ECOLOGICAL EFFECTS OF FIRE IN THE MONTANE GRASSLANDS OF NATAL

COLIN STUART EVERSON

Submitted in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Grassland Science
Faculty of Agriculture
University of Natal
Pietermaritzburg

December 1985

DECLARATION

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

C.S. Everson

The Author

ECOLOGICAL EFFECTS OF FIRE IN THE MONTANE GRASSLANDS OF NATAL

EVERSON, C.S., Ph.D. University of Natal, 1985.

Although controlled burning has been used to manage Highland Sourveld grasslands, little was known of its effects on the vegetation. This study examined the effects of past fire treatments on veld condition, species composition, dry matter production, quality and canopy recovery growth rates of these grasslands. Also, six techniques of estimating the species compostiion of grasslands were compared in order to decide on a standard technique for monitoring these grasslands. From this work it was concluded that the wheel point method is the most satisfactory.

Veld condition scores were significantly lower in grassland protected from fire than where veld had been burnt or burnt and grazed at regular intervals. Frequent defoliation was found to maintain the grassland composition largely unchanged over a period of 30 years. Individual species were, however, found to react strongly to defoliation frequency. Plant demographic studies were therefore carried out to explain this differential response to burning. Three Decreaser and two Increaser I species were studied.

In all species examined, recruitment of secondary tillers was stimulated by regular burning, each species being well adapted to a regular fire regime. Differential responses to burning were best explained by the combined effects of the different reproductive capacities and mortality rates of tillers of these species. A biennial spring burning regime

was shown to be most suitable for maintaining the most important grass species at their present levels of abundance.

Annual winter and biennial spring burning did not result in significant differences in dry matter production. Maximum net productivity was approximately 230 g/m^2 in both treatments, placing them amongst the more productive areas of Southern Africa.

Examination of canopy recovery growth rates showed that there is little difference in the percentage canopy cover at the end of the growing season when veld is burnt annually in winter or biennially in spring. However, differences in season of burn resulted in exposure to erosive forces at different times of the year.

The results of this investigation have highlighted the importance of regular burning during the dormant period in the montane grasslands of Natal.

TABLE OF CONTENTS

Page

Page

Page

Page

Page

CHAPTER 1

INTRODUCTION

1.1 Background to the study

In the Republic of South Africa, where at least two thirds of the area may be classified as arid or semi-arid, the need for conserving water is of national importance (Dyer, 1963). The only means by which these water resources can be conserved is by the judicial management of the plants which vegetate mountain catchment areas.

The Drakensberg mountains form the main catchment area of Natal and at present most of the area falls under the jurisdiction of the Department of the Environment Affairs. The major portion of this area is covered by grassland (Veld types Nos. 44 and 48; Acocks, 1953), the condition of which is maintained by a regular burning regime. Present management goals include: 1) the production of high quality water and preservation of the soil mantle, 2) the maintenance of faunal and floral species diversity within communities, and 3) the prevention of accelerated extinction of any component species (Bainbridge & Scott, 1981). Although prescribed burning is used to attain these goals there is little knowledge on the long term effects of burning at different times of the year and at different frequencies on species composition and floristic diversity. This has resulted in controversy over different burning regimes used by management in the past. For instance, Nanni (1969) suggested that an irregular fire regime would maintain species diversity, since no species or community would be favoured at the expense of others. Results from a burning experiment at Giant's Castle Game Reserve led Edwards (1969) to propose that biennial spring (September) or annual winter (August) burns be applied to maintain good vegetative cover and palatable species for grazing. Mentis, Meiklejohn & Scotcher (1974) suggested a biennial summer burning regime to encourage woody vegetation while maintaining good grass cover.

At the Cathedral Peak Forestry Research Station, different fire treatments have been applied to the grassland over the past 30 years. These experiments provided an ideal opportunity for examining the effects of various long term burning treatments on the grasslands within the research catchments. In addition to assessments of long term burning treatments, there has recently been greater emphasis on the need to assess the effect of current management practices (Mentis, 1984; Tiedman & Wiedland, 1983). This can be achieved by regularly monitoring community-composition, by which is meant "the maintenance of regular surveillance to test the null hypothesis of no change in predefined properties of a system which is vulnerable to impacts, the nature, timing and location of which are not necessarily known" (Mentis, 1984).

The Directorate of Forestry has recently proposed a monitoring programme in the Natal Drakensberg to determine the degree to which the objectives of management are being achieved. There are however a number of techniques which are used for monitoring species composition. During the course of this study the author was requested by management to determine which technique was most suitable for assessing changes in grassland species composition.

An experiment was therefore carried out to assess six different monitoring methods, including the one used in the present study. Standardization of the methods used will be the first step towards a sound monitoring programme.

1.2 Objectives of the study

The main objectives of the study were:

- to provide management with a technique suitable for assessing grassland species composition,
- to develop a prescribed burning policy which would meet the objectives of management.

1.3 Approach

In order to achieve the stated objectives a number of goals were developed to provide direction to the research and enable its progress to be assessed. The goals of the study were:

1) To compare six methods of measuring grassland species composition and determine the most suitable method for Highland Sourveld.
2) To investigate the effects of thirty years of burning on the species composition of the grassland catchments at Cathedral Peak.
3) To identify the most important grass species and study their population dynamics to understand their differential responses to burning.
4) To determine the effects of the long term burning treatments on the dry matter production and quality of Highland Sourveld.
5) To study the redevelopment of the grass canopy under different fire regimes in order to gauge their potential effects on water quality.

It was hoped that achievement of the above goals would provide a scientific basis for the formulation of a prescribed burning policy for the Natal

Drakensberg catchments.

Results pertaining to each of these goals are organized into discrete chapters. Thus the procedures, results, discussion and conclusions relating to each goal are all presented in their respective chapters. It was felt that this would facilitate easy reference to the various topics.

1.4 Historical background

Acocks (1953) suggested that the Highland Sourveld of the Drakensburg (between 1 350 m and 2 150 m) has replaced woody communities that originally extended over the Little Berg. Thus, protection of these fire sub-climax grasslands may result in the invasion of woody species. This is evident in a catchment at Cathedral Peak Forest Research Station which has been protected from fire for approximately 20 years. Other examples of suppression of fire favouring plant succession have been cited by West (1951), Killick (1963), Phillips (1965), Scott (1971) and Westfall, Everson & Everson (1983). However, it is unlikely that fire exclusion has been maintained over large tracts of the Little Berg, since this area has a long history of high frequency, natural firing (Watson, 1981). Manry (1983) reported that some of the highest lightening ground-strikes recorded in South Africa (> 9,0 strikes/km/annum) occur in the Drakensberg. In addition to these natural fires, human influence has served to increase the frequency of fires, particularly in the dry season (Watson, 1981). Although it is uncertain how long primitive man has modified the natural fire regime (Mentis, Meiklejohn & Scotcher, 1974), there is evidence of occupation by man in the Drakensberg approximately 7 000 years ago (Cable, Scott & Carter, 1980).

By the early eighteenth century regular veld burning was practised by the Bantu people to temporarily improve grazing and aid hunting (Bryant, 1929). More recently the European settlers of the early nineteenth century burned extensively in August to promote early growth for grazing (Nanni, 1969).

This use of fire had deleterious effects on water yield and prompted the proclamation of the Soil Conservation Act in 1946. This act virtually eliminated the use of fire to ensure efficient erosion control. Total protection of the Drakensberg grasslands was, however, impractical (Nanni, 1969), and Scott (1970) questioned the wisdom of this policy.

Throughout this period there was a growing recognition of need for planned management of mountain catchment areas. This led to a new burning policy in the Department of Forestry by which management units were burnt at two-yearly intervals after the first spring rains. However, in spite of an inherent comprehension of the role of burning as a management tool (Scott, 1951), little was known about the effects of fire on vegetation in montane grasslands, since the research work which led to this comprehension had largely been undertaken on lower altitude grasslands.

In 1936 Scott (1984), laid out veld burning experiments in the Highland Sourveld of Thabamhlope to determine the effect of various treatments on species composition, soil factors and run-off. This comprehensive study included treatments of protection from fire, grazing, mowing and burning in winter, spring and autumn at intervals of 1, 2 and 3 years. Although this study and others (Edwards, 1969; Dillon, 1979) have clarified some aspects of veld burning, much more research is required on this subject

CHAPTER 2

STUDY AREA

2.1 Introduction

The Drakensberg mountains, situated 160-240 km inland from the eastern seaboard of South Africa, form the edge of the great elevated inland plateau of South Africa. This range varies in altitude between 1 380 m and 3 350 m a.s.l. and creates a natural boundary between the province of Natal and Lesotho between latitudes 28°30'S and 30°30'S, and longitudes 28°30'E and 29°30'E (Fig. 2.1).

The great uplifting which took place in this area during the late pliocene accelerated the erosion cycle, particularly of the rivers draining eastwards. This resulted in the formation of a deeply dissected terrain below the main escarpment, known as the Little Berg. Killick (1963) describes this as "a terrace consisting of finger-like spurs projecting into Natal more or less at right angles to the escarpment". The spurs, lying between 1 675 m and 2 130 m, are capped with basalt and end abruptly in conspicuous cave sandstone cliffs.

The Cathedral Peak Forestry Research Station (29°00'S; 29°15'E) was established in 1935 to examine the influences of various management practices on the vegetation and water yield of the local mountain catchments. As a consequence, its topography, geology, hydrology and vegetation have been extensively studied and are described in detail by Killick (1963), Nanni (1956; 1970; 1972), Schulze (1974), Granger (1976), Tyson, Preston-Whyte & Shulze (1976), Bosch (1979) and Watson (1981).

1 850 m and 2 150 m) Acocks recognized a second veld type i.e. Themeda-Festuca Alpine Veld. This is a short dense grassveld, dominated by T. triandra and other species common to Highland Sourveld, as well as a high proportion of temperate grasses, particularly on the cool southern aspects and at higher altitudes. Common species are Festuca costata, Merxmuellera disticha, Koelaria cristata, Pentaschistis spp. and Poa binata (Scotcher, 1982). Where fire has been absent, a form of Fynbos is a common component of the vegetation, consisting chiefly of Passerina montana, Erica spp., Cliffortia nitidula, Encephalartos ghellenckii and Widdringtonia nodiflora.

The most comprehensive study carried out on the vegetation at Cathedral Peak is that by Killick (1963). He recognized three altitudinal vegetation belts, corresponding with three climax communities, viz.:

(1) Montane Belt: Podocarpus latifolius forest (1 280 m - 1 829 m).
(2) Subalpine Belt: Passerina - Philippia - Widdringtonia Fynbos (1 829 m - 2 865 m).
(3) Alpine Belt: Erica - Helichrysum Heath (2 865 m - 3 353 m).

The research catchments, situated between 1 675 m and 2 130 m, fall into the subalpine belt. This vegetation belt consists mainly of fire-maintained tussock grassland, chiefly Themeda triandra Grassland. Also present are temperate grassland occurring on mesocline slopes, tall grassland, Rendlia altera grassland and the Merxmuellera maçowanii consocies. Woody communities include Cliffortia linearifolia scrub, Leucosidea sericea scrub, Buddleja salviifolia scrub, and the climax community Passerina - Phillippia - Widdringtonia fynbos (Killick, 1963).

Associated with these grasses are a wide variety of perennial forbs, most of which are non-woody. Bayer (1955) separated these forbs into vernal aspects and autumnal aspects species. The former depend on regular fires for their survival whilst the latter are fire sensitive (Scotcher, 1982).

2.2 Climatic conditions during the study period

Climatic data were obtained from the central meteorological station situated north-west of the study area (Fig. 2.2). Ecologically significant climatic parameters recorded during both the study period (climatograms), and for the 33 year period from 1948 to 1981 (climatic diagram), are summarized in Fig. 2.3.

The Cathedral Peak research area lies in the summer rainfall zone of South Africa and as a result the summers are wet and humid, and the winters are dry and cold. This is clearly evident in the climatic diagrams (Fig. 2.3). The long term average annual rainfall is 1 380 mm. Precipitation during the study period was 1 706, 1 278, 1 337 and 1 230 mm for 1978, 1979, 1980 and 1981 respectively. 1978 therefore represented a wetter than average year (+326 mm), while 1981 was drier than normal (-150 mm). The mean annual temperatures were 14,0°C for 1978, 14,3°C for 1979 and 13,8°C for 1980. These did not differ markedly from the long term average of 13,8°C. The only year during the study period which was colder than average was 1981 (12,0°C).

Drought periods (dotted areas in Fig. 2.3) were experienced between May and July for 1978, 1980 and 1981, while June was the only month in which drought was recorded in 1979. The early part of the growing season (September - November) for the years 1979 to 1980 were characterized by a higher than average precipitation in August/September followed by lower than average precipitation in September/October.

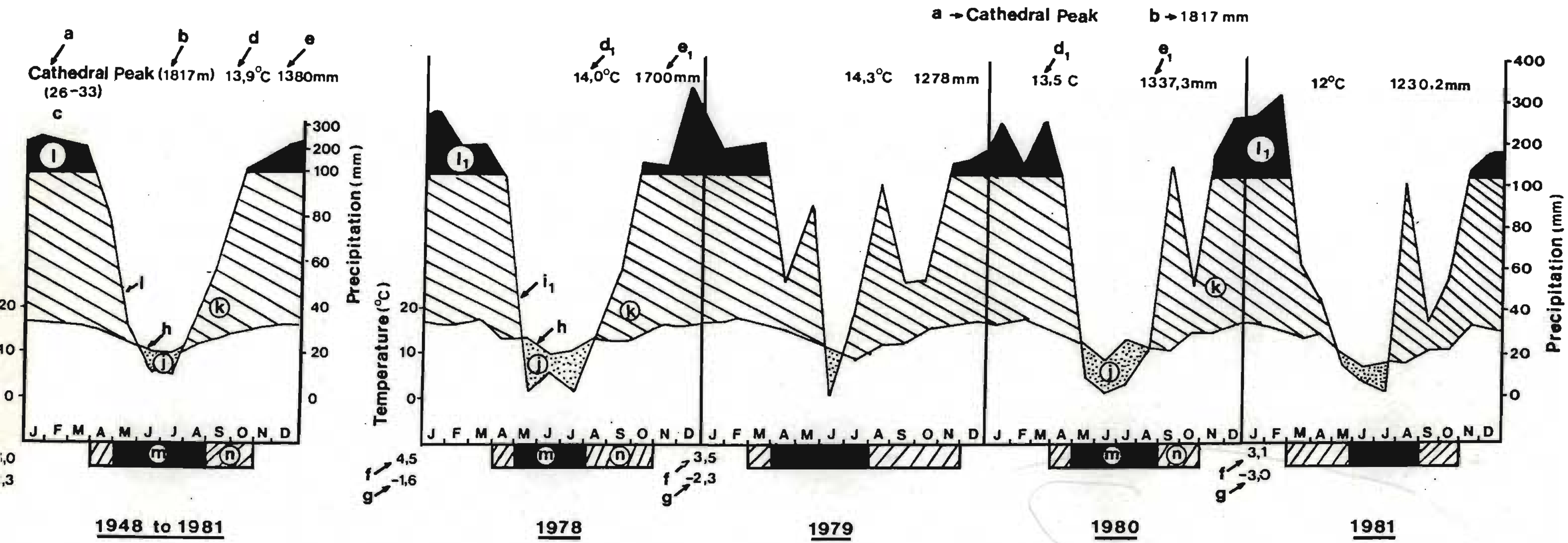


Fig 2.3. A climatic-diagram representing a period of 33 years (1948 to 1981), and annual climatograms for 1978 to 1981, for the central meteorological station at Cathedral Peak. The symbols and figures on the diagrams have the following meanings: a, station; b, height above sea level; c, number of observation years (first figure for temperature, second for precipitation); d, mean annual temperature; d_1, mean monthly temperature; e, mean annual precipitation; e_1, annual precipitation; f, mean daily minimum temperature of the coldest month; g, lowest absolute minimum temperature recorded; h, curve showing monthly mean temperatures; i, curve showing mean monthly precipitation; i_1, curve showing monthly precipitation; j, drought period (dotted); k, humid period (vertical hatching); ℓ, mean monthly precipitation exceeding 100 mm with the scale reduced to 1/10 (black area); ℓ_1, monthly precipitation exceeding 100 mm with the scale reduced to 1/10 (black area); m, months with mean daily grass minimum less than 0°C (black); n, months with absolute grass minimum less than 0°C (diagonally hatched), (after Walter, 1971). For the assessment periods, the figures mean: o, mean monthly temperature; and p, total precipitation; for the marked intervals.

CHAPTER 3

A COMPARISON OF SIX METHODS OF BOTANICAL ANALYSIS IN THE MONTANE GRASSLANDS OF NATAL

3.1 Introduction

In nature conservation it is necessary to monitor ecosystems for changes which may indicate the success or otherwise of current management policies. Public authorities (for example the Department of Environment Affairs) control large tracts of montane grasslands which are comprised of the most important river catchments and mountain nature reserves in South Africa. To monitor these it is essential to follow changes in species composition. These changes are then interpreted as being desirable or undesirable, according to management objectives.

A large variety of methods of botanical analysis are available to the ecologist for quantitatively assessing grassland condition, of which various have been used in the Natal Drakensberg. With administrative arrangements now being made to monitor the vegetation changes in these large areas, it has become essential to standardize the methods used. Of the several techniques recommended for use in grasslands by various experienced ecologists, five techniques for estimating percentage frequency and one for estimating above-ground biomass for dominant species have been reported to be promising (Walker 1970). The purpose of the study reported here was to evaluate these techniques with regard to relative accuracy and precision especially as affected by inter-operator variation and information return.

3.2 Study area

The study site, which was chosen for its proximity to the research station, represented grassland in good condition and the vegetation was visibly uniform. An area of 120 X 120 m was demarcated for the study. This area was then subdivided into plots, each 20 X 20 m.

3.3 Methods

There are a number of measurable species parameters available for sampling vegetation. The more important of these are: 1. density, the number of individuals; 2. frequency, the number of times a species is recorded in a given number of small quadrats; 3. cover, either of crown and shoot area or of basal area. In addition there are other measurable quantities such as height, stem diameter and biomass (Mueller-Dombois & Ellenberg, 1974).

Density is readily determined but because its determination is time consuming and laborious (Greig-Smith, 1983) it was not included in this study.

Frequency provides an objective measure similar to denisty, but in contrast it is a nonabsolute measure. This means that the result is dependent on the size and shape of the quadrat frame. Frequency is usually the easiest of the quantitative measures to determine (Greig-Smith, 1983).

In order to measure percentage frequency a quadrat method was introduced into the experiment. When a sampling quadrat is reduced to a dimensionless point, frequency becomes an absolute measure of cover. In order to attain a reasonable level of precision, however, a very large number of points is necessary (Mentis, Collinson & Wright, 1980). Recently the nearest plant method has been used as an alternative, where the plant species nearest the point is recorded. The results provide an estimate of the proportional species composition rather than cover.

Three point techniques were included in this study viz.: the Levy bridge, the wheel point and the step point. These techniques differ principally in the distance between successive points. This may be important because if the points are located too close to one another relative to the diameters of most of the plants then the observations will not be independent, and the variance is consequently under-estimated (Tidmarsh & Havenga, 1954).

Cover is defined as the proportion of ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration (Greig-Smith, 1983). Top-cover, the proportion of ground covered by the aerial portions of the species, is the more easily determined measure. The metric belt transect technique was included to assess species composition by cover.

The contribution of biomass of individual species is an objective measure of the vegetation in terms of the percentage composition by weight. The techniques of estimating biomass are generally laborious and destructive. The method of 't Mannetje and Haydock (1963), whereby species composition is estimated by ranking the first three species in relation to their biomass, overcomes these problems and was included in this study.

3.3.1 Frequency techniques

3.3.1.1 Quadrat method

The 0,4 X 0,4 m quadrat frame used in the experiment was divided into three; two 0,1 X 0,1 m sub-quadrats and one 0,2 X 0,2 m sub-quadrat. These were allocated the symbols A, B and C respectively. The quadrat was placed randomly in the plot, after which all rooted species in the A portion were recorded. The operator then recorded any new species in section B, followed by new species in section C. In each placement the species were recorded without regard to their quantity or number of individuals. The results were expressed as the percentage frequency, i.e. the percentage of samples in which each species was found. A preliminary analysis of the data showed that the 0,1 X 0,1 m quadrat resulted in a frequency of about 80% for the common species and was therefore considered to be an acceptable size to use (Hyder _et_ _al_., 1966).

The size of the sample was not determined for any of the methods as each operator worked with each method for a specified period of time (see experimental design 3.3.4).

3.3.1.2 Levy bridge

The Levy bridge is a frame supporting 10 needles, each 0,15 m apart (Levy & Madden, 1933). To conduct a survey the bridge is located randomly within the sample plot. At each random emplacement of the bridge, the needles are lowered vertically through the grass sward. When the needle reaches ground level the plant struck or if there is no strike, the plant nearest to the point, is recorded. Thus the diameter of the needle and of the needle point are not important.

3.3.1.3 Wheel point

The principle of this method is the same as that of the Levy bridge. The apparatus consists of a simple spoked wheel (3 m circumference) that runs on its spoke ends. A handle is attached through the axle of the wheel in such a way that it can easily be pushed in an upright position. As sampling was restricted to only one of the spokes, the distance between points was 3 m. This results in a less clumped distribution of point positions within the sample site when compared with the Levy bridge.

3.3.1.4 Step point

This method requires only one operator and no equipment. The operator marks a point on the toe of his shoe, and uses this mark to define the point positions. The species nearest the mark in front of the shoe was recorded at every second step to give the percentage species composition (Mentis, 1981).

3.3.2 Estimation of relative biomass

3.3.2.1 't Mannetje & Haydock

This is a dry-weight rank method ('t Mannetje & Haydock, 1963) in which a 0,4 X 0,4 m quadrat is placed randomly in the site. All species present are recorded, after which the three most common species are ranked on the basis of their dry mass. The proportion of quadrats in which each species occurred in first, second and third place is then calculated. These values are then weighted by multiplying them against three previously determined constants, and the sum of these values, for each species, gives the percentage contribution of that species to the total mass of the sward. The constants used in this study are those derived by 't Mannetje and Haydock (1963).

3.3.3 Species composition by aerial cover

3.3.3.1 Metric belt transect

The metric belt transect method described by Schmutz, Reese, Freeman & Weaver (1982) involves the emplacement of a 0,316 square frame along a tape stretched across the ground. After the emplacement of the frame the tape is relocated and the method repeated. The cover of each species in the quadrat is estimated by using the frame which is divided into two halves, each 0,1 m^2. One half is further subdivided into five 0,01 m^2 units. Percentage crown cover is then converted to percentage species composition by dividing total transect cover of each species by total cover of all species in the transect.

3.3.4 Experimental design

The techniques were tested by 6 operators each assisted by a scribe. Three of the operators were trained (familiar with botanical assessments) and 3 were relatively untrained. A day was spent before testing started in familiarising the operators with the different techniques and plant names. Plants which could not be identified were allocated nicknames until proper identification could be made at the end of a time period or day. In this way plant names could be standardised.

The precision, repeatability and accuracy of the six methods were examined using a 6 X 6 Latin square design (Fig. 3.1). Precision, the degree of clustering of the observations around a central value, was estimated using the coefficient of variation. Repeatability, the scatter of mean results between workers, was estimated in the same manner. Accuracy, regarded in this study as the degree of bias, was gauged according to the frequency distribution of the results.

The efficiency of the various methods (i.e. in terms of man hours per sample), was not measured directly as each operator worked continuously throughout each time period, regardless of how many observations were made. Efficiency was therefore gauged by the precision, repeatability and accuracy of the information obtained per unit of time.

The experiment was conducted over six days, each day being split into six 45 minute time periods. Sampling was arranged in such a way that each operator visited six plots every day, using a different technique each time. Thus the operator effect, technique effect, day effect and time of day effect were all mutually orthogonal. However, a direct comparison of the scores obtained using the six different techniques is difficult. The point techniques give a score for the proportional species composition; the quadrat gives percentage frequency; the 't Mannetje & Haydock method gives ranked species composition by mass and the metric belt transect estimates proportional species composition by aerial cover. In order to make comparisons, functional relationships between the various techniques were sought using regression analysis. In this way it was possible to standardize the scores.

DAY 1

OPERATORS

TIME PERIODS	3	4	5	6	1	2
3	E	D	A	C	B	F
4	C	B	E	A	F	D
5	F	E	B	D	C	A
6	D	C	F	B	A	E
1	B	A	D	F	E	C
2	A	F	C	E	D	B

DAY 2

	1	2	3	4	5	6
1	C	B	E	A	F	D
2	A	F	C	E	D	B
3	D	C	F	B	A	E
4	B	A	D	F	E	C
5	F	E	B	D	C	A
6	E	D	A	C	B	F

DAY 3

	5	6	1	2	3	4
5	A	F	C	E	D	B
6	E	D	A	C	B	F
1	B	A	D	F	E	C
2	F	E	B	D	C	A
3	D	C	F	B	A	E
4	C	B	E	A	F	D

DAY 4

	6	1	2	3	4	5
6	B	A	D	F	E	C
1	F	E	B	D	C	A
2	C	B	E	A	F	D
3	A	F	C	E	D	B
4	E	D	A	C	B	F
5	D	C	F	B	A	E

DAY 5

	4	5	6	1	2	3
4	F	E	B	D	C	A
5	D	C	F	B	A	E
6	A	F	C	E	D	B
1	E	D	A	C	B	F
2	C	B	E	A	F	D
3	B	A	D	F	E	C

DAY 6

	2	3	4	5	6	1
2	D	C	F	B	A	E
3	B	A	D	F	E	C
4	E	D	A	C	B	F
5	C	B	E	A	F	D
6	A	F	C	E	D	B
1	C	E	B	D	C	A

Figure 3.1 The 6 X 6 Latin square design used in the experiment. The letters A, B, C, D, E and F refer to the quadrat, Levy bridge, metric belt, step point, wheel point and 't Mannetje & Haydock methods respectively.

3.4 Results and discussion

3.4.1 Analysis of relationships between methods

The homogenous nature of the plots meant that variation in scores for any single species across plots was small. This resulted in clumping of points for each individual species so that very little opportunity existed for relationships between the methods to be manifested in species analyses. This was confirmed by the data (see example Fig. 3.2 and Table 3.1 for *Themeda*).

