plant data were recorded.

Management of the plot simulated the treatment that an individual camp in a reasonably sophisticated but practicable management system would receive; and it was grazed by Bonsmara steers three times during the 1981/82 growing season (November 1981; February 1982 and June 1982). Animal numbers were set so that periods of occupation would be approximately 10 days. The first two periods of occupation occurred during the growing season, and in order to ensure rapid grass regrowth, animals were removed after reasonably lenient defoliation. The third period of occupation occurred during winter, and the sward was subjected to severe defoliation. Thirty tufts of each of the four most abundant species were marked and numbered before each period of occupation. The same tufts were returned to each day during grazing, and classified according to the utilisation classes of Kruger & Edwards (1976). The RUP of each of these species was calculated on a daily basis. The mean height of the tallest leaves of each marked plant was also recorded.

The overall forage on offer was estimated each day during periods of occupation by means of 100 standard disc pasture meter readings.

2.2.2 Results and discussion

2.2.2.1 Species composition

The species compositions of the plots at Adelaide were calculated as the mean of the percentage composition recorded each day during periods of occupation on each plot repectively. These means, their coefficients of variation (CV) and the percentage composition at Kroomie are listed in Table 2.1.

The CV of the percentage composition recorded between days at Adelaide was less than 10% for all species comprising 10% or more of the total botanical composition. The CV for species comprising from three to 10% of the total composition was less than 20% in all cases. For species comprising less than 3% of the sward, the CV between days increased considerably. At Adelaide, the six most abundant species comprised more than 90% of the total composition on all plots. Only these species (*Cymbopogon plurinodis, Digitaria eriantha, Eragrostis obtusa, Panicum stapfianum, Sporobolus fimbriatus and Themeda triandra*) were considered for preference rating since too few individuals of other species were encountered to give a reliable estimate of their utilisation. At Kroomie four species comprised more than 90% of the whole sward (*D. eriantha, Eragrostis chloromelas, S. fimbriatus and T. triandra*). The seven species identified as being the most abundant within the plots are probably also the most abundant in the veld type as a whole.

2.2.2.2 Relative utilisation percentage and overall forage availability

The RUP of the six most abundant grasses during each period of occupation at Adelaide are presented in Figure 2.1. Also shown on Figure 2.1 are the relations between overall herbage availability and time during periods of occupation. Time is expressed in animal unit grazing days per ha (GD/ha) calculated from the metabolic mass of each steer. By this means the different periods of occupation by animals of different mass can be expressed on a comparable scale.

Danckwerts (1981) suggested that forage availability during periods of occupation on sweet grassveld will diminish not linearly, but in two identifiable phases : an initial phase of rapid herbage disappearance when availability is high and intake per head constant, and a second phase where insufficient forage availability limits intake per head and herbage disappears less rapidly. During the summer, autumn and winter periods of occupation at Adelaide (Figure 2.1b, c and d) both phases were identified, and, on the basis of the proposals of Danckwerts (1982*b*), described by separate linear regressions. During the spring period, intake was restricted because insufficient herbage was available even at the beginning of the period of occupation. Accordingly, only a single linear regression was fitted to the data.

The RUP of the marked tufts of the four most abundant species during periods of occupation at Kroomie are presented in Figure 2.2. The relations between herbage availability and time during periods of occupation are also superimposed on Figure 2.2. During the first two periods of occupation (Figure 2.2a & b) the sward was leniently grazed, and no deviation from linearity was observed in the rate of herbage disappearance with time. During the third period of occupation, utilisation was more complete, and the rate of herbage disappearance apparently deviated from linearity. Here separate linear regressions were fitted to each phase of herbage disappearance (Figure 2.2c).

In terms of the definition of preference (Mentis, 1981), the species preference exhibited by animals at any time during a period of occupation will be reflected by a comparison of the mean relative utilisation by mass of the various species. Expressing utilisation as a percentage thus allows inter-species comparisons to be made. The procedure used for calculating relative utilisation was based on subjective classification of individual plants into utilisation classes. Since the objective was not to measure absolute utilisation of grasses, but rather to rate the extent to which certain species were preferred to others, the procedure was considered adequate for these purposes.

The results from both sites (Figures 2.1 & 2.2) imply that animals exhibit differential preference for species throughout periods of occupation. The question is at what points during periods of occupation should species be ranked for preference by cattle? Since animals graze preferred species first, ranking should be made before animals are forced to utilise unpalatable plants through an insufficient availability of herbage. On the basis of the proposals by Danckwerts (1981), the point in time where forage availability deviates from linearity is a logical point for ranking species. Before this point, available forage is wasted, and after this point, animals may be forced to graze normally unattractive feeds.

At Adelaide, the expected deviation from linearity did not occur on the spring grazed treatment (Figure 2.1a), but since the order of the preference exhibited by cattle remained virtually unchanged throughout that period of occupation, the preference rating was made in the middle of the grazing period. During the other three periods of occupation (Figure

2.1b, c & d) the preference rating was made when herbage disappearance with time deviated from linearity. The preference ratings of species at Adelaide are listed in Table 2.2.

At Kroomie, swards were grazed leniently during the first two periods of occupation (Figure 2.2a & b) and here preference rating was made at the end of grazing periods. During the third grazing (Figure 2.2c), preference rating was made when herbage disappearance with time deviated from linearity. The preference ratings of species at Kroomie are listed in Table 2.3.

The most preferred species at both sites was generally *T. triandra*, but the degree of preference for this species changed with time of year. At Adelaide the species was highly preferred in spring (October). However, in summer and autumn, the presence of dry flowering culms resulted in decreased preference for the species. In winter, the dry culms had largely disappeared, and *T. triandra* was once more highly preferred. At Kroomie, the first grazing took place in November when *T. triandra* was seeding profusely. *S. fimbriatus* was grazed in preference to *T. triandra* at this time. During the two following periods of occupation, most of the culms had been removed, and *T. triandra* became the most preferred species.

Sporobolus fimbriatus was generally the second most attractive species at both sites. However, *P. stapfianum* (Adelaide) and *D. eriantha* (both sites) were also highly preferred species. A further species, *Setaria neglecta* was a minor constituent at the experimental sites, but experience indicates that this species, too, is a highly preferred plant in the veld type.

At Adelaide, the least preferred species in three of the four assessments was *C. plurinodis*, probably a result of the presence of aromatic turpines in the plant. At Kroomie, the least preferred species was *E. chloromelas*. This species was avoided during winter in particular, when leaves were dry, tough and tightly rolled.

If preference for species declines with diminishing overall availability, the relative utilisation percentages of species would be expected to converge towards the ends of periods of occupation. This generally did not occur (Figure 2.1 & 2.2). The result suggests that the strategy of non selective grazing is unlikely to be successful in the veld type studied, since animals still exhibited preference between species even when forced to graze swards very severely (Figure 2.1 & 2.2c).

Themeda triandra was apparently less preferred relative to the other species at Kroomie than at Adelaide. This suggests that, other factors being equal, animals may show preference for the less abundant species in the sward.

2.2.2.3 Plant height

The mean heights of the tallest leaves of the six most abundant species at the beginning of periods of occupation at Adelaide are presented in Table 2.4, and those of the four most abundant species at Kroomie are listed in Table 2.5.

With the exception of *C. plurinodis* (Adelaide) and *E. chloromelas* (Kroomie), preference for species within a site increased with ascending mean plant height. At Adelaide *Eragrostis obtusa* was avoided, probably because of its being relatively unavailable when compared with other species. It is, however, of note that the mean heights of *S. fimbriatus* and *D. eriantha* at Kroomie were often lower than the height of *E. obtusa* at Adelaide. This resulted from the fact that the plot at Kroomie was grazed three times in the same season, while plots at Adelaide were grazed only once per year. Also, the rainfall recorded during the 1981/82 season was considerably lower than that in the 1979/80 season.

The results suggest that unless there is a chemical or physical deterrent to grazing (as is the case with *C. plurinodis* and *E. chloromelas* respectively), animals may prefer the taller species within a sward. However, the "critical" height below which animals avoid grazing plants is not absolute, but will depend on the mean height of all the grasses in the sward.

2.2.3 Summary of results

i. Cattle exhibit preference for different herbaceous species in the False Thornveld of the Eastern Cape, *T. triandra* being the most preferred species, followed by *S. fimbriatus*.

ii. The degree of preference can change with time of year, but these changes are not large.

iii. Animals continue to graze selectively even when the grazing pressure is very high.

iv. When other factors are equal, animals apparently prefer the less abundant of two species in a sward.

v. Cattle may exhibit preference for the taller species in a particular sward, provided those species have no physical or chemical deterrents to grazing.

2.3 Forage production of grass species

It has been indicated that the species composition of the diets of animals will be a function of the acceptability and availability of those species. In turn, availability will be a function of species abundance in the sward and the production of available material by the individual species. In view of this, an investigation was undertaken to establish forage production of the most common species identified in the preceding section.

2.3.1 Procedure

In addition to the procedure listed in Section 2.2, thirty randomly selected tufts of each of the most abundant species at both sites were clipped at soil level at the beginning and a further 30 at the end of each respective period of occupation. The circumference of each tuft was recorded after clipping and the yield expressed in g/cm². The species clipped at Adelaide did not include *E. obtusa*, despite this being one of the six most abundant species. This is because the extremely low shoot mass of the species made clipping difficult, and the stoloniferous habit of plants made it impossible to measure tuft area. The species clipped at Kroomie included all four of the most abundant species.

2.3.2 Results and discussion

The main effects of grazing, grass species and time of year on the dry matter yields of tufts clipped before and after each period of occupation at Adelaide were all statistically significant ($P<0,01$) (Figure 2.3). Since treatments were grazed very severely, it is logical that the main effect of grazing over all species and all times of year should have been statistically significant. Regarding the main effects of individual species, the results in Figure 2.3 represent the mean of the yield before and after grazing, and are thus confounded by the preference shown by animals during grazing. However, the mean yield of *T. triandra* was still considerably greater than that of any other species, despite *T. triandra* being the most preferred species (Figure 2.1). The results (Figure 2.3) also show that mean yield increased significantly as the growing season progressed. This resulted from increasing resting periods before each respective period of occupation. Yield during winter was not significantly different from that in autumn, probably because very little growth takes place in the veld type between the end of April and July.

Of more relevance than the significant main effects at Adelaide, is the significant interaction between the effects of grazing, grass species and time of year on herbage yield (Table 2.6). This implies that some species had significantly more material removed per unit basal area than others, and that this difference was not consistent as time of year progressed. *Themeda triandra* was grazed to a significant extent during all periods of occupation. *Panicum* *stapfianum* and *S. fimbriatus* were significantly grazed during summer, autumn and winter. During spring, the overall yields of tufts were low, and large samples of utilised tufts would have been required to show significant differences. *Cymbopogon plurinodis*, despite having the second highest overall herbage yield before grazing commenced, was not grazed to significant degree; a result of the unpalatability of the species. *Digitaria eriantha* had the lowest yield of all the clipped species, and thus it was generally not possible to show significant differences before and after grazing in this species.

The least significant difference between two differences (Table 2.6) shows that the amount of material grazed per unit basal area of *T. triandra* was significantly higher than all other species at all times of the year. *Sporobolus fimbriatus* generally had the second most material removed per unit basal area, although this difference was not significantly greater than *P. stapfianum*.

The main effects of grazing, grass species and time of year at Kroomie are presented in Figure 2.4 The overall effect of grazing was not statistically significant. This was probably a result of the fact that the plot was only lightly grazed during the first two periods of occupation in order to allow rapid sward recovery. Regarding differences between species, the main effects are again misleading as a result of yield being determind both before and after grazing. However, as at Adelaide, the mean yield of *T. triandra* was greater than that of other species (P<0,01), despite this being the most preferred species (Figure 2.2). The overall yield of herbage was more during winter (P<0,05) than during early summer, and the yield during autumn was not significantly different from either of these. The effect of time of year was not large, and this is expected since, unlike at Adelaide, the same plot was grazed at three different times within a single season.

In addition to the main effects at Kroomie, there was a significant interaction (P<0,01) between all three parameters (Table 2.7). Again, this implies that some species had more material removed per unit basal area than others, and this difference was not consistent as the growing season progressed.

The amount of material per unit basal area removed per species during the first two periods of occupation was not significant, with the exception of *T. triandra* during the early summer. This was a result of the lenient grazing during these two periods. During the third period of occupation, animals were forced to graze the sward severely, and all clipped species except *D. eriantha* had their yield significantly reduced by grazing (Table 2.7).

The tendency was for the amount of material of *T. triandra* grazed per unit basal area to be greater than for other species, although this difference was not usually significant (as shown by the least significant difference between two differences; Table 2.7).

2.3.3. Ranking of species according to productivity

Ranking of species according to the above ground yield of dry matter clipped at the beginning of periods of occupation at the different times of the year at both sites is presented in Table 2.8.

The results in Table 2.8 represent ranking according to total above-ground yield and are not necessarily related to the production of material eaten by animals. The absolute amount of each species eaten during periods of occupation is represented by the difference in above-ground yield at the beginning and end of each period of occupation, provided it is assumed that no growth took place during the grazing periods. Ranking of species according to amount eaten is presented in Table 2.9.

The ranking of species in Tables 2.8 and 2.9 is very similar, with the exception of two species, *C. plurinodis* at Adelaide and *E. chloromelas* at Kroomie. These species yielded relatively high amounts of above ground herbage, but contributed very little to the amount of forage eaten by animals. This suggests that amount eaten is proportional to above ground yield unless there is a physical (*E. chloromelas*) or chemical (*C. plurinodis*) deterrent to grazing.

2.3.4 Summary of results

i. The highest yielding species in the veld type is generally *T. triandra*.

ii. The yield of grazable forage is generally in proportion to the yield of above ground herbage unless there is a physical or chemical deterrent to grazing.

iii. The species producing the greatest amount of grazable forage per unit basal area in the False Thornveld is *T. triandra*, generally followed by *S. fimbriatus*.

2.4 Identification of key species in the False Thornveld

If the management objective is maximised livestock production off grassveld, key species should not necessarily be identified according to the absolute contribution they make to the diet of grazing animals at any particular site. This is because on degraded veld, the potentially most acceptable species may be rare, and therefore contribute little to the diet of animals. In order to facilitate improvement in veld condition, it would be necessary to regard these "rare" desirable species as key species for management purposes. Therefore, where a nucleus of desirable species exists, key species should be ranked according to the potential contribution they make to livestock production. Such ranking will be a function of the preference exhibited by animals and the availability of species only in terms of their productivity per unit basal area, and not in terms of their abundance in the sward.

The difference between forage yield before and after grazing (amount eaten) (Tables 2.6 & 2.7) is one means by which such ranking can be made, provided animals are forced to utilise swards until insufficient availability severely restricts intake per head, and regrowth during grazing periods is negligible relative to amount eaten. Under such circumstances, amount eaten is a function of both acceptability and availability per unit basal area. This is because animals in the veld type under consideration continue to graze selectively even when grazing pressures are very high (Figure 2.1 & 2.2) and restricted intake per head at the ends of periods of occupation ensures amount eaten is not merely a reflection of chance encounters between animals and plants.

Indices for ranking species according to their potential importance were thus calculated at the experimental sites from the differences in forage yield before and after grazing (Tables 2.6 & 2.7). This was done by assigning a value of 100 to the largest amount eaten per species per unit basal area during a period of occupation, and expressing remaining amounts eaten as percentages of this (Figure 2.5). Expressing this index as a percentage of the most important species during each period of occupation allows relative comparisons between grazing periods and sites to be made. At Kroomie importance indices would be meaningless for the first two periods of occcupation since animals were removed before insufficient availability restricted intake per head. During the third period of occupation, however, animals were forced to utilise the sward very severely. Consequently relative importance indices at Kroomie are calculated only for the third period of occupation.

Ranking of species according to these indices (Figure 2.5) suggests that *T. triandra* was potentially by far the most important species during all seasons at Adelaide and at least during winter at Kroomie. Potentially, the second most important species was generally *S. fimbriatus* at both sites, although *P. Stapfianum* and *S. fimbriatus* had similar importance indices during spring and summer at Adelaide.

It is of note that *D.eriantha*, generally considered to be an important species in the False Thornveld, was found to be potentially a relatively unimportant species on veld in both good and poor condition, at least within the limitations of the procedure used in the investigation.

In addition to the results in Figure 2.5, *T. triandra* and *S. fimbriatus* were identified as the species most preferred by beef cattle at Adelaide and Kroomie (Tables 2.2 & 2.3). On the basis of these results and those in Figure 2.5, *T. triandra* and *S. fimbriatus* are identified as key species in the False Thornveld of the Eastern Cape.

It is, however, conceded that a possible key species at certain sites in the veld type is *Setaria neglecta*. The species was not sufficiently abundant at the experimental sites to be evaluated, but where it does occur, it has been subjectively observed to be both highly preferred and productive.

CHAPTER 3

ONTOGENY OF UNUTILISED KEY GRASS SPECIES

3.1 Introduction

The species *T. triandra* and *S. fimbriatus* have been identified as key grasses for management purposes in the False Thornveld of the Eastern Cape (Chapter 2). Since livestock production is *inter alia* a function of plant growth, an understanding of the growth of key species is an essential prerequisite towards improved veld management. This investigation is aimed at developing an understanding of the growth of *T. triandra* and *S. fimbriatus* in the False Thornveld of the Eastern Cape, and more specifically at studying the developmental morphology (ontogeny) of the species in an unutilised situation.

Langer (1972) reviewed the general pattern of grass morphological development and indicated that grass plants consist of a number of tillers, each with its own root system. Once a new tiller reaches the stage of assimilate independence, and has a functional root system, it can act as an independent unit. The tiller is thus the ecological unit of growth in grasses (Evans, Wardlaw & Williams, 1964). It is therefore logical that a study of grass ontogeny should take place at tiller level.

It is of note that germination and seedling establishment form an integral part of grass ontogeny. These aspects are, however, excluded from the current investigation. This study deals specifically with the developmental morphology of vegetatively initiated tillers. A review of information available regarding ontogeny of veld grasses is appropriate. Aspects of particular interest are shoot apex and stem development, leaf development, root development and the development of lateral tillers.

3.1.1 Shoot apex and stem development

The shoot apex of an individual tiller is that whole region comprising the apical dome and alternating leaf primordia (Langer, 1972).

In order that regrowth can commence rapidly after defoliation, it is necessary that within the remaining stubble and crown of each plant, there should be as many as possible intact shoot apices in a condition for immediate production of new leaves. If these apices are removed at the time of defoliation, then the development of new leaves must await activation of new shoot apices from the axes of the leaves on the decapitated tillers. The timing of shoot apex elevation through internodal elongation is relevant in pasture management, since it will determine the degree of shoot apex susceptibility to defoliation at different times and at different intensities (Booysen, 1966). Such investigations on veld grasses have been conducted, chiefly in Natal and almost invariably on sourveld, and reported in a series of publications including those of Scott, 1956; Tainton & Booysen, 1963; Booysen, Tainton & Scott, 1963; Tainton, 1964; Tainton & Booysen, 1965*a* & 1965*b* and Rethman 1971. Of particular interest is the finding that the apex of *T. triandra* is elevated to a susceptible height while still in the vegetative condition and remains so for approximately six months.

Shoot apex elevation is a result of cell division and elongation in the internodes of the stem immediately below the apical dome. During the early stage of tiller development, the successive leaf primordia produced by the shoot apex remain closely spaced without being separated by identifiable internodes. Separation occurs later through cell division in the region between adjoining nodes. Initially this involves all cells, but as the internode grows, meristematic activity becomes restricted to the basal portion. Internodal elongation generally only occurs with the advent of the reproductive stage, although it can sometimes occur during the vegetative stage (Langer, 1972).

Tainton & Booysen (1965*a* & *b*) recorded nodal development of two veld grasses, *T. triandra* and *Hyparrhenia hirta*, in the Tall Grassveld of Natal. The authors found that these species produced 17 and 15 nodes respectively in an unutilised situation. In both grasses, approximately half the nodes were closely associated at the base of the stem, while the nodes produced in the later life of the tiller were separated by elongated internodes. It is of note that authors found that in the case of *T. triandra*, defoliation during the vegetative life of the tiller reduced the number of culm nodes relative to basal nodes, but had little effect on the total number of nodes produced. This had the effect of delaying shoot apex elevation.

In addition to their elevation, shoot apices undergo physiological and morphological changes from the vegetative through to the reproductive condition. Physiological changes and successful completion of morphological changes are often under strict control of the environment. The variables affecting these changes in tropical - subtropical grasses are likely to be day length, energy substrates available in the plant, light energy input and an interaction of these factors (Tainton, 1969). Elucidation of this process would require a complex investigation under a strictly controlled environment. Tainton (1964) did, however, characterise the morphological change of the shoot apex of *T. triandra* from the vegetative to the reproductive condition. In the case of spring initiated tillers this change took place during the following winter.

It is clear that shoot apex development of *T. triandra* has received considerable attention in the literature. However, no such studies have been undertaken in the False Thornveld of the Eastern Cape. The fact that the behaviour of the species in the Transvaal Highveld is different from that in the Tall Grassveld of Natal (Rethman, 1971) suggests that the results of previous workers are not likely to be of general application. Shoot apex development of *S. fimbriatus* has not been documented in the literature.

3.1.2 Leaf development

Leaves generally constitute the primary source of grazable material in grasses, and, as such, grasses (and other forage crops) are unique among agricultural plants in that the harvestable product is the photosynthetic "factory" of the plant. Despite this, grasses are extremely well adapted to defoliation, since during the vegetative stage, leaf formation continues after defoliation. This is because the meristematic zones are located close to the soil surface, and even if these are removed, they may readily be replaced by the initiation of new tillers. Leaves are formed from leaf primordia occurring alternately along the opposite flanks of the apical dome at the centre of a tiller. The process of leaf formation is repeated successively as long as the shoot apex remains vegetative (Langer, 1972).

At its inception the whole leaf primordium is meristematic, but soon cell division actively becomes confined to a meristematic zone near the base. This meristematic area becomes divided into two by a band of cells that later becomes the ligule, the upper portion of the meristem being associated with the growth of the lamina and the lower portion with the growth of the leaf sheath. Cell division and expansion cause the lamina to move up inside the sheaths of older leaves. Cell expansion in the lamina is restricted to the portion protected by the older leaf sheaths. Emergence of the lamina results in a cessation of expansion in the exposed portion accompanied by the commencement of photosynthesis and transpiration. Meristematic activity in the lamina comes to an end as soon as the ligule is differentiated, but the sheath continues to elongate until exposure of the ligule. The leaf then reaches its final size but meanwhile the next leaf moves up inside its sheath. Once leaves have reached their final size they remain active for a certain period before they die. Senescence begins at the tip of the leaf and spreads downwards (Langer, 1972).

This general pattern is similar in all grasses, and appears to be genetically controlled within species. The achievement of this genetic potential is, however, dependent on environmental conditions (Langer, 1972).

Since leaves form the bulk of the herbage grazed by animals, quantification of the developmental morphology of leaves is presumably a prerequisite for planning the proper use of swards. In particular, the timing of each defoliation used to harvest grasses should bear some relation to the rate of appearance of leaves and their longevity (Anslow, 1966). The rate of leaf primordia initiation is not necessarily the same as the rate of visible appearance of leaves (Anslow, 1966), and the number produced per tiller ranges from about five in some cereals to as many as 20 in some perennial grasses (Sharman, 1947).

The rate of leaf emergence varies markedly between species and within species between seasons (Anslow, 1966; Silsbury, 1970). Seasonal variation appears largely to reflect changing temperatures (Anslow, 1966). Age of the shoot apex, illumination and defoliation appear to have little direct effect on the rate of leaf emergence, but illumination and defoliation may influence the rate of leaf emergence indirectly through their influence on the amount of assimilated carbon (Anslow, 1966).

Apparently the rate of leaf senescence is approximately equal to the rate of leaf emergence, so that the number of living leaves on a tiller varies within relatively narrow limits (Ryle, 1964; Langer, 1972). Once leaves have senesced, they begin to decay. Thus, in an ungrazed situation, forage can be lost through leaf decay and abscission. Hunt (1964) estimated that on a cultivated ryegrass pasture, eight kg per ha per day of dry matter is lost through death and subsequent decomposition of leaves.

Little attention has been given to quantifying the leaf growth and development patterns of veld grasses in South Africa. Tainton (1964) described the process of leaf initiation in *T. triandra* without indicating the rate of this process. Tainton & Booysen (1965*a* and *b*) recorded the total number of leaves produced, leaf length and leaf mass per tiller of *T. triandra* and *H. hirta* in the Tall Grassveld of Natal. The authors found that undisturbed tillers produced 17 to 18 leaves, but that defoliation reduced this number as well as the total mass and length of leaves. Only the former species occurs in significant quantities in the False Thornveld of the Eastern Cape, and it cannot be assumed that the species will behave in a similar manner in this semi-arid situation.

3.1.3. Root development

On morphological, anatomical and physiological grounds, plants can be differentiated into root and shoot growth systems. These perform contrasting and complementary functions: the shoot photosynthesises and transpires, while the root absorbs water and minerals (Troughton, 1977).

Grasses have both seminal and adventitious root systems. Seminal roots arise from primordia present on the embryo. They comprise a small proportion of the total root system and in perennial grasses, disappear after the plant has developed a functional adventitious root system (Langer, 1972). In the context of vegetatively initiated tillers, seminal roots are thus of little interest. Adventitious roots arise from the nodes of tillers and in tufted grasses this normally occurs at, or close to, ground level (Langer, 1972).

After vegetative tiller reproduction, new tillers are dependent on parent tiller roots for moisture and minerals. As the new tillers grow, they develop their own root systems, but the stage at which they become "independent" of primary tillers is somewhat debatable. The simplistic approach of regarding tillers as independent units suggests that roots grow and senesce concurrently with the tiller that produces them. This implies that the maximum longevity of a root is somewhat less than that of a tiller (Troughton, 1977). In cultivated temperate grasses, the life span of roots has been reported to be of the order of weeks or months, rarely years (Garwood, 1967; Perkins, 1968), while other workers have indicated root longevity of a year or more (Troughton, 1977; Marshall, 1965). In a review, Troughton (1977) suggested that roots probably live longer than tillers, so that the concept of independent tillers is not strictly applicable. This implies that the ratio of root : shoot mass for a grass sward would be greater than that of individual tillers.

Marshall (1977) investigated production partitioning in seven North American grassland types, and concluded that the proportion of biomass occurring below ground was generally considerably greater than that above ground at peak standing crop (56% to 96% of total biomass). Such high proportions of below ground biomass are not usually experienced in other vegetation types.

Below ground biomass includes viable roots of both living and senescent tillers, as well as dead root material. Because of the difficulty in identifying living and dead root material, there is a lack of information on the relative proportions of the two in the soil (Marshall, 1977; Parkinson, 1977). Singh & Coleman (1977), however, estimated that at any one time, approximately 60% of the roots of shortgrass prairie in North America are functional, and that considerable mortality takes place in winter. In view of this and since tillers predecease their root systems, viable roots produced by a current population of living tillers may well comprise less than 50% of the total root biomass in the soil. In contrast, above ground phytomass is replaced relatively rapidly. Marshall (1977) estimated that the turnover rate of root biomass was 64% per annum on North American Grassland, compared with 123% in the case of above ground biomass.

Since root : shoot ratios, as measured in practice are generally a measure of what is instantaneously present (living and dead phytomass), on the basis of the above argument, they do not necessarily reflect what proportion of growth has been partitioned below ground. Ryle (1970*a*) found that 44% of assimilated carbon was partitioned below ground in annual ryegrass, but the same author (1970*b*) indicated that perennial grasses transfer relatively more assimilate below ground than annuals. Apparently translocation of carbon to roots also increases as the season and/or plant age progresses. Dahlman & Kucera (1968) found that in vigorously growing American tallgrass prairie, 50% of assimilated carbon moved to roots while in mature plants the proportion was 80%. Singh & Coleman (1977) recorded 38% and 71% assimilated carbon translocation to roots in young and old populations of tillers respectively in American shortgrass prairie. Translocation to roots will, however, vary according to stage of recovery after defoliation, as well as in response to environmental factors such as drought, temperature and light intensity.

Little research has been undertaken on root growth and development of perennial veld grasses in South Africa. What work has been conducted, has generally been directed not at the tiller level but rather at investigating all roots per unit area regardless of the number of tillers. Thus, results are likely to be confounded with the effect of previous treatments on tiller number, as opposed to describing root growth *per se*. In addition, research on roots has largely been aimed at identifying the effect of various treatments (usually different levels of utilisation and/or fertiliser) on the carbohydrate reserve status in the roots. Investigations of this nature include work by Murray & Glover, (1935); Weinmann (1940*a*, 1940*b*, 1943, 1944, 1961); Coetzee, Page & Meredith (1946); Weinmann & Reinhold (1946); Daitz (1954); Bartholomew & Booysen (1969) and Nursey (1971).

While such research is necessary, it is also desirable that the inherent morphological root growth pattern from tiller initiation to senescence be determined. This is necessary in order to avoid confusion between treatment effects on roots, and the effect of factors such as tiller age, number and morphological state on the root system.

Murray & Glover (1935) conducted a preliminary study on the root morphology of some grass species in the Transvaal Highveld. The authors divided the species into three categories: those with a surface root system; those with a deep root system; and those with deep roots as well as surface lateral roots. Most species fell into the first category, including *T. triandra* and *C. plurinodis*, although results from water utilisation studies in the False Thornveld of the Eastern Cape (Stuart-Hill, 1984*a*) suggests that *C. plurinodis* has access to deeper soil moisture than *T. triandra*. It is also of note that *Elionurus muticus*, a common South African grass species, was classified by Murray & Glover (1935) as having a deep root system. Coetzee, Page & Meredith (1946) indicated that grasses in the Transvaal Highveld were generally characterised by shallow root systems, over 50% of the mass of roots being found in the top 10cm of soil and 70% in the top 20cm. However, the authors found large variations in root distribution between species, as well as within species between soil types, soil textures and different intensities of utilisation. This work was conducted on root material per unit area and not per individual tiller.

In terms of root number per tiller, Tainton & Booysen (1965*a* and *b*) reported on research into this aspect of two grasses, *T. triandra* and *H. hirta*, in the Natal Tall Grassveld. The authors showed that the number of roots that developed at the basal nodes of primary tillers of *T. triandra* increased steadily during the growing season for two consecutive growing seasons, finally reaching an average of 5,2 roots per tiller when the tillers reached maturity. However, the authors reported difficulty in interpreting the results for *H. hirta* and stated that root development was an aspect that required further investigation before conclusions could be drawn.

No published information is available as to the root growth and development of the most important grasses in the False Thornveld of the Eastern Cape.

3.1.4 Lateral tillering

New tillers (secondary tillers) arise as axillary buds on the shoot apex of the primary tiller. New buds are thus initiated at the same rate as leaf primordia, being laid down in succession from the base upwards. Each bud is a replica of the parent structure, complete with apical meristem, leaf primordia and axillary buds. Production of tiller initials is dependent on leaf initiation and is thus largely genetically controlled. However, like leaf emergence, the development of tiller initials into active tillers is dependent on environmental factors (Langer, 1972).

The number of tillers that ultimately develop as units is also largely dependent on the prevailing utilisation regime. This was shown by Tainton, Groves & Nash (1977) who recorded higher yields of herbage on mown than burned veld in the Tall Grassveld of Natal. Since no difference in the yield of living material per tiller could be established between treatments, the authors concluded that the difference in yield per unit area must have resulted from a greater density of tillers on mown than burned veld. This was subsequently shown by Dillon (1980).

In addition to the effects of the utilisation regime it is likely that specific grasses have inherent tendencies to produce lateral tillers at certain times of the year. Booysen (1966) stressed the importance of establishing these capacities and times in order that optimal replacement of mature tillers by daughter tillers can be accommodated by management practices.

The formation of secondary tillers was studied on two veld grasses, *T. triandra* and *H. hirta*, by Tainton & Booysen (1965*a* & *b*) in the Tall Grassveld of Natal. No studies have been conducted on the tillering properties of the important grasses in the False Thornveld of Eastern Cape.

3.1.5 Conclusion

Although a certain amount of information exists regarding the ontogeny of veld grasses in South Africa, this information has invariably been collected in mixed and sourveld situations. In addition, of the key species identified in the False Thornveld of the Eastern Cape, only *T. triandra* has received attention in the literature. The fact that the behaviour of the species in the Transvaal Highveld (Rethman, 1971) is different to that in the Tall Grassveld of Natal (Booysen, Tainton & Scott, 1963; Tainton & Booysen, 1963; 1965*a*), suggests that the results of previous workers are not likely to be of general application, and particularly with regard to semi-arid sweetveld situations.

An investigation was therefore undertaken to study the developmental morphology of unutilised tillers of *S. fimbriatus* and *T. triandra* in the False Thornveld of the Eastern Cape. In view of the considerable limitation moisture places upon growth in the veld type (Stuart-Hill, 1984*a*) the investigation was undertaken both under unamended moisture conditions and where moisture stress was eliminated, thus allowing characterisation of the genetic potential of the species.

3.2 Procedure

The majority of investigations were undertaken at two field sites in the False Thornveld of the Eastern Cape, although some recordings were made in the controlled environment of the greenhouse. The two field sites consisted of an area of veld dominated by *T. triandra* situated on the University of Fort Hare Research Farm (Site A) and an area dominated by *S. fimbriatus* situated on the Adelaide Experimental Station (Site B). Site A was situated on a gentle (Slope < 5%) north western aspect on a soil of the *Glenrosa* form with an effective rooting depth of approximately 50cm. Site B was flat and situated on a soil of the *Swartland* form with an effective rooting depth in excess of 50cm. The greenhouse trial was conducted at the Dohne Research Station.

The data were collected from six separate trials. Field trials were under two moisture regimes: a control where no additional moisture was added, and an irrigated treatment where soil water was maintained between wilting point and field capacity.

3.2.1 Experiment 1

The experimental areas were mown to a height of 1cm during winter 1980, and 5 000 newly emerged tillers were marked in stratified transects on each moisture treatment and at both Sites (A and B) during the following spring. Tillers were marked with plastic coated wire rings using the procedure illustrated by Gammon (1976). This was done as soon as tillers were sufficiently developed to avoid chance dislodgement of the wire rings.

Starting on 26 September 1980, a sample of 30 tillers was haphazardly removed at soil surface (with secondary tillers, if present) approximately every 14 days from all except the non-irrigated *S. fimbriatus* treatment. On the non-irrigated *S. fimbriatus* treatment, tiller development was slower than on other treatments and the first sample of 30 tillers could be removed no earlier than 13 October. Even by this date, the tillers were still insufficiently developed to facilitate marking. Thereafter, a period of dry weather resulted in the population of tillers wilting and it was not until good rains fell at the end of November and beginning of December 1980, that tillers reached an adequate stage of development to be marked with plastic coated wire rings. Sampling of the non-irrigated *S. fimbriatus* tillers therefore recommenced on 22 December 1980. Sampling from all treatments continued until surviving tillers reached maturity. Only living or mature tillers were sampled. Tillers that had senesced prematurely were not harvested.

After harvesting, tillers were taken to the laboratory where the following characteristics were recorded:

1. Primary tiller development

1.1 Height of shoot apex
1.2 Tiller mass (whole tiller, leaf mass and stem mass)
1.3 Leaf development (leaf area, number of emergent green leaves and number of dead leaves attached to the tiller.

2. Secondary tiller development

2.1 Number per primary tiller
2.2 Height of lateral tiller bases on the stems of primary tillers.
2.3 Secondary tiller mass per primary tiller.

Leaves were classified as green if any portion of the leaf blade was subjectively assessed to be both green in colour and not permanently wilted. Leaf blades considered to be either in a permanent wilt or to have lost all chlorophyll were classified as senescent. Furthermore, since dead leaves do not abscise cleanly, but decay gradually, individual leaves were considered to be abscised if more than 50% of the leaf blade was subjectively assessed to have been lost.

Leaf area was recorded using a light interception planimeter and all masses were recorded on an oven dry basis. Leaf blades were removed from stems before recording of leaf area and drying. For practical reasons, it was not possible to measure masses and leaf areas per individual tiller. Instead, tillers were pooled before measurements were made. However, 30 tillers per treatment per fortnight were considered adequate to provide a pattern of development despite there being no estimate of error at each sampling date. Tainton & Booysen (1965*a* and *b*) considered six tillers per harvest to be adequate for plotting similar trends at this high frequency of sampling.

In this experiment and those which follow, the term "leaves" refers to leaf blades only, while "stems" refers to both the culm and leaf sheaths.

3.2.2 Experiment 2

Areas of irrigated and non-irrigated veld at each site were mown to a height of 1-2cm at the end of July 1980. Five hundred newly emerged tillers were marked in each treatment as soon as tillers were sufficiently developed. This procedure was repeated on newly mown areas at two-monthly intervals and thereafter for a period of 12 months. This resulted in a series of populations of tillers initiated at different times of the year.

Commencement of initiation of each successive population of tillers was assumed to be the date of mowing of each new area. Thirty marked tillers were removed from each population of tillers at two monthly intervals after mowing. Sampling continued until surviving tillers on each treatment reached maturity . The phenological state of tillers was recorded, and each sample of tillers was oven dried in order to record tiller mass.

3.2.3 Experiment 3

During spring 1981, fifty newly emerged tillers were permanently marked with plastic coated wire rings on both moisture treatments and at each site, following intense defoliation the previous winter. Tillers were marked in such a manner that individuals could be returned to in the same order at successive sampling dates. At approximately fortnightly intervals, until these tillers reached maturity, each newly emerged leaf on each tiller was marked with a stain containing a dye in organic solvent (typist's correcting fluid) and recorded, thus allowing the total number and date of emergence of leaves produced through the lifespan of the tiller to be calculated. Leaves were classified as they emerged and marked with dye as soon as part of the blade became visible, and not after the leaf had fully emerged. In addition, the number of green leaves attached to tillers was recorded, the height of the growing point of each tiller was estimated (by previous experience from dissected tillers in the laboratory), and premature senescence of tillers was monitored.

3.2.4 Experiment 4

During autumn 1980, 250 tufts of both *T. triandra* and *S. fimbriatus* were removed from previously wetted soil at the two respective experimental sites already described, using a specially designed auger. The auger was such that it removed a cylinder of undisturbed soil of the same diameter as greenhouse pots and approximately 15cm deep. It was thus possible to remove whole tufts with a minimum of root disturbance below tufts. After removal, tufts were planted in greenhouse pots (25cm deep), using soil from the respective experimental sites as filler, and transported to the greenhouse at Dohne Research Station. Temperature was controlled at approximately 25^0 C (day) and 15^0 C (night) although these did vary somewhat with changing weather conditions as a result of a faulty air conditioning system. In particular, day temperatures during summer were often considerably higher than 25^0 C. All pots were watered to field capacity twice per week.

As soon as plants had become well established during early spring 1980, all tufts were harvested to a height of 1cm in order to stimulate a population of new tillers. When these newly emerged tillers were sufficiently developed, approximately 15 tillers were marked in each pot using plastic coated wire rings.

Commencing on 23 September 1980 and at approximately three weekly intervals thereafter, five pots of each species were selected at random. Sods were removed with the soil from each pot and the soil carefully "washed away" from the roots. Five marked living tillers were then removed with their roots, if present, from each pot, resulting in a sample of 25 tillers of each species. These tillers were taken to the laboratory where the following characteristics were recorded:

1. Number of roots per tiller
2. Root length
3. Tiller mass (Shoot mass, root mass and whole tiller mass)

As in the field trials, it was not possible to measure masses per individual tiller, and tillers were pooled before drying.

In addition to the above procedure, the material that remained after removal of marked tillers was separated into roots and above ground material and oven dried to constant temperature on an individual pot basis.

Sampling of tufts of both species continued until the marked population of tillers reached maturity.

3.2.5 Experiment 5

After observing the growth of *T. triandra* and *S. fimbriatus* tillers in the greenhouse (Section 3.2.4), it was considered that the morphological development of these species was atypical of field conditions. In particular, favourable environmental conditions resulted in unusually rapid growth. This in turn probably resulted in a depletion of nutrients in the pots and the observed response was an elongation of roots considerably in excess of expectations from literature.

Consequently, during winter 1981, areas of veld were mown to a height of 1cm at both Sites A & B in order to stimulate a new population of tillers. As soon as newly emerged tillers were sufficiently developed, 200 tufts of *T. triandra* and *S. fimbriatus* respectively were marked with metal pegs and approximately 20 tillers on each tuft were marked by the procedure already described.

Commencing on 9 Cctober, 1981, and at approximately three weekly intervals thereafter, five tufts of each species were removed using the specially designed auger already described.

The soil was "washed" from roots, and five marked tillers were removed with their roots, if present, from each tuft. Tillers were taken to the laboratory where root length and root number were recorded. Leaves, stems and roots were separated and dried in order to record their respective masses. Sampling continued until surviving tillers of the original marked population reached maturity.

This trial was conducted only on irrigated treatments since removal of tufts without damage to roots would have been virtually impossible in the non-irrigated situation. It should also be noted that roots were removed intact only to a depth of 15cm and only within the vertical cylinder of soil removed by the auger (diameter 18cm). Roots deeper than 15cm and those that spread laterally more than 9cm from the centre of the tuft were severed, and thus the estimate of mean root length could well be an underestimate of their true length.

3.2.6 Experiment 6

The two preceding trials were designed to characterise root number, root length and root mass per individual tiller, but gave no indication of the vertical distribution of roots within the soil. Such information is of value since it would indicate the depth in the soil from which grasses extract moisture.

Thus, in order to investigate root distribution, non-irrigated areas at Sites A and B were mown during winter 1981. Four plots ($40cm^2$) were demarcated at each site and all vegetation other than *T. triandra* at Site A and *S. fimbriatus* at Site B was removed from the plots and from a border area 50cm wide surrounding the plots. The key species in the respective plots were rested for an entire growing season, but other vegetation was continually removed. The areas where the plots were situated were selected so that the respective key species comprised more than 50% of the living basal cover at the two sites.

During winter 1982 tufts in all plots were clipped at the soil surface (*T. triandra* at Site A and *S. fimbriatus* at Site B). The soil in each plot was then removed in five layers: 0-5cm; 5-10cm; 10-20cm; 20-30cm and 30-40cm. All roots were washed from each individual layer of soil and oven dried to constant mass.

This trial was conducted only under unamended moisture conditions and not repeated under irrigation.

3.2.7 Statistical considerations in presentation of results

The most meaningful way of presenting a picture of the developmental morphology of plants is by graphic presentation of the parameter under consideration plotted against time. This can be done by plotting raw data by making use of moving averages, or by fitting mathematical functions to the data. Considerable attention in the literature has been given to the functional (regression) approach to plant growth.

Three prerequisites exist for implementation of the functional approach. Firstly, that an independent variable (X) should be measured without, or virtually without, error; secondly, that the distributions of replicated Y values at each X should be normal; and thirdly that the variance of the subpopulations of Y should be uniform and not change in magnitude with X. The first condition is not difficult to satisfy since in plant growth, time can be measured with much greater accuracy than other parameters. The second and third conditions, however, usually require attention. The means of overcoming this problem is to transform the values of the primary data and to perform the regressions on these transformed data. For this reason, the logarithmic transformation is almost standard (Hunt,1982).

A further prerequisite exists where the objective of regression analysis is a statistical comparison of two or more growth functions. This is that the measurements of the dependent variable (Y) be made on a different set of individuals at each value of X. Should this not be done, the variance of the subpopulations of Y values would be correlated. This would result in an underestimate of error and statistical comparison of curves (by means of confidence limits) would be spurious. There is, however, no objection to fitting curves to data with correlated variance if the objective is simply to describe the data. Under such circumstances, transformation of data is still desirable if variance heterogeneity is suspected (Clarke, 1984; *pers. comm.*).

Logarithmic transformation of primary data has an added advantage. Since changes in the dependent variable are often large, very little of the first phases of growth are revealed in a simple plot of the variable against time on an arithmetic scale. Log transformation of the data gives a clearer description of these initial stages of growth (Hunt, 1978).

The functional approach can be implemented by making use of either mechanistic or empirical models. The former attempt to fit single continuous functions to growth data in order to describe growth in terms of the mechanism of the system, while the empirical approach simply re-describes the data and does not give rise to any information that is not contained therein (Thornley, 1976).

These two approaches are conflicting. Mechanistic models were favoured by Waddington (1956) who pointed out that if formulae are used merely as a convenient means of summarising empirical observations, then the theoretical gain of knowledge regarding plant growth is small. However, this opinion was disputed by Williams & Bouma (1970) who suggested that fitting of continuous functions to extensive growth data in an attempt to achieve a mechanistic model of growth is rarely justified, since it is unreasonable to expect growth to be governed by a single set of parameters throughout its course, even in a controlled environment.

In moving from mechanistic to empirical models, the particular mathematical form of the function used is regarded as of no special physiological significance. Accuracy in the fit achieved becomes the primary aim and the resulting curve summarises the growth data in a convenient manner. The original data, disturbed by irregular errors, are replaced by a smooth continuous function (Richards, 1969). The literature, particularly in recent years, favours empirical models for describing plant growth (Williams, 1964; Hammerton & Stone, 1966; Hughes & Freeman, 1967; Richards, 1969; Evans, 1972; Hunt, 1973, 1978, 1979, 1982; Hunt & Parsons, 1974, 1977; Thornley, 1976; Williams & Bouma, 1970; Hurd, 1977).

In simple terms, the rationale behind the empirical approach is as follows: if attempts to assess the reality of growth, result in a series of observations scattered randomly about that reality, then a suitable function fitted to those observations may be expected to regain much of the clarity with which reality is perceived by the researcher (Hunt, 1979).

A useful means of implementing empirical models is by making use of splined functions. These are piecewise polynomials of degree that join together in so called "knots" and fulfil continuity conditions for the function itself and the first n-1 derivatives (Wold, 1974). The simplest form of splined function is in the case of moving averages, which can be considered as splines of degree zero. Moving averages were used by Tainton & Booysen (1965*a* & *b*) to describe the growth of various components of *T. triandra* and *H. hirta* in Natal.

Parsons & Hunt (1981) provided the methodology for a more sophisticated use of splined functions; fitting of smooth curves to lengthy series of data by means of splined third order polynomials fitted to logarithmically transformed data. Practical applications of this method have been provided by Hunt (1980) and Hunt & Evans (1980).

The growth data collected from the trials described above (3.2.1; 3.2.2; 3.2.3; 3.2.4; 3.2.5 & 3.2.6) will be described where applicable, by the methodology of Parsons & Hunt (1981). The number of knots used in each splined function are chosen according to the guidelines of Hunt (1982). However, no more than two knots are used in each function. This is considered to provide a compromise between statistical exactitude and the experimenter's biological expectation.

Where applicable, fitted curves are presented on both a log scale and an arithmetic scale. The advantages of the former means of presentation have been stated. In addition, the methodology of Parsons & Hunt (1981) fits 95% confidence limits to log transformed data, implying that these limits would be asymmetrical on untransformed data. Curves are, however, also presented on an arithmetic scale to provide a clearer mental picture of absolute growth.

3.3 Results and discussion

3.3.1 Rainfall

The monthly rainfall recorded at the experimental sites from July 1980 to June 1983 is presented in Figure 3.1. The mean annual rainfall at Site A over a period of 38 years is 521mm (Danckwerts, 1981). Rainfall records at Site B exist only since 1975. However, the mean annual rainfall recorded at the Adelaide Police Station, situated approximately 2km from Site B, over a period of 65 years is 422,2mm (Anon,1984). Unusually dry conditions occurred at both sites during the latter part of the 1981/82 season and particularly during the 1982/83 season (Figure 3.1).

3.3.2 Premature tiller mortality

During the process of sequential harvesting of marked tillers of *T. triandra* and *S. fimbriatus* initiated during spring 1980 (Experiment 1), it was observed that a considerable number of the wire rings used to mark the tillers were no longer encircling living tillers. It was assumed that the tillers that had been marked with these rings had senesced prematurely. This provided one of the justifications for non-destructive recording of permanently marked and numbered tillers (Experiment 3). From this trial, it was possible to monitor the cumulative percentage of permanently marked tillers initiated during spring 1981 that senesced prematurely (Figure 3.2).

The rate of premature senescence of *T. triandra* tillers was similar on both moisture treatments until March 1982. At that stage, a late summer drought (Figure 3.1) accelerated the rate of tiller mortality, and 90% of non-irrigated tillers had died by the end of April 1982 (Figure 3.2). Unstressed *T. triandra* senesced at a fairly consistent rate, and even here, by the time the remaining tillers reached maturity, 70% of the original population of tillers had died while still in the vegetative phase (Figure 3.2). This can probably be attributed to competition for space as a result of prolific tillering and consequent high tiller densities of this species after heavy defoliation during winter.

Tillers of *S. fimbriatus* senesced more rapidly on the non-irrigated than on the irrigated treatment even from the beginning of the growing season (Figure 3.2). As was the case with *T. triandra*, summer drought (Figure 3.1) resulted in increased mortality of non-irrigated *S. fimbriatus* tillers and nearly all (94%) of these had died by autumn 1982. On the unstressed treatment, only 40% of tillers senesced prematurely. This can probably be explained by the fact that the tiller density of this species was less than that of *T. triandra* during the spring and summer.

It is, however, important to note from the results that a considerable proportion of the tillers of both species dies while still in the vegetative phase of growth and never reaches maturity, even when the plants are not subjected to moisture stress and are not defoliated. A severe drought such as that which occurred during the late summer of 1981/82 has a devastating effect on tiller populations.

3.3.3 Elevation of shoot apices

3.3.3.1 Shoot apex elevation of spring initiated tillers

Shoot apex elevation of *T. triandra* and *S. fimbriatus* tillers was recorded by means of dissection of sequentially harvested samples of living tillers growing under irrigated and non-irrigated conditions (Experiment 1).

After recording apex elevation of spring (1980) initiated tillers of the species *S. fimbriatus*, it became clear that they could be separated into two distinct populations: those which elongated and flowered in the autumn after marking (1981), and those which remained vegetative with growing points close to the soil surface throughout autumn and winter 1981. That these two populations of tillers all emerged after winter 1980, was not in doubt. This was because when tillers were marked, it was ensured that the oldest leaf was intact and had not been clipped during the severe defoliation in winter 1980. It would be meaningless to express the elevation of the shoot apices of these tillers as the mean of both populations. The data from the populations were thus analysed separately once the tillers could be distinguished as separate populations, and shoot apex elevation of *S. fimbriatus* described only in terms of the early flowering population. The early flowering population was defined as all tillers whose apices had elevated to a height in excess of 15mm by autumn 1981. This height was chosen because the apices that remained vegetative during autumn and winter 1981 were maintained at elevations below this height. Shoot apex elevation of *S. fimbriatus* tillers initiated in spring 1980 is thus described in terms of the mean height of apices of all harvested tillers until such time as the two populations could be differentiated (February 1981), and thereafter as the mean height of those apices in excess of 15mm (Figures 3.3 (log scale) and 3.4 (arithmetic scale)).

In contrast to *S. fimbriatus* tillers, those of *T. triandra* virtually all elongated and flowered during the spring of the year after tiller initiation (1981). Shoot apex elevation of spring (1980) initiated tillers of the latter species is thus described in terms of the mean height of the apices of all harvested tillers. (Figure 3.3 (log scale) and 3.4 (arithmetic scale)).

The pattern of shoot apex development of *T. triandra* (Figures 3.3 & 3.4) was similar to that reported by Tainton & Booysen (1965*a*) in the Natal Tall Grassveld. However, the initial elevation of apical buds of irrigated tillers during autumn 1981 was significantly greater (P<0,05) than that of non-irrigated tillers (Figure 3.3), despite the fact that the 1980/81 season was considerably moister than average (Figure 3.1). Moreover, this initial elevation was only of the order of 20mm in the case of non-irrigated tillers, suggesting that these apices would not have been vulnerable to grazing animals, particularly cattle, during the winter. This early elevation is likely to be even less pronounced during normal or dry seasons. Winter elevation of apical buds of unstressed tillers was approximately 120mm (Figure 3.4), a little higher than that recorded by Tainton & Booysen (1965) in moist Natal Tall Grassveld (100mm).

When final elevation of *T. triandra* apices took place at flowering (spring 1981), there was no significant difference between irrigated and non-irrigated tillers (Figure 3.3). The function fitted to the shoot apex data of irrigated *T. triandra* tillers suggests that apices were continuing to elevate when sampling ceased (November 1981). In practice this did not happen and flowering tillers had already commenced senile mortality at this time. Extremely high tiller densities made sampling difficult after this date, but had sampling continued after tiller maturity as on the non-irrigated treatment, the fitted functions would probably have followed similar trends on both moisture treatments. The final elevation reached by apices of *T. triandra* tillers was approximately 600mm on both treatments (Figure 3.4), similar to that recorded by Tainton & Booysen (1965*a*) in Natal.

In contrast to *T. triandra*, elevation of apices of the early flowering population of *S. fimbriatus* tillers began in the summer (1980/81) after tiller initiation, and continued through to maturity after flowering, which took place during autumn 1981 (Figure 3.3). The rate of elevation of irrigated tillers was apparently rapid during January/February 1981, followed by a deceleration during March. This was probably caused by the fact that from February 1981 onwards, only those apices above 15mm were used to construct the fitted function, thus resulting in an apparent rapid elevation of apices of irrigated *S. fimbriatus* tillers at that time; a result that is not considered biologically meaningful.

The final height achieved by *S. fimbriatus* tillers was not significantly different between moisture treatments (Figure 3.3). However, this was a result of log transformation of the primary data, and on an arithmetic scale, irrigated tillers reached a mean height of 650mm while stressed tillers achieved a mean height of only 410mm, a difference that was very obvious from observation in the field. This does not necessarily imply that culm height achieved by *S. fimbriatus* is more sensitive to moisture stress than that of *T. triandra*, since the rainfall recorded at Site A was considerably higher than that at Site B during 1980 and 1981 (Figure 3.1).

Regarding differences between species, the mean height of shoot apices of early flowering *S. fimbriatus* tillers was significantly greater than that of *T. triandra* tillers after mid-December 1980 and early February 1981 ($P<0,05$) on irrigated and non-irrigated treatments respectively (Figure 3.4). This was essentially a result of a difference in timing of shoot apex elevation, and there was no significant difference in the final culm height attained between species (Figure 3.4).

3.3.3.2 Timing and rate of elevation of individual shoot apices within populations

Figures 3.3 & 3.4 represent the mean height of shoot apices of whole populations of tillers, but give no indication of the timing or rate of elevation of individual apical buds. From sequentially harvested samples of spring initiated tillers (Experiment 1) it was observed that flowering of tillers within populations did not occur simultaneously, but sporadically over a number of months. The perçentage of sequentially harvested samples of *T. triandra* and *S. fimbriatus* tillers with flowering culms at each harvest date and in both moisture treatments, are presented in Figure 3.5. Flowering of *T. triandra* was first encountered on 19 June and 27 July 1981 on irrigated and non-irrigated treatments respectively. The percentage of harvested tillers in flower increased as sampling date progressed through winter and the following spring, until 11 November and 27 October on the two respective treatments, by which time all harvested tillers were in flower. However, the increase was inconsistent, a reflection of sampling variability.