TABLE 3.1 Correlation matrix of the relationships between the six methods for *Themeda*

Method	Quadrat	Levy bridge	Metric belt	Step point	Wheel point	't Mannetje & Haydock
Quadrat	1,0000					
Levy bridge	0,4962	1,0000				
Metric belt	-0,0634	0,3220	1,0000			
Step point	0,2718	0,3250	0,2172	1,0000		
Wheel point	0,1964	0,4205	0,4306	0,2611	1,0000	
't Mannetje & Haydock	-0,0020	0,1043	0,2093	0,2500	0,1720	1,0000

In order to overcome this problem the mean scores for every species for all plots were compared for all combinations of methods. The resulting values were used to plot scatter diagrams for the 22 most common species (Fig. 3.3 a-d). In Fig. 3.3a the mean scores for the various species using the quadrat are plotted against those obtained for the other methods. In this example the most abundant species had a mean relative frequency of 72% and the rarest species a relative frequency of 1%. This

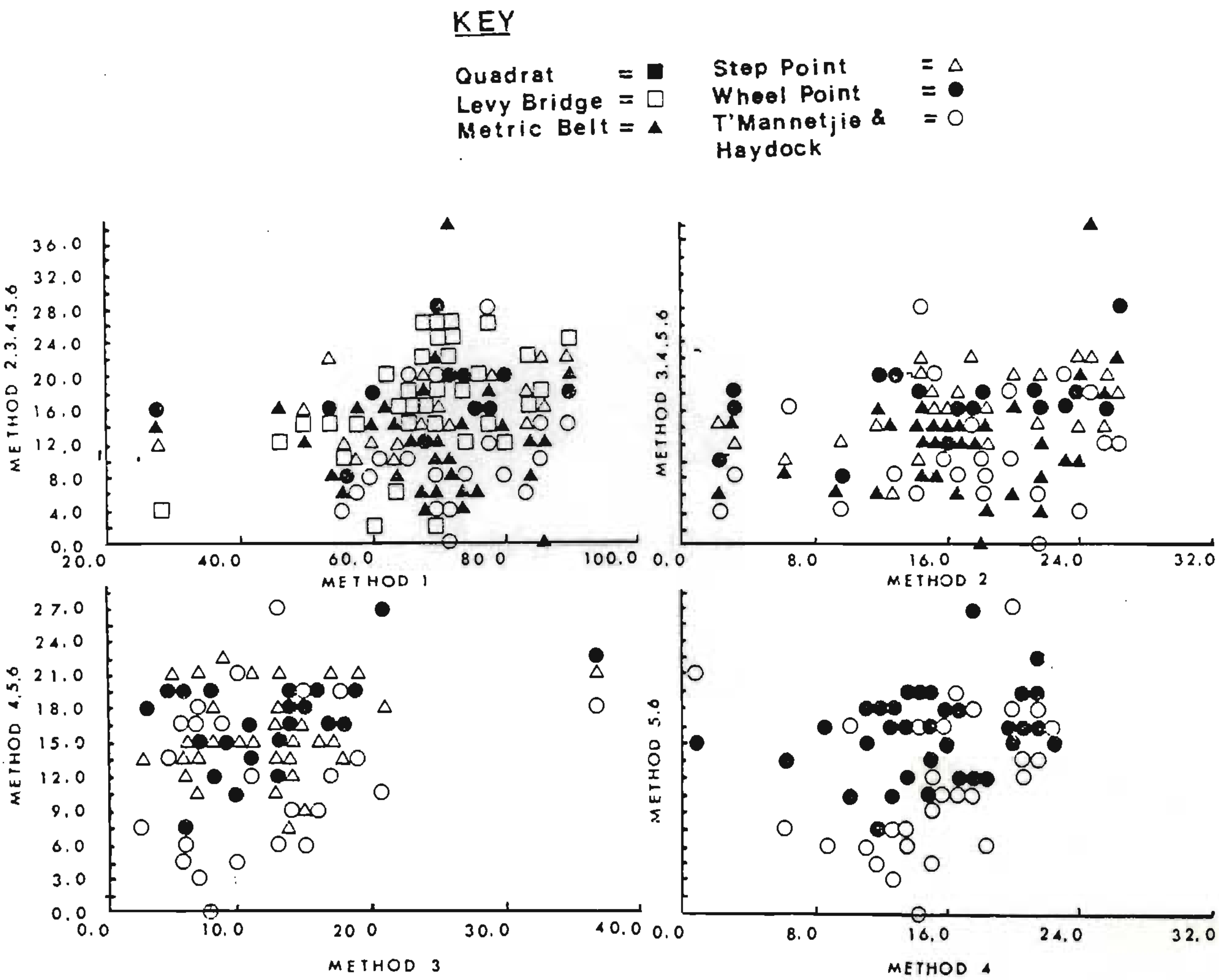


Figure 3.2 Scatter diagrams of the various methods for Themeda. Methods 1, 2, 3, 4, 5 and 6 refer to the quadrat, Levy bridge, metric belt, step point, wheel point and 't Mannetje & Haydock methods respectively.

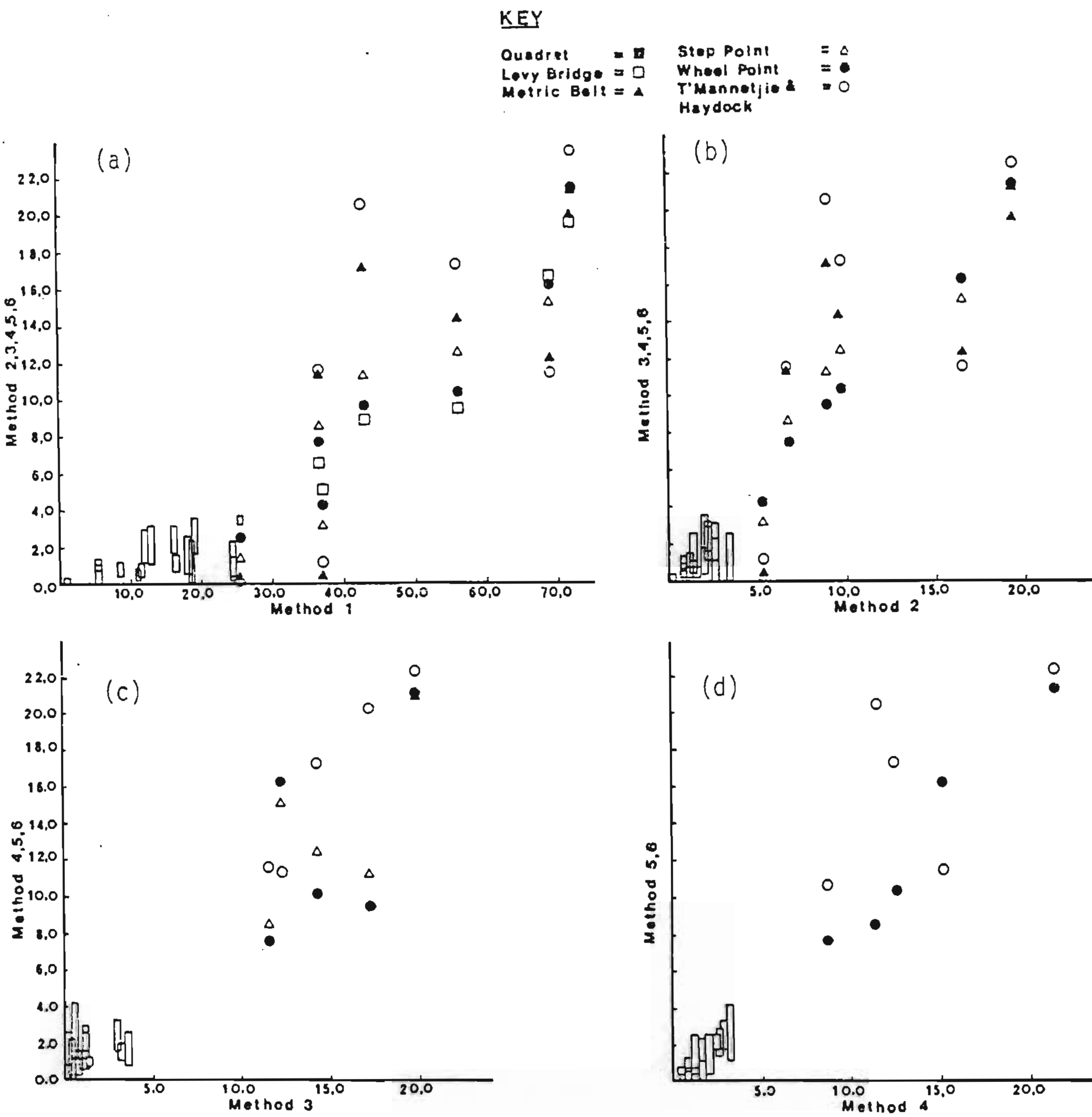


Figure 3.3 a-d Scatter diagrams of the mean scores of all the plots for 14 species for all combinations of methods. Open bars represent areas where methods overlap. The numbers 1 – 6 refer to the quadrat, Levy bridge, metric belt, step point and 't Mannetje & Haydock methods respectively.

provided a range of 71% over which the methods could be compared. The ranges obtained for methods 2, 3 and 4 in this manner (Fig. 3.3 a-c respectively) were ca 20%. In each case the relationship between any one method and any other was approximately curvilinear.

From these data, quadratic regression lines were fitted by arbitrarily relating the score for the quadrat method as a dependent variable to the scores for each other method in turn as independent variables. Both regressions through the origin and regressions with arbitrary intercept were fitted. However the intercepts were not significantly different and the simple models were subsequently used. Fig. 3.4 illustrates both sets of curves.

Table 3.2 shows the values of the estimated parameters and other relevant details for the regressions through the origin. In all cases the regression lines fitted the data very well, (R^2 varying between 0,74 and 0,68). Logarithmic functions fitted the data less well. The quadratic regressions were therefore used to make all data comparable to that of the quadrat. This is referred to as quadrat adjusted data.

3.4.2 Analysis of variance on quadrat adjusted data

Quadrat adjusted data were used in analyses of variance in which the main effects of days, operators, methods and their interactions were examined. The fourteen most common species (species exceeding 10% relative frequency as measured with the quadrat) were examined in this way.

An examination of the interaction between methods and operator revealed that the wheel point, quadrat and Levy bridge methods were least affected

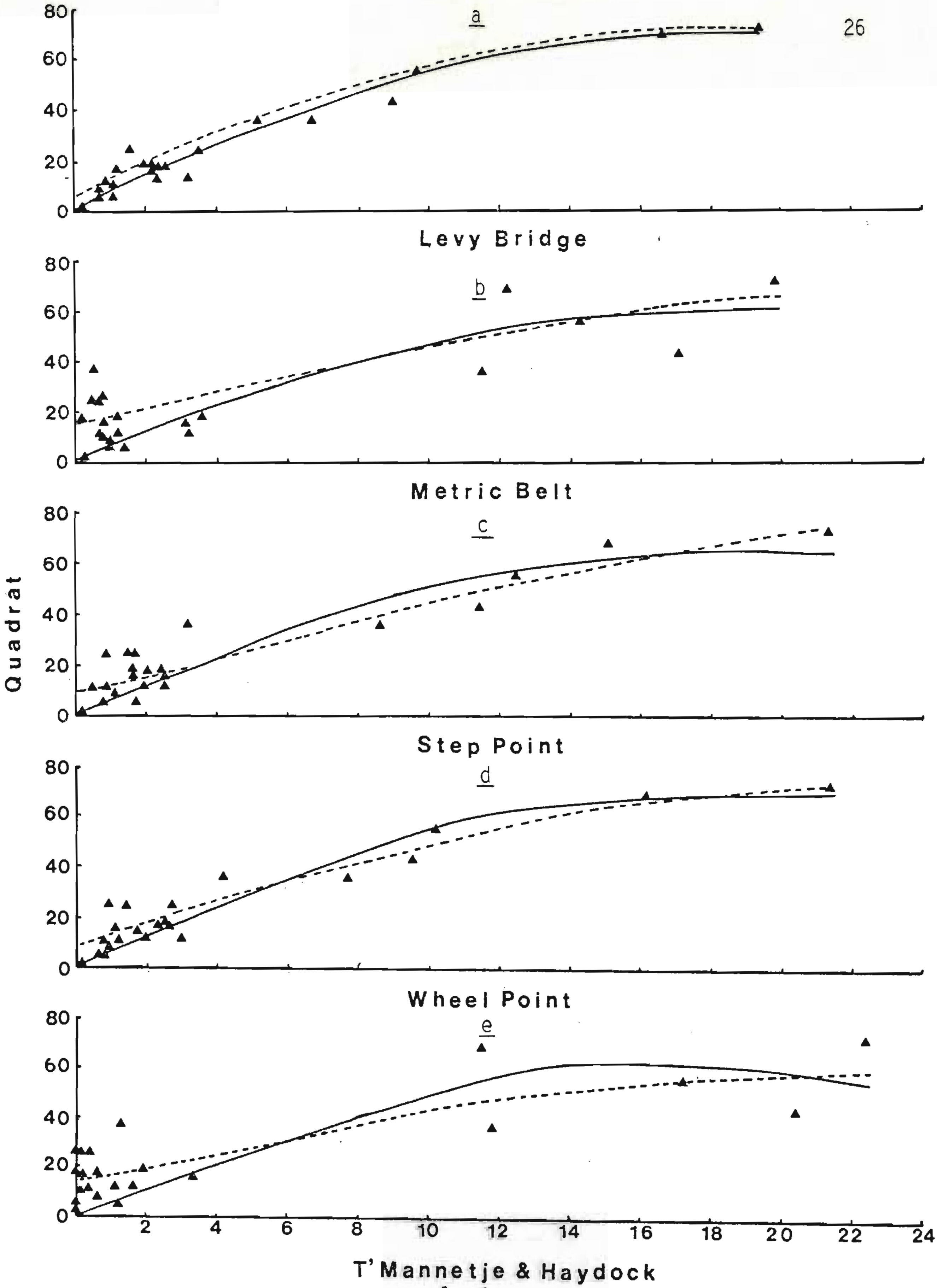


Figure 3.4 a-e Relationships between relative frequency (y axis) as measured with the quadrat and the proportional species composition measured by the other methods (x axis).

by operator differences. This can be seen by examining Table 3.3 in which the coefficients of variation have been presented for each method and each of the fourteen species. No single method is universally best for every species. But if the methods are ranked according to the coefficients of variation for each species and the mean rank for each technique calculated, then the wheel point has the lowest mean rank.

TABLE 3.2 Regression equations with the quadrat score as the dependent variable

Independent variable	Regression equations		R^2
x = Levy bridge score	$y = 7{,}50\ x$	$- 0{,}201\ x^2$	0,968 ***
	$\pm\ 0{,}52$	$\pm\ 0{,}03$	
x = Metric belt score	$y = 6{,}74\ x$	$- 0{,}191\ x^2$	0,792 ***
	$\pm\ 1{,}70$	$\pm\ 0{,}105$	
x = Step point score	$y = 7{,}07\ x$	$- 0{,}183\ x^2$	0,917 ***
	$\pm\ 0{,}854$	$\pm\ 0{,}051$	
x = Wheel point score	$y = 7{,}405\ x$	$- 0{,}195\ x^2$	0,954 ***
	$\pm\ 0{,}593$	$\pm\ 0{,}035$	
x ='t Mannetje & Haydock	$y = 7{,}022$	$- 0{,}204\ x^2$	0,764 ***
	$\pm\ 1{,}731$	$\pm\ 0{,}090$	

*** = Significant at the 1% probability level

TABLE 3.3 The coefficients of variation and ranks for the method x operator interaction for the fourteen most common species

Species	Quadrat CV	Quadrat Rank	Levy Bridge CV	Levy Bridge Rank	Metric Belt CV	Metric Belt Rank	Step Point CV	Step Point Rank	Wheel Point CV	Wheel Point Rank	't Mannetje & Haydock CV	't Mannetje & Haydock Rank
Becium	14.3	2	13.3	1	17.6	5	15.5	3	16.5	4	22.2	6
Diheteropogon	8.0	4	10.3	6	10.1	5	7.9	3	7.8	2	4.9	1
Harpechloa	9.9	1	12.8	2	15.3	4	18.1	5	13.5	3	41.9	6
Helichrysum	19.1	4	30.2	5	26.4	2	28.3	3	21.8	1	45.3	6
Hypoxis	10.1	1	10.5	2	19.4	4	20.9	5	15.6	3	31.9	6
Oxalis	21.4	3	19.6	2	32.0	5	30.1	4	17.6	1	-	6
Rendlia	5.5	2	5.2	1	9.7	5	9.3	4	9.2	3	12.6	6
Scilla	18.9	4	16.7	2	29.9	5	17.9	3	12.9	1	48.3	6
Senecio	16.2	4	9.7	2	41.7	5	8.9	1	12.5	3	102.3	6
Themeda	3.4	4	2.9	3	7.3	6	2.2	2	1.1	1	5.8	5
Trachypogon	15.4	1	21.8	4	25.2	6	24.0	5	16.2	2	21.2	3
Tristachya	2.0	2	3.9	4	9.2	5	3.0	3	1.4	1	15.1	6
Vernonia	5.5	1	10.7	2	15.0	5	13.1	4	11.6	3	17.5	6
Alloteropsis	4.6	3	4.7	4	2.7	2	2.2	1	7.3	6	6.9	5
Mean rank		2.57		2.79		4.50		3.29		2.50		5.29

Although the mean ranking of the quadrat and wheelpoint were very close, the coefficients of variations for the quadrat method will vary with variations in quadrat size. The relationships between the wheel point and the other methods were therefore examined more closely.

3.4.3 Wheel point adjusted data

Quadratic regression lines were fitted relating the score for the wheel point method as dependent variable to the scores for each other method as the independent variable as described previously. Fig. 3.5 illustrates the regressions through the origin and the regressions with arbi-

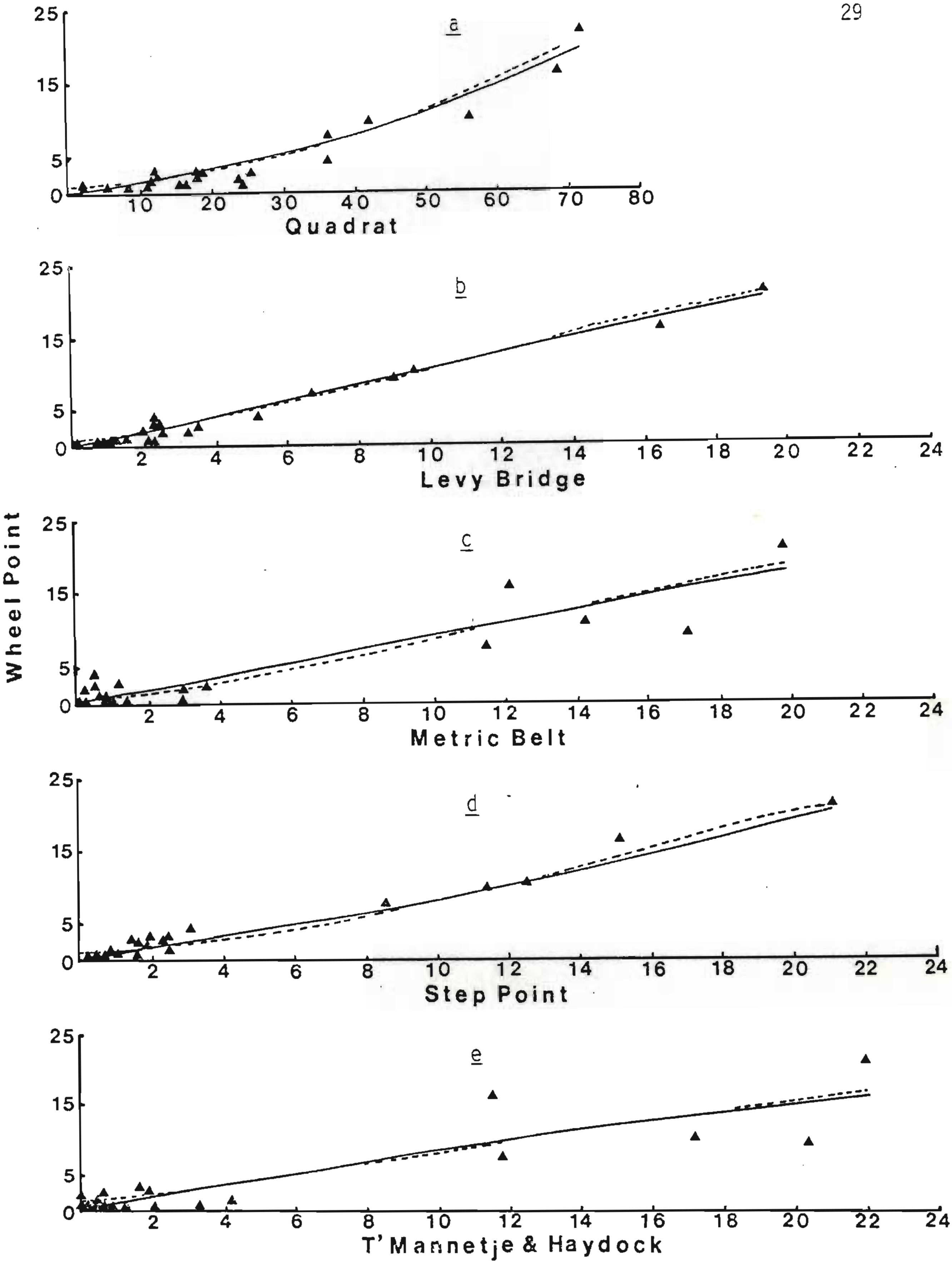


Figure 3.5 a-e Relationships between proportional species composition (y axis) as measured with the wheel point and the other methods (x axis).

trary intercept. The intercepts were not significantly different and the simpler models were used. Table 3.4 shows the values of the estimated parameters and other relevant details. Comparison of these data with Table 3.2 reveals that the fit obtained using the wheel point method was in all cases better than that using the quadrat. Wheel point adjusted data were therefore used in all subsequent analyses.

TABLE 3.4 Regression equations with the wheel point score as the dependent variable

Independent variable	Regression equations	R^2
x = Quadrat score	$y = 0{,}049\ x \quad 0{,}003\ x^2$ $\pm\ 0{,}024 \quad \pm\ 0{,}004$	0,966 ***
x = Levy bridge score	$y = 0{,}947\ x \quad 0.006\ x^2$ $\pm\ 0{,}058 \quad \pm\ 0{,}004$	0,992 ***
x = Metric belt score	$y = 0{,}796\ x \quad 0{,}005\ x^2$ $\pm\ 0{,}294 \quad \pm\ 0{,}018$	0,872 ***
x = Step point score	$y = 0{,}902\ x \quad 0{,}079\ x^2$ $\pm\ 0{,}004 \quad \pm\ 0{,}005$	0,985 ***
x = t' Mannetje & Haydock score	$y = 1{,}074\ x - 0{,}017\ x^2$ $\pm\ 0{,}313 \quad \pm\ 0{,}016$	0,840 ***

*** = Significant at the 1% probability level

3.4.4 Analysis of variance on wheel point adjusted data

Wheel point adjusted data were used to perform an analysis of variance in which the main effects of the days (DA), time of day (TI), operators (OP) and methods (ME) were examined. Because analysis of these four factors could not be performed simultaneously (due to confounding of interactions between pairs of factors in certain cases) two separate analyses were performed.

The first involved examining the factors DA, OP and ME and their first order interactions (Appendix A). In the second analysis, TI replaced OP. The fourteen most common species were examined in this way. A summary of both analyses is presented in Table 3.5. Differences between methods were significant at the 1% level for most species examined. These differences were in most cases attributable to low values recorded using the metric belt transect and 't Mannetje & Haydock methods. For example the values recorded for Themeda by the quadrat, Levy bridge, metric belt, step point, wheel point and 't Mannetje & Haydock method were 10,11; 15,68; 10,66; 14,08; 16,17 and 9,64% respectively. Results for the metric belt and 't Mannetje & Haydock methods were, in general 4% to 8% lower when compared with the other four methods.

Differences between days were significant (at the 1% level) for Hypoxis and Tristachya (Table 3.5). For Hypoxis this was due to the fact that for the first three days operators did not distinguish between different species (note that only one of the three Hypoxis species encountered is included in this analysis). After three separate species had been identified by day four, the mean decreased from 4,92 to 2,76. Significant differences between operators and the first-order interactions between

DA x OP and OP x ME for these two species can also be explained in this way. There appears to be no obvious reason as to why days were significantly different for Tristachya.

TABLE 3.5 Summary of analysis of variance on wheel point adjusted data

Species	Methods	Days	Times	Operators	DA x OP	DA x ME	TI x ME	OP x ME
Bcium	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Diheteropogon	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Harpechloa	N.S.	N.S.	N.S.	***	N.S.	N.S.	N.S.	N.S.
Helichrysum	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Hypoxis	***	***	N.S.	***	**	N.S.	N.S.	**
Oxalis	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Rendlia	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Scilla	***	N.S.	N.S.	***	N.S.	N.S.	N.S.	***
Senecio	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Themeda	***	N.S.	***	N.S.	N.S.	N.S.	***	N.S.
Trachypogon	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Tristachya	***	***	N.S.	***	***	N.S.	N.S.	N.S.
Vernonia	**	N.S.	N.S.	N.S.	N.S.	N.S.	***	N.S.
Alloteropsis	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = Not significant
*** = Significant at the 1% probability level
** = Significant at the 5% probability level

Themeda was the only species where time of day was significant at the 1% level (Table 3.5). The means of Themeda for times one to six were 14,05; 16,02; 14,24; 12,86; 14,81 and 12,30% respectively. Lower values recorded just prior to the midday meal break (Time 4) and the last period of the day (Time 6), when the effects of fatigue would be most noticeable, may account for this difference. The fact that time of day did not significantly affect the results for other species was surprising, as many other workers have reported on the effects of human stress on botanical analysis techniques (Walker, 1970). However, Walker (1970) found that actual sampling time should be limited to between four and five hours a day, which was within the four-and-a-half hour sample time used in this study.

Perhaps the most surprising result was that differences between operators were not significant for most of the species examined. This may be due to the fact that common grasses at Cathedral Peak are morphologically distinct and therefore easily recognizable. The only species in which operator differences were significant were the herbs Hypoxis and Scilla. The confusion arising from the three different species of the genus Hypoxis has already been discussed. Similarities between the herbs Scilla and Ledebouria may have caused similar identification problems for the untrained operator 2.

The first order interaction of DA x OP was only significant for Hypoxis and Tristachya. Since both days and operators were significant for Hypoxis, this could be expected. There appears to be no obvious reason as to why the DA x OP interaction is significant for Tristachya.