The first flowering tillers of *S. fimbriatus* were encountered on 16 February and 3 March 1981 respectively on irrigated and non-irrigated treatments. The proportion of flowering tillers in samples increased with progressive harvest dates until early- to midwinter. As with *T. triandra*, this increase was inconsistent, particularly on the non-irrigated treatment.

It is of note that all harvested tillers of *T. triandra* had flowered by spring 1981. In contrast, only of the order of between 45% and 65% of *S. fimbriatus* tillers had flowered by winter 1981 (Figure 3.5). This again suggests the existence of sub-populations of reproductive and vegetative *S. fimbriatus* tillers referred to in the previous section.

Despite sampling variability, the data (Figure 3.5) suggest that flowering of both *S. fimbriatus* and *T. triandra* was spread over a period of about three months during autumn and spring respectively. However, since these results were derived from destructively sampled tillers of spring initiated populations, it was not possible to identify the date of flowering or rate of shoot apex elevation of individual tillers. This was recorded on permanently marked and numbered tillers that were non-destructively sampled from the spring of 1981 onwards (Experiment 3). In this trial, all growing points of *T. triandra* tillers remained near the soil surface until 3 February 1982, when one of the irrigated tillers elevated its apex to a height of 30mm although still in the vegetative phase. Thereafter, vegetative apices of individual tillers were elevated sporadically throughout the autumn and winter until the end of July 1982, by which time 92% of all surviving irrigated tillers had their growing points elevated to a height of 30mm or more. This initial elevation of apices, however, was rapid and was completed in approximately 14 days.

On the non-irrigated treatment, most *T. triandra* tillers senesced as a result of drought during autumn 1982 (Figure 3.2). However, on the few remaining tillers similar trends were observed, but the initial elevation was to a height of only about 15mm.

Flowering of irrigated *T. triandra* tillers began on 3 May 1982 and continued until the end of September, when the final tiller flowered (Figure 3.6). Although flowering covered a time span of 210 days, the majority of tillers flowered between the beginning of August and the end of September (60 days).

As with vegetative shoot elevation, the later (reproductive) elevation of individual shoot apices was rapid, the mean length of time from the start of piping to flower emergence per individual tiller being 18,4 days (CV 33,8%).

It is of note (Figure 3.6) that only 73% of surviving irrigated *T. triandra* tillers initiated during spring 1981 came into flower during spring 1982. This is in contrast to sequentially harvested tillers where 100% of tillers sampled were in flower during the second spring after tiller initiation. Possible explanations are firstly that in the case of the permanently marked and numbered tillers, the site was being irrigated for the second successive season, and tiller densities were very high. Thus, competition between tillers could have been responsible for suppressing flower formation. Secondly, it is also possible that the sampling procedure of sequentially harvested tillers was biased (Experiment 1) since it is easier to "find" marked flowering tillers than those still in the vegetative phase.

As a result of drought, none of the few surviving non-irrigated *T. triandra* tillers flowered during spring 1982. It was, however, observed that a very limited number of unmarked tillers growing on the same treatment flowered that spring.

The question that arises is the fate of the *T. triandra* tillers that remained vegetative during the spring in the year after tiller initiation. On the irrigated treatment, these tillers all senesced as the season progressed into late spring and summer. This was probably a result of a combination of overshading and competition. The non-flowering individuals were in any event the less vigorous of the marked tillers, and in a situation where moisture is not limited, survival of such tillers for a further season is considered unlikely, even under a defoliation regime where shading would be unlikely. The few surviving non-irrigated *T. triandra* tillers all senesced during the summer of 1982/83 as a result of the very severe drought (Figure 3.1).

With regard to *S. fimbriatus* tillers marked and numbered during spring 1981 (Experiment 3), all growing points remained near the soil surface from spring through to midsummer. Thereafter, a few individual apices began to elongate on the irrigated treatment, and the first tiller flowered on 16 February 1982. Thereafter flowering of individuals occurred sporadically and at a fairly constant rate until 2 June when the last of reproductive tillers came into flower (Figure 3.6). Flowering thus covered a time span of 107 days. As with *T. triandra* tillers, however, the elevation of individual apices was rapid, and the mean length of time for a growing point to elevate from 15mm to flower emergence was 20,3 days (CV 39,1%).

Once again, the existence of two subpopulations of *S. fimbriatus* tillers of the same age is indicated by the fact that only 40% of surviving tillers initiated in spring 1981 flowered in autumn 1982 on the irrigated treatment (Figure 3.6).

On non-irrigated treatment, nearly all marked *S.fimbriatus* tillers senesced as a result of drought during autumn 1982 (Figure 3.2). The growing points of the very few surviving tillers did not elevate that autumn. A limited number of unmarked tillers did flower that autumn, but it was not known whether these tillers had been initiated the previous spring or earlier.

The fate of the sub-population of *S. fimbriatus* tillers initiated in spring 1981 that did not flower in autumn 1982 is debatable. On the irrigated treatment, vegetative tillers continued to grow through to the next summer. At that stage recordings became virtually impossible since no utilisation for 18 months resulted in a considerable accumulation of herbage. However, although the growing points of marked tillers remained near the soil surface at this time, the individuals had become small and "spindly" as a result of excessive shading, and probably would have senesced the following autumn. On the non-irrigated treatment, the few surviving tillers senesced as a result of severe drought during summer 1982/83 (Figure 3.1).

Despite these observations, it is likely that under a utilisation regime where excessive shading does not occur, at least some of the vegetative sub-population of tillers would survive and flower during the second autumn after tiller initiation, provided tillers do not die as a result of drought. This is suggested by subjective observations made while marking newly emerged tillers during spring 1981. At this time a large number of "older" vegetative tillers were present, and these flowered profusely during 1982.

In concluding discussion on timing and rate of elevation of individual apices of *T. triandra* and *S. fimbriatus*, of special significance is the fact that while individual apices elevate relatively rapidly (two to three weeks), the timing of this elevation covers a period of two to three months or longer. This implies that flowering of these species cannot be controlled by critical periods of grazing or resting during spring and autumn respectively.

3.3.3.3 Effect of season of tiller initiation on apex elevation

The results illustrated in the preceding sections are relevant only to spring initiated tillers. The timing of flowering in populations of *T. triandra* and *S. fimbriatus* tillers initiated progressively at two-monthly intervals during the 1980/81 season (Experiment 2) was, however, also recorded. The percentage of surviving marked *T. triandra* and *S. fimbriatus* tillers, initiated at different times during this season, which flowered during spring 1981 (*T. triandra*) and autumn 1981 (*S. fimbriatus*) respectively, are presented in Table 3.1. For *T. triandra*, these data are calculated as the mean of the percentage of tillers in flower at the end of September 1981 and the end of November 1981 harvest dates for each series of tiller populations; these being dates after spring flowering had taken place. For *S. fimbriatus*, the percentage of tillers in flower was calculated from the end of May 1981 and the end of July 1981 harvest dates.

The majority of irrigated *T. triandra* tillers initiated as late in the season as the end of November, set seed the following spring. A limited number of irrigated tillers initiated even at the end of January, flowered in the next spring. In the case of the non-irrigated *T. triandra* treatment, most tillers initiated up to the end of September came into flower the following spring. Approximately half of the tillers initiated at the end of November set seed the next spring (Table 3.1). In view of the fact that good rains fell during autumn 1981 (Figure 3.1) the only difference in treatment between the irrigated and non-irrigated tillers initiated at the end of November and the end of January was moisture stress on the non-irrigated tillers during the summer. These results suggest that tillers must have reached a critical stage of development by the beginning of autumn in order to flower the next spring.

Regarding the species *S. fimbriatus*, all populations of tillers (irrigated and non-irrigated) initiated up to the end of November 1980 produced at least some flowering individuals the next autumn. The percentage of tillers initiated at the end of November that flowered the next autumn was, however, apparently smaller than that of tillers initiated earlier. Even where there was no moisture stress, no tillers initiated after midsummer produced flowers during autumn 1981 (Table 3.1)

Once again, the data suggest sub-populations of reproductive and vegetative *S. fimbriatus* tillers within each treatment.

3.3.3.4 Summary of results

i. Elevation of *T. triandra* shoot apices in an un-utilised situation in the False Thornveld of the Eastern Cape follows a similar trend to that reported by Tainton & Booysen (1965) in the Natal Tall Grassveld; apices of spring initiated tillers remain near the soil surface until the next autumn when they elevate while still in the vegetative stage of growth. During the following spring the apical buds undergo a second phase of elevation and flowering takes place.

ii. Under unamended moisture conditions, the initial elevation of apical buds of *T. triandra* is less than 20mm, implying that these apices would not be vulnerable to grazing in winter, particularly by cattle. This is in contrast to moist conditions where the apices elevate to a vulnerable height.

iii. Spring initiated *S. fimbriatus* tillers can be divided into two sub-populations, those that flower the next autumn, and those that remain vegetative during the autumn and winter.

iv. The apices of the early flowering population of *S. fimbriatus* tillers remain near the soil surface until late summer, after which they elevate rapidly as flowering culms develop.

v. Un-utilised spring initiated *S. fimbriatus* tillers that do not flower in the autumn of the same season senesce as a result of excessive shading during the following summer. In a utilised situation, they would probably survive and flower during the second autumn after initiation.

vi. Shoot apices within tiller populations of both species do not elevate simultaneously, but do so sporadically over periods of about three months.

vii. Elevation of individual apices is rapid, and takes place within a period of two to three weeks.

viii. *T. triandra* tillers initiated before the beginning of autumn can flower the next spring, provided there is no moisture stress. Even mild stress necessitates that tillers be initiated earlier in the growing season than midsummer in order to flower the next spring. Severe drought during the growing season causes mortality of *T. triandra* tillers, and those that do survive generally do not flower the next spring.

ix. *S. fimbriatus* tillers must be initiated before midsummer in order to flower in autumn of the same season. As with *T. triandra*, drought causes mortality of most tillers, and those that survive do not flower during the autumn.

3.3.4 Above ground mass of primary tillers

3.3.4.1 Mass of spring initiated tillers

The cumulative total mass, leaf mass and stem mass of *T. triandra* and *S. fimbriatus* tillers initiated during spring 1980 (Experiment 1) are presented in Figures 3.7 (log scale) and 3.8 (arithmetic scale). Each figure was derived from the data of approximately 30 sampling dates. Since the fitted functions were derived from the means of separate samples of tillers, the confidence intervals can be used for within and between species comparisons of these functions.

Within each species, the whole tiller mass on irrigated treatments was significantly greater ($P<0,05$) than that under non-irrigated conditions from approximately midsummer 1980/81 (Figure 3.7A). Between species, the trend was for *T. triandra* tillers to have a smaller mass than similarly treated *S. fimbriatus* tillers up to mid-autumn 1980; thereafter the mass of *T. triandra* tillers exceeded that of the other species (Figure 3.8A). This result was, however, not statistically significant (Figure 3.7A).

The maximum mass achieved by irrigated *T. triandra* tillers was 0,75g/tiller, approximately equal to that recorded by Tainton & Booysen (1965*a*) in the Natal Tall Grassveld. Non-irrigated *T. triandra* tillers reached a maximum mass of nearly 0,5g/tiller and those of *S. fimbriatus* approximately 0,5 and 0,3g/tiller on irrigated and non-irrigated treatments respectively (Figure 3.8).

With regard to leaf mass per tiller, supplementary irrigation had little effect during the initial stages of growth after tiller emergence. However, the leaf mass of irrigated tillers of *T. triandra* and *S. fimbriatus* exceeded those on non-irrigated treatments after December 1980 and February 1981 respectively ($P<0,05$) (Figure 3.7B). Between species, the leaf mass of *T. triandra* tillers exceeded that of *S. fimbriatus* tillers after January 1981 and March 1981 ($P<0,05$) on irrigated and non-irrigated treatments respectively (Figure 3.7B). On the irrigated treatment, this difference was no longer significant by the end of winter 1981.

Stem mass per tiller, like total tiller mass, differed little between treatments within each species up to midsummer 1980/81. Thereafter, irrigated tillers had significantly higher stem masses ($P<0,05$) than non-irrigated tillers (Figure 3.7C). This difference ceased to be significant at the end of March 1981 in the species *S. fimbriatus*. On similar treatments, *T. triandra* tillers had significantly lower stem masses than those of *S. fimbriatus* during most of the vegetative life of tillers: until mid-March 1981 on irrigated sites and mid-June 1981 on non-irrigated sites (Figure 3.7C). However, the stem mass of *T. triandra* increased markedly at the end of the life cycle of tillers, exceeding that of the other species (Figure 3.8C).

In general, it is of note that because of log transformation of data, small absolute differences in tiller mass during early stages of growth were often significant, while much larger differences during the later stages of growth were not significant.

3.3.4.2 Stem : leaf mass ratio

The ratio of stem mass to leaf mass over the life span of spring initiated populations of *T. triandra* and *S. fimbriatus* tillers (Experiment 1) is presented in Figure 3.9. The leaf mass of both stressed and unstressed *T. triandra* tillers was greater than their stem mass for most of the vegetative growing period. Only when tillers were small, and again after shoot apex elevation had taken place the following winter, was the mass of stem material greater than that of leaf blades. In contrast, the proportion of leaf blade material of *S. fimbriatus* was less than that of stem material throughout the life cycle of tillers. It is, however, of note that while the stem:leaf mass ratio of *T. triandra* was less than that of *S. fimbriatus* throughout the vegetative life of tillers, at the end of their life cycle (flowering stage), the ratio for *T. triandra* increased considerably, and was considerably greater than that of flowering *S. fimbriatus* tillers (Figure 3.9).

If it is assumed that palatability of grasses is, *inter alia*, related to their leafiness, then it could be expected from the results that *T. triandra* would be more attractive to grazing animals than *S. fimbriatus* at all times except during flowering in spring. The results from the previous indicate chapter (Section 2.2.2.2) that *T. triandra* was generally the most preferred species, but that it was relatively less preferred when flowering culms were present. When *T. triandra* was flowering profusely during November, cattle grazed *S. fimbriatus* in preference to the former species (Figure 2.2A).

3.3.4.3 Effect of time of initiation on tiller mass

The mean tiller mass of *T. triandra* and *S. fimbriatus* populations initiated progressively during the 1980/81 season (Experiment 2) are presented in Figures 3.10 & 3.11 respectively. Since, in this trial, tillers were harvested at 60 day intervals, each curve was derived from the data recorded at 10 or less harvest dates (although each point in Figures 3.10 & 3.11 represents the mean of 30 tillers). Thus, although splined functions were fitted to the data using the methodology of Parsons & Hunt (1981), because of the policy of harvest dates the functions are not quantified by confidence limits and are presented only on an arithmetic scale (Figure 33.10 & 3.11).

As in the case of spring initiated tillers, irrigated tillers tended to have a higher mass than non-irrigated tillers (Figures 3.10 & 3.11). In addition, mature tiller mass apparently declined progressively the later in the season that tillers were initiated. This occurred under both moisture treatments and with both species, and even with tillers that did not flower during the season of initiation (Table 3.1).

Each series of tiller populations can be subdivided into two apparent groups: those initiated before midsummer and those initiated after midsummer. The former group experienced the greatest increment in mass in the late summer/autumn after initiation, while those initiated after midsummer grew little during the season of initiation, and their greatest mass increment took place during the following season (Figures 3.10 & 3.11). These groups correspond roughly to those populations where flowering took place during 1981 and those that remained vegetative during this period (Table 3.1). An exception is in the case of irrigated *T. triandra* tillers initiated during early February 1981. A limited number of these tillers did flower during 1981, although the mean tiller mass for the whole population followed a similar trend to those that remained vegetative at this time and flowered during spring 1982 (Figure 3.10).

3.3.4.4 Summary of results

i. Moisture apparently plays an overwhelming role in determining the total mass and stem mass achieved by tillers of *T. triandra* and *S. fimbriatus*.

ii. *T. triandra* tillers have considerably more leaf blade material than those of *S. fimbriatus* throughout the vegetative life of the tillers.

iii. Young tillers of *T. triandra* have a smaller mass than those of *S. fimbriatus*, but this difference does not persist beyond six to seven months after tiller emergence.

iv. The leaf mass of *T. triandra* tillers is greater than their stem mass for the greater part of their vegetative life. In contrast, the leaf mass of *S. fimbriatus* tillers is always less than their stem mass. When flowering takes place, however, the stem mass of *T. triandra* increases considerably, and the stem:leaf mass ratio of tillers becomes considerably greater than that of flowering *S. fimbriatus* tillers.

v. Tillers initiated early in the season achieve greater mass when mature than those initiated late in the season.

vi. Spring initiated tillers undertake most of their vegetative growth during the autumn of the same season; autumn initiated tillers grow vegetatively during the next season.

3.3.5 Leaf development

3.3.5.1 Leaf area

The total green leaf area per tiller in populations of *T. triandra* and *S. fimbriatus* tillers initiated during spring 1980 (Experiment 1) is presented in Figure 3.12 (log scale) and 3.13 (arithmetic scale).

Leaf area per tiller followed a similar trend over all treatments, increasing steadily after tiller initiation and reaching a peak at the end of the following autumn (May 1981) (Figures 3.12 & 3.13). Non-irrigated *S. fimbriatus* tillers reached this peak earlier than unstressed tillers, probably a result of the dry autumn experienced at Site B during 1981 (Figure 3.1).

Confidence limits of the expected logarithms of leaf area are fairly wide (Figure 3.12), so that differences between leaf areas of irrigated and non-irrigated treatments within species were not significant. This was probably caused by the "error" involved in the measurement of leaf area. The trend was, however, for irrigated treatments to have larger leaf areas than non-irrigated treatments within each species. In absolute terms, this difference was large, nearly double on an arithmetic scale (Figure 3.13).

Between species the recorded leaf areas of *T. triandra* tillers were significantly greater than those of *S. fimbriatus* from approximately the end of December 1980 and the end of January 1981 on irrigated and non-irrigated treatments respectively. However, comparison of leaf areas between species and even between irrigated and non-irrigated treatments in the case of *S. fimbriatus* is to some extent misleading. The leaves of irrigated *S. fimbriatus* tillers became rolled soon after harvesting, while those of the non-irrigated tillers remained expanded. In contrast, the area of *T. triandra* leaves were relatively easy to measure and results are comparable between different moisture treatments. Here, leaves were generally folded, and it was ensured that leaves were always folded before passing them through the planimeter. The recorded leaf area was thus twice the planimeter reading.

Nevertheless, in general terms, it is reasonable to conclude that leaf area of irrigated tillers of both species was larger than that of stressed tillers, and the leaf area of *T. triandra* tillers greater than that of *S. fimbriatus* tillers.

3.3.5.2 Leaf number

The number of emerged green leaves and the number of dead leaves attached to *T. triandra* and *S. fimbriatus* tillers initiated during spring 1980 (Experiment 1) are presented in Figures 3.14 (log scale) and 3.15 (arithmetic scale).

There was no significant difference in the number of emerged green leaves per tiller between irrigated and non-irrigated treatments within species (Figure 3.14A). The trend was, however, for irrigated tillers to have more green leaves at most times than non-irrigated tillers (Figure 3.15A).

T. triandra tillers had significantly more green leaves attached than *S. fimbriatus* tillers after the end of autumn 1981 on both moisture treatments (Figure 3.14A). This was a result of flowering of tillers of the latter species during autumn 1981 (Figure 3.5).

The general trend was for the number of green leaves on *T. triandra* tillers to increase rapidly during the spring after tiller initiation (1980). Thereafter the number remained fairly constant (between three and five leaves per tiller throughout the following summer, autumn and winter, but dropped sharply after flowering the next spring (1981). The number of green leaves on *S. fimbriatus* tillers also increased rapidly after tiller initiation in spring 1980, but reached a peak of approximately four leaves per tiller in early summer. Thereafter, green leaf number decreased steadily as flowering took place through to winter 1981 (Figure 3.15A).

The results imply therefore that from the summer after tiller initiation, the rate of leaf emergence is equal to, or less than the rate of leaf senescence in both species.

Regarding the number of dead leaves attached to tillers, there was little significant difference between treatments within species or between species within treatments (Figure 3.14B).

The mean number of senescent leaves attached to *T. triandra* tillers increased to six and four leaves per tiller on irrigated and non-irrigated sites respectively during the summer following tiller initiation (1980/81) (Figure 3.15B). For the rest of the vegetative period of growth, the number of dead leaves attached to irrigated tillers declined and that on non-irrigated tillers remained constant, although this difference was not significant (Figure 3.14B). The implication is that dead leaves of *T. triandra* abscised through desiccation at a rate equal to (on the non-irrigated treatment) or more rapidly (on the irrigated treatment) than the rate of leaf senescence during the summer, autumn and winter following tiller emergence. During and after flowering (spring, 1981), the number of dead leaves attached to irrigated *T. triandra* tillers increased proportionately to the decrease in the number of green leaves per tiller, while that on non-irrigated tillers of the species remained constant (Figure 3.15).

The number of dead leaves attached to *S. fimbriatus* tillers also increased rapidly during the spring after tiller initiation, until a maximum of between four and five leaves was reached on both moisture treatments during summer 1980/81. Thereafter the number of dead leaves per tiller decreased into the winter. The implication is that during this latter phase, the rate of leaf abscission was greater than the rate of leaf senescence. During winter 1981 after flowering had taken place, the number of dead leaves per tiller increased on both treatments, and this increase coincided with a concurrent decrease in the number of green leaves per tiller (Figure 3.15).

Considering the dynamics of both species in general terms; during the spring of the season of tiller initiation, leaves emerge at a rate greater than the rate of leaf senescence which in turn is greater than the rate of leaf abscission. Thus during this period, in the absence of utilisation, both green leaves and dead leaves accumulate. For the rest of the period of vegetative growth, leaves emerge at a rate less than or equal to the rate of leaf abscission through desiccation. The implication is that on sweetveld rested for a whole growing season, at least some forage will be wasted as a result of leaf decay. After tillers have flowered, leaf emergence ceases.

The number of emerged green leaves attached to tillers was also recorded on permanently numbered non-destructively sampled tillers that were initiated during spring 1981 (Experiment 3). As was indicated in Section 3.3.3.2, irrigated tillers of both species consisted of two sub-populations, those that flowered during the year after tiller initiation and those that remained vegetative during this period . Since in this trial tillers were numbered and non-destructively sampled, it was possible to separate the data of each tiller sub-population and consider them independently. This separation of data was considered worthwhile since the leaf dynamics of vegetative and reproductive tillers were considerably different after flowering of the latter sub-population had taken place. Non-irrigated tillers were, however, considered as single populations within each species, as drought prevented these tillers from flowering during autumn 1982 (Figure 3.2). In any event the sizes of the samples of remaining non-irrigated tillers were considered insufficient to monitor leaf development patterns after this time.

The number of green leaves attached to the various populations of non-destructively sampled tillers initiated during spring 1981 are presented in Figure 3.16. The curves in Figure 3.16 are presented on an arithmetic scale, being untransformed values of curves fitted to logarithms of primary data. Measurements were made on the same individual tillers at each date, implying correlated variance between recording dates. Confidence limits fitted to the curves would thus have been meaningless. It is, however, of note that such correlated variance (successive measurements on the same tillers) resulted in small and consistent changes between dates. The fitted curves thus followed the primary data very closely.

In the case of both non-destructively sampled sub-populations of irrigated *T. triandra* tillers initiated in spring 1981, green leaves increased in number after emergence (Figure 3.16) at a rate similar to that of the destructively sampled tillers initiated during the previous season (Experiment 1) (Figure 3.15A). However, the number of green leaves on non-destructively sampled tillers dropped during the winter following tiller initiation (1982) (Figure 3.16). This drop was not observed on sequentially harvested tillers, possibly a result of variability in the primary data as reflected by the confidence limits in Figure 3.14A. In the reproductive sub-population of permanently marked *T. triandra* tillers green leaves senesced during spring 1982 after flowering took place, although there was a small increase in green leaf number immediately prior to flowering. In the irrigated vegetative sub-population, green leaf numbers increased with a rise in temperature during spring 1982 (Figure 3.16). The number of green leaves on non-irrigated permanently marked *T. triandra* tillers decreased progressively through spring and summer 1981/82 as a result of drought.

The number of green leaves attached to irrigated non-destructively sampled *S. fimbriatus* tillers followed a similar trend to that recorded on sequentially harvested tillers during the previous season. Green leaf number reached a peak of four to five leaves per tiller during summer 1981/82, then decreased steadily through autumn and winter. Green leaves on the reproductive sub-population of *S. fimbriatus* tillers senesced completely during winter 1982 after flowering had taken place. The vegetative sub-population of irrigated tillers also experienced a drop in green leaf numbers during winter, but this increased once more the next spring. On non-irrigated *S. fimbriatus* tillers, the green leaf number dropped sharply in summer and autumn as tillers died as a result of drought (Figure 3.16).

In all these sub-populations of tillers, sampling in spring 1981 began after approximately three green leaves had emerged per tiller (Figure 3.16). This was because it was not possible to mark and number the new popoulations of tillers before this stage of development.

It is clear from the preceding discussion as well as the review of the literature that the leaf system of a tiller does not remain static, but leaves are continuously being replaced by new individuals. It is thus of interest to determine the total number of leaves produced by individual tillers in their life cycle. This was possible to calculate for sub-populations of destructively sampled tillers since all newly emerged leaves on each tiller were marked and recorded (Experiment 3). The cumulative number of leaves produced by the various sub-populations of tillers initiated in spring 1981 are presented in Figure 3.17.

Irrigated reproductive tillers of *T. triandra* and *S. fimbriatus* produced 23 and 14 leaves during their life cycles respectively (Figure 3.17). This is in contrast to the results of Tainton & Booysen (1965 *a*) who recorded a total of 17,4 leaves on undisturbed *T. triandra* tillers. Irrigated vegetative tillers had produced a mean of 21 leaves per tiller in both species by the second summer after tiller initiation (Figure 3.17). After December 1982 sampling of permanently numbered tillers ceased for reasons already given.

Non-irrigated tillers of *T. triandra* and *S. fimbriatus* had produced eight and 10 leaves respectively by the end of March 1982 (Figure 3.17). Severe drought had resulted in the death of the majority of non-irrigated tillers by this time (Figure 3.2).

3.3.5.3 Rate of leaf emergence and leaf longevity

The rate of leaf emergence and leaf longevity is of obvious importance to grazing management since the timing of each defoliation should, presumably, bear some relation to the current rate of appearance of leaves and their longevity (Anslow, 1966).

The rate of leaf emergence (R) can be calculated by differentiating the cumulative total number of emergent leaves per tiller (x) with respect to time (t)

$$\text{i.e.}\quad R = dx/dt$$

This procedure was undertaken for the various populations of permanently marked and non-destructively sampled tillers that were initiated in spring 1981 (Figure 3.17). The results are presented as the reciprocal of R (days between emergence of leaves) in Figure 3.18.

Leaves on irrigated *T. triandra* tillers emerged at intervals of approximately 10 to 20 days during the spring, summer and autumn after tiller initiation, although the rate of emergence was most rapid during late summer/autumn. The interval between leaf emergence increased considerably during the following winter (Figure 3.18). Review of the literature (Anslow, 1966) suggests that this was probably a result of cold winter temperatures. Figure 3.18 suggests a true interval of 110 days between the emergence of successive leaves during winter. This slow rate comes about as a result of mathematical differentiation of the functions in Figure 3.17. In practice, however, the midwinter period when no leaves emerged was not maintained for as long as 110 days. The longest time intervals (observed from the raw data) between emergence of successive leaves on irrigated reproductive and vegetative sub-populations of *T. triandra* tillers during winter 1982 were 77 and 103 days respectively. During spring 1982 the time interval between emergence of successive leaves dropped once more, but this was short lived in the case of the reproductive population where leaf emergence ceased after flowering. Vegetative tillers continued to produce leaves during spring until these tillers senesced the following summer (Figure 3.18).

Non-irigated *T. triandra* tillers produced new leaves every 24 days until summer 1981/82, when drought resulted in the cessation of leaf production (Figure 3.18). This was followed by mortality of nearly all tillers (Figure 3.2).

Irrigated populations of *S. fimbriatus* tillers produced new leaves approximately every 20 days during the spring and summer after tiller initiation. In autumn 1982, flowering resulted in cessation of leaf production in the reproductive sub-population of tillers. The vegetative sub-population of irrigated tillers continued to produce new leaves every two to three weeks during the autumn, but as with *T. triandra*, the rate of leaf production dropped considerably during winter 1982. The rate of leaf emergence of the vegetative *S. fimbriatus* tillers increased once more as temperatures rose during the subsequent spring and summer (Figure 3.18).

The rate of leaf emergence on non-irrigated *S. fimbriatus* tillers was between 20 and 30 days per leaf until the late summer after tiller emergence, when drought resulted in the cessation of leaf production (Figure 3.18) followed by tiller mortality (Figure 3.2).

In general terms, leaves emerge in both species during the growing season at apparently two to three week intervals, provided tillers are experiencing no moisture stress. However, both moisture stress and declining temperature during winter cause a considerable drop in the rate of leaf emergence.

Determination of leaf longevity is more complex. In order to establish the longevity of emergent leaves, it is necessary to calculate the dates of emergence and senescence of each successive leaf. The mean dates of emergence of succussive leaves ($tx_1....tx_n$) in the respective populations of permanently numbered and non-destructively sampled tillers that were initiated in spring 1981 can be determined from the cumulative total number of leaves per tiller (x) (Figure 3.17); where tx_n is the date of emergence of the nth leaf.

In order to establish the date of senescence of each successive leaf ($tz_1 \ldots tz_n$), it is necessary first to determine the cumulative total number of dead leaves per tiller (z). This can be calculated for the non-destructively sampled tiller populations from the difference of the integrals of the cumulative total number of leaves produced per tiller (x) (Figure 3.17) and the number of living green leaves attached per tiller (y) (Figure 3.16).

$$\text{i.e.} \quad \int Z = \int X - \int Y$$

The cumulative total number of dead leaves per tiller calculated in this manner for the various populations of permanently marked tillers is presented in Figure 3.19. From this figure it is possible to determine the date of senescence of each successive leaf ($tz_1 \ldots tz_n$), where tz_n is the date of senescence of the nth leaf.

The longevity (L) of leaves 1 to ....n can now be calculated as;

$$L_1; \ldots; L_n = (tz_1 - tx_1); (tz_2 - tx_2); \ldots; (tz_n - tx_n).$$

The mean longevity of leaves emerging at different times of the year in the various non-destructively sampled tiller populations are presented in Figure 3.20. The longevity of spring and summer emerging leaves of irrigated *T. triandra* tillers was between 70 and 90 days. However, the longevity of autumn emerging leaves dropped to a low of about 60 days, possibly a result of low winter temperatures causing premature senility of these leaves once they had fully expanded. In apparent contradiction to this, the longevity of late autumn and winter emerging leaves increased considerably (approximately 140 days). However, this phenomenon is explained as follows: with the onset of winter 1982, low temperatures resulted in virtual cessation of meristematic activity and therefore a corresponding slow rate of leaf emergence (Figure 3.18). This resulted in a decrease in the number of living leaves attached to tillers (Figure

3.16), which would have been promoted by premature senility of already fully expanded leaves (Figure 3.20) caused by low winter temperatures. The remaining living leaves would thus have consisted largely of young unexpanded leaves whose tips emerged during autumn 1982. Since the meristematic areas of young leaves are protected within leaf sheaths (Langer, 1972), and because of slow meristematic activity in winter, these leaves were able to remain viable within the protection of the leaf sheaths of older leaves during winter, despite the fact that their tips had already emerged.

During spring 1982, the longevity of newly emerged *T.triandra* leaves again dropped to about 80 days per leaf (Figure 3.20).

The longevity of leaves of non-irrigated *T. triandra* tillers was approximately 50 days per leaf and already declining when sampling began during spring 1981. Leaf longevity declined progressively with increasing aridity during summer (Figure 3.20), until drought resulted in tiller mortality.

Spring and summer emerging leaves of irrigated *S. fimbriatus* tillers remained viable for about 70 to 90 days. The reproductive sub-population of tillers ceased producing leaves after flowering had taken place in autumn 1982. However, the vegetative sub-population continued to produce leaves, and the longevity of these leaves followed similar trends to those recorded on irrigated *T. triandra* tillers; that is leaves emerging in late autumn and winter survived for considerably longer than those emerging in the growing season. The reasons for this are probably the same as those stated for *T. triandra*. The following spring (1982), longevity of newly emerged leaves on irrigated *S. fimbriatus* tillers reverted to approximately 80 days per leaf (Figure 3.20).

The longevity of leaves on non-irrigated *S. fimbriatus* tillers was also approximately 80 days per leaf when sampling began during spring 1981. However, as the summer approached, drought caused premature senility of leaves and their longevity dropped considerably (Figure 3.20).

Regarding leaf longevity in general terms, leaves of both species can remain viable for approximatley 80 days during the growing season. However, moisture stress, and to a lesser extent the onset of cool winter temperatures, result in premature senility of leaves. Leaves emerging in late autumn and winter remain protected within leaf sheaths in a semi-dormant, unexpanded state until the end of winter. The longevity of these leaves is therefore considerably greater than that of leaves during the growing season.

In terms of grazing management, if one assumes that all green leaves contribute to plant growth, then periods of absence between grazing should be long enough to allow the rate of leaf senescence to equal the rate of leaf emergence. Before this occurs, green leaves would still be accumulating on tillers, and presumably defoliation would serve no purpose other than diminishing the means whereby the plant can trap light energy for growth and replenishment of carbohydrates. Even if older green leaves are not particularly useful photosynthetically, they are continuously being replaced by newly emerging green leaves. Furthermore, in sweetveld, where dead grass leaves remain palatable, no forage would be lost by withholding veld from grazing until such time as decay causes abscission of the oldest leaves.

Thus, in terms of tiller leaf dynamics, periods of absence in sweet grassveld should be at least long enough for green leaves to accumulate to the point where the rate of leaf emergence is equal to the rate of leaf senescence, but they should also be short enough so that forage is not lost through abscission of the oldest leaves.

Unstressed vegetative tillers of both *T. triandra* and *S. fimbriatus* accumulated between four and six green leaves per tiller, and leaves emerged at two to three week intervals. Consequently, vegetative tillers would be expected to grow for approximately 80 to 90 days before the rate of leaf senescence equalled the rate of leaf emergence. This period of time coincided with the recorded longevity of the individual leaves of both species (Figure 3.20).

After senescence, leaves do not abscise immediately, but accumulate on tillers until their number is at least equal to the number of green leaves per tiller. Thus, assuming dead leaves are palatable, a period of absence of considerably more than 80 to 90 days could be tolerated without loss of grazing.

The implication is that on sweetveld growing without moisture stress, from a point of view of leaf growth, periods of absence between grazing should be at least three months.

In practice, however, three consecutive months without moisture stress are rarely experienced in these situations. The effect of moisture stress on tiller leaf dynamics is to slow down the rate of leaf emergence and reduce leaf longevity (Figures 3.18 & 3.20). This suggests that the equilibrium stage, where the rate of leaf senescence equals the rate of emergence, would be reached sooner in a normal than in an unstressed situation. This would be true should the growth that does take place, commence immediately after grazing. Rainfall, however, is unpredictable and periods of two or more months without effective rain during the growing season in sweetveld, are not uncommon. It is therefore concluded that periods of absence of at least three months during the growing season would still be desirable, particularly since even if regrowth did take place immediatly after grazing, early senescing leaves would not abscise before the next grazing took place. This is illustrated by the fact that even in an unstressed situation, it took at least six months for the rate of accumulation of dead leaves to slow down through leaf decay (Figure 3.15B).

Two exceptions to this principle are likely to apply. Firstly, during winter, the rate of leaf emergence slows down considerably (Figure 3.18), while the rate of senescence of expanded leaves increases (Figure 3.20), and presumably the rate of leaf abscission is likely to remain constant. The implication is that little forage will accumulate, even where there is no moisture stress, while decay will continue to take place. This suggests that there is little objective in long periods of absence in winter, other than to maintain a fodder bank in case of drought the next spring.

The second exception is where severe drought occurs, such as that during summer 1981/82. Here leaf emergence virtually ceased (Figure 3.18) and green leaves senesced rapidly (Figure 3.20), followed by tiller mortality (Figure 3.2). However leaf decay presumably continued at a constant rate, or even accelerated as a result of hot dry conditions, particularly when accompanied by berg winds. Under these circumstances no forage accumulation would take place, while forage loss through leaf decay would continue or even accelerate and there would thus be no purpose in withholding such veld from grazing in order to increase forage production. Maintaining a fodder bank for fodder-flow purposes could, however, still be necessary, despite a net loss of grazing through leaf decay.

3.3.5.4 Summary of results

i. Leaf area per tiller increases after tiller initiation in spring and reaches a peak the following autumn, whereafter it declines during the winter.

ii. Leaf area per tiller is greater under unstressed conditions than where moisture stress occurs, and the leaf area of *T. triandra* tillers is greater than that of *S. fimbriatus* tillers.

iii. Green leaves attached to *T. triandra* tillers increase in number through the spring and summer after tiller initiation, reaching a maximum of between four and six leaves per tiller. This number remains constant or drops during the next winter, and green leaves senesce completely after flowering the next spring.

iv. Green leaves on *S. fimbriatus* tillers also increase during the spring and summer after tiller initiation, reaching a peak of four to five leaves per tiller. The number decreases during the following autumn and winter and green leaves senesce completely on tillers that flower during the autumn after tiller initiation. Tillers that do not flower produce more green leaves during the next spring.

v. Severe drought causes senescence of all green leaves.

vi. Dead leaves attached to tillers increase in number during the spring and summer after tiller initiation, reaching a number approximately equal to that of the green leaves attached to the tillers. Thereafter abscission through desiccation causes the number of dead leaves per tiller to remain fairly constant.

vii. During the spring and summer after tiller initiation, leaves emerge at a rate greater than the rate of leaf senescence which in turn is greater than the rate of leaf abscission. During the rest of the period of vegetative growth, the rate of emergence is less than or equal to the rate of senescence which is less than the rate of abscission, implying that at least some forage is lost through leaf drop.

viii. Unstressed reproductive tillers of *T. triandra* and *S. fimbriatus* produce 23 and 14 leaves during their life cycles respectively.

ix. Leaves emerge at approximately two to three week intervals on unstressed tillers of both species. Both moisture stress and declining winter temperatures result in a considerable drop in this rate.

x. Individual leaves live for approximately 80 days. Both moisture stress and, to a lesser extent, the onset of cool winter temperatures result in premature senility of leaves. Juvenile leaves emerging during the winter period have their meristematic areas protected by older leaf sheaths, and since growth is very slow at this time, the longevity of these leaves is considerably greater than that of leaves emerging during the growing season.

xi. Tiller leaf dynamics indicate that periods of absence from grazing should be at least three months. This period can be reduced during winter or in the case of severe drought.

3.3.6 Root development

Root development of *T. triandra* and *S. fimbriatus* was measured in three trials. The development of individual tiller roots was recorded by sequential sampling of pots in the greenhouse (Experiment 4), as well as by sequential removal of marked spring initiated tillers under irrigation in the field (Experiment 5). Root development in tiller populations was recorded from the total mass of all root material in pots (Experiment 4), as well as by removal of soil strata on sites dominated by the two respective species (Experiment 6).

3.3.6.1 Number of roots per tiller

The number of roots attached to spring initiated tillers of *T. triandra* and *S. fimbriatus* growing in pots in the greenhouse (A) and under irrigation in the field (B) are presented in Figures 3.21 (log scale) and 3.22 (arithmetic scale).

There were no significant differences between species within treatments regarding the number of roots produced per tiller or the timing therof (Figure 3.21). However, tillers of both species growing in the field produced more roots earlier in the season than those in the greenhouse (P<0,05). After midsummer, differences between treatments ceased to be significant. Tillers of both species growing in the greenhouse subtended approximately four roots each while in the field; *T. triandra* and *S. fimbriatus* produced six and three roots per tiller respectively. In the field, both species had subtended two roots per tiller respectively. In the field, both species had subtended two roots per tiller by the midsummer after initiation.

The general trend in the number of roots produced by irrigated *T. triandra* tillers in the field was similar to that recorded by Tainton & Booysen (1965*a*) in the Natal Tall Grassveld.

3.3.6.2 Root length

The mean length of individual roots attached to spring initiated tillers of *T. triandra* and *S. fimbriatus* growing in pots in the greenhouse (A) and under irrigation in the field (B) are presented in Figures 3.23 (log scale) and 3.24 (arithmetic scale). There were no significant differences in root length between species within treatments (Figure 3.23). The mean length of roots in the field were, however, significantly greater than those in the greenhouse up to midsummer ($P<0,05$). Thereafter, there was no significant difference between treatments (Figure 3.23).

The results recorded after midsummer are, however, misleading, particularly in the field experiment. After this time root elongation had reached the stage where it was difficult to "wash" soil away from roots without breakage, and in the case of the field trial, all roots growing laterally or deeper than 200mm would in any event have been severed by the auger. The recorded results (Figure 3.24) are thus an underestimate of the actual root elongation that took place from summer onwards. In the case of tillers growing in pots (Experiment 4), individual root lengths of 250 to 300mm were not uncommon approximately one year after tiller initiation, provided "breakage" had not taken place in the "washing" process. The relatively wide confidence limits of mean root length recorded on this treatment (Figure 3.23A) are likely to be a reflection of the variability in recorded lengths as a result of root breakage.

On tillers growing in the field (Experiment 5), maximum individual root lengths varied between 100 and 150mm and breakage as a result of removal with an auger was generally apparent. Consistent breakage of roots in this trial is reflected by relatively narrow confidence limits of mean root lengths (Figure 3.23B).

In addition to variability in root length as a result of breakage, it was also apparent that the presence of short unbroken roots (shorter than 50mm) together with long roots (greater than 100mm) on the same tiller was a fairly common occurrence.

The fact that root development (both in terms of root number and root length per tiller) took place earlier in the field than in the greenhouse is difficult to explain, particularly since intense clippings of tufts on both treatments during the preceding winter resulted in above ground senescence of all parent tillers. The explanation may be associated with the fact that parent tillers in the greenhouse had better developed root systems than those in the field, a result of more favourable conditions prior to commencement of the trial. Since, according to the literature, tillers predecease their root systems (Troughton,1977), the implication is that new tillers in the greenhouse may have been more adequately supplied with water and minerals from the still viable roots of parent tillers than those in the field, thus obviating the necessity for new tillers to develop their own root systems in the former case.

That marked tillers both in the field and in the greenhouse had emerged after midwinter, was not in doubt. This was because only tillers with intact oldest leaves were marked in spring. Had these tillers emerged before midwinter, at least one of the leaves would have shown signs of clipping.

3.3.6.3 Root mass

The total mass (root and shoots) of tillers of *T. triandra* and *S. fimbriatus* growing in pots in the greenhouse (A) and under irrigation in the field (B) are presented in Figures 3.25 (log scale) and 3.26 (arithmetic scale). The mass of these tillers partitioned between roots and shoots is presented in Figures 3.27 (log scale) and 3.28 (arithmetic scale) respectively.

Between species, the only significant difference was that *T. triandra* tillers in pots had a lower total and shoot mass than those of *S. fimbriatus* during the autumn and winter after tiller initiation (Figures 3.25 & 3.27). This was a result of the latter species flowering at this time, and there was no significant difference between species once they had both flowered.

Within species, tillers growing in the field had greater total root masses than those in pots up to about midsummer after tiller initiation ($P<0,05$). Therafter, the significant difference disappeared (Figure 3.25 & 3.27), but the trend was reversed so that the final mass of tillers in pots was apparently considerably greater than that of tillers in the field (Figure 3.26 & 3.28). The more rapid early development of tillers in the field is difficult to explain, particularly in view of the favourable environmental conditions in the greenhouse.

The recorded mass of roots per tiller was considerably less than that of shoots throughout the life of tillers of both species and in both treatments. This result is misleading, and is probably a consequence of breakage of both primary roots and root branches during the harvesting process. Root breakage, resulting in erroneous recordings of root mass per tiller, is illustrated by the fact that confidence limits of root mass are considerably wider than those of shoot mass (Figure 3.27). The extent to which recorded root mass per tiller (Figure 3.28) is an underestimate of actual root mass per tiller is difficult to assess. In terms of the literature review (Section 3.13), the mass of roots produced by a tiller probably represents at least 50% of the carbon assimilated by that tiller, and these roots represent about 50% of all root material in the soil, so that at any one time, the biomass of root material is greater than the biomass of shoot material.

The total biomass (living and dead) of root and shoot material in populations of *T. triandra* and *S. fimbriatus* tillers was recorded in pots in the greenhouse (Experiment

4). Since sampled pots were replicated, and since a new set of pots was destructively sampled at each date, analysis of variance of the data was possible. The main effects of plant age ($P<0,05$) plant part (shoot and roots) ($P<0,05$) and grass species ($P<0,05$) on recorded biomass in pots were also statistically significant. In addition, the interactions between harvest date and plant part, and between harvest date and species were also statistically significant ($P<0,05$). These results are presented graphically as untransformed values of splined third order polynomials fitted to logarithmically transformed primary data (Figure 3.29). The least significant differences listed in Figure 3.29 are those between any two of the means used to construct the various functions. These are thus those of the second order interaction in the case of total mass (Figure 3.29A) and of the third order interaction in the case of partitioned mass (Figure 3.29B)

The fact that total plant mass increased during the summer and autumn after tiller initiation, but changed little (*T. triandra*) or dropped (*S. fimbriatus*) the following winter, is attributable to the drop in root mass and not shoot mass (Figure 3.29B) and is a reflection of the significant interaction between the main effects of harvest date and plant part. The maximum total biomass of *S. fimbriatus* in pots was significantly greater than that of *T. triandra*, a trend that was not observed in field experiments.

Root mass in pots of both species was greater than shoot mass during the summer and autumn after tiller initiation. However, a drop in root mass the following winter suggests that the roots of aerially senescent parent tillers were still present during the autumn following tiller senescence, but thereafter decomposition took place. In this context it is of note in the literature that Singh & Coleman (1977) recorded considerable root mortality during winter in North American grassland.

After spring initiated tillers of both species had flowered, root mass in pots continued to increase (Figure 3.29B) again suggesting that root growth continued after senescence of aerial growing points of tillers.

Shoot mass in pots increased steadily in both species during summer and autumn after tiller initiation. *S. fimbriatus* shoot mass reached a maximum after flowering in late autumn, while *T. triandra* shoots continued to grow through the winter, reaching maximum biomass the following spring after flowering.

Regarding the interaction between the main effects of harvest date and species and between harvest date and plant part, the implication is that the change in total mass in pots with time was not consistent between species, and that the ratio of roots to shoots did not remain constant as time progressed. However, the non-significant interaction between plant part and species suggests that the root:shoot mass ratio while changing with time, remained fairly consistent between species (Figure 3.30).

In both species, the mass of roots in pots was at all times greater than the mass of non-desiccated shoot material. The fact that root mass was greater than shoot mass even during early summer, despite the fact that roots on spring initiated tillers only started developing at this time (Figure 3.22A), suggests that a considerable number of roots of older parent tillers must have been present. As new shoots developed in summer, the root:shoot ratio increased, reaching a peak the following autumn (Figure 3.30). The ratio decreased during winter, probably as a result of decay of older roots. After flowering had taken place, the ratio increased once more, a combined result of aerial desiccation and continued growth of roots (Figure 3.29). There is, however, a lack of quantitative information on the rate of root decomposition in the soil (Parkinson, 1977).

The above results provide comparative data regarding root biomass of *T. triandra* and *S. fimbriatus* with changing seasons and progressively ageing tiller populations. However, since they were recorded in pots in the greenhouse, they give no indication of the absolute mass of roots in veld dominated by the two respective species. This information can be calculated from the recorded total mass of roots in 40cm3 soil cores removed from sites dominated by the two species (Experimant 6).

The total mass of roots in winter in a pure *T. triandra* stand rested for 12 months was 5 955kg/ha, as opposed to 4 473kg/ha in an *S. fimbriatus* stand. The difference between the two species was statistically significant ($P<0,01$; CV 22%). The results reflect the mass of roots in the top 40cm of soil but it will be shown that density of roots below this depth is of minor consequence.

It is of note that the maximum above-ground dry matter yields recorded at the same sites during the same season (1981/82) were 1 470 and 270kg/ha for *T. triandra* and *S. fimbriatus* respectively (4cm clipping height) (results reported in Chapter 7). Danckwerts & Trollope (1980) estimated that after clipping to a height of 4cm at least 1 000kg/ha of herbage remained above the soil surface. Assuming remaining tuft crowns accounted for a further 1 000 kg/h, the maximum above ground "standing crop" accumulated during the 1981/82 growing season would still only have been approximately 50% of the below-ground biomass during winter 1982.

3.3.6.4 Vertical distribution of roots in the soil

The distribution of root material (living and dead) at different depths in the soil was determined from stratified soil cores (40cm3) removed during winter 1982 from non-irrigated pure stands of *T. triandra* and *S. fimbriatus* rested for 12 months (Experiment 6).

Because root density decreased sharply with increasing soil depth (Table 3.2), the variance of the primary data also diminished with increasing soil depth. Thus, in order to conduct analysis of variance, the data were log transformed.

This analysis (Table 3.2) showed the main effects of soil depth and species both to be statistically significant (P<0,01). Root density dropped markedly with increasing soil depth, and the density of *T. triandra* roots in the soil was greater than that of *S. fimbriatus* roots. The latter result is expected since it has already been shown that the total mass of *T. triandra* roots per unit area, was greater than that of the other species.

The interactions between the effect of rooting depth and species on root density was nearly, but not quite significant. The statistical result is thus that *T. triandra* had consistently more roots than *S. fimbriatus* at all depths, but the trend was for the difference in the logs of the density of roots between species to increase with increasing soil depth (Table 3.2). Considering the untransformed values in relative terms, the density of *S. fimbriatus* roots was between 80% and 100% of the density of *T. triandra* roots in the top 10cm of soil. However, at all depths between 10cm and 40cm, the density of *S. fimbriatus* roots was less than half of the density of roots of the other species. In addition, in terms of the absolute mass of roots (as opposed to density), only 70,6% of *T. triandra* roots occurred in the top 10cm of soil, while 83,4% of *S. fimbriatus* root occurred in the same zone. It is thus concluded that despite a statistically non-significant interaction between the effect of species and depth on root densities, the data suggest that the proportion of *T. triandra* roots occurring at soil depth below 10cm is greater than that of *S. fimbriatus* roots.

Although basal cover at the two sites was different, this was not considered to affect differences in rooting densities. This is because competition between species was eliminated by physical removal of all species other than *T. triandra* and *S. fimbriatus* at each site respectively. Roots of the two species were thus allowed a period of 12 months to exploit the soil profiles at the two respective sites. In addition, the density of both species was fairly high before the trial commenced, comprising more than 50% of living basal cover.

3.3.6.5 Summary of results

i. Spring initiated tillers of both species begin producing roots during the summer after initiation.

ii. Both *T. triandra* and *S. fimbriatus* tillers produce approximately four to six roots.

iii. Individual root length can reach 300mm or more, but the occurrence of both short and long roots on the same tillers is common.

iv. The total biomass of roots in the soil is considerably (at least twice) greater than the total aerial biomass at any one time. Total root biomass, however, includes both living and dead root material, and functional roots may constitute about half of the total.

v. Tillers predecease their roots so that root longevity is apparently greater than that of the tillers.

vi. Considerable root decay apparently takes place during winter.

vii. The root:shoot mass ratio is approximately the same in both *S. fimbriatus* and *T. triandra*.

viii. The majority of roots of *T. triandra* and *S. fimbriatus* occur in the top 10cm of soil. *T. triandra*, however, has relatively more roots at lower soil depths than *S. fimbriatus*.

3.3.7 Secondary tiller development

Secondary tiller development of *T. triandra* and *S. fimbriatus* was monitored on sequentially harvested primary tillers initiated during spring 1980 both under irrigation and unamended moisture conditions (Experiment 1). The number of secondary tillers per primary tiller (A), the mean height of lateral tillering (B) and the mass of secondary tillers per primary tiller (C), are presented in Figures 3.31 (log scale) and 3.32 (arithmetic scale).

Within species, secondary tiller development followed similar trends and was not significantly different between the two moisture treatments. Between species, however, secondary tiller development was considerably different (Figure 3.31).

Secondary tillers began to appear on spring initiated primary tillers of *T. triandra* during the following autumn, but these were both very few and appeared inconsistently until flowering took place the following spring. The number of secondary tillers per primary tiller then increased sharply to about two per tiller (Figure 3.32A). Spring initiated *S. fimbriatus* tillers also began producing secondary tillers the following autumn, but again these were few in number. Unlike *T. triandra*, however, the number of secondary tillers per primary tiller remained low even after flowering of the reproductive population of *S. fimbriatus* tillers (Figures 3.32A). It is possible that this result is confounded by the fact that only about half the population of spring initiated *S. fimbriatus* tillers flowered the following autumn, the rest remaining in the vegetative condition.

The increased rate of tillering of *T. triandra* tillers after flowering was accompanied by a sharp rise in the height at which lateral tillers formed on the parent tiller (Figure 3.32B). The height of lateral tillering at this stage (in excess of 100mm) was such that secondary tillers would not have been able to establish their own root systems. This suggests that *T. triandra* requires utilisation even after a single year's rest in order to persist vegetatively. In contrast, the height of lateral tillering of *S. fimbriatus* remained near the soil surface even after flowering (Figure 3.32B), suggesting that this species may not require utilisation to persist vegetatively.

The mass of secondary tiller per primary tiller of *T. triandra* increased progressively as the number of secondary tillers increased. In *S. fimbriatus*, however, this mass remained fairly constant (Figure 3.32C). Since the number of secondary tillers per primary tiller in the latter species also remained fairly constant (Figure 3.32A), these results suggest that the mass of secondary tillers themselves did not increase markedly while they were still dependent on living primary tillers.

In general, the results suggest that *T. triandra* is a more prolific tillering species than *S. fimbriatus*, but that the former species requires utilisation in order that secondary tillers should survive.

3.3.7.1 Summary of results

i. Primary tillers of both *T. triandra* and *S. fimbriatus* produce few lateral tillers while still in the vegetative stage. Flowering promotes prolific tillering in the case of the former species but not the latter.

ii. The height at which lateral tillers develop on primary tillers after flowering of *T. triandra* is such that secondary tillers would not be able to establish their own root systems, suggesting that utilisation is necessary for the species to persist vegetatively. *S. fimbriatus* tillering remains near the soil surface even after flowering.

iii. Individual secondary tillers do not grow markedly when still apparently dependent on living primary tillers.

CHAPTER 4

ANALYSIS OF TILLER GROWTH OF UNUTILISED KEY GRASS SPECIES

4.1 Growth analysis - its relevance to pastoral agriculture

"Plant growth analysis" is an informal title used to describe a range of quantitative techniques developed to derive comparative information about the growth of plants under natural or artificial conditions. These techniques require the simplest of basic data (Hunt, 1979). The traditional role of growth analysis has primarily involved derivation of indices for describing dry matter production, leafiness and leaf efficiency (Hunt, 1982). The general objective of such analysis is to provide information regarding how fast and efficiently plants work (Evans, 1972).

The practical significance of growth analysis has been questioned. Woolhouse (1980) suggested that it is "at best a useful method for obtaining preliminary descriptions of plant growth as a framework for more detailed studies of the underlying biological processes, and at worst an end to itself leading to nothing". Hunt (1982) examined the justification for continuing with plant growth analysis, when more recent and elaborate methods, such as gasometric exchange studies, can be used to measure plant photosynthetic efficiency. The author pointed out that while gasometric observations provide the most precise means of studying short term apparent assimilation, they cannot replace growth analysis as a long term measure of photosynthesis. Furthermore, Evans (1976) pointed out the problems arising in interpretation of observations made over periods of minutes and hours when trying to relate them to plant growth over months and years. The author went on to suggest that the study of undisturbed growing plants was the only means of dealing with the natural plant/environment system without external interference over periods of the order of a week or longer.

In pasture crops the material harvested for economic yield (leaves) is also the basis whereby light energy is trapped to synthesise assimilates for formation of new plant tissue (Ryle, 1964). In order to maximise yield from a pasture, growth after defoliation must commence as quickly as possible, and a rapid rate of regrowth must be maintained up to the time of the next defoliation (Booysen, 1966). Rapid commencement of growth after defoliation will depend on the availability of reserve carbohydrates as well as the remaining photosynthetic substrate (green leaves). Once new growth has become independent of reserve carbohydrates, regrowth will be dependent on the leaves themselves for energy for new growth. The rate of this regrowth will be determined by the size of the photosynthetic substrate (green leaf area) and the efficiency with which it can assimilate light energy for manufacture of substrate (Booysen, 1966). Growth analysis of pasture plants is thus of obvious importance in achieving the objective of maximised forage yield since it will provide a means of establishing the optimum frequency and degree to which plants should be defoliated.

In this chapter, the growth of unutilised tillers of *T. triandra* and *S. fimbriatus* in the False Thornveld of the Eastern Cape is analysed in an attempt to provide additional information towards optimal utilisation of semi-arid grassveld.

4.2 Plant growth indices

Fundamental to the field of growth analysis is a series of measurements of plant size, form or number (the primary data). From these, one or more of the following principle types of derived quantities can be constructed:

i. simple rates of change involving one variate and time;

ii. simple ratios between two variates; and

iii. compounded rates of change involving more than one variate (Hunt, 1982).

Implicit in the objective of plant growth analysis (analysis of the speed and efficiency of plant growth) is measurement of the growth rate of plants. The rate of change of individual plant mass per unit time is termed the absolute growth rate (AGR), and in calculus terms is defined as:

$$AGR = dM/dt$$

Absolute growth rate is thus the instantaneous slope of the plot of total mass per plant (M) against time (t); a plain and simple measure of the rate of increase in mass (Hunt, 1982). Absolute growth rate is thus a derived quantity of "type i" listed above.

Absolute growth rate is generally considered to give little information concerning the physiological efficiency of plants in terms of dry matter production, since simple observation has shown that very often AGR is simply proportional to plant size (Causton & Venus, 1981). It is thus a poor tool for comparative purposes unless the plants being compared are of the same size. The deficiencies of AGR were recognised by Blackman (1919) who developed an index to describe the increase in mass per unit of plant mass per unit time. Briggs, Kidd & West (1920) termed the parameter relative growth rate (RGR) and it is most simply expressed in calculus nomenclature as an instantaneous value:

$$RGR = 1/M \quad dM/dt$$

Relative growth rate is a "Type iii" expression of those listed above, and provides a convenient integration of the combined performance of the various parts of the plant. It is particularly useful when the need arises to compare the growth rate of species and treatments where there are plants of different sizes. The index, however, provides no information of the causal processes that contribute to the plant's growth performance. Relative growth rate thus treats all the mass of the plant as being equally productive. However, as plants grow, the proportion of purely structural material they contain increases. A consequence of this is that RGR generally declines with increasing plant age (Hunt, 1982).

To overcome this problem, an index was derived to describe the efficiency of plants in terms of the size of the photosynthetic substrate (green leaf area). This quantity is commonly termed net asssimilation rate (NAR) (Gregory, 1926), or unit leaf rate (Briggs *et al.*, 1920). Like RGR, it is a "type iii" quantity of those listed above and the expression for its instantaneous value is:

$$NAR = 1/L \quad dM/dt$$

where L is the total living leaf area present on the plant (Hunt, 1982).

Net assimilation rate is thus an estimate of the carbon assimilatory capacity of the leaves. This index, together with the extent of leafiness of the plant , will therefore determine its overall RGR. Alternatively, starting with RGR, some index of leafiness is the other quantity that can be derived together with NAR, to produce an informative subdivided summary of the plant's performance. Briggs *et al.* (1920) termed such an index of leafiness "leaf area ratio", which they defined as the ratio of total leaf area to total plant dry mass, a "type ii" quantity of those listed above. In general terms, LAR represents the ratio of photosynthesising to respiratory material within the plant.

Simply expressed, the growth rate of a plant depends simultaneously on both the efficiency of its leaves as producers of new material (NAR) and upon the leafiness of the plant itself (LAR). Theoretically therefore:

$$RGR = NAR \times LAR \text{ (Hunt, 1982)}$$

Many other quantities have been derived for use in plant growth analysis (Hunt, 1978; 1982; Causton & Venus, 1981; and Evans, 1982). However, the objective of this investigation is not to review plant growth analysis, but to use it as a tool to assist in explaining the growth of key grass species in the False Thornveld of the Eastern Cape from a viewpoint of maximising dry matter production. For this purpose, the four derived quantities briefly described (AGR, RGR, NAR, and LAR) will be used. These indices will be calculated from primary measurements of tiller mass and tiller leaf area.

4.3 Derivation of functions to describe plant growth indices

Growth analysis can be implemented in practice using two different methodologies, the classical and functional approaches (Causton & Venus, 1981). In the former approach, mean values of the required quantities are derived over a period intervening between two harvests. The harvests are relatively infrequent and large, with much replication of measurements (Hunt, 1978). Such growth analysis methods were originally designed to be independent of underlying mathematical functions because of the considerable difficulties of function fitting in practice at that time. However, in recent decades, computer technology has resulted in increasing use of curve fitting methods, and this has given rise to the functional approach (Causten & Venus, 1981). In this approach, harvests supplying data for curve fitting involve less replication of measurement, but at more frequent intervals (Hunt, 1978). Instantaneous values and their errors are then derived from equations fitted to the observed data. Reviews covering both approaches have been provided by Radford (1967), Evans (1972), Hunt (1978) and Causton & Venus (1981).

Parsons & Hunt (1981) provided a complete computer methodology for fitting splined cubic polynomial exponentials to lengthy series of primary data, the application and rationale of which is described in the previous chapter (Section 3.2.7). In addition to fitting functions to primary data, the methodology of Parsons & Hunt (1981) provides the means of deriving AGR, RGR, NAR and LAR by manipulating the equations of the original fitted curves. Detailed application of this methodology is described by Hunt & Evans (1980).

In this chapter, AGR, RGR, NAR and LAR are derived for various populations of unutilised *T. triandra* and *S. fimbriatus* tillers using the method of Parsons & Hunt (1981). Many of the functions fitted to the primary data are presented in the preceding chapter.

4.4 Growth analysis of spring initiated tillers

4.4.1 Procedure

The data used in this investigation are those already used to characterise the ontogeny of tillers of *T. triandra* and *S. fimbriatus* initiated during spring 1980 and sequentially harvested both under unamended moisture conditions and without moisture stress. The details of the procedure are described in Section 3.2 (Experiment 1). The data are particularly suited to the functional approach to growth analysis in view of the high frequency of sampling (fortnightly). Application of the classical approach to such data would be misleading since absolute changes between harvest dates were small, and chance variation in primary data would have resulted in erroneous estimates of growth analysis indices during inter-harvest periods.

4.4.2 Results and Discussion

4.4.2.1 Primary data

Curves fitted to the natural logarithms of total tiller mass and green leaf area of irrigated and non-irrigated tillers of *T. triandra* and *S. fimbriatus* are presented in Figures 3.7A and 3.12, and the results have been discussed in Sections 3.3.4 and 3.3.5.

Of note in terms of the growth analysis to follow, is the fact that tiller mass (Figure 3.7A) reflects only above-ground mass and does not include root mass. The growth analysis functions to follow are therefore a reflection of the growth efficiency of tillers in terms of above-ground material only. While this is a limitation, in pastoral agriculture the usable portion of plants is that which occurs above ground. The pastoralist is therefore primarily concerned with the efficiency of production of above-ground material. It is, however, conceded that below-ground growth probably plays a role in determining above-ground yield, particularly during the initial stages of growth after defoliation when carbohydrate reserves presumably play an important role.

4.4.2.2 Absolute growth rate of tillers

Absolute growth rates of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers initiated during spring 1980 are presented in Figure 4.1.

In both species and on both treatments, AGR increased rapidly during the spring and summer after tiller initiation, reaching a peak in mid- to late summer on irrigated treatments and during late summer/autumn on non-irrigated treatments. The rate then dropped sharply, but on the non-irrigated *T. triandra* treatment and on both *S. fimbriatus* treatments, AGR increased once more when flowering took place during the spring and autumn of the year after tiller initiation, respectively (Figure 4.1). The latter phenomenon was possibly a result of mobilisation of underground storage carbohydrates during the time of flowering and/or possibly also of greater photosynthetic efficiency of culm leaves produced at this time. In any event, it was not a result of increased leaf area since this parameter decreased at the time of flowering (Figure 3.12).

In both species, the maximum AGR achieved was greater on irrigated treatments than on non-irrigated treatments, particularly in the case of *T. triandra*. The maximum AGR achieved on the *T. triandra* treatment was considerably greater than on any other. Despite the fact that AGR was lower on non-irrigated treatments, growth rate on these treatments nevertheless increased consistently through to autumn and thereafter decreased, also consistently, until the onset of flowering (Figure 4.1). However, this was probably a result of "smoothing" of the primary data (Figures 3.7A and 3.12), since subjective observation revealed that growth during the growing season took place sporadically depending on the presence or absence of water. The implication is that there was considerable absolute variation in AGR between harvest dates on non-irrigated treatments, but that fitting curves to primary data eliminated this variability, and at the same time resulted in lower apparent growth rates than on irrigated treatments throughout the vegetative life of tillers.

On non-irrigated treatments, the maximum derived AGR for the two species was similar. However, *T. triandra* tillers maintained a high AGR for a longer period of time than did *S. fimbriatus* tillers (Figure 4.1). This explains the greater mass achieved by non-irrigated tillers of the former species (Figure 3.7A).

The sharp drop in apparent AGR on all treatments during the latter part of the growing season (Figure 4.1) may not have been observed if growth analysis had been undertaken on the whole plant. This is because root development takes place later in the season than shoot development (Section 3.3.6).

Causton & Venus (1981) point out that AGR is very often proportional to plant size. On this basis the index is criticised as a comparative parameter for analysing plant growth rates. However, during spring after initiation, all tillers were newly emerged and inter-treatment comparisons are valid. In addition, pastoral agriculture is concerned with the absolute amount of forage produced and not necessarily the efficiency of this production per unit of phytomass. On this basis, AGR is a more appropriate parameter to use to predict forage production rates than RGR. From the observed above-ground AGRs (Figure 4.1), it can be concluded that the rate of forage production per unit tiller is greater where there is no moisture stress, than where plants grow under unamended moisture conditions, even in a well above average rainfall year (1980/81; Figure 3.1). Also, the rate of forage production of *T. triandra* tillers is higher and/or remains at a high level for a longer duration than that of *S. fimbriatus* tillers.

Finally, the sharp drop in the derived AGR that took place in the latter part of the growing season (Figure 4.1) may not have been observed had growth analysis been undertaken on the whole plant. This is because root growth takes place later in the season than shoot growth (Section 3.3.6).

4.4.2.3 Relative growth rate of tillers

Relative growth rates of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers initiated during spring 1980 are presented in Figure 4.2.

The general trend of the RGR of above-ground material of tillers was similar on both treatments and for both species up to the time of flowering. Relative growth rate increased sharply during spring after tiller initiation, reaching a peak during summer. Thereafter, RGR decreased through autumn and into winter (Figure 4.1). This trend is expected since young vegetative tillers have a relatively low proportion of purely structural material during spring and early summer (Figure 3.9), and furthermore, environmental conditions become increasingly more favourable for rapid growth in terms of day length and temperature as summer approaches, provided moisture is not limiting. After midsummer, the proportion of purely structural material increases (Figure 3.9)., while environmental conditions for growth become less favourable.

Within species, the maximum RGR on irrigated treatments was considerably greater than that on non-irigated treatments (Figure 4.2). Since good rains fell during the 1980/81 season (Figure 3.1) the results illustrate the sensitivity of the biological performance of grass tillers even to moderate moisture stress. What is not apparent from results is the fact that growth, and therefore RGR on the non-irrigated treatment, was subjectively observed to take place sporadically, depending on the presence or absence of soil moisture. However, fitting curves to the primary data masked this effect and resulted in a lower apparent RGR on this treatment than where there was no moisture stress. In reality, the RGR of non-irrigated tillers probably fluctuated considerably between harvest dates.

Between species, the maximum RGR of *T. triandra* was greater than that of *S. fimbriatus* on the irrigated treatment but lower on the non-irigated treatment. The absolute inter-species difference in maximum RGR on similarly treated tillers was, however, not large. Despite this, *T. triandra* tillers maintained a relatively high and/or positive RGR for longer than similarly treated *S. fimbriatus* tillers (Figure 4.2). This result explains why *T. triandra* tillers achieved greater mature mass than those of *S. fimbriatus*, although there was little difference in mass between species for the first 200 days of growth (Figures 3.7A; 3.8A). The conclusion is thus that there is little difference in the rate of above-ground biological performance between species, but that *T. triandra* tillers maintain a high rate of performance for longer than those of *S. fimbriatus*, and therefore achieve a greater mature size than those of the latter species.

Non-irrigated *T. triandra* tillers, and *S. fimbriatus* tillers on both treatments, experienced increased RGRs with the onset of flowering during spring and autumn 1981 respectively. As with AGR, this was possibly a result of carbohydrate relocation from underground organs and/or possible greater biological efficiency of culm leaves produced at this time.

4.4.2.4 Net assimilation rate of tillers

Net assimilation rates of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers initiated in spring 1980, derived from the natural logarithms of above-ground mass (Figure 3.7A) and leaf area (Figure 3.12) and using the procedure of Parsons & Hunt (1981), are presented in Figure

4.3. The NARs presented in this figure are only apparent estimates of the assimilatory capacity of leaves, since they do not include photosynthate translocated below ground, but conversely do include relocated storage carbohydrates from below-ground sources as apparent assimilation. The results must therefore be assessed in this context. Furthermore, it was pointed out in Section 3.3.5 that comparison of leaf areas between species was spurious since *S. fimbriatus* leaves become rolled shortly after harvesting, resulting in an underestimate of leaf area. Since NAR is derived from leaf area, comparisons of NAR between species is invalid.

Within species the NAR of irrigated *T. triandra* tillers increased sharply during the spring after tiller initiation, reaching a peak in midsummer. Thereafter it dropped steadily as winter approached, and sharply after flowering the next spring (Figure 4.3). Booysen (1966) suggested that NAR is a property of both the availability of the raw materials for photosynthesis (CO_2, light, water and temperature) as well as of the age of the plant. Net assimilation rate as determined by the environment would be expected to peak in mid-summer and be at its lowest in midwinter, provided moisture supply is adequate. As determined by plant age, however, NAR would be expected to decline whenever the plant becomes well grown, a result of an increasing proportion of old inactive leaves, mutual shading and decreased CO_2 concentrations (Booysen, 1966).

In terms of Booysen's hypothesis (1966), the NAR of irrigated *T. triandra* tillers followed the expected trend, the midsummer peak occurring presumably as a result of favourable environmental conditions, and the fact that tillers were still juvenile. Thereafter, increasing plant age, accompanied by declining light intensities and temperatures, were coupled with an observed drop in NAR (Figure 4.3).

The NAR of non-irrigated *T. triandra* tillers did not follow the same trend as that on the irrigated treatment. Instead, NAR dropped steadily after tiller emergence in spring through to the next winter. This drop can only be attributed to moisture stress counteracting the influence of increased day length and temperature (Figure 4.3). However, as with AGR and RGR, inter-harvest variability in NAR as a result of soil moisture fluctuations was probably masked by fitting curves to the primary data. During spring 1981, the apparent NAR of flowering non-irrigated *T. triandra* tillers increased considerably and exceeded that at any stage during the vegetative phase of growth, before dropping again as tillers senesced (Figure 4.3). While it is conceded that culm leaves, because of their physical elevation, could have been more efficient photosynthetically than basal leaves, this effect is certainly unlikely to be great enough to account for the extent of the increase in NAR at the time of flowering. The observed increase is probably largely a result of mobilisation of carbohydrates from underground storage organs at the time of flowering, accompanied by an overall decrease in green leaf area (Figure 3.12). The NAR of irrigated *T. triandra* tillers did show this marked increase at the time of flowering. This was because irrigated tillers reached maximum mass earlier (September) than non-irrigated tillers (Figure 3.8), and at this time the leaf area of irrigated tillers was still relatively high (Figure 3.12). Non-irrigated tillers achieved maximum mass in November/December, a time that corresponded with a very low leaf area, (Figures 3.8 & 3.12), resulting in a high apparent NAR.

The derived NAR of irrigated *S. fimbriatus* tillers followed a similar general trend to that of similarly treated *T. triandra* tillers, increasing during spring after emergence and reaching a peak during midsummer. Thereafter, NAR dropped sharply through to the winter, although an apparent small increase was observed during flowering in autumn (Figure 4.3), possibly as a result of carbohydrate mobilisation. The mechanisms behind this general trend are probably the same as those discussed for irrigated *T. triandra* tillers.

As on the irrigated treatment, the NAR of non-irrigated *S. fimbriatus* tillers followed the same basic trend as that for similarly treated *T. triandra* tillers. However, there was a small increase in NAR immediately after tiller emergence (Figure 4.3). The results once again suggest an effect of moisture stress on photosynthesis.

Finally, it is of note that the apparent NAR on irrigated treatments of both species peaked at approximately the same time during the summer. This suggests that the environmental determinant of NAR discussed by Booysen (1966) may dominate that of plant age, provided moisture is not limiting.

4.4.2.5 Leaf area ratio of tillers

Leaf area ratios of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers initiated in spring 1980 are presented in Figure 4.4. Like NAR, leaf area ratios are derived from leaf area, and since the leaf areas of *S. fimbriatus* and *T. triandra* are not comparable on an absolute scale, comparison of LAR between species is invalid.

The general trend of LAR on all treatments was for the index to increase during the spring after tiller emergence, to reach a maximum and then decline. This maximum was reached in early to midsummer on irrigated treatments, but not until autumn on the non-irrigated treatments (Figure 4.4). Since LAR is basically a measure of the green leafiness of plants (Hunt, 1982), this result is not unexpected. Irrigated tillers grew more rapidly than those under unamended conditions (Figures 4.1; 4.2), and thus the former treatment would be expected to accumulate purely structural material more rapidly than the latter. Added to this is the fact that non-irrigated treatments reached maximum leaf area at the same time (*T. triandra*) or earlier (*S. fimbriatus*) than irrigated treatments (Figure 3.12). It is thus logical to expect that the ratio of leaf area to plant mass should have declined earlier on unstressed than on stressed treatments.

4.4.3 Summary of results

i. Absolute growth rate of spring initiated tillers of

T. triandra and *S. fimbriatus* increases rapidly after emergence and reaches a maximum in late summer or autumn, after which it declines sharply.

ii. Relative growth rate follows a similar trend to AGR, but reaches maximum values earlier in the growing season.

iii. Maximum growth rates are considerably depressed under moisture stressed conditions.

iv. Growth rates of *T. triandra* tillers are higher, or maintained at a relatively high level for a longer duration than those of similarly treated *S. fimbriatus* tillers, thus explaining why the former species achieves a greater mature mass than the latter.

v. Net assimilation rates are potentially maximal in midsummer after tiller emergence. However, moisture stress during summer can mask the beneficial effect of increased day length and temperature, resulting in a lower NAR during summer than in spring. The results illustrate the adverse effect of even partial moisture stress on photosynthesis and thus plant growth.

vi. Leaf area ratio increases after tiller emergence, but reaches a peak while tillers are still in the juvenile phase; thereafter the index declines as time progresses.

vii. Leaf area ratio reaches maximum values earlier in the growing season under irrigated than under non-irrigated conditions.

viii. Experimental procedure was such that absolute comparisons between growth indices derived from leaf area were not possible.

ix. Fitting of curves to primary data masked variability between harvest dates that occurred as a result of rapidly fluctuating soil moisture conditions, and produced estimates of mean values of what were probably widely fluctuating actual values. The result was that the maximum values achieved for the different growth indices (AGR, RGR and NAR) were apparently consistently lower on irrigated than on non-irrigated treatments. In reality, however, growth indices probably fluctuated considerably between high and low levels depending on moisture availability on non-irrigated treatments.

4.5 Influence of time of year and plant age on growth indices of key grass species

4.5.1 Implications of time of year and age on tiller growth

Once grass tillers reach the stage of carbohydrate independence, new leaves themselves provide the energy for new growth (Booysen, 1966). Thereafter the rate of growth of tillers (AGR and RGR), and therefore the ultimate production of forage, will depend on the size of the photosynthetic substrate available for trapping sunlight (leaf area) and the efficiency with which this leaf area can photosynthesise (NAR) (Watson, 1958). In turn, leaf area is essentially dependent on the internal properties of the plant (Gregory, 1926), although attainment of this genetic potential is affected by the environment (Anslow, 1966), while NAR is a property of the raw materials for photosynthesis (CO_2, light, water and temperature), and the age of the plant's leaf system (Booysen, 1966). Consequently, any growth analysis index determined from a single population of tillers will reflect the combined effect of the influences of age and the favourability of the environment for photosynthesis to take place.

In order to isolate the influences of time of year and age on any growth analysis index, sequential growth measurements must be made on a succession of plants of the same genetic material that commence growth at different times of the year. The influence of time of year on the growth index in question can then be determined at any time of the year as the mean value for plants of all ages at that particular time of year (harvest date). The NAR curve resulting from this data will depict the potential of the environment to facilitate photosynthesis in a particular species (Watson, 1963), and can be abbreviated NARp. Such a curve will typically have a peak in midsummer and will be lowest in winter (Booysen, 1966). This trend is hypothetically depicted in Figure 4.5.

Conversely, the effect of plant age *per se* on any growth index can be determined from the means of the index in question, of plants of the same age at all times of the year (harvest dates). The curve of NAR against time as influenced by plant age (NARa) is expected to decline sharply as soon as the plant is well grown (Figure 4.5) (Booysen, 1966). The corresponding expected combined effect of NARp and NARa on changes in leaf area, AGR and cumulative dry matter production with time, are also depicted in this figure.

The considerations of Booysen (1966) led to the author postulating that grasses should be defoliated at the so-called optimum leaf area (Figure 4.5), that is the leaf area corresponding to maximum growth rate; and the intensity of defoliation should be such that sufficient leaf area remains so that the plant is not dependent on carbohydrate reserves for regrowth. By harvesting each time the pasture reaches optimum leaf area, the NAR of the plant should never drop below NARp as would be the case were the plant defoliated at maximum leaf area (Figure 4.5). Booysen (1966) showed how the postulated defoliation regime was theoretically superior to defoliating at maximum leaf area or defoliating at optimum leaf area but to an intensity where most leaf material was removed. With regard to intensity of utilisation, however, Booysen (1966) did not consider the possible change in photosynthetic efficiency of plants within a vertical plane, and the fact that animals probably graze the youngest photosynthetically active leaves first, so that the remaining leaves may have a low NARa. With this in mind, the intensity of leaf removal may have relatively little influence on the rate of regrowth and thus herbage yield, when compared with the influence of the timing of each defoliation. Steinke (1975) did, however, show that lenient defoliation of *Eragrostis curvula* resulted in only a relatively small depletion of carbohydrates reserves. Similar results were reported by Weinmann (1961), who indicated that carbohydrate reserves were used after any defoliation, but that the degree of depletion of reserves increased with severity of defoliation.

The influence of intensity of defoliation on regrowth will be reported in a chapter to follow. In this section, an investigation aimed at isolating the effects of seasonality and plant age on growth indices of unutilised tillers of *T. triandra* and *S. fimbriatus* is reported, the objective being to provide information regarding the timing of defoliation from a viewpoint of maximising dry matter production.

4.5.2 Procedure and analysis of data

The procedure and data used in this trial were those already used to describe the ontogeny of *T. triandra* and *S. fimbriatus* tillers initiated at different times of the year, both under unaltered moisture conditions and without moisture stress. The details of the procedure are described in Section 3.2 (Experiment 2). In addition to the procedure already listed, the green leaf area of samples of tillers was recorded.

New populations of tillers were stimulated to develop by intense defoliation of plants at intervals through the season. The date of initiation of each population of tillers was regarded as the date when defoliation took place, despite the fact that the new populations of tillers did not necessarily emerge immediately after defoliation, particularly during dry conditions and in winter. Nevertheless, it was considered reasonable to use cutting date as the date when lateral buds started to develop since it is likely that bud activity would have been stimulated to commence once apical dominance was removed by shoot apex decapitation, even though inadequate moisture or temperatures could have restricted this development.

Since, in this trial, tillers were harvested at 60 day intervals (Section 3.2; Experiment 2), the primary data consisted of no more than 10 mean observations from each population of tillers. Consequently, the data are not particularly suited to functional growth analysis (Hunt, 1982). The data from each population were nevertheless subjected to analysis by the methodology of Parsons and Hunt (1981) both for fitting curves to the primary data, and for derivation of indices of AGR, RGR, NAR and LAR, but in view of the paucity of observations, the fitted and derived functions should be regarded only as trends.

The effect of time of year and plant age on growth indices were then isolated from the derived indices of the successive tiller populations initiated at different times. In terms of the effect of time of year, this was done by pooling the values of all plant ages at each particular harvest (6 times per year) on each treatment (irrigated and non-irrigated *T. triandra* and *S. fimbriatus*). Conversely, the effect of plant age was isolated on each treatment by pooling the values of similar plant ages derived at different times of the year. The data were, however, partially confounded by the fact that tiller longevity was to some extent dependent on the date of tiller initiation, tillers initiated before midsummer generally flowering during the following calendar year, while those initiated after this date remained vegetative (Table 3.1). Furthermore, immediately after tiller emergence, and again when flowering took place, it is probable that carbohydrate relocation was taking place, and it is thus likely that apparent growth indices at these times would have been overestimates of true assimilation, as was indicated with spring initiated tillers (Section 4.4).

Thus, in an attempt to eliminate the confounding effects of tiller longevity and carbohydrate relocation, it was decided to isolate the effects of time of year and plant age only on vegetative tillers twelve months old or younger, but excluding tillers less than two months old. Consequently, six harvest dates and thus six estimated growth index values were available for most sub-populations of tillers. Exceptions were the twelve month old, and ten and twelve month old recordings of irrigated *T. triandra* tillers initiated at the end of September and November respectively;

the twelve month old recordings of non-irrigated *T. triandra* tillers initiated at the end of September; and the ten and twelve month old recordings of *S. fimbriatus* tillers (both treatments) initiated at the end of July and end of September. In all these instances, the majority of tillers were flowering and values were excluded for calculation of mean effects of time of year and plant age. In the tiller populations in question, these particular harvests were considered as "missing plots" for purposes of analysis. "Missing plots" thus represented two and one out of 36 observations on irrigated and non-irrigated *T. triandra* treatments respectively, and four out of 36 observations on both *S. fimbriatus* treatments.

With respect to each derived growth function (AGR, RGR, NAR and LAR), variability of the derived means for determining the influence of time of year and plant age could be attributed to three main sources in addition to error. These were the main effects of species, moisture treatment and time of year or plant age respectively. Furthermore, each growth index mean was derived from six independent observations on separate samples of tillers (replications). Since variance heterogeneity did not occur, and since the data were apparently normally distributed, analysis of variance in terms of the three main effects and their interactions (with provision made for missing plots) was considered appropriate. Such analysis was conducted twice, to make provision for the respective influences of time of year and plant age. These main effects could not be included in the same analysis since the means for describing them represented different combinations of the same data.

In addition, with respect to the growth indices NAR and LAR, separate analyses were conducted for each of the species. This was because, for reasons already given, comparison of leaf area between species was not valid, and the growth indices NAR and LAR are derived from leaf area.

Analysis of variance of the data is particularly useful since, within treatments, the size of the variability between times of year or tiller ages relative to the respective least significant difference on any particular treatment represents the dependence of the growth index in question on time of year or tiller age. For this purpose, a ratio was calculated between the largest observed and the least significant difference of the effects of time of year and tiller age on each treatment. The least significant difference used was that between any two mean observations within a treatment and was thus that of the third order interaction in the case of the growth indices AGR and RGR (where there were three main effects), and of the second order in the case of the indices NAR and LAR (where the main effect of species was not considered).

4.5.3 Results and discussion

4.5.3.1 Primary data

The mean mass of *T. triandra* and *S. fimbriatus* tillers initiated progressively during the 1980/81 season is presented in Figures 3.10 & 3.11 and the corresponding green leaf areas in Figures 4.6 & 4.7. Because of the paucity of harvest dates (10 or less), the functions are not qualified by confidence limits and are presented on an arithmetic scale.

The results concerning tiller mass have been discussed in Section 3.3 & 3.4. The difference in green leaf area between treatments showed the same trend as those of tiller mass. Irrigated treatments had greater leaf areas than non-irrigated treatments, and maximum leaf area apparently declined progressively the later in the season that tillers were initiated. In addition, those tillers initiated before midsummer achieved maximum leaf area during the season of tiller initiation, while those initiated after midsummer achieved maximum leaf area during the following season (Figure 4.6 & 4.7).

As with spring initiated tillers, tiller masses reflect only above groung material and do not include root mass. Consequently, growth indices reflect changes in above-ground material only.

The growth indices AGR, RGR, NAR and LAR were calculated from the primary data by the methodology of Parsons & Hunt (1981), and from these the influence of time of year and plant age was isolated by the procedure already described.

4.5.3.2 Effect of time of year and tiller age on absolute growth rate

The effect of time of year (A) and tiller age (B) on the AGR of irrigated and non-irrigated tillers of *T. triandra* and *S. fimbriatus* in a vegetative condition is presented in Figure 4.8.

In terms of the AGR of tillers of all ages at different times of the year (Figure 4.8A), the main effects of time of year, irrigation and species were all statistically significant (P<0,01), and there was a significant interaction between time of year and moisture treatment (P<0,05). The results show thus that AGR increased in all treatments as time of year progressed from spring through to summer (*S. fimbriatus*) or autumn (*T. triandra*), and then decreased as winter approached. There was, however, no significant difference in the timing of maximum AGR between species (time of year/species interaction). Nevertheless, between species, the overall AGR of *T. triandra* was greater than that of *S. fimbriatus* (P<0,01). Moisture treatment resulted in an overall higher AGR on irrigated treatments (P<0,01), but this effect became apparent only after the commencement of summer (P<0,05) (time of year/irrigation treatment interaction).

In terms of the AGR of tillers of different ages at all times of the year (Figure 4.8B), the main effects of age, irrigation and species were all statistically significant (P<0,01), but there were no significant interactions between treatments. The implication is thus that AGR increased with age up to about six months, after which it dropped; that the AGR of irrigated tillers was greater than that on the non-irrigated treatment; and that *T. triandra* tillers increased in mass more rapidly than those of *S. fimbriatus*. No significant interactions show that differences between species and irrigation treatments were consistent with increasing plant age, and that the effect of irrigation was consistent both with increasing plant age and between species. The tendency was, however, for maximum AGR to occur slightly later and be maintained at a high level for longer on *T. triandra* tillers than those of *S. fimbriatus*.

The size of the ratios between largest observed differences and least significant differences suggest that AGR was slightly more dependent on time of year than on plant age, on irrigated treatments. However, on non-irrigated treatments the difference between the ratios was small, and the influences of both time of year and plant age were probably to some extent masked by moisture stress. The latter result is expected since moisture stress causes growth to cease regardless of whether plant age, day length and temperatures are favourable for growth.

In general terms then, AGR of vegetative tillers is potentially maximal during late summer and when tillers are six to eight months old. Thus, spring initiated tillers are likely to be the highest yielding since they reach an age of six to eight months in late summer.

4.5.3.3 Effect of time of year and tiller age on relative growth rate

The effect of time of year (A) and age (B) on the RGR of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers in a vegetative condition is presented in Figure 4.9.

The RGR of vegetative tillers of all ages was significantly different at different times of the year (Figure 4.9A) (P<0,01) but was not affected by irrigation and was not different for the two species, although the effect of the former was nearly significant. There were no significant interactions between treatments. The results thus show that RGR increased sharply as time of year progressed from early spring, reaching a peak that same spring (*S. fimbriatus*) or early summer (*T. triandra*), and thereafter declined as summer progressed through to autumn and winter. This trend was consistent for the two species, and RGR tended to be higher on irrigated than non-irrigated treatments.

The RGR of tillers of different ages at all times of year (Figure 4.9B) was significantly affected only by age ($P<0,01$), and not by species, irrigation or interactions between these effects. Relative growth rate decreased progressively with increasing tiller age. This is to be expected since mass increment per unit plant mass is likely to drop as plants become larger. Although there was no significant interaction between plant age and species, *T. triandra* tillers apparently maintained a positive RGR throughout their vegetative life, while *S. fimbriatus* tillers maintained a high RGR for a shorter period and the parameter even became negative when tillers approached one year of age.

With the exception of the non-irrigated *T. triandra* treatment, the sizes of the largest difference/least significant difference ratios (Figure 4.9) suggest that RGR was more dependent on plant age than time of year. The index was approximately equally affected by both time of year and plant age on non-irrigated *T. triandra* tillers.

Comparing changes in RGR and AGR; maximum absolute growth of tillers apparently takes place later in the season than maximum physiological efficiency. This is probably a result of the fact that spring initiated tillers were the largest of the various populations (Figures 3.10 & 3.11) and the plant growth rate indices are therefore weighted in favour of these populations. It is expected that spring initiated tillers should reach maximum RGR while still small (Figure 4.2), but maximum AGR when larger (Figure 4.1). In terms of tiller age, physiological efficiency declined progressively as tillers aged after two months, but reached maximum AGR at six to eight months. This result is expected since AGR is often a reflection of plant size (Causton & Venus, 1981) and six to eight month old tillers are obviously larger than those only two months old.

4.5.3.4 Effect of time of year and tiller age on net assimilation rate

The effect of time of year (A) and tiller age (B) on the NAR of irrigated and non-irrigated *T. triandra* tillers is presented in Figure 4.10, and the effect of these parameters on similarly treated *S. fimbriatus* tillers in Figure 4.11. For reasons already given, deficiencies in the experimental procedure made quantitative comparisons of NAR between species invalid.

In the species *T. triandra*, the NAR of tillers of all ages was significantly affected by both time of year and irrigation (P<0,01). In addition, there was a significant interaction between these two main effects (P<0,01). Under both moisture treatments, NAR increased as season progressed from winter through to summer, reaching a peak in midsummer. Net assimilation rate then declined through autumn and into winter. The summer increase in NAR was considerably greater on the non-irrigated than on the irrigated treatment (Figure 4.10A). This is probably a result of high leaf areas resulting in mutual shading and therefore depressed photosynthetic efficiency on the irrigated treatment, as well as possible experimental underestimation of leaf area as a result of wilting on the non-irrigated treatment. In addition, under dryland conditions, leaf death proceeded more rapidly than under irrigation (Chapter 3). Therefore irrigated tillers probably carried a large proportion of older photosynthetically inactive inefficient leaves which died off early on the non-irrigated tillers.

In contrast to *T. triandra*, there was no significant effect of time of year on the NAR of *S. fimbriatus* tillers (Figure 4.11A). However, the NAR of *S. fimbriatus* tillers declined with increasing tiller age (Figure 4.11B) (P<0,05). In addition, the effect of irrigation was nearly significant in both analyses (Figure 4.11 A & B). The decline in NAR of tillers of this species with increasing age (Figure 4.11B), in contrast to the non-significant result recorded on *T. triandra* tillers (Figure 4.10B), is possibly a result of the shorter longevity of flowering *S. fimbriatus* tillers. Flowering *S. fimbriatus* tillers commenced senile mortality within the 12 month period listed in Figure 4.11B, and therefore presumably experienced a drop in NAR. In contrast, 12 month old *T. triandra* tillers were usually still vegetative.

The largest difference/least significant difference ratios for the effect of time of year and plant age on *S. fimbriatus* tillers show that error involved in determining NAR in this species was relatively high (Figure 4.11). This was probably caused by inaccurate measurement of leaf area in this species, resulting from experimental procedure (both moisture treatments) and wilting of leaves as a result of drought (non-irrigated treatment).

The fact that the NAR of *S. fimbriatus* tillers was not affected by time of year (Figure 4.11A) suggests that this species may be a more opportunistic assimilator of light energy than *T. triandra*, photosynthesising whenever the environment/moisture/grazing situation is favourable. This inference is consistent with the fact that *S. fimbriatus* is generally considered to dominate at a lower seral stage than *T. triandra* (Roberts, 1973) in terms of classical Clementsian plant succession.

As has been indicated, the effect of irrigation on the NAR of *S. fimbriatus* tillers was nearly significant, and the trend was for non-irrigated tillers to have greater NARs than those on the irrigated treatments (Figure 4.11). The reasons are probably the same as those given for a similar result on *T. triandra* tillers. Although unlimited moisture apparently reduced the overall NAR of tillers of both species (Figures 4.10 & 4.11), young newly emerged leaves are situated at the top of tillers of both species, and are therefore unlikely to be affected by mutual shading. The lower overall NAR on irrigated treatments was thus probably a result of mutual shading in the vicinity of the oldest still-green leaves near the bases of tillers. Animal preference is such that they presumably graze youngest leaves first, a result of both their palatability and physical placement (Daines, 1976). Consequently, the implication is that while lenient utilisation of actively growing swards may result in a certain amount of green leaf area remaining after utilisation, the leaves that remain could well not be particularly active photosynthetically.

4.5.3.5 Effect of time of year and tiller age on leaf area ratio

The effect of time of year (A) and age (B) on the LAR of irrigated and non-irrigated *T. triandra* tillers is presented in Figure 4.12, and the effect of these parameters on similarly treated *S. fimbriatus* tillers is presented in Figure 4.13. Deficiencies already discussed in the experimental procedure made quantitative comparison between treatments spurious.

In the species *T. triandra*, there were no significant differences in the LARs recorded between different times of year or irrigation treatment (Figure 4.12). However, the tendency was for LAR to drop during midsummer on the non-irrigated treatment, a consequence of diminished leaf area on this treatment at this time, a result, in all probability, of wilting brought about by drought. The LAR of *T. triandra* tillers did, however, drop progressively with increasing plant age (Figure 4.12B) ($P<0,01$).

The results regarding the effect of time of year and plant age on the LAR of *S. fimbriatus* tillers (Figure 4.13) followed the same trend as those on *T. triandra* tillers (Figure 4.12), although the absolute values were different. Once again, the only significant result was that LAR diminished with increasing plant age of *S. fimbriatus* tillers (Figure 4.13B, ($P<0,01$)).

The implication in both species is thus that as tillers get older, they become less leafy, and the proportion of palatable material decreases with increasing plant age. Leafiness is, however, not expected to change materially on plants of the same age at different times of the year.

4.5.4 Practical significance of dependence of growth indices on time of year and tiller age.

From the effect of plant age on AGR (Figure 4.8B), it is possible to determine the cumulative mass of vegetative tillers with increasing age meaned over all times of year (Figure 4.14). It is clear from this figure that the average size achieved by vegetative *T. triandra* tillers after 12 months is considerably greater than that of *S. fimbriatus* tillers. However, up to six months of age *S. fimbriatus* tillers are as large or larger than those of *T. triandra*. After six months of age, the growth rate of *S. fimbriatus* tillers declined sharply (Figure 4.8B), resulting in less production of herbage than *T. triandra* after this time (Figure 4.14).

The theoretical effect of frequency of complete utilisation on herbage production per tiller can be calculated from Figure 4.14. Assuming total utilisation of above-ground material, and that tillers utilised in this manner regrow at the same rate as newly initiated tillers, the effect of interval between harvests on the above-ground production of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tillers, expressed in terms of mean annual production, is presented in Figure 4.15.

Figure 4.15 does not reflect the total herbage production at the end of a specific 12 month period under the various harvest frequencies, but rather the mean production of herbage over an extended period under the various harvest intervals, expressed on an annual basis. For this reason, a 10 month harvest interval produced more forage than that of a 12 month interval on irrigated *T. triandra* tillers, despite the mass increment from zero to two months being less than that from 10 to 12 months. Over an extended period, the mean rate of herbage production from zero to 10 months is greater than that from zero to 12 months. Annual yield (AYn) at the n month harvest interval was thus calculated as the cumulative tiller yield after n months (Yn) (presented in Figure 4.14) multiplied by 12/n.

$$\text{i.e.} \quad AYn = Yn \times 12/n$$

Maximum yield of irrigated and non-irrigated *T. triandra* tillers would be achieved at harvest intervals of 10 and 12 months respectively, while that of *S. fimbriatus* tillers would be achieved at an interval of six months on both treatments (Figure 4.15). In the case of *T. triandra* tillers, the increase in mass after six months is probably a result of an increase in stem mass (includes leaf sheaths) and not leaf blade mass. In Chapter 3 (Section 3.3.5) it was shown that tillers of the species attain a constant number of leaf blades (living and senescent) after about six months.

Total harvesting of all above-ground material of tillers as assumed in Figure 4.15 would result in decapitation of growing points and death of the tillers. Thus the theoretical yields listed in Figure 4.15 represent not the production of individual tillers, but the yields of newly initiated tillers plus that of their consecutive descendants commencing growth after each harvest, expressed on an annual basis. In practice, however, tillers are not totally defoliated. Thus initial regrowth of a tiller after defoliation would be more rapid than that shown in Figure 4.14, and would vary in degree according to the assimilate reserves available to the tiller, and the ability of the tiller itself to commence assimilation from residual leaf. The important inference to be made from Figure 4.15 is the considerable relative difference in optimal utilisation frequency between the two species. This is consistent with the fact that *S. fimbriatus* was classified in the veld type by Danckwerts (1983) as an Increaser II species - it increases in abundance when veld is overutilised (Foran, Tainton & Booysen, 1978). Conversely, *T. triandra* was classified as a Decreaser species - it is abundant in well-managed veld (Danckwerts,1983).

The results (Figure 4.15) further provide justification for periodic implementation of a complete growing season rest, particularly where the intention is to maintain the health and vigour of *T. triandra*. This is because maximum mean growth rate (and yield) of *T. triandra* tillers was attained with a 10 to 12 month defoliation frequency. Presumably, tillers should be allowed to attain this occasionally in order to allow reserve carbohydrate accumulation, despite a net loss of forage through leaf decay (Section 3.3.5.3). However, in terms of the effect of plant age on the AGR of *S. fimbriatus*, there is apparently little justification in resting this species for more than six months. Also of relevance in terms of long rests is the fact that LAR decreases with increasing plant age (Figures 4.12 & 4.13). Thus rested veld will be less leafy and therefore less palatable than veld not rested for a long period, implying that excessively long rests should not be implemented unnecessarily.

The results discussed above are based on the mean growth of plants of the same age at all times of the year. In practice, plants potentially grow fastest in late summer (Figure 4.8A), implying that when water is readily available, the grazing rotation can be accelerated. Of note in this context is the fact that leaves of unstressed tillers emerge more rapidly (Figure 3.18) and have a shorter longevity (Figure 3.20) during late summer than leaves emerging at other times of the year.

Although the AGR of tillers was most rapid during late summer/autumn (Figure 4.8A), they were physiologically most efficient in terms of growth per unit plant mass in spring/early summer (Figure 4.9A) and when still young (Figure 4.9B). Since tillers were also leafiest when young (Figures 4.12 & 4.13), the implication is that tillers are particularly vulnerable to overgrazing while young and during the early part of the growing season. (When young, a high proportion of their mass is both palatable to animals and physiologically active). Since the majority of new tillers are likely to emerge during spring, the spring period is probably the most critical time of the year in terms of veld management. As has been indicated, it may be difficult to control defoliation so that photosynthetically active leaves remain after defoliation, and in view of this, actively growing veld should be rested as far as possible during the spring. This critical period extends until after midsummer in the species *T. triandra* since the photosynthetic efficiency of leaves of this species reaches a peak in midsummer (Figure 4.10A).

The primary data indicate that spring initiated tillers grow more rapidly and achieve greater size than tillers initiated at any other time of the year. This is probably because they are able to make use of favourable summer conditions while still vegetative, but at the same time are sufficiently developed to be independent of reserve carbohydrates and have adequate photosynthetic substrate (leaves) to make full use of these favourable conditions. It is also likely that spring is the natural time for tiller emergence to take place. In view of this, management should be geared towards stimulating emergence of tillers in spring, and maintenance of their health and vigour through the growing season. An exception to this is where profuse seeding of *T. triandra* is specifically required. Here the management action that stimulates tiller production (severe) utilisation in winter, could also result in decapitation of primary tillers (Section 3.3.3) and thus suppress flowering.

Finally, although in this chapter the effects of grazing were not tested, leaf arrangement on tillers is such that it may be difficult to control defoliation in order that photosynthetically active leaves be left on tillers after grazing. Consequently the contention of Booysen (1966) that defoliation should be such that a reasonably high green leaf area remains after grazing, may not be an applicable principle in practice.

4.5.5 Summary of results

i. Absolute growth rate of tillers of *T. triandra* and *S. fimbriatus* are influenced by both time of year and plant age. The index is maximal during late summer and when tillers are six to eight months old.

ii. Time of year has a greater effect on AGR than plant age on irrigated treatments, but not where tillers are subject to moisture stress.

iii. The AGR of *T. triandra* tillers is generally greater than that of *S. fimbriatus* tillers, and the index is higher under irrigated than under non-irrigated conditions.

iv. The RGR of both species, like AGR, is affected by both time of year and tiller age. However, the index is maximal during spring or early summer, and declines with increasing plant age after two months.

v. Relative growth rate is more sensitive to changing plant age than time of year.

vi. During the 1980/81 season, relative growth rate was not significantly affected by species or irrigation, although irrigated tillers tended to have a greater RGR than those on non-irrigated treatments.

vii. The NAR of *T. triandra* tillers is significantly affected by time of year, reaching a maximum in midsummer, but the parameter is not influenced by plant age in this species.

viii. The NAR of *S. fimbriatus* tillers is not influenced by time of year, but declines with increasing plant age.

ix. During the 1980/81 season, irrigated tillers of both species had lower NARs than those of non-irrigated tillers. This was probably a result of mutual shading and a large proportion of old inactive leaves on the irrigated treatments.

x. Leaf area ratio of both species is independent of time of year and moisture treatment but diminishes with increasing plant age.

xi. Meaned over all times of the year, *T. triandra* tillers achieve considerably greater size after 12 months than those of *S. fimbriatus*. However, up to six months there is little difference between species.

xii. Theoretically, *S. fimbriatus* tillers will achieve maximum herbage production with a considerably shorter harvest interval than is optimal for *T. triandra*.

xiii. Plants grow most rapidly in late summer/autumn. The grazing rotation can thus be accelerated at this time provided active growth is taking place.

xiv. Tillers are physiologically most efficient during spring and while still young, and therefore probably most susceptible to overgrazing at this time.

xv. Spring initiated tillers potentially achieve greater size than those initiated at other times. Management should thus be aimed at spring initiation of new tiller populations.

xvi. Leaf arrangement of tillers is such that it may be difficult to control defoliation in order that photosynthetically active leaves are left on tillers after grazing.

CHAPTER 5

NON-STRUCTURAL CARBOHYDRATE ACCUMULATION AND DEPLETION IN UNUTILISED KEY GRASS SPECIES

5.1 Traditionally accepted role of storage carbohydrates

Non-structural carbohydrates are traditionally accepted as the primary source of carbon for initial growth of new tillers or regrowth of old tillers after defoliation (includes reviews by Weinmann, 1961; White, 1973; Trlica, 1977 and Briske & Woie, 1984). These carbohydrates are stored in various plant organs for use at a later date (Beevers, 1979), and form a small proportion of total assimilated carbon relative to that used for respiration or that metabolised into structural carbohydrate and protein (Gordon, Ryle & Powell, 1977). Considerable research aimed at determining seasonal and post-defoliation trends in the concentration of total non-structural carbohydrates in various plant tissues has been conducted (includes work by Weinmann, 1940*a*, 1940*b*, 1943, 1944; Weinmann & Reinhold, 1946; Daitz, 1954; Hyder & Sneva, 1959, 1963; Bartholomew & Booysen, 1969; Trlica & Cook, 1971, 1972; Nursey, 1971; Gifford & Marshall, 1973; Steinke, 1975; Buwai & Trlica, 1977; Daer & Willard, 1981 and Menke & Trlica, 1981, 1983).

From the work and reviews of previous authors, the generalised reserve carbohydrate accumulation and depletion pattern in grasses can be summarised as follows: Initially, new tillers import substrate from established parent tillers for a period of time. Thereafter, the newly initiated tiller develops sufficient leaf area to become photosynthetically self sufficient. The tiller may nevertheless remain dependent on water and nutrients absorbed by the root systems of the primary tiller. The stage of development where a tiller no longer imports carbon from an organically attached parent tiller is termed that of "physiological independence". As the tiller approaches maturity, sugars and polymers are photosynthesised by the leaves at a rate exceeding the requirements of aerial growth, and the excess is translocated via the phloem to the roots, stem base and other storage organs. The grass then draws on the reserves whenever new growth takes place. This occurs not only with the emergence of new tillers but whenever new growth is produced after cutting or grazing. In addition, Briske & Woie (1984) suggest that a physiologically independent tiller can itself revert to being an importer of carbon following a reduction in carbon-gain capacity of that tiller. In this context, the authors contend that carbon transport may occur continually among tillers regardless of the stage of vegetative development, and this transport can increase several fold within minutes of either shading or partial defoliation. Work by Sagar & Marshall (1966) and Marshall & Sagar (1968) on temperate pasture species, led the authors to conclude that the overall response to differential defoliation suggests that a grass tuft is a highly integrated organism, and instead of becoming dominant, intact shoots supply damaged shoots with assimilates, so that each tiller tends towards an evenness of size. However, this conclusion was drawn from observed carbon transfer from older to younger tillers. In contrast, Langer (1972), in review on growth of grasses, suggests that carbohydrate movement between older tillers appears to be restricted. Furthermore, unpublished results of research at the M~~o~~atopos Research Station in what was then Rhodesia (1966-67), suggested that reserve re-allocation among established tillers of *T. triandra* and *Hyparrhenia hirta* may well have been minimal, even after partial defoliation of tufts (Barnes, 1984: *pers. comm.*). It thus appears that while new tillers almost certainly draw on carbon resources of older tillers until they become physiologically independent, the question of carbon interdependence among organically linked older tillers is not fully understood. It may well be that differences exist between species, and even within species growing in different areas and under different utilisation regimes.

When tillers reach maturity and begin flowering a considerable demand is placed on the rest of the plant to supply substrate for seed formation. Work with radioactive carbon has shown that this is largely supplied by the flag leaf and other leaves occurring near the top of the tillers (Langer, 1972). However, it seems reasonable that tillers should draw on their carbohydrate reserves, or even those of other tillers after defoliation or shading, but not for flower and seed development.

Carbohydrate accumulation and depletion patterns in unutilised veld grasses in South Africa were studied by Weinmann (1940*b*) who showed that carbohydrate reserves were depleted in the roots of Highveld grasses during spring and early summer, a time associated with rapid shoot growth. Without interference through clipping, carbohydrates increased in autumn and winter, reaching a maximum in mid-winter. Weinmann & Reinhold (1946) investigated the corresponding pattern of carbohydrates in the shoots during early summer. However, the authors indicated that the total amount of carbohydrates probably increased during this period since the drop in percentage was associated with a time of rapid aerial growth. Carbohydrate percentage in shoots increased during late summer but dropped sharply in autumn and winter. This tends to support the earlier work of Weinmann (1940*b*). These results were later supported by Daitz (1954) who studied carbohydrate reserves in *T. triandra* in a potting experiment on the Transvaal Highveld. Root reserves reached a maximum in winter (18-19%) and a minimum during summer (8,4%).

Further work by Nursey (1971), who studied starch grain accumulation and depletion in *T. triandra* in the Orange Free State, showed that while starch grains were always present, the positioning of these grains varied. Factors affecting the location of these grains included growth activity and flowering of the plant, as well as the prevailing moisture regime. The author concluded from the results that *T. triandra* could be vulnerable to defoliation after a drought, but indicated that further research was needed on the location of carbohydrates in South African grasses. In addition, the work of Weinmann & Reinhold (1946) points to the danger of drawing conclusions from starch alone, since *T. triandra* has greater proportions of other non-structural carbohydrates in both roots and shoots.

No published information is available regarding carbohydrate accumulation and depletion patterns of key grass species in the False Thornveld of the Eastern Cape. The species *T. triandra* has received attention by previous researchers, but this work was conducted on sourveld ecotypes either in the field or in a greenhouse. An investigation was thus undertaken to characterise carbohydrate accumulation and depletion patterns of unutilised *T. triandra* and *S. fimbriatus* tillers.

5.2 Procedure

Non-structural carbohydrate accumulation and depletion patterns of *T. triandra* and *S. fimbriatus* were monitored in sequentially harvested populations of unutilised spring initiated tillers growing both in the field and in pots in the greenhouse. The tiller samples used for total non-structural carbohydrate analyses from the field trial were the same as those used to characterise the developmental morphology of tillers of both species initiated in spring 1980. The field procedure of this trial has thus already been described in Section 3.2 (Experiment 1). Before samples were dried, in addition to removal of leaves from stems, stems themselves were cut at a height of 2cm above the base, thus separating stubble from upper stems. Leaves (green and dry pooled), stems and stubble were then freeze-dried to constant mass and analysed in the laboratory for percentage non-structural carbohydrates.

The tiller samples analysed for non-structural carbohydrates from the potting trial were those used to characterise the root development of *T. triandra* and *S. fimbriatus*. The experimental procedure has thus been described in Section 3.2

(Experiment 4). As in the field trial, stem bases were separated from upper stems at a height of 2cm, and after freeze-drying, leaves, stems, stubble and roots were analysed in the laboratory for non-structural carbohydrate content.