The interactions between DA x ME were not significant for any species (Table 3.5). This implies that the manner in which a method was used remained unchanged over six days and that six consecutive days of botanical analysis did not appear to affect this interpretation. This reflects the simplicity of the techniques studied.

The TI x ME interaction was significant for only two out of the fourteen species examined. This indicates that time of day has little effect on the results derived from methods used. Exceptions to this were Themeda and Vernonia.

The OP x ME interaction is the most important one since it provides a measure of how much variation is a result of the way in which different operators use the various techniques. In the OP x ME interaction confusion in the identification of Hypoxis and Scilla once again resulted in significant differences. There were however no significant differences for the remaining species. The coefficient of variation for this interaction (Table 3.3) shows that the wheel point, Levy bridge and quadrat methods were the most consistent. However, the coefficient of variation is not necessarily a reliable indicator of the relative merits of the methods. The tendency of certain methods to record zero values for inconspicuous species would give erroneously low coefficients of variation, and other features such as extreme skewness are not revealed. The alternative approach adopted was to examine the frequency distribution of the data for the various methods.

3.4.5 Frequency distribution of the data for the various methods

The design of the experiment was such that by the end of the experiment, each method had been used once in every plot. Because operator differences were generally not significant, it seems reasonable that the scores for all 36 plots could be used to plot histograms of the frequency distributions for each method by species. The fourteen most common species were examined in this way (Fig. 3.6 a-n).

The method of 't Mannetje & Haydock exhibits a frequency distribution which for most species differs markedly from the other methods. The distribution of the frequency classes appears to be related to the abundance of a particular species. For species low in abundance the distribution is positively skew or positive J-shaped. Scilla, Harpechloa,

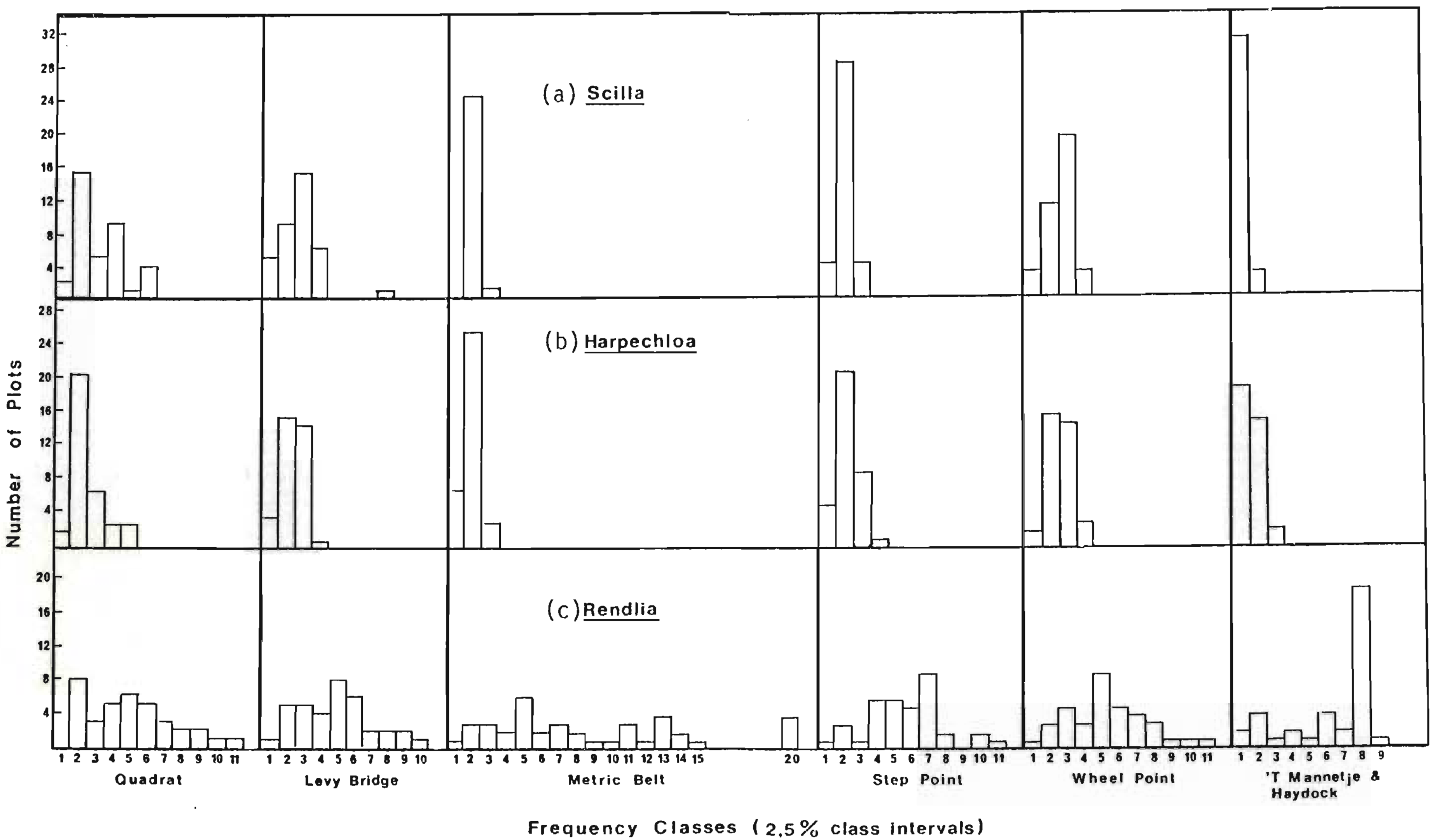


Figure 3.6 a-n Frequency distributions obtained for 14 different species using the various methods.

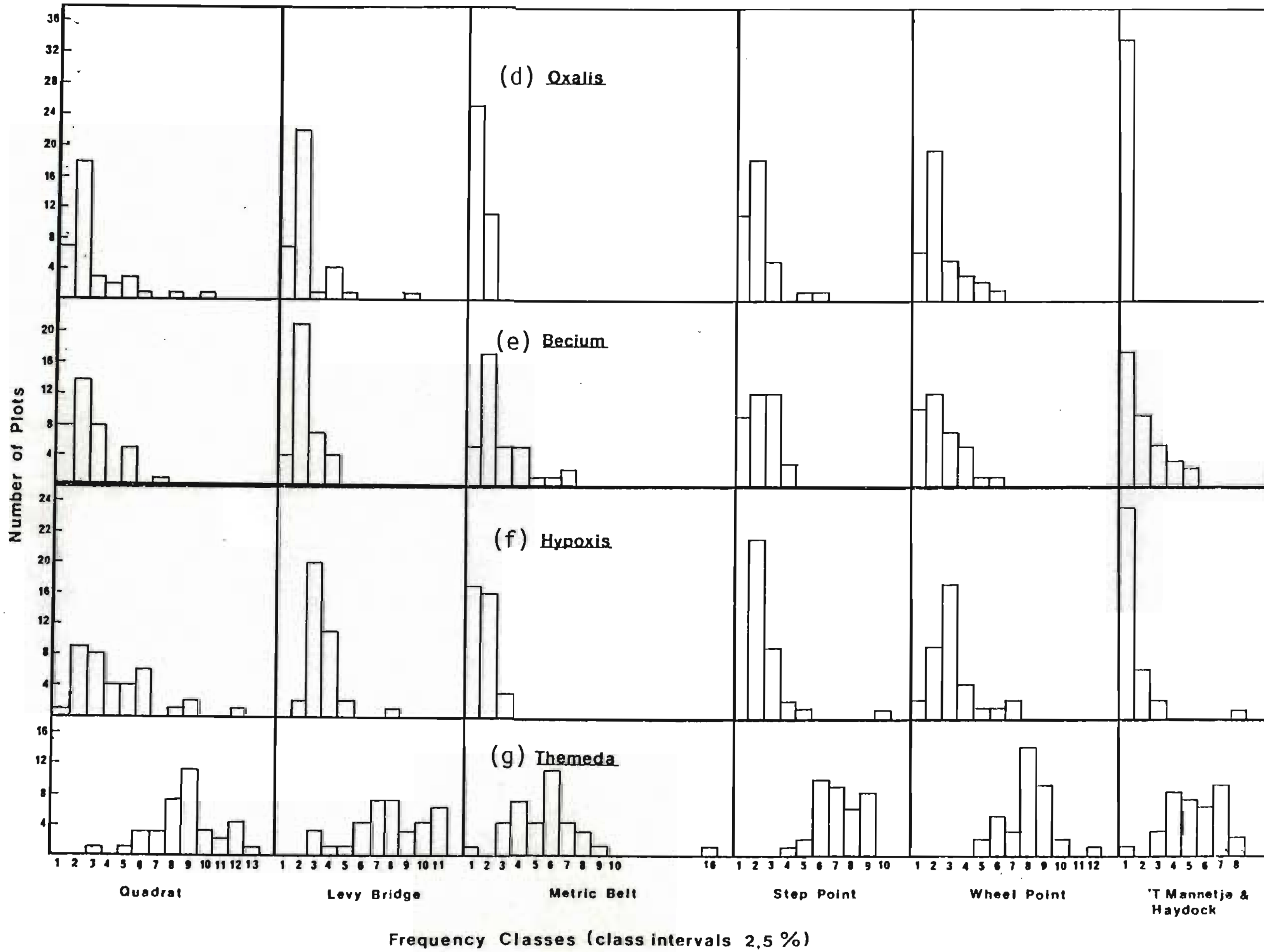


Figure 3.6 a-n continued

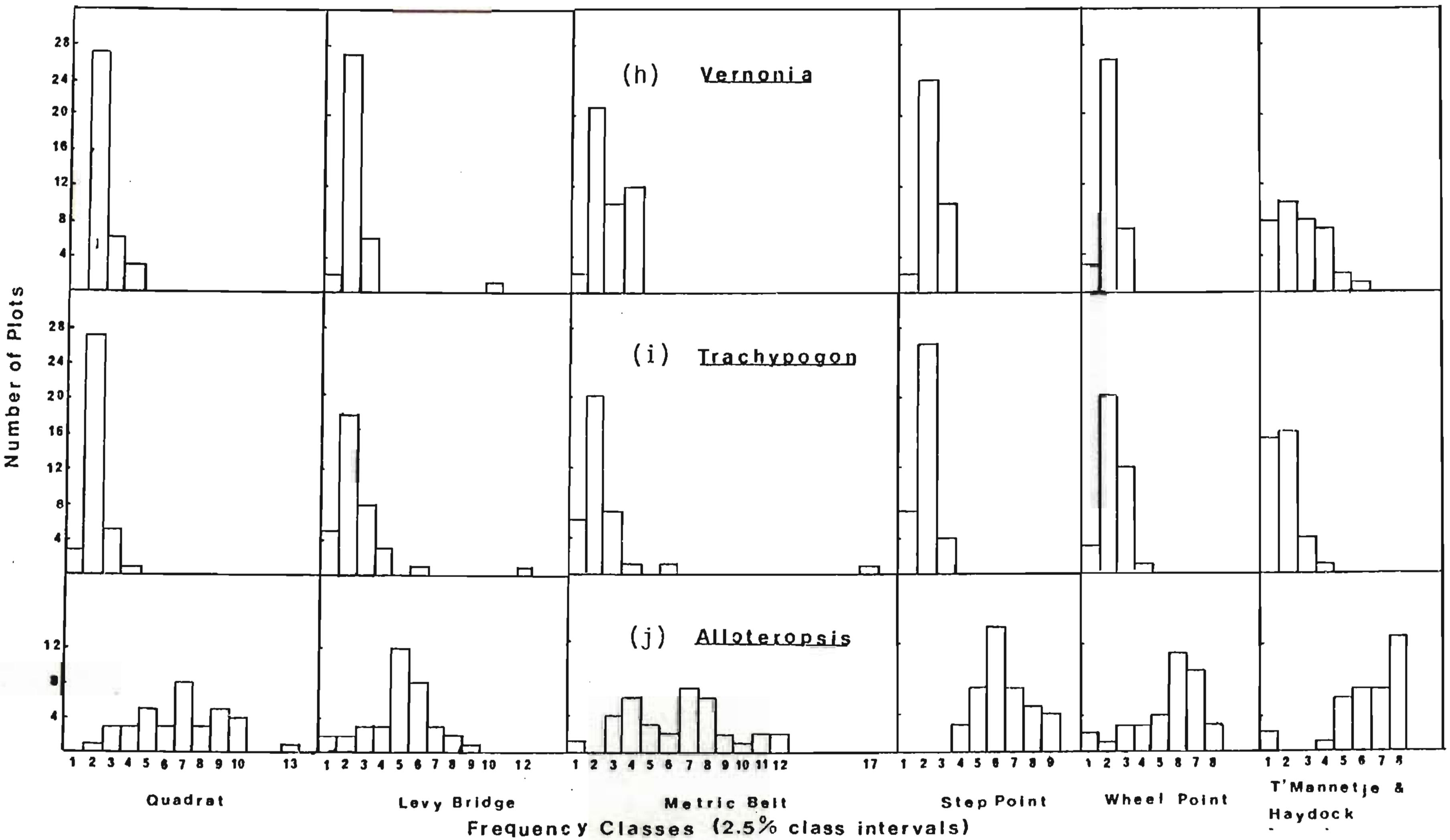


Figure 3.6 a-n continued

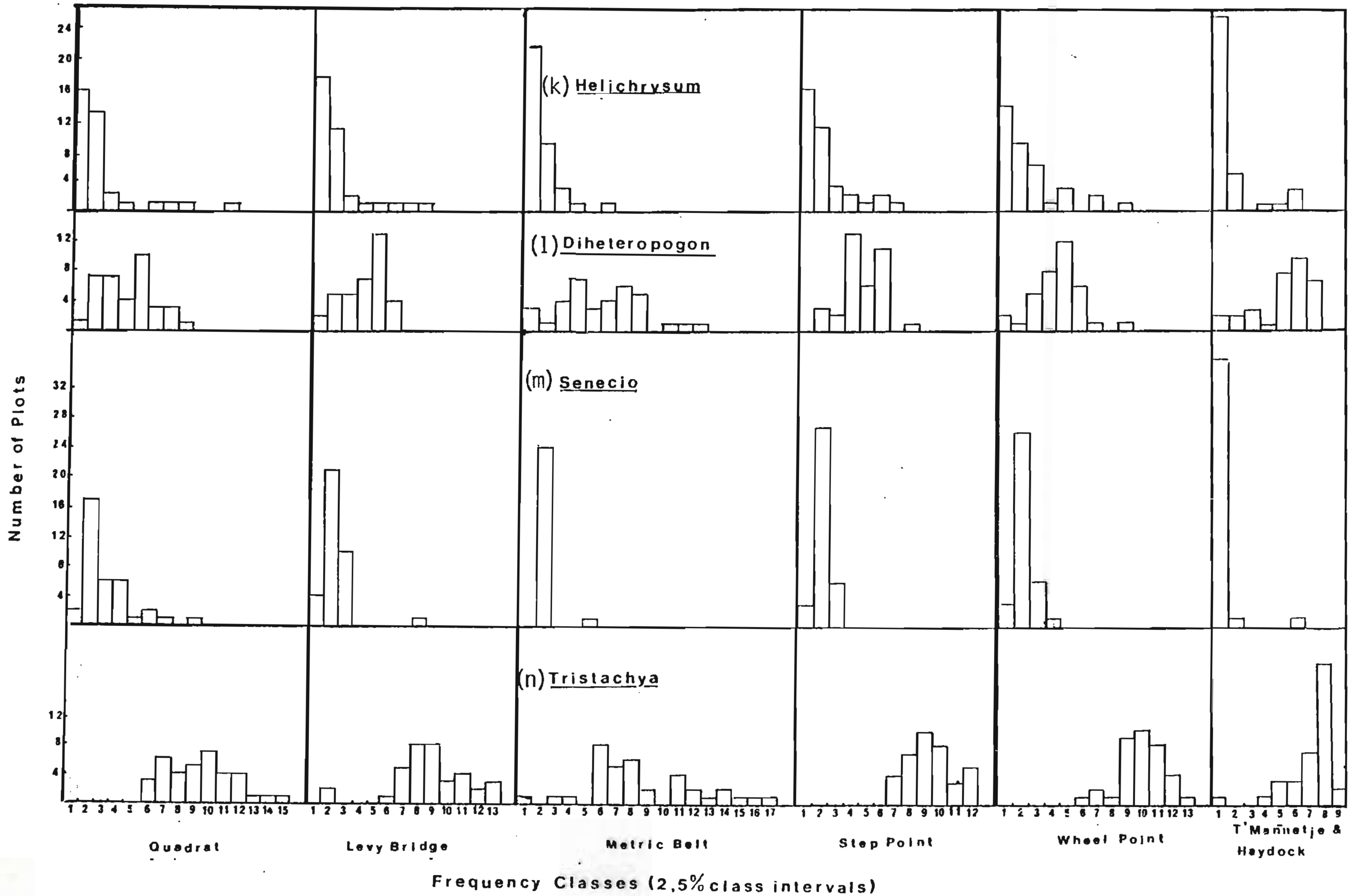


Figure 3.6 a-n continued

Hypoxis, Becium, Oxalis, Senecio and Trachypogon fall into this category (Fig. 3.6 a-n). For the common species the distribution is negatively skew. Rendlia, Tristachya, Diheteropogon, Alloteropsis and Themeda are examples. Thus the proportional composition of inconspicuous species is underestimated (or not recorded at all) while that for common species is overestimated. Although the 't Mannetje & Haydock method has advantages when trying to estimate the mass contribution of various species, its usefulness is limited when species composition is the important parameter. For the less common species such as Oxalis, Hypoxis, Scilla and Senecio, the distribution is skewed to the right. For the common species the metric belt transect exhibits a much flatter (i.e. platykurtic) frequency distribution when compared with the other methods. Rendlia, Alloteropsis and Tristachya clearly illustrate this feature. These frequency distributions appear to be complex, with more than one peak. The platykurtic nature of the frequency distribution for the metric belt data indicates a large variance for this method. The metric belt method was therefore not considered suitable for the measurement of species composition.

A critical examination of Fig. 3.6 a-n reveals that for eight of the species (Themeda, Oxalis, Trachypogon, Vernonia, Rendlia, Harpechloa, Scilla and Diheteropogon), the least biased distribution (i.e. closest to normal) was obtained using the wheel point. The Levy bridge showed similar results for Becium, Hypoxis and Alloteropsis and the step point for Senecio and Tristachya. Helichrysum was omitted from this assessment as the frequency distributions are positively skew for all methods. Although the quadrat method did not rank first for any species the frequency distribution was not as biased as 't Mannetje & Haydock and the metric belt transect.

3.4.6 A comparison of veld composition scores obtained using the various methods

A modified form of the quantitative climax method of Dyksterhuis (1949) (referred to as the veld condition assessment technique) has been developed to enable the rapid assessment of the agro-ecological condition of grassveld in Natal (Foran, Tainton & Booysen, 1978; Tainton, Edwards & Mentis, 1980). In order to use this technique the proportions of the different plant species at a site must be known. The wheel point has been commonly used for this purpose. There is, however, no reason why other techniques should not be used. The present experiment provided an ideal opportunity for evaluating the effect of different methods of determining botanical composition on the calculation of the veld condition score.

Veld composition scores were calculated for the 36 plots for each method and an analysis of variance was performed on standardized data. The main effects of days, operators, methods and their first order interactions were examined separately for each of the ecological groups and the veld condition score, and the results summarised in Table 3.6.

The factor days was only significantly different (at the 1% level) for the Increaser I scores. This difference was a result of the low score obtained on day 2 (20,1%) when compared with the other days (23,2%; 23,5%; 23,4%; 23,9% and 24,0%). The DA x ME interaction table for Increaser I scores showed that the Levy bridge (17,3%), metric belt (17,2%) and 't Mannetje & Haydock (14,6%) methods all recorded low scores on this day when compared with the quadrat (20,6%), step point (24,5%) and wheel point (26,2%) methods.

TABLE 3.6 Summary of analysis of variance on the ecological groups and veld condition score

Species class	Days	Operators	Methods	DA x OP	DA x ME	OP x ME
Decreaser	N.S	N.S.	***	N.S.	N.S.	N.S.
Increaser I	***	N.S.	***	N.S.	N.S.	N.S.
Increaser II	N.S.	N.S.	***	N.S.	N.S.	N.S.
Inceaser III	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Veld condition score	N.S.	N.S.	***	N.S.	N.S.	N.S.

N.S. = Not significant

*** = Significant at the 1% probability level

No significant operator effects were found (Table 3.6) indicating that even relatively untrained operators can use these methods. The interactions DA x OP, DA x ME and OP x ME were all non-significant.

The methods were significantly different for the Decreaser, Increaser I, Increaser II, and veld condition scores (Table 3.6). In all cases these differences can be attributed to low scores obtained using the metric belt transect and 't Mannetje Haydock methods. These two methods resulted in a mean veld condition score which was 10% lower than that for the point or quadrat methods. Differences between the latter methods were small (2 - 3%).

3.4.7 A comparison of the methods using multivariate techniques

Ordination techniques have recently been proposed for interpreting the results of monitoring experiments (Mentis, 1984). Principal co-ordinates analysis (PCO) was used to examine the effects of the six methods on a sample by species ordination. PCO was chosen simply because the computer programmes were readily available.

The 36 plots represented the samples, and the 15 most common plants, the species. Since wheel point adjusted data would mask the true ordination picture, non adjusted data were used in the analysis. For brevity, only the plot of the first and second principal co-ordinates for each method are presented (Fig. 3.7). The first PCO shows that the quadrat, Levy bridge, step point and wheel point are most similar. Samples 13 and 7, and 12 and 30 at the two extremes of the axes illustrate this. The percentage variation accounted for by these methods was similar, ranging between 43,1 and 44,5 for the first two axes. The samples from the

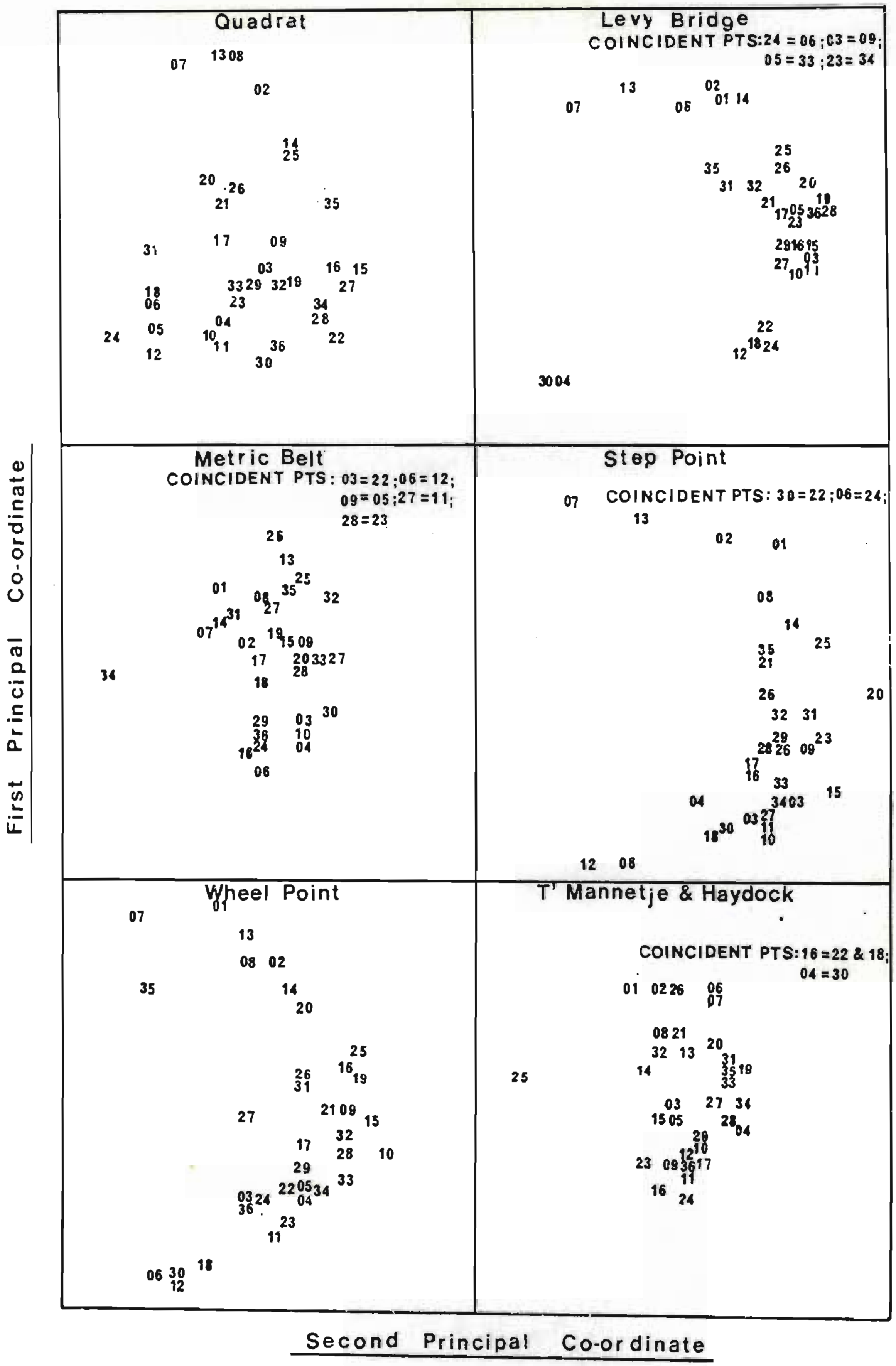


Figure 3.7 Ordination of the 36 plots for each method using non-standardized data.

metric belt and 't Mannetje & Haydock methods are more clumped when compared with the other methods. This indicates that these methods are not as sensitive as the others to ordination techniques.

Visual comparison of these diagrams is difficult and a measure of comparing the configuration obtained by the various methods was sought. This was achieved by using the method of 'Procrustes Rotation', where two configurations are compared by moving the centroid of the second configuration until it coincides with the first (Gower, 1971). After translation, the axes are orthogonally rotated and isotropically stretched until the distance between the samples is minimized. The figure obtained is a distance measure (residual) between the two configurations. In this study all combinations of configurations were compared in this way. The results (Table 3.7) confirmed the earlier observation that the configurations obtained using the wheel point, step point and Levy bridge were the most similar. The quadrat was similar to the step point and wheel point, with residuals of 0,4211 and 0,4095 respectively. The metric belt and 't Mannetje & Haydock methods did not compare favourably between themselves or with any of the other methods, their residuals being 0,92 for all comparisons.