Work by Weinmann & Reinhold (1946) has shown that the non-structural carbohydrates occurring in South African veld grasses are made up largely of sugars (reducing and non-reducing) and the polymer, starch. This is in contrast to temperate grasses where the most important polysaccharides are fructosans and not starch. For this reason, the acid hydrolysis method of analysis for total non-structural carbohydrates developed by Wylam (1954) and commonly used in temperate grasses, is not appropriate for indigenous South Afican grasses. The mild conditions for the enzymic hydrolysis of starch makes the takadiastase method used by Weinmann (1947) particularly suitable for determination of total non-structural carbohydrate content of indigenous grasses. It is further preferable to methods employing acid hydrolysis since these are subject to error resulting from hydrolysis of some structural polysaccharide and partial destruction of fructose, which ocurrs as a free sugar in all grass species (Marais, 1969). The procedure used to analyse samples for total non-structural carbohydrate content in this trial was thus that developed by Weinmann (1947), but included refinements suggested by Marais (1969). Owing to the high frequency of sampling (fortnightly in the field and every three weeks in the greenhouse) each sample was analysed only once. Cost and logistics made duplicate analysis of the large number of samples impracticable. Also, the pooled sample sizes of some of the plant parts were not large enough to analyse for non-structural carbohydrate content during the initial stages of growth immediately after tiller emergence. In these instances, analyses began on the sampling dates when sample size was sufficient.

The seasonal progression of non-structural carbohydrate content in the various plant parts is described graphically by fitting splined third order polynomial functions to the primary data, using the methodology of Parsons & Hunt (1981).

However, the primary data were not log transformed before performing the regressions as was the case in describing the developmental morphology of grass tillers (Chapter 3). This was because non-stuctural carbohydrate content did not increase from very small values to relatively high values (as, for instance, was the case with tiller mass). Thus, variance heterogeneity between harvest dates was not suspected and log transformation in terms of the reasoning provided by Hunt (1982) was considered inappropriate.

5.3 Results and discussion

The percentage concentration by mass of non-structural carbohydrate in leaves, upper stems and stubble of irrigated and non-irrigated tillers of *T. triandra* and *S. fimbriatus* growing in the field after initiation during spring 1980 are presented in Figures 5.1, 5.2, and 5.3 respectively. The percentage non-structural carbohydrate content of leaves, upper stems, stubble and roots of tillers of the same species growing in pots in the greenhouse are presented in Figures 5.4, 5.5, 5.6 & 5.7 respectively. Since each analysis was conducted on a separate sample of tillers, the curves of carbohydrate content are qualified by confidence limits, and statistical comparison of all curves with each other is acceptable.

The concentration of non-structural carbohydrates in the leaves (green and dead pooled) of both species and on all treatments (Figures 5.1 & 5.4) increased from values of 1-2% after tiller initiation in spring 1980, to reach maximum values a little under 2% (*S. fimbriatus*) and a little over 2% (*T. triandra*) during the following autumn (1981). Thereafter, non-structural carbohydrate concentration in leaves dropped through the winter. This drop in concentration is expected, since the proportion of dry leaves increased as tillers grew older and winter approached (Figure 3.14), and dead leaves are likely to contain less non-structural carbohydrates than green leaves. There were no significant differences in the concentration of non-structural carbohydrates in leaves between species or between treatments (Figures 5.1 & 5.4). The tendency was, however, for non-structural carbohydrate concentration in leaves of *T. triandra* tillers to be higher during the summer after tiller initiation (1980/81) than that of *S. fimbriatus* tillers. Also, leaves of *T. triandra* tillers tended to achieve peak non-structural carbohydrate content later in the growing season than those of *S. fimbriatus* (Figures 5.1 & 5.4). The latter trend is probably a result of the fact that *S. fimbriatus* tillers flowered during autumn 1981, while *T. triandra* tillers remained vegetative at this time and flowered the following spring (Figure 3.4).

The confidence limits of the recorded non-structural carbohydrate content of the upper stems (include sheaths above 2cm) of both species and all treatments (Figures 5.2 & 5.5) are proportionately wide, relative to those qualifying the non-structural carbohydrate content of other plant organs. There were thus no significant differences in non-structural carbohydrate content in stems both between species and between treatments. The wide confidence limits (Figures 5.2 & 5.5) reflected variability in the primary data, probably a result of both absolute variability (otherwise confidence limits would be equally wide for all plant organs) and error resulting from laboratory procedure. It is thus difficult to draw conclusions regarding trends of non-structural carbohydrate concentration in stems. However, in general terms, non-structural carbohydrates comprised approximately 2% of the mass of all tillers during the vegetative growing period. This concentration apparently dropped after culm development and flowering (winter 1981 for *S. fimbriatus* tillers and spring 1981 for *T. triandra* tillers).

The non-structural carbohydrate content of stem bases (Figures 5.3 & 5.6) increased steadily from a low value (less than 2%) after initiation of tillers of both species and in all treatments (spring 1980). In the species *T. triandra* non-structural carbohydrates accumulated, reaching a maximum of 5-6% in the late winter approximately one year of tiller emergence (1981) on all treatments. Thereafter the concentration dropped when flowering took place during spring and summer. There was no significant difference in non-structural carbohydrate content of stem bases between treatments within this species (Figures 5.3 & 5.6).

In the species *S. fimbriatus*, non-structural carbohydrates in stem bases followed a similar trend to those in the species *T. triandra*. However, maximal concentrations were achieved during the autumn following tiller emergence (1981), some months earlier than in the case of *T. triandra*. In addition the maximum concentrations of non-structural carbohydrates in the stem bases of *S. fimbriatus* tillers were 5,5-7% in the field (where there were no significant differences between treatments), and only 4,7% in pots in the greenhouse, significantly less than in the field. However, the timing of these maxima were the same within species (Figures 5.3 & 5.6).

In both species and on all treatments, non-structural carbohydrates accumulated in stem bases, reaching a maximum immediately prior to flower formation, and dropped sharply with culm development and flower formation (Figures 3.4, 5.3 & 5.6). Since secondary tillers produced at these times were both few in number and very small in size (Figure 3.32), the implication is that carbohydrate reserves in the stem bases were drawn on for stem, flower and seed formation. These results agree with those of Nursey (1971) who reported that starch granules in *T. triandra* diminished at the time of flowering. Mobilisation of reserves at the time of flowering thus probably account at least partially for an increased apparent photosynthetic efficiency of grass leaves at this time (Figure 4.3).

The non-structural carbohydrate content of roots of tillers growing in pots in the greenhouse comprised 2-3% of total root mass, and there was no significant difference between species (Figure 5.7). Observed trends in the data were small relative to data variability as indicated by the confidence intervals. However, non-structural carbohydrate concentration in roots apparently declined during the subsequent winter. While it is possible that root reserves were used for culm development at this time, the change in non-structural carbohydrate concentration in roots was too small relative to data variability to make this inference (Figure 5.7).

Comparing differences between plant organs, there was little significant difference in the non-structural carbohydrate concentration in leaves, upper stems and roots of spring initiated tillers (Figures 5.1, 5.2, 5.4, 5.5 & 5.7). However, the tendency was for roots to contain greater concentrations than leaves and upper stems, and for the concentration of non-structural carbohydrates in all these organs to decline as tillers approached maturity. In contrast, stem bases accumulated non-structural carbohydrates as tillers matured. Concentrations were low immediatly after tiller emergence (less than 2%) and reached a level significantly higher than in all other plant organs during the summer (Figures 5.4 &5.6). The concentration gradient of non-structural carbohydrates between stem bases and other plant organs diminished after flowering took place. Of note is the fact that the non-structural carbohydrate concentration in leaves was initially equal to or greater than that in stem bases. This is presumably a result of the fact that sugars are always present in active leaves since they are the substrates from which carbohydrates are manufactured, while stem bases (the sink) depend on translocation of carbohydrates from the source.

Gordon, Ryle & Powell (1977) indicated that while translocation of carbohydrates from leaves is rapid, the primary demand for non-structural carbohydrates is at meristematic sites, and a relatively small proportion of metabolites is converted to storage products.

In general terms, the results suggest that non-structural carbohydrate accumulation and depletion patterns in unutilised tillers of *T. triandra* and *S. fimbriatus* in the False Thornveld of the Eastern Cape are as follows: after tiller emergence and during vegetative growth, soluble carbohydrates in leaves, upper stems and roots remain at a fairly low concentration, but accumulate in stem bases. Stem bases are therefore the main storage organs. These stored carbohydrates are drawn on when culm elongation and flowering takes place. The carbohydrate reserves stored in stem bases are presumably also remobilised after tiller defoliation both for regrowth of the same tiller and growth of new individuals. However, the latter conclusion is speculative since tillers were not defoliated in the trial reported in this chapter.

5.4 Summary of results

i. Non-structural carbohydrates in leaves and stems of *T. triandra* and *S. fimbriatus* tillers are maintained at a low concentration of about 2% during vegetative growth. This concentration diminishes as tillers approach maturity and flowers develop.

ii. Non-structural carbohydrates in stem bases accumulate and reach a maximum of about 6% immediately prior to flower development. This maximum occurs in autumn in *S. fimbriatus* tillers and in late winter in *T. triandra* tillers. At flowering, non-structural carbohydrates in stem bases diminish, probably a result of translocation up the culm for flower and seed formation.

iii. Non-structural carbohydrates in roots are maintained at a concentration of 2-3%, and the concentration shows relatively little variability with changing season and plant age.

? dubious result

iv. Soil moisture treatments have relatively little influence on non-structural carbohydrate concentrations within plant organs.

5.5 The role of reserve carbohydrates - a critical examination

Reserve carbohydrates are traditionally considered to be the main source of energy for regrowth and respiration following defoliation of pasture plants (Booysen, 1966). The necessity of maintaining a high level of carbohydrate or "root" reserves to facilitate vigorous regrowth after defoliation has become a "corner-stone" of veld management philosophies advocated by extension officers (King, 1984, *pers. comm.*; Smart 1984, *pers. comm.*). To quote an experienced and senior extension officer in the Eastern Cape: "Where grasses grow poorly, the inference has been that this lack of vigour is due mainly to a depletion of root reserves. Much use of the role of root reserves has been made by extension workers when advising farmers on veld management. Lack of vigour in veld has been used to penalise participants in judging farm competitions as it has been accepted as a criterion on which to judge *inter alia*, the extent to which veld has been afforded rests to build up root reserves". (Smart, 1984, *pers. comm.*). It is thus evident that carbohydrate reserves have been used as a convenient means of explaining declining plant vigour with increasing defoliation.

Discussion

Booysen, 1966, however, questioned the traditional role of carbohydrates in determining the rate of regrowth after defoliation. The author indicated that although much attention in the literature had been directed towards the role of reserve carbohydrates, many questions remained unanswered for the great majority of pasture species.

Despite considerable research effort directed at establishing correlations between non-structural carbohydrate concentrations in storage organs and the rate of regrowth after defoliation, the success of these attempts has been limited (May, 1960); Ward & Blaser, 1961; Caldwell, Richards, Johnson, Nowak & Dzurec, 1981; Richards 1984 and Richards & Caldwell 1984). Caldwell *et al.* (1981) suggested that total reserve carbohydrate pools (the product of reserve carbohydrate concentrations and biomass) are a more appropriate measure of carbohydrate reserves than a simple measure of non-structural carbohydrate concentrations. Nevertheless, the authors found no correlation between regrowth following defoliation and reserve carbohydrate pools.

Richards & Caldwell (1984) suggest three possible causes for a lack of correlation between non-structural carbohydrate pools or concentrations and regrowth. These are:

i. non-structural carbohydrate reserves as assessed by traditional procedures do not adequately present available substrates for regrowth;

ii. the contribution of concurrent photosynthesis in determining regrowth is large relative to that of reserve substrate; and

iii. meristematic restrictions limit regrowth.

Dealing firstly with the question of whether non-structural carbohydrates adequately represent the plant's carbon reserve, Richards & Caldwell (1984) suggested that these reserves represent only a portion of the stored carbon used for regrowth. The authors came to this conclusion after studying etiolated regrowth (growth in the dark) of *Agropyron* species. They found that changes in the total available carbohydrate pool could explain only 19% of changes in crown biomass. Since plants were grown in the dark and photosynthesis could not have taken place, the conclusion was that soluble compounds other than carbohydrates must have been utilised as a source of carbon. Similar results have been reported with other pasture species by Davidson & Milthorpe (1966), Chung & Trlica (1980) and Dewald & Sims (1981). The identity of the soluble compounds other than non-structural carbohydrates used as a source of carbohydrate is not clear. Richards & Calwell (1984) suggested that crude protein could be one such source of labile protein, and showed that in *Agropyron* species, the carbon pool derived from this source could be as large as that present in acid-soluble carbohydrates.

The second suggested cause for unrelated growth response to reserve carbohydrates was that the contribution of concurrent photosynthesis is large relative to that of reserve substrate. Studies of carbon balance and of redistribution of 14C-labeled reserves following defoliation have, in a number of instances, shown little or no mobilisation of root or crown reserves for regrowth (Marshall & Sagar, 1965; Davidson & Milthorpe, 1966; Smith & Marten, 1970; Chung & Trlica, 1980; Richards, 1984 and Richards & Caldwell, 1983). Smith & Marten (1970) suggested that the contribution of concurrent photosynthesis varies considerably between species and phenological state, thus obscuring correlations between regrowth and reserve carbohydrates. The work of Richards & Caldwell (1984) showed that the contribution of stored carbon to the regrowth of *Agropyron* species was at most 10%, but probably considerably less. Only after very severe defoliation did the contribution of reserve carbon exceed that of photosynthesis, and this was for only a few days after defoliation. Furthermore, Caldwell *et al.* (1981) showed that culms and sheaths themselves can be important photosynthetic surfaces after defoliation. A situation not considered by previous authors is where photosynthetic substrate (green leaf area) is not removed by defoliation, but senesces as a result of moisture stress. This phenomenon commonly arises in semi-arid grassveld such as that in the False Thornveld of the Eastern Cape. In situations where photosynthetic substrate is eliminated by severe defoliation or drought, or a combination of the two, regrowth must inevitably be triggered by reserve labile carbon, provided meristematic sites for regrowth are available. Under these circumstances reserve carbon is essential, even if only for a short period. The question is whether the quantities required are large enough to make rests aimed at allowing reserves to accumulate, an important managemant consideration.

The third suggested cause for a lack of correlation between regrowth and reserve carbohydrates is the question of meristematic limitations. Richards & Caldwell (1984) found considerable differences in the etiolated regrowth of two *Agropyron* species, even though large amounts of stored carbohydrate were present in both species. The authors attributed this difference to the inability of *A. spicatum* to produce secondary tillers readily, relative to the more rapidly responding *A. desertorum* after apical meristems of both species had been removed. Similar results were reported by Caldwell *et al.* (1981). In addition, Richards (1984) showed that removal of apical meristems of either *Agropyron* species affected 'etiolated regrowth considerably more than the presence or absence of carbohydrate reserves. The author thus concluded that photosynthetic carbon fixation is the most important carbon source for regrowth, and that morphological characteristics of the plant limit this regrowth to a greater extent than availability of carbon resources. Tainton (1984) in reviewing the findings of Richards (1984) did not dispute the importance of meristematic sites in determining regrowth, and even suggested that their absence may be responsible for reduced forage production in midsummer in many grassland systems. However, Tainton, (1984) pointed out that this did not diminish the importance of energy reserves in triggering immediate development of new photosynthetic surfaces.

Meristematic limitations are particularly relevant in semi-arid grassland, where shoot apices are not only susceptible to defoliation, but also to senescence as a result of drought. Consequently, regrowth after a drought may be particularly slow, despite the presence of adequate labile carbon reserves. Research effort thus needs to be directed at the developmental constraints which restrict activation of basal buds following apical meristem removal or drought.

In conclusion, it is clear that many questions remain unanswered regarding the role of reserve carbohydrates and other physiological and morphological characteristics in determining the regrowth of grasses following defoliation or drought. Answers to the following questions are thus regarded as critical in order to model optimal sward management in the False Thornveld of the Eastern Cape.

i. What are the relative roles of reserve labile carbon, concurrent photosynthesis and presence of active meristematic sites in determining regrowth of key grasses after defoliation or drought?

ii. What is the chemical form of the stored labile carbon, and in which plant organs does it occur?

iii. How much reserve substrate is required to activate regrowth, and is this quantity sufficient to justify management strategies aimed at reserve accumulation?

iv. How long does it take before primary tillers become independent of reserve carbohydrate after defoliation or drought, and how long does it take newly initiated secondary tillers to become physiologically independent of their parents?

v. To what extent do defoliated tillers draw on the reserves of organically attached undefoliated tillers?

vi. What are the meristematic limitations of key grass species in terms of seasonal susceptibility of apical meristems to defoliation or drought, and in terms of the ability of basal buds to be activated following defoliation or drought at different times of the year.

In the absence of answers to these questions, the following hypothesis is proposed: "After defoliation, drought or winter, the rate of growth of individual secondary tillers is dependent on the availability of reserve carbon and the number of active lateral buds. Reserve carbon is, however, only drawn on for a relatively short period, probably no longer than after the emergence of at most two green leaves. This short period refers only to that time after growth has commenced, since unavailability of moisture can delay commencement of growth after defoliation or winter. The number of active lateral buds varies seasonally and is dependent on the severity of defoliation, the severity of the drought that has been experienced, and the species in question. Lateral buds are most readily activated in spring, and this activity diminishes as the season progresses, reaching a minimum in winter. Increasing severity of defoliation of primary tillers promotes lateral bud activation, particularly if primary tiller shoot apices are removed. Increasing drought severity results in progressive mortality of lateral buds downwards from the top of the tiller. Very severe drought results in the mortality of all lateral buds and regeneration then becomes dependent on seedlings. *T. triandra* activates lateral buds more readily than many other species".

"The rate of regrowth of primary tillers following defoliation, drought or winter is dependent on availability of reserve carbon and the extent of desiccation of the tiller. As with secondary tillers, reserve carbon is used only for a relatively short period, until one or two new leaves have emerged. These reserves are drawn on even after reasonably lenient defoliation since, defoliation results in removal of the youngest and the most photosynthetically active leaves first. During drought, however, the youngest leaves are the last to decay and reserve carbon is used only after the severity of drought reaches the stage where all leaves senesce. After winter the youngest leaves remain viable and thus relatively little carbon reserve is used by primary tillers at this time. After partial defoliation of tufts, defoliated tillers make preferential use of their own carbon reserves but if these are insufficient, they will draw on reserves of organically attached undefoliated tillers".

"The response of regrowth to the size of the reserve carbon pool is correlated only when the pool is below a certain critical level. Reserves in excess of this level are not used for regrowth. This critical level of reserves can be maintained in a rotational grazing and resting system where periods of occupation are short enough to avoid grazing regrowth, periods of absence are long enough to allow the rate of leaf decay to equal the rate of emergence, and veld receives a full growing season's rest at least once every four years".

It should be noted that the hypothesis set out above does not consider regrowth response to the net rate of leaf assimilation in different seasons - this was discussed in Chapter 4.

Finally, the proposed hypothesis regarding the role of reserve carbon was generated from the results that have been discussed, and a review of the literature. The investigations to be discussed in ensuing chapters were previously designed and thus were not specifically aimed at testing this hypothesis. However, some of the data will provide means of testing some of the suggested concepts and possible answers to some of the critical questions regarding the role of reserve carbohydrates.

CHAPTER 6

EFFECT OF MOISTURE STRESS ON GROWTH AND SURVIVAL OF KEY GRASS SPECIES

6.1 Introduction

In Chapters 3 and 4 it was shown that even in a well above average rainfall year, insufficient moisture considerably retards growth and production of tillers of key grass species in the False Thornveld of the Eastern Cape. In addition, it was shown that drought has a devastating effect on the survival of tiller populations. These results are consistent with the sentiments of Brown (1977) who cited water availability as the most important factor limiting growth and survival of range plants.

Under conditions of adequate moisture, water moves through the soil-plant-atmosphere continuum down a gradient of free energy (decreasing water potential). However, when the rate of transpiration exceeds the rate of absorption, water deficits develop in the plant. This subjects the aerial parts of the plant to stress, which results in reduced growth rates and biochemical processes in the plant. Severe stress may result in protoplast collapse in response to negative turgor pressures, at which point most biochemical reactions cease, and ultimately death occurs (Brown 1977).

The first impact of moisture stress in plants is reduced cell enlargement, followed by a decrease in the rate of cell division (Slatyer, 1967). In pasture plants, the observed response is a reduced rate of leaf enlargement. Leaf enlargement generally shows a marked decrease at values of leaf water potential below -4 bars (Turner & Begg, 1978). Stomatal closure and reduced photosynthesis are less sensitive to moisture stress than leaf extension in all species in which comparisons have been made (review by Turner & Begg, 1978). It is generally recognised that stomata do not respond to changes in leaf water potential until a critical threshold is reached, whereafter stomatal closure occurs over a narrow range in water potential (Turner & Begg, 1978). A similar observation was made by Mes & Aymer-Ainslie (1935) who found the transpiration intensity of *T. triandra* was not affected by diminishing soil moisture when soil water was in excess of 36% of water-holding capacity. However, closure of individual stomata does not occur at a unique leaf water potential, but varies between species, leaf ages and positioning of leaves in the canopy (Turner & Begg, 1978). Since stomata regulate CO_2 exchange, water deficits that close stomata also depress photosynthesis. Moisture stress also causes further reduction in photosynthesis not related to stomatal closure, but this usually occurs at leaf water potentials lower than those where stomatal closure takes place (Slatyer, 1973). Additional effects of moisture stress in pasture plants are a reduced rate of lateral tillering, decreased leaf longevity (also shown in Figure 3.20) and ultimately, tiller death.

Since leaf expansion is more sensitive to plant water deficit than photosynthesis, pasture plants, whose economic yield consists largely of vegetative growth, are more sensitive to moisture stress than plants where marketable yield is reproductive growth (Turner & Begg, 1978).

In South Africa, semi-arid grassland is particularly susceptible to drought (Skinner, 1981; Booysen & Rowswell, 1983). In these areas, the effect of moisture stress on the growth and survival of the important plant species is of obvious importance in formulating veld management strategies. Despite this, water relations in South African veld grasses have received little attention in the literature. Early work by Mes & Aymer-Ainslie (1935) was concerned with certain aspects of the moisture relations of various ecotypes of *T. triandra* found in the Northern Transvaal and what was then Bechuanaland (Botswana). The authors found that stomatal distribution on leaves varied considerably between ecotypes, times of the year and utilisation treatment, and even between leaves on the same plant. Young leaves and leaves with "hairy" cuticles transpired less than older leaves or leaves with smooth surfaces. Burning increased transpiration of leaves, a result also reported by Kruger & Van Ginkel (1975). Mes & Aymer-Ainslie (1935) further showed that transpiration was not affected by soil moisture provided the soil moisture content was greater than 36% of soil moisture at field capacity. However, when comparing transpiration at different times of the year but under conditions of similar humidity and temperature, the authors found that it peaked in midsummer. They thus concluded that *T. triandra* would suffer from low soil water content more during midsummer than at any other time of the year. Of particular interest in the results of Mes & Aymer-Ainslie (1935) was the fact that cuticular transpiration (as opposed to stomatal transpiration) was high, approximately half to two thirds of total transpiration. This suggests that grasses, or at least *T. triandra*, continue to lose moisture even after stomatal closure, explaining why tillers desiccate and die during droughts after wilting point has been reached.

Grass mortality as a result of drought was reported by Donaldson (1967) who found approximately 80% mortality of the three major perennial grass species in the Kalahari Thornveld after the 1964-66 drought. Where woody plants were eliminated before drought, only 10% mortality of grasses was recorded. This was probably a result of elimination of competition for moisture by the woody plants. More recently, work by Opperman, Human & Roberts (1977) showed that the response of *T. triandra* to moisture stress varied according to defoliation treatment. Lenient defoliation before or during stress seemed more beneficial than severe or no defoliation. Opperman *et al.* (1977) also found that short periods of stress apparently resulted in increased root growth and non-structural carbohydrate accumulation. The latter result corroborates the fact that photosynthesis continues after leaf elongation has ceased.

Studies on moisture use in *T. triandra* dominated, semi-arid grassveld in the Orange Free State showed that the mean evapo-transpiration (Et) in a field situation was approximately 0,35 of evaporation from a Class "A" pan open water surface (Eo) over a three-year period (Opperman, Human

& Viljoen, 1977). The authors did, however, indicate that the Et/Eo ratio changed considerably with time of year, phenological state of the grass, and between years of different rainfall. Subsequent work by Snyman, Opperman & Van den Berg (1980) recorded Et in the same situation but where soil moisture was never limiting. The recorded Et thus represented the potential evapo-transpiration (PEt). These authors showed that PEt varied considerably with time of year, veld condition, phenological state of the grass and extent of regrowth after defoliation. PEt was highest during summer, on veld in good condition, when grass was reproductive and when the sward had recovered after defoliation. On veld in good condition, a maximum Et/Eo ratio of 1,0 was recorded during summer after grass was well grown, and a minimum of 0,5 during early spring immediately after defoliation.

Opperman, Human & Viljoen (1977) suggested that the PEt/Eo ratio could be used to predict soil moisture and duration of regrowth after rain had fallen. However, since at least one of the factors affecting PEt is always changing, precise predictions are probably difficult.

Snyman *et al.* (1980) also studied water use efficiency of veld in various seral stages. The authors found that sub-climax veld (in terms of Clementsian succession) produced more phytomass per unit of moisture than pioneer veld. Further research by Snyman & Opperman (1983) in the same area established that a 20% reduction of normal incoming moisture resulted in reduced basal cover and a retrogression in plant species composition.

None of the investigations listed above was able to quantify degree of stress that plants are able to tolerate before growth ceases and varying degrees of desiccation takes place. The following information regarding water relations in key grass species is thus considered essential in order to optimise management and predict system responses in semi-arid grassveld:

i. the growth response of grasses to diminishing water availability and the level of water availability where growth ceases;

ii. the ability of leaves to remain viable through increasing levels of stress so that they recommence growing and/or photosynthesis after water replenishment;

iii. the ability of tillers to persist through increasing levels of stress; and

iv. the ability of grass to regenerate from lateral buds after existing tillers have senesced as a result of increasing levels of stress/drought.

An investigation was thus undertaken to quantify these relations for key grass species occurring in the False Thornveld of the Eastern Cape. Also of importance regarding water relations of key grass species is their moisture-use efficiency in terms of their forage production per unit of incoming rainfall. This aspect is being investigated by Stuart-Hill (1984*a*).

6.2 Procedure

The investigation was undertaken in two parts:

i. a potting trial in the greenhouse where water application was controlled (Experiment 1); and

ii. a field trial where data regarding the mortality of marked grass tufts became circumstantially available as a result of the 1982/83 drought (Experiment 2).

6.2.1 Experiment 1

During autumn 1982 representative tufts of *T. triandra* and *S. fimbriatus* were removed from the field in the False Thornveld of the Eastern Cape using the auger described in Section 3.2.4 and transplanted into greenhouse pots (25cm deep). Soil from the sites where the tufts were removed was used as filler. Although derived from different sites, the texture of the soil in which the tufts were established was similar for the two species (sandy clay loam), and in both cases contained 15 to 35% clay. Pots were free draining and kept in the greenhouse at the Dohne Research Station. Favourable conditions in the greenhouse resulted in rapid establishment of tufts and these were defoliated at a height of 2cm during August 1982. In the spring, a number of the pots containing tufts of both species were randomly selected and the soil washed away to ensure that roots had exploited all the soil in the pots.

On 14 September 1982, twelve pots of both species were irrigated to field capacity (watered in excess the previous day and allowed free drainage for 24 hours). Four healthy vegetative tillers in each pot were marked with wire rings of different colours enabling the same tillers to be returned to at successive sampling dates. All living green leaves on marked tillers were marked with a stain containing a dye in organic solvent. No further water was added to pots until after stress symptoms had developed in potted plants. Successively severe degrees of phenological stress symptoms were allowed to develop in respective individual pots before water replenishment. The degree of stress symptoms allowed to develop covered the range from the stage where leaves had wilted and commenced senescence in the most leniently treated pots, through successive stages of leaf and tiller senescence to the point where all tillers were completely dead. This was in an attempt to characterise the various levels of stress where leaf, shoot apex and total tiller mortality took place.

Since tiller populations and leaf areas varied between pots, the rate of water depletion was variable so that intervals between successive water replenishment in pots did not necessarily coincide with corresponding increased levels of stress. It was, however, ensured that the complete range of phenological stress symptoms from wilting through to tiller senescence was covered. Of particular note is the fact that vegetative *S. fimbriatus* tillers in the greenhouse were larger than those of *T. triandra*, and stress symptoms were observed sooner in the former species. Intervals between replenishment of water in successive pots were thus shorter in the case of *S. fimbriatus* than with *T. triandra*.

After the initial irrigation of pots to field capacity, and until replenishment of moisture, a number of parameters were recorded at least every second day, but more often in the initial stages when tillers were actively growing

i. Each pot was weighed using a triple beam balance in order to characterise soil moisture depletion.

ii. The number of living green leaves on each marked tiller was recorded. Leaves that had emerged since the initial irrigation of pots were also marked and recorded. Leaves were classified as living and green if any portion of the leaf blade was subjectively assessed to be both green in colour and not permanently wilted. Leaf blades considered to be either in a permanent wilt or to have lost all chlorophyll were classified as senescent.

iii. The total length of the living green portion of leaves on all marked tillers was measured. The living portion of leaves was defined as that portion which was subjectively assessed to be both green in colour and not permanently wilted.

iv. The leaf water potential of four randomly selected unmarked tillers (each from a separate pot) of each species was recorded. The tillers were destructively sampled at the same time each day (8 am) and leaf water potential was recorded using the procedure described by Scholander, Hammel, Bradstreet & Hemmingsen (1965). The technique could not be used after leaves had wilted because the pressure required to neutralise leaf water potential became too high for precise measurements.

v. The evaporation from an open water surface was monitored. The evaporation from the container used in the greenhouse was subsequently calibrated against a Class "A" evaporating pan, in order that potential evaporation in the greenhouse could be expresseed in terms of standard Class "A" pan evaporation from the two respective water surfaces.

After relief of stress, the pots concerned were maintained at field capacity, and a further set of parameters was recorded.

i. The number of marked leaves per marked tiller that recovered after stress relief was recorded. These were identifiable within days after water replenishment.

ii. The number of marked tillers whose apices senesced during the period of moisture stress was recorded. This could be assessed in terms of whether the tiller continued to produce leaves after stress relief. This was identifiable within a fortnight after water replenishment.

iii. The number of marked tillers that senesced completely as a result of the stress was recorded. These were identified as tillers that produced no new leaves or lateral secondary tillers after relief of moisture stress and were identifiable within three weeks of replenishment of moisture.

iv. The number of secondary tillers produced per marked primary tiller within about four weeks of water replenishment after stress was also monitored.

After completion of the trial, the soil from each pot was removed and dried to constant mass, enabling soil moisture content to be calculated in terms of soil dry mass.

6.2.2 Experiment 2

This trial was undertaken at the Adelaide Experimental Station and at a site approximately 20km east of Adelaide (Kroomie). Both sites were typical of the False Thornveld of the Eastern Cape. The vegetation consisted of both a herbaceous and a woody component, the latter comprising predominantly *Acacia karroo* at a density of not more than 1000 individuals per ha. The chief difference in the herbaceous vegetation at the two sites was that the species composition at Kroomie corresponded to what Danckwerts (1981) described as veld in good condition, while that at Adelaide was in moderate condition.

Thirty living tufts of the most abundant species at each site had been permanently marked prior to the 1982/83 drought for purposes of a separate study of utilisation patterns by animals (Chapter 10). Both sites received a full growing season's rest during the 1982/83 season, but were grazed by cattle during winter 1983. Thereafter, the sites were again rested for the whole of the 1983/84 season. Approximately eight weeks after the drought had been broken in spring 1983, marked tufts were returned to and mortality assessed. Tufts were classified as dead, only if there was no sign of any living tillers. Even if one green secondary tiller was present on a tuft it was classified as living.

Both sites were characterised in terms of species composition by means of wheel point surveys of 500 points before the 1982/83 drought and again during winter 1984, approximately one year after the drought had broken. Strikes and nearest plant data were recorded. In addition, adjacent sites that had not received a full growing season's rest after the 1982/83 drought were also characterised in terms of species composition. These adjacent sites received identical management and were similar in all other aspects prior to the drought. At Kroomie, the adjacent site had in fact been part of the same production camp until the experimental site was camped off at the commencement of the trial.

The soil at both sites was of the Glenrosa form with an effective rooting depth in excess of 50cm. However, the soil at Adelaide contained a large proportion of free boulders, approximately 50% by volume recorded in an adjacent separate research project on soil of the same series (Stuart-Hill, 1984b). In contrast the soil at Kroomie was boulder free.

Rainfall was recorded at both sites. Evaporation was recorded using a Class "A" pan only at Adelaide. For logistical reasons, it was not possible to monitor evaporation at Kroomie.

6.3 Results and discussion

6.3.1 Effect of controlled stress on growth and mortality of tillers of key grass species (Experiment 1)

6.3.1.1 Cessation of growth as determined by moisture stress (Experiment 1)

Probably the most meaningful way of expressing the effect of moisture stress on growth and senescence of grass tillers is by means of functional representation of changes in growth or senescence in relation to progressive depletion of moisture available to the plant. In order to do this, a prerequisite is the availability of sensitive and readily quantifiable indices of both growth and moisture stress. In this trial, the measurement used to monitor growth was total green leaf length per tiller. This is because cell expansion and division is the most sensitive response of grasses to moisture stress (Turner & Begg, 1978). In order that this technique should be successful, the oldest leaves must be young enough not to be undergoing normal senile senescence; otherwise senile senescence of oldest leaves could mask expansion of youngest leaves, and thus recorded net growth. In order to avoid this all pots were defoliated approximately one month prior to the commencement of stress, and on the basis of the results discussed in Chapter 3, oldest leaves were considered to be young enough not to be undergoing normal senile senescence. It is of note that this technique can be adapted for use as an index of cumulative tiller growth over an extended period. In order to do this, the maximum absolute length of each successive leaf would have to be recorded, irrespective of whether it was green or not. This procedure has been used with considerable success by Stuart-Hill (1984*a*).

The green leaf length technique used in this trial reflects net green leaf expansion, and thus changes in plant size. The literature indicates that the photosynthesis continues for a short period after cessation of visible growth. However, in order to monitor this, gasometric measurements are required. Apparatus was not available for such measurements in this trial, and the term growth refers only to net visible growth as reflected by net green leaf expansion. In contrast to indices for monitoring growth, indices of senescence are relatively easy to quantify. These include leaf, shoot apex and total tiller mortality. The procedure for recording these has been described in Section 6.2.2.

If growth (or senescence) is to be functionally presented in terms of progressive moisture depletion, it is essential that in order to fulfil the preconditions for regression analysis laid down by Hunt (1982), moisture availability should be measured without, or virtually without error. One of the most attractive means of expessing the moisture available in plants is leaf water potential. The advantage of this index is that it reflects the total plant response to available moisture and is thus independent of soil texture, structure and depth. However, for leaf water potential to be a meaningful expresson of water depletion, it must be measured at the same time each day, and preferably at dawn. This is because leaf water potential changes markedly with time of day, and it is at dawn that the parameter is equal to (when soil water is abundant) or closest to soil water potential. In this trial leaf water potential was recorded using the procedure of Scholander *et al.*(1965). However, the procedure could only be used while leaf water potential was fairly high. When leaves approached wilting point, leaf water potential dropped sharply (lower than -200 bars). At these low potentials the procedure of Scholander *et al.* became unreliable, since the point where cell sap potential was in equilibrium with air pressure in the "Scholander bomb" could only be identified within a wide range of pressures. Consequently, use of leaf water potential as the independent variable in regression analysis would be expected to result in increasingly wide confidence intervals with decreasing leaf water potential, particularly below -200 bars.

An alternative index for expressing moisture availability is soil moisture. This was recorded relatively accurately in each pot by weighing pots to the nearest gram when pots were at field capacity and at each sampling date thereafter. Soil water content was calculated as the mass of soil water per unit dry mass of soil. In order to spread the range over which soil moisture varied, the parameter was expressed as the percentage depletion of the soil moisture content at field capacity.

A comparison between measured leaf water potential and the corresponding soil moisture content is presented in Figure 6.1. The relationship in Figure 6.1 is described in terms of a splined third order polynomial fitted to the primary data according to the methodology of Parsons & Hunt (1981) and is presented on an arithmetic scale. The relationship is qualified by 95% confidence intervals. Fitting confidence intervals to the curves is acceptable since leaf water potential was measured on new randomly selected tillers at each sampling date. Figure 6.1 suggests that leaf water potential remained relatively constant while water availability in the soil was abundant (up to 30% and 60% depletion of soil water in pots containing *T. triandra* and*S. fimbriatus* plants respectively). Thereafter, leaf water potential declined sharply with diminishing soil moisture. The presence of reasonably wide confidence intervals (Figure 6.1) suggests error in measurement of at least one of the indices for expressing water availability. A difference in the recorded leaf water potential of tillers removed from the same pot at each date, as well as the fact that it was difficult to measure the parameter when pressures dropped below -200 bars, suggests that at least some of the variability arose from the "Scholander bomb" method (Scholander *et al.*, 1965) of estimating leaf water potential. In contrast, soil moisture content in each pot could be measured relatively accurately (to within 1g of water whose mass was the order of 1,5kg at field capacity). However, a possible source of error in using soil water as an index of moisture availability is possible variability between pots both within species and between species, particularly the latter since soil was derived from different sites. Comparisons of the soil water content at field capacity, soil water content at maximum green leaf length (cessation of visible growth), the amount of soil water (as a percentage of soil dry mass) available for visible growth, and the depletion of soil water as a percentage of soil water at field capacity between individual pots of the two species are presented in Table 6.1.

The results in Table 6.1 show that the soil on which *S. fimbriatus* tufts were growing contained more water at field capacity ($P<0,01$) and at cessation of visible growth ($P<0,05$) than the soil on which *T. triandra* tufts were growing. In addition, the absolute amount of water used for expansive leaf growth was greater ($P<0,05$) in the soil in which the former species was growing. However, although statistically significant, these differences were small, and generally no more than the standard errors between species. There was no significant difference in the percentage of soil water depletion between species at the point of maximum visible growth in individual pots. It is thus concluded from Table 6.1 that although there was error in using soil water content as an index of moisture availability (both between and within species), in absolute terms this error was relatively small. The variability was certainly smaller than that involved in measuring leaf water potential at pressures lower than -200 bars.

Mean green leaf length per tiller per pot plotted against moisture availablity expressed in terms of soil water depletion (A) and plant water potential (B) recorded for both species at each sampling date is presented in Figure 6.2. The relations in Figure 6.2 again represent splined third order polynomials fitted to the primary data and presented on an arithmetic scale. Although 95% confidence intervals are fitted to the curves, these are only intended to give an indication of the variability in the primary data. They cannot be used to test statistical differences between curves since successive measurements from the same 12 pots of each species were used to construct the regressions and thus variance is partially correlated. These confidence limits are considerably wider when green leaf length is plotted against leaf water potential (Figure 6.2B), than when the parameter is plotted against soil water depletion (Figure 6.2A). This suggests error in the recorded values of leaf water potential, particularly at pressures below -200 bars when confidence intervals widened markedly (Figure 6.2B). Thus, despite the attractiveness of leaf water potential as a measure of water available to the plant, practical limitations made the "Scholander bomb" technique a poor measure of water availability for growth of grasses. In contrast, despite variability in moisture-holding capacity between pots (Table 6.1), the relatively narrow confidence limits in Figure 6.2A suggest that soil moisture depletion was a more reliable method of assessing the moisture available for plant growth than leaf water potential.

The results (Figure 6.2A) show that maximum green leaf length was considerably greater in *S. fimbriatus* tillers than in those of *T. triandra*. This is attributed to the difference in the absolute size of the tillers of the two species and has already been noted in the procedure (Section 6.2.2). The trend in leaf extension with progressive moisture depletion was, however, the same between species. Green leaf length per tiller increased steadily while water was abundant, reaching a maximum at approximately 40% water depletion. Thereafter, green leaf degenerated rapidly, beginning from the tips of oldest leaves (Figure 6.2A). The actual mean length of time taken for tillers of the two species to reach maximum green leaf length was six and 10 days for *S. fimbriatus* and *T. triandra* respectively. The fact that water was depleted more rapidly by the former species is attributed to greater evapo-transpiration because *S. fimbriatus* tillers were considerably larger than those of *T. triandra*. It is of note that soil moisture depletion at maximum green leaf length (Figure 6.2A) did not coincide precisely with that listed in Table 6.1 for both species. This is because the curves in Figure 6.2B are derived from green leaf expansion data recorded at all sampling dates, while the means in Table 6.1 are only from those data where green leaf length was maximal in each pot.

Regarding cessation of leaf expansion as determined by moisture stress in general terms, the results suggest that this takes place after approximately 40% soil water depletion. It is, however, conceded that cessation of leaf expansion could take place at different levels of soil moisture depletion depending on soil texture. Nevertheless, the soils used in this trial were typical of the veld type as a whole.

These results can be used to extrapolate the duration of active leaf expansion of *T. triandra* and *S. fimbriatus* in the field at various times of the year and after rains of different sizes. In order to do this, it is necessary to know the potential evapo-transpiration (PEt) at various times of the year of veld on which the grasses occur. The duration of leaf expansion (days) could then be simply calculated by dividing 40% of the rain that has fallen by the daily PEt at that time of the year. Assumptions would be that soil is dry before the rain, that all rain enters the soil and there is no run-off, and that water in the soil after the rain can be uniformly extracted by grass roots throughout the wetted profile. Obviously the extrapolation would also be based on the assumption that the level of soil moisture depletion where leaf expansion ceases in the field, is equal to that recorded in the greenhouse.

Potential evapo-transpiration data are not available in the False Thornveld of the Eastern Cape. However, Class "A" pan evaporation data are available for a period of seven years from the Adelaide Experimental Station (1977 to 1983 inclusive). These data are considered to provide a reasonably reliable estimate of mean monthly evaporation since evaporation data are considerably less variable than those of rainfall. This is shown by the fact that coeficients of variation of evaporation calculated for individual months over seven years, ranged from 11% to 17%.

In contrast, those calculated from rainfall recorded at the Adelaide Police Station over a period of 65 years, range from 71% to 127% between individual months (Anon,1984). The best available means of converting Class "A" pan evaporation data recorded at Adelaide to PEt is by using PEt/Eo ratios recorded for semi-arid grassveld in the Orange Free State by Snyman *et al.* (1980). These authors derived mean PEt/Eo ratios for the periods September to January and February to May inclusive. In addition, separate ratios were derived for veld in various seral stages.

The monthly rainfall recorded at the Adelaide Police Station over a sixty-five-year period, the mean monthly evaporation at the Adelaide Experimental Station, (Anon, 1984) and the corresponding monthly PEt for the months September to May inclusive (growing season) are presented in Table 6.2. PEt is calculated from PEt/Eo ratios derived by Snyman *et al.* (1980) for both of what these authors termed "climax" and "sub-climax" veld. However, for the purposes of this discussion they are more appropriately termed veld in good and moderate condition, respectively. It is stressed that the PEt/Eo ratios derived by Snyman *et al.* (1980) are merely estimated means. In addition to variation between times of year and veld condition types (already considered in Table 6.2), the ratios would change considerably according to grass phenology and extent of regrowth after defoliation (Snyman *et al.* 1980). In addition, during severe drought, green leaves would presumably senesce and initial PEt would approach that on a bare soil surface which, according to Snyman *et al.* (1980) is only 0,18 of Eo.

The data in Table 6.2 are used to estimate the duration of green leaf expansion growth (Figure 6.3B) for veld in good and moderate condition respectively in the False Thornveld of the Eastern Cape. These durations are calculated assuming that extension growth ceases at 40% soil water depletion. In addition, the results in Figure 6.3B are calculated on the assumption that all rainfall from September to May enters the soil, 40% of which is used during leaf expansion growth.

At first glance, the results in Figure 6.3 seem unlikely.

The data suggest that active leaf expansion on veld in good condition persists for approximately five, four and seven days during spring, summer and autumn, respectively, after a rain of 50mm. If these estimated periods of leaf expansion are excessively short, then one or more of the following apply:

i. green leaf expansion in the field continues after soil water depletion in excess of 40%;

ii. the PEt/Eo ratios of Snyman *et al.*(1980) are an overestimate; or

iii. soil water is not uniformly available for extraction by grass roots through the vertically wetted profile or, with time as water is depleted. In fact, the latter statement is probably true since water deep in the soil profile will require more energy for extraction than water near the surface and, as water is depleted, soil water potential drops, requiring greater energy for extraction. This would imply a somewhat longer duration and slower rate of leaf expansion as surface water is depleted, and an actual evapo-transpiration correspondingly lower than PEt. Of further note is the fact that the Eo values in Table 6.2 are means for entire months. In practice, however, Eo values during the first few days after a rain are often lower than normal, implying less daily Et than that suggested in Table 6.2, and consequently, a longer period of leaf expansion growth.

Nevertheless, inferences from the results of other workers suggest that the results in Figure 6.3 are not totally misleading. Stuart-Hill (1984*c*) found that after a rain of approximately 50mm at the Adelaide Experimental Station at the end of October 1983, 40% soil moisture depletion took place within five days. The veld at the site was in moderate condition, and furthermore, total available soil water depletion took place within 12 days after the rain had fallen. In the semi-arid grassveld of the Orange Free State, both Opperman *et al.* (1977) and Snyman *et al.* (1980) recorded evapo-transpiration values in midsummer of more than 10mm/day, suggesting very rapid depletion of soil moisture and thus short periods of growth after rain.

In the greenhouse trial reported in the current discussion, maximum green leaf length (Figure 6.2) occurred six to ten days after soil had been watered to field capacity. The mean daily evaporation in the greenhouse at this stage was 4,8mm, less than the mean for September at the Adelaide Experimental Station (Table 6.2). Added to this is the fact that tillers had been defoliated only one month before, suggesting a relatively low leaf area and thus, rate of evapo-transpiration from pots.

The results in Figure 6.3, as well as those of Opperman *et al.* (1977), Snyman *et al.* (1980) and Stuart-Hill (1984*c*), emphasise that growth after rain takes place for a very short period in semi-arid grassveld (Figure 6.3A). In addition, the total number of days during which leaf expansion growth takes place are relatively few, probably no more than 40 to 50 per year in an average season (Figure 6.3B). Even if expansion continued until 60% soil water depletion and not 40% as suggested in the greenhouse trial, the PEt/Eo values derived by Snyman *et al.* (1980) would imply a duration of leaf expansion on veld in moderate condition after 50mm rain in midsummer of approximately six days.

Of further note, regarding the results in Figure 6.3, is the fact that growth after a given amount of rain continues for considerably longer during autumn than at any other time of the year (Figure 6.3A). This is a result of relatively low Eo value at this time combined with lower PEt/Eo ratios during autumn than at any other time of the year (Table 6.2). This trend, coupled with a peak in average rainfall during autumn (Table 6.2), implies a considerably longer duration of leaf expansion growth during February, March and April than in any other month in an average year in the False Thornveld (Figure 6.3B).

The duration of leaf expansion after rain presented in Figure 6.3A applies only to swards with living green leaves. Snyman *et al.* (1980) showed that the PEt/Eo ratio decreased markedly after defoliation. In addition, during severe drought leaf senescence takes place (Section 3.3.5). The PEt/Eo ratio after a severe drought will initially approach that of a bare soil surface and thus the duration of leaf expansion growth after rain at the end of a drought will be longer than under normal conditions. However, if Et after a drought remained equal to that on a bare soil surface (0,18 of Eo; Snyman *et al.* (1980)) 40% moisture depletion in midsummer would still take place after only 12 days, assuming the Eo values listed in Table 6.2.

The results (Figure 6.3) have important implications regarding grazing management. It is widely advocated by extension officers that the grazing rotation should be rapid during periods of active growth, accompanied by longer periods of occupation and absence when the sward is dormant. The theory is that short periods of occupation will incur minimal damage while still allowing regrowth to take place after animals have been removed. However, if the duration of leaf expansion growth after the rain is less than a week, periods of occupation would have to be extremely short to allow the camps grazed during and after the rain, to make use of this moisture for regrowth. It is suggested that a more judicious practice after rain is not to move animals, but rather to sacrifice (temporarily) the camp or camps where the animals were grazing at the commencement of the rain, by keeping them there for the duration of expansion growth after the rain. This would ensure the accumulation of forage on the maximum possible portion of a farm and the "sacrificed" camps could then be given special treatment after subsequent rains. Such a practice could result in animals staying in the "sacrificed" camps longer than originally intended, thus causing possible stress to these animals through insufficient forage availability. However, such a stress period would be short (generally less than one week) and would probably not result in noticeably impaired animal performance. Even preferable to this suggestion in terms of dry matter production would be to kraal animals for the duration of leaf expansion growth after rain. Additional feeding costs (R2.60 per cow per day; (Aucamp, 1984*a*)) would probably make the economics of such a practice questionable except after severe drought. This practice is particularly desirable after drought when meristematic limitations and low levels of reserve substrate probably seriously inhibit regrowth. However, because of leaf mortality the period of regrowth after drought is probably longer than after a rain in a normal season, and thus feedlot cost would be higher under such circumstances.

Another possible management strategy after a rain would be to spread animals over a whole farm at the lowest possible stocking density for the duration of expansion growth. The rationale behind this practice would be to minimise the probability of any particular plant being grazed while active growth is taking place. However, this option is considered questionable in view of the selective grazing that could result subsequent to recommencement of normal rotational grazing.

6.3.1.2 Effect of stress on leaf senescence and recovery

In the preceding section, soil water depletion was considered a more precise means of characterising leaf expansion growth in terms of water availability than leaf water potential. This was largely a result of technical limitations in the procedure used for monitoring leaf water potential, particularly where moisture availability was less than that required for positive leaf expansion growth. Soil water depletion was thus also used to characterise the number of viable green leaves per tiller of *T. triandra* and *S. fimbriatus* as determined by moisture stress (Figure 6.4A). These relations represent splined third order polynomials fitted to primary data recorded on each marked tiller at each sampling date and are presented on an arithmetic scale. Since the data represented successive measurements of the same 48 marked tillers in 12 individual pots of each species, variance between harvest dates was correlated. The 95% confidence intervals plotted in Figure 6.4A are thus merely an indication of the variability in the primary data (between pots and tillers within pots) and cannot be used to test differences between populations statistically.

The results (Figure 6.4A) suggest that leaves remained viable (*S. fimbriatus*) or senesced at a slow rate (*T. triandra*) with depleting soil moisture until approximately 70% soil water depletion. Thereafter the rate of leaf senescence increased markedly with diminishing moisture. Most leaves had senesced by the time 90% soil moisture had been lost. The results suggest further that although *T. triandra* leaves commenced senescing at a higher soil moisture content than those of *S. fimbriatus*, when soil water became severely depleted (greater than 80%) remaining leaves of *T. triandra* were apparently more tolerant of stress than those of the other species.

The relations in Figure 6.4A do not represent leaf senescence on a time scale. Soil water diminished more or less constantly with time until approximately 70% soil water depletion, after which soil water was extracted progressively more slowly. The primary data used to construct the relations in Figure 6.4A thus occurred most frequently in the range of greater than 70% soil water depletion. The paucity of observations at soil water depletion values less than 70% is illustrated by the relatively wide confidence intervals at less than this level of soil water depletion (Figure 6.4A). The results thus suggest that leaf senescence takes place over a narrow range of soil water depletion in excess of 70%. This will presumably apply to the mortality of other plant parts, particularly those that senesce after leaves have died such as growing points and lateral buds. Thus, since the process of plant senescence takes place over a narrow range of soil water content, soil water depletion is not particularly attractive for expressing water stress when the objective is prediction of plant mortality.

Another means of expressing stress is in terms of atmospheric evaporative demand (Eo). One of the problems associated with using this parameter in the investigation reported in this chapter (Experiment 1) is that the PEt in individual pots varied according to tiller density and leaf area. The rate of water depletion and thus stress would obviously be greatest in pots with highest leaf areas. This problem was partially overcome by determining Eo for each pot from the date of cessation of leaf expansion. This would largely have eliminated differences in water loss between pots arising from stomatal transpiration, and it is during the period when stomata were open that major differences in Et between pots would have occurred. Nevertheless, differences in the rate of moisture loss between pots would still have occurred as a result of greater cuticular transpiration from pots with highest leaf areas. These differences would, however, have diminished as leaves wilted, and disappeared completely after leaf senescence. In view of the above argument, the major consequence of expressing stress in terms of Eo after cessation of leaf expansion growth in this trial is that stress symptoms in the species *S. fimbriatus* would be likely to occur after an apparently lower level of stress (Eo) than for the species *T. triandra*. This is because *S. fimbriatus* pots had higher leaf areas than those of the other species. Within species, leaf areas within pots appeared to be relatively uniform.

The relations between the number of viable leaves per tiller and moisture stress expressed as Eo after cessation of leaf expansion growth for the species *T. triandra* and *S. fimbriatus* are presented in Figure 6.4B. These relations are once again splined third order polynomials fitted to primary data on an arithmetic scale, and 95% confidence intervals, because of correlated variance, merely represent the variability in the data. These relations (Figures 6.4B) show that the number of green leaves per tiller declined at a fairly constant rate over most of the range of recorded Eo, suggesting that Eo is a more attractive measure of stress that the plant has endured at the levels where mortality takes place. In addition, within the limited duration of the greenhouse trial, cumulative Eo was virtually linearly related to time, and thus there was a relatively even distribution of the primary data over the range of observations in Figure 6.4B. This resulted in more symmetrical confidence limits at the two ends of the relations in Figure 6.4B as compared with those in Figure 6.4A. Nevertheless, the number of recordings in Figure 6.4B still became progressively fewer as levels of stress increased as a result of the fact that pots were being successively replenished with water as increasingly severe stress symptoms developed. Thus an increasing number of pots did not contribute to the data as time progressed. This explains why confidence intervals in Figure 6.4B became wider at levels of stress (Eo after cessation of leaf expansion) greater than 175mm. A further advantage of using Eo after cessation of leaf expansion as a measure of stress to predict mortality is the fact that it allows extrapolation into the field. It would not be possible to use soil water depletion for this purpose since the PEt/Eo ratio presumably drops sharply after cessation of growth and in any event has not been quantified. In addition, changes in soil water at this time would be very small, implying that predictions of soil water depletion and corresponding effects on the plant would be difficult.

It is thus concluded that for the purposes of this investigation, while soil water depletion was the best means of quantifying the effect of stress on leaf expansion (Section 6.3.1.1), Eo after cessation of leaf expansion is a better means of quantifying the effect of stress on leaf mortality. In short, the rationale is that Eo would have been a poor expression of stress during active growth in view of variability in leaf area between pots. However, after cessation of growth, wilting would have commenced and Et would have been less affected by leaf area than when stomata were fully open. It is, however, conceded that cuticular transpiration after cessation of growth would still have resulted in different levels of moisture stress between pots because of differences in leaf area.

The results (Figure 6.4B) show that after cessation of growth, relatively little leaf mortality took place up to 50mm Eo. Thereafter, leaves of each species senesced at a constant rate with increasing Eo until approximately 160mm Eo had taken place after cessation of expansion growth. At this stage, most green leaves of both species had senesced. The results suggest that *T. triandra* leaves were more resistant to stress (expressed as Eo) than those of *S. fimbriatus*, but this is probably largely a result of differences in leaf areas between species. Nevertheless, when viewed in conjunction with the result in Figure 6.4A, the results do indicate the *T. triandra* leaves may be more tolerant of stress than those of *S. fimbriatus* at levels of severe moisture stress. This observation was also subjectively made in the field during the the 1981/82 and 1982/83 droughts, where *T. triandra* leaves apparently remained green for longer than those of most other species.

Of note, with respect to leaf senescence as a result of stress, is the fact that oldest leaves died first, implying that the leaves most vulnerable to grazing (at the top of tiller) are the last to die as a result of drought.

The results in Figure 6.4 are based on subjective assessment of the viability of individual leaves as stress progressed. This meant that estimation of the precise point where leaves were no longer viable (permanent wilt) was difficult. However, precise estimation of the ability of leaves to recover after stress was possible by considering the number of leaves marked per tiller before stress that recovered after water replenishment. Of course, this gives no indication of progressive leaf mortality, but only of the proportion of leaves that recovered after relief from varying degrees of stress. The proportions of leaves on marked tillers that recovered when water was replenished after progressive levels of stress in individual pots of *T. triandra* and *S. fimbriatus* are presented in Figure 6.5. Each symbol in Figure 6.5 represents the mean percentage leaf recovery of the four marked tillers in each pot. The data are described by simple logarithmic regressions which were statistically different between species. Simple mechanistic models were used on the basis that there were too few points to regress the data by means of spline functions (empirical models), but correlation coefficients (Figure 6.5) show that the fitted functions followed the data reasonably closely. The choice of the mathematical form of the simple regression was made after testing the goodness of fit of linear, exponential, logarithmic and power functions. Not included in the regressions in Figure 6.5 are those observations made long after all leaves had died. These observations (denoted by bold symbols in Figure 6.5) were made for the purpose of monitoring lateral bud activity after very severe stress and would have altered the mechanistic regressions, resulting in unrealistic fits to the data in the range of moisture stress where leaf mortality was taking place.

The results (Figure 6.5) indicate that after cessation of leaf expansion, periods of stress equivalent to 90mm and 125mm Eo resulted in only 50% recovery of leaves of *S. fimbriatus* and *T. triandra* respectively, once water had been replenished. No recovery of leaves took place after stress periods equivalent to 160mm and 210mm in the two respective species.

The results (Figure 6.5) and the Eo data for the Adelaide Experimental Station (Figure 6.2) are used to estimate durations of periods of no rainfall once leaf expansion has ceased, after which 50% and 100% mortality of leaves of *T. triandra* and *S. fimbriatus* may be expected to take place in the False Thornveld of the Eastern Cape (Figure 6.6). These results (Figure 6.6) are obviously only a rough estimate in view of extrapolation from the greenhouse and the effect that changing leaf area (canopy cover) would have on the amount of water lost through cuticular transpiration. In fact, the differences between species (Figure 6.6) are probably a result of the fact that the leaf areas in *S. fimbriatus* pots were greater than those in pots of *T. triandra*, implying more rapid desiccation in the former species. Nevertheless, the estimated difference between species (Figure 6.6) is not particularly large considering that the actual duration of leaf expansion in pots was approximately twice as long in the species *T. triandra* as compared with that of *S. fimbriatus*. This implies that the effect of leaf area on the time taken for stress symptoms to develop is considerably less after growth has ceased than when leaves are growing and stomatal transpiration is taking place. Added to this is the fact that the actual duration of leaf expansion growth in the greenhouse was similar to that estimated for field conditions from soil water depletion in pots in the greenhouse (Section 6.3.1.1). In the absence of quantitative data from the field, the results (Figure 6.6) thus at least give a rough estimate of the effect of drought on leaf longevity.

The results (Figure 6.6) suggest that in midsummer, green leaves will senesce completely approximately 21 days after cessation of leaf expansion if there is no rainfall during this period. (It is of note that despite large differences in leaf areas between species, the estimated difference in the duration before total leaf senescence between species was only five days at this time of the year (Figure 6.6)). In other words, the implication is that after cessation of leaf expansion, tillers can recommence growing in midsummer through photosynthetic assimilation by existing leaves provided rain falls within about three weeks. After three weeks, tillers would have to make use of labile carbon reserves for initial regrowth. This period becomes considerably longer in spring and autumn as a result of lower Eo (approximately four weeks in October and March (Figure 6.6)). These results can be partially corroborated from data depicted in Figures 3.1 and 3.16. Virtually all green leaves on permanently marked tillers died during summer 1981/82 (Figure 3.16), and it was only for a period of little more than one month (January 1981) that no significant rain was recorded (Figure 3.1).

The results from the potting trial in this investigation do not take into account the fact that in the field, differential rooting depths of species might affect the amount of water available to them and thus their ability to retain green leaves. In Section 3.3.6.4 it was indicated that *T. triandra* has more roots at a greater depth than *S. fimbriatus*, suggesting that the former species might be able to retain green leaves for longer than the latter.

The management implication of the results in Figure 6.6 is that when stress periods are long enough to cause total leaf mortality, regrowth after rain will be slower than normal. This will arise from the fact that labile, as opposed to assimilatory carbon, has to be used to lay down new structural material before photosynthesis can take place. In addition, this period of regrowth will continue for longer than normal as a result of low PEt after the rain. In terms of the grazing rotation, animals should then be kept off camps not occupied at the time of moisture replenishment for longer than would be the case where leaf senescence had not taken place before the rain. Insufficient forage in occupied camps could thus make supplementary or pen feeding necessary under such circumstances.

6.3.1.3 Effect of moisture stress on tiller mortality

Two degrees of tiller mortality were monitored : firstly, mortality of the growing point of the primary tiller, disregarding whether or not lateral buds remained viable; and secondly, total mortality of the tiller so that no lateral buds recovered after water replenishment. The procedure for doing this is described in Section 6.2.1.

For the same reasons already given in the preceding section, Eo after cessation of leaf expansion was considered the most appropriate means of expressing stress at the levels of stress where tiller mortality took place. The percentage growing point mortality (A) and percentage total mortality (including lateral buds) (B) of marked tillers in individual pots of *T. triandra* and *S. fimbriatus* after progressive levels of moisture stress are presented in Figure 6.7.

Each symbol in Figure 6.7 represents the mean percentage mortality of the four marked tillers in an individual pot. The data are described by simple mechanistic regressions which were statistically different between species in both cases. Mechanistic models were used for the same reason that they were used to describe leaf recovery (Figure 6.5), and the mathematical form of the regressions were chosen according to goodness of fit. Not included in Figure 6.7A were those observations made long after growing points had died, again for the same reasons that they were excluded in Figure 6.5. All observations were included in the regressions in Figure 6.7B since there were no observations made long after those that first recorded 100% total tiller mortality.

The results show that the growing points of *S. fimbriatus* and *T. triandra* commenced senescence after approximately 80mm and 115mm Eo respectively. The proportion of growing point mortality increased progressively with increasing stress until all *S. fimbriatus* growing points had senesced at 160mm Eo and those of *T. triandra* at 240mm Eo (Figure 6.7A). Of particular note is the fact that 100% growing point mortality (Figure 6.7A) occurred at levels of moisture stress equal to (*S. fimbriatus*), or only a little more severe (*T. triandra*) than those where 100% leaf mortality took place (Figure 6.5). This suggests that once the youngest leaf of a tiller senesces, the tiller ceases to produce new leaves and regrowth will be dependent on secondary tiller development. This observation was also subjectively made by Stuart-Hill (1984*d*, *pers. comm.*) in recording data reported by the same author (Stuart-Hill, 1984*a*). The implication of this observation is that regrowth after total leaf senescence will be even slower than that suggested in Section 6.3.1.2 since it will be dependent on emergence of secondary tillers.

Mortality of whole tillers (apical meristem and lateral buds (Figure 6.7B)) commenced at similar levels of stress as those where growing points started to senesce (Figure 6.7A). However, a proportion of tillers maintained viable lateral buds after their growing points had died, and this can be observed from both the primary data and the fitted regressions (Figure 6.7B). Lateral bud mortality increased progressively with increasing stress until complete mortality of tillers took place after 275mm Eo (*S. fimbriatus*) and 330mm Eo (*T. triandra*).

The results in Figure 6.7 and the Eo data from the Adelaide Experimental Station (Figure 6.2) are used to estimate duration of periods of no rainfall once leaf expansion has ceased after which 50% and 100% mortality of growing points (A) and complete mortality (shoot apex and lateral buds) (B) of *T. triandra* and *S. fimbriatus* will take place in the False Thornveld of the Eastern Cape (Figure 6.8). As with predictions of leaf mortality (Figure 6.6), the results in Figure 6.8 are only a rough estimate in view of extrapolation from the greenhouse and the effect changing canopy cover would have on cuticular transpiration and thus the rate of desiccation. Once again, the differences between species in both Figures 6.7 and 6.8 probably arise from the fact that *S. fimbriatus* had a greater leaf area in pots in the greenhouse than *T. triandra*.

The results suggest (Figure 6.8) that during midsummer all growing points of *T. triandra* and *S. fimbriatus* will have senesced within 27 and 19 days respectively, after cessation of leaf expansion growth provided there is no rainfall during this period (Figure 6.8A). The corresponding periods for complete senescence (including lateral buds) are 37 and 31 days for the two respective species. It is of note that these differences between species are not large in view of the fact that the duration of leaf expansion in the pots was approximately twice as long for the species *T. triandra* than for *S. fimbriatus*. The implication is that if there is no rain after cessation of growth in midsummer for a period of about three to four weeks, regrowth when rain does fall will be from lateral tiller buds, and it will be slow, since use would have to be made of labile carbon reserves for initial regrowth. If the dry period continued for about five weeks, the lateral buds themselves would senesce and regrowth after relief of the drought would be dependent on seedling establishment. These critical periods become considerably longer in spring and autumn as Eo drops (approximately five weeks for growing point mortality and seven weeks for lateral bud mortality in October and March).

As with prediction of leaf mortality (Figure 6.6), the suggested trends in Figure 6.8 do not take into account the fact that species that have different rooting depths are likely to show different responses to moisture stress. Also, although pots were initially watered to field capacity, they were only 25cm deep. In Table 3.2 it was shown that by far the majority of the roots of *T. triandra* and *S. fimbriatus* occur within this depth. However, the few roots below 25cm may play an important role in extracting moisture from lower soil horizons, particularly in order to keep plants alive after water in the upper soil has been depleted, suggesting that rainless periods before tiller mortality might be longer than those suggested in Figure 6.8.

Nevertheless, approximately one month without rain in January 1982 (Figure 3.1) resulted in virtual total mortality of all marked tillers that did not receive irrigation in the field trial. The results (Figure 6.2), in fact, show that total tiller mortality took place somewhat after January, but this is misleading. Tillers could not be classified as dead until well after good rains had fallen, since before that, the difference between a dead or merely dormant tiller with senescent leaves could not be identified. Perusal of rainfall records in the False Thornveld, however, reveals that periods of one month or more where no rain falls are extremely rare during the growing season. Relatively long periods during which only small rains occur (less than 10mm rain) are reasonably common. The suggestion is that if tiller mortality does not take place during these periods (an observation made in the field during the 1981/82 season; Figures 3.1 and 3.2), then small rains, while not being large enough to stimulate growth, probably play an important role in keeping grass plants alive.

The management implications of the results in this section are that where rainless periods are long enough to cause growing point mortality (approximatley one month in midsummer if the period of leaf expansion growth is included), then regrowth following rain will be extremely slow. In addition, this regrowth will arise from secondary tillers which will be dependent on reserve substrate for initial growth. If the rainless period continues for so long that lateral buds also senesce, then regrowth would depend on seedling growth. The suggestion is thus that after severe drought, regrowth when it does rain probably continues for longer than normal (as a result of low PEt), and is likely to be extremely sensitive to grazing (since labile carbon has to be used for initial regrowth in the case of lateral tillers, and in the case of seedlings root systems are undeveloped and carbon reserves have not been accumulated). It thus becomes important to keep animals off the veld for as long as possible after a severe drought has been broken. Pen feeding of animals during these times is probably highly desirable.

6.3.1.4 Effect of moisture stress on secondary tillering

The mean number of secondary tillers produced per marked tiller within each individual pot containing *T. triandra* and *S. fimbriatus* at the end of a four week period after water replenishment following progressively severe levels of stress are presented in Figure 6.9. Each symbol in Figure 6.9 thus represents the mean of four marked primary tillers regardless as to whether they were still viable or senescent. Fitted to the data of each species are simple mechanistic regressions, the mathematical forms of which were chosen according to their goodness of fit.

The results (Figure 6.9) show that the number of secondary tillers produced per primary tiller decreased sharply at levels of stress in excess of 10mm Eo after cessation of leaf expansion. After a level of stress equal to about 150mm Eo, both species produced on average a lateral tiller only on every second primary. This level of stress corresponds to a rainless period of about two to three weeks in midsummer and three to four weeks during October and March. These results emphasise the fact that after drought periods, regrowth is extremely slow. This is not only a result of the fact that initial regrowth is dependent on labile carbon, but also of the fact that only a limited number of the original primary tillers produce any laterals. After periods of stress of 200mm Eo following cessation of leaf expansion, very few of the initial population of primary tillers produced any laterals (less than one in ten). Since primary tiller growing points had mostly senesced at this level of stress (Figure 6.7A), under corresponding circumstances in the field (a month or more with no rain during midsummer) the rate of grass recovery would be very slow and to a large degree dependent on seed germination and establishment.

In conclusion, the results (Figure 6.9) once more emphasise that after a period of severe drought, slow and vulnerable regrowth make it necessary to keep animals off the veld for as long as possible after the drought has broken. Thus, in semi-arid grassland, drought management strategies must be geared towards not only pen feeding animals during the drought (if there is no accumulated forage), but also towards pen feeding the animals after rain has fallen for a period at least as long as the duration of active growth, even if accumulated forage is available in the form of rested veld.

6.3.1.5 Summary of results

i. In the greenhouse experiment in this investigation, soil water depletion was found to be the best means of expressing moisture availability during active growth, while accumulative Eo after cessation of leaf expansion was the best means of expressing stress at those levels where plant mortality took place.

ii. Net leaf expansion growth of *T. triandra* and *S. fimbriatus* ceases after 40% water depletion in soils such as those used in the greenhouse trial reported in the current investigation. Using mean monthly Eo figures recorded at Adelaide and PEt/Eo ratios recorded in the Orange Free State, extrapolation to the field suggests that the duration of net green leaf expansion after rain is extremely short, probably less than a week for most of the growing season.

iii. In an average rainfall season, the extrapolated number of net green leaf expanding days in the False Thornveld of the Eastern Cape is of the order of 40 to 50.

iv. During autumn, low Eo values, PEt/Eo ratios and peak in rainfall normally result in considerably more green leaf expansion days than at any other time of the year.

v. After drought or grazing, low areas of green leaf result in low PEt values and thus a longer duration of leaf expansion growth than when canopy cover is high.

vi. The management implication of the duration of green leaf expansion under normal conditions is that after rain, animals should not be moved in the normal rotation, but kept in the camps where they were before the rain fell until the cessation of green leaf expansion growth. This would ensure accumulation of forage on the maximum possible portion of a farm after rain has fallen.

vii. Green leaf viability is affected relatively little by moisture stress until approximately 70% soil water depletion or 50mm Eo following cessation of leaf expansion. Thereafter leaves desiccate progressively with increasing levels of stress, beginning with oldest leaves. No green leaves recovered when water was replenished after stress of the order of 200mm Eo following cessation of leaf expansion.

viii. Extrapolation of results to the field suggest that in midsummer all green leaves will senesce approximately three weeks after cessation of leaf expansion if there is no rainfall during this period. The corresponding period is approximately four weeks in October and March.

ix. Growing point mortality more or less coincides with mortality of the youngest emerged green leaf on a tiller.

x. A proportion of tillers maintain the ability to activate lateral buds after growing point mortality. However, complete mortality (including lateral buds) of tillers takes place after approximately 300mm Eo following cessation of leaf expansion. Extrapolation to the field suggests that after cessation of leaf expansion in midsummer, a period of approximately five weeks with no rain will result in total tiller mortality. The equivalent period is approximately seven weeks in October and March.

xi. Small rains (less than 10mm) apparently play an important role in maintaining tiller viability.

xii. The number of lateral buds produced per primary tiller decreases sharply with increasing stress in excess of 100mm Eo after cessation of leaf expansion. At levels of stress greater than 200mm Eo after cessation of leaf expansion, very few of the original population of tillers retain the ability to activate lateral buds.

xiii. The results suggest that after severe drought (one month or more with no rain in midsummer, longer in spring and autumn) regrowth is in the form of secondary tillers and seedlings. Such regrowth is likely to be extremely slow, as well as vulnerable to grazing. The management strategy after severe drought should thus be to pen feed animals for a period at least as long as the duration of active regrowth.

6.3.2 The effect of severe drought on tuft mortality and species composition (Experiment 2)

One way of expressing the severity of drought experienced at the field sites during the 1982/83 season is by means of water budgets. These have the objective of estimating the extent to which moisture requirements of crops are met by rainfall, and involve a comparison between PEt and rainfall (Marais, 1975). Water budgets have thus been compiled for the Adelaide (A) and Kroomie (B) field sites for 1982/83 season (Figure 6.10). Also presented in Figure 6.10 is a mean long-term budget for Adelaide (C). The data are plotted on a monthly basis. Rainfall was recorded at both sites during the 1982/83 season, but long-term records are available at neither site. However, 65 years of rainfall data were recorded at the Adelaide Police Station situated approximately 2km from the Adelaide Experimental Station. These are the data used for the long-term water budget.

Potential evapo-transpiration is calculated from Eo values recorded at the Adelaide Experimental Station. Evaporation data are unavailable from both Kroomie and the Adelaide Police Station. However, use of the Eo data from the Experimental Station to determine PEt at all these sites is considered meaningful since they were all situated within reasonably close proximity in the same veld type, on similar aspects and topogophy and at the same altitude. Class "A" pan evaporation was converted to PEt using PEt/Eo values determined for semi-arid grassveld in the Orange Free State by Snyman *et al.*(1980). These authors derived PEt/Eo ratios for veld described as being in "climax", "sub-climax" and "pioneer" condition, as well as for bare ground. In terms of the descriptions of the authors, the Kroomie site would have corresponded roughly to "climax" condition, while that at Adelaide would have been described as "sub-climax". The PEt/Eo ratio used for deriving PEt during the winter months (June to August) was taken to be that derived by Snyman *et al.* (1980) on bare ground. This is probably an underestimate since winters in the False Thornveld are not as severe as those in the Orange Free State, and some growth does take place at this time. The mean long term budget (Figure 6.10C) is presented for both of what Snyman *et al.* (1980) termed "climax' and "sub-climax" veld. For the purpose of this discussion they are more appropriately termed veld in "good" and "poor" condition, respectively.

Since potential evapo-transpiration was derived using factors extrapolated from the Orange Free State, the water budgets depicted in Figure 6.10 merely reflect estimates of the water deficits experienced. They are nevertheless considered useful, particularly for comparative purposes. It is clear from Figure 6.10 that severe drought occurred at both sites during the summer and autumn of the 1982/83 season. This drought was described by many farmers as "the worst in living memory". The situation was aggravated by the fact that what rain did occur, fell mostly in spring 1982. The last rain in excess of 30mm during the 1982/83 season fell at the end of October 1982. Thereafter, the only rain of any consequence was on 17 November, approximately 28mm at both sites. Otherwise, no rains greater than 10mm fell during the growing season. Good rains fell in July 1983 and again during the following spring. The 1982/83 drought was thus characterised by its intensity rather than its duration. In particular, the most severe period of stress occurred between 6 December 1982 (when 10mm fell at both sites) and 18 March when a further 10mm fell at both sites. During this period of 97 days covering most of the midsummer period, only 24,8mm and 32,7mm fell at Kroomie and Adelaide, respectively. Most of this precipitation fell in individual rains of less than 5mm, the exception being a single downpour of approximately 7mm at both sites at the end of January.

In view of the results from the greenhouse trial (Experiment 1), it is expected that the growing points of all tillers should have senesced during the summer of 1982/83, and in addition, that secondary tillering from lateral buds after the drought should have been minimal.

The percentage compositions of the experimental sites at Adelaide and Kroomie before the 1982/83 drought, after a full season's rest following the drought, and of veld adjacent to experimental sites after a season of normal grazing following the drought, are presented in Table 6.3. The species in Table 6.3 are classified into ecological categories and veld condition scores are calculated according to the procedure of Foran *et al.* (1978) adapted for use in the False Thornveld of the Eastern Cape by Danckwerts (1981). Also listed is the percentage composition of the benchmark site for the False Thornveld and the maximum limits of each species used for calculating veld condition score by the procedure described by Danckwerts (1981). The results (Table 6.3) show that before the 1982/83 drought, at least in terms of the scoring technique of Danckwerts (1981), the veld at the Kroomie site was in excellent condition while that at Adelaide could be termed moderate. The relatively high proportion of *C. plurinodis* at Adelaide is presumably a result of proliferation of this species owing to lenient grazing on the Adelaide Experimental Station. The site had been previously severely overgrazed prior to being taken over as an Experimental Station, thus also accounting for the relatively high proportion of Increaser II species.

Tufts of five of the species occurring at Adelaide (*C. plurinodis, D. eriantha, P. stapfianum, S. fimbriatus and T. triandra*) were permanently marked before the drought. These species included all but one of the species that comprised more than 90% of the composition of the whole sward at that time (Table 6.3A; Adelaide). The species not marked was *E. obtusa*, since its stoloniferous growth habit made it impossible to identify individaul tufts and thus assess mortality . At Kroomie, the permanently marked species were *D. eriantha, E. chloromelas, S. fimbriatus and T. triandra* and these four species comprised more than 90% of the composition of the whole site before the drought (Table 6.3A; Kroomie). The six species marked at the two sites are probably also the most abundant and important in the veld type as a whole.

None of the tillers in marked tufts that were viable before the 1982/83 drought survived the summer of that season, thus corroborating the results from the greenhouse trial. The percentage total mortality of tufts of these marked species recorded after relief of the drought during spring 1984 is presented in Table 6.4. Since a tuft was considered alive even if one viable secondary tiller was produced, the results mask the fact that the vast majority of the original population of tillers produced no secondary tillers. In most instances, surviving tufts produced less than a total of five lateral tillers from the original primary tiller population.

The results in Table 6.4 show that the mean total mortality of marked tufts was higher at Kroomie where veld condition was good than Adelaide where the condition was poor. A general higher mortality on veld in good condition (and in particular when *T. triandra* is abundant) than in veld in poor condition is explained by greater moisture extraction from the soil in the former case. Snyman *et al.* (1980) showed that the PEt/Eo ratio on *T. triandra* dominated veld is greater than that on veld in poor condition. In addition, cuticular transpiration (Mes & Aymer-Ainslie, 1935) would have continued after closure of stomata, and since *T. triandra* has a greater leaf area than *S. fimbriatus* (Section 3.3.5.1), it is likely that drought desiccation under conditions of similar evaporative demand could be greater on veld dominated by the former species. It is thus not unexpected that tiller mortality as a result of drought would be greater on veld in good condition than on veld in poor condition. The same argument would lead one to expect that mortality would be greater on rested (tall) than on utilised (short) veld during a severe drought. This trend was observed, but not quantitatively assessed when comparing mown veld in passages between rested plots in a trial at the University of Fort Hare Research Farm (Trollope, 1984: *pers. comm.*).

Of particular significance from the results listed in Table 6.4 is the fact that the key species *T. triandra* experienced considerably greater mortality than the species *S. fimbriatus* at Kroomie, but at Adelaide, the soil comprised 50% rock by volume while at Kroomie the soil was stone-free. Stuart-Hill, Tainton, Aucamp & Danckwerts (1984) showed that on stony soil of this type, incoming moisture penetrates approximately twice as deep (10mm deep/mm rainfall) as on stone-free soil (5mm deep/mm rainfall).

During the 1982/83 season, the last single rain that penetrated to any appreciable depth, fell at the end of October 1982 (35mm and 32mm at Adelaide and Kroomie respectively). At Adelaide in a trial adjacent to, and on similar soil to that discussed in this investigation, this rain was reported to penetrate approximately 40cm into the soil (Stuart-Hill, 1984*c*). Although the precise penetration of this rain was not monitored at Kroomie, the results of Stuart-Hill *et al.* (1984) suggest that moisture would have penetrated the soil to a depth of only about 16cm. In Table 3.2 (Section 3.3.6.4) it was observed that *T. triandra* has at least double the concentration of roots in the soil at a depth of 20-40cm than is the case with *S. fimbriatus*. This suggests that *T. triandra* is better suited to using soil moisture at depth than *S. fimbriatus*. At Adelaide, the 31 October rain penetrated to the 20-40cm depth, thus providing moisture that would have been preferentially used by *T. triandra*. If this is so, it would explain the lower mortality of this species than in the case of *S. fimbriatus*. It is of note that Stuart-Hill (1984*a*) has found *C. plurinodis* to have access to even deeper water than *T. triandra*, and consistent with this finding is the observation that no marked tufts of *C. plurinodis* died at Adelaide during the 1982/83 drought (Table 6.4).

In contrast to Adelaide, at Kroomie no moisture is thought to have penetrated to a depth below 20cm. Both *T. triandra* and *S. fimbriatus* have extensive root systems in the top 20cm of soil (Table 3.2), and therefore probably have equal access to available water. After extraction of available surface water, it is expected that tillers of *T. triandra* should desiccate more rapidly than those of *S. fimbriatus* as a result of their greater leaf area and thus higher rates of cuticular transpiration in the former species. This would explain the greater mortality of *T. triandra* tufts than those of *S. fimbriatus* at Kroomie.

Turning to changes in overall species composition Table 6.3, the results show that despite a full growing season's rest after the 1982/83 season, the veld condition scores one year after the drought had dropped to 52,4 and 72,4 at Adelaide and Kroomie, respectively, compared with 63,4 and 89,6 before the drought. These changes were due almost entirely to a decrease in the proportion of decreaser species at both sites, with a concomitant increase in the percentage of forbs. However, the drop in veld condition score was surprisingly small when viewed in the light of the high percentage mortality of tufts of the key species *T. triandra* and *S. fimbriatus* after the drought (Table 6.4). The observed recovery after a season's rest (Table 6.3B) was largely a result of profuse emergence of seedlings during spring 1983, particularly in the case of *T. triandra* at Kroomie. The results indicate the resilience of sweet grassveld to drought, provided an adequate period of recovery is ensured after the drought is broken. In this context, a resilient system is one which may be changed considerably in terms of the amounts of its state variables, but remains attracted towards its equilibrium (Walker, 1980). In contrast, where the veld was grazed during the season after drought (Table 6.3C), the veld condition score dropped to approximately half of what it had been before the drought. This was largely a result of a considerable decrease in the proportion of the key species *T. triandra* and *S. fimbriatus* at the two sites. The observed difference between the recovery on rested veld (B) and that on grazed veld (C) after the drought is attributed to the ill-effect grazing had on seedling establishment and tuft regeneration from a limited number of secondary tillers. This result is consistent with the conclusion drawn from the potting trial that grazing should be avoided for as long as possible after a severe drought. Pastoralists in semi-arid grassveld should thus weigh the costs of pen feeding after relief from a severe drought versus their long-term losses associated with reduced veld condition as a result of injudicious grazing after the drought.

The consequences of the changes in veld condition score (Table 6.3) in terms of changes in the grazing capacity of the sites are illustrated in Table 6.5. These grazing capacities (Table 6.5) are calculated from each of the veld condition scores in Table 6.3 using the model developed for the False Thornveld of the Eastern Cape by Danckwerts (1982*a*) and assuming a mean annual rainfall equal to that recorded at the Adelaide Police Station (422,2mm (Anon.,1944)). The results (Table 6.5) show that the estimated grazing capacities of the veld at Adelaide and Kroomie following a full season's rest after the 1982/83 drought had dropped by only 23,5% and 22,2% respectively when compared with the grazing capacities before the drought. In contrast, the estimated grazing capacities on veld grazed immediately after the drought dropped by 58,8% and 55,5% at the two respective sites in comparison with the before-drought carrying capacities. These results once again emphasise the considerable importance of resting veld after good rains following a severe drought.

The results in Tables 6.3 and 6.4 can be further used to compare the responses of representative species in the various ecological categories defined by Foran *et al.* (1978) to severe drought. The categories defined by Foran *et al.* (1978) were:

i. Increaser I species - those that increase with under-utilisation;

ii. Decreaser species - those that are typically found in veld in good condition and that decrease in abundance with under- and over- utilisation; and

iii. Increaser II species - those that increase with overgrazing.

In this comparison, the terms stability and resilience are used to describe the response of species to stress. A species is described as being stable if it changes little in abundance when subjected to outside stress, while a resilient species is one that may (or may not) change considerably in abundance when subjected to stress, but returns quickly to its original equilibrium once the stress is removed.

The only Increaser I species occurring at either of the sites was *C. plurinodis*. Tufts of this speices remained viable through the 1982/83 drought (Table 6.4), and its contribution to the community remained relatively constant before and after the drought regardless of the post-drought treatment (Table 6.3). The suggestion is thus that Increaser I species are very stable in terms of their resistance to drought. In contrast, the Decreaser species *T. triandra* was able to regenerate reasonably rapidly after the drought, provided it was protected from grazing. It was not able to recover if grazed immediately after the drought (Table 6.3). Thus, although less stable than *C. plurinodis*, *T. triandra* appeared to be reasonably resilient to drought. Dealing finally with Increaser II species, three examples are *S. fimbriatus*, *D. eriantha* and *E. chloromelas*. *Sporobolus fimbriatus* which has been identified as a highly preferred species, behaved in much the same way as *T. triandra*. That is, although suffering considerable mortality during the drought (Table 6.4) it was able to recover completely if protected from grazing (Table 6.3). However, it was not able to recover if grazed during the season after the drought (Table 6.3).

Digitaria eriantha and *E. chloromelas* have been identified by Danckwerts (1983) as Increaser II species that increases with severe overgrazing, as opposed to *S. fimbriatus* that has been identified (Danckwerts, 1983) as an Increaser II species that increases with moderate overgrazing. *Digitaria eriantha* and *E. chloromelas* also suffered severe mortality during the 1982/83 drought (Table 6.4), but these species recovered after the drought regardless of whether the veld was rested or grazed. The results thus suggest diminishing stability of species in moving from Increaser I species through the Decreaser category to Increaser II species, but that their resilience in terms of their ability to recover after drought (or possibly heavy grazing) (at least with respect to Decreaser and Increaser II species) follows an opposite trend. This result is consistent with the hypothesis of Walker (1980) who argued that well-managed highly productive veld (presumably dominated by Decreaser species) is less resilient, in terms of its ability to recover, than veld that is subjected to severe or excessive grazing (presumably dominated by Increaser II species).

In conclusion, the major implication arising from the field trials at Kroomie and Adelaide is that severe drought can have a devastating effect on the survival of perennial grasses and the condition of the veld in semi-arid grassveld. It is essential that the veld be allowed to rest for as long as possible after the drought has broken in order to allow seedling establishment and tuft regeneration.

6.3.2.1 Summary of results

i. A very severe drought occurred at the experimental sites during the 1982/83 growing season. The drought was characterised more by its intensity than its duration.

ii. Severe drought such as that which occurred during the 1982/83 season results in considerable mortality of tufts of perennial grasses.

iii. Tuft mortality as a result of drought is higher on veld in good than on veld in poor condition.

iv. Tuft mortality as a result of drought apparently varies between species purely in response to soil physical characteristics.

v. Species composition can recover fairly rapidly after a drought provided the veld is withdrawn from grazing after the drought breaks. Grazing after a drought results in considerably more deterioration in veld condition than occurs on rested veld.

vi. Grazing capacity also decreases markedly when veld is grazed rather than rested immediately after a drought has broken.

vii. Increaser I species are apparently more able to resist drought than Decreaser species, which in turn are more stable than Increaser II species. Resilience in terms of ability to recover after a drought apparently follows an opposite trend.

viii. It is highly desirable that veld be rested as long as possible after relief from a severe drought in order to allow seedling establishment and tuft regeneration.

CHAPTER 7

HERBAGE PRODUCTION OF SWARDS DOMINATED BY KEY SPECIES

7.1 Introduction

The species *T. triandra* and *S. fimbriatus* have been identified as key grass species in the False Thornveld of the Eastern Cape (Chapter 2). Subsequent investigations have been aimed primarily at characterising the growth and response to moisture stress of individual plants or tillers of these species (Chapters 3, 4, 5 & 6). Implicit in the objective of improved livestock production is knowledge of the overall production patterns of the veld to be utilised. The objective of this investigation is thus to describe the overall herbage production and production patterns of veld dominated by *T. triandra* and *S. fimbriatus* respectively in the False Thornveld of the Eastern Cape.

7.2 Procedure

The investigation was undertaken at two field sites in the False Thornveld of the Eastern Cape. These consisted of a site dominated by *T. triandra* situated on the University of Fort Hare Research Farm (Site A) and an area dominated by *S. fimbriatus* on the Adelaide Experimental Station (Site B). The two sites were those already described in Chapter 3, and the respective soil types and aspects are reported in Section 3.2.

The trial consisted of 10 treatments at each site. All treatments were defoliated to a height of 4cm, using a self-driven sickle bar mower, at the end of June 1980. Thereafter, a separate treatment was harvested at the same height at monthly intervals starting at the end of August 1980 until the end of June 1981 (10 treatments). Treatments were replicated six times at both sites and arranged in randomised block designs. Gross plot size was 2m x 10,4m and net plot size, after removal of border areas, 1,2m x 8m.

On the final harvest date (30 June 1981) all plots were clean-cut and the procedure repeated during the 1981/82 season, and again during the 1982/83 season. Treatments were re-randomised each season.

After harvesting, net plot yield was oven-dried to constant mass and expressed in terms of kg dry matter per ha.

Each site was characterised in terms of botanical composition by means of a wheel point survey of 500 points (strikes and nearest plant data were recorded) during the 1980/81 season. Rainfall was also recorded.

7.3 Considerations in presentation of results

The original intention was to present the results as cumulative yield plotted against time in the form of a mechanistic mathematical model fitted to the means of the data at each harvest date. Expressing undisturbed cumulative yield on a seasonal basis (as opposed to consecutive series of cumulative growth curves covering shorter regrowth periods within seasons) is considered justified on the basis that Tainton, Booysen & Scott (1970) found that the clipping frequency which resulted in highest herbage yield of Natal Tall Grassveld was once per year. This suggests that optimum leaf area index as defined by Booysen (1966) was not attained by the sward even after a full season's undisturbed growth. If this is true in the relatively moist Natal Tall Grassveld, it is also likely to be true in semi-arid grassveld. This hypothesis was corroborated in Chapter 4 at least as far as the species *T. triandra* is concerned, since it was found that it took at least 10 to 12 months for the overall mass increment of this species to benefit from defoliation.

The question that arises is the validity of expressing this seasonal cumulative growth in terms of a mechanistic mathematical model. In Chapter 3 it was pointed out that mechanistic models of growth are rarely justified since it is unreasonable to expect growth to be governed by a single set of parameters throughout its course (Williams & Bouma, 1970). In addition, in Chapter 6, it was shown that growth in semi-arid grassveld is opportunistic, occurring sporadically after each successive rainfall. On this basis, it would be more appropriate to describe cumulative herbage production in the False Thornveld of the Eastern Cape by means of empirical models fitted to the data. However, one of the problems associated with using empirical models, and splined functions in particular, is that data should be recorded at frequent intervals, although little or no replication is required (Hunt, 1978).

In the current investigation, there were only 10 harvest dates with six replications at each date. Describing the data by making use of the methodology of Parsons & Hunt (1981) to fit splined polynomial functions to means of the primary data is thus questionable in view of the paucity of harvest dates. However, one means of overcoming this is to fit the splined functions not to the means of the primary data, but to disregard replications and to fit functions to all the individual observations. This would result in 60 observations for each curve as opposed to 10 which would be the case should means of the primary data be used.

The seasonal cumulative growth of swards dominated by *T. triandra* and *S. fimbriatus* is thus described by means of splined third order polynomials fitted to logarithms of the primary data according to the methodology of Parsons & Hunt (1981). The functions are qualified by 95% confidence intervals, and since each observation within a season took place on a different plot, and treatments were re-randomised each year, use of these confidence limits for statistical comparisons between sites and years is valid. Functions are fitted to logarithms of the primary data for reasons already stated in Chapter 3. However, fitted curves are also presented on an arithmetic scale together with growth rates in order to provide a clearer mental picture of the magnitude of growth that took place.

7.4 Results and discussion

The monthly rainfall recorded at the experimental sites has already been presented in Figure 3.1, and the implications discussed in Section 3.3.1.

The species compositions of the two sites recorded during the 1980/81 season are presented in Table 7.1. The species (Table 7.1) are also classified into ecological classes as described by Foran *et al.* (1978) and the veld condition scores at each site calculated by the method described by Danckwerts (1981). Veld condition is scored against the maximum limits of the benchmark site listed in Table 6.3.

The cumulative herbage production (log scale) at both sites over three seasons 1980/81 to 1982/83 is presented on an arithmetic scale together with derived crop growth rates in Figure 7.2.

The results show that the herbage yield per ha was at all times greater at Site A than at Site B ($P<0,05$). Rainfall at Site A was greater than at Site B for the first two seasons, but not the third (Figure 3.1), and this probably contributed towards differences between sites within seasons. However, the recorded differences between sites were considered to be too large to be accounted for by rainfall alone, particularly since the rainfall during the 1982/83 season was greater at Site B than at Site A. The overriding factor responsible for differences between sites is thus considered to be veld condition, with veld in good condition (Site A) yielding considerably more herbage than veld in moderate condition (Site B). This was also shown by Danckwerts & Barnard (1981) who measured herbage production at three veld condition sites, but under similar rainfall and edaphic environments in the False Thornveld of the Eastern Cape. The authors concluded that veld condition played an overwhelming role in determining herbage production and thus output of saleable animal products per hectare in the veld type.

Within sites, total herbage production and the pattern of this production were closely related to total seasonal rainfall and within seasonal rainfall distribution respectively (Figure 3.1 & 7.2). At both sites, maximum total herbage yield was recorded in the 1980/81 season (2120kg/ha and 870kg/ha at Sites A and B) followed by the 1981/82 and 1982/83 seasons respectively (Figure 7.2). Total rainfall followed the same trend, with the 1980/81 rainfall being 30% and 12% higher than the long-term averages of 521mm and 422,2mm at Sites A and B respectively. Rainfall during the 1981/82 season was 5% and 10% below average and during the 1982/83 season 43% and 25% below average at Sites A and B respectively (Figure 3.1, Section 3.3.1).

In terms of seasonal distribution of forage production, crop growth rates during spring 1980 were lower than those recorded at the same sites during spring 1981 and spring 1982 (Figure 7.2). Herbage production up to the summer period was, in fact, significantly higher ($P<0,05$) during both the 1981/82 and 1982/83 seasons than during the 1980/81 season (Figure 7.2), despite the fact that total rainfall during the experimental period was greatest during the 1980/81 season (Figure 3.1). This result is attributed to relatively good late winter and/or spring rains during 1981 and 1982 (Figure 3.1).

After the spring period, relatively poor summer rains during the 1981/82 and 1982/83 seasons resulted in little or even negative growth. During the 1980/81 season, particularly good summer rains fell at Site A, resulting in rapid herbage accumulation at this time. At Site B, good early summer rains fell during the 1980/81 season, resulting in rapid growth up to midsummer. However, Site B did not experience the good rains that fell at Site A during January 1981, and this is reflected in a decline in the herbage production at Site B at this time (Figures 3.1; 7.1 & 7.2).

During the autumn period, good rains fell at both sites during the 1980/81 season and to a lesser extent during the 1981/82 season (Figure 3.1). This resulted in continued growth during autumn 1981 (although it was very much slower at Site B than at Site A), and a recommencement of growth during autumn 1982. During the 1982/83 season, the severe summer drought continued through autumn 1983, and during this period negative herbage accumulation took place at both sites, although the fitted curves did suggest a short period of positive growth at Site A during late autumn 1983 (Figures 3.1; 7.1 & 7.2).

The fitted curves (Figure 7.1 & 7.2) suggest a negative crop growth rate at Site A during summer 1981/82, although this decline could have been accounted for by variability in the primary data as is indicated by the confidence intervals in Figure 7.1. During the 1982/83 season, both sites experienced negative crop growth rates during summer and autumn (Figure 7.2), and the recorded drop in yield of standing herbage was statistically significant (P<0,05) (Figure 7.1). This drop in yield coincided with the extremely severe 1982/83 summer/autumn drought. The data thus clearly show that in an unutilised situation, forage can be lost within a growing season through leaf loss. This phenomenon has already been discussed at the individual tiller level in Chapter 3. Leaf senescence and abscission presumably occurs at all times and not only during severe drought, but its influence on the yield of standing herbage is masked by net positive growth when drought is not severe.

The maximum rate of forage loss was recorded during summer 1982/83, and reached approximately 4kg/ha/day and 2kg/ha/day at Sites A and B respectively (Figure 7.2). The rate of forage loss diminished during autumn 1983, despite a very small increase in rainfall at this time (Figure 3.1). This suggests that even if herbage loss does take place at all times of the year, it is promoted by hot dry conditions, and may be more closely related to water deficit (as illustrated in Figure 6.10) than to actual rainfall.

The crop growth rates presented in Figure 7.2 were derived from mean yields recorded at monthly intervals. It was apparent from results in Chapter 6 (Figure 6.3) that active growth takes place for a relatively short period of time following rain and is thus a sporadic process and not a continuous one through the season as suggested in Figure 7.2. The crop growth rates after rain are thus probably considerably higher than those presented in Figure 7.2, but are maintained for short periods. Between these periods crop growth rates are likely to be very slow or even negative as a result of herbage decay. If, as indicated in Figure 6.3, there are only 40 active growing days in normal years on veld in good condition, and if herbage production is 1500kg/ha (approximately that recorded at Site A during the 1981/82 season), then mean crop growth rate would be 37,5 kg/ha/day. The maximum derived crop growth (Figure 7.2) was approximately 18kg/ha/day at Site A during spring 1981.

Finally, the results discussed in this chapter represent herbage yield above a 4cm clipping height. Yield thus consisted primarily of leaf material during periods of vegetative growth, but included culms after tillers began piping. Danckwerts & Trollope (1980) showed that as much as 1000kg/ha of stubble may remain after mowing to a height of 4cm on dense swards in the False Thornveld of the Eastern Cape. This stubble is, however, probably not utilised by grazing animals.

7.5 Summary of results

i. Veld in good condition produces considerably more herbage than veld in moderate condition.

ii. Within veld condition sites, herbage production is largely determined by rainfall. Total herbage production in the 1980/81 season was greater than that in the 1981/82 season, which in turn was greater than that in the 1982/83 season.

iii. Distribution of rainfall within a season affects the pattern of herbage production during that season. During the 1981/82 and 1982/83 seasons more herbage was produced in spring than during spring of the 1980/81 season, despite the fact that greatest total production was achieved during the

1980/81 season. This was probably a result of relatively low rainfall during spring 1980.

iv. During a drought, leaf decay can result in a negative rate of herbage accumulation. Presumably leaf loss takes place whenever leaves are allowed to accumulate on tillers, but this is usually masked by growth rates in excess of rates of leaf loss. Leaf loss is, however, apparently most rapid under hot, dry conditions.

CHAPTER 8

EFFECT OF DEFOLIATION ON KEY GRASS SPECIES

8.1 Introduction

Preceding chapters have been aimed primarily at quantifying growth of key grass species, or swards dominated by key grass species in unutilised conditions in the False Thornveld of the Eastern Cape. Although these investigations provide considerable information regarding the probable effects defoliation would have under various conditions, a study of the precise effects of defoliation on key grasses is essential in order to formulate optimal management strategies in the veld type.

Barnes (1972) stated that, while knowledge of the defoliation effects in grasses is a prerequisite to rational use of veld, quantitative data with respect to this subject was far from adequate. This sentiment is particularly relevant in the False Thornveld of the Eastern Cape where very little information is available regarding the response to defoliation of the important grass species. Danckwerts & Barnard (1981) did, however, undertake a preliminary investigation aimed at assessing the short-term effects of various frequencies and intensities of defoliation on herbage production at three veld condition sites in the False Thornvled of the Eastern Cape. The authors showed that veld condition was overwhelmingly the most important factor affecting herbage yield. While yield did respond to different frequencies and intensities of defoliation their effect was relatively minor when compared to the effect of veld condition and the rainfall during any particular season. The yield response to different frequencies and intensities of defoliation was, however, not constant over veld condition types. Veld in good condition (dominated by *T. triandra*) appeared to be more sensitive to utilisation treatments than veld in poor condition (dominated by Increaser II species). In addition, the effect of various utilisation treatments was manifested not only during the season of application, but also during the subsequent season. Despite these responses, Danckwerts & Barnard (1981) concluded that the most important aspect of the defoliation regime in the False Thornveld may be the role it plays in maintaining or improving veld condition. However, this role could not be assessed because of the short-term nature of the trial and the fact that no physiognomic or physiological characteristics were recorded when treatments were applied. In addition, the study of Danckwerts & Barnard (1981) was aimed at overall yield response of the whole sward to frequency and intensity of defoliation. No consideration was given to the responses of individual plants and tillers that ultimately affected the yield response of the whole sward. In this context, Drewes (1979) investigated the response of *T. triandra* tillers to various forms of defoliation in the Natal Tall Grassveld. The author found that intensity of defoliation affected subsequent yield, flowering, lateral tiller activation and death, and herbage digestibility. It is of note that the most severely utilised treatment (by means of a fire) produced not only less yield from the whole sward, but also a lower yield from lateral tillers, despite the fact that more laterals were initiated than on any of the other treatments. It is logical that severe defoliation will result in the mortality of primary tillers as a result of apical bud removal, and thereby a reduction in subsequent overall yield. However, the fact that the yield from lateral tillers was also lower on the burned treatment suggests that mechanisms other than meristematic limitations affected regrowth after defoliation.

The parameters involved in any utilisation regime include intensity, frequency and season of defoliation, the physiognomic and physiological state of the grass when the defoliation is applied, and the defoliating agent itself. The size of an experiment aimed at an investigation of the main effects and interactions of two or more of these parameters would increase explosively with the inclusion of each additional variable. As an alternative, two separate investigations were undertaken to study the effect of defoliation on key grass species in the False Thornvled of the Eastern Cape. The first (Experiment 1) was aimed specifically at investigation of the effect of intensity and season of defoliation on individual tufts and tillers of key grass species, while the second (Experiment 2) considered the effect of frequency of defoliation *per se* on these species. The physiognomic development of the plant at time of defoliation was of necessity, also a variable in these trials, since defoliation at different frequencies or at different times of the year inevitably involved defoliation of plants of different ages, and thus physiognomic development.

8.2 Procedure

The investigations were undertaken on an area of veld dominated by *T. triandra* situated on the University of Fort Hare Research Farm, and an area dominated by *S. fimbriatus* situated at the Adelaide Experimental Station. The sites were those already described in Chapter 3 (Site A and B respectively; Section 3.2). Both trials were conducted under unamended moisture conditions, and under irrigation where soil water was replenished to field capacity once per week.

8.2.1 Intensity and season of defoliation (Experiment 1)

Three defoliation intensities were applied to randomly chosen tufts of *T. triandra* (at Site A) and *S. fimbriatus* (at Site B) during spring, summer, autumn and winter. The defoliation intensities were severe (1-2cm), moderate (3-4cm) and lenient (7-8cm) and were replicated five times using new sets of tufts at each season. Treatments were applied by placing frames of the specified heights over the tufts and clipping all material above the frame. Prone and angled tillers were held upright so that all tillers within the tufts were clipped at the required distance from their bases.

The first treatments were applied during late winter 1982 (15 August), and were applied to tufts that had been resting for an entire growing season after undergoing severe defoliation (1-2cm) during the previous (1981) winter. On the initial treatment date (15 August 1983) new areas were mown to a height of 1-2cm at each site and on both moisture treatments. Thereafter, follow-up treatments were applied to tufts on each of these mown sites successively during the growing season following the initial clean cut, using new individual tufts at each treatment date. The follow-up treatment dates were 18 October 1982 (spring), 12 January 1983 (summer) and 29 March 1983 (autumn). Intensity of defoliation treatments were thus applied to grass tufts in successive stages of physiognomic development in spring, summer, autumn and winter respectively, even though the winter treatments were applied to tufts that had matured during the previous (1981/82) growing season.

Immediately prior to application of defoliation treatments five randomly selected tufts were removed with their roots, at each site and on each treatment using the auger described in Section 3.2.4. Approximately two months after the application of treatments, the defoliated tufts were removed in the same manner. After removal from the soil, tuft circumference was measured, soil was "washed away" from the roots and tufts were taken to the laboratory. In the laboratory, tufts were separated in living and senescent primary and secondary tillers. Tillers were classified as living if they had viable shoot apices. Primary tillers were defined as those that had emerged before intensity of defoliation treatments were applied. There were thus considered to be no secondary tillers in tufts removed immediately prior to application of treatments. Separated tillers were further sub-divided by clipping into roots, herbage up to the original clipping height and herbage above the original clipping height. Tillers of tufts removed before applying treatments were not separated into herbage above and below clipping height since these tufts had not been subjected to differential defoliation intensities.

After separation of tufts into the various components, roots that had been attached to senescent tillers were discarded, and all other plant parts oven-dried to constant mass. All recordings were made on an individual tuft basis (replications) in order to allow statistical comparison of treatment effects.

The following parameters were determined for each tuft:

1. Tuft yield per unit basal area

1.1 Tuft mass per unit area above soil level

1.2 Tuft mass per unit area above clipping height

1.3 Root mass of living tillers per unit area

2. Tiller densities

2.1 Number of living primary tillers per unit area

2.2 Number of living secondary tillers per unit area

2.3 Number of living secondary tillers per primary tiller (living and dead)

3. Primary tiller mass

3.1 Mass per living primary tiller above soil surface

3.2 Mass per living primary tiller above clipping height

3.3 Root mass per living primary tiller

4. Flowering tillers

4.1 Percentage of primary tillers with flowering culms

It is of note that root mass represented only those roots that were removed by the auger; that is, those roots within a radius of 8cm from the centre of the tuft and to a depth of 15-20cm. In addition, many of the fine feeder roots were lost in the process of "washing away" the soil. Of further note is the fact that the number of secondary tillers per primary was determined in terms of all primary tillers regardless as to whether they had viable apices or not. This was because tillers with decapitated or senescent apices continued to activate lateral buds.

For each of the 10 parameters listed above, the effect of three intensities of defoliation (as well as the pre-defoliation values where applicable) could be compared between two species, two moisture treatments and at four different times of the year (or stages of physiognomic development). Since all treatments were replicated five times and tufts were randomly selected, analysis of variance of each of the recorded parameters was considered the most appropriate means of comparing treatment effects.

However, after removal of the first series of tufts (winter treatments), it was questioned as to whether the parameters recorded would adequately describe treatment effects on the regrowth of individual tillers. Consequently, after applying spring treatments, three tillers were marked with plastic-coated wire rings on each tuft. The wire rings marking each tiller were differently coloured within each tuft, and tufts were numbered so that individual tillers could be returned to in the same order at each sampling date. Immediately after marking, any remaining green leaf blades on tillers were marked with a stain containing a dye in organic solvent. Only leaves with at least 5mm of remaining green leaf blade were marked, and leaf blade was classified as green if it was subjectively assessed to be both green in colour and not permanently wilted. After marking, and at approximately fortnightly intervals thereafter until removal of tufts, tillers were returned to and the following characteristics non-destructively recorded.

1. The number of living marked leaves per tiller
2. The number of unmarked living leaves per tiller
3. The total length of green leaf blades per tiller
4. The height of the shoot apices of tillers above the soil surface

The latter characteristic was estimated from previous experience of dissecting tillers in the laboratory (Chapter 3).

Since the same tillers were returned to within each period between clipping and tuft removal, variance between dates but within seasons, was correlated. Consequently, analysis of variance between dates was invalid. However, it was possible to compare treatment effects individually at each recording date.

8.2.2 Frequency of defoliation (Experiment 2)

Fifty randomly selected tufts were marked and numbered with steel pegs on both moisture treatments and at both sites (*T. triandra* at Site A; *S. fimbriatus* at Site B) at the end of July 1982. All tufts were clipped to a height of 1-2cm on the same date and each group of 50 tufts randomly separated into five sets (treatments) of 10 tufts (replications). Each treatment was subjected to a different frequency of defoliation during the 1982/83 season. The dates of defoliation on the various treatments were as follows:

1. 28 June 1983;
2. 12 January 1983 and 28 June 1983;
3. 2 December 1982, 8 March 1983 and 28 June 1983;
4. 3 November 1982, 12 January 1983, 2 February 1983, 28 March 1983 and 28 June 1983; and
5. 5 October 1982, 3 November 1982, 2 December 1982, 12 January 1983, 2 February 1983, 8 March 1983, 28 March 1983, 9 May 1983 and 28 June 1983.

The treatments thus represented one, two, three, five and nine clipping frequencies during the 1982/83 growing season respectively. With the exception of the final harvest date (28 June 1983), clipping intensities were not at a fixed height, but were approximated on each tuft at a height above the shoot apices but below the collar regions of the majority of vegetative tillers. The final defoliation was, however, applied at a uniform height of 1-2cm, thus allowing comparisons of yield between treatments. After each harvest, tuft circumference was recorded in order that yield could be expressed per unit tuft basal area.

After the final defoliation (28 June 1983), tufts were removed with their roots using the auger described in Section 3.2.4. Soil was "washed away" from the roots and tufts were taken to the laboratory where the number of tillers per tuft was counted and the stubble was separated from roots by clipping. All harvested material, stubble and roots were oven-dried to constant mass. The following parameters were recorded from the destructively sampled material:

1. Individual harvest yields per unit tuft area on treatments clipped more than once per year

2. Total treatment yields per unit area over the whole season

3. Stubble yield per unit area after the final harvest

4. Root yield per unit area after the final harvest

5. Number of tillers per unit area after the final harvest.

Since individual harvest yields at different dates were derived from the same 10 tufts within each treatment, variance between harvest dates would have been correlated and thus statistical comparison of individual harvest yields within treatments was not possible. The other parameters (total yield, stubble yield, root yield and tiller density) were derived from independent sets of 10 replicated tufts per treatment, and were thus considered suitable for analysis of variance.

After the initial clean cut in winter 1982, and after each harvest date thereafter, two living tillers on each tuft (except those to be subjected to one cut per year) were marked using plastic-coated wire rings. Immediately before each cut, the two marked tillers in tufts were removed, dissected, and the height of the shoot apex above the stem base recorded. Statistical comparison of these heights between treatments and clipping dates was accepted since new individuals (20 per treatment) were marked after each harvest. Tillers were marked after each harvest in order to avoid bias in the removal of tillers at the time of the next clip. Unbiased selection of unmarked tillers for removal would have been a problem particularly when some tillers had elevated their apices (or flowered) and others not. Shoot apex elevation was not monitored on treatments clipped once at the end of the growing season. This was because elevation of these apices up to the time of tuft removal would have been the same as that on unutilised tufts described in Chapter 3 (Section 3.3.3).