3.5 Conclusions

Examination of various techniques reveals that species composition can be measured by one of four criteria: frequency of occurrence, number of individuals, area covered and mass (Brown, 1954). In this study at least one example of each has been compared. Although numerous studies have compared these methods (Brown, 1954; Johnstone, 1957; Walker, 1970; Poisson et <u>et al.</u>, 1973 and others) the present study differs from these in

TABLE 3.7 Results of the procrustes rotation (residuals) for all combinations of methods

Method	Quadrat	Levy bridge	Metric belt	Step point	Wheel point
Quadrat	-				
Levy bridge	0,7668	-			
Metric belt	0,9436	1,0063	-		
Step point	0,4211	0,4071	0,7966	-	
Wheel point	0,4095	0,5207	0,8966	0,3659	-
't Mannetje & Haydock	0,9232	0,9210	1,0573	0,9380	0,9279

two main respects. Firstly, relationships were sought between the methods and the raw data were standardised to make the comparisons more meaningful. Secondly, for the point methods the nearest plant technique rather than basal cover was used to estimate species composition. This removes any bias associated with determining a strike as well as greatly increasing the efficiency of these methods.

The results of this study show that area covered (metric belt) and weight methods ('t Mannetje & Haydock) are not suitable for detailed botanical analysis. The choice therefore is between measuring frequency of occurrence (quadrat) or proportional species composition (point methods). The results of the analysis of variance showed that while there was little difference between the quadrat, the wheel point and the Levy bridge, the least biased frequency distributions were obtained using the wheel point.

Frequency data can be used as a basis for defining the limits of communities. However, since they only supply information about the presence or absence of species, frequency data are not the best method for determining changes in the relative proportion of species of a particular site. Frequency readings can be converted to density through the logarithm of percentage absence, which will provide exact information for investigating critical and intensive vegetation changes (Brown, 1954).

Unfortunately this relationship only applies to species which are randomly distributed, a situation rarely found in the field. Because frequency is measured using quadrats, problems associated with selecting optimum quadrat sizes are encountered. In addition the disturbance caused by placing the quadrat in position and the difficulty of deciding whether a plant occurs in or out may create edge effects (Tothill, 1978).

The point methods are free of problems associated with quadrat size. Of the three point methods assessed in this study the wheel point was the most consistent, followed by the Levy bridge. Although the wheel point has been shown to be the most suitable method, it does have the disadvantage of requiring three people to operate it. In situations where three people cannot be afforded the Levy bridge could be substituted.

Most studies comparing different methods of measuring species composition agree that the choice of method depends on the objectives and precision required (Walker, 1970; Becker & Brockett, 1973). However, the mathematical relationships developed in this study enable the wheel point data to be easily converted to the parameters measured by other methods. Similar relationships were found by Poissonet et al. (1973) in dense herbaceous vegetation. The results obtained in the present study (together with the applicability of the mathematical relationships) have shown that the wheelpoint is the best method for monitoring grassland vegetation in the Natal Drakensberg.

3.6 Summary

(i) An evaluation of sampling techniques was conducted on Highland Sourveld in the Natal Drakensberg. The quadrat, Levy bridge, step point, metric belt transect and 't Mannetje & Haydock methods were used. In order to compare the methods the scores were standardized against the wheel point.

(ii) Analysis of variance showed that the methods were significantly different for most species examined. These differences are attributable to low values recorded using the metric belt transect and 't Mannetje & Haydock methods. Operator differences and time of day had little effect on the results.

(iii) The frequency distributions obtained for each species using the different methods showed that the best distributions were obtained using the wheel point.

(iv) Principal co-ordinates analysis was used to examine the effects of the six methods on a sample by species ordination. The results indicate that the metric belt transect and 't Mannetje & Haydock methods are not as sensitive to ordination techniques as the other methods.

(v) It is concluded that the wheel point method is most suitable for determining grassland species composition in the Natal Drakensberg.

CHAPTER 4

THE EFFECTS OF THIRTY YEARS OF BURNING ON SPECIES COMPOSITION

4.1 Introduction

In their review of fire in grasslands, Tainton & Mentis (in Booysen & Tainton, 1984) conclude that fire has played a major role in the development and maintenance of grassland communities in the montane grassland regions of South Africa. Controlled burning is therefore the logical form of management of this ultra-sensitive environment. Watson (1981) reports that controlled burning of Themeda triandra dominated grassland communities may modify the structural and functional dynamics of the floral constituents. At the Cathedral Peak Forest Research Station a number of different fire treatments have been applied to the grassland over the past thirty years. These experiments provided an ideal opportunity for examining the effects of various long term burning treatments on the species composition of Highland Sourveld.

4.2 Procedure

The research catchments are protected by permanent firebreaks which have been burnt annually in winter for the last thirty years. This winter treatment was used as a control against which the other treatments were compared. The location of the firebreaks between the treatments enabled the demarcation of 14 paired plots and 6 triplicate plots having a wide range of treatments, aspects, slopes and altitudes (Table 4.1 & Fig. 2.2). Direct comparison of all combinations of treatments over most land facets represented in the research area was therefore possible.

TABLE 4.1 Treatments and topographical characteristics of the different plots

Plot	Treatment	Altitude (m)	Slope	Aspect
1a	Annual winter burning	1 960	17° 40'	13°
1b	Biennial spring burning + grazing		16° 0'	12°
2a	Annual winter burning	1 905	4° 0'	338°
2b	Biennial spring burning + grazing		2° 30'	350°
3a	Annual winter burning	1 890	12° 40'	235°
3b	Biennial spring burning + grazing		16° 30'	174°
4a	Annual winter burning	1 875	20° 0'	132°
4b	Biennial spring burning + grazing		20° 40'	140°
5a	Annual winter burning	1 875	12° 0'	330°
5b	Biennial spring burning + grazing		12° 40'	310°
6a	Annual winter burning	1 829	37° 0'	354°
6b	10 yrs protection	1 800	25° 20'	350°
6c	10 yrs protection	1 768	4° 40'	13°
7a	Annual winter burning	1 890	1° 10'	270°
7b	Biennial spring burning		0° 40'	275°
8a	Annual winter burning	1 829	12° 30'	164°
8b	Unknown protection		8° 20'	157°
9a	Annual winter burning	1 960	21° 0'	75°
9b	Biennial spring burning		21: 10'	62°
9c	18 yrs protection		22° 0'	83°
10a	Annual winter burning	1 900	3° 50'	84°
10b	Biennial spring burning		3° 30'	103°
10c	18 yrs protection		1° 10'	83°
11a	Annual winter burning	1 890	15° 0'	297°
11b	Biennial spring burning		11° 40'	301°
11c	18 yrs protection		14° 20'	298°
14a	Annual winter burning	2 280	35° 0'	343°
14b	20 yrs protection		32° 40'	343°
15a	Annual winter burning	2 130	29° 30'	165°
15b	Biennial spring burning		17° 40'	186°
16a	Annual winter burning	2 130	31° 0'	17°
16b	Biennial spring burning		31° 40'	17°
17a	Annual winter burning	1 980	7° 10'	80°
17b	Biennial spring burning		11° 30'	162°
18a	Annual winter burning	1 965	22° 40'	347°
18b	Biennial spring burning		19° 20'	340°
18c	5 yrs protection		27° 10'	342°
19a	Annual winter burning	1 900	7° 20'	348°
19b	Biennial spring burning		9° 20'	336°
19c	5 yrs protection		10° 40'	6°
20a	Annual winter burning	1 920	16° 30'	280°
20b	Biennial spring burning		12° 40'	275°
21a	Annual winter burning	1 950	11° 0'	40°
21b	Biennial spring burning		15° 40'	12°
22a	Annual winter burning	1 829	22° 30'	210°
22b	Biennial spring burning		24° 40'	196°

A ten point bridge (with points spaced 150 mm apart) was used to derive estimates of species composition. Two hundred point positions were sampled in plots of 25 X 25 m. The data were then compared against a benchmark site. This site represented vegetation considered to have optimal species composition and basal cover in terms of the management objectives of the area. Sample sites were scored against this benchmark to determine the veld composition score according to Tainton, Edwards & Mentis (1980). This method classifies plants into four ecological groups: Decreaser species which decrease in abundance with lenient utilization (in the context of the mountain catchments this implies infrequent defoliation) or heavy utilization (frequent defoliation); Increaser I species which increase with lenient utilization; Increaser II species which increase with heavy utilization and Increaser III species which increase with selective grazing. Mentis & Collinson (1979) have described the use of this technique for managing natural areas. They suggest that maximising on-site species diversity implies fair to good veld condition, and therefore little soil-loss.

Recently the identity and membership of the ecological groups has been questioned since no formal objective techniques of ordination and classification have been applied (Mentis, 1980). In the present study important species were ordered by both the methods of direct and indirect gradient analysis (Gauch, 1982).

4.3 Results and Discussion

The mean proportional species composition for the annual winter burn, biennial spring burn with grazing, biennial spring burn and protected treatments are presented in Table 4.2. The effects of these treatments

TABLE 4.2 Mean species composition of the benchmark site and different burning treatments at Cathedral Peak

Treatment	Benchmark	Protection	Annual winter burning	Biennial spring burning	Biennial spring burning + grazing
DECREASER					
Themeda triandra	31.5	18.9	29.2	25.5	28.3
Trachypogon spicatus	10.8	2.1	6.4	7.9	7.3
Heteropogon contortus	10.31	0.9	6.0	3.4	6.9
Diheteropogon amplectans	3.4	1.2	2.3	1.7	1.3
Panicum natalense	0.0	0.1	0.5	0.4	0.2
Monocymbium ceresiiforme	0.1	-	0.5	0.4	-
Eragrostis capensis	0.0	-	0.4	0.5	0.9
Stiburus alopecuroides	0.1	-	0.3	-	-
Eragrostis racemosa	0.0	-	2.7	0.4	1.4
INCREASER I					
Tristachya leucothrix	16.8	17.9	8.1	12.2	9.3
Alloteropsis semialata	0.0	14.7	5.0	6.5	6.5
Andropogon apendiculatus	1.3	1.1	0.2	1.4	-
Harpechloa falx	4.9	12.3	3.0	6.6	5.8
Cymbopogon validus	0.0	0.3	-	-	-
Aristida monticola	0.0	0.5	-	-	-
Helictotrichon turgidulum	0.0.	0.1	-	-	-
Unidentified grass spp.	0.0	4.4	2.2	1.8	2.4
INCREASER II					
Hyparrhenia hirta	0.0	-	-	-	-
Microchloa caffra	0.1	0.2	1.0	0.8	1.0
Eragrostis curvula	0.0	-	-	0.2	-
Digitaria monodactyla	0.0	-	-	0.1	-
Spring forbs	10.5	5.7	3.3	2.3	3.2
Herbs	1.1	12.6	8.8	11.7	3.7
Sedges	4.0	1.3	12.8	5.2	9.8
INCREASER III					
Elionurus muticus	0.0	1.2	0.6	0.6	1.5
Diheteropogon filifolius	1.3	0.4	1.5	0.9	2.0
Koeleria cristata	2.8	3.7	2.0	3.5	1.1
Rendlia atera	0.0	0.6	3.0	4.6	7.4
Loudetia simplex	0.0	-	-	0.1	-
Festuca costata	0.0	-	0.3	0.7	-

on the mean relative proportion of the most important grass species are shown in Table 4.3. Only species whose mean composition exceeded 5% in any one treatment are included.

Themeda triandra, Heteropogon contortus, Tristachya leucothrix, Trachypogon spicatus, Harpechloa falx and Alloteropsis semialata were selected in this way. The responses of these species to fire frequency are shown in Fig. 4.1.

T. triandra, H. contortus and T. spicatus all decrease and T. leucothrix, A. semialata and H. falx increase in abundance with a decrease in defoliation frequency. These six species and the sample plots have been ordered by the methods of indirect gradient analysis using the technique of detrended correspondence analysis (Gauch, 1982). The results are presented in Fig. 4.2. Samples 1 to 19, 20 to 30, 31 to 35 and 36 to 40 represent the annual winter burn, biennial spring burn, biennial spring burn and grazing and protected treatments respectively. This ordination places similar entities in close proximity in a two dimensional space. The majority of the annual winter burn plots fall together to the right; biennial spring burn and grazing and biennial spring burn samples occupy a middle position and the protected plots ordinate to the left. The species ordination (Fig. 4.2) shows T. triandra, H. contortus and T. spicatus falling to the right on the first ordination axis and T. leucothrix, H. falx and A. semialata falling to the left. This difference in dominant species indicates a gradient from frequent burning to protection (Fig. 4.2) as was also shown by the sample ordination. Plot 44 appears to be an outlier. It is interesting to note that the period of protection for plot 44 (plot 44 in the sample ordination is plot 8b in Table 4.1) is unknown. It is possible that the protected period of

TABLE 4.3 The effect of the various burning treatments (with and without grazing) on the mean species composition (%) of the most important grass species

Species	Burning Treatment			
	Protection	Biennial Spring	Biennial Spring + Grazing	Annual Winter
Alloteropsis semialata	14.7	6.5	6.5	5.0
Tristachya leucothrix	17.9	13.2	9.3	8.1
Harpechloa falx	12.3	6.6	5.8	3.0
Themeda triandra	18.9	25.5	28.3	29.2
Trachypogon spicatus	2.1	7.9	7.3	6.4
Heteropogon contortus	0.9	3.4	6.9	6.0

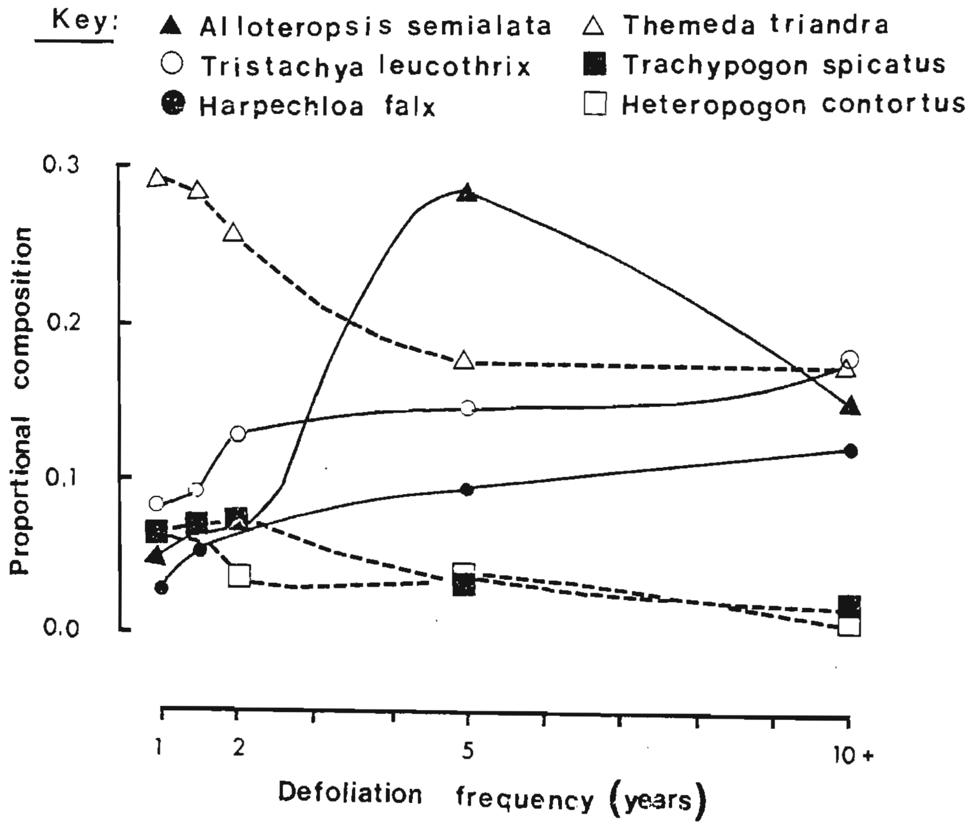


Figure 4.1 Response of the various species along a defoliation frequency gradient for Highland Sourveld. *T. triandra*, *T. spicatus* and *H. contortus* decrease in abundance and *H. falx*, *T. leucothrix* and *A. semialata* increase in abundance with decreasing defoliation frequency. The BS + G treatment is related at a mean frequency of 1,5 yr.

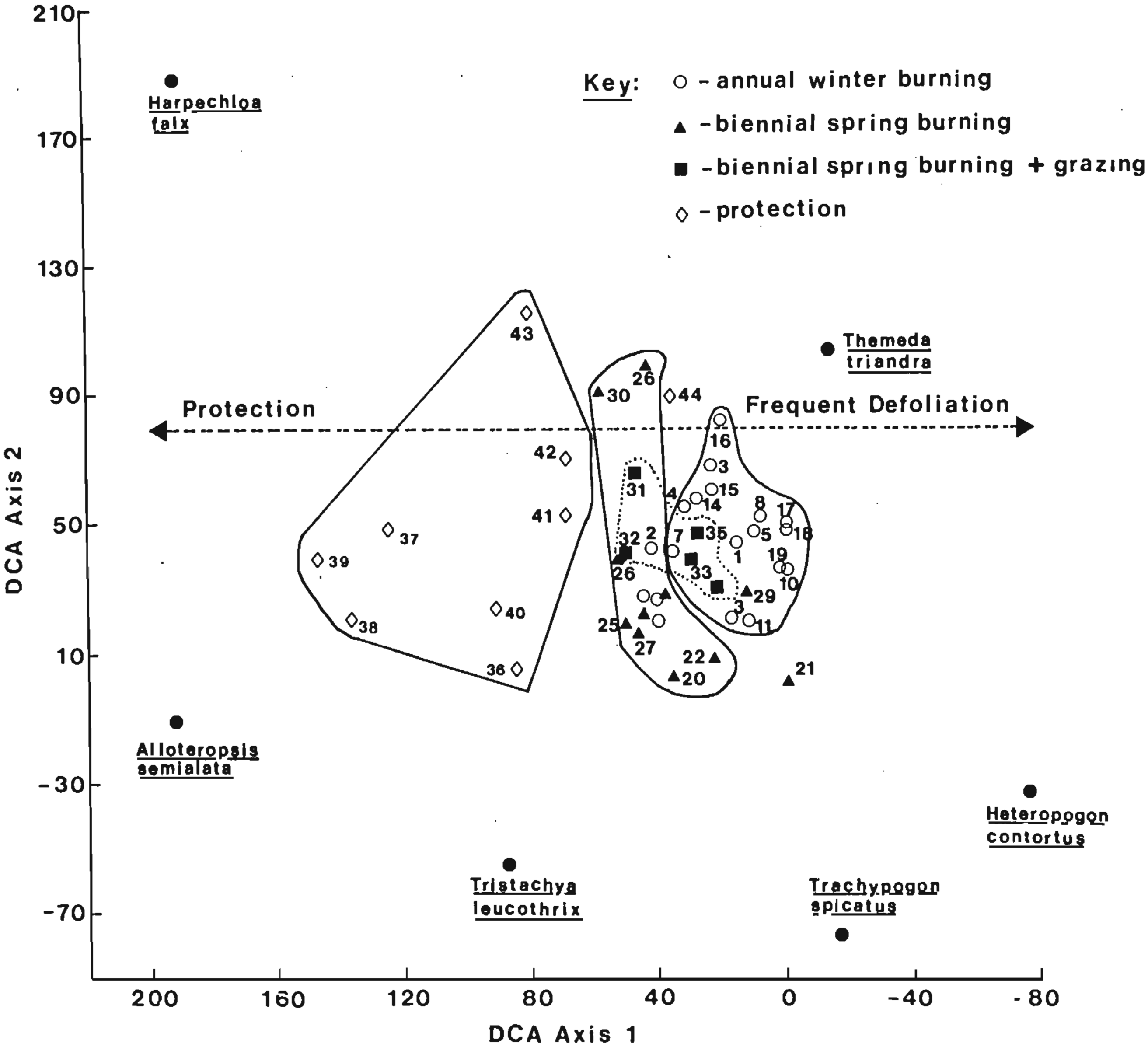


Figure 4.2 Detrended correspondence analysis (DCA) ordination of the Cathedral Peak samples and species. The first DCA axis represents a frequent-to-protection fire regime.

this plot has been too short for the species composition to move to the left on the ordination axis.

The second axis spreads the samples less than the first axis but the individual species are still widely separated. This spread may result from the environmental gradients of altitude, slope and aspect. However, sampling sites were not representative of sufficiently wide ranges in these factors to permit an explanation of the gradients which were recorded.

Both the direct and indirect ordinations confirmed the identity of the ecological groups Decreaser and Increaser I. Species not ordinated in this study were classified according to Tainton et al., (1980).

A least squares analysis in which the individual veld condition and group scores for each plot were adjusted to remove the effects of slope, altitude and aspect is shown in Table 4.4a. These results showed that veld composition scores in grassland protected from fire ($\overline{x}$ = 34,7) were significantly lower than those in the annual winter burn ($\overline{x}$ = 58,0), biennial spring burn ($\overline{x}$ = 56,6) and biennial spring burn and grazing ($\overline{x}$ = 66,3) treatments.

Differences in veld composition scores between the latter three treatments were non significant. It would appear therefore that a regular fire regime, whether in the winter or spring, will maintain the condition of these grasslands, whereas protection from fire resulted in a 42% drop in veld condition. Although differences in veld composition scores between the regularly burnt treatments were non significant, examination of the individual group scores (Tables 4.4 b-e) revealed significant

TABLE 4.4a Comparisons of veld composition scores between treatments

Treatment	Mean	Versus annual winter burning			Versus biennial spring burning + grazing			Versus biennial spring burning		
	$\bar{x}$	t	SE	Sig.	t	SE	Sig.	t	SE	Sig.
Annual winter burning	58.0		-							
Biennial spring burning + grazing	66.3	8.3	±7.2	NS		-				
Biennial spring burning	56.6	0.6	±5.0	NS	- 7.7	±8.7	NS		-	
Protection	34.7	-23.4	±5.4	xx	-31.7	±9.0	xx	-23.9	±5.9	xx

TABLE 4.4b Comparisons of Decreaser scores between treatments

Treatment	Mean	Versus annual winter burning			Versus biennial spring burning + grazing			Versus biennial spring burning		
	$\bar{x}$	t	SE	Sig.	t	SE	Sig.	t	SE	Sig.
Annual winter burning	48.8		-							
Biennial spring burning + grazing	52.0	3.2	±3.0	NS		-				
Biennial spring burning	36.6	-12.2	±2.1	xx	-15.4	±3.7			-	
Protection	26.2	-22.5	±2.2	xx	-25.7	±3.8	xx	10.4	±2.5	xx

TABLE 4.4c Comparisons of Increaser I scores between treatments

Treatment	Mean	Versus annual winter burning			Versus biennial spring burning + grazing			Versus biennial spring burning		
	$\bar{x}$	t	SE	Sig.	t	SE	Sig.	t	SE	Sig.
Annual winter burning	17.3		-							
Biennial spring burning + grazing	23.4	6.1	±4.2	NS		-				
Biennial spring burning	26.4	9.1	±2.9	xx	3.0	±5.1	NS		-	
Protection	45.8	28.6	±3.1	xx	22.5	±5.2	xx	19..5	±3.4	xx

TABLE 4.4d Comparisons of Increaser II scores between treatments

Treatment	Mean	Versus annual winter burning			Versus biennial spring burning + grazing			Versus biennial spring burning		
	$\bar{x}$	t	SE	Sig.	t	SE	Sig.	t	SE	Sig.
Annual winter burning	32.9		-							
Biennial spring burning + grazing	20.8	-12.1	±4.5	x		-				
Biennial spring burning	31.2	- 1.6	±3.1	NS	10.5	±5.5	NS		-	
Protection	31.3	- 1.6	±3.4	NS	10.5	±5.6	NS	0.1	±3.7	NS

TABLE 4.4e Comparisons of Increaser III scores between treatments

Treatment	Mean	Versus annual winter burning			Versus biennial spring burning + grazing			Versus biennial spring burning		
	$\bar{x}$	t	SE	Sig.	t	SE	Sig.	t	SE	Sig.
Annual winter burning	8.4		-							
Biennial spring burning + grazing	8.4	0.1	±0.3	NS		-				
Biennial spring burning	8.8	0.4	±0.2	NS	0.4	±0.4	NS		-	
Protection	8.1	-0.4	±0.2	NS	0.4	±0.4	NS	0.8	±0.3	xx

treatment differences. For example, treatment means for the Decreaser species were 48,8% in the annual winter burn; 52,0% in the biennial spring burn and grazing; 36,6% in the biennial spring burn and 26,2% in the protected treatments (Table 4.4 b). Comparisons between these treatments were significant at the 1,0% probability level, with the exception of the annual winter burn versus biennial spring burn and grazing treatments. This implies that in order to maintain a high proportion of Decreaser species, defoliation needs to be more frequent than once in two years.

Similar differences were apparent when comparing the mean Increaser I scores between treatments viz. annual winter burn = 17,3%; biennial spring burn and grazing = 23,4%; biennial spring burn = 26,4%; protection = 45,8% (Table 4.4 c). Here, all comparisons against the protected treatment in addition to the biennial spring burn versus annual winter burn were significant at the 1,0% probability level. Thus, both infrequent burning in the absence of grazing, and complete protection, resulted, not unexpectedly, in a high percentage of Increaser I species. Comparison of the Increaser II and Increaser III scores (Tables 4.4 d & 4.4 e) generally showed no significant differences between treatments. Since there has been no heavy utilization or selective grazing at Cathedral Peak it is not surprising that no differences were found in the proportion of Increaser II and III species.

It would appear that the ecological groups, Decreaser and Increaser I are responding along a gradient of defoliation frequency (from annual or biennial burning with grazing to protection). The theory of classical succession or relay floristics assumes that each group of species modifies the site conditions so that it becomes less suitable for its own persistence and more suitable for its successor (Clements, 1936). However the existence of all the important grass species in each plot (Table 4.2) would rather support Egler's (1954) initial floristic composition theory. Thus species shifts reflect the gradual emergence and dominance of species which may have been present but inconspicuous prior to the burning treatment.

By using data collected by Killick (1963) in 1950 for catchment IV it is also possible to examine changes in species composition within treatments over the past 30 years. A comparison between the species composition found by Killick in 1950 and that found in the present study is shown in Table 4.5.