8.3 Results and discussion

8.3.1 Effect of intensity of defoliation on key grass species (Experiment 1)

8.3.1.1 Tuft yield per unit basal area

The above-ground mass per unit area of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts before defoliation and two months after three different intensities of clipping at different times of the year is presented in Figure 8.1. The listed least significant differences are those between any two treatment means in the figure.

The main effect of intensity of clipping on above-ground mass of herbage was statistically significant ($P<0,01$), lenient defoliation resulting in higher mass than moderate defoliation which in turn resulted in higher yield than severe defoliation. This result is expected, since lenient defoliation involved less material being removed at clipping than severe defoliation, and the results represent the sum of both regrowth and the material that remained after the harvest. The main effect of irrigation was also statistically significant (P<0,01), additional moisture resulting in greater above-ground yield per unit area. However, of note was a significant interaction between moisture and time of year (P<0,01), showing that moisture had less effect in spring than at other times of the year. This is a result of the good rains that fell in spring and early summer 1982 (Figure 3.1).

Regarding differences between species, clipping affected the above-ground yield of *S. fimbriatus* less than that of *T. triandra*. This is illustrated by the fact that the before-clip yields of *T. triandra* were higher than most of the yields two months after clipping. This trend occurred even where there was no moisture stress during the two months after clipping, and even at the light utilisation intensity during autumn and winter. In contrast; *S. fimbriatus* yields before clipping were usually less than those two months after clipping. This inter-action between species and the effect of clipping was statistically significant (P<0,01). The results, however, do not necessarily imply that *T. triandra* is more sensitive to defoliation than *S. fimbriatus*. The interaction between the effect of species and cutting could be a result of *S. fimbriatus* having a greater proportion of stem material below cutting heights than *T. triandra*, thus causing a smaller proportion of the former species to be removed by clipping at equivalent cutting heights than the latter. This is suggested by the fact that above-ground mass of *T. triandra* before clipping was greater than that of *S. fimbriatus* (P<0,01), but two months after clipping the trend was reversed (P<0,01).

The main effect of time of clipping on above-ground yield of tufts (Figure 8.1) was that yield increased as the season progressed from spring onwards, a result of the fact that tufts had been clean-cut the previous winter, and thus had been growing for progressively longer periods before cutting as the season progressed. However, the effect of intensity of clipping was consistent with treatments as the season progressed.

To conclude discussion on above-ground mass per unit area, the results are not particularly useful in terms of assessing the effect of intensity of clipping on productivity. This is because the yields represent not only regrowth that took place after clipping but also stubble that remained below clipping height. The latter would also have included old dead material that remained after the initial clean cut. A more useful means of comparing the effect of intenisty of clipping on post-harvest productivity is in terms of tuft regrowth above clipping height.

The mass per unit area above clipping height of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts two months after three different intensities of clipping at different times of the year is presented in Figure 8.2. The main effects of height of clipping (P<0,05), season of clipping (P<0,01) and irrigation (P<0,01) were all statistically significant. The main effect between species was not significant. The effect of irrigation on regrowth yield was overwhelmingly a result of the 1982/83 drought (Figure 3.1). This drought effect is considered to have masked most other treatment effects on non-irrigated tufts, although *S. fimbriatus* tufts were apparently able to make better use of what little moisture there was at the intense clipping height. On the irrigated treatments, the effect of time of year resulted in greatest regrowth during summer (Figure 8.2). In Chapter 4, it was shown that provided there is no moisture stress, summer is the most favourable time of the year for growth, at least with the species *T. triandra*. Regrowth in spring was significantly lower than at all other times of year, probably a result of the fact that tufts consisted of populations of young tillers since they had been intensely defoliated during the preceding winter.

Over all treatments, severe clipping resulted in greater herbage production than moderate clipping which in turn produced more than lenient clipping. However, a significant third order interaction between species, time of year and clipping height (P<0,01) showed that this effect was not consistent within species and time of year. Increasingly severe intensities of defoliation generally favoured regrowth during summer, autumn and winter in the species *S. fimbriatus*, while in the species *T. triandra*, intensity of defoliation had no significant effect during all seasons except winter. After winter defoliation, *T. triandra* tufts were favoured by lenient defoliation on the irrigated treatment (Figure 8.2). This was probably a result of the fact that many shoot apices had elevated on the irrigated treatment by this stage (as has already been discussed in Chapter 3 (Figures 3.3 & 3.4)). Intense defoliation thus resulted in decapitation of these apices at this time. This does not necessarily imply that lenient defoliation of *T. triandra* is desirable during winter since the consequent prolific flowering of tillers could result in production of unpalatable herbage and aerial lateral tillering (Section 3.3.7). It is thus concluded that when tufts growing without moisture stress are subjected to a single defoliation, regrowth per unit basal area will be favoured by severe defoliation in the species *S. fimbriatus*, while intensity of defoliation has little effect on regrowth in the species *T. triandra* except during winter. In winter regrowth in the latter species is favoured by lenient defoliation. The results (Figures 8.2), however, do not show whether these effects are caused by differences in tiller growth rates, or changes in the density of tillers per unit area. During drought the effects of intensity of clipping on tuft regrowth are largely masked by the effects of moisture stress.

The mass of roots attached to living tillers per unit basal tuft area before defoliation and two months after three intensities of clipping of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts at different times of the year is presented in Figure 8.3. It is stressed that these results represent roots only on living tillers and within the circumference of the auger used to remove tufts to a depth of 15-20cm. Also, many of the fine roots were lost through the "soil washing" and tiller separation process, and thus the results are an underestimate of actual root mass and are subject to error.

Despite this, the main effects of intensity of clipping (P<0,05), time of year (P<0,01), irrigation (P<0,01) and species (P<0,01) were all statistically significant. *T. triandra* tufts had more root material attached to living tillers per unit area than *S. fimbriatus*, irrigated tufts had more roots than those not under irrigation, and the mass of roots per unit area increased as the season progressed. The species and irrigation effects are expected from the results discussed in Chapter 3, while the effect of time of year is also expected since tillers in tufts had been growing undisturbed for progressively longer periods before each successive season of defoliation.

With respect to the effect of clipping (Figure 8.3), where significant differences occurred, root mass before cutting was greater than that of the severely clipped treatment two months after cutting. This result was not apparent in spring, since at the time of clipping, tillers were still young and had not yet established their own root systems. In addition, where significant differences occurred, leniently clipped tufts usually had a greater mass of roots attached to living tillers than severely clipped tufts. In view of these results, and the fact that defoliated tufts were allowed two months growth after clipping before measurements were made, it is concluded that defoliation reduces the mass of roots attached to living tillers per unit area. In addition, intense defoliation apparently has a more marked effect than lenient defoliation. As with regrowth after clipping, however, the results do not show whether the reduced root mass as a result of clipping is caused by reduction in root mass per tiller or a reduced density of tillers.

8.3.1.2 Tiller density per unit basal area

The number of living primary tillers (those present before clipping took place) per unit area in irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts before defoliation and two months after three different intensities of clipping at different times of the year is presented in Figure 8.4. The main effects of species, irrigation, intensity of clipping and time of year were all statistically significant (P<0,01). In addition, a significant interaction (P<0,05) between all these factors showed that their effects were inconsistent.

In the species *T. triandra*, severe cutting always resulted in a reduced density of living primary tillers, except on the non-irrigated summer treatment, where, as a result of drought, the density of living tillers was not significant even before the drought. The more moderate clipping intensities sometimes, but not always, reduced tiller densities in this species. During spring, tillers were newly emerged and densities of *T. triandra* tillers were high. All clipping treatments resulted in a significant decrease in tiller densities. This could, however, have been an effect of self-thinning particularly on the non-irrigated treatment where initial tiller densities were very high. In Chapter 3 (Figure 3.2) it was shown that a large proportion of tillers senesced prematurely even where there was no defoliation. Summer defoliation of irrigated *T. triandra* tufts had a similar effect on tiller densities to that experienced in spring. Again, self-thinning could have been largely responsible for the results, and this is suggested by lower densities of tillers before clipping in autumn and winter. On the non-irrigated treatment, the initial density of tillers was considerably lower than that in spring, and very few tillers remained alive two months after clipping. These results are most likely largely a response to the 1982/83 drought, the effects of which are discussed in Chapter 6. During autumn, the effects of intensity of defoliation on the density of non-irrigated *T. triandra* tillers were also masked by this drought. However, during this season, the density on the irrigated treatments was significantly reduced at the severe and moderate clipping heights, but was unaffected by lenient clipping. This is probably a result of decapitation of shoot apices of living tillers at the two most severe intensities. In Chapter 3 (Figure 3.4) it was shown that the mean height of shoot apices of irrigated spring emerged tillers was in excess of 50mm by March during the following autumn. Defoliation of *T. triandra* tufts during winter resulted in significantly reduced tiller densities at the moderate and severe intensity on the non-irigated treatment. Lenient defoliation also resulted in reduced tiller densities, but this effect was not significant. These treatments took place during late winter (15 August) and the results in Figure 3.4 show that year-old tillers had begun piping by this stage and their apices were therefore susceptible to decapitation by clipping. Of note is a much higher ($P<0,01$) density of non-irrigated *T. triandra* tillers before clipping than was present in autumn. This was because winter treatments were applied to tufts that had grown during the previous (1981/82) growing season which, despite a midsummer drought, was considerably moister than the 1982/83 season (Figure 3.1) during which the other treatments were applied.

The density of living primary tillers of *S. fimbriatus* was generally lower ($P<0,01$) than that of *T. triandra* tufts, particularly before clipping treatments were applied (Figure 8.4). The 1982/83 drought, however, had a very similar effect on tiller densities on the non-irrigated treatments to that experienced by *T. triandra* tufts during summer and autumn. Otherwise, clipping had no significant effect on the density of *S. fimbriatus* tillers except during autumn on irrigated treatment. Here, all clipping intensities significantly reduced the density of tillers two months after clipping ($P<0,05$). This was probably a result of the removal of flowering culms during this defoliation. However, the effect of defoliation on irrigated *S. fimbriatus* tufts at this time was less marked than that on similarly treated *T. triandra* tufts. This also, is expected since in Chapter 3 (Figures 3.5 & 3.6) it was shown that a considerably smaller proportion of *S. fimbriatus* tillers elevated their apices than that of *T. triandra*. There was at no stage a significant difference in the number of primary tillers per unit area in *S. fimbriatus* tufts subjected to different intensities of defoliation two months after defoliation took place.

It can thus be concluded that when moisture is not limiting, defoliation of *T. triandra* tufts with dense populations of young primary tillers results in a considerable drop in the density of these tillers, but this could be a result of natural self-thinning. If tufts of this species are allowed to grow out until autumn, when tillers elevate their apices, severe defoliation results in decapitation of many of these apices and a significant drop in the density of primary tillers takes place. Lenient defoliation at this time has no effect on primary tiller densities. If tufts are allowed to grow out still further (late winter), tillers become even more susceptible to defoliation. In contrast to *T. triandra*, *S. fimbriatus* tufts have a considerably lower density of young primary tillers in spring and summer. However, tiller densities of this species are not significantly affected by defoliation regardless of its intensity, except during autumn when tillers elevate their apices and flowering takes place. At this time clipping results in decapitation of flowering apices and consequently a drop in the density of primary tillers.

The number of secondary tillers that emerged per unit area and were still alive within two months after three different intensities of clipping of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts at different times of the year, is presented in Figure 8.5. The main effect of intensity of clipping was not statistically significant, but time of year, irrigation and species all significantly ($P<0,05$) affected secondary tiller densities per unit area. *Themeda triandra* produced more laterals per unit area than *S. fimbriatus*, and irrigated treatments more than under unamended moisture conditions. The effect of time of year interacted significantly with irrigation ($P<0,05$), a consequence of the fact that non-irrigated treatments produced very few lateral tillers during summer and autumn of the 1982/83 drought. Where there was no moisture stress, *T. triandra* tufts produced more lateral tillers after defoliation during winter than at any other season. Similarly treated *S. fimbriatus* tufts produced more laterals after defoliation in autumn and winter than during spring or summer. The trend was thus for tufts to produce more lateral tillers per unit area after defoliation during dormancy and/or when primary tillers in tufts approached maturity, provided drought did not prevent the development of lateral apices. Intensity of clipping, however, had little consistent effect on the number of laterals produced per unit area.

The number of secondary tillers that emerged per unit primary tiller (living and dead) and were still alive two months after three different intensities of clipping of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts at different times of the year are presented in Figure 8.5. In contrast to the number of laterals produced per unit area (Figure 8.5), the mean number of laterals produced per primary tiller did not differ significantly between species (Figure 8.6). Consequently, the greater mean number of lateral tillers produced per unit area in *T. triandra* tufts than in those of *S. fimbriatus* (Figure 8.5) was a result of greater primary tiller densities in the former species.

The number of lateral tillers produced per primary tiller did, however, vary between moisture treatments ($P<0,01$), times of year ($P<0,01$) and between clipping intensities ($P<0,05$). Non-irrigated tillers of both species produced significantly fewer laterals after defoliation in summer and autumn than at other times of the year, a result of 1982/83 drought. Otherwise, the trend was for more lateral tillers to be produced per primary as time of year progressed, or possibly more appropriately as physiognomic development of the primary tillers at time of cutting progressed. The effect of intensity of clipping was significant only after winter clipping of the species of *T. triandra*. Here, severe defoliation resulted in significantly more laterals being produced per primary than lenient defoliation (irrigated, $P<0,05$; non-irrigated, $P<0,01$). Intensity of clipping had no significant effect on the number of laterals produced per primary during spring, summer and autumn in the species *T. triandra*, and no significant effect at all times of year in the species *S. fimbriatus*.

It is thus concluded that a single defoliation results in greater production of lateral tillers per unit area in the species *T. triandra* than in the species *S. fimbriatus*. However, this is a result of greater primary tiller densities in the former species and there is little overall difference in the number of laterals produced per primary tiller of the two species. Lateral tillering increases after defoliation as the season progresses from spring through to dormancy in winter, and/or as plant physiognomic development advances towards maturity. Intensity of defoliation has little influence on the number of laterals produced per unit area or per primary tiller, the exception being when year-old *T. triandra* tillers are defoliated during winter. At this time, lateral tillering per primary tiller is stimulated by severe defoliation.

8.3.1.3 Primary tiller mass

The above-ground mass of living primary tillers growing in irrigated and non-irrigated tufts of *T. triandra* and *S. fimbriatus* before defoliation and two months after three different intensities of defoliation applied at different times of the year is presented in Figure 8.7.

The main effects of irrigation, time of year and clipping were statistically significant ($P<0,01$). The effect of irrigation on tiller mass both before and after clipping was overwhelming, a result of the 1982/83 drought. In addition, tiller mass over all treatments increased as time of year progressed. This is expected since tufts had been clean-cut during winter before spring treatments were applied, and thus most primary tillers would have been progressively older as successive seasonal treatments were applied after spring. The effect of intensity of cutting meaned over all treatments showed that lenient defoliation resulted in heavier tillers than moderate defoliation which in turn resulted in tillers of higher mass than severe defoliation. This result, too, is expected since lenient defoliation involved less material being removed at clipping than severe defoliation, and the results represent the sum of both regrowth and the material that remained after the harvest. In order to evaluate the effect of intensity of clipping on herbage production of tillers (regrowth), it is necessary to consider not above-ground mass, but rather the mass of regrowth above clipping height.

Of particular interest in Figure 8.7, however, is a comparison of above-ground mass of cut tillers two months after clipping with the above-ground mass of tillers in tufts removed before clipping at the next time of year treatment. Since tuft removal two months after clipping took place at approximately the same time that clipping intensities were applied on the following time of year treatments, these tillers would have been approximately the same age. Such a comparison would give an indication of the extent to which any clipping favours or retards growth of tillers in successive stages of physiognomic development. In the species *T. triandra*, tiller mass two months after clipping (regardless of intensity) was always lower (and often significantly so) than tiller mass before clipping at the following time of year clipping (Figure 8.7). In contrast, leniently clipped *S. fimbriatus* tillers on the irrigated treatment always had greater mass two months after clipping than unclipped tillers of the next time of year treatment. On the non-irrigated treatment, the mass of leniently clipped tillers was nearly as high or greater than that of unclipped tillers of the next time of year treatment. The results thus suggest that recovery of *T. triandra* tillers is slower after clipping than that of *S. fimbriatus* tillers, and furthermore, total tiller size of the latter species is nearly as large, or larger, two months after lenient clipping than in the case of no clipping. In contrast, clipped *T. triandra* tillers are always smaller than unclipped tillers two months after clipping. These results corroborate the theoretical comparison made between the two species from growth rates of unutilised tillers (Chapter 4; Figures 4.14 & 4.15).

In Figure 8.7 it can be seen that tillers recovered to the pre-clipping mass more rapidly after lenient than after severe defoliation. However, no indication is given of the absolute amount of herbage produced by tillers after clipping of different intensities (regrowth). The living tiller mass above clipping height two months after three different intensities of clipping of irrigated *T. triandra* and *S. fimbriatus* tillers at different times of the year is presented in Figure 8.8. The living tiller yields above harvest height on the non-irrigated treatments were negligible (a result of 1982/83 drought), and thus had much smaller variances than above-clip yields of irrigated tillers. They were thus excluded from analysis of variance. The effect of clipping on non-irrigated treatments was in any event confounded by the effect of the drought.

The mean effect of time of year on regrowth of irrigated tillers (Figure 8.8) was statistically significant ($P<0,01$), with greatest regrowth taking place after cutting in summer, followed by winter, autumn and spring. Greatest regrowth after clipping in summer is expected since it was shown in Chapter 4 that growth rates as determined by the environment are greatest in summer, provided moisture is not limiting. Slowest regrowth of tillers after clipping in spring and autumn is explained in the first instance (spring) by the fact that tillers were still very young, while regrowth after autumn clipping took place in April and May, a time of year when growth rates slow down considerably. Regrowth of tillers after winter clipping was reasonably rapid, and significantly greater than that after clipping in spring and autumn. This was presumably because tillers cut at this time were well-developed (tufts had been rested for one year), and since defoliation took place in late winter, regrowth took place in spring when temperatures were favourable for growth.

There were no significant main effects of clipping intensity in species on the mass of living tillers above clipping height. However, a significant interaction between the effects of clipping intensity and species (P<0,01) showed that tiller regrowth was favoured by lenient clipping in the species *T. triandra*, while the opposite trend took place with *S. fimbriatus* tillers (Figure 8.8). The results thus suggest that not only is the recovery of *T. triandra* tillers slower than those of *S. fimbriatus* tillers after clipping (Figure 8.7), but also that *S. fimbriatus* tillers are less sensitive to severe clipping than those of the other species. *T. triandra* tiller regrowth was particularly favoured after winter clipping when tillers were well-developed. However, as was indicated with tuft regrowth after clipping, lenient utilisation of this species is not necessarily desirable in winter. This is because lenient defoliation would presumably result in shoot apex elevation of these tillers in the subsequent spring, the consequence of which could be rejection of the species by grazing animals (shown in Chapter 2) and aerial tillering (Chapter 3). It may well be preferable to apply intense defoliation to *T. triandra* in winter in order to stimulate vegetative reproduction by means of lateral tillering (Figure 8.6) near the soil surface.

The mass of roots per living primary tiller in irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts before defoliation and two months after three different intensities of clipping at different times of the year is presented in Figure 8.9. Because of the means used for removing tufts, the root masses presented in Figure 8.9 are an underestimate of actual root mass, and this was explained in Section 8.3.1.1.

The main effects of irrigation, time of year, species and clipping on root mass per living tiller were all statistically significant. Because of the 1982/83 drought, root mass per tiller on non-irrigated treatments was considerably lower than on irrigated treatments. On irrigated treatments, root mass increased as the season of defoliation progressed from spring through to the following winter. This was presumably a result of increasing tiller age at time of clipping. In addition, the mean mass of living *T. triandra* primary tillers was greater than that of *S. fimbriatus* tillers, a result that corroborates those reported in Chapter 3.

With respect to the effect of clipping on primary tiller root mass (Figure 8.9), comparison of before-cut masses with after-cut masses at the same season are not particularly meaningful. Two months growth was allowed to take place after clipping, and when tillers were still young with few or no roots attached, a two-month period is likely to have had a positive effect on root growth with or without defoliation. Once tillers were older, with developed root systems, the two-month growing period after clipping is likely to have had a less critical effect. This trend is illustrated by the results on the irrigated treatments (Figure 8.9), where young tillers generally had lower root masses before clipping than two months after clipping. However, two months after autumn and winter clipping of irrigated *T. triandra* tufts, tillers had significantly lower (P<0,01) masses than before clipping. In similarly treated *S. fimbriatus* tufts, before-clip root mass per tiller exceeded after-clip mass only on the winter treatment, and here the result was not significant.

Of more relevance, with respect to the effect of clipping on tiller root mass, is to compare the mass of roots per tiller two months after clipping with that of tillers before clipping at the subsequent time of year treatment, these tillers being of roughly the same age. In nearly all instances, severe defoliation resulted in tiller root mass two months after clipping being lower than that of undefoliated tillers of the same age. On irrigated treatments this effect was usually significant. In contrast, leniently defoliated tillers often did not have a significantly lower root mass than undefoliated tillers of the same age. Furthermore, the main effect of intensity of defoliation showed statistically (P<0,01) that root mass per tiller meaned over all moisture treatments, species and time of year diminished with increasing intensity of defoliation.

8.3.1.4 Leaf emergence and growth

It was explained in the procedure (Section 8.2.1) that after defoliation of tufts in spring, summer and autumn, three tillers per tuft were permanently marked. In addition, living, or portions of living leaf blades (longer than 5mm) that remained after defoliation were marked with a stain in organic solvent. Marked tillers were returned to and leaf emergence and growth monitored at approximately fortnightly intervals until tuft removal. Observation and monitoring of defoliated tillers showed that leaves that were partially defoliated after their ligules had emerged, did not continue to expand after defoliation. However, leaves with ligules that had not emerged from the covering of leaf sheaths at time of defoliation, continued to expand after clipping. The degree of this post-defoliation expansion was greater the younger the leaf. These concepts are described in Figure 8.10. In this figure, the distance between successive ligules is enlarged to facilitate easier interpretation of the diagram. Four typical stages in the defoliation process of a moderately clipped vegetative *T. triandra* tiller are illustrated.

(A) A vegetative *T. triandra* tiller before clipping. Two of the living leaves have emergent ligules, while the three youngest emerged leaves have their ligules protected within the older leaf sheaths.

(B) The same tiller immediately after moderate clipping. The two youngest leaves that had emerged before clipping no longer have any portion of their leaf blades emerged.

(C) The same tiller approximately two weeks after clipping. The two oldest leaves which had ligules that had already emerged at time of clipping have not expanded, while the younger clipped leaves have continued expanding. The degree of expansion increases with diminishing leaf age. The oldest leaf with an unemerged ligule at time of clipping is now fully expanded.

(D) The tiller approximately four to six weeks after clipping. The two oldest leaves have senesced and the three leaves that were still expanding at time of clipping are now fully expanded (ligules emerged). Two new unclipped leaves have emerged, but their ligules are protected within the older leaf sheaths. The tiller has five emergent green leaves, the same number it had before clipping.

This process illustrates the remarkable adaptation of grasses to defoliation. While leaves were still expanding, their meristematic sites were protected within the leaf sheaths, and only once leaves were fully expanded did the ligule area emerge. The meristematic regions of leaves are thus protected from all but the most intense utilisation. In addition, the results to be reported in Chapter 10 will show that stems of vegetative grass tillers which consist essentially of leaf sheaths, are avoided by grazing animals unless stocking pressures are extremely high. Thus the meristematic regions of vegetative tillers are largely protected from grazing animals.

The mean number of emerged green leaves that remained (marked with a stain in organic solvent) on marked tillers after three intensities of defoliation of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts in spring, summer and autumn and the number of these leaves that remained alive after subsequent sampling dates is presented in Figure 8.11. The mean number of unmarked leaves that emerged (or re-emerged in the case of previously emergent leaves whose emerged part was removed by clipping) on these tillers after defoliation is presented in Figure 8.12, and the sum of these two (total green leaves per tiller) is presented in Figure 8.13. The least significant differences listed on these figures represent those between any two treatment means at each sampling date. Statistical comparisons between sampling dates could not be made since they represented sequential recordings of the same individual tillers.

Immediately after clipping at all times of year (Figure 8.11), virtually no green leaves remained on severely clipped tillers. In spring, three to four green leaves (or portions of green leaves) remained attached to tillers of both species and on both moisture treatments at the moderate and lenient defoliation intensities. These senesced progressively with time until tufts were removed in mid-December approximately two months after clipping, by which time there remained less than one viable leaf per tiller of those that had emerged before defoliation. There was no significant difference in the number of marked green leaves per tiller between the moderate and lenient clipping intensities at time of clipping or at time of tuft removal on the various treatments. However, approximately one month after clipping (November), leniently defoliated tillers had more marked green leaves than moderately defoliated tillers ($P<0,05$). This suggests that the oldest marked leaves survived longer on the leniently defoliated treatment.

After defoliation in summer, the number of marked green leaves followed a similar trend to that after spring defoliation on the irrigated *T. triandra* treatment (Figure 8.11). On the irrigated *S. fimbriatus* treatment, however, there was no significant difference between clipping intensities. On the non-irrigated treatments, the number of marked green leaves per tiller was initially less than that on equally defoliated irrigated tillers of the same species, and these remaining leaves senesced rapidly, a result of the 1982/83 drought. After autumn defoliation, moderately defoliated *T. triandra* tillers had significantly fewer green leaves remaining than leniently defoliated tillers. This was probably a result of the fact that the apices of these tillers had elevated by this time, and thus defoliation at a height of 4-5cm resulted in complete removal of most leaves. In contrast to *T. triandra*, there was no significant difference in the number of green leaves remaining on irrigated *S. fimbriatus* tillers that were moderately or leniently utilised. Very few green leaves remained on non-irrigated tillers of both species after autumn defoliation, a result of the 1982/83 drought.

The number of unmarked green leaves per tiller (Figure 8.12) increased sharply after marking on all treatments and times of year, provided moisture was not limiting. However, the number of unmarked leaves per tiller increased more rapidly on severely defoliated tufts than on moderately and leniently clipped treatments. Severe defoliation of tillers generally resulted in significantly more unmarked green leaves per tiller than lenient defoliation at first and second sampling dates after defoliation, provided moisture was not limiting. This difference, however, diminished at subsequent sampling dates and in most instances was no longer significant by the time tufts were removed. The trend is attributed to the fact that after severe defoliation, young, expanding, previously emerged leaf blades were removed by clipping, but re-emerged rapidly after treatments were applied, thus initially resulting in more unmarked emerging leaves than on leniently defoliated treatments. The results thus suggest that, after emergence of all clipped leaves, there was no major difference in the rate of emergence of new leaves between intensity of defoliation treatments.

With respect to the total number of green leaves per tiller, the results (Figure 8.13) show that immediately after defoliation, provided drought was not being experienced, severely defoliated tillers had significantly fewer green leaves than leniently or moderately defoliated tillers. At the same time (immediately after defoliation) there were no significant differences between moderately and leniently defoliated tillers. An exception is in the case of autumn defoliated *T. triandra* tillers under irrigation. Here, leniently defoliated tillers had more green leaves than moderately defoliated tillers immediately after clipping. As was suggested in the case of previously emerged leaves that remained after clipping (Figure 8.11), this was probably a result of shoot apices on this treatment being elevated at this time, and thus moderate defoliation resulted in complete defoliation of most leaves.

The difference between the total number of leaves attached to severely clipped tillers and the number attached to leniently and moderately clipped tillers became progressively less at each sequential sampling date after clipping. By the time tufts were removed, there was no significant difference in the number of leaves attached to tillers subjected to different defoliation intensities on any of the treatments. The results thus show that severe defoliation physically removed more emerged leaf blades than lenient defoliation. However, clipped expanding leaves re-emerged rapidly after defoliation on severely defoliated treatments, (provided moisture was not limiting), and within two months these tillers attained the same number of leaves as those on leniently clipped tillers.

Since tillers clipped at each time of year had received identical treatment before clipping intensities were applied, the labile carbon reserves of differentially clipped tillers within species and moisture treatments would have been the same when clipping treatments were applied. Consequently, differences in regrowth of tillers between clipping intensities at each time of year can be attributed to differences in living leaf area remaining after clipping, provided apices were not decapitated. Leaf area per tiller could not be non-destructively sampled. However, total green leaf length per tiller was measured immediately after clipping and at each sampling date thereafter until tufts were removed. Green leaf length is presumably closely related to green leaf area, and the recorded green leaf lengths per tiller immediately after clipping at subsequent sampling dates are presented in Figure 8.14.

The total green leaf lengths per tiller on non-irrigated treatments in summer and autumn were variable and extremely small, a reflection of the 1982/83 drought. Although there was a significant amount of green leaf material on leniently clipped, non-irrigated summer treatments immediately after defoliation, this leaf material senesced rapidly (Figure 8.14). The green leaf length data from the non-irrigated summer and autumn treatments are thus considered largely to reflect the effects of the drought which mask the effect of clipping intensity. Reasonably good rains fell during spring 1982 (Figure 3.1), however, and clipping effects on non-irrigated spring treatments are considered meaningful.

In virtually all other instances, the green leaf length per tiller was significantly greater immediately after lenient clipping than after moderate clipping which in turn was greater than the green leaf length of intensely clipped tillers (Figure 8.14). As time progressed after clipping, the difference between clipping treatments of *T. triandra* tillers growing with adequate moisture in spring and summer became larger. This implies that the more leniently clipped treatments would have had progressively more photosynthetic material as time progressed after clipping during these seasons. After autumn clipping of irrigated *T. triandra* tillers, the same trend occurred initially, but with the onset of winter, the green leaf length on the more leniently clipped tillers diminished, probably a result of early mortality of oldest leaves at this time of year, a phenomenon discussed in Chapter 3 (Section 3.3.5.3). On the intensely defoliated treatment, oldest leaves were removed at time of clipping, and thus all green leaf material emerged after clipping. Leaf senescence thus did not take place as rapidly on this treatment.

The green leaf length of *S. fimbriatus* tillers growing with adequate moisture followed a similar trend to that of *T. triandra* tillers (Figure 8.14). However, on irrigated treatments the green leaf length of the leniently clipped treatments had reached a peak and begun declining by the time tufts were removed. On the non-irrigated spring defoliated treatment, the green leaf length per tiller of all defoliation intensity treatments had begun declining by the time tufts were removed. By the time tufts were removed, there was no significant difference in green leaf length per tiller on all except the irrigated spring treatments in the species *S. fimbriatus*. This is in contrast to *T. triandra* where, provided there was a reasonable amount of moisture available, leniently clipped treatments always had significantly greater leaf lengths per tiller than severely clipped treatments at time of tuft removal. Thus, lenient clipping resulted in greater green leaf material remaining immediately after clipping than severe clipping in both species (Figure 8.14). However, in the species *T. triandra*, the difference between treatments remained (or increased) over a two-month period after clipping while in the species *S. fimbriatus* the difference between clipping intensities generally diminished two months after clipping. Of note is the fact that the yield above clipping height of leniently clipped *T. triandra* tillers two months after clipping was inclined to be higher than that of severely clipped tillers, a difference that was significant after winter defoliation (Figure 8.8). In contrast, intensity of clipping had an opposite trend in terms of yield of tiller above clipping height in the species *S. fimbriatus* (Figure 8.8). It is thus concluded that the green leaf area remaining after partial defoliation of tillers of the species *T. triandra* plays an important role in determining regrowth of tillers after clipping. In the species *S. fimbriatus*, however, green leaf material remaining after partial defoliation apparently does not affect regrowth of tillers, and regrowth in this species is dependent on labile carbon reserves and photosynthetic assimilation by newly-emerged leaves. These results are consistent with the findings reported in Chapter 4 (Section 4.5.3.4) that the rate of photosynthetic assimilation of *T. triandra* tillers is less affected by age than by time of year, while in the species *S. fimbriatus*, age had a far greater effect on NAR than time of year.

The results (Figures 8.8 and 8.14) also refute the hypothesis of Booysen (1966) that intensity of defoliation should be such that sufficient leaf area should remain so that regrowth is not dependent on carbon reserves as far as its application to the species *S. fimbriatus* is concerned. However, results corroborate the hypothesis as far as its application to *T. triandra* is concerned. The question that arises is the extent to which intensity of tiller defoliation by grazing animals can be manipulated through animal management. This aspect will be considered in Chapter 10.

Unfortunately, green leaf length measurements (Figure 8.14) cannot be used to compare net green leaf length increment after different intensities of defoliation. This results from the fact that what was measured was green leaf and not total leaf length. The results thus reflect the combined effect of expanding young leaves and senescing older leaves. In retrospect, it would have been meaningful to measure total length of each individual leaf in addition to the length of its green portion. By returning to leaves in the same order at sampling dates, this would have allowed the maximum length of each leaf to be determined and thus the net increment of leaf material (expressed in terms of leaf length) to be compared between intensity of defoliation treatments. This procedure has been used to compare tiller growth between species by Stuart-Hill (1984*a*).

Finally, the results discussed in this, and preceding sections (Experiment 1) consider the effect of intensity of defoliation where whole tufts are defoliated uniformly. In practice, it is likely that animals only partially defoliate tufts, defoliating some tillers and not others, and the difference in height between individual bites could well also be different. Under such circumstances, defoliated tillers could make use of carbon reserves from organically attached undefoliated tillers, as was suggested in Chapter 4. The question of tiller interdependence after partial defoliation of tufts is likely to be of fundamental importance in formulating grazing management strategies, and was not investigated in the series of trials reported in this dissertation. The aspect of tiller interdependence and carbon reserve re-allocation after partial defoliation of tufts requires further attention in the future.

8.3.1.5 Shoot apex elevation and flowering

The mean height of shoot apices of marked tillers after three intensities of defoliation of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts in spring, summer and autumn is presented in Figure 8.15. Least significant differences are those between any two means at each individual sampling date with the exception of irrigated *S. fimbriatus* tillers after summer defoliation. This was the time when *S. fimbriatus* tillers normally elevate their apices and flower, and thus the mean height of the tillers of this species on the irrigated treatment was considerably higher than those of any other treatment. (On the non-irrigated *S. fimbriatus* treatment, flowering at this time was suppressed by drought). Since only a limited number of irrigated *S. fimbriatus* tillers flowered in autumn after summer defoliation, the standard error of the mean height of the apices of these tillers was high (considerably higher than on any other treatment) at this time. Consequently, a separate statistical analysis was conducted for the means of heights of shoot apices of irrigated *S. fimbriatus* tillers once the first of these means had exceeded 50mm, and separate least significant differences are listed for these means in Figure 8.15. In addition, the means are presented on a different scale once they exceeded 50mm, and the least significant differences are also listed on this scale.

After spring defoliation, there was little difference in the height of apices at different intensities of defoliation on any of the treatments within the two-month sampling period after tufts had been clipped. However, the apices of leniently clipped irrigated *S. fimbriatus* tillers were nearly significantly higher than those of the other treatments at the end of the two-month period. These results may be expected since Figure 3.4 shows that the apices of unutilised *T. triandra* and non-irrigated *S. fimbriatus* tillers had not commenced noticeable elevation by the end of December, while the elevation of irrigated *S. fimbariatus* apices had just become noticeable.

The results recorded after different intensities of defoliation on non-irrigated treatments in summer and autumn (Figure 8.15) are not considered meaningful since shoot apex elevation was in any event suppressed by the 1982/83 drought (Figure 3.1). However, where there was adequate moisture, intensity of defoliation had a significant effect on subsequent shoot apex elevation of these times. On irrigated *T. triandra* tillers, there was no significant difference between the height of shoot apices immediately after clipping in summer. However, as autumn approached, leniently clipped tillers elevated their apices significantly higher than moderately clipped tillers, which in turn elevated their apices significantly (or nearly significantly) higher than severely clipped tillers. Severely defoliated irrigated *T. triandra* tillers did not elevate their apices significantly by the end of March 1983 after clipping in January (Figure 8.15). The height of the apices of irrigated *T. triandra* tillers subjected to lenient defoliation in summer was of the order of 30mm, approximately equal to, or a little less than that of undefoliated tillers at the same time of year (Figure 3.4).

Immediately after autumn defoliation of irrigated *T. triandra* tufts, the height of the apices of leniently and moderately clipped tillers was not different, but the apices of severely clipped tillers were significantly lower. This results from the fact that severe clipping decapitated the apices, and those that were marked were still in the juvenile phase. On the leniently and moderately clipped treatments, defoliation intensity was such that most of the elevated apices remained intact, and marked tillers belonged to this population. However, after autumn defoliation, leniently clipped tillers continued to elevate their apices, and two months after defoliation the apices of leniently clipped tillers were significantly higher than those of the moderately clipped treatment. The mean height of the apices of the irrigated *T. triandra* tillers subjected to lenient defoliation in autumn was approximately 35mm two months after clipping (beginning of June). This height was considerably lower than that of undefoliated tillers of the same age at the same time of the year (higher than 100mm; Figure 3.4).

It is thus concluded that in the species *T. triandra*, where shoot apex elevation is not restricted by inadequate moisture, defoliation suppresses the normal vegetative elevation of shoot apices as described in Chapter 3. However, the degree of suppression of vegetative shoot apex elevation increases with increasing severity of utilisation intensity. Very severe defoliation after shoot apex elevation has commenced, results in decapitation of these apices.

In the species *S. fimbriatus*, as with *T. triandra*, there was no significant difference between the height of shoot apices immediately after clipping in summer. As autumn approached, a number of marked tillers began to elevate their apices, and flower. The number of tillers that flowered after lenient clipping was, however, greater than on the moderately or severely defoliated treatments. This resulted in leniently clipped tillers having a significantly higher mean height of shoot apices two months after clipping than moderately or severely clipped tillers (Figure 8.15). The height of the flowering culms of the tillers that did flower was, however, apparently not different between intensity of defoliation treatments.

After autumn defoliation of irrigated *S. fimbriatus* tufts, it was difficult to assess whether the apices of tillers that were already elevated had been defoliated by clipping or not. Consequently, only tillers with unelevated apices were marked after clipping. The results (Figure 8.15) show that these tillers did not elevate their apices and flower within two months after clipping and there was little difference in the height of apices between clipping treatments at this time. There were, however, tillers that did flower after clipping at this time, but these were not marked for fear of marking tillers with decapitated apices.

Thus, considering shoot apex elevation of irrigated *S. fimbriatus* tillers in general terms, increasing intensity of defoliation in summer (without decapitating apices), increasingly suppresses the number of tillers that elevate their apices and flower in autumn. The height achieved by the tillers that do flower appears to be unaffected by defoliation intensity. Defoliation in autumn results in decapitation of those tillers that have already elevated their apices or flowered.

The percentage of flowering primary tillers in irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts before defoliation and two months after three different intensities of clipping at different times of the year is presented in Figure 8.16. In the species *T. triandra*, the low percentage of flowering tillers before clipping in spring, summer and autumn were a result of those few tillers whose growing points had not been removed by the initial clean-cut of the experimental site in winter 1982, and thus flowered during spring of the same year. The tillers that flowered after winter clipping represent the population of tillers that emerged after the initial clean-cut. Before clipping, approximately 6% and 15% of irrigated and non-irrigated primary tillers were in flower. These would have represented the early flowering tillers, and in Chapter 3 (Section 3.3.3.2) it was shown that flowering of *T. triandra* tillers covers a period from approximately June through to November. These tillers were, of course, decapitated at clipping. Two months after clipping, very few irrigated *T. triandra* tillers had flowered on the severe and moderate clipping intensities, but a significantly greater percentage (42%) of leniently clipped tillers were in flower. On the non-irrigated treatment, significantly fewer leniently defoliated tillers flowered than in similarly treated irrigated tufts (P<0,01). However, a significant number of non-irrigated *T. triandra* tillers flowered in spring after moderate and severe defoliation, and on the severely defoliated treatment, the percentage was significantly higher (P<0,01) than on similarly treated tufts under irrigation. The results thus support the contention in Chapter 3 that flowering of *T. triandra* under non-irrigated conditions cannot be avoided by critical defoliation in winter, provided the intensity of clipping is not more severe than 2cm. This results firstly from the fact that non-irrigated *T. triandra* tillers do not elevate their apices to a height in excess of about 2cm while still in the vegetative condition, even if rested for a full growing season (Figure 3.4). Secondly, although piping and flowering of individual tillers is reasonably rapid, between tillers it occurs sporadically, covering a period from June to November (Section 3.3.3.2).

Regarding *S. fimbriatus* tillers, no flowering took place during the 1982/83 growing season on the non-irrigated treatments, a result of the drought. Approximately 5% of non-irrigated tillers were in flower before cutting in winter (Figure 8.16) but this was because this treatment was applied at the end of the 1981/82 season, and tufts had thus not experienced the very severe 1982/83 drought. On the irrigated treatment flowering was first encountered when tufts were removed after the summer treatment. Here, significantly more tillers were in flower after lenient defoliation than after moderate or severe clipping ($P<0,05$), an observation that has already been pointed out in Figure 8.15. Before autumn defoliation of irrigated *S. fimbriatus* tillers, approximately 5% of tillers had already flowered. Two months after autumn defoliation, significantly more leniently defoliated tillers were in flower than moderately or severely clipped tillers ($P<0,01$) (Figure 8.16). During winter, flowering *S. fimbriatus* tillers were decapitated, and no tillers flowered after clipping at this time.

In conclusion, severe clipping of both species supresses flowering of primary tillers more than lenient clipping. However, in *T. triandra* flowering of tillers experiencing some moisture stress is not completely supressed by severe defoliation in winter. Where there is no moisture stress, severe defoliation results in decapitation of apical buds. In the species *S. fimbriatus*, severe clipping in summer or autumn suppresses the number of tillers that flower even when apical buds are not removed.

8.3.1.6 Summary of results

i. Increasing intensity of clipping of tufts of *T. triandra* and *S. fimbriatus* at different times of the year results in decreasing above-ground yield per unit area two months after clipping.

ii. Regrowth per unit area (mass above clipping height) is favoured by severe clipping in the species *S. fimbriatus*, but is not significantly affected by intensity of defoliation in the species *T. triandra*, except after winter, when regrowth of the latter species is favoured by lenient clipping.

iii. During drought the effects of intensity of clipping are masked by the effects of moisture stress.

iv. Defoliation reduces the mass of roots of the two species per unit area, and the reduction in root mass increases with increasing severity of clipping.

v. The density of primary tillers in *T. triandra* tufts with elevated vegetative shoot apices (autumn and winter) drops markedly with increasing intensity of defoliation, a result of shoot apex decapitation. *S. fimbriatus* primary tiller densities are affected by clipping only during autumn when tillers elevate their apices and flowering takes place.

vi. Clipping results in more lateral tillers being produced per unit area in the species *T. triandra* than in the species *S. fimbriatus*. However, this is a result of greater primary tiller densities in the former species and not in the number of laterals produced per primary.

vii. Lateral tillering increases after defoliation as the season progresses from spring through to winter and/or as the physiognomic development of primary tillers advances towards maturity, particularly in the species *T. triandra*.

viii. Intensity of defoliation has little influence on the number of lateral tillers produced per unit area or per primary tiller, the exception being when mature *T. triandra* tillers are defoliated during winter. At this time lateral tiller production per primary is stimulated by increasing intensity of defoliation.

ix. Primary tillers of *T. triandra* take longer to recover to their original above-ground mass after clipping than *S. fimbriatus* tillers.

x. Regrowth of *S. fimbriatus* primary tillers after clipping is favoured by intense clipping, while in the species *T. triandra*, regrowth is favoured by lenient clipping.

xi. Leaves on tillers of both species with emerged ligules at time of clipping do not expand after defoliation. Leaves with ligules that have not emerged from within their covering of leaf sheaths at time of clipping continued to expand after defoliation. The degree of expansion of clipped leaves after defoliation is greater the younger the leaf.

xii. More green leaves remain on tillers immediately after lenient than after severe defoliation. Immediately after defoliation, however, leaves emerge more rapidly after severe than after lenient clipping, the rapidly emerging leaves being those that were already emerged before defoliation, but the emerged portions of which are removed by the clipping process. The rate of emergence of new leaves is apparently not affected by intensity of defoliation. Two months after defoliation, there is no difference in the number of green leaves attached to differentially defoliated tillers.

xiii. Lenient clipping results in a greater amount of green leaf material remaining immediately after clipping than severe clipping in both species. However, in the species *T. triandra* the difference between clipping treatments remains (or increases) over a two-month period after clipping, while in the species *S. fimbriatus*, the differences between clipping treatments generally diminish within two months after clipping.

xiv. The green leaf area remaining after partial defoliation of *T. triandra* tillers continues to photosynthesise after defoliation and plays an important role in regrowth. In the species *S. fimbriatus* green leaf remaining after partial defoliation apparently does not affect regrowth of tillers.

xv. The expected (when moisture is not limiting) elevation of shoot apices of *T. triandra* tillers while still in the vegetative phase is suppressed by defoliation, even when apices are not decapitated. The degree of this suppression increases with increasing severity of utilisation. Very severe defoliation after vegetative shoot apex elevation has commenced, results in decapitation of these apices.

xvi. Clipping of primary tillers of both species suppresses the development of flowers. The degree of suppression increases with increasing defoliation intensity. In the species *T. triandra*, flowering of tillers receiving some moisture stress is not completely suppressed even by very severe defoliation of this species in winter. However, where there is no moisture stress, severe defoliation of this species in winter results in decapitation of apical buds and completely suppresses flowering. In the species *S. fimbriatus*, severe clipping in summer or autumn reduces the number of primary tillers that flower even when apical meristems are not removed.

xvii. The results consider the effects of intensity of defoliation where whole tufts are defoliated uniformly. In a grazed situation it is likely that tufts are partially defoliated, with some tillers grazed and others not. Under such circumstances reserve carbon re-allocation between tillers could play an important role in regrowth, an aspect that requires further investigation.

8.3.2 Effect of frequency of defoliation on key grass species (Experiment 2)

8.3.2.1 Total tuft yield

The mean total yields (sum of individual cuts) per unit area of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts subjected to five different clipping frequencies in the 1982/83 season are presented in Figure 8.17. After examination of the data, it became apparent that total yields on irrigated treatments were considerably greater than those on non-irrigated treatments as a result of the 1982/83 drought. Variance heterogeneity was suspected and statistical comparison between irrigated and non-irrigated treatments would have required transformation. However, differences between irrigation treatments were obvious, and separate analyses of variance were conducted on untransformed data from each of the irrigation treatments. Least significant differences (Figure 8.17) are thus those between any two treatment means within irrigation treatments.

Dealing first with irrigated treatments, the mean effects of species, frequency of clipping and the interaction between the two were all statistically significant ($P<0,01$). This implies that the clipped yield of irrigated *T. triandra* tufts was greater than that of *S. fimbriatus* tufts, and the yields of both species were affected by clipping frequency, but the effect of clipping frequency was not consistent between species (Figure 8.17).

Irrigated *T. triandra* tufts produced greatest yield (dry mass) at a clipping frequency of three times per year, but this was not quite statistically higher than the yield produced on treatments clipped twice and once per year. However, one, two and three cuts per year all produced significantly more clipped herbage than five cuts per year ($P<0,01$) which in turn produced more herbage than nine cuts per year ($P<0,05$) (Figure 8.17). The conclusion is thus that on irrigated *T. triandra* tufts, very infrequent clipping (once and twice per year) produced nearly significantly less herbage above clipping height than clipping three times per year, probably a result of herbage loss through leaf senescence and abscission on the least frequently defoliated treatments. On the treatments clipped three times per year, the second cut (early March) took place at the critical stage when tillers had commenced piping, and flowering was suppressed on this treatment. No flowering took place on treatments cut five and nine times per year, but vegetative growth of these tufts was apparently depressed by clipping. It is thus concluded that increased frequency of cutting reduced yield of irrigated *S. fimbriatus* tufts, but that this was only significant when tufts were clipped five or more times per year. As with *T. triandra*, the differences between treatments are attributed to the fact that frequently defoliated tufts spent a relatively long period with low leaf areas and/or the pool of reserve carbon in these tufts became progressively smaller in these plants.

The degree to which the yield of irrigated *S. fimbriatus* tufts was reduced by frequent clipping (five and nine cuts per year) was not as marked as with *T. triandra*. This is shown by the fact that irrigated *T. triandra* tufts clipped once, twice and three times per year all produced considerably more herbage than similarly treated *S. fimbriatus* tillers (P<0,01) (Figure 8.17). However, while irrigated *T. triandra* tufts clipped five times per year still produced more than equally treated *S. fimbriatus* tillers, the difference between species was not as large (P<0,05). Finally, irrigated *T. triandra* tillers clipped nine times per year did not produce significantly more than similarly treated *S. fimbriatus* tillers.

On the non-irrigated treatments, the main effects of species and frequency of clipping were still statistically significant (P<0,01), but there was no significant interaction between these two main effects. The implication was thus that non-irrigated *T. triandra* tufts produced significantly more herbage above clipping height than *S. fimbriatus* tufts, and although frequency of cutting affected yield, this was fairly consistent between species. The latter result is not unlikely in view of the overwhelming effects of the 1982/83 drought (Figure 8.17).

treatments. However, frequent defoliation (five times and nine times per year) considerably reduced herbage production. Since tufts were always defoliated above the height of shoot apices (except at the last harvest when all tufts were defoliated to a height of 1-2cm), the results cannot be attributed to meristematic limitations. However, harvest height was also such that all green leaf blades were removed, so that the only photosynthesising material that remained after clipping was leaf sheaths, and thus was fairly constant between species. Consequently differences between treatments were probably not a result of differences in the amount of photosynthetic substrate remaining after defoliation. The results are thus attributed to the fact that frequently defoliated plants spent a relatively longer period with low leaf areas (shortly after each defoliation) than infrequently defoliated plants, and/or the fact that the pool of reserve carbon was progressively diminished in frequently defoliated plants. Unfortunately, the relative importance of these two parameters could not be assessed since no estimate was made to labile carbon reserves.

The maximum yield achieved with three clips per year on irrigated *T. triandra* tufts approximately coincides with the optimal period between successive defoliations suggested from rates of leaf emergence and senescence in Chapter 3 (Section 3.3.5.3).

With reference to irrigated *S. fimbriatus* tufts (Figure 8.17), yield diminished with increasing clipping frequency, but there was no significant difference between one, two and three cuts per year. Five cuts yielded less herbage than one cut (P<0,05), but not less than two or three clips. Nine cuts per year produced significantly less herbage than one and two cuts per year (P<0,05), but not significantly less than the other treatments. The highest yields achieved with one and two clips per year on irrigated *S. fimbriatus* tufts is attributed not necessarily to the fact that these treatments produced greater leaf material than other treatments, but rather to the fact that more flowering culms were produced on the two most infrequently clipped

Comparing individual treatment means shows that two cuts per year, followed by three cuts, produced the greatest amount of herbage on non-irrigated tufts of both species. However, these fequencies did not result in significantly greater yields than one cut per year in the species *T. triandra*, or greater than five cuts per year in species *S. fimbriatus*. In the species *T. triandra*, two and three cuts per year both yielded significantly more herbage than five cuts and nine cuts ($P<0,05$), while in the species *S. fimbriatus*, nine cuts produced less forage than two cuts ($P<0,05$), but not significantly less than any other treatment.

Thus, despite no significant interaction between species and frequency of cutting on non-irrigated tufts, the results (Figure 8.17) suggest that even in a severely stressed situation, *S. fimbriatus* is less sensitive to frequent cutting than *T. triandra*. The very low yield recorded with one cut at the end of the growing season on non-irrigated *S. fimbriatus* tufts is probably a result of leaf senescence and abscission on this treatment. In Chapter 7 it was shown that considerable forage loss took place as a result of desiccation on veld dominated by *S. fimbriatus* during the 1982/83 season.

Of particular note is the fact that frequent defoliation had a negative effect on the yield of both species, even where there was no irrigation, despite there being virtually no growth from January 1983 onwards. The results, in fact, probably underestimate the detrimental effect of frequent defoliation since more forage loss through desiccation is likely to have taken place on the infrequently cut than on the frequently cut treatments. The results thus illustrate the ill-effect of frequent defoliation even during a relatively short part of the growing season. In addition, in Chapter 4, it was suggested that tillers were probably more adversely affected by defoliation during spring than at any other time of the year.

Regarding the effect of frequency of defoliation on the total seasonal yield of *T. triandra* and *S. fimbriatus* in general terms, it appears that five or more cuts per growing season have an adverse effect on herbage production, both where there is no moisture stress and where stress is very severe. However, the species *S. fimbriatus* is apparently less adversely affected by frequent defoliation than *T. triandra*. The optimum frequency of defoliation in terms of the results in Figure 8.17 is about three times per year.

In a rotational grazing system with fairly short periods of occupation (two to three weeks), a defoliation frequency of three times per year would result in periods of absence of three to four months. This period approximately coincides with that suggested in Chapter 3 from the rates of leaf emergence and decay on tillers of *T. triandra* and *S. fimbriatus* (Section 3.3.5.3).

Finally, the effect of frequency of defoliation considered in this discussion arises from a situation where whole tufts were completely defoliated (Experiment 2). In practice, animals may well only partially defoliate tufts (graze some tillers and not others, and possibly not remove all green leaves on a tiller). Labile carbon re-allocation in partially defoliated tufts may alter regrowth patterns after defoliation and thus the optimum defoliation (partial) frequency. This aspect requires further investigation.

8.3.2.2 Tiller density per unit basal area

When tufts were removed after the final clip in June 1983, the number of living tillers per tuft was counted and expressed per unit basal tuft area. This could only be done on irrigated treatments since the difference between living and senescent tillers could not be identified on non-irrigated treatments. The results for irrigated treatments are presented in Figure 8.18. There was no significant difference in the number of living tillers per unit basal tuft area between frequency of defoliation treatments at the end of the 1982/83 season, at least on irrigated treatments. This may be expected since tufts were defoliated above the estimated height of the majority of growing points at all but the final defoliation treatment. Differences in tuft yields (Section 8.3.2.1) are thus also a reflection of differences in tiller yields. In addition, the results in Figure 8.18 suggest that differences in total yield between different clipping frequencies were not caused by meristematic limitations in any of the irrigated treatments. On non-irrigated treatments, many shoot apices and lateral buds could well have senesced as a result, but this would not have affected the results during the 1982/83 season, since no significant rain (Figure 3.1) or growth took place after January 1983.

Differences in yield between frequency of clipping treatments as has been suggested, would thus have been a result of diminishing availability of storage carbon for regrowth on frequently clipped treatments, and/or the fact that frequently clipped plants spent relatively longer periods with small leaf areas than infrequently defoliated tufts.

8.3.2.3 Individual cut yields

The individual cut yields per unit area of irrigated and non-irrigated *T. triandra* tufts clipped more than once per year are presented in Figure 8.19, and the individual cut yields of similarly treated *S. fimbriatus* tufts in Figure 8.20.

The differences between yields of individual cuts within each frequency of clipping treatment cannot be tested statistically since the same 10 tufts were returned to at each clipping date within treatments. However, the data can be used to illustrate trends. Individual cut yields apparently declined at successive clipping dates on irrigated treatments of both species clipped five and nine times per year (Figures 8.19 & 8.20; C & D). This suggests progressively diminishing vigour after clipping as the season progressed.

In irrigated tufts cut three times per year (Figures 8.19B & 8.20B) the first cut produced the highest yield in both species, probably a result of a longer inter-clip growing period before the first clip than before the other two clips. The third clip produced more herbage than the second, and although this could have been a result of a longer inter-clip growing period and more intense defoliation, the results do suggest that the vigour of the plants had not been greatly impaired.

The yield of irrigated tufts of both species cut twice per year (Figures 8.19A & 8.20A) was lower at the first cut than at the second. The first cut took place during mid-January, suggesting an equal inter-clip growing period before each cut. It can thus be inferred from the results that clipping did not impair the vigour of tufts on this treatment.

On non-irrigated tufts of both species, yields were recorded only at the first three cutting dates on treatments cut nine times per year (Figures 8.19D & 8.20D) and at the first two cuts of treatments cut five times per year (Figures 8.19C & 8.20C). Treatments cut twice (Figure 8.19A & 8.20A) and three times (Figures 8.19B & 8.20B) per year resulted in measurable yields only after the first cut. The results thus show that the ill-effect of frequent cutting in terms of its effect on herbage production were manifested within a relatively short period at the beginning of the growing season. On the non-irrigated *T. triandra* treatment clipped five times per year (Figure 8.19C) yield was recorded only at the first two harvest dates, and yield at the second harvest date was very low. On non-irrigated tufts of the same species clipped three times per year (Figure 8.19B), yield was recorded only at the first harvest date. Thus, the major difference between these two treatments was that the frequently clipped tufts were subjected to defoliation earlier in the growing season. This suggests that *T. triandra* tufts that consist primarily of young tillers, are particularly sensitive to defoliation in spring, a point that was suggested from the analysis of growth of unutilised tillers in Chapter 4.

8.3.2.4 Stubble mass

The stubble mass (living and dead material) per unit area of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* tufts during June 1983 after they had been subjected to different frequencies of defoliation during the 1982/83 growing season is presented in Figure 8.21. Tufts had been subjected to equal intensities of defoliation during the June 1983 defoliation, implying that meaningful comparisons could be made between irrigation treatments, so a combined analysis of variance was conducted on all the data. Least significant differences listed in Figure 8.21 are thus those between any two treatment means.

Frequency of defoliation had no significant effect on the mass of stubble after different frequencies of clipping within species or irrigation treatments. However, stubble on irrigated treatments had significantly higher mass per unit area than stubble on non-irrigated treatments ($P<0,05$), and the stubble mass of *S. fimbriatus* tufts was significantly higher than that of *T. triandra* tufts ($P<0,01$), despite the fact that both species were subjected to the same intensity of clipping during June 1983. The results again illustrate the high proportion of stem material in the species *S. fimbriatus*. The stubble mass of *S. fimbriatus* was, in fact, higher than the total clipped yield of the same species (Figure 8.17). With the species *T. triandra*, stubble mass was greater than clipped mass only on the non-irrigated treatments (Figure 8.17 & 8.21). This results from the fact that clipped yields on non-irrigated treatments were low during the 1982/83 drought. Of further note is the fact that the relative difference between stubble on irrigated and non-irrigated treatments (Figure 8.21) was considerably smaller than the differences in clipped yield between the two moisture treatments (Figure 8.17).

Finally, the fact that there was no significant difference between stubble mass at different clipping frequencies (Figure 8.21) is not unexpected in view of the fact that there was no difference in the number of living tillers between frequency of clipping treatments, at least under irrigated conditions (Figure 8.19).

8.3.2.5 Root mass

The mass of roots (removed using the auger already described) per unit basal tuft of irrigated and non-irrigated *T. triandra* and *S. fimbriatus* plants during June 1983 after they had been subjected to different frequencies of defoliation during the 1982/83 season is present in Figure 8.22. Despite fairly large variability between treatment means, variance between treatments was reasonably constant, and a single analysis of variance was conducted on all the data. Least sigificant differences in Figure 8.22 are thus those between any two treatment means.

In discussing the results (Figure 8.22), it should be remembered that estimated root masses are an underestimate of true root mass for reasons already discussed. Analysis of variance showed that the main effects of irrigation and defoliation frequency were both statistically significant $(P<0,01)$. Irrigated tufts had considerably greater root mass per unit basal tuft area than non-irrigated tufts (an effect of the 1982/83 drought), and root yield with increasing defoliation frequency. The latter effect was significant on irrigated treatments, but not on non-irrigated *S. fimbriatus* treatments. On non-irrigated *T. triandra* treatments, tufts cut three times per year had higher root mass $(P<0,05)$ than other treatments.

In conclusion with respect to frequency of defoliation and root mass, the results suggest that frequent defoliation reduces root mass provided severe drought such as that in 1982/83 does not mask the effects of clipping. Root mass and distribution in a frequently defoliated situation is thus probably small. One implication is that swards in such a situation may have less access to soil water than infrequently defoliated swards. Thus, with the onset of drought, the advantages that a frequently defoliated sward has as a result of a low level of potential evapo-transpiration (discussed in Chapter 6) may be counteracted by the fact that an infrequently defoliated sward has greater access to soil water (through a better developed root system) than in a frequently defoliated situation.

8.3.2.6 Elevation of shoot apices

The height of shoot apices was determined as the mean of those of marked tillers (two per tuft) removed before each cut on all treatments. Since two new tillers were marked per tuft after each cut, a separate sample of 20 tillers was removed at each individual cut and on all treatments (except those defoliated once per year). Thus statistical comparison between all means so derived (individual cuts both between and within treatments) was considered acceptable. The mean heights of shoot apices of marked tillers before each individual clip of irrigated and non-irrigated *T. triandra* tufts clipped more than once per year are presented in Figure 8.23, and those of similarly treated *S. fimbriatus* tillers in Figure 8.24. Least significant differences represent those between any two means, excluding those before the second clip on irrigated *S. fimbriatus* tufts on treatments cut twice and three times per year. These means were excluded from the analysis since they included a few flowering tillers together with a majority of vegetative individuals, and would have resulted in heterogeneous variances between height estimates. The fact that some *S. fimbriatus* tillers did flower at these times is, however, important to note.

In the species *T. triandra*, there was no significant difference in the mean height of shoot apices between any defoliation treatments or between any individual cuts where there was no irrigation. Presumably, shoot apex elevation was suppressed by severe drought. Moreover, most marked non-irrigated *T. triandra* tillers senesced from January 1983 onwards.

On the irrigated *T. triandra* treatments, there was no significant difference in the heights of shoot apices before individual cuts on treatments defoliated five and nine times per year (Figure 8.23C & D). On these treatments, and on all non-irrigated *T. triandra* treatments where marked tillers were not senescent, the mean height of shoot apices was approximately 10mm. Consequently, frequent defoliation, even though above shoot apex height (where there was sufficient moisture) and drought both effectively suppressed the vegetative elevation of *T. triandra* expected in autumn and winter in an unutilised situation.

On irrigated *T. triandra* tufts defoliated three times per year (Figure 8.23B), the height of shoot apices at the second cut (March) was significantly higher (P<0,01) than the height of shoot apices before the first cut (beginning of December). By the time the third cut was applied (end of June), apices had elevated to a height significantly higher than that at the second cut (P<0,01). The mean height of shoot apices by the time the third (final) cut was applied was 28,5mm. This height was still considerably lower than that achieved by irrigated *T. triandra* tillers during June in an unutilised situation (approximately 120mm; Figure 3.4).

The heights of shoot apices in *T. triandra* tufts cut twice per year (Figure 8.23A) were significantly higher (P<0,01) at the second cut (June) (4mm) than at the first cut in January (10,5mm). The height of these apices in June (Figure 8.23A) was also significantly higher (P<0,01) at the same time of year than those of tillers in tufts cut three times per year (Figure 8.23B). However, the height of apices in tufts cut twice per year at the time of the second cut (June) was also considerably lower than that of unutilised tillers at the same time (approximately 120mm; Figure 3.4).

Consequently, although the apices of irrigated *T. triandra* tillers subjected to infrequent defoliation above shoot apex height (once or twice during the growing season) do elevate in autumn while still in the vegetative phase, the height of these apices during the winter before flowering is considerably lower than in an unutilised situation. In a situation defoliated twice during the growing season (once in winter) (Figure 3.23B), the height of the apices was still only 25mm above soil surface during the mid-winter before flowering. Such a frequency of defoliation corresponds roughly to that already suggested for optimal herbage production. Thus in a rotational system grazed three times per year, very severe defoliation would be required during winter in order to decapitate *T. triandra* apices, even where there is no moisture stress. It is thus concluded that in a rotational grazing system grazed three or more times per year, complete prevention of flowering of *T. triandra* by severe grazing in winter is highly unlikely. Drought, however, effectively prevents flowering of *T. triandra* tillers.

In the species *S. fimbriatus*, where there was no irrigation, the 1982/83 drought suppressed shoot apex elevation and there was no significant difference between the heights of shoot apices of any living tillers (Figure 8.24). Under irrigation, nine cuts per year (Figure 8.24D) and five cuts per year (Figure 8.24C) also suppressed elevation of shoot apices. On irrigated tufts cut three times per year (Figure 8.24B), the second cut took place at the time of year when primary tillers of the species normally elevate and flower (March). At this time 15% of marked tillers had elevated their apices and flowered. The mean height of all apices was not tested statistically against other means at this time for reasons already given. At the third cut, none of the tillers marked after the second cut had flowered, and the mean height of shoot apices at this time was no higher than on more frequently cut treatments.

On the irrigated *S. fimbriatus* treatment cut twice per year (Figure 8.24A), the first cut took place in mid-January when unutilised apices have normally just commenced elevation (Figure 3.4). The height of the shoot apices at this time (Figure 8.24A) was significantly ($P<0,05$) or nearly significantly higher than that on more frequently clipped treatments at the same time of year. When these tufts were again cut in winter, 20% of marked tillers had flowered, resulting in an increased mean height of shoot apices, although not tested statistically. The percentage of tillers that flowered even after one growing season defoliation before the normal time of flowering was still considerably less than that of irrigated *S. fimbriatus* tillers subjected to no growing season defoliation (Figure 3.5 & 3.6).

It is thus concluded that in the species *S. fimbriatus*, defoliation suppresses the number of tillers that elevate their apices and flower even where there is no moisture stress. The degree of this suppression increases with increasing frequency of defoliation, even when apical meristems are not removed. It has also been shown that flowering of *S. fimbriatus* tillers is also supressed by increasing intensity of defoliation (Figure 8.16).

8.3.2.7 Summary of results

i. Frequent defoliation (five or more cuts per year) reduces the clipped yield of *T. triandra* and *S. fimbriatus* tufts, both where there is no moisture stress and where moisture stress is very severe.

ii. The yield of the species *S. fimbriatus* is less adversely affected by frequent clipping than that of *T. triandra*.

iii. The optimum frequency of defoliation (above shoot apex height) in terms of herbage production is approximately three times per year.

iv. Frequency of clipping, provided it is above average height of shoot apices, does not affect the number of living tillers per unit area.

v. Frequent defoliation commencing on vigorous tufts in spring results in regrowth becoming progressively less vigorous after each successive defoliation. Infrequent defoliation within a season apparently does not affect vigour.

vi. Tufts consisting of young vegetative tillers particularly those of *T. triandra*, are apparently adversely affected by defoliation in spring.

vii. Stubble mass is not significantly affected by frequency of defoliation within one season. However, *S. fimbriatus* tufts contain a significantly higher proportion of stubble than those of *T. triandra*.

viii. Root mass per unit area decreases with increasing frequency of defoliation.

ix. Root mass per unit area after a severe drought is considerably lower than that in a situation of abundant water.

x. Shoot apex elevation of *T. triandra* tillers while still in the vegetative phase is suppressed by increasing frequency of defoliation. Drought suppresses vegetative shoot apex elevation of the species even under infrequent defoliation.

xi. Increasing frequency of defoliation of *S. fimbriatus* tufts suppresses the percentage of tillers that elevate their apices and flower even where there is no moisture stress. Drought effectively prevents *S. fimbriatus* tillers from elevating their apices and flowering.

8.4 Conclusion

In this chapter, the short-term effects of intensity and frequency of defoliation were studied on the key grass species *T. triandra* and *S. fimbriatus*. The combined and long-term effects of these parameters was not investigated. Furthermore, treatments were applied uniformly to all tillers within tufts. In grazed situations, however, it is likely that tufts are only partially defoliated, with some tillers grazed and others not. Also, the intensity at which tillers are grazed may vary both within and between tufts. Assimilated and reserve labile carbon re-allocation between tillers may well play an important role in the rate of regrowth in partially defoliated tufts. The question of tiller interdependence would thus be of fundamental importance in formulating grazing management strategies.

Of further note is the fact that active growth of swards takes place in a series of short flushes after rain. Regrowth of tillers and tufts in swards under occupation by grazing animals at these times could be subjected to repeated defoliation. This could result in depletion of reserve carbon pools and decreased sward vigour, implying that these swards could require preferential attention in order to allow them to recover at a later date.

It is thus concluded that many questions remain unanswered regarding the response of key grasses to defoliation by grazing animals in the False Thornveld of the Eastern Cape. In order to predict optimal sward utilisation in the veld type, it is necessary that the growth of grasses in response to the parameters and combinations of parameters outlined above be quantitatively assessed. Nevertheless, the results discussed in this and previous chapters provide useful information towards improving veld utilisation and livestock production in the False Thornveld of the Eastern Cape.

CHAPTER 9

ADAPTATION OF KEY GRASS SPECIES TO DEFOLIATION

9.1 Introduction

In Chapter 2, *T. triandra* and *S. fimbriatus* were identified as key grass species for management purposes in the False Thornveld of the Eastern Cape. Subsequent chapters have considered their growth and development, response to moisture stress and response to utilisation in some detail. The results suggest that the two species have developed different adaptive responses to defoliation, or possibly that the species have become adapted to different defoliation regimes. It is also of note that the species are considered to dominate different seral stages in terms of classical Clementsian succession (Roberts, 1973). Furthermore, the species have been considered by Danckwerts (1983) to belong in different ecological categories as defined by Foran *et al.* (1978). *Themeda triandra* was classified as a Decreaser species, one that is typically found in well-managed veld and decreases with over- or under-utilisation. In contrast, *S. fimbriatus* was considered to be an Increaser II species that increases with moderate overgrazing.

In this chapter, the adaptive responses of the two species will be considered and contrasted. These will be used to infer the defoliation regimes to which the two species are best adapted. From this a defoliation strategy, providing a means towards improved sward utilisation in the False Thornveld of the Eastern Cape, will be suggested.

9.2 Adaptive responses of key grass species

In a review, Stuart-Hill & Mentis (1982) contended that African grasslands have evolved under the impact of herbivory and fire. These authors suggested that grasses have developed through natural selection to deter, escape and tolerate grazing and to escape and tolerate fire.

Deterrents exist when plants possess chemical or physical characteristics which are unneccessary except that they render the plants to a greater or lesser degree, unacceptable to herbivores. These occur in the form of chemical deterrents - the chemical properties (specific or general chemical substances) of the plants make them unacceptable to herbivores - and physical deterrents. There are disadvantages attached to reliance of plants on deterrents. Their manufacture requires diversion of plant resources from other physiological processes. This may be influenced in dense swards where there is inter-plant competition for light. Also, deterrents to herbivory would not necessarily confer protection against fire (Stuart-Hill & Mentis,1982).

Plants escape defoliation in a number of ways, but in grasses the most important of these is the development of a low growth habit. Thirdly, plants may become adapted to defoliation by developing mechanisms to tolerate repeated use. Escape and tolerance strategies are effective against both grazing and burning (Stuart-Hill & Mentis, 1982).

The authors hypothesised that grasses adapted to heavy herbivore usage would have well-developed deterrents to grazing (and also possibly escape and tolerance mechanisms) while grasses adapted to fire and not grazing would have developed escape and tolerance mechanisms, but would have no deterrents. Stuart-Hill & Mentis (1982), however, suggested that these two extreme situations are unlikely and indicated that in South African grasslands, plants were probably selected for defoliation by fire and grazing.

A factor not considered by Stuart-Hill & Mentis (1982) is the adaptation of grasses to physical environment. The environmental constraints in semi-arid grassland (drought, extremes of temperature, shallow soils) are probably considerably different to those in humid grasslands (infertile soils, low temperatures, low sunlight). Plants in these situations would then also be selected for environmental adaptations.

The ensuing discussions will thus consider and contrast responses of *T. triandra* and *S. fimbriatus* to defoliation (deterrents, escape and tolerance) and to environmental constraints in the False Thornveld of the Eastern Cape.

9.2.1 Deterrents

1. **Chemical deterrents.** In Chapter 2 it was shown that *S. fimbriatus* and *T. triandra* are both highly acceptable to cattle at all times of the year, and even during winter after a full season's rest. The latter result is expected of palatable grasses in sweet grassveld. It can thus be inferred from the results that the two species under consideration have not developed any noticeable specific or general chemical deterrents to grazing. Although *T. triandra* was not quite as palatable during summer as at other times of the year, this was a result of the presence of flowering culms and not chemical substances.

2. **Stubble barrier.** Vegetative *S. fimbriatus* tillers have a considerably greater stem/leaf mass ratio than those of *T. triandra* (Figure 3.2), and tufts of the former species contain a significantly higher proportion of stubble mass than the latter. Despite the fact that *T. triandra* produces more herbage per unit area and has higher tiller densities than *S. fimbriatus* there was no significant difference in the stubble mass per unit area between species (Figure 8.21). If it is assumed that leaf blades are more readily grazed than stems or stubble, then the species *S. fimbriatus* partitions a greater portion of its structural substrate into unpalatable material than *T. triandra*, the effect being that herbivores are deterred from grazing a greater portion of the former species. Of further note is the fact that Stuart-Hill & Mentis (1982) suggested that one of the disadvantages of the reliance of plants on deterrents is that their manufacture requires a diversion of plant reserves from essential physiological processes. This seems applicable to the two species *S. fimbriatus* and *T. triandra*. *Sporobolus fimbriatus* directs the major portion of its above-ground substrate into

unpalatable (and photosynthetically inactive) stubble, while *T. triandra* apportions most of its above-ground substrate into the manufacture of photosynthetically active leaf blades. The observed response is that the species *T. triandra* is more productive at the tiller, tuft and sward level (Figures 3.8; 2.3 & 7.2 respectively).

The inference from the existence of a "stubble barrier" in the species *S. fimbriatus* is that this species is better adapted to withstand herbivory than *T. triandra*, but not necessarily to make better use of incoming radiation.

9.2.2 Escape

1. **Forage availability and height.** In Chapter 2 it was shown that the above-ground mass per unit area (Tables 2.6 & 2.7) and mean height of the tallest leaves (Tables 2.4 & 2.5) of tufts of *T. triandra* are considerably greater than those of *S. fimbriatus*. Thus where basal cover of the two species is equal, grazing animals would have a greater probability of encountering *T. triandra* herbage than that of *S. fimbriatus*. If one adds to this the fact that animals prefer to graze the taller of two species (Section 2.2.2.3) then in terms of forage availability and height *S. fimbriatus* tufts have a greater chance of escaping herbivory than those of *T. triandra*.

2. **Shoot apex elevation.** In the absence of defoliation, elevated shoot apices are presumably to the advantage of plants in view of competition for light. Consequently, the fact that grasses usually maintain their apices close, or relatively close to the soil surface, except for a short period when they flower (Langer, 1972), is a clear indication of the adaptation of these plants to defoliation (Stuart-Hill & Mentis, 1982). When grasses flower, they elevate their apices rapidly, presumably in the interests of pollination and seed dispersal. The species *S. fimbriatus* maintains its shoot apices near the soil surface except just before flowering when apex elevation is rapid (Section 3.3.3), thus following the expected trend of grasses whose growing points

are adapted to escaping from defoliation. In contrast, in unutilised and moist situations, *T. triandra* tillers partially elevated their apices to a height of about 10cm while still in the vegetative phase and the apices remained elevated for a period of about six months (Section 3.3.3). Defoliation and moisture stress suppressed vegetative shoot apex elevation. The degree of this suppression increased with increasing intensity (Figure 8.15) and frequency (Figure 8.23) of defoliation. Stuart-Hill & Mentis (1982) suggested that such suppression of shoot apex elevation could be a function of both diminished plant vigour as a result of defoliation, and the fact that the apices of defoliated tillers could receive more intense radiation which could stunt internodal elongation. In Chapter 8, however, it was suggested that the vigour of tillers defoliated two or three times per year above shoot apex height is not impaired. On these treatments, the height of vegetative shoot apex elevation of *T. triandra* tillers was still considerably less than that in a totally unutilised situation.

The capability of *T. triandra* tillers to elevate their apices while still vegetative during the growing season and the fact that this elevation is suppressed even by lenient defoliation, suggests that the species is adapted to both situations where no defoliation and some defoliation during the growing season takes place. In contrast, *S. fimbriatus* tillers maintain their growing points near the soil surface until immediately before flowering whether defoliated or not. This suggests that the latter species is adapted to situations where defoliation during the growing season is highly probable.

Defoliation under natural conditions would result from either herbivory or fire. Veld fires have been a feature of South African grasslands since prehistoric times (Scott 1970), and Roux (1969) stated that burning of veld in winter was a common occurrence long before settled agriculture. Trollope (1983) suggested that the season of burning under the natural fire regime would have occurred most frequently at the end of the dry season (winter) just prior to the first spring rains.

It is thus reasonable to contend that in the pristine state, South African grasslands were subjected to fairly regular defoliation by fire, usually during the dormant season. Defoliation during the growing season would have been chiefly in the form of herbivory. Species adapted to defoliation during the growing season would thus be adapted to herbivory, while grass species not adapted to defoliation during the growing season would more likely have developed under a fire regime. The shoot apex ontogeny of *S fimbriatus* suggests that this species is well-adapted to year-long herbivory. Shoot apex ontogeny of *T. triandra*, however, suggests that this species is adapted both to defoliation (herbivory) and no defoliation during the growing season.

3. Leaf emergence and expansion. Leaf ontogeny of grasses suggests that most of the graminae are exceptionally well adapted to defoliation. Leaves are initiated from leaf primordia occurring alternately along the opposite flanks of the apical dome, which is itself encased within the basal portions of leaf sheaths and situated near the soil surface for most of the life of the tiller (Langer,1972). The rate of emergence of these leaves is genetically and environmentally controlled and is not directly affected by defoliation (Anslow 1966). The process of leaf initiation and emergence on *T. triandra* and *S. fimbriatus* tillers appears to follow this pattern (Sections 3.3.5 & 8.3.1.4) suggesting that these species are well-adapted to escaping defoliation (be it in the form of herbivory or fire).

Leaves themselves are well adapted to escaping defoliation since meristematic areas of expanding leaves are protected within the covering of leaf sheaths, and thus can continue expanding after defoliation. This process was observed in both species *T. triandra* and *S. fimbriatus* and is illustarated in Figure 8.10.

9.2.3 Tolerance

1. Timing and rate of culm elongation. When tillers of both *T. triandra* and *S. fimbriatus* elongate their culms in order to flower, the rate of elevation of individual apices is rapid, approximately two to three weeks (Section 3.3.3.2). However, within tiller populations culm elongation and flowering does not occur simultaneously, but sporadically over a period of about three months. This suggests that both species are adapted to tolerating defoliation during the season of flowering - culm elongation per tiller is rapid but spread over a long period in the whole sward, ensuring that at least some shoot apices escape decapitation at critical times in order that they can elevate and flower.

Since culm elongation of *T. triandra* and *S. fimbriatus* occurs during the growing season (spring and autumn respectively), the implication is that the spread in timing of individual apex elevation is an adaptation to herbivory. Fire would be most likely during the dormant season (Trollope, 1983), and, should it occur immediately before culm elongation, would in all likelihood be of an intensity that damages all shoot apices that are about to elevate and flower.

2. Stem : Leaf mass ratios. The fact that *S. fimbriatus* has a higher ratio of stem to leaf material than *T. triandra* has already been suggested as a deterrent to grazing in the former species. It follows from this that *S. fimbriatus* is better adapted to tolerating herbivory than *T. triandra* since a smaller portion of the plant is removed in the former species.

3. Lateral tillering. Lateral tillering allows some grasses to reproduce themselves vegetatively after removal of apical primordia and thus indicates their tolerance of defoliation (Stuart-Hill & Mentis, 1982). Both *T. triandra* and *S. fimbriatus* produce lateral tillers in an unutilised situation, but these are few in number and remain small while primary tillers are still actively growing (Section 3.3.7). The species *T. triandra* does produce an increased number of lateral tillers when unutilised primaries reach maturity, but the height of this lateral tillering is such that secondary tillers would not be able to establish their own root systems (Figure 3.3.2). The rate of lateral tillering of both species after defoliation during the early part of the growing season remains low , but defoliation promotes lateral tillering as primaries become more mature, particularly in the species *T. triandra* (Figures 8.5 & 8.6). Intensity of defoliation has little effect on lateral tillering except when applied to mature tillers of *T. triandra* during winter. At this time, intense defoliation promotes prolific tillering (Figure 8.6).

These results thus illustrate the tolerance of *T. triandra* and *S. fimbriatus* to defoliation through their ability to produce lateral tillers. In *T. triandra*, defoliation appears obligatory to the vegetative persistence of the species. In the absence of defoliation, aerial tillering takes place and tufts become moribund. However, in terms of its capacity to produce viable lateral tillers, the species seems best adapted to severe defoliation when tufts are mature during the dormant season. This treatment is what would occur under a natural fire regime (intense defoliaton during the dormant season). In the absence of fire occurring or at the end of winter, *T. triandra* tillers would elevate their apices and flower in spring, thus providing means for persistence through seedling germination.

In contrast to *T. triandra*, the height of lateral tillering of *S. fimbriatus* remains near the surface even when tufts are mature (Figure 3.3.2), and the capacity to produce lateral tillers is not as dependent on time of year or intensity of defoliation (Figures 8.5 & 8.6). *Sporobolus fimbriatus* is thus apparently adapted to reproducing itself vegetatively at all times of year and over any range of utilisation intensities. This would be well-suited to tolerating a system of year-long herbivory.

4. Growth patterns. Growth rates (AGR) of *T. triandra* tillers are maintained at a high level for a longer duration than those of *S. fimbriatus* tillers (Section 4.4). Meaned over all times of year, *T. triandra* tillers would achieve greater size after 12 months than those of *S. fimbriatus*, but up to six months there would be little difference between

species (Figure 4.14). Theoretically, if the AGR of *T. triandra* tillers is meaned over all times of year, greatest long-term production of above ground biomass would be achieved if successive individuals were replaced every 10-12 months. The equivalent period for *S. fimbriatus* tillers would be approximately 6 months (Figure 4.15). This suggests that *T. triandra* tillers are adapted to spending relatively long periods (up to 12 months) without defoliation, while *S. fimbriatus* tillers tolerate more frequent defoliation. Natural defoliation at more frequent intervals than once per year would most probably be in the form of herbivory, while defoliation as infrequent as once per year could well be in the form of fire. If this is so, then the growth patterns of *S. fimbriatus* tillers are well-suited to tolerating salient herbivory, while those of *T. triandra* are adapted to defoliation that would occur under a fire regime.

5. **Primary production.** Defoliation during the growing season has a negative effect on the mass of *T. triandra* tillers and tufts when compared with undefoliated tillers and tufts of the same age two months after clipping (Figures 8.1 & 8.7). However, if defoliated, the species produces most regrowth after lenient clipping (Figures 8.2 & 8.8). *Sporobolus fimbriatus* tillers and tufts show an opposite trend. Two months after defoliation, defoliated tillers and tufts often have greater mass than undefoliated individuals of the same age (Figures 8.1 & 8.7), and more regrowth takes place after severe than after lenient clipping (Figures 8.2 & 8.8). *Sporobolus fimbriatus*, in terms of its regrowth, thus appears to be tolerant of defoliation. The capacity of this species to withstand defoliation may in fact be so well developed that its net primary production may be higher under grazing than in its absence. This reaction has been observed in other African grasslands by Mc Naughton (1976; 1979). In contrast, *T. triandra* is apparently adversely affected by defoliation within one growing season, but the more lenient the defoliation, the less adverse its effect.

Of further note in this regard is the fact that after defoliation of *S. fimbriatus*, remaining green leaf material is apparently not used for photosynthesis, thus implying that the species is able to tolerate intense defoliation without affecting its subsequent regrowth. *Themeda triandra* makes use of what green leaf material remains after defoliation for subsequent photosynthesis and regrowth (Section 8.3.1.4), explaining why this species is adversely affected by severe defoliation.

The primary production of both *T. triandra* and *S. fimbriatus* is adversely affected by frequent defoliation (Figure 8.17), but *S. fimbriatus* is less adversely affected than *T. triandra*. The vigour of both species is apparently not affected by infrequent defoliation (Figures 8.19 & 8.20) and, in fact, the production of palatable material (leaves) may be enhanced in both species.

Thus, to conclude discussion on the primary productivity of the two species, it seems that both are to some extent adapted to defoliation. However, *S. fimbriatus* is more tolerant of severe and frequent defoliation than *T. triandra*. Tolerance to herbivory would imply that the primary production of species should be relatively unaffected by frequent (within-season) severe and moderate defoliation - a trend observed in *S. fimbriatus*. The growth response of *T. triandra* after within-season defoliation suggests that this species is less well adapted to herbivory than *S. fimbriatus*.

6. **Physiological efficiency.** Tillers of all ages of both *T. triandra* and *S. fimbriatus* are physiologically most efficient in spring/early summer (Figure 4.9A). Meaned over all times of year, the tillers are most efficient while still young (Figure 4.9B). At these times, tillers are likely to be most vulnerable to defoliation since a high proportion of their mass is both palatable and physiologically active. This is illustrated by the fact that both species are adversely affected by defoliation during spring when tillers are still young (Section 8.3.2.3), but *S. fimbriatus* less so than *T. triandra*. Herbivory in spring is likely to be relatively intense since grazing pressure would be high as a result of little herbage accumulation during winter. Tolerance of

spring defoliation is thus considered to be a positive reaction to herbivory. In view of *S. fimbriatus* being less sensitive to defoliation than *T. triandra* at this time, it is suggested that *S. fimbriatus* is better adapted to a regime of resident herbivores than the other species.

7. **Labile carbon reserves.** The ability of grasses to store assimilates and re-use them for regrowth after defoliation is cited by Stuart-Hill & Mentis (1982) as an adaptation to tolerate grazing. Both *T. triandra* and *S. fimbriatus* accumulate carbohydrates in their stem bases (Chapter 5). It can also be inferred from their response to frequent defoliation (Section 8.3.2), that these stored assimilates play a significant role in determining the rate of regrowth. These results emphasise the fact that both *T. triandra* and *S. fimbriatus* are adapted to tolerating some form of defoliation.

9.2.4 Environmental adaptations

1. **Tiller Longevity.** The minimum longevity of tillers of *T. triandra* (that do not senesce prematurely) is considerably longer than those of *S. fimbriatus* (Table 3.1). As longevity of plants increases, it can be inferred that they become adapted to more mesic environments (where favourable growth conditions are maintained for longer) than short-lived plants. The contrasting longevities of *T. triandra* and *S. fimbriatus* tillers are thus consistent with the suggestion of Roberts (1973) that *S. fimbriatus* occupies a niche in a lower stage in plant succession than *T. triandra* (in terms of classical Clementsian succession).

2. **Time of tiller emergence.** Spring initiated tillers potentially achieve greater size than those initiated at other times of the year, a result of the fact that these tillers can make use of a full growing season. *Themeda triandra* shows a strong tendency to produce lateral tillers in early spring, with (Figures 8.5 & 8.6) or without (Figure 3.32) defoliation. *Sporobolus fimbriatus* does not show this strong seasonal tendency in lateral tiller production. It is

thus contended that adaptation to environmental conditions has resulted in *T. triandra* developing a tendency to tiller in spring. In *S. fimbriatus*, other constraints have resulted in the species producing laterals at all times of the year. It is likely that year-long herbivory would select against tiller emergence in spring, since grazing pressure would be highest at this time as a result of low herbage availability. It can thus be inferred that *S. fimbriatus* is adapted to a situation where year-long herbivory is an overriding constraint, while *T. triandra* is adapted to situation where there is less herbivory, allowing the species to make full use of environmental conditions.

3. **Assimilation of sunlight energy.** The photosynthetic efficiency of *T. triandra* is strongly dependent on time of year (Figure 4.10). The NAR of *S. fimbriatus* is not affected by time of year, indicating that this species may be a more opportunistic assimilator of light energy than *T. triandra* photosynthesising whenever the environment/moisture/ grazing situation is favourable. In addition, *T. triandra* is better adapted to competing for incoming light by being able to elevate shoot apices while still in the vegetative condition. These results are again consistent with the suggestion that *S. fimbriatus* occupies a lower successional niche than *T. triandra*.

4. **Moisture use.** Insufficient moisture is an overriding constraint in semi-arid grassveld. Both *T. triandra* and *S. fimbriatus* are adapted to this by retaining green leaves in a semi-dormant state during periods of moisture stress except during severe drought when they senesce. Growth takes place in flushes after rain, and on average, there are probably no more than 40 to 50 days per year during which active leaf expansion takes place (Chapter 6).

However, where deep subsoil moisture is available, *T. triandra* is better able to tolerate drought than *S. fimbriatus* (Table 6.4; Adelaide). This is probably because *T. triandra* has more roots at lower soil depths than *S. fimbriatus* (Table 3.2). This confers greater stability (as defined in Chapter

6) on *T. triandra*, a property expected of a plant that occupies a higher successional niche.

5. **Response to drought.** During severe drought, both species experience extensive mortality (Table 6.4). After drought, the species are able to recover if protected from grazing. Grazing during the year after drought prevents *T. triandra* and *S. fimbriatus* from recovering to the pre-drought levels, and they are replaced by less productive and less palatable plants accompanied by decreased grazing capacity (Table 6.3). Under natural conditions, it is probable that large herbivores would also experience heavy mortality during severe drought. This would imply that the vegetation would be afforded an opportunity to recover during the period of low stocking pressures after drought. It is thus suggested that *T. triandra* and *S. fimbriatus* are adapted to periods of very light herbivory after severe drought. In pastoral agriculture, domestic herbivores are kept alive during severe drought by supplementary feeding, the cost of which is often subsidised by State aid schemes. After the drought breaks, the animals are usually returned to the veld as soon as there is sufficient feed available, thus delaying or even preventing the recovery of the key species.

Of particular interest in this regard is a comparison of effects of the 1982/83 drought on veld used for tribal pastoralism in the Ciskei with that on veld farmed in a cash economy system in adjacent parts of South Africa. The veld in the Ciskei was subjected to considerably more intense utilisation before and during the drought than on the adjacent South African farms. However, considerable mortality of livestock took place in the Ciskei during the drought, while livestock was kept alive with the assistence of drought relief schemes in South Africa. After the drought, recovery of the veld was conspicuous in much of the Ciskei, but slow and often accompanied by a considerable increase of forbs such as *Senecio pterophorus* in adjacent parts of South Africa. (Aucamp, 1984*b*).

9.3 Defoliation regimes to which *Themeda triandra* and *S. fimbriatus* are best adapted - an hypothesis.

Both *T. triandra* and *S. fimbriatus* possess many characteristics enabling them to survive defoliation. Defoliation appears to be obligatory for vegetative persistence of *T. triandra*, and emergence of potentially viable lateral tillers of the species is best stimulated by severe defoliation during the dormant season. In contrast, production of lateral tillers of *S. fimbriatus* is not as affected by time of year. *Sporobolus fimbriatus* is, however, better adapted to both frequent and intense defoliation during the growing season and has better developed physical deterrents to herbivory than *T. triandra*. It is therefore concluded that *T. triandra* is better adapted to fire during the dormant season than *S. fimbriatus*, while the latter is better adapted to year-long herbivory.

The following hypothesis is put forward: **T. triandra** ***is well-adapted to a situation of relatively frequent (inter-season) fire and no more than modest herbivory;*** **S. fimbriatus** ***is well adapted to a situation of heavy (within-season) herbivore usage, but infrequent fire*** .

This hypothesis is in keeping with the classification of *T. triandra* as a Decreaser species (Danckwerts, 1983) - one that is typically found in well-managed veld and decreases with under- and overgrazing. *Sporobolus fimbriatus* was classified as a modest Increaser II species (Danckwerts, 1983) - one that increases with moderate over-grazing. Other Increaser II species in the False Thornveld include *D. eriantha* and *E. chloromelas* that increase with heavy overgrazing (Danckwerts, 1983). These species have even better developed deterrents to grazing than *S. fimbriatus*. It is logical that species that are typically found in well-managed veld (Decreasers) should have poorly developed deterrents to grazing (although they could have well-developed escape and tolerance mechanisms). This is because these species decrease with increasing levels of herbivory. It follows that Decreaser species will be difficult to maintain under commercial pastoralism, and the tendency will be for species composition to move to one adapted to year-long herbivory - an abundance of Increaser II species.

It may well be that the long-term solution to commercial pastoralism is to replace the natural vegetation with artificially bred plants adapted to grazing, but without strongly developed deterrents. However, the grazing pressure under commercial pastoralism implies strong selection for deterrents (Stuart-Hill & Mentis, 1982) and the plant breeder's task is a daunting one.

In the absence of well-adapted artificial pastures, in semi-arid grassveld, it is necessary to make the best use of natural pasture while retaining sustainability of the resource. From the point of view of the pastoralist, the most desirable species composition is one that is both highly productive and acceptable to domestic herbivores, but at the same time it should be well-adapted to being grazed. As has been pointed out, this is an unlikely situation. Walker (1980) pointed out that stable high production comes with a cost, a decrease in the resilience of the ecosystem and an increased susceptibility to degradation by poor management. *Themeda triandra* fulfils the first two requirements of grasses desirable to pastoralists. It is generally the most productive and most palatable grass species of those studied in the False Thornveld (Chapter 2). It is, however, only modestly adapted to herbivory, although it is most suited to fire accompanied by long rests. In contrast, *S. fimbriatus* is less productive, but better adapted to herbivory. The stated objective in the introduction to this dissertation was to provide means towards improved livestock production off veld in the False Thornveld of the Eastern Cape. It is contended that maintenance and/or an increase in the proportion of *T. triandra* in the veld is a prerequisite towards achieving this objective. It is further suggested that in order to do this, defoliation strategies must at least periodically simulate what would happen under a regime of relatively frequent fire accompanied by no more than moderate herbivory. This can be implemented in practice by use of fire followed by resting, as suggested by Stuart-Hill & Mentis (1982). Alternatively, the treatment that would be applied in a fire regime could be simulated by critical herbivore management strategies. The latter alternative is more attractive to pastoralists in semi-arid grassveld since it precludes wastage of herbage through combustion.

The following section will thus suggest a defoliation strategy, using domestic herbivores, aimed at maintaining or increasing the proportion of *T. triandra* in the False Thornveld.

9.4 Towards improved veld utilisation in the False Thornveld of the Eastern Cape - a defoliation strategy.

9.4.1 Rotational resting

It has been inferred from the data that *T. triandra* is adapted to fire accompanied by lenient grazing. In addition, it was shown that meaned over all times of year, *T. triandra* tillers take about one year to reach maximum size. The production of the species is favoured by infrequent and lenient defoliation during the growing season, but some defoliation may be obligatory to its vegetative persistence. Lateral tillering was best stimulated by severe defoliation during winter.

It is thus suggested that a portion of the veld under a commercial pastoral enterprise should be rested for a full growing season on a rotational basis annually. The veld to be rested should be subjected to severe and uniform defoliation during the winter before the rest, and rested camps should be grazed during the spring after the full season's rest is complete.

The decision as to the proportion of veld to be rested each year is an arbitrary one, but the strategy of resting a third of the veld annually has proved to be a highly successful one on "Tukulu", a well-known conservation farm in the False Thornveld (Trollope 1984*b*). On this property, *T. triandra* is by far the most abundant species, and grazing capacity is high (Trollope 1984*b*), at least double the average for the veld type (Danckwerts & King, 1984).

It is stressed that the veld being rested should be subjected to uniform severe defoliation during the winter before the rest commences. The severity is necessary to stimulate lateral tillering, and the uniformity avoids ungrazed tufts becoming moribund and unpalatable at the end of the rest. In fact, the "severe graze" before the rest is the treatment that simulates fire. Fire could be used as an alternative to the "severe graze", but this would involve wasted herbage, and would also probably require an additional rest before the fire in order to attain a uniform burn. It is, however, conceded that fire is a possible management tool in sweet grassveld, particularly in view of the additional role it plays in controlling bush encroachment (Trollope, 1983).

Finally, it is appreciated that during the full season's rest, some forage will be lost through leaf decay and abscission (Chapter 3 & 7). It is, nevertheless, contended that this loss is more than compensated for by the role a resting programme plays in maintaining the condition of the veld. In addition, resting a third of the veld has the further advantage of buffering the effect of seasonal rainfall fluctuation. During a dry year, there is a reasonable probability of the previous year having been wet, and the third of the property that was rested during that year provides a "fodder bank" for the dry year.

9.4.2 Rotational grazing

Considerable attention has been given to the development of rotational grazing management systems in South Africa. Pioneer investigations by Scott (1948), Botha (1957) and Tidmarsh (1977) led to recommendation and application of conventional two, three and four camp systems. Subsequent publications by Acocks (1966); Pienaar (1968); Booysen

(1969); Booysen, Klug & York (1974); Howell (1976); Tainton, Booysen & Nash (1977) and Fourie, Redelinghuys & Opperman (1984) have suggested that more than four camps per group of animals are necessary.

The basic operator dependant variables in a rotational grazing system are season, frequency and intensity of grazing. These are manipulated by means of camp numbers, periods of occupation and periods of absence. It is not the intention of this discussion to consider the *pros* and *cons* of various rotational grazing systems, but rather to use the results reported in preceding chapters to construe a rotational grazing system aimed at maintaining the presence and promoting the productivity of *T. triandra* in those camps not receiving a full season's rest.

1. **Season of grazing.** In Chapter 8 it was shown that both *T. triandra* and *S. fimbriatus*, but particularly the former, are adversely affected by defoliation during spring. This problem can be partially overcome by commencing the grazing rotation during spring on those camps that have just completed a full season's rest. The herbage in these camps would consist of mature plants at this stage with low populations of young tillers. Commencing the grazing rotation with these camps would stimulate a new crop of vegetative tillers, while allowing undisturbed growth on the other camps, where presumably vegetative tillers have already emerged. A further advantage of commencing the spring rotation on previously rested camps is that forage availability in other camps at the end of winter is likely to be low.

After the spring period (September, October, November), the tillers in previously grazed camps will have been allowed time to establish, and the normal rotation could continue.

During autumn, and as winter approaches, those camps that are due to rest the following season would require severe defoliation, and the grazing rotation might have to be adjusted to ensure that this takes place. Achieving the "clean" defoliation of camps to be rested might even be at the expense of animal performance.

2. **Frequency of defoliation.** In Chapter 8, it was suggested that three cuts per year did not impair the vigour of *T. triandra* tufts within one season. Furthermore, in Chapter 3 it was suggested that periods of absence in sweet grassveld should be at least long enough for green leaves to accumulate to the point where the rate of leaf emergence is equal to the rate of leaf senescence, but they should also be short enough so that forage is not lost through abscission of the oldest leaves. It was concluded that under conditions of both no moisture stress and severe moisture stress, periods of absence of at least three months during the growing season are desirable. However, periods of absence between grazing should not be longer than about five months, since after this time forage would be lost through leaf decay.

In order to optimise the grazing rotation, it is necessary also to determine optimal periods of occupation in camps. These, together with periods of absence, allow the operator to calculate the number of camps required per group of animals.

Recent extension effort has been directed towards encouraging operators to keep periods of occupation short. The rationale behind this recommendation is that short periods of occupation avoid grazing of regrowth within a single grazing period. However, in Chapter 6 it was argued that if the duration of leaf expansion growth after a rain is less than a week, periods of occupation would have to be extremely short to allow the camps grazed during and after the rain to make use of this moisture for regrowth. It is suggested that a more judicious practice after rain is not to move animals, but rather to temporarily sacrifice the camp or camps where the animals were grazing at the commencement of the rain by keeping them there for the duration of expansion growth after rain. This would ensure the accumulation of forage on the maximum possible portion of a farm and the "sacrifice" camps could then be given special treatment after future rains.

This argument thus suggests that periods of occupation need not be "very" short (less than a week). The question is how long can periods of occupation be? Increasing periods of occupation (together with a fixed period of absence) would imply decreasing numbers of camps, and, consequently, an increasing proportion of the veld under occupation by animals at any one time. The basis of the preceding argument is that the maximum possible portion of a farm should be unoccupied after any particular rain in order to allow maximum possible forage accumulation. Booysen *et al.* (1974) showed that the advantage accrued (in terms of shorter periods of occupation and longer periods of absence) through increasing camp numbers becomes minimal at more than eight grazing camps per group of animals. Ninety-day periods of absence and eight grazing camps would give imply average periods of occupation of 13 days and 87,5% of the area of the grazing camps unoccupied at any one time. If one adds to this the third of the property undergoing its seasonal rest, then 92% of the entire property would be unoccupied at any one time. However, periods of occupation as short as 13 days are probably unnecessary. Average periods of occupation of two to three weeks and periods of absence of 90 days would require approximately six grazing camps per group of animals and if the rested camps are added, a total of nine camps per group of animals. Under such a system, 87% of the property would still be unoccupied at any one time. Regrowth only occurs for a short period after rain and it seems unlikely that periods of occupation of two to three weeks or even longer would be harmful to the veld under non-grazing conditions. When active growth is taking place, animals should in any event not be moved to the next camp on the basis of the argument in Chaper 6.

To conclude, the grazing rotation can thus probably be optimised by periods of absence of at least 90 days, but no longer than 150 days, and average periods of occupation of two to three weeks or longer. Such a system can readily be implemented in six grazing camps per group of animals if the proportion of veld rested for a full growing season is added to this, then nine camps per group of animals is the optimum in the False Thornveld.

It has been argued recently that considerably more than nine camps per group of animals are required. This is in order that periods of occupation can be extremely short (three to four days), allowing animals to repeatedly graze new forage and not be forced to graze lignified growth (Parsons, 1984). However, this argument is fallacious since stocking densities and thus grazing pressure will be considerably higher within such a system, thus if anything, forcing animals to graze more unpalatable material. The extent to which animals are forced to graze unpalatable material will be more dependent on stocking rate than on the management system applied.

3. **Intensity of defoliation.** From the adaptive responses of *T. triandra* (Section 9.2), it was suggested that the species is suited to infrequent intense defoliation in the ? during winter, and lenient defoliation during the growing season. Infrequent severe defoliation is catered for by intense grazing during winter every third year. Theoretically, during the normal grazing rotation, intensity of utilisation should be lenient. It is questionable, however, to what extent intensity of defoliation can be manipulated by animal management.

9.4.3 Defoliation strategies during and after drought

The defoliation strategies suggested apply to moist, normal and even moderately below normal rainfall conditions. However, periodic severe droughts are a feature of the False Thornveld and other semi-arid grassveld areas. During these times supplementary feeding of livestock is essential, and since this is a costly process, all but nucleus breeding and replacement stock should be sold. Remaining stock should be fed in pens and not on the veld. The latter practice results in trampling and soil disturbance, accompanied by invasion of weeds after drought has broken. Weed infestation after the 1982/83 drought was particularly conspicuous on farms (and camps in farms) where supplementary feeding had taken place on the veld (Aucamp 1984*b*).

Of greater significance than management during the drought, is management after the drought. Continued withdrawal of veld from grazing after severe drought is essential to allow veld rehabilitation (Chapter 6). This practice is expensive, and thus often avoided by pastoralists. State subsidisation schemes do, however, make provision for supplementary feeding until the veld has recovered after severe drought.

9.4.4 Conclusion

A strategy of rotational resting and rotational grazing has been suggested to provide a means towards improved sward utilisation in the False Thornveld of the Eastern Cape. The suggested strategy is aimed entirely at proper use of the species *T. triandra*, and does not consider whether it is compatible with acceptable levels of animal performance. Consequently, in Chapter 10, the compatibility of the suggested defoliation strategy with acceptable levels of animal performance will be tested. The results will be used in an attempt to determine an acceptable compromise between sward utilisation and animal performance.

CHAPTER 10

INFLUENCE OF DIMINISHING AVAILABILITY ON ANIMAL PERFORMANCE AND ON SWARD DEFOLIATION PATTERNS DURING PERIODS OF OCCUPATION

10.1 Introduction

The preceding chapters have resulted in a proposed defoliation strategy for the False Thornveld, assuming the objective of the pastoralist is commercial pastoralism. The question is whether the suggested defoliation strategy, inferred from studies on grass ontogeny, physiology and the results of clipping trials, is compatible with adequate animal performance? In this chapter the dynamics of herbage availability, animal performance and sward defoliation patterns are investigated. From this, the practicability of the suggested defoliation strategy will be assessed in an attempt to achieve a compromise between sward utilisation and animal performance. A brief review of the relation between herbage availability and animal performance is appropriate.

10.2 Effect of forage availability on animal performance - a brief review

The argument developed in this review deals specifically with rotational grazing systems, and it is assumed that sward growth is negligible relative to the rate of removal of herbage during periods of occupation.

A theoretical model was proposed by Jones (1971) to describe the rate of herbage disappearance with time during periods of occupation in rotational grazing systems. According to this model, the quantity of available herbage should decrease linearly with time while herbage is abundant. When animals start searching for feed, daily intake per head should diminish, and the rate of disappearance of herbage would deviate from linearity decreasing progressively with time.

Bransby & Tainton (1977) explained how such a relationship could be characterised using the disc pasture meter.

If the model of Jones (1971) holds in practice, it would allow a point in time to be identified during periods of occupation where animals stop performing at their maximum capabilities on the pasture under consideration. This would have useful application in grazing experimentation since, if treatment effects on pasture are to be measured in terms of livestock products, the level of utilisation must be more severe than that which just causes animal production to be depressed through a limitation on the amount of forage available.

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However, the model of Jones (1971) is based on the assumption that forage requirement of grazing animals during a period of occupation is constant, and that when forage is in free supply, intake is equal to requirement. These assumptions may, or may not be valid in certain specific pasture situations.

10.2.1 Regulation of intake

It is not the purpose of this investigation to undertake a detailed review of the mechanisms controlling feed intake by animals. However, since the rate of disappearance of herbage during a period of occupation by a specific number of animals will be dependent on daily intake per head, it is necessary to outline briefly the most important factors that are likely to influence the daily consumption of feed per head during a period of occupation.

The first factor influencing daily intake per head in a pasture situation is the quality (*intrinsic* characteristics) of the herbage on offer to animals. In the past, it was generally assumed that ruminants consumed more of feeds of high than of low nutritive value. However, comparatively recent work has suggested that a more accurate generalisation is that ruminants attempt to eat to constant energy intake, but that this can be achieved only with feeds of high nutritive value, containing greater than 2,2kcal metabolisable energy per g dry matter (kcal/MEg DM) (Ulyatt, 1973) (Figure 10.1). The author indicated that this level of nutritive value corresponded to a digestibility of approximately 65% to 70%. Ulyatt (1973) concluded that where the digestibility of feeds is less than 67%, resistance to digestion within the gastro-intestinal tract forms the basis for the control intake, causing intake per head to increase with increasing nutritive value up to this level. At digestibilities above 67%, intake is controlled by changes within the animal tissues, caused by the absorbed end products of digestion, and here daily intake per head decreases with increasing nutritive value in order to achieve constant energy intake.

Despite the generalised trend depicted in Figure 10.2, a number of workers (Milford & Minson, 1966; 1968; Raymond, 1969 and Thomson, 1971) have shown that the relation between intake and digestibility can differ markedly between pasture types. The argument developed in this review is, however, not dependent on a quantifiable general relation between intake and digestibility. While the principle is accepted that intake per head will increase with increasing nutritive value up to a critical level (Ncrit.), after which intake decreases with further increase in nutritive value, it is appreciated that the value of Ncrit. can vary between forage sources. Consequently, if forage quality should change during a period of occupation, daily forage requirement per head would not be constant, even if herbage were in free supply, thus refuting one of the assumptions of Jones (1971).

A second factor affecting intake is the quantity of herbage on offer to animals. If herbage is abundant, animals will attempt to graze a constant energy intake. As the quantity of herbage on offer becomes limiting, animals will start searching for feed, and daily intake per head will be restricted. The necessity of adequate herbage on offer was recognised as early as 1797 by James Anderson who stated: "as it would be necessary to allow fattening beasts always to have a full bite, it would not be proper to keep so many of these as would at any time eat one of these fields quite bare". Johnstone-Wallace & Kennedy (1944) reported that grazing cows required to be presented with at least 1120kg of pasture per ha (measured on a dry mass basis), of height approximately 10-15cm, for maximum daily intake to be achieved. Intake per head fell when pasture was shorter or less dense than this. Johnstone-Wallace & Kennedy (1944) found that restricted intake at levels of herbage availability below 1120kg per ha could not be obviated by increasing the area available to the animal. The authors concluded that grazing cows will attempt to gather about 15kg of dry material per day, but when forage availability drops below a critical value (1120kg per ha in the example cited by the authors), the task becomes an impossible one.

A third factor that may affect daily intake per head is competition between animals. Bransby & Tainton (1977) stated that in theory, for any set of grazing conditions, there exists a "critical level" of utilisation beyond which competition between animals results in a reduction in the daily consumption per head. Mentis & Tainton (1981), however, show that the "competitive factor" *per se* is of very minor importance.

For the purposes of this argument, intake per head during periods of occupation is thus considered to be controlled by changes in the quality and quantity of the herbage on offer to animals.

10.2.2 The relation between herbage availability and intake per head in sweet grassveld

Consider the situation where quality remains fairly constant during periods of occupation up to, or after the quantity of herbage on offer has become limiting. Here, intake per head should remain constant until a point in time (ti) is reached where quantity becomes limiting. Thereafter, intake is restricted and should drop sharply (Figure 10.2). The corresponding rate of depletion of herbage is expected to be linear with time, until the quantity of herbage on offer restricts intake (ti). Thereafter, the relationship should deviate from linearity (Figure 10.2).

Both relations in Figure 10.2 deviate from linearity when the quantity of herbage on offer becomes limiting. This event is expected to occur over a relatively short period of time when compared with the length of periods of occupation and with changes in the quality of herbage on offer. It is thus logical that the trends in Figure 10.2 should be described by two separate functions for the periods where quantity is abundant (to to ti) and where quantity is limiting (t>ti). Intake (I) would be constant with time (t) up to time ti:

$$I\ (to\ to\ ti) = C$$

where C is constant. Thereafter, intake could be described by a modified exponential function of the form:

$$I(t>ti) = k - abt$$

when k, a and b are constants.