Killick used a wheel point apparatus and only recorded basal strikes. His basal cover figures have therefore been converted to reflect the relative proportions of the different species present. Data from plot 6 (the closest protected site to C IV) have also been included to illustrate the effects of protection on the species composition. Linear correlation between the 1950 and 1980 data showed that $r = 0,86$; $p < 0,001$ for the biennial spring burn treatment and that $r = 0,87$, $p < 0,001$, for the annual winter burn treatment (Table 4.5). From these data it is apparent that 30 years of biennial spring or annual winter burning have had no significant effect on the species composition. However, the correlation between the protected treatment and the 1950 data ($r = 0,05$) was non significant. Although not a repeat survey of the same site, the data nevertheless suggest changes which may have occurred with protection. For instance, the percentage Decreaser species found at this protected site was only 4,5% compared with 49,5% found in C IV in 1950. This decrease was particularly noticeable in *T. triandra* which dropped

TABLE 4.5 Comparison between the species composition of Catchment IV found by Killick (1950) and the present study (1980)

Species	C IV (Killick 1950)	C IV, 1980 (30 years biennial spring burning)	C IV, firebreak (30 years annual winter burning)	Plot 6, (10+ years protection)
DECREASER				
Themeda triandra	25,8	27,5	28,0	1,0
Trachypogon spicatus	13,0	4,0	3,8	3,0
Heteropogon contortus	9,8	12,0	11,3	0,5
Eragrostis racemosa	0,1	0,0	3,8	0,0
Diheteropogon amplectens	0,0	1,0	1,0	0,0
Monocymbium ceresiiforme	0,8	0,0	2,5	0,0
TOTAL	49,5	44,5	50,4	4,5
INCREASER SPECIES				
Tristachya leucothrix	11,0	11,0	9,3	24,5
Harpechloa falx	7,3	3,5	2,5	16,5
Rendlia altera	7,3	1,5	5,0	0,0
Diheteropogon filifolius	0,0	2,0	4,0	1,0
Alloteropsis semialata	6,9	13,5	3,3	21,0
Microchloa caffra	0,0	2,5	0,0	0,0
Koelaria cristata	1,6	4,5	0,5	7,5
Elyonurus muticus	3,9	0,0	0,0	5,5
Andropogon apendiculatus	2,0	0,0	0,0	0,0
Eragrostis capensis	0,0	0,0	0,0	12,5
TOTAL	40,0	38,5	24,6	88,5

Catchment IV 1950 compared to C IV 1980 : $r = 0{,}86$; $p = < 0{,}001$

Catchment IV 1950 compared to firebreak 1980: $r = 0{,}87$; $p = < 0{,}001$

Catchment IV 1950 compared to plot 6 1980 : $r = 0{,}05$; p = Not significant from 25,8% to 1,0%. In addition there was a marked increase in Increaser I species. This is reflected in A. semialata which increased from 6,9% to 21,0%. Similar changes were found by Granger (1976), who noted a striking decrease in the abundance of T. triandra in Catchment IX and an increase in Andropogon appendiculatus. He also noted an increase in A. semialata in the grass dominated communities of C IX.

4.4 Conclusion

The general conclusion which can be drawn from these experiments, is that 30 years of veld burning has not resulted in a significant change in the veld condition of Highland Sourveld burnt annually in winter, biennially in spring or biennially in spring with light summer grazing. However, even after short periods of protection (only 5 years) there has been a change in species composition. Particularly noticeable is the decrease in T. triandra and increase in A. semialata, with a corresponding drop in veld condition. In order to maintain natural areas of Highland Sourveld in optimal condition (implying maximum species diversity and minimal soil loss) it is obvious that a regular fire regime is essential.

These results support the view that the ecological groups (Decreaser and Increaser I) can be arranged along a successional axis, with defoliation frequency as the experimental variable. The evidence presented also suggest that annual winter and biennial spring burning with and without light summer grazing is capable of maintaining the status quo in these mountain grasslands.

4.5 Summary

i) A veld condition assessment was used to determine the effect of past burning treatments on the species composition of Highland Sourveld at Cathedral Peak.

ii) Veld condition scores in grassland protected from fire were significantly lower than where veld had been burnt or burnt and grazed at regular intervals.

iii) Frequent defoliation was found to maintain the grassland composition largely unchanged over a period of 30 years.

iv) Individual species were found to react strongly to defoliation frequency.

v) The results support the view that the ecological groups (Decreaser and Increaser I) can be arranged along a successional axis, with defoliation frequency as the experimental variable.

CHAPTER 5

POPULATION DYNAMICS OF SELECTED GRASS SPECIES IN RELATION TO BURNING IN THE NATAL DRAKENSBERG

5.1 Introduction

In spite of a long history of burning, and current practices of applying prescribed fire regimes to montane grasslands, there remains little factual data on the responses of vegetation to fire.

Early work in this field addressed the developmental behaviour of individual tillers and the influence of defoliation treatments on their development (Booysen, Tainton & Scott, 1963; Tainton & Booysen, 1963; Tainton, 1964; Tainton & Booysen, 1965). Similar work on developmental tiller morphology in relation to burning and grazing was carried out in the semi-arid grassveld in the Eastern Cape (Danckwerts, Aucamp & Du Toit, 1984) and the Eastern Transvaal (Rethman, 1971).

Results from the present study (Chapter 4) show that individual species react markedly to the frequency of burning. In particular *Themeda triandra*, *Heteropogon contortus* and *Trachypogon spicatus* decreased in abundance with infrequent burning while *Tristachya leucothrix*, *Alloteropsis semialata* and *Harpechloa falx* increased. The reasons for such differential responses are unknown. It was hypothesized in this study that changes in the relative abundance of these grass plants are brought about by changes in the birth and death rates of tillers as a direct result of fire (or its absence). An elaboration of these changes could, hopefully, lead to general principles which could be applied across all species, and would therefore provide valuable information which could be used in the design of scientific management programmes for these grasslands. The objective of this investigation was to monitor the population dynamics of the above species in order to test the above hypothesis.

Studies of this nature can operate at two levels: counting of 'individuals' (genets) or counting of sub-units (tillers) within a plant (Harper & White, 1974; Harper, 1977). Since species abundance is often better represented by number of tillers than genets, tillers were used as the ecological unit of growth in this study. As far as the author is aware, with the exception of Themeda triandra and Tristachya leucothrix, there are no similar demographic data for the species examined in this study. Comparisons between the present and other studies were therefore not possible.

5.2 Methods

On a representative area of veld two paired plots (25 X 25 m) were each subdivided into 25 sub-plots (5 X 5 m). Within each sub-plot, two tufts of each of T. triandra, H. contortus, T. spicatus, T. leucothrix, A. semialata and H. falx were randomly located and marked with wire stakes to facilitate relocation. The treatment allocated to the paired plots were annual winter and biennial spring burning.

The annual winter burn treatment was applied in July 1979, June 1980 and July 1981. The biennial spring burn treatment was applied in October 1979 and October 1981. In November 1979 five tillers were tagged on each of the two marked tufts within each sub-plot, resulting in a total of 250 tagged tillers on each species within each plot. Only newly emerged tillers were tagged to represent an even aged population or cohort. Initially the tillers were tagged with 5 mm plastic sleeving. Prior to the treatment burns this was replaced with wire tags covered with asbestos string. As young tillers of A. semialata are enclosed in the leaf sheaths of the parent plant they were impossible to locate without damaging the parent plant. This species was therefore omitted from the study.

In the initial phase of the programme a number of new tufts were marked and tagged to compensate for tillers that died. This enabled sufficient marked tillers to last the entire study period.

The relocation of individual tillers was aided by silver tags placed on the edge of the tuft next to the tagged tiller. In addition, a detailed map was drawn showing the position of each tuft and records were kept on each tiller (i.e. whether removed by sampling, dead, live or lost). Thus the fate of virtually every tiller could be followed throughout the study period.

Collecting marked tillers commenced in December 1979 and continued to March 1982 (a period of 27 months). Five tillers were removed randomly from each plot approximately every fortnight until growth ceased in winter. Thereafter sampling proceeded at monthly intervals until growth commenced in the next spring.

The tillers collected were dissected and the following characteristics recorded:

(a) height of main shoot apex;

(b) dry mass (living and dead material combined);

(c) presence of flowers;

(d) number of lateral (secondary) tillers;

(e) mean mass of secondary tillers.

A total count of all living tillers was also carried out before and after each treatment burn. This enabled the calculation of mortality rates in both plots. To test whether the difference in the mortality of a species in the different treatments was significant, the following formula (Clarke, 1985 pers. comm.) was applied:

$$u = \frac{P_1 - P_2}{\frac{P_1(1 - P_1)}{n_1} + \frac{P_2(1 - P_2)}{n_2}}$$

where u (standardized normal variate) was significant at 5% if $> 1{,}96$ and 1% if $> 2{,}54$. P_1 and P_2 were the proportions dying (i.e. number dead divided by the expected number living) and n_1 and n_2 were the number of living tillers.

Two additional plots were included in the experiment in 1980, their respective treatments being summer and early winter burning. The procedure was the same as that already described, with the exception that only tufts of T. triandra were tagged. Sampling in these plots commenced in December 1980 and continued to March 1982 (a period of 16 months).

5.3 Presentation of Results

In this study graphical representation of the raw data was considered to be most suitable for illustrating the developmental morphology of the species (Clarke, 1985; pers. comm.).

Because the study was continued over a 27-month period, it was possible to follow the fate of uniform aged populations of tillers from birth to death. The data were used to construct life tables similar to those used by Silvertown (1982), in which the important events in a population are summarized.

The first column in these tables (eg. Table 5.1) shows the age interval. The second column records the length in days between two successive censuses, and the third column records the number of survivors (Nx), present at the beginning of an age interval. Survivorship (ℓx) is calculated as the proportion surviving to day x. The average mortality rate per day, qx, is obtained by dividing the number dying, dx, during an interval by the length of the interval, Dx.

In order to predict the fate of successive cohorts of tillers from the raw data, a transition matrix model was used, based on the Leslie Matrix (Leslie, 1945; 1948). These models are deterministic and are based on the age distribution of the population, predicting the distribution of age classes at successive intervals.

The Leslie matrix places the numbers of individuals in the different classes of the population in a column vector (a) in which the numbers of each age class of the population are one unit older each row down the vector. This is premultiplied by a transition matrix (A) of fertility rates (F) and probability (P) of surviving to the next class corresponding to classes in the column vector.

$$\begin{array}{ccc} A & & a \\ \begin{bmatrix} F & F & F & \cdots\cdots & F & F \\ P & 0 & 0 & \cdots\cdots & 0 & 0 \\ 0 & P & 0 & \cdots\cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots\cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots\cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots\cdots & P & 0 \end{bmatrix} & \times & \begin{bmatrix} N \\ N \\ N \\ \cdot \\ \cdot \\ N \end{bmatrix} \end{array}$$

The product of multiplication is the column vector a_{t+1}, representing the population structure after one unit of time,

$$Aa_t = a_{t+1}.$$

5.4 Results and Discussion

In the following section the overall reaction of the tillers of each species to fire is dealt with individually. Comparisons between species are highlighted in the general discussion.

5.4.1 Themeda Triandra

5.4.1.1 Primary tiller mass

The mean mass of primary tillers of *T. triandra* burnt annually in winter and biennially in spring is illustrated in Fig. 5.1 a. Tillers from both treatments increased in mass from December 1979, reaching a maximum of 0,15 g in April/May 1980. After the frosts in April, tiller mass decreased. From spring (September) tiller mass increased rapidly, reaching a maximum of 0,23 g (February) and 0,21 g (April) in the biennial spring and annual winter burn treatments respectively.

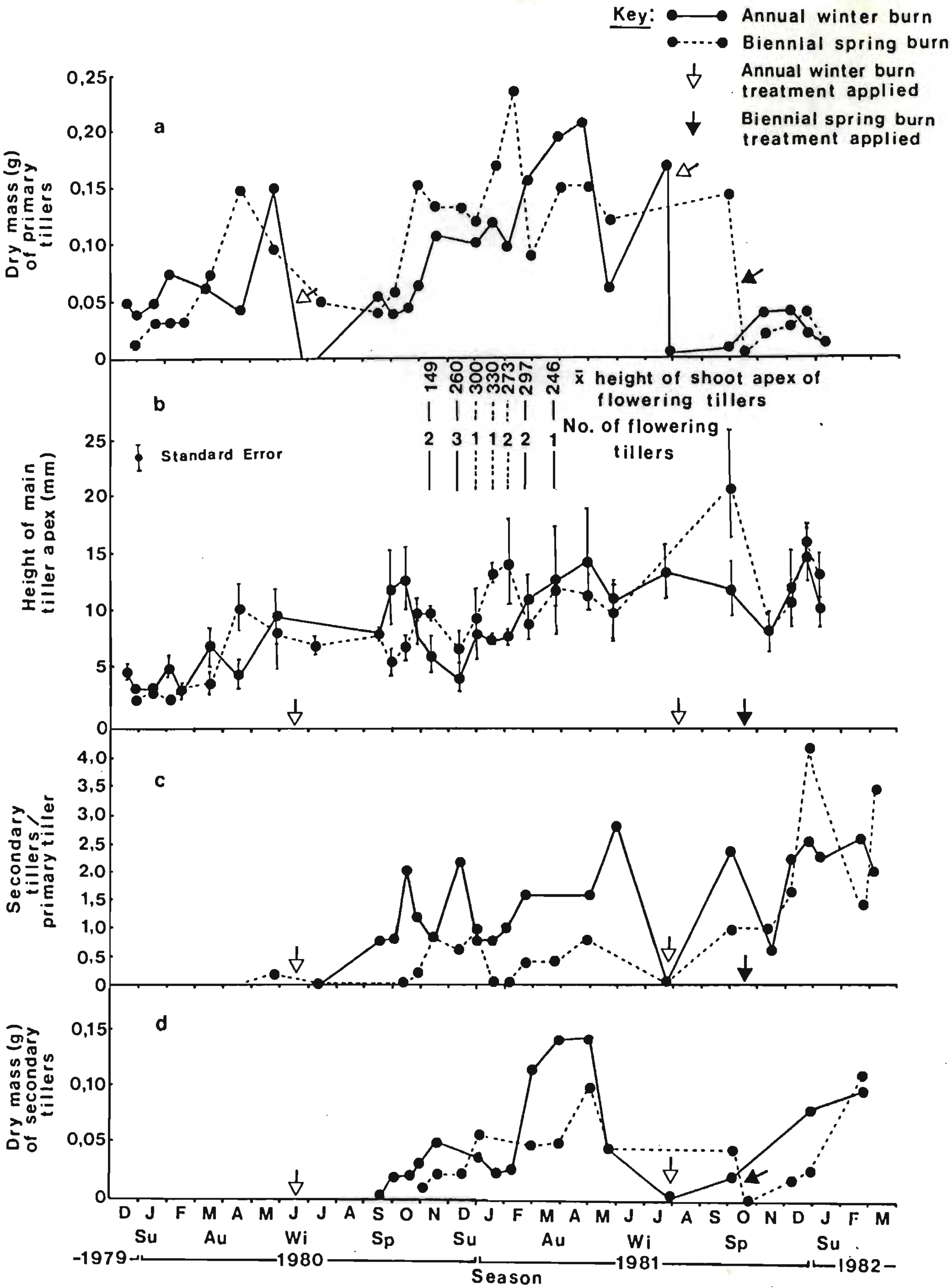


Figure 5.1 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of *Themeda triandra* subjected to annual winter and biennial spring burn treatments.

Similar results were obtained by Danckwerts _et al_., (1984) who recorded a mass of 0,14 g for _T. triandra_ tillers growing in a winter mow treatment in the False Thornveld of the Easter Cape. Tiller mass followed similar trends in both treatments during the 1980/81 growing season. In the following season however, only the basal sections, which continued to support daughter tillers, remained and little increase in tiller mass was recorded, indicating that irrespective of these treatments, primary tillers had a life span of two years.

Growth of primary tillers in the summer and early winter burn treatments is illustrated in Fig. 5.2 a. Both plots were initially burnt in July 1980 to synchronize treatments. Although growth commenced in spring, a uniform population of new tillers could only be recognized and tagged in December 1980. Following this, tiller mass increased until January 1981, reaching a maximum of approximately 0,15 g. From mid February until late April tiller mass decreased to 0,08 g per tiller. Here the early winter burn treatment resulted in complete removal of the above ground material. Following the dormant winter period, growth resumed in spring 1981 with tiller mass again reaching a maximum of approximately 0,15 g in both treatments. As the tillers were already established, this peak was recorded two months earlier than in the 1980 season. Tiller mass then decreased steadily in the early winter treatment until early March.

The summer burn treatment was applied on 21.12.1981, resulting in a sharp decline in tiller mass. In those tillers that survived, growth was resumed in January, reaching a value of 0,18 g in early March.

5.4.1.2 Elevation of shoot apices

In the first growing season (December 1979 to the end of May 1980) the

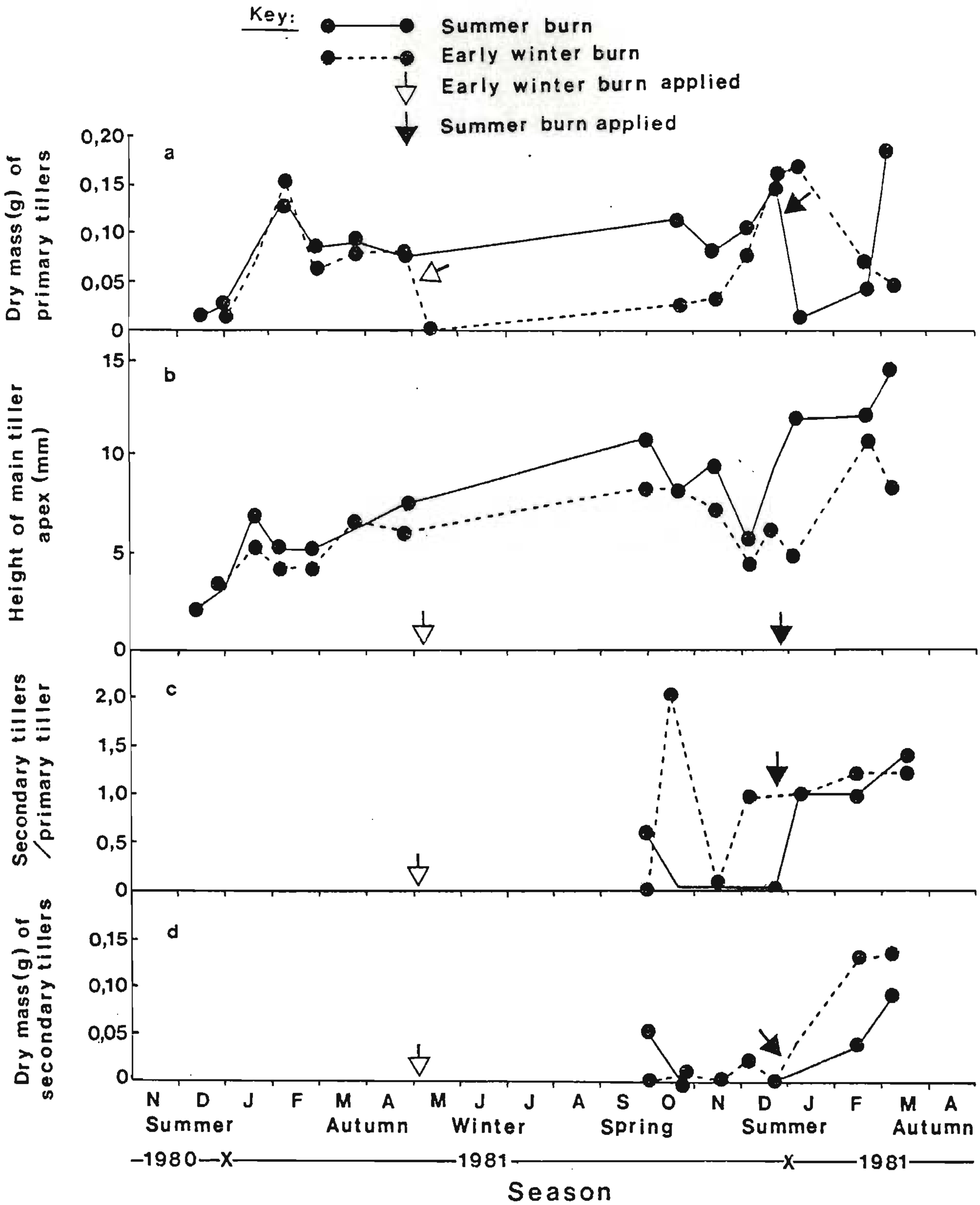


Figure 5.2 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of Themeda triandra subjected to early winter and summer burn treatments.

shoot apices of tillers in the annual winter and biennial spring burn treatments were elevated to only 10 mm above the soil surface (Fig. 5.1 b). Tillers that remained vegetative generally did not elevate their shoot apices beyond 12 mm throughout the rest of the study period. Nevertheless, they continued to grow during the flowering and post-flowering period (Fig. 5.1 a) and produced the bulk of the above ground living material. These results are very similar to those of Rethman (1971), who was working at similar altitudes in the Transvaal highveld. As pointed out by Rethman (1971), elevation of apices during summer in the highveld is much slower than at the lower altitudes in which Tainton & Booysen (1963; 1965) worked, where shoot apices reached 90 mm by the end of the growing season.

During the study period a high proportion of vegetative to fertile tillers was recorded, even at the peak flowering period. In the annual winter burn treatment this ratio was 31 : 1, while in the biennial spring burn treatment the ratio was 62 : 1. Similar results were found by Tainton & Booysen (1963), where the ratio of vegetative to fertile tillers for *T. triandra* was 47 : 1. The heights of fertile and vegetative shoot apices are presented separately (Fig. 5.1 b). Inflorescences were elevated to approximately 300 mm above the soil surface. Unfortunately, the sampling technique used did not allow the exact determination of time of flowering. Thus inflorescences sampled in March could have been produced earlier in the season. However, it would appear that the majority of tillers that produced flowers, did so between November and February.

The results indicate that tillers in the annually burnt treatment produced more inflorescences (8) in the season following a burn than those in the biennially burnt treatment (4) in their second year after a burn. These results imply, contrary to common observation, that the annual winter burn did not adversely affect initiation and survival of inflorescences. Also, the data showed that, at least in the tiller cohort which was investigated, flowering did not occur in the season following initiation. Tillers flowered only in the second season after initiation. These results are, however, inconclusive as so few fertile tillers were recorded.

The height of shoot apices in the early winter and summer burn treatment followed similar trends to the annual winter and biennial spring burn treatments. Shoot apices elevated to approximately 7 mm in the first season (1980/81) and only increased to approximately 12 mm in the 1981/82 season (Fig. 5.2 b). No flowers were recorded on marked tillers in either of these treatments. Season of burn therefore had no positive effect on flowering. From the results of this investigation it would appear that flowering is of minimal importance for the propagation of *T. triandra* plants in the Highland Sourveld of Natal.

5.4.1.3 Secondary tiller development

In the 1979/80 growing season, no secondary tillers were produced from marked primary tillers in either the annual winter or the biennial spring treatment (Fig. 5.1 c). Development of secondary tillers in the annual winter burn treatment commenced in mid-September, and continued through to the end of the growing season in May 1981. During this period primary tillers produced an average of 0,8 to 2,8 secondary tillers. In the biennial spring burn treatment however, fewer secondary tillers were produced (0-1,0). Annual winter burning thus appeared to stimulate production of secondary tillers during the first growing season. Similarly, Tainton & Booysen (1963) found that the average number of secondary tillers produced on each primary tiller of T. triandra was greatest in burnt plots and least in rested plots. Tiller production ceased in both treatments with the onset of winter.

In the following growing season, primary tillers in the annual winter burn treatment carried approximately 2,5 laterals per primary tiller. In contrast, the number of lateral tillers on primary tillers in the biennial spring burn treatment increased to 4,15 following the treatment burn in October 1981. This difference in tillering rate may be due to a greater accumulation of food reserves during the two year inter-burn period in plants burnt biennially in spring. In spite of this increase, it is apparent from Fig. 5.1 c that the average number of secondary tillers carried by primary tillers during the 27 months study period was higher in the annual winter burn treatment. Similar results were found by Tainton & Booysen (1965), where veld burnt in early spring after a two year rest, produced a large number of lateral tillers (3,1 per primary tiller) immediately after the burn.

The development of secondary tillers from T. triandra plants burnt in early winter and summer is shown in Fig. 5.2 c. During the first growing season (1980/81) no secondary tillers were produced in either treatment. These results, together with those of the annual winter and biennial spring burn treatment, indicate that primary tillers need to reach a certain stage of maturity before they produce basal secondary tillers.

During the second growing season (1981/82), the number of secondary tillers in the early winter burn treatment had reached a maximum of 2 by October. After decreasing sharply in November to zero through tiller death, initiation continued to produce about 1 per parent during the rest of the season. In contrast, the rate of tiller initiation was low in the summer burn plot until the treatment burn was applied in mid December. Although the number of secondary tillers increased to approximately 1,4 by the end of the season, the high mortality rate of the primary tillers necessitated the termination of the experiment in March 1982.

5.4.1.4 Mass of secondary tillers

The mass of secondary tillers produced in the annual winter burn treatment was generally higher than that of the biennial spring burn treatment during their first growing season (Fig. 5.1 d). The treatment burns appeared to have no marked effect on mass of these tillers by the end of their second growing season.

In contrast, the summer burn treatment applied in December resulted in a low secondary tiller mass in the early growing season (Fig. 5.2 d). This treatment was so severe that by the end of the growing season these tillers had not recovered fully. They were on average approximately 0,4 g less than the secondary tillers in the early winter treatment, which had steadily increased in mass during the growing season.

5.4.1.5 Population dynamics of _T. triandra_ subjected to various burning treatments

Life tables and survivorship curves of _T. triandra_ subjected to various burning treatments are presented in Table 5.1 and Fig. 5.3 respectively. For comparative purposes the annual winter, biennial spring and summer burn treatments have been plotted on the same axes. The data for the early winter burn treatment were incomplete and were excluded.

TABLE 5.1 Life tables of populations of *Themeda triandra* subjected to annual winter, biennial spring and summer burning treatment

Treatment	Days on which burn applied	Age interval (days) x-x'	Length of interval (days) Dx	No. surviving to day x Nx	Survivorship ℓ x	No. removed by sampling	No. remaining	No. dying during interval dx	Ave. mortality rate/day qx
annual	-	0-151	151	268	1,0000	35	233	51*a-	0,338
	198	151-305	154	209	0,7798	20	162	10 b-	0,065
winter	-	305-488	183	196	0,7313	50	102	25 c-	0,137
	490	488-700	211	148	0,5522	25	52	10 d+	0,047
burn	-	700+	-	120	0,4477	-	-	-	-
biennial	-	0-151	151	268	1,0000	30	225	49 a-	0,325
	-	151-305	154	208	0,7761	25	151	13 b-	0,084
spring	-	305-488	183	184	0,6865	50	88	20 c-	0,109
	660	488-700	211	173	0,6455	20	48	6 d+	0,028
burn	-	700+	-	119	0,4440	-	-	-	-
summer	-	0-166	166	331	1,0000	35	296	81	0,488
	-	166-357	191	225	0,6797	15	200	13	0,068
burn	360	357-456	99	220	0,6646	25	162	141	1,424
	-	456+	-	28	0,0846	-	-	-	-

*Values sharing the same letter indicate comparisons between treatments (Standardized normal variate). - = Not significant

+ = Significant at the 1% probability level

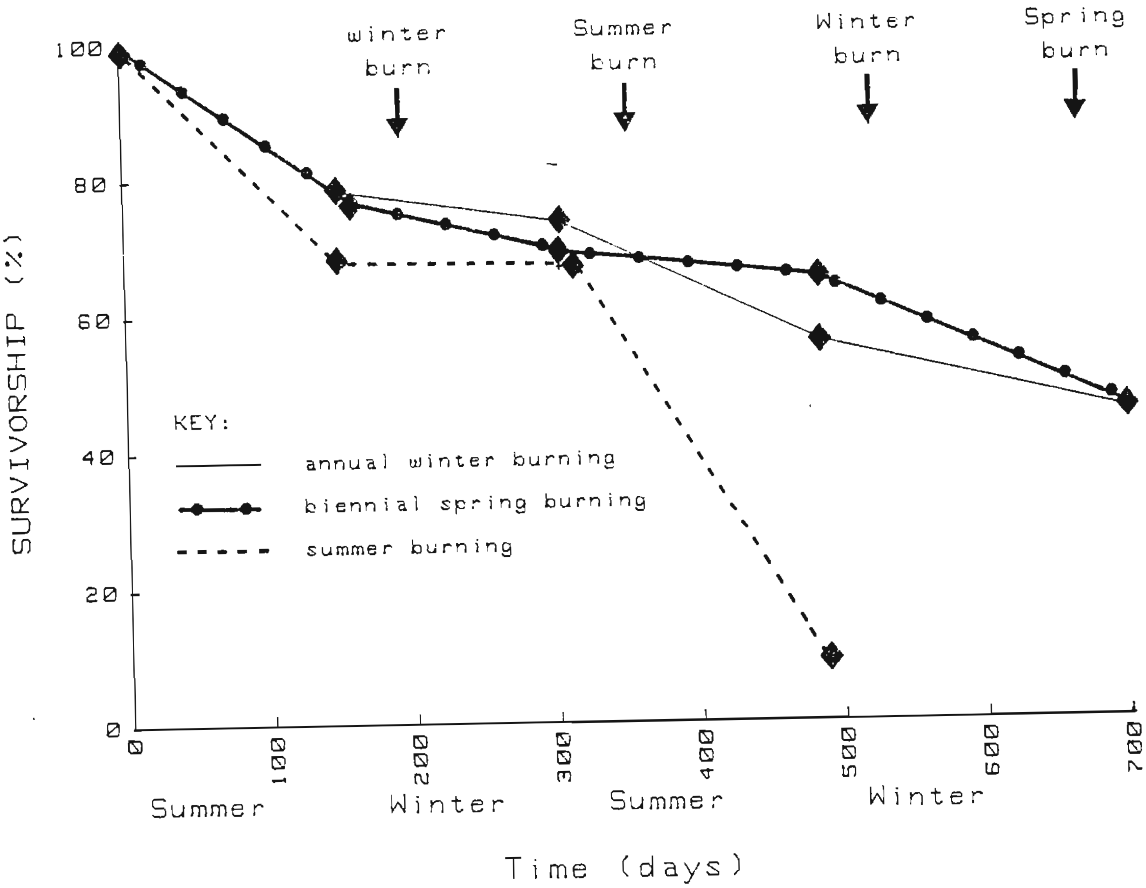


Figure 5.3 The survivorship curves of Themeda triandra in Highland Sourveld grassland when subjected to annual winter, biennial spring and summer burn treatments.

In the first growing season (day 0 to 151) there was little difference in the survivorship of T. triandra with the three treatments. The average mortality rate (qx) was 0,38 tillers per day. Approximately 77% of the original populations survived to the first winter period, when the mortality rate declined to 0,065 - 0,084 tillers per day for all treatments (Table 5.1). The annual winter burn treatment applied during this period had no effect on the mortality rate.

During the second growing season (day 305 to 488), the large increase in the mortality of tillers in the summer burn treatment is particularly noticeable. Here, the mortality rate averaged 1,4 tillers per day, until only 8 % of the original population remained alive at day 456. There was little difference between the annual winter and biennial spring treatments, their mortality rates being 0,137 and 0,109 tillers per day respectively. The treatment burns applied between days 488 and 700 appeared to have no effect on the tillers which had survived to this period. By the end of the recording period only 44 % of the original populations were still surviving.

Fig. 5.3 illustrates quite clearly a stepwise survivorship curve of tillers. This phenomenon, in which mortality is most severe at a time of rapid growth in spring and early summer, was also described by Sarukhan & Harper (1973) for Ranunculus. The survivorship curves for T. triandra for the annual winter and biennial spring burn treatments exhibited an exponential decline of numbers with age over the study period - a death risk that is independent of the age of the tillers. This survivorship curve described as Type II (Deevey, 1947) is characteristic of populations where a fixed proportion of individuals die per unit of time. Following this interpretation, the half life (the time taken for a population to fall by 50 %) of T. triandra was calculated to be 20 months.

From the life tables it was possible to construct matrices to predict the rate of growth or decline of populations of T. triandra receiving different treatments (Table 5.2). Five age classes of tillers were recognized viz. 0-151; 151-305; 305-488; 488-700 and 700+ days. Fertility rates were calculated as the number of daughter tillers produced per primary tiller for each age interval. Since the study period was 700 days and the transition matrix defines the transition from one step to the next,

TABLE 5.2 Transition matrices (A) and vectors (a) used to derive predicted values of population growth of Themeda triandra populations in annual winter (i), biennial spring (ii) and summer burn treatments (iii).

$$\text{(i)}\quad A = \begin{bmatrix} 0{,}00 & 1{,}20 & 1{,}33 & 1{,}53 & 2{,}32 \\ 0{,}78 & 0 & 0 & 0 & 0 \\ 0 & 0{,}93 & 0 & 0 & 0 \\ 0 & 0 & 0{,}75 & 0 & 0 \\ 0 & 0 & 0 & 0{,}80 & 0 \end{bmatrix} \quad X \quad a = \begin{bmatrix} 268 \\ 209 \\ 196 \\ 148 \\ 120 \end{bmatrix}$$

$$\text{(ii)}\quad A = \begin{bmatrix} 0{,}03 & 0{,}05 & 0{,}51 & 1{,}00 & 2{,}80 \\ 0{,}79 & 0 & 0 & 0 & 0 \\ 0 & 0{,}91 & 0 & 0 & 0 \\ 0 & 0 & 0{,}77 & 0 & 0 \\ 0 & 0 & 0 & 0{,}87 & 0 \end{bmatrix} \quad X \quad a = \begin{bmatrix} 268 \\ 208 \\ 184 \\ 173 \\ 119 \end{bmatrix}$$

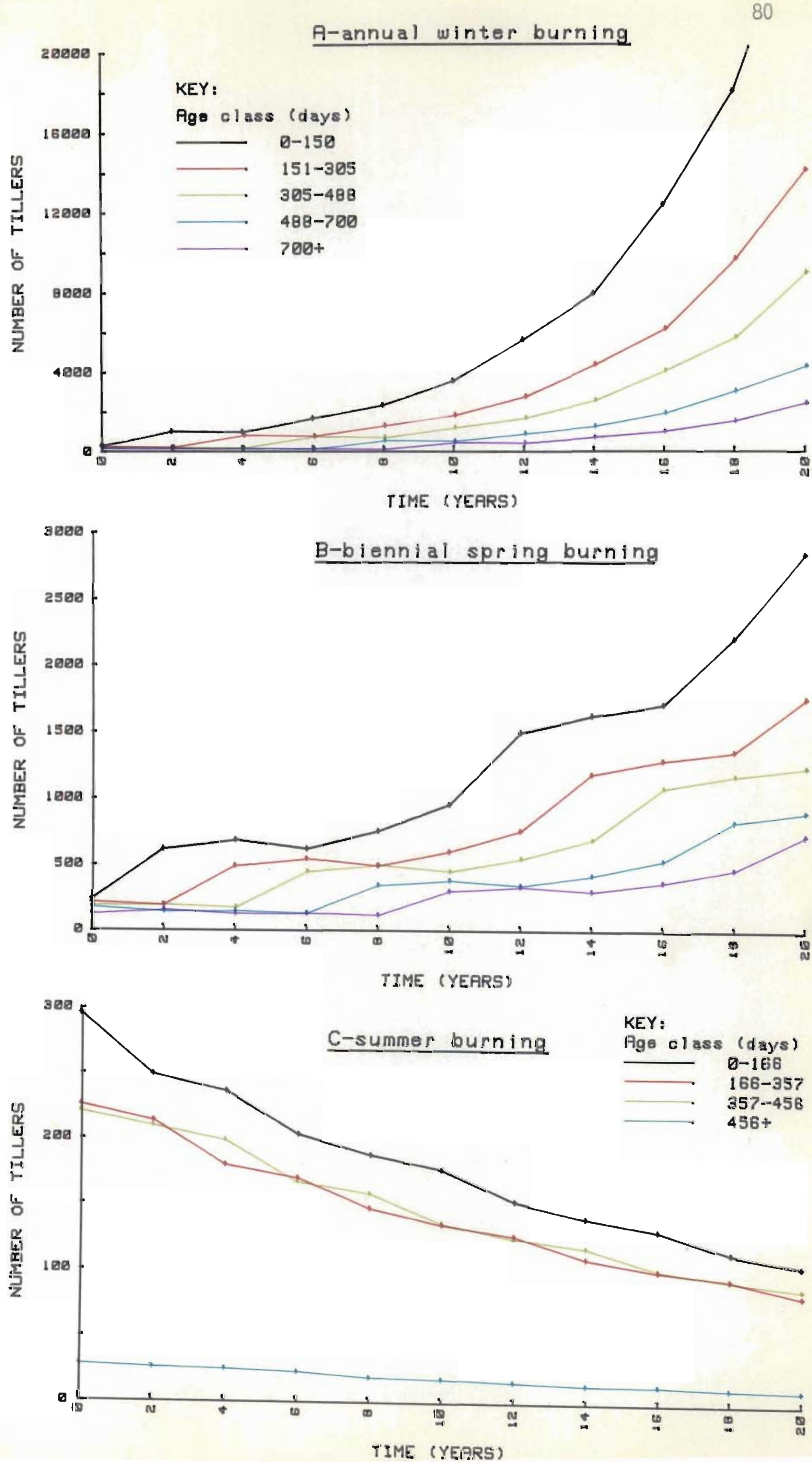
$$\text{(iii)}\quad A = \begin{bmatrix} 0{,}00 & 0{,}12 & 1{,}01 & 0{,}00 \\ 0{,}72 & 0 & 0 & 0 \\ 0 & 0{,}93 & 0 & 0 \\ 0 & 0 & 0{,}12 & 0 \end{bmatrix} \quad X \quad a = \begin{bmatrix} 331 \\ 225 \\ 220 \\ 28 \end{bmatrix}$$

The results (based on actual mortality and birth rates) are presented in Fig. 5.4. The model predicts that *T. triandra* will increase exponentially with annual winter burning (Fig. 5.4 a), gradually increase with biennial spring burning (Fig. 5.4 b) and will decline with summer burning (Fig. 5.4 c). These results concur with those in Chapter 4 (Table 4.2) where after 30 years of burning, *T. triandra* was found to be more abundant in annually burnt firebreaks (29,2 %) than in biennially burnt veld (25,5 %). It is unlikely, however, that the exponential growth predicted for annual burning will be realized, since at some stage the effects of overcrowding will bring the population down to a supportable size. The deleterious effect on veld condition and decrease in *T. triandra* by summer burning has been shown by Scotcher & Clarke (1981), Tainton, Groves & Nash (1977) and Tainton & Mentis (1984).

5.4.1.6 Conclusions

The results of the study suggest that in Highland Sourveld flowering is of minimal importance for the propagation of *T. triandra*, the majority of tillers remaining vegetative until death. Shoot apices remained close to the soil surface, enabling the plants to survive frequent defoliation. Tiller mortality was not adversely effected by burning either in winter or spring, whereas burning in summer had a catastrophic effect on tiller survival.

Tiller survival showed a stepwise pattern, indicating that mortality was most severe at the time of rapid growth in spring and summer. Tillers of *T. triandra* had a half-life of 20 months, the survivorship curve being classed as Deevey Type II. Mortality was thus shown to be independent of the age of the tillers at least up to an age of 700 days. It was not, as might be expected, greater in winter than in summer, and did not appear


A-annual winter burning
KEY:
Age class (days)
0-150
151-305
305-488
488-700
700+
NUMBER OF TILLERS
20000
16000
12000
8000
4000
0
0 2 4 6 8 10 12 14 16 18 20
TIME (YEARS)
B-biennial spring burning
NUMBER OF TILLERS
3000
2500
2000
1500
1000
500
0
0 2 4 6 8 10 12 14 16 18 20
TIME (YEARS)
C-summer burning
KEY:
Age class (days)
0-166
166-357
357-456
456+
NUMBER OF TILLERS
300
200
100
0
0 2 4 6 8 10 12 14 16 18 20
TIME (YEARS)

to be related to the stage of morphological development of the tiller. This insensitivity of the survival pattern to morphological development was probably related to the poor flowering in the tiller population examined.

Predictions of population growth of T. triandra tillers indicated that (a) annual winter burning would exponentially increase the population, (b) biennial spring burning would gradually increase the population and (c) summer burning would result in a loss of T. triandra from the sward. If T. triandra is to be maintained at its present levels of abundance in the Natal Drakensberg, then a two year burning cycle is likely to be the most suitable. Annual burning would tend to increase its abundance relative to that of other species.

5.4.2 Heteropogon Contortus

5.4.2.1 Primary tiller mass

The mean mass of primary tillers of H. contortus burnt annually in winter and biennially in spring is presented graphically in Fig. 5.5 a. In the 1979/80 growing season the increase in tiller mass was low, with a maximum of 0,05 g in the annual winter burn and 0,03 g in the biennial spring burn. After the frosts in April 1980, tiller mass decreased until spring (September). Tiller mass then increased rapidly, reaching a maximum of 0,11 g (April) in the 1980/81 growing season. There was little difference between the two burning treatments. In the 1981/82 growing season little increase in tiller mass was recorded. At this stage the life span of the primary tillers was completed and only the basal sections, which continued to support daughter tiller, remained.

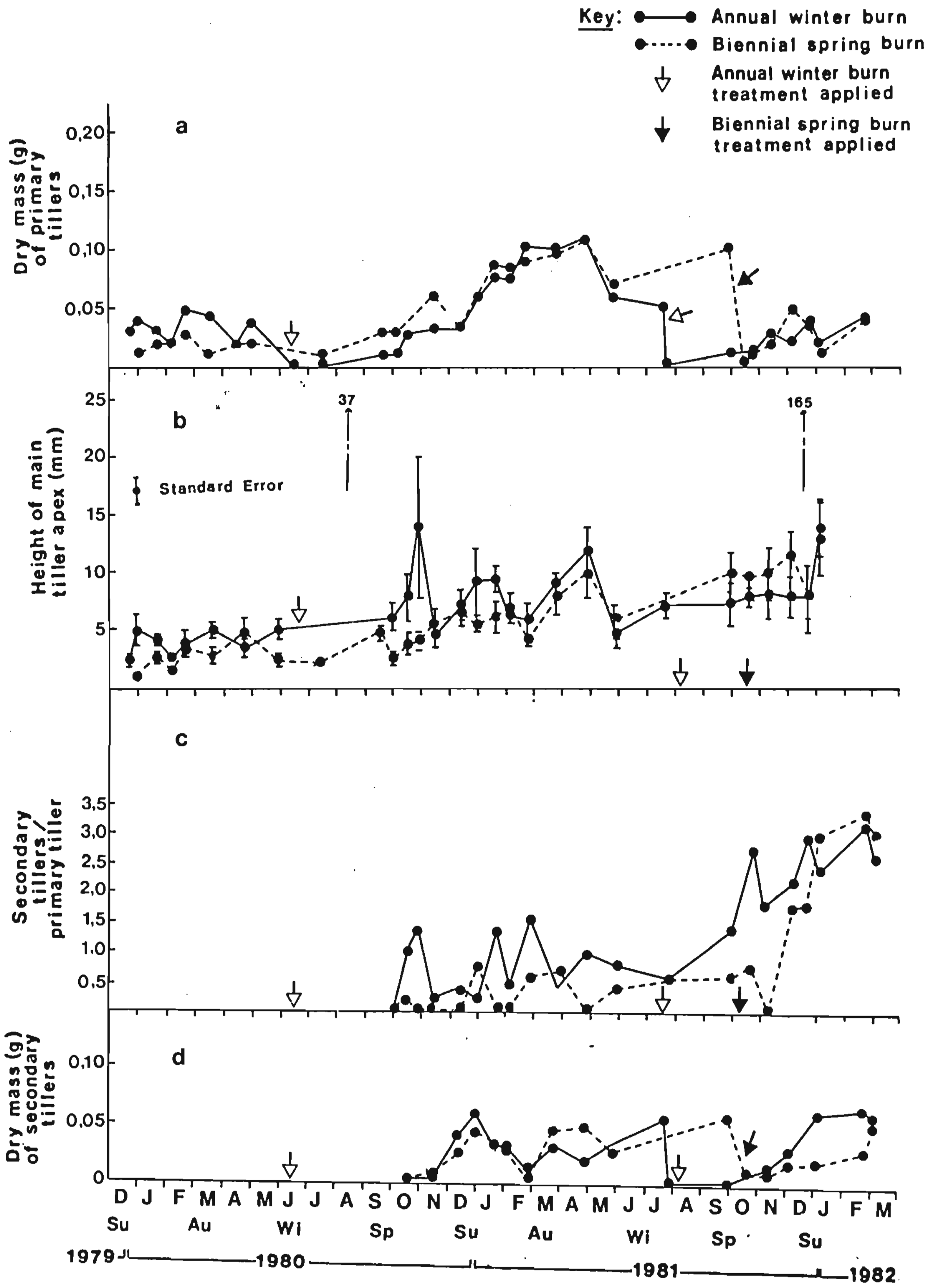


Figure 5.5 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of <u>Heteropogon contortus</u> subjected to annual winter and biennial spring burn treatments.

5.4.2.2 Elevation of shoot apices

In the first growing season (December 1979 to the end of May 1980) the shoot apices of tillers in both the annual winter and biennial spring burn treatments were elevated to only 5 mm above the soil surface (Fig. 5.5 b). Tillers that remained vegetative generally did not elevate their shoot apices beyond 10 mm throughout the rest of the study period. They did, however, continue to grow during this period (Fig. 5.5 a) and produced the bulk of the above ground living material.

Only two fertile tillers, recorded in the annual winter burn treatment, were sampled during the study period. The proportion of vegetative to fertile tillers was therefore high in both treatments. Thus vegetative propagation of tillers appears to be the most important means of reproduction in this species. The results are similar to those presented for _T. triandra_, where season of burn had no positive effect on flowering.

5.4.2.3 Secondary tiller development

No secondary tillers were produced from marked primary tillers in either treatment until mid-October 1980 (Fig. 5.5 c). Development of secondary tillers was sporadic during the 1980/81 growing season, varying between 0,2 to 1,5 and 0,2 to 0,7 per parent in the annual winter and biennial spring burn treatments respectively. The annual winter burn treatment therefore stimulated greater production of secondary tillers than the biennial spring burn treatment.

In the following growing season, primary tillers in the annual winter burn treatment carried approximately 1,5 laterals per primary tiller in September, increasing to a maximum of 3,2 at the end of February 1982.

In contrast, the number of lateral tillers in the biennial spring burn treatment remained low ($<1,0$ per primary tiller) until after the treatment burn in October 1981. Thereafter the number of laterals per primary tiller increased sharply, reaching a maximum of 3,4 in February. It is apparent from Fig. 5.5 c that the average number of secondary tillers produced per primary tiller during the study period was considerably lower in the biennial spring burn treatment than in the annual winter burn treatment.

5.4.2.4 Mass of secondary tillers

Secondary tiller mass increased steadily from October 1980, reaching a maximum of 0,05 g and 0,06 g in the annual winter and biennial spring burn treatments respectively (Fig. 5.5d). Between January and June 1981 secondary tiller mass varied between 0,02 g and 0,05 g in both treatments. There appeared to be no discernable pattern in the data. The winter and spring burns applied in July and October 1981, respectively, resulted in a marked decrease in secondary tiller mass. Although there was little difference in secondary tiller mass at the beginning of the 1981/82 growing season, by January values in the annual winter burn treatment were considerably higher (0,065 g) than in the biennial spring burn treatment (0,025 g). These differences were no longer as apparent by March, indicating that initial differences between treatments were related to season of burn.

5.4.2.5 Population dynamics of _H. contortus_ subjected to annual winter and biennial spring burning

Life tables and survivorship curves of _H. contortus_ subjected to annual winter and biennial spring burning are presented in Table 5.3 and

TABLE 5.3 Life tables of populations of *Heteropogon contortus* subjected to annual winter, biennial spring and summer burning treatments

Treatment	Days on which burn applied	Age interval (days) $x-x^1$	Length of interval (days) Dx	No. surviving to day x Nx	Survivorship ℓ x	No. removed by sampling	No. remaining	No. dying during interval dx	Ave. mortality rate/day qx
annual	-	0-151	151	238	1,0000	35	203	30*a-	0,199
	198	151-305	154	203	0,8529	20	153	36 b-	0,233
winter	-	305-488	183	162	0,6807	50	67	14 c-	0,077
	490	488-700	211	138	0,5798	25	28	14 d-	0,066
burn	-	700+	-	115	0,4832	-	-	-	-
biennial	-	0-151	151	240	1,0000	30	210	36 a-	0,238
	-	151-305	154	199	0,8292	25	149	29 b-	0,188
spring	-	305-488	183	165	0,6875	50	70	13 c-	0,071
	660	488-700	211	143	0,6958	20	37	8 d-	0,038
burn	-	700+	-	131	0,5458	-	-	-	-

*Values sharing the same letter indicate comparisons between treatments (Standardized normal variate). - = Not significant

\+ = Significant at the 1% probability level

Fig. 5.6. In the first growing season (day 0-151) there was no significant difference in the survivorship between the two burning treatments. The average mortality rate (qx) was approximately 0,20 tillers per day. Nearly 85 % of the original populations survived to the first winter period. The annual winter burn treatment applied during this period (day 198) had no effect on the mortality rate (qx = ca 0,20) which was similar to that recorded in the previous summer season (Table 5.3).

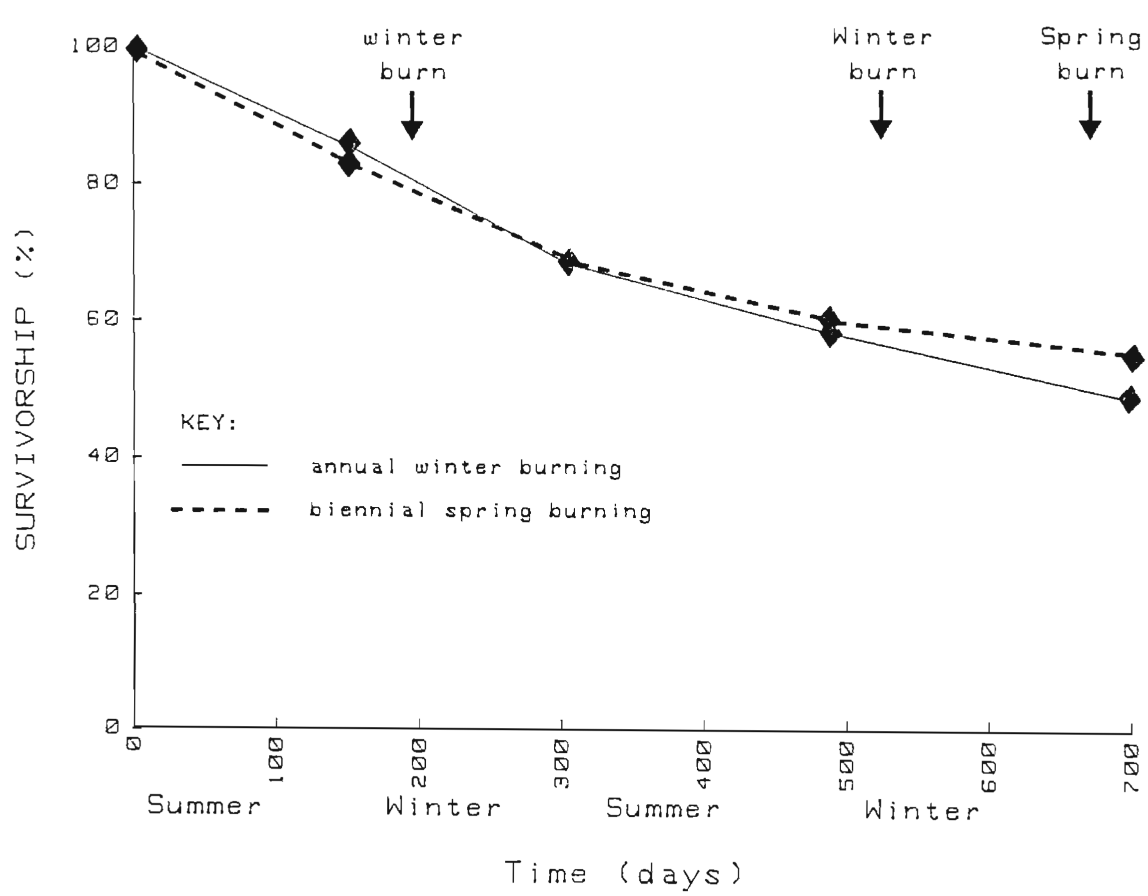


Figure 5.6 The survivorship curves of <u>Heteropogon contortus</u> in Highland Sourveld grassland when subjected to annual winter and biennial spring burn treatments.