When quantity is abundant (to to ti), the relation between herbage on offer (Y) and time (t) would be a linear function of the form:

$$Y(to\ to\ ti) = g - ht$$

where g and h are constants. After time ti herbage disappearance could be described by an exponential function of the form:

$$Y(t>yi) = ne-mt$$

where n and m are constants.

Time ti when herbage disappearance with time deviates from linearity (or where quantity of herbage on offer restricts intake) occurs at the point of intersection of the two functions describing the two phases of herbage disappearance with time.

The relationship between herbage on offer and time presented in Figure 10.2 is of the same form as that postulated by Jones (1971) who assumed that forage requirements of grazing animals remain constant, and that when forage is in free supply, intake is equal to requirement. These assumptions will hold only if the nutritive value of herbage during a period of occupation remains constant and at a level higher than Ncrit. However, the linear relationship between herbage on offer and time when forage is in free supply does not require that nutritive value be higher than Ncrit., but only that it remain constant during this period.

It is suggested that the trends depicted in Figure 10.2 are likely to hold on sweet grassveld where it is ***contended that the quality of feed is likely to remain fairly constant while forage is still abundant during periods of occupation.*** This hypyothesis might appear to be dubious, but is generated from research results in the sweet grassveld of the False Thornveld of the Eastern Province. Some of these results follow.

Aucamp (1980) used the Cr2 03 marking method to estimate daily intake of cattle over an 18 month period on a grazing experiment using two stocking rates in the False Thornveld of the Eastern Province. The mean daily intake per head was statistically higher ($P<0,01$) at the light than at the heavy stocking rate (14,6 and 12,3kg dry matter per animal per day respectively.) Over the same period, there was no statistical difference between the *in vitro* digestibility of herbage samples from fistulated steers on each of the stocking rates (52.2% and 51.8% respectively). This suggests that the observed difference in intake was a result of differences in the quantity, and not the quality of herbage on offer.

In the same veld type, Danckwerts & Trollope (1980) sequentially estimated herbage yield using the disc pasture meter during periods of occupation on three different species dominated swards that had been previously rested for a growing season. In each case, the data suggested two distinct phases of depletion of herbage with time: an initial phase where herbage disappeared rapidly and apparently linearly with time and a second phase towards the end of the period of occupation where herbage disappeared less rapidly.

Subsequently, Danckwerts (1981) repeated the procedure during periods of occupation on a considerable number of swards under a range of simulated rotational grazing systems. In most cases, two distinct phases of herbage disappearance were again observed. Only where the quantity of herbage on offer at the start of the grazing period was low (less than 1000kg per hectare as estimated with the disc meter), did the data not suggest two phases. Here, it was assumed that insufficient quantity of herbage on offer restricted intake per head even at the beginning of the period of occupation.

Danckwerts (1981) also indicated that the rate of disappearance of herbage during the phase of limited quantity was very nearly linear, and that there was little statistical justification in fitting an exponential function to the data during this phase. Consequently, linear functions were fitted to both the phases of abundant and limited quantity respectively. Fitting linear functions to both phases is particularly attractive since, if the functions describing the phases of abundant and limited quantity are of the form:

$$Y(to\ to\ ti) = g - ht,$$

and

$$Y(t>ti) = n - mt$$

respectively, then the point in time (ti) where insufficient quantity restricts intake and the rate of depletion or herbage deviates from linearity can simply be derived by:

$$ti = \frac{g - n}{h - i}$$

Fitting linear regressions to both phases of herbage disappearance described in Figure 10.2 implies that intake per head would not drop gradually after time ti as depicted in the figure. Instead, two linear regressions would imply an instantaneous drop in intake per head at time ti, after which intake per head would again be constant, but at a low value. In practice, no matter how short the period of time is over which forage on offer becomes limiting, the process of changing intake per head and herbage availability must be continuous ones. Fitting separate regressions to the phases of abundant and restricted intake is thus a simplification of a more complicated biological process. This would be in an attempt to identify a point where intake per head drops as a result of insufficient herbage availability as opposed to other factors such as changing forage quality. Assuming constant quality with diminishing herbage availability, time ti would represent the point in time where insufficient availability noticeably affects intake per head. Fitting linear regressions to both phases of herbage disappearance is thus rather a means of identifying ti than an accurate description of the rate of herbage disappearance with time.

In this chapter, the change in herbage quality during periods of occupation within a rotationally grazed system such as described in Chapter 9 is investigated in order to test the hypothesis illustrated in Figure 10.2. The results will also be related to corresponding sward utilisation patterns in an attempt to determine an acceptable compromise between veld utilisation and animal performance.

10.3 Procedure

The trial was undertaken on veld in both good and moderate condition in the False Thornveld of the Eastern Cape. The site in good condition was situated at Kroomie (about 20km east of Adelaide) and the site in moderate condition at the Adelaide Experimental Station. A general description of the sites has been given in Section 6.2.2 where the effect of the 1982/83 drought on the mortality of various species was assessed.

A single 4 ha plot was demarcated at each site during winter 1981. Plots were fairly intensely grazed during June/July 1981 so that nearly all tufts of key species had been defoliated. The sites had previously been managed within reasonably sophisticated rotational grazing systems, similar to that proposed in Chapter 9. Sites were characterised in terms of botanical composition and soil type.

The plots simulated individual camps within a rotational grazing system where a third of the area is rested annually and where the average periods of absence and occupation are about three months and two to three weeks respectively. The simulated grazing rotation began after winter 1981 and sites were first grazed approximately three months later. Plots were each subjected to three periods of occupation during the 1981/82 growing season. At Kroomie these were from 25 November to 4 December, 1981 (10 days) (summer); 23 February to 2 March, 1982 (8 days) (autumn); and 13 to 25 July, 1982 (13 days) (winter). At Adelaide they were from 5 to 11 December, 1981 (7 days) (summer); 3 to 10 March, 1982 (8 days) (autumn); and 27 July to 2 August 1982 (7 days) (winter). For practical purposes, periods of occupation were shorter than would occur in the suggested rotational grazing system, and to achieve the same level of utilisation, higher stocking densities were used. This will be borne in mind when discussing the results. Also, the period of absence between the second and third periods of occupation was longer than three months. This period extended into winter 1982 and thus would probably not have affected the dynamics of leaf emergence. Furthermore, it was considerably less than 150 days, after which forage loss through decay is expected to take place. Utilisation intensity at the end of the first two periods of occupation was reasonably lenient since plots were supposed to simulate camps during normal rotational grazing. However, the winter treatment simulated that in a camp entering a full season's rest, and animals were forced to utilise the sward very severely.

Swards were always grazed by cattle of the *indicus* type, and these included a group of oesophageal fistulated steers and filler animals, the number of which were set so that periods of occupation would not exceed two weeks. All animals were weighed before and after each period of occupation.

The fistulated steers were used to collect herbage samples at dawn each day during periods of occupation. These steers were fistulated according to the procedure described by Chapman & Hamilton (1962). Six steers were originally fistulated. The mean mass of the fistulated steers was 344kg, 401kg and 420kg during the three respective periods of occupation in the 1981/82 season and 445kg during winter 1983. An attempt was made to collect a minimum of four herbage samples each day. Fistula samples were individually dried at 800C until they reached constant mass. Samples were then individually analysed for percentage digestibility at the Glen Agricultural College Laboratories using the conventional *in vitro* technique described by Engels & Van der Merwe (1967). The true percentage digestibility of organic matter was interpolated from the regression relationship between *in vitro* and *in vivo* digestibility, developed from a range of standards by Engels, De Waal, Biel & Malan (1981). The authors found a close relationship between *in vitro* and *in vivo* digestibility. It is, however, appreciated that differences in pasture type could result in error in the predicted absolute value, but this error is likely to be consistent, thus not affecting relative values. All digestibility analyses were replicated twice and a mean value derived for each sample.

In addition to digestibility determinations, all fistula herbage samples were analysed for crude protein content, while those obtained from periods of occupation during winter 1983 were also analysed for phosphorus (P) and potassium (K) content.

Herbage disappearance was monitored each day using the standard disc pasture meter described by Bransby & Tainton (1977), and the procedure followed was that described by Danckwerts & Trollope (1980), but further refined by Danckwerts (1981).

Sward utilisation patterns were monitored from individually marked tufts. Thirty tufts of each of the five most abundant species at Adelaide and the four most abundant species at Kroomie (these are already listed in Table 6.4) were permanently marked at the beginning of each period of occupation. The tufts were marked so that they could be returned to in the same order at successive sampling dates. When any marked tuft had been grazed, the bite height was recorded and the ends of the "bitten" leaves were marked with a dye in organic solvent (typists' correcting fluid). This enabled subsequent regrazing of partially grazed tufts to be recorded. The number of marked individuals of each species regrazed once, twice, or more than two times during a period of occupation was calculated on a daily basis. It had been established in a separate investigation the previous season that the dye itself had no effect on animal preference.

10.4 Results and Discussion

10.4.1 Species composition, soil and rainfall

The species composition of the two sites before the 1982/83 drought is listed in Table 6.3, and is discussed in Section 6.3.2. The soil at both sites was of the *Glenrosa* form, with an effective rooting depth in excess of 50cm. However, the soil at Adelaide contained a large proportion of free boulders and the effect of these on water infiltration during drought is discussed in Section 6.3.2. The rainfall at Adelaide during the 1981/82 and 1982/83 seasons is presented in Table 3.1 (Site B). The total rainfall at Kroomie during the 1981/82 season was 413mm, approximately 30mm more than at Adelaide. The additional rainfall was recorded during February and April. Otherwise the rainfall distribution at the two sites during the 1981/82 season was practically identical. The rainfall patterns during the 1982/83 season were also virtually identical, and these are illustrated in Figure 6.10.

10.4.2 Forage quality

Forage quality was estimated from fistula samples collected each day during periods of occupation. These samples were collected using six oesophageal fistulated steers during the 1981/82 season. One of the steers died during 1983, and only five steers were used during periods of occupation in winter that year. An attempt was made to obtain at least four fistula samples at each sampling date. Herbage quality was monitored in terms of digestibility of organic matter and crude protein during the 1981/82 season. In winter 1983, these two parameters as well as the P and K content of herbage were recorded. Before considering the dynamics of forage quality within periods of occupation, between times of year and between sites, it is necessary to investigate any differences between the individual steers (replications) used to collect the herbage samples.

10.4.2.1 Differences between animals

The organic matter digestibility estimated from *in vitro* analyses of samples collected by individual fistulated steers during each period of occupation at Kroomie and Adelaide in the 1981/82 season is presented in Figure 10.3. Least significant differences and coefficients of variation are presented for each period of occupation. During autumn at Adelaide, and winter at Kroomie, there are no recorded values for steer numbers 2 and 3 respectively. The fistulae of these animals were inflamed at these times, and they were not used for sampling. The corresponding crude protein values collected by individual steers during each period of occupation at the two sites in the 1981/82 season are presented in Figure 10.4.

There was no significant difference in the digestibility of herbage selected between steers, despite low sampling variability as illustrated by small coefficients of variation (Figure 10.3). There was generally also no significant difference in the crude protein content of herbage selected by steers, although data variability was greater than that where digestibility was recorded (Figure 10.4). During autumn and winter at Adelaide, the difference between the highest and lowest crude protein values, recorded from samples of individual steers, were just significantly different ($P<0,05$). There were no other significant differences (Figure 10.4).

The organic matter digestibility of samples collected by individual fistulated steers at Kroomie and Adelaide during winter 1983 is presented in Figure 10.5, and the crude protein content of the same samples in Figure 10.6.

Again, there was little difference in the digestibility of samples between steers. At Adelaide, the digestibility of samples collected by steer number 1 was just higher ($P<0,05$) than that of samples collected by steer number 6 (Figure 10.5). There was no significant difference in the crude protein content of samples collected by different steers (Figure 10.6). In both these Figures (10.5 & 10.6), there are values listed for only five steers. Steer number 6 died during 1983.

From the results (Figure 10.3; 10.4; 10.5; & 10.6), it appears that there is little inherent difference in the quality of herbage grazed by animals of the same breed and class. It is thus considered acceptable to use samples collected by individual steers as replications for comparing the quality of herbage at different levels of forage availability within periods of occupation.

It is noted, however, that the quality of herbage consumed between different breeds and classes of animal may vary very considerably. The quality of herbage consumed by fistulated steers is, nevertheless, considered adequate to make relative comparisons between time within periods of occupation, between seasons and between sites.

10.4.2.2 Changes in herbage quality within periods of occupation

The mean digestibility of organic matter and crude protein content of forage samples collected at each sampling date during periods of occupation at Kroomie in the 1981/82 season is presented in Figure 10.7. Least significant differences represent those between sampling dates within periods of occupation. The corresponding data for periods of occupation at Adelaide during the 1981/82 season are presented in Figure 10.8.

The mean digestibility of organic matter and crude protein content of herbage samples collected by fistulated steers at each sampling date during winter 1983 at Kroomie and at Adelaide is presented in Figure 10.9. In all these figures (10.7; 10.8 & 10.9) time is expressed in animal unit grazing days per ha (GD/ha). These were calculated from the mean metabolic masses (Mass to the power 0,75) of each grazing animal used during each period of occupation. Expressing time in this way allows the different periods of occupation by animals of different mass both within and between sites to be expressed on a comparable scale.

There were no significant changes in the digestibility of herbage grazed by fistulated steers within any period of occupation both at Kroomie and at Adelaide (Figures 10.7; 10.8 & 10.9). The biological significance of this result is emphasised by the low coefficients of variation of digestibility values recorded within periods of occupation (no more than 6%).

Crude protein content of samples also changed little during periods of occupation. Only during the summer period of occupation at Kroomie during the 1981/82 season (Figure 10.7) and at the same site in winter 1983 (Figure 10.9) were any significant differences in crude protein content between sample dates observed. During summer 1981/82 at Kroomie (Figure 10.7), the crude protein value of herbage at the first sampling date was just significantly higher than the lowest recorded value ($P<0,05$). However, the highest recorded value was not significantly higher than the rest of values other than the lowest, and the data did not show a trend to decrease as the period of occupation progressed. During winter 1983 at the same site (Figure 10.9) the two highest values were significantly higher than the lowest ($P<0,05$). Again, however, there was no trend for the data to decrease in value as the period of occupation progressed, and mean crude protein content of samples at the end of the period of occupation were as high as those at the beginning.

It is thus concluded that the quality of forage consumed by animals changed little within periods of occupation. This trend was observed within periods of occupation of up to two weeks, on rested and on rotationally grazed veld, and veld in good and moderate condition. In addition, quality of intake did not change within periods of occuption despite very severe grazing during winter periods of occupation. The hypothesis that the quality of forage consumed is likely to remain fairly constant while forage is abundant during periods of occupation in sweet grassveld has not been refuted, and has withstood fairly rigorous testing in the False Thornveld of the Eastern Cape. Quality did not change even after quantity had become severely limiting during winter periods of occupation. The trends suggested in Figure 10.2 are thus likely to be applicable in the False Thornveld provided periods of occupation are short enough that the rate of forage removal is very much greater than the rate of herbage regrowth.

10.4.2.3 Changes in herbage quality between seasons

The mean organic matter digestibility of fistula samples collected during each period of occupation (summer, autumn and winter) of the 1981/82 season and in winter 1983 at Kroomie and Adelaide are presented in Figure 10.10A. Least significant differences represent those between periods of occupation within sites. The corresponding crude protein content of samples is presented in Figure 10.10B.

Digestibility of herbage at Kroomie and at Adelaide dropped significantly (P<0,01) at each successive period of occupation during the 1981/82 season. Digestibility after a full season's rest (winter 1983) was significantly lower than digestibility during winter after a season of normal rotational grazing (winter 1982) at Adelaide (P<0,01), but not at Kroomie. The magnitude of the drop in herbage digestibility was, however, not large: 62,5% in early summer to 56,2% in winter at Kroomie, and 64,2% in early summer to 57,2% in winter at Adelaide during the 1981/82 season. The digestibility after a full season's rest was 54,5% and 52,5% at Kroomie and Adelaide respectively. Despite the relatively small change in digestibility as the season progressed, it is concluded that this change is biologically meaningful since the same trend was observed at both sites.

In contrast to digestibility, crude protein did not drop as the season progressed (Figure 10.10B). Crude protein content during autumn 1982 at Kroomie and winter 1982 at Adelaide was significantly higher (P<0,05) than the crude protein content of herbage during all other periods of occupation at the two respective sites. Within sites, there was no significant difference in crude protein content of herbage between all other periods of occupation. It is thus concluded that crude protein content of herbage remains relatively constant as the season progresses, or if veld is rested for a whole season. Crude protein content during winter certainly appears to be no lower than that during early summer.

It can thus be inferred from Figure 10.10 that the ratio between digestible organic matter and crude protein content changed as the season (1981/82) progressed. This can also be seen in Figures 10.7 and 10.8 where the scales on which daily digestibility and crude protein values are plotted remain constant for each period of occupation. Organic matter digestibility diminished relative to crude protein content of samples with each successive period of occupation in both these figures.

Reference to tables of feeding standards (Kearl 1982) shows that the quality of herbage consumed during the 1981/82 season was sufficient for growing steers 350 to 400kg in mass (similar to those used for sampling) to gain at least 0,75kg per day without supplementation. This is, of course, provided animals are offered sufficient forage to consume the required amount of herbage (8,4kg dry material per day). Aucamp, Venter & Barnard (1981) measured animal performance within a practical management system in the veld type, and recorded mass gains of growing steers in excess of 1,0 kg per day. What is illuminating, however, is the fact that digestibility values recorded in the early part of the growing season (Figure 10.10) were high, in excess of the levels laid down by Kearl (1982) for growing steers to gain 0,75kg per day. If winter digestibilities are high enough to achieve this level of animal performance, (and the results of Aucamp *et al.* (1981) suggest that they are) then there is a surplus of digestible energy in the herbage during the early part of the season. At the risk of encroaching on the territory of the animal nutritionist, this surplus may explain why animals in the False Thornveld often become extremely fat, even when still in the actively growing stage. Furthermore, these results (Figure 10.10) provide the basis for investigation into the possibility of protein (or nitrogen) supplementation not during winter (as is the common practice in sourveld), but during the early part of the growing season. This could perhaps allow growing and possibly lactating animals to make better use of the high digestible energy diets offered to them at this time of the year. The preceding discussion is obviously based on the assumption that insufficient herbage availability does not limit daily intake per head.

10.4.2.4 Herbage quality between sites

The mean organic matter digestibility and crude protein content of fistula samples collected at Kroomie and at Adelaide during the 1981/82 season and during winter 1983 are presented in Figure 10.11. Least significant differences are those between sites, calculated separately for each year. Digestibility was significantly higher ($P<0,05$) at Adelaide than at Kroomie during the season of simulated rotational grazing (1981/82). This trend was reversed in winter 1983 after a full season's rest ($P<0,05$). These differences were, however, small, no more than 2% between sites. Crude protein content of forage consumed at Kroomie was significantly lower than that at Adelaide during both seasons ($P<0,01$). The reasons for this are not clear, but may be associated with soil fertility. It is not necessarily true that veld in good condition (Kroomie) is generally likely to be of lower quality (and protein content in particular) than veld in moderate (Adelaide) or poor condition.

10.4.2.5 Phosphorus and potassium

The mean P and K content of fistula samples collected at Kroomie and Adelaide during winter 1983 is presented in Figure 10.12. Least significant differences are those between sites in terms of each of the two respective minerals. There was no significant difference in the amount of P in herbage grazed by the animals, but samples at Adelaide contained considerably more K than those at Kroomie ($P<0,01$). Zeeman (1984) has pointed out that K analyses from fistula samples are not particularly reliable since saliva contains a fairly high proportion of K, thus confounding the results. The P content of the samples are, however, of particular interest. Year-round feeding of licks containing a mixture of salt and bonemeal, mainly as a source of P, is a fairly common procedure in the False Thornveld, particularly amongst more advanced farmers. The recorded values of P in veld rested for a whole growing season, and having experienced the desiccating effects of a severe dought were approximately 1,5% at the two sites. This is considerably higher than the requirements of growing and lactating cattle (0,2% to 0,5%) specified in tables of feeding standards by Kearl (1981). The necessity of providing salt/bonemeal licks in the False Thornveld is therefore questioned.

10.4.3 The rate of herbage disappearance during periods of occupation

From the results in Section 10.4.2.1, it was concluded that herbage quality changes very little during periods of occupation of two weeks, even when swards are grazed very severely. On this basis, it is argued that herbage should disappear linearly, or very nearly linearly, with time while forage is in free supply. Moreover, a deviation in this linear relationship will imply that daily intake per head has dropped. Since forage quality remains constant during periods of occupation, the point in time where this deviation occurs corresponds to the time during the grazing period when insufficient forage availability restricts intake per head.

The relations between herbage availability and time during periods of occupation at Kroomie during the 1981/82 season are presented in Figure 10.13, at Adelaide during the 1981/82 season in Figure 10.4, and both sites during winter 1983 in Figure 10.15. Time is expressed in animal unit grazing days per ha (GD/ha) calculated from the metabolic mass of each steer. By this means the different periods of occupation by animals of different mass can be expressed on a comparable scale.

During the first two periods of occupation at Kroomie in the 1981/82 season (Figure 10.13), the sward was leniently grazed and animals were removed before deviation in linearity could be observed in the rate of herbage disappearance with time. Here, single linear regressions were fitted to the primary data. During the third period of occupation, animals were forced to utilise the sward severely, and the primary data suggested a deviation from linearity in the rate of herbage disappearance with time. On the basis of the rationale outlined in Section 10.2.2, separate linear regressions were fitted to the periods of abundant and insufficient availability. The regressions were fitted to the data by the procedure described by Danckwerts (1981), and ti represents where the two regressions intersected (Figure 10.13). Time ti was thus considered as the point where insufficient forage availability restricted intake per head.

The plot at Adelaide was also leniently grazed during the first two periods of occupation of the 1981/82 season (Figure 10.14). Here too, animals were removed from the sward before a deviation from linearity could be observed in the rate of herbage disappearance with time. Single linear regressions were fitted to the primary data. During the third (winter) period of occupation, utilisation was more complete, and the primary data suggested a deviation in linearity in the rate of herbage disappearance with time. During this period, however, herbage availability before grazing was low - it has already been stated that less rain fell at Adelaide during Autumn 1982 than at Kroomie (Section 10.4.1). In addition, the stocking density was high, implying that herbage disappeared rapidly. Consequently, only three observations were made during the phase of herbage disappearance when forage was considered to be abundant. Despite this, separate linear regressions were fitted to the two phases of herbage disappearance. Owing to the paucity of data, the positioning of time ti (Figure 10.14) is probably not as precise as that during the third period of occupation at Kroomie (Figure 10.13).

It is noted that the estimated level of herbage availability when intake became restricted in winter 1982 was 1000kg to 1100kg per ha at both sites. This level corresponds fairly closely with that recorded by Johnstone-Wallace & Kennedy (1944) on cultivated pastures in the USA.

After a full season's rest during the 1982/83 season, both sites were subjected to very heavy utilisation during the winter (Figure 10.15). Two phases of herbage disappearance were identified from the primary data recorded during grazing periods at both sites. Linear regressions were once again fitted to each phase, and the time when intake became limited (ti) identified as the point where the lines intersected.

Despite a full season's rest herbage availability at the beginning of periods of occupation during winter 1983 was still low. This was a result of the 1982/83 drought, and herbage availability after resting for a normal season would be considerably higher. Danckwerts & Trollope (1980) and Danckwerts (1981) recorded herbage disappearance in veld rested for a whole growing season when rainfall was normal and above average. Here, herbage availability before grazing was considerably higher than that during winter 1982 (up to 3000kg per ha). The two distinct phases of herbage disappearance were, nevertheless, still observed .

Time ti (the point where insufficient availability restricts intake per head) occurred at a level of availability somewhat lower during winter 1983 than during winter 1982. This was probably a result of a lower mass of stubble being present during winter 1983, a result of the drought. Danckwerts (1981) found that the level of forage availability at ti varied considerably according to sward density, and was higher after a wet than a dry year.

It can be seen from the results (Figures 10.13; 10.14 & 10.15) that animals were forced to utilise swards very severely during winter periods of occupation. This is reflected by the very slow rate of herbage removal at the ends of periods of occupation. Despite this, forage quality was no lower at the ends of periods of occupation than at the beginning (Figures 10.7; 19.8 & 10.9) emphasising the fact that quality remains constant within periods of occupation in rotational grazing systems in the veld type.

It has been pointed out that no matter how short the period of time is over which forage on offer becomes limiting, the processes of changing intake per head and herbage availability must be continuous ones. Fitting separate linear regressions to the two phases of herbage disappearance identifies an instant in time (ti) within a continuously changing biological system. Thus, assuming constant quality, time ti represents a point during periods of occupation where insufficient availability noticeably restricts intake per head. In terms of animal production per head, when this point is reached during a period of occupation, animals should be moved to the next paddock. Danckwerts (1981) used the point ti during periods of occupation in simulated rotational grazing systems to estimate the grazing capacity of sweet grassveld. Danckwerts (1981) also conducted economic analyses of the relation between GD/ha and gain/ha, and showed that the most profitable number of GD/ha were not considerably different to those at ti. The most profitable number of GD/ha were in some instances higher than those recorded at ti. Furthermore, Danckwerts & King (1984) estimated the profitability of different veld condition types under rotational grazing systems stocked at a rate corresponding to the grazing capacity recorded by Danckwerts (1981). The authors concluded that profitability at this stocking rate (based on moving animals every time ti is reached) was considerably higher than that currently achieved by farmers in the False Thornveld.

It is thus suggested that within the rotational grazing system proposed in Chapter 9, from the point of view of adequate animal performance (and profitability) ***animals should be moved out of a camp and into the next when intake per head becomes noticeably restricted through insufficient availability.*** An exception to this, of course, is when significant rain has fallen during the period of occupation. Here animals should not be moved into a new camp until the cessation of leaf expansion growth, despite possible animal stress. The rationale behind this is explained in Chapter 6.

Derivation of the relations in Figures 10.13; 10.14 & 10.15 occurred during periods of occupation shorter than would occur within the rotational grazing system proposed in Chapter 9. Periods of occupation in the experimental plots at Kroomie and Adelaide ranged from one to two weeks, while two to three week periods of occupation were considered adequate in the suggested utilisation strategy. The periods of unrestricted grazing in the experimental plots were even shorter during the winter periods of occupation when animals were forced to graze swards severely. The short periods of occupation came about as a result of the high stocking densities. These were deliberately set in order to make the trial logistically possible. The mean stocking densities during periods of occupation on the experimental plots at Kroomie and Adelaide were 4,3 and 3,7 mature livestock unit equivalents (MLU) per ha. The actual stocking densities that would be applied within the proposed rotational grazing system (nine camps per group of animals with three rested each season) can be calculated if the overall stocking rate is known. Mean stocking rates equal to the mean grazing capacities of the veld before the 1982/83 drought are assumed (3,7 and 5,8 ha per MLU at Kroomie and Adelaide respectively; Table 6.5). These stocking rates would result in stocking densities of 2,5 MLU per ha and 1,6 MLU per ha at Kroomie and Adelaide, respectively, within a nine camp system. However, the expected trends in the rate of herbage disappearance are not likely to be affected by stocking densities (provided regrowth during the period of occupation is negligible). While stocking density would affect the rate at which herbage disappears, it is unlikely to change the overall trend, since the time scale could, in any event, be equated over all stocking densities by expressing it in animal unit grazing days per unit area. Of note in this regard is the fact that Mentis & Tainton (1981) showed that the competitive factor between animals is of minor importance in determining intake. Furthermore, Johnstone-Wallace & Kennedy (1944) showed that when insufficient availability per ha restricted intake, increasing the area available to cows did not affect the amount of forage consumed per head. Stocking density could well affect area selective grazing, but this was not investigated.

The question that now arises is whether moving animals into a new camp when insufficient availability restricts intake per head results in an acceptable level of sward utilisation. In order to do this, tuft defoliation patterns were monitored during all periods of occupation in the plots at Kroomie and Adelaide.

10.4.4 Tuft defoliation patterns during periods of occupation

The percentage of marked tufts grazed once, twice three or more times, and the total percentage of grazed tufts of each species during periods of occupation at Kroomie in the 1981/82 season are presented in Figures 10.16; 10.17 & 10.18. The data for the same site during the winter 1983 period of occupation are presented in Figure 10.19. The corresponding results for each period of occupation at Adelaide are presented in Figures 10.20; 10.21; 10.22 & 10.23. Superimposed on the figures are the mean daily bite heights for each species, and where relevant, the time ti where insufficient herbage availability was considered to noticeably restrict intake per head. The results are considered fairly representative of the swards as a whole since the marked species constituted about 90% of the composition at each site.

During the first and second periods of occupation at Kroomie and Adelaide in the 1981/82 season, animals were removed before intake became restricted (Figures 10.13 & 10.14). The percentage of plants of any species subjected to more than one bite was low (except *T. triandra* at Adelaide) (Figures 10.16; 10.17; 10.20 & 10.21). When swards were severely grazed (Figures 10.18; 10,19; 10.22 & 10.23) a fairly high proportion of plants were returned to by animals. Even then, only *T. triandra* and *S. fimbriatus* at Kroomie, and these two species together with *P. stapfianum* at Adelaide were regrazed in any meaningful proportion. By the ends of periods of occupation, the percentages of these species grazed more than once were sometimes as high or higher than the percentage of tufts of less preferred species subjected to any grazing. These results suggest that initially cattle will avoid partially grazed tufts within a species, but will return to partially grazed tufts of preferred species before attempting to graze all the less preferred species.

It is worth noting that it was qualitatively observed that when animals did return to regraze tufts within periods of occupation, they did not graze the same part of the tuft as was previously grazed. Thus, individual tillers were generally subjected to only a single defoliation during periods of occupation. This is further illustrated by the fact that there was no real tendency for bite heights within a species to decline as periods of occupation progressed (Figures 10.16; 10.17; 10.18; 10.19; 10.20; 10.21; 10.22 & 10.23).

It is thus suggested that when forage availability is relatively low (less than 2000kg per ha) as was the case in the experimental plots, tillers are unlikely to be grazed twice during periods of occupation of two weeks. This is provided no significant regrowth takes place during the grazing period, which could happen if good rains fall during the period of occupation. When this happens, however, rapid rotation will not avoid grazing of regrowth, but will spread it over more than one camp. The rationale for not moving animals into new camps while active growth is taking place is explained in Chapter 6. Where forage availability is high, as for example on veld rested during a wet year (and not during a drought as occurred in the 1982/83 season) or in sourveld situations, the grazing habits of animals may well change. Under these circumstances, individual tillers may be grazed more than once during periods of occupation. The observation that individual tillers are not regrazed within periods of occupation would explain why quality of intake does not change as the period of occupation progresses, assuming, of course, that all tillers are of constant quality.

It can be observed from the figures that bite height within species and periods of occupation changed little as the grazing period progressed. There were, however, fairly large differences in bite heights between species. Where bite height appeared to drop slightly as periods of occupation progressed, this was probably a result of animals being forced to graze smaller tillers in the sward. This is logical since in Chapter 2 it was suggested that animals show preference for taller tufts within a sward. In most species bite height was generally a little above the ligule region of tillers, with very little leaf blade material remaining per tiller after a single bite. Exceptions were *E. chloromelas* at Kroomie and *C. plurinodes* at Adelaide. Tillers of these two species were generally only lightly defoliated, a result of their unpalatability which was discussed in Chapter 2. The implication of the observed bite heights during periods of occupation is that, within an acceptable range of animal performance, intensity (height) of defoliation cannot be controlled by manipulating the length of the grazing period. Thus, although *T. triandra* tufts respond differently to different intensities of defoliation, this is probably not a management option within rotational grazing systems where forage availability is less than 2000kg per ha. Within the simulated grazing management system, the bite height of *T. triandra* tufts corresponded roughly with the moderate defoliation intensity applied in Chapter 8. The preceding argument again applies to a situation where herbage availability is relatively low. Where availability is high, such as on rested veld (after a normal season) or in sourveld, the initial bite may not remove all leaf material. If this is the case, bite height could be controlled by manipulating the period of occupation.

A further observation from the results (Figures 10.16; 10.17; 10.18; 10.19; 10.20; 10.21; 10.22 & 10.23) is that at the ends of periods of occupation, a number of tufts remained ungrazed, and the majority had been grazed only once, even where utilisation intensities were very severe.

Thus, by the time ti is reached during grazing periods, a large proportion of ungrazed tillers will remain unutilised. The role of assimilate interdependence between tillers in partially grazed tufts in determining regrowth is thus fundamental to an understanding of sward response to grazing. This aspect was not considered in the investigations that have been reported in previous chapters, and therefore must be considered as a research priority in the False Thornveld.

The level of sward utilisation at time ti (optimal animal performance) seems reasonably compatible with the rotational grazing strategy (as opposed to rotational resting) suggested in Chapter 9 for optimal use of *T. triandra*. At time ti, most *T. triandra* tufts had been at least partially defoliated at a moderate intensity (Figures 10.18; 10.19; 10.22; 10.23). Although utilisation intensity was more severe than that suggested from clipping trials, this can in any event probably not be manipulated. In terms of tiller leaf dynamics (Chapter 3), partial defoliation of tufts will result in forage wastage through leaf decay, but this is likely under any sustained system of herbivory. Partial defoliation of tufts would, to some extent, be overcome by ensuring periodic severe defoliation (before the prescribed season's rest). It is noted that relatively few *T. triandra* tufts were grazed at Kroomie during early summer (Figure 10.16). This was a result of profuse flowering of the species at this time, but this did not prevent the tufts from being preferentially grazed during the next period of occupation.

Severe grazing of swards before rotational resting for an entire season does appear to be a problem with regard to animal performance. On swards that were severely grazed (Figures 10.13; 10.14 & 10.15), intake per head appeared to be very restricted by the end of periods of occupation and, despite this, utilisation of swards was not complete. Nevertheless, this management strategy is still considered essential for the maintenance of *T. triandra* (Chapter 9). The question the pastoralist must answer is whether he is prepared to concede this periodic stress to the animals in favour of the very much greater productivity of swards dominated by *T. triandra*? The results from previous chapters, and those of Danckwerts (1981), show that veld dominated by *T. triandra* is overwhelmingly more productive than veld even in moderate condition. The species *T. triandra* is also more preferred by animals, than other species during normal periods of occupation. The short period of animal stress involved in severe defoliation of camps to be rested thus seems a small price to pay for maintenance of a sward dominated by *T. triandra*. In addition, rotational resting has further advantages already discussed, including provision of a fodder bank. A strict rotational resting programme accompanied by intense grazing during winter before the rest has been applied for many years on the well-reputed conservation farm "Tukulu" situated in the False Thornveld of the Eastern Cape. Within this system, sward domination by the species *T. triandra* has been achieved (and maintained) and the enterprise has proved to be economically viable (Trollope 1984*b*).

The necessity for periodic complete utilisation of the veld makes fire a practicable management tool in the False Thornveld. Burning could be applied on camps about to be rested, provided there is adequate fuel for a complete burn. This could normally occur only in very good seasons. However, Trollope (1983) too, has stressed the role of fire as a management tool in the veld type.

The proposed rotational grazing and resting programme (Chapter 9) is thus generally considered compatible with adequate animal performance despite periodic stress to grazing animals. The problem facing the pastoralist is thus a practicable means of identifying time ti (intake per head starts to drop through insufficient availability) during periods of occupation. The pastoralist cannot be expected to monitor herbage disappearance by means of a disc meter during each period of occupation. In any event, this technique can be used to identify ti only if swards are grazed well beyond the point where intake per head is restricted, and by this time animals should have been moved to the next camp. In the experimental plots at Kroomie and Adelaide, time ti was generally reached when 80% to 90% of tufts of *T. triandra* had been at least partially grazed. At the same time, about 10% to 20% of the least preferred species (*E. chloromelas* at Kroomie; *C. plurinodis* at Adelaide) had been partially defoliated. An appropriate adage could thus be "***move animals when nearly all (80% to 90%) of the tufts of the most preferred species have been grazed and animals have commenced grazing (10% to 20%) the less preferred species***". This is merely a suggested "rule of thumb" and is not infallible. For instance, during early summer when *T. triandra* is profusely in flower, restricted intake is likely to be reached well before 80% of tufts are grazed (Figure 10.16).

In addition, the "indicator" less preferred species could become relatively palatable at certain times of the year. *Eragrostis chloromelas* was relatively palatable during autumn when leaves were green (Chapter 2), resulting in a reasonably high number of tufts of the species being grazed at this time (Figure 10.17).

Whether there is a dependable, quantitative and practicable means of pastoralists identifying the point in time when animals should be moved from one paddock to the next is questionable. In this context, the development of grazing pattern diagrams such as those used by Daines (1980) in the Dohne Sourveld could be of relevance.

10.5 Summary of results

i. There is little difference in the quality of herbage consumed by animals of the same breed and class in the False Thornveld.

ii. The quality of herbage (measured in terms of organic matter digestibility and crude protein content) consumed by animals changes negligibly within periods of occupation of two weeks.

iii. Forage digestibility drops as the season progresses from spring through to winter. In contrast, crude protein content of forage changes little with time of year.

iv The quality of forage consumed by animals was higher on veld in moderate than on veld in good condition in the investigation reported in this chapter. However, this is not necessarily considered to be a general rule.

v. The phosphorus content of herbage consumed by animals in the False Thornveld is higher than the requirement listed in feeding standards at all times of the year.

vi During periods of occupation, herbage apparently disappears linearly with time until insufficient availability restricts daily intake per head. Thereafter, the rate of herbage disappearance diminishes.

vii. From a point of view of animal production, they should be moved from one camp and into the next when intake per head becomes noticeably restricted through insufficient availability.

viii. Cattle tend initially to avoid partially grazed tufts within a species in favour of ungrazed plants, but will return to preferred species before attempting even partial grazing of all less preferred species.

ix. Grazed tillers, as opposed to tufts, are very rarely re-grazed within periods of occupation of two weeks.

x. Bite height within species remains fairly constant as periods of occupation progress and forage availability diminishes, provided initial herbage availability is less than 2000kg per ha.

xi. Intensity (height) of grazing can probably not be manipulated by varying the duration of periods of occupation in rotational grazing systems in the veld type.

xii. A large number of ungrazed tillers remain in the sward even after fairly severe defoliation.

xiii. The suggested rotational grazing and resting programme appears to be reasonably compatible with adequate animal performance. Animals will, however, have to undergo some stress when camps to be rested are severely utilised before the rest commences.

xiv. The adage "move animals when nearly all (80% to 90%) of the tufts of the most preferred species have been grazed, and animals have commenced grazing (10% t0 20%) the less preferred species" seems appropriate for use during the normal grazing rotation in the False Thornveld.

CHAPTER 11

TOWARDS IMPROVED LIVESTOCK PRODUCTION

The stated objective of the investigations reported in previous chapters was to provide quantitatively the means towards improved livestock production of sweet grassveld, with particular reference to the False Thornveld of the Eastern Cape. It is therefore appropriate to conclude by collating the information reported in Chapters 2 to 10 together with other available information, into a management model for sweet grassveld. To this end, an algorithm suggesting a means towards improved livestock production on a pastoral enterprise in the False Thornveld of the Eastern Cape is presented in Figure 11.1. The algorithm is constructed essentially from information gathered in the False Thornveld. Nevertheless, many of the suggested actions will also be applicable to other sweetveld areas.

Figure 11.1 is primarily a synthesis of the results reported in the preceding series of chapters together with those reported by Danckwerts, (1981). However, to provide a holistic management model, the work of other authors is incorporated where applicable. The objective of improved livestock production is within the context of sustained commercial pastoralism. This implies that the maximum sustainable financial benefit should be enjoyed at the present (or within the planning horizon of the individual pastoralist), but the potential of the environment should be retained in order to satisfy the needs of future generations.

A step by step explanation of Figure 11.1 follows:

1. **Identify and separate veld types.** Identification and separation of veld types has become virtually axiomatic as a prerequisite for proper veld management. Veld types in this context imply land types within a pastoral enterprise (as determined by veld condition, aspect, slope, soil etc.) as opposed to the broader use of the term "veld type" as defined by Acocks (1953). Veld types are separated in order that all

vegetation within a single unit (camp) should be as uniform as practicably possible in order to promote uniform veld utilisation (Edwards, 1981). There is surprisingly little quantitative data showing the ill-effects of not separating veld types. Perhaps this is because the area selective grazing that arises when veld types are not separated is obviously visible, avoiding the necessity for quantitisation. Matthews (1956) and Trollope (1984*b*) have indicated that in the False Thornveld, camps should be fenced with particular attention given to soil types, soil depth and aspect. However, veld types may also change according to changes in species composition.

2. **Conduct veld condition assessment.** Veld condition is the overriding factor determining grazing capacity within the False Thornveld of the Eastern Cape (Danckwerts, 1981). Thus, in order to plan what animals (type and number) to run on a property, veld condition assessment of each veld type is essential. Techniques for assessing veld condition in the veld type are currently in review, but the most successful procedure in the False Thornveld at present is that described by Danckwerts (1981).

3. **Are there browse species?** After conducting veld condition assessment, the number and size of browse species present should be determined.

4. **Calculate mean long-term browsing capacity.** If there are browse species present, the browsing capacity would be calculated. The most up-to-date procedure is that reported by Teague, Trollope & Aucamp (1981).

5. **Calculate mean long-term grazing capacity.** Regardless of the browsing capacity, the mean long-term grazing capacity of the property should be estimated. The mean grazing capacity (for commercial pastoralism) in the False Thornveld can be fairly precisely calculated using the model developed by Danckwerts (1981). This model predicts mean grazing capacity in terms of herbaceous species composition score, the density of woody species, and mean annual rainfall.

6. **Is property an economic unit?** Having calculated the browsing and grazing capacity of his property, the operator can estimate the number of animals he will carry in an average year. With this knowledge, it is possible to determine the theoretical profitability of the property as demonstrated by Danckwerts & King (1984). The pastoralist will then be in a position to determine whether the property is large enough to fulfil his personal financial requirements in an average year. (It is assumed that the owner will not attain his requirements from repeated borrowings, using his continually appreciating property as security - a possibility pointed out by Danckwerts & King (1984)).

7. **Does the operator wish to remain a rancher?** If the property is not adequate to fulfil the owner's financial requirements, the owner must decide whether he wishes to remain a pastoralist.

8. **Purchase more property.** Should the owner of a sub-economic unit wish to remain a rancher, it is obviously necessary to purchase more property, and to begin again from Step 1.

9. **Sell property.** If the owner does not wish (or cannot afford) to remain a rancher, it would be necessary to sell the property.

10. **Invest in an alternative business or retire.** Danckwerts & King (1984) pointed out that the value of pastoral property is extremely high, three to thirteen times higher than its value calculated on the basis of its productive potential. The original owner would thus probably have the option of undertaking a new (non-pastoral) enterprise or retiring and living off the interest earnings of his invested capital.

11. **Is browsing capacity sufficient.** If the owner's property is a large enough economic unit, the next step is for him to assess whether the browsing capacity of the farm is high enough to warrant introduction of an additional farming enterprise (goats).

12. Introduce goats and manage according to published principles. If the property possesses a significant browsing capacity, the operator would introduce goats as an additional farming enterprise. It is not the purpose of this investigation to discuss how this should be done, but Teague *et al.* (1981) provided a basic guideline as well as references of more detailed explanations of how to manage goats in the False Thornveld.

13. Calculate optimum stocking rate of breeding and replacement grazing animals. Regardless of whether the property has a significant browsing capacity or not, the operator must calculate the number of grazing animals that he should run. The grazing animals are assumed to be beef cattle, this being the generally recommended grazing enterprise in sweet grassveld. Sheep grazing is considered to be detrimental to sweet grassveld, but this aspect was not investigated and requires elucidation in the future.

It would be short-sighted to set stocking rate of breeding cows, unweaned calves, replacement animals and bulls at the mean grazing capacity of the veld. This would require culling of breeding stock (or poor animal performance and severe sward utilisation) in any year of below average rainfall. A suggested strategy is rather to set the stocking rate of breeding, unweaned and replacement animals at the grazing capacity one would expect during 75% of years. The procedure for calculating this stocking rate was undertaken by Holcraft & Trollope (1984) for a farm in the False Thornveld. It was found that the rainfall that can be expected in 75% of years in the veld type can be approximated by multiplying mean annual rainfall by a factor 0,85. This stocking rate of breeding and replacement animals would thus be calculated by using 0,85 of the mean annual rainfall in the model of Danckwerts (1981).

14. Determine minimum number of groups of animals. Once the owner is aware of the number of cows he can run on a property, he can determine the number of herds that he will require. These should be kept to the minimum practicable number in order to facilitate fewer camps on the property.

15. **Plan fences - approximately nine camps per group of animals.** In addition to fencing off veld types, the property should have sufficient camps to facilitate proper rotational grazing. It was suggested (Chapter 9; Page 256) that nine camps per group of animals is probably in the region of optimal. More camps (12 per group of animals) would also be acceptable, but very high camp numbers such as used in "short duration grazing" systems (20 or more per group of animals) are not recommended. In such systems, grazing pressures would become very high if periods of occupation were extended for the duration of leaf expansion growth after rain (Step 37).

16. **Are camps bigger than 50 ha?** Having planned the number of camps, it is now possible to calculate mean camp size. On a large property, despite multi-camp systems, it is possible that mean camp size could be in excess of 50ha. (On a 2000ha property with three groups of animals and nine camps per group, mean camp size would be about 75ha.)

17. **Area selective grazing is likely to occur.** Little quantitative information is available regarding the effect of camp size on area selective grazing. However, the qualitative statement that large camp size results in area selective grazing has often been made (including by Edwards, 1981). In the False Thornveld, area selective grazing was effectively controlled on the farm "Tukulu" where mean camp size was 26 ha (Trollope, 1984*b*). On this property, there were, however, a limited number of camps in excess of 40 ha in size, and here too, there was little evidence of area selective grazing. Thus, in the absence of better information, it is suggested that area selective grazing can be controlled in camps of 50ha or smaller, but that area selection is likely in camps larger than 50 ha.

18. **Make provision for more groups of animals.** If camp size is in excess of 50 ha, it would be necessary to run more than

the minimum number of groups of animals, and return to Step 15.

19. **Rest a third of camps for a full growing season.** A third of all camps must be set aside for a full growing season's rest each year on a rotational basis. The rationale for doing this is explained in Chapter 9 (Page 252).

20. **Ensure camps to be rested receive intense defoliation during winter before rest commences.** Again the rationale for this is set out in Chapter 8 and 9 (Page 201 and 253). The practice is considered necessary despite probable animal stress. Fire is an alternative during wet seasons.

21. **Calculate current optimum stocking rate in terms of prevailing moisture regime.** Danckwerts (1981) pointed out that grazing capacity varies considerably from year to year depending on rainfall. A procedure was suggested for calculating current optimum stocking rate in terms of rainfall over the past 12 months. The procedure is currently successfully in practice at the University of Fort Hare Research Farm (Trollope, 1984*a*).

22. **Is property currently overstocked?** Using the model of Danckwerts (1981), it is now possible to determine whether the current stocking rate is in excess of the optimum calculated on the basis of rainfall over the past 12 months.

23. **Sell non-breeding and non-replacement animals.** If the property is overstocked, the owner should then sell as many non-breeding and non-replacement animals as is necessary to equate the stocking rate with the optimum calculated on the basis of rainfall over the past 12 months.

24. **Is property still overstocked?** The situation may arise whereafter selling all non-breeding and non-replacement animals the stocking rate is still in excess of the current optimum. If not, the operator would proceed to Step 28.

25. **A severe drought is being experienced.** If, after selling all readily disposable animals, the property is still overstocked, then one of the 25% of years where rainfall is

below that which was used to calculate stocking rate of breeding animals (Step 13) is being experienced. The situation could be classified as one of severe drought.

26. **Pen feed or cull surplus breeding animals.** During a severe drought it would be necessary to pen feed (or cull) the number of breeding animals in excess of the current optimum stocking rate. It is essential that such supplementary feeding should take place in pens and not on the veld. Heavy infestation of weeds is commonly experienced after the drought, a result of soil disturbance through trampling, when supplementary feeding is undertaken on the veld. Jones (1983) provided a practicable procedure for farmers to calculate the size of the fodder bank they should maintain in the event of drought.

27. **Pen feed all animals for at least three months after drought has been broken.** After a very severe drought, it is essential that all animals be kept off the veld for as long as possible in order to allow it to recover. The necessity for doing this is illustrated in Chapter 6 (Table 6.3). After the veld has been given an opportunity to recover, the operator would return to Step 21 and calculate the optimum stocking rate.

28. **Is property currently understocked?** If property is not overstocked in terms of rainfall over the last 12 months (Step 22), the operator must assess whether stocking rate is below the optimum. If not he would proceed to Step 33.

29. **Keep non-replacement growing animals.** If the current stocking rate is below the optimum, the operator would be wise to keep growing non-replacement animals that would normally be sold in an attempt to equate his stocking rate to optimum.

30. **Is property still understocked.** The situation could arise where after keeping all surplus growing animals, the stocking rate is below the current optimum. If not, the operator would proceed to Step 33.

31. Unusually wet conditions are being experienced. If after keeping all surplus animals, the property is still understocked, then one could conclude that an extremely good season is being experienced.

32. Purchase additional growing animals, or burn veld if conditions are favourable. When extremely good conditions are being experienced, the operator has the opportunity of increasing his stocking rate by purchasing more animals which he can dispose of readily when conditions return to normal. Alternatively, the operator may wish to take the opportunity to burn surplus veld, provided conditions are favourable. The latter alternative is particularly relevant where there is a bush encroachment problem. Wet seasons would provide the opportunity for accumulation of fuel loads large enough to affect a top-kill of woody species as is explained by Trollope (1983).

33. Rotationally graze all non-resting camps beginning in spring with camps that have just received a full season's rest. Having set the correct stocking rate, animals should be rotationally grazed in non-resting camps according to the guidelines set out in Chapters 9 & 10 (Pages 253-257; 286-287).

34. Has it rained more than 25mm during period of occupation? In Chapter 6 (Pages 148-152) it was suggested that growth takes place for very short periods after rain and that animals should not be moved into an ungrazed camp while this growth is taking place. For practical purposes, a rain of 25mm is considered to cause significant growth to take place. If a rain of 25mm does not fall during the grazing period, the grazing rotation would continue as normal and the operator would proceed to Step 40.

35. Do not continue with grazing rotation for one week after rain. In the event of rain of 25mm or more falling, animals should not be moved to a new camp, thus allowing herbage to accumulate in the maximum possible portion of the property.

36. Is there sufficient herbage for tolerable levels of animal stress? The question the operator now needs to answer is whether there is sufficient herbage in the camp occupied at the time of the rain in order to sustain the animals, at least at tolerable levels of animal stress, for a period of a week after the rain has fallen.

37. Stay in current grazing camps for duration of one week after rain. Where there is sufficient forage, animals would be kept in the occupied camp until the cessation of leaf expansion growth (one week).

38. Supplementary feed, preferably in pens, until end of week. Where there is insufficient feed in the occupied camp to sustain the animals until growth ceases, then supplementary feeding becomes necessary. For reasons already given (Step 26), this should preferably take place in pens. Situations may arise where repeated rains make the period of active growth long and financial constraints may force the operator to move animals into new camps instead of supplementary feeding. Such repeated rains are most likely to occur in the autumn in the False Thornveld (Figure 6.10). If the operator is forced to move animals into new camps during active growth at this time, he should move them into camps due to receive a full year's rest the next season. These camps would in any event require intense defoliation before the end of winter (Step 20).

39. Continue with normal grazing rotation one week after cessation of rain. After cessation of leaf expansion growth, the operator should continue with the normal grazing rotation (Step 40). On the basis of the results in Chapter 6, the period would probably not exceed one week.

40. Move animals into next camp when intake per head drops. In Chapter 10 (Pages 280; 287) it was suggested that during the normal grazing rotation (assuming it has not rained more than 25mm), animals should be moved from one camp and into the next when intake per head drops, through insufficient forage availability. This point can possibily be identified in the field as the time when nearly all (80% to 90%) of the tufts of the most preferred species (usually *T. triandra*) have been at least partially grazed, while relatively few (10% to 20%) of tufts of the least preferred grasses have received any grazing.

41. Is period of absence less than 90 days? Within the suggested system, periods of absence should be 90 to 150 days (Chapter 9; Pages 255-257). The length of the period of absence thus provides an effective check of whether the property is over- or understocked.

42. Veld is overstocked. If the operator finds that within the grazing rotation animals return to the same camp within a period of 90 days, then there is not sufficient forage to sustain animals in camps for mean periods of two to three weeks and the property is overstocked. The operator must then return to Step 21 and re-assess his current optimum stocking rate.

43. Is period of absence greater than 150 days?

44. Veld is understocked. If periods of absence are longer than 150 days, it implies that there are insufficient animals to rotationally graze herbage in camps to the point where availability restricts intake and still return to previously grazed camps before forage is wasted through leaf decay. Under these circumstances, the property is understocked and the operator must re-assess his current stocking rate.

45. Repeat veld condition assessment every two to three years. In addition to the suggested management system, the operator should repeat veld condition assessment at regular intervals to monitor long-term changes, possibly through mismanagement.

46. Has veld condition changed? If veld condition has not changed the operator will continue with his normal management system (Step 19), although he might wish to modify this, if he had been anticipating veld improvement.

47. Have veld types changed? If veld condition has changed (improved or deteriorated), it is necessary for the operator to assess whether veld types, too, have changed. If there is no change in veld types, the operator would return to Step 3 and sequentially proceed along the algorithm as has been described. If change in veld condition has also resulted in change in veld types, the operator would then be required to revert to Step 1 and re-identify and separate veld types.

Figure 11.1 is intended to provide a simplistic management guide for the False Thornveld of the Eastern Cape and by extrapolation, also for other sweet grassveld types. As has been indicated in preceding chapters, there are still many questions unanswered with respect to optimal management and livestock production in sweet grassveld. The algorithm should thus be continually modified and updated as additional information becomes available.

In conclusion, three prerequisites are considered essential in achieving the goal of improved livestock production off sweet grassveld:

1. Stocking rates should be conservative and no higher than the grazing capacity (for commercial pastoralism) of the veld. This conclusion is largely a result of the work of Danckwerts (1981).

2. Rotational resting of a third of the veld for a full growing season each year.

3. Rotational grazing of non-rested veld within a multi-camp system. The basis for the rotation should be periods of absence of 90 to 150 days, and periods of occupation of two to three weeks.

Of particular note is that most of the proposed guidelines emanating from the research reported in this dissertation were intuitively applied on the renowned conservation farm "Tukulu" by Edgar Matthews and his son Ted Matthews (Matthews, 1956; Trollope 1984*b*). "Tukulu" has become synonymous with the concept of economically viable veld management and conservation in sweet grassveld (Trollope,1984*b*). The achievements on this property are evidence that the goal of improved livestock production off sweet grassveld is attainable.

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