During the second growing season (day 305 - 488), the mortality rate declined in both treatments to ca 0,07 tillers per day. Approximately 59 % of the original population survived to the end of this period (Fig. 5.6). The treatment burns applied between days 488 and 700 therefore appeared to have no detrimental effect on the mortality of these plants. By the end of the study period approximately 50 % of the original populations were surviving. The half-life of H. contortus tillers was therefore 27 months.

The survivorship curves for H. contortus in both treatments exhibited an exponential decline of numbers with age (Fig. 5.6). Thus the death risk is independent of the age of the tillers (Deevey, Type II), a fixed proportion of individuals dying per unit of time.

Following the procedure already described for T. triandra, it was possible to construct matrices (Table 5.4) to predict the rate of growth or decline of populations of H. contortus receiving either annual winter or biennial spring burning. The results are presented in Fig. 5.7. The transition matrix models predict that H. contortus will increase exponentially with annual winter burning (Fig. 5.7 a) and remain essentially constant with biennial spring burning (Fig. 5.7 b). The results agree with those in Chapter 4 (Table 4.2) where after 30 years of burning, H. contortus was found to be more abundant in annually burnt firebreaks (6,0 %) than in biennially burnt veld (3,4 %). It is unlikely, however, that the exponential growth predicted for annual winter burning will be realized, since at some stage the effect of some or other density dependent factor (eg. competition with other plants) would reduce the population to a supportable size.

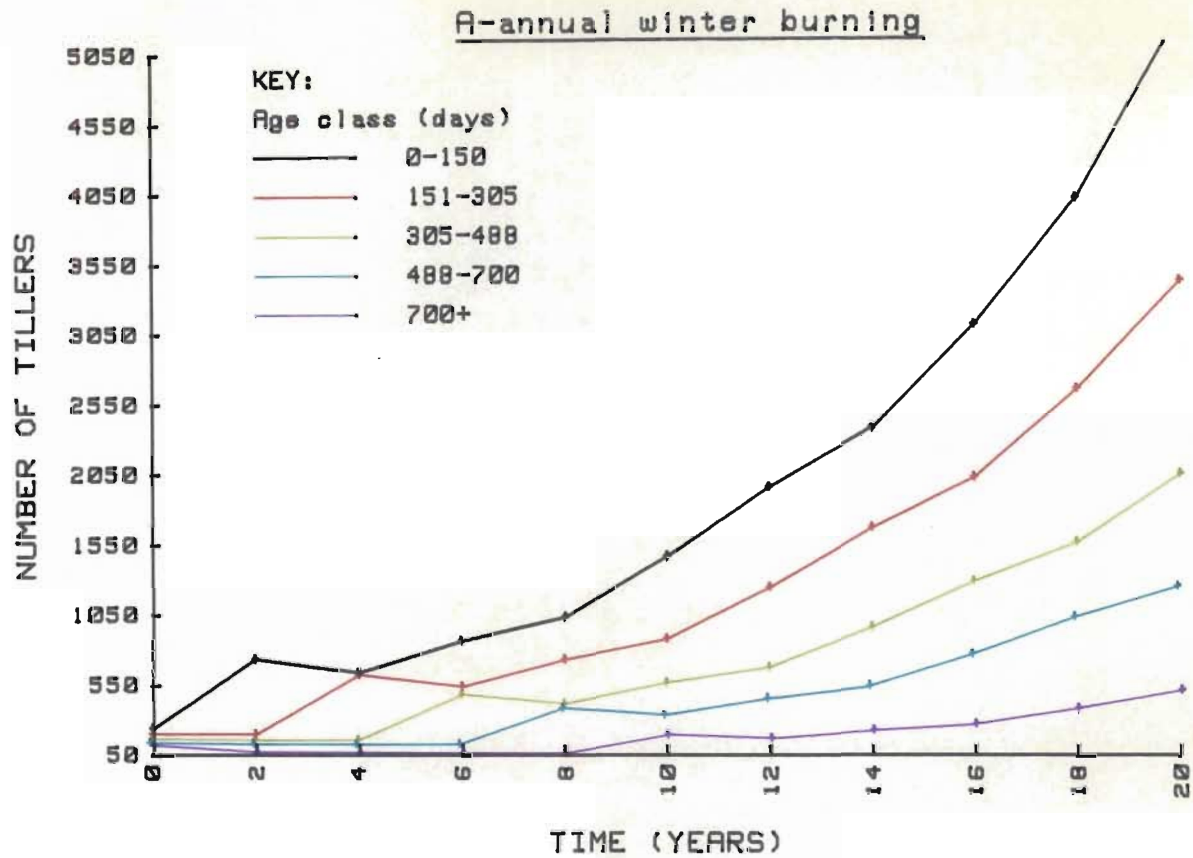
TABLE 5.4 Transition matrices (A) and vectors (a) used to derive predicted values of population growth of *Heteropogon contortus* populations in annual winter (i), and biennial spring burn treatments (ii).

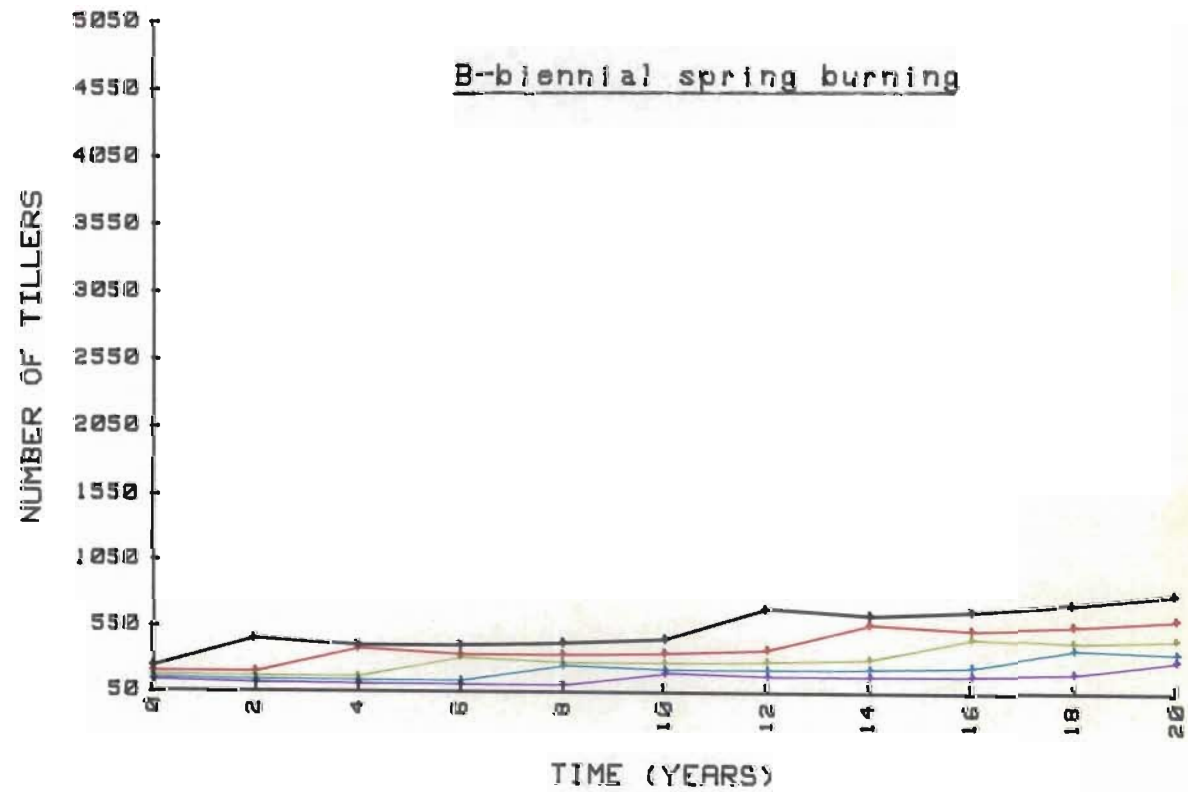
$$\text{(i)}\quad \overset{A}{\begin{bmatrix} 0{,}09 & 0{,}60 & 0{,}64 & 1{,}32 & 2{,}68 \\ 0{,}85 & 0 & 0 & 0 & 0 \\ 0 & 0{,}77 & 0 & 0 & 0 \\ 0 & 0 & 0{,}79 & 0 & 0 \\ 0 & 0 & 0 & 0{,}50 & 0 \end{bmatrix}} \quad X \quad \overset{a}{\begin{bmatrix} 238 \\ 203 \\ 162 \\ 138 \\ 115 \end{bmatrix}}$$

$$\text{(ii)}\quad \begin{bmatrix} 0{,}00 & 0{,}12 & 0{,}24 & 0{,}35 & 2{,}60 \\ 0{,}83 & 0 & 0 & 0 & 0 \\ 0 & 0{,}81 & 0 & 0 & 0 \\ 0 & 0 & 0{,}81 & 0 & 0 \\ 0 & 0 & 0 & 0{,}78 & 0 \end{bmatrix} \quad X \quad \begin{bmatrix} 240 \\ 199 \\ 165 \\ 143 \\ 131 \end{bmatrix}$$

5.4.2.6 Conclusions

The results of this investigation suggest that flowering is of minimal importance for the propagation of *H. contortus*, the majority of plants being recruited as ramets. Shoot apices remained close to the soil surface, enabling the plants to survive frequent defoliation. Recruitment of new tillers was stimulated by regular burning, the annual winter


A-annual winter burning
KEY:
Age class (days)
0-150
151-305
305-488
488-700
700+
NUMBER OF TILLERS
5050
4550
4050
3550
3050
2550
2050
1550
1050
550
50
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)


B-biennial spring burning
NUMBER OF TILLERS
5050
4550
4050
3550
3050
2550
2050
1550
1050
550
50
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)

burn treatment producing on average more secondary tillers per primary tiller than the biennial spring burn treatment.

Tiller mortality was not adversely effected by burning either in winter or spring. The survivorship curves (classed as Deevey Type II) showed that mortality was independent of tiller age during the study period, and that H. contortus had a half life of 27 months.

Predictions of population growth of H. contortus tillers indicated that annual winter burning would exponentially increase the population while biennial spring burning would result in a stable population. If H. contortus is to be maintained at its present levels of abundance in the Natal Drakensberg, then a biennial burning cycle is likely to be the most suitable, since annual burning would tend to increase its abundance relative to that of other species.

5.4.3 Trachypogon spicatus

5.4.3.1 Primary tiller mass

Fig. 5.8 a illustrates the seasonal pattern of primary tiller mass for both the annual winter and biennial spring burn treatments. Tillers from both treatments increased in mass from December 1979, reaching a maximum of approximately 0,1 g. Following the first frosts in May tiller mass in both treatments decreased. From spring (September) tiller mass increased rapidly, reaching a maximum in February 1980 of 0,20 g and 0,24 g in the annual winter and biennial spring burn treatments respectively. In the following season, however, only the basal sections remained and little increase in tiller mass was recorded. The results showed that there were

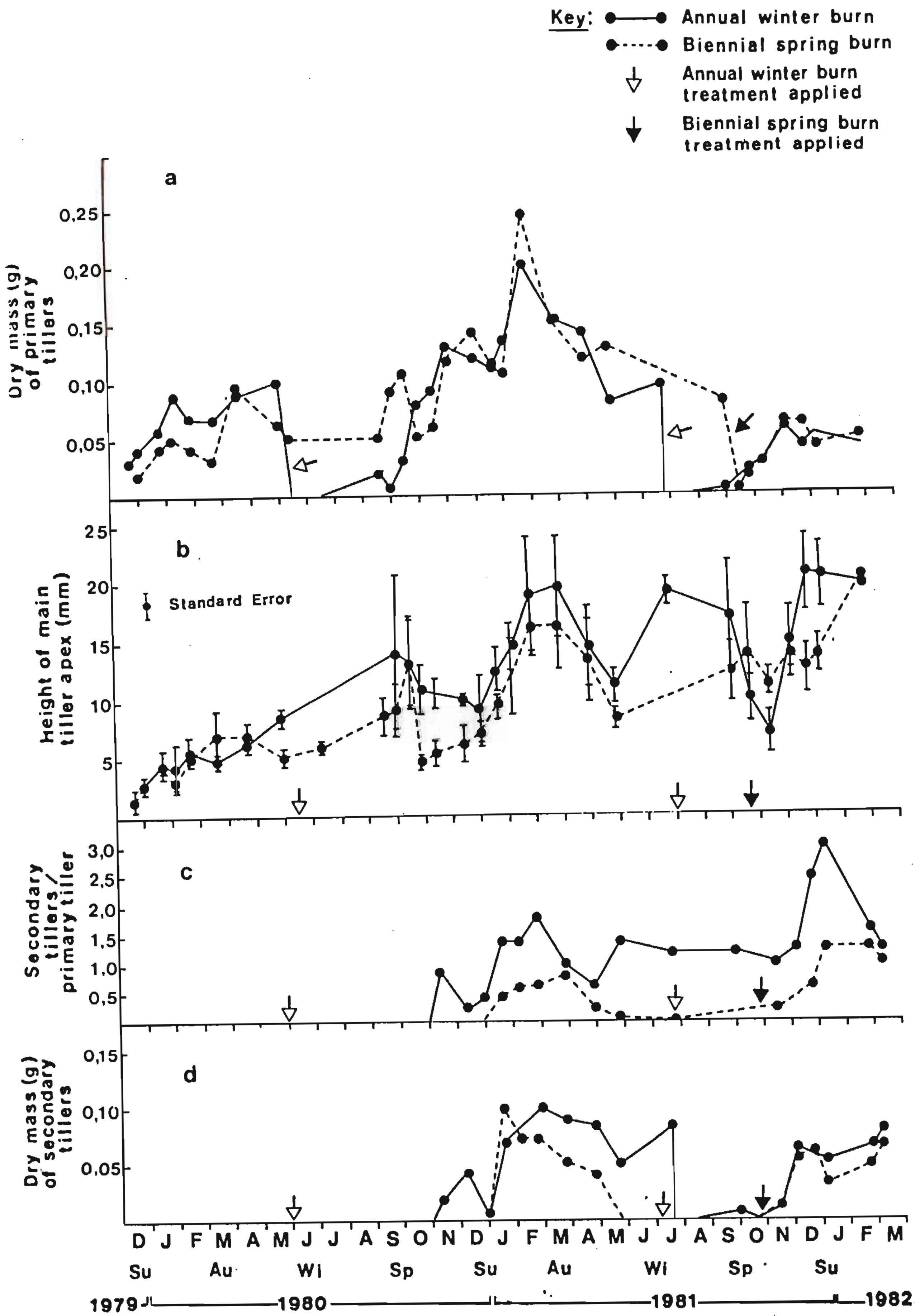


Figure 5.8 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of <u>Trachypogon spicatus</u> subjected to annual winter and biennial spring burn treatments.

generally no differences in primary tiller mass between treatments. This indicates that the different seasons and frequency of treatment burns had little effect on primary tiller mass.

5.4.3.2 Elevation of shoot apices

Shoot apices in both treatments increased steadily from a minimum of approximately 1 mm in December 1979 to a maximum of 20 mm in February 1982 (Fig. 5.8 b). Differences between treatments were generally not significant (13 and 26 mm).

No fertile tillers were recorded from marked tillers from either treatment during the study period. Season of burn therefore had no positive effect on flowering. Although this implies that T. spicatus does not produce flowers, flowering heads were observed on unmarked tillers. The results suggest that T. spicatus depends mainly on vegetative reproduction for its continued existence in these montane grasslands.

5.4.3.3 Secondary tiller development

Secondary tiller development in the annual winter burn commenced in November 1980, with a maximum of 1,75 daughters being produced per primary tiller (Fig. 5.8 c). Secondary tiller development in the biennial spring burn commenced three months later in January 1981, reaching a maximum of only 0,75 daughters per primary tiller. For the period June to July 1981 the annual winter burn produced an average of approximately 1,25 daughters per parent, while there were no tillers produced in the biennial spring burn treatment. In the following growing season (1981/82) tiller initiation increased markedly in the annual winter burn treatment (3,0 daughters per parent), but remained comparatively low (1,25 daughters per parent), in the biennial spring burn treatment. The annual winter burn treatment was therefore a greater stimulus in initiating secondary tillers than the biennial spring burn treatment.

5.4.3.4 Mass of secondary tillers

During the 1980/81 growing season secondary tiller mass reached a maximum of 0,10 g in both the biennial spring (January, 1981) and annual winter (February, 1981) burn treatments (Fig. 5.8 d). From February onwards secondary tiller mass in the annual winter burn varied between 0,10 and 0,05 g. The application of the winter burn in July resulted in the removal of all the above ground material. Secondary tiller mass in the biennial spring burn treatment decreased steadily during this period, until no tillers were produced between May and October.

In the 1981/82 growing season there was little difference in secondary tiller mass between treatments. Maximum masses of 0,05 g (annual winter burn) and 0,04 g (biennial spring burn) were recorded at the end of the growing season in March. The results therefore show that frequency and season of burn had little effect on the maximum tiller mass attained in the annual winter and biennial spring burn treatments.

5.4.3.5 Population dynamics of _T. spicatus_ subjected to annual winter and biennial spring burning

The life tables and survivorship curves for _T. spicatus_ subjected to different burning regimes are presented in Table 5.5 and Fig. 5.9 respectively. During the first growing season (day 0-151) the average mortality rate (qx) was low in both the annual winter (0,132 tillers/day) and biennial spring burn treatments (0,199 tillers/day). This

TABLE 5.5 Life tables of populations of *Trachypogon spicatus* subjected to annual winter, biennial spring and summer burning treatments

Treatment	Days on which burn applied	Age interval (days) x-x1	Length of interval (days) Dx	No. surviving to day x Nx	Survivorship ℓ x	No. removed by sampling	No. remaining	No. dying during interval dx	Ave. mortality rate/day qx
annual	-	0-151	151	225	1,0000	35	190	20*a-	0,132
	198	151-305	154	201	0,8933	20	150	14 b-	0,091
winter	-	305-488	183	185	0,8222	50	86	25 c-	0,137
	490	488-700	211	145	0,6444	25	36	33 d+	0,118
burn	-	700+	-	89	0,3756	-	-	-	-
biennial	-	0-151	151	230	1,0000	30	200	30 a-	0,199
	-	151-305	154	196	0,8522	25	145	11 b-	0,071
spring	-	305-488	183	183	0,7957	50	84	20 c-	0,109
	660	488-700	211	151	0,6565	20	44	10 d+	0,047
burn	-	700+	-	136	0,5913	-	-	-	-

*Values sharing the same letter indicate comparisons between treatments (Standardized normal variate). - = Not significant

+ = Significant at the 1% probability level

difference was not significant (Table 5.5), and the majority (ca 85%) of the initial populations in both treatments survived to the following winter (Fig. 5.9). During this winter period (day 151-305), the mortality rate declined to 0,091 and 0,071 tillers/day in the annual winter and biennial spring burn treatments respectively. The annual winter burn treatment applied during this period therefore had no effect on the mortality of plants.

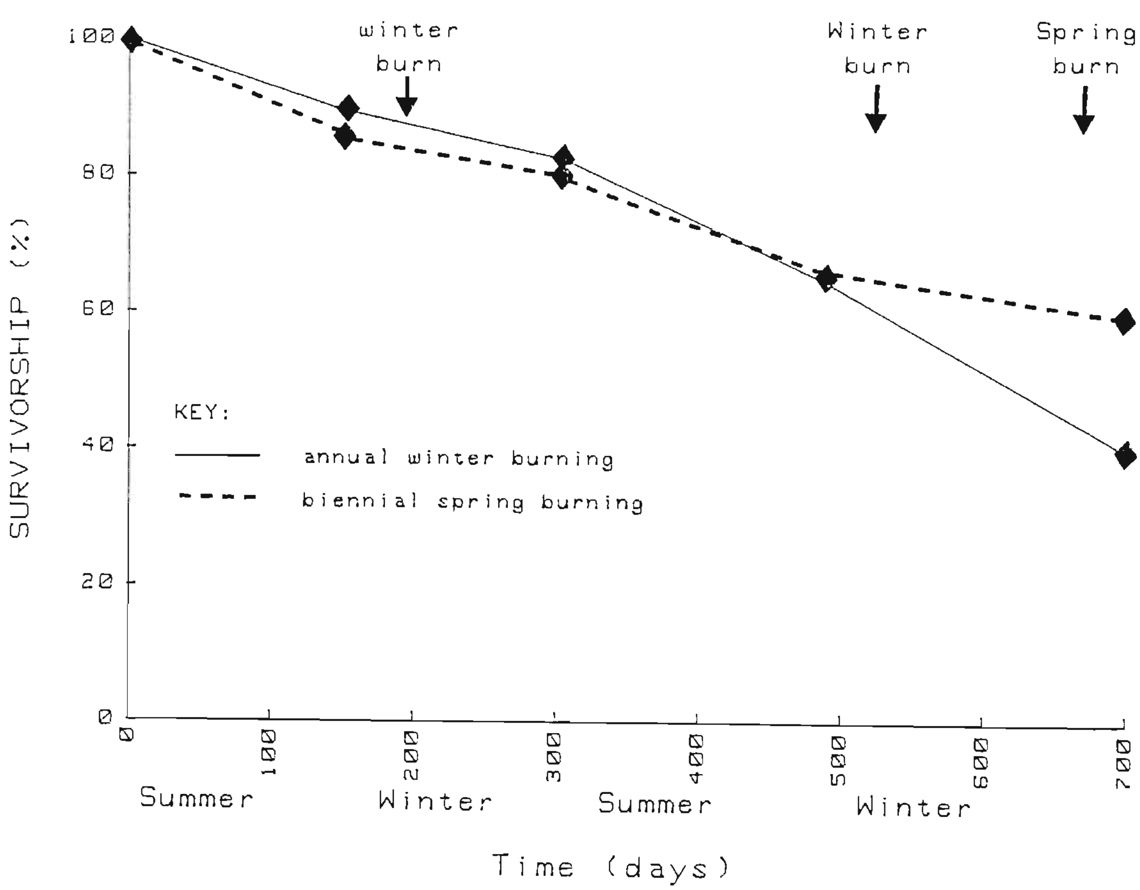


Figure 5.9 The survivorship curves of Trachypogon spicatus in Highland Sourveld grassland when subjected to annual winter and biennial spring burn treatments.

During the second year of the study the pattern of tiller mortality was similar to that of the first year, with the rate increasing during the growing period (day 305-488) and then declining in the dormant winter months. However, by day 700 (Fig. 5.9) there were still 39% and 59% of the original populations surviving in the annual winter and biennial spring burn treatments respectively. This difference was significant at the 1% probability level. This is explained by the fact that mortality in the annual winter burn treatment during the second winter remained relatively high (qx = 0,118) when compared with that in the biennial spring burn treatment (qx = 0,047). This difference was possibly a result of the treatment burns applied between days 488 and 700.

The survivorship curves of T. spicatus (Fig. 5.9) for the annual winter and biennial spring burn treatments followed a pattern where the death risk was low for young individuals, the majority (ca 80%) reaching at least an age of one year. This survivorship curve described as Type I (Deevey, 1947) is characteristic of populations where most individuals survive to an old age for the species (eg. laboratory populations of Drosophila, Hydra and man). Although similar curves were found for perennial grasses in Arizona (Canfield, 1957) they differ from any other populations described for plants (Harper, 1977).

The transition matrices used to predict the fate of successive age classes of T. spicatus tillers are shown in Table 5.6. The results (Fig. 5.10 a) indicate that annual winter burning would result in fluctuations in the numbers of the different age classes. However, there was an overall tendency for an increase in the population. For example, in the 0-150 age class an initial 225 tillers increased to 431 tillers after 20 years .

In comparison, the transition matrix model for biennial spring burning

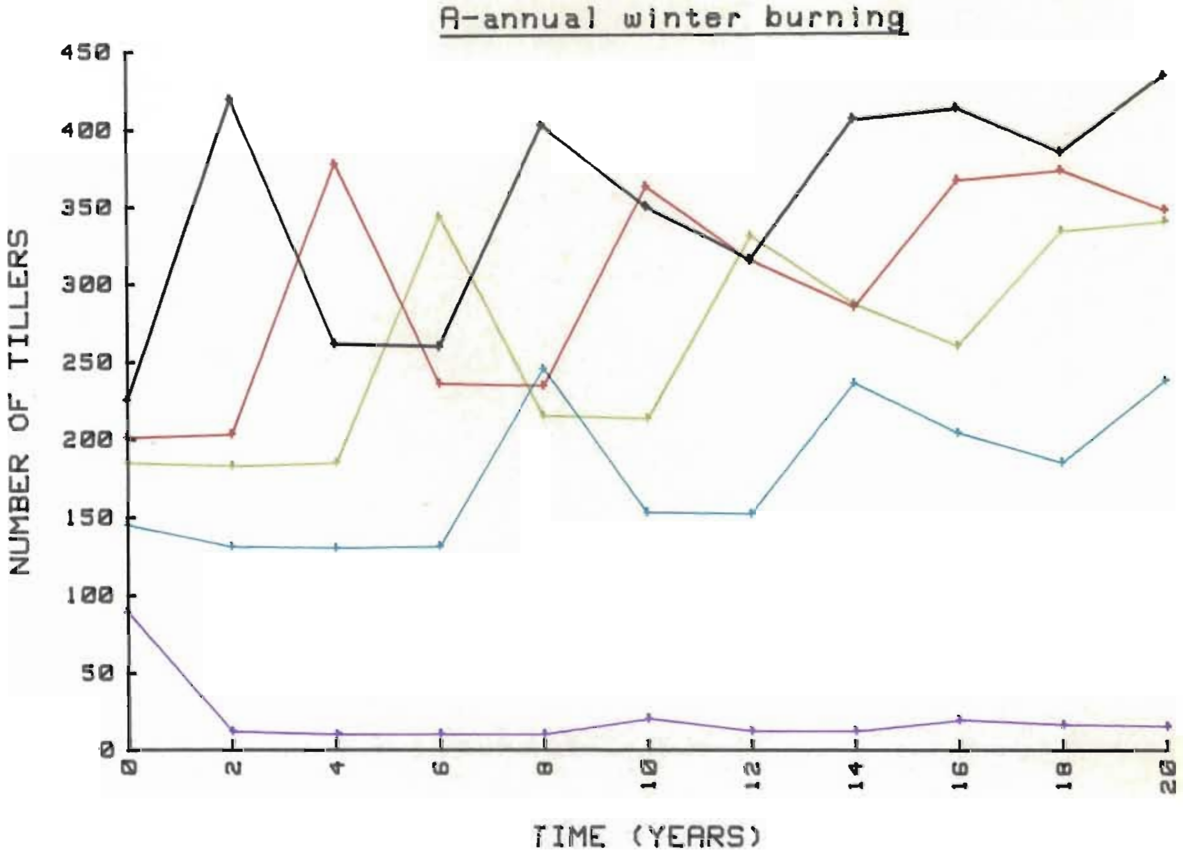
(Fig. 5.10 b) predicted an initial decline in T. spicatus numbers in the first 10 years and thereafter a relatively stable population of tillers.

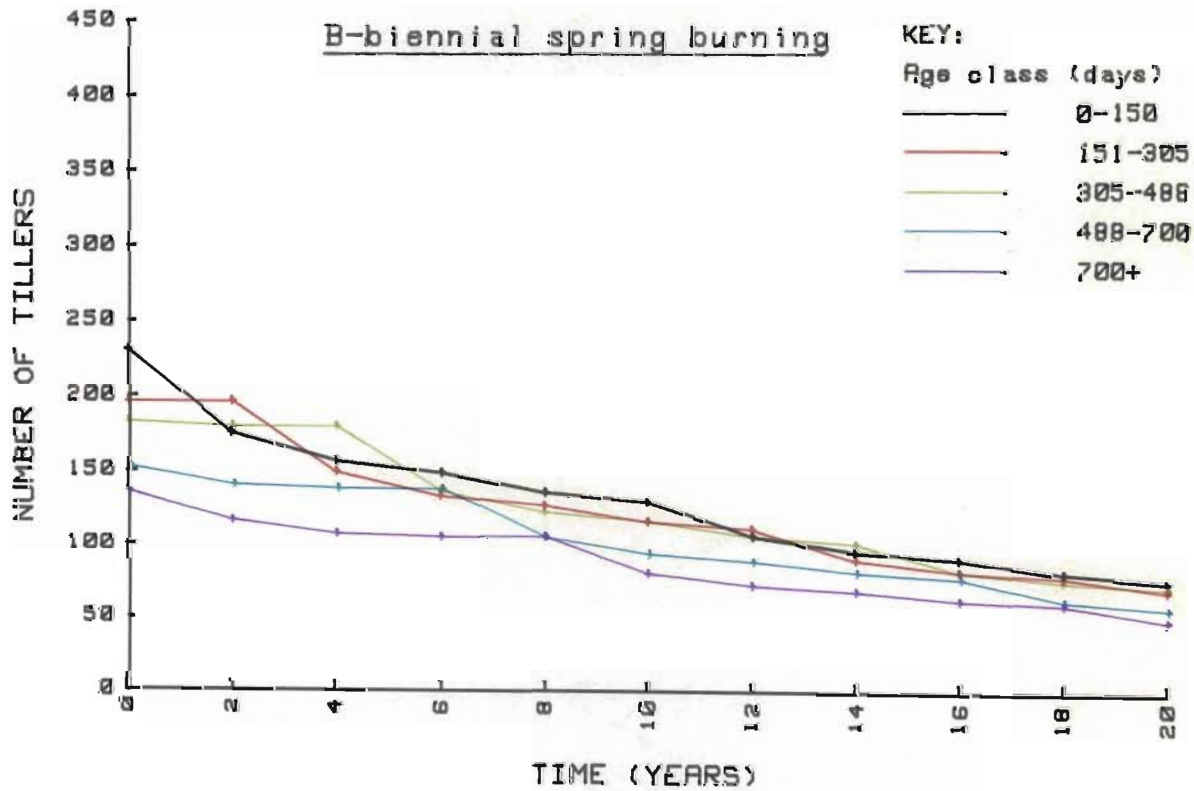
TABLE 5.6 Transition matrices (A) and vectors (a) used to derive predicted values of population growth of *Trachypogon spicatus* populations in annual winter (i), and biennial spring burn treatments (ii).

$$\text{(i)}\quad A = \begin{bmatrix} 0{,}00 & 0{,}00 & 0{,}90 & 0{,}56 & 1{,}92 \\ 0{,}90 & 0 & 0 & 0 & 0 \\ 0 & 0{,}91 & 0 & 0 & 0 \\ 0 & 0 & 0{,}71 & 0 & 0 \\ 0 & 0 & 0 & 0{,}08 & 0 \end{bmatrix} \times \; a = \begin{bmatrix} 225 \\ 201 \\ 185 \\ 145 \\ 89 \end{bmatrix}$$

$$\text{(ii)}\quad A = \begin{bmatrix} 0{,}00 & 0{,}00 & 0{,}90 & 0{,}56 & 1{,}92 \\ 0{,}90 & 0 & 0 & 0 & 0 \\ 0 & 0{,}91 & 0 & 0 & 0 \\ 0 & 0 & 0{,}71 & 0 & 0 \\ 0 & 0 & 0 & 0{,}08 & 0 \end{bmatrix} \times \; a = \begin{bmatrix} 418 \\ 202 \\ 182 \\ 131 \\ 116 \end{bmatrix}$$

These results show that T. spicatus increases slightly with annual burning and decreases slightly with biennial spring burning. The small difference in the proportional composition between these two treatments observed in Chapter 4, Table 4.2 (1,5%) would tend to support the above


A-annual winter burning
NUMBER OF TILLERS
450
400
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)


B-biennial spring burning
KEY:
Age class (days)
0-150
151-305
305-488
488-700
700+
NUMBER OF TILLERS
450
400
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)

observations.

5.4.3.6 Conclusions

The results show that there were no significant differences in primary tiller mass between treatments. Shoot apices were not elevated beyond a height of 20 mm, enabling the apical buds of T. spicatus plants to avoid the effects of fire. This strategy, however, appears to result in these plants being dependent on the production of ramets (rather than genets) for its continued existence. Regular burning (i.e. the annual winter burn treatment) was once again a major stimulus in the recruitment of secondary tillers.

Tiller survival showed an unusual pattern for plants where the risk of death was low in middle age, followed by a higher death risk in older plants. This is a survivorship curve of the type described by Deevey as Type I.

Predictions of population growth of T. spicatus tillers indicated that either annual winter or biennial spring burning would be capable of maintaining T. spicatus at acceptable levels in the Natal Drakensberg.

5.4.4 Tristachya leucothrix

5.4.4.1 Primary tiller mass

The mean mass of primary tillers followed similar trends in the annual winter and biennial spring burn treatments during the study period (Fig. 5.11a). In the first growing season (1979/80) the maximum mass attained was approximately 0,1 g. In the following season masses were three times

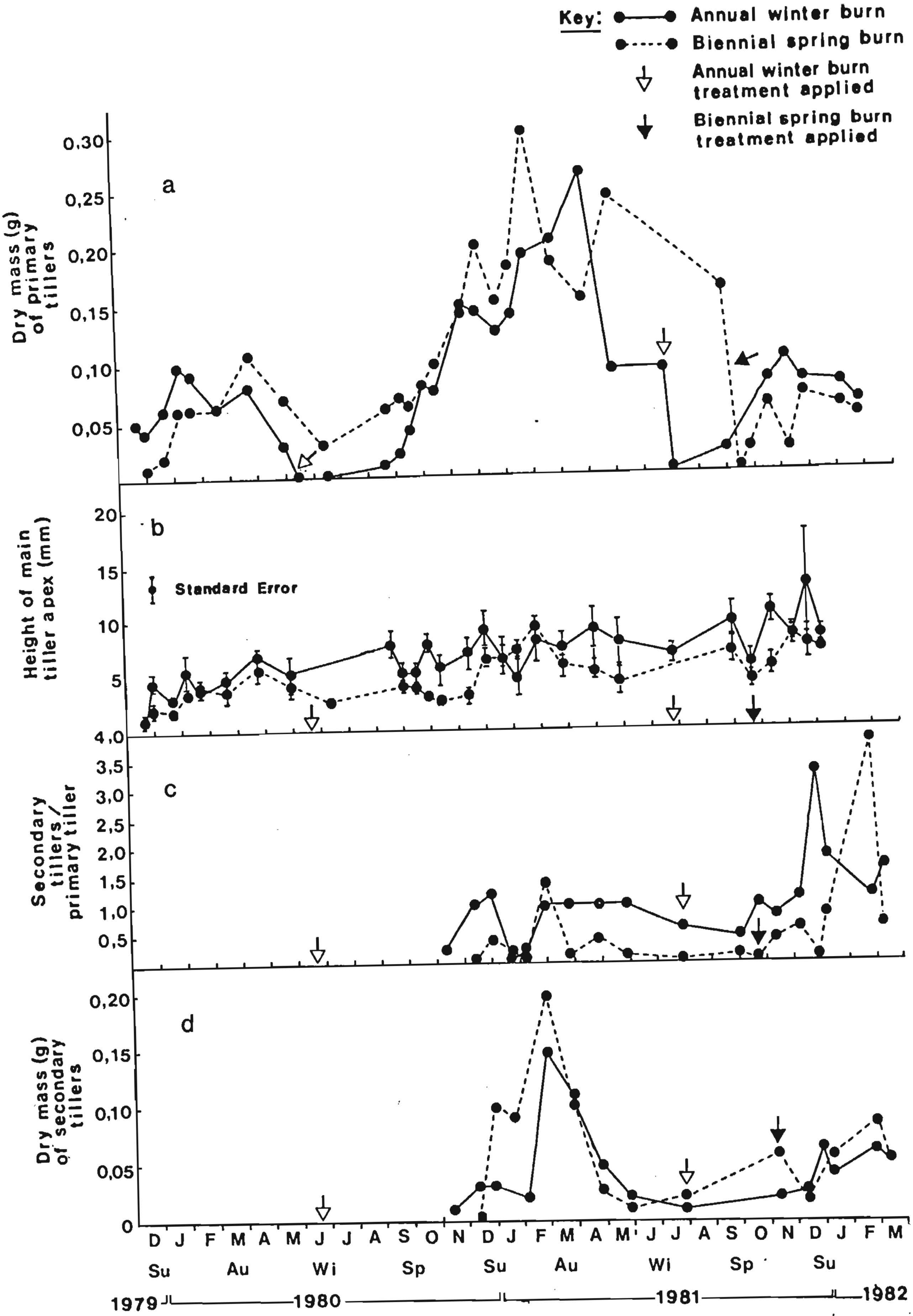


Figure 5.11 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of Tristachya leucothrix subjected to annual winter and biennial spring burn treatments.

greater, reaching a maximum mass of 0,3 g in February 1980 in the biennial spring burn treatment, and 0,24 g in April 1980 in the annual winter burn treatment. In the third growing season masses were low (less than 0,1 g) since only the basal portions remained. This indicates that irrespective of these treatments, primary tillers had a life span of at least 27 months.

5.4.4.2 Elevation of shoot apices

The apical buds of T. leucothrix in both the annual winter and biennial spring burn treatments remained close to the soil surface (<10 mm high) for the entire 27 month study period (Fig. 5.11 b). This indicates that the growing part of the grass is protected from fire during this period. Low elevations of T. leucothrix apices were also recorded by Tainton & Booysen (1963) in the first season of a biennial spring burn treatment. In the second season however, these authors recorded elevations of up to 140 mm. In contrast, no flowers were produced from marked tillers in the present study. These results once again illustrate the major role played by vegetative reproduction in these Highland Sourveld grasses.

5.4.4.3 Secondary tiller development

Secondary tillers were initiated in November/December 1981, when the primary tillers were approximately one year old (Fig. 5.11 c). With the exception of January/February 1981, approximately one secondary tiller per primary tiller was stimulated by annual winter burning between November 1980 and July 1981. In contrast tiller initiation in the biennial spring burn treatment during 1981 was generally low, seldom exceeding a mean of 0,5 laterals per parent. In the following season (1981/82) tiller initiation was high, reaching maximum values of 3,25 in the annual winter and 3,75 in the biennial spring burn treatments. Overall, the average number of secondary tillers per primary tiller was higher in the annual winter burn treatment.

5.4.4.4 Mass of secondary tillers

The mass of secondary tillers produced in the biennial spring burn treatment ($<$ 0,2 g) was generally higher than that of the annual winter burn treatment ($<$ 0,15 g) during the first growing season (Fig. 5.11 d). Although more laterals were produced per parent during the 1981/82 growing season (Fig. 5.11 c), their mean dry mass was approximately half that (i.e. ca 0,08 g) of the previous season (Fig. 5.11 d). There appeared to be little difference between the burning treatments.

5.4.4.5 Population dynamics of *Tristachya leucothrix* subjected to annual winter and biennial spring burning

Life tables and survivorship curves of *T. leucothrix* subjected to annual winter and biennial spring burn treatments are presented in Table 5.7 and Fig. 5.12 respectively. During the first growing season (day 0-151) mortality (qx) in the annual winter burn (0,298 tillers/day) was almost four times as great as in the biennial spring burn (0,082 tillers/day). This difference (significant at $p<0,1$) resulted in only 79% of the annual winter population surviving to the first winter period, in comparison with 90% in the biennial spring burn treatment. This difference in mortality between the two treatments remained significant throughout the entire study period and eventually resulted in only 31,6% of the original population surviving to day 700, as opposed to 70,9% in the biennial spring burn population.

TABLE 5.7 Life tables of populations of *Tristachya leucothrix* subjected to annual winter, biennial spring and summer burning treatments

Treatment	Days on which burn applied	Age interval (days) x-x1	Length of interval (days) Dx	No. surviving to day x Nx	Survivor-ship ℓ x	No. removed by sampling	No. remain-ing	No. dying during interval dx	Ave. mortality rate/day qx
annual	-	0-151	151	250	1,0000	35	215	45* a+	0,298
	198	151-305	154	198	0,7920	20	150	28 b+	0,182
winter	-	305-488	183	166	0,6640	50	72	25 c+	0,137
	490	488-700	211	124	0,4860	25	22	21 d+	0,100
burn	-	700+	-	79	0,3160	-	-	-	-
biennial	-	0-151	151	220	1,0000	30	190	18 a+	0,082
	-	151-305	154	199	0,9045	25	147	11 b+	0,091
spring	-	305-488	183	183	0,8318	50	83	7 c+	0,038
	660	488-700	211	172	0,7818	20	56	12 d+	0,057
burn	-	700+	-	156	0,7091	-	-	-	-

*Values sharing the same letter indicate comparisons between treatments (Standardized normal variate). - = Not significant

+ = Significant at the 1% probability level

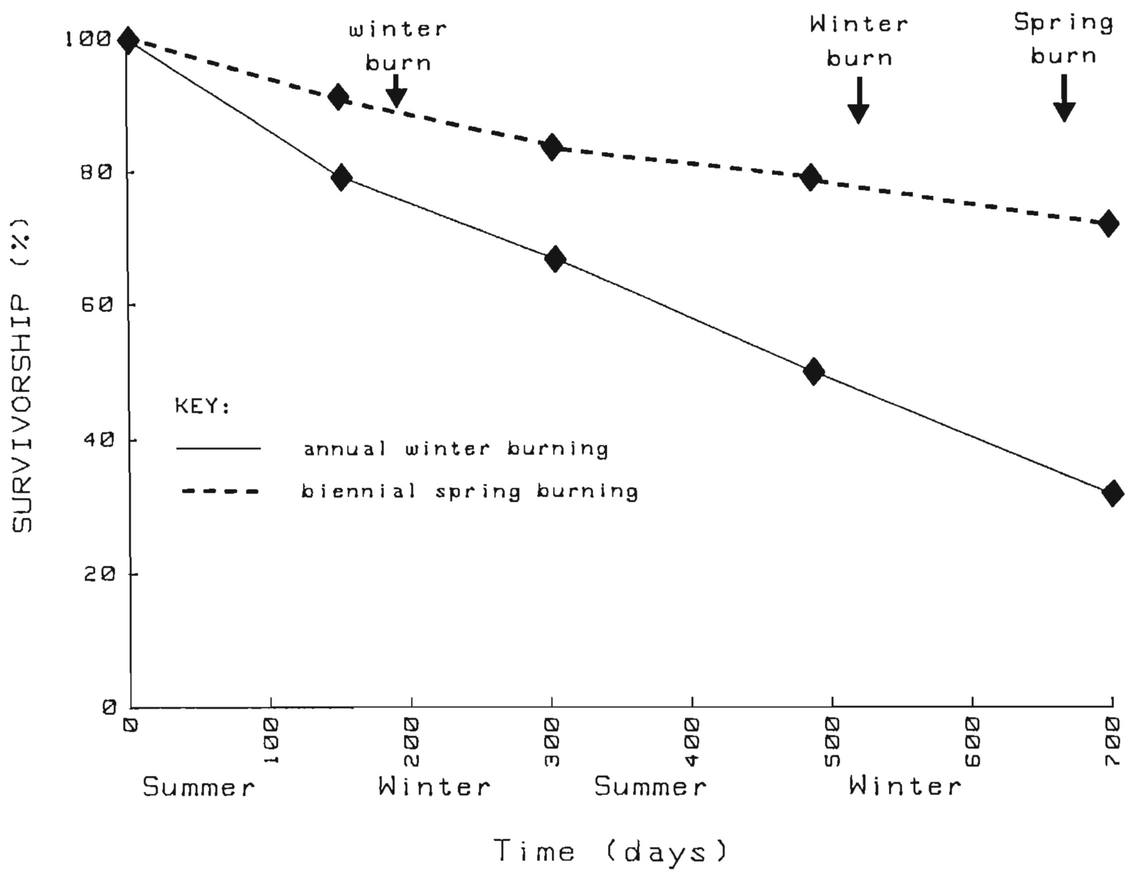


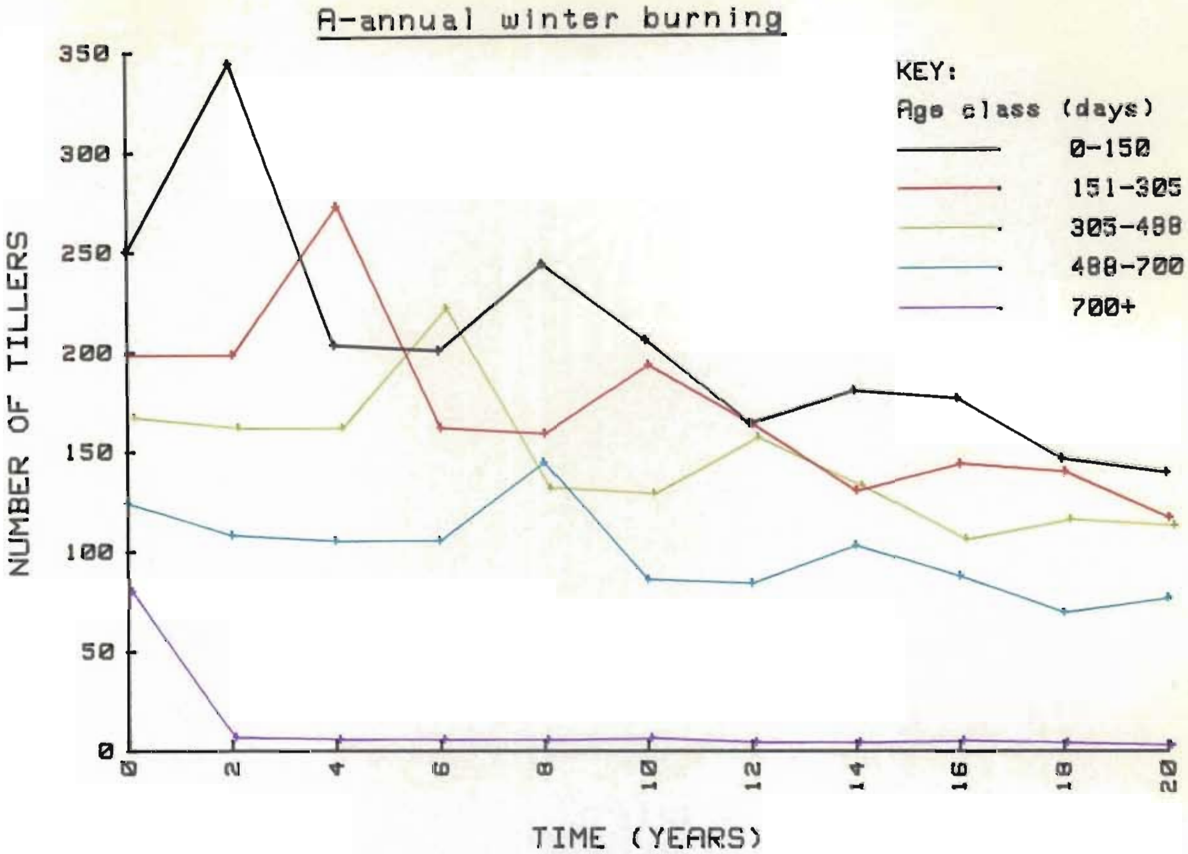
Figure 5.12 The survivorship curves of Tristachya leucothrix in Highland Sourveld grassland when subjected to annual winter and biennial spring burn treatments.

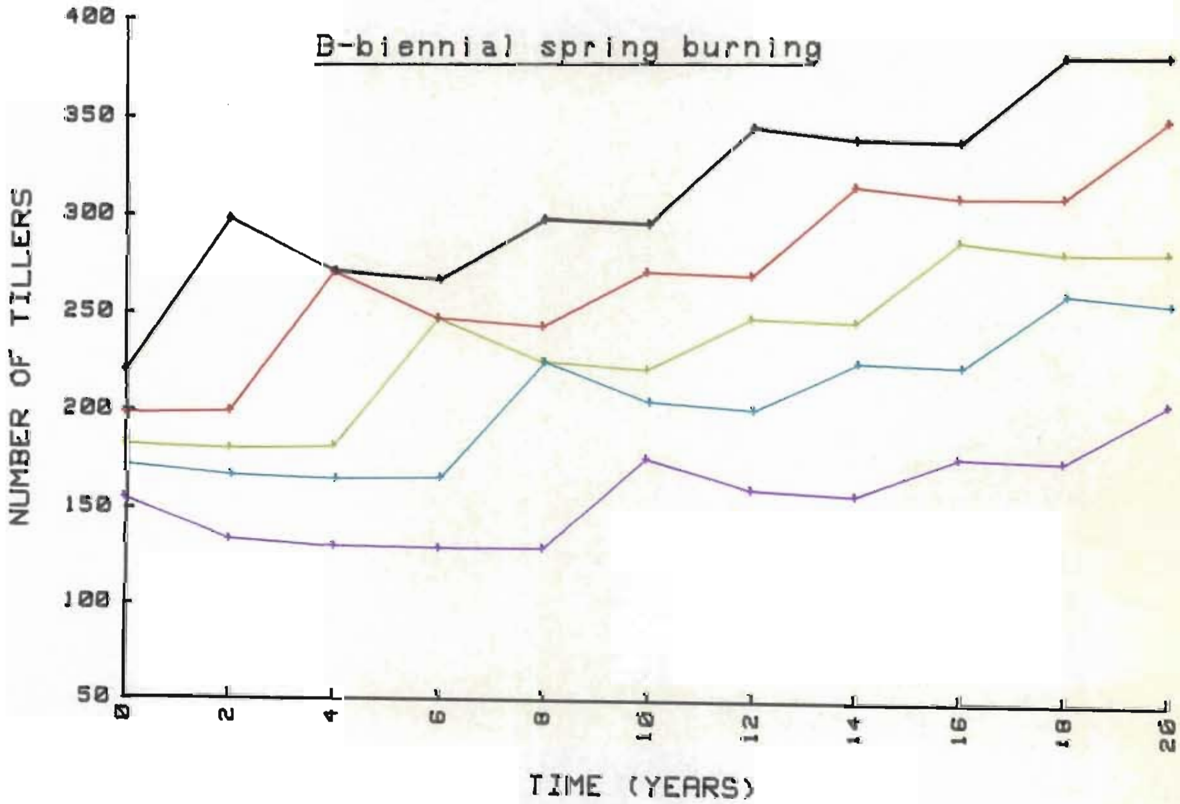
These differences are clearly illustrated in the survivorship curves for T. leucothrix for annual winter and biennial spring burn treatments (Fig. 5.12). Thus plants in the biennial spring burn treatment exhibited a survivorship curve where the majority of individuals survived to an old age for the species (Deevey Type I). In the annual winter burn population however, there was an almost constant number of individuals dying per unit of time after an initially high mortality in the first summer season. This type of survivorship curve, although approximated by some plants (Jain, 1979; Solbrig & Solbrig, 1979) was not classified by Deevey (1947).

The Leslie matrices used to predict the increase or decrease of tiller populations in annual winter and biennial spring burning are presented in Table 5.8. The model predicts that T. leucothrix tillers will decrease in number with annual winter burning and increase with biennial spring burning. This difference is a direct result of the higher mortality in the annual winter burn treatment since the birth rates were in fact higher in this treatment than in the biennial spring burn treatment (Fig. 5.13).

TABLE 5.8 Transition matrices (A) and vectors (a) used to derive predicted values of population growth of Tristachya leucothrix populations in annual winter (i), and biennial spring burn treatments (ii).

$$\begin{array}{cccc} & A & & a \\ (i) & \begin{bmatrix} 0,00 & 0,00 & 0,73 & 0,70 & 1,72 \\ 0,79 & 0 & 0 & 0 & 0 \\ 0 & 0,81 & 0 & 0 & 0 \\ 0 & 0 & 0,65 & 0 & 0 \\ 0 & 0 & 0 & 0,05 & 0 \end{bmatrix} & X & \begin{bmatrix} 250 \\ 198 \\ 166 \\ 124 \\ 79 \end{bmatrix} \\ (ii) & \begin{bmatrix} 0,00 & 0,00 & 0,50 & 0,15 & 1,16 \\ 0,91 & 0 & 0 & 0 & 0 \\ 0 & 0,91 & 0 & 0 & 0 \\ 0 & 0 & 0,92 & 0 & 0 \\ 0 & 0 & 0 & 0,79 & 0 \end{bmatrix} & X & \begin{bmatrix} 220 \\ 199 \\ 183 \\ 172 \\ 156 \end{bmatrix} \end{array}$$


A-annual winter burning
KEY:
Age class (days)
0-150
151-305
305-488
488-700
700+
NUMBER OF TILLERS
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)


B-biennial spring burning
NUMBER OF TILLERS
400
350
300
250
200
150
100
50
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)

These results agree with the classification of *T. leucothrix* as an increaser I species, as noted in Chapter 4 (Table 4.2), where 30 years of burning resulted in a proportional composition of 8,1% in annual winter and 12,2% in biennial spring burn treatments.

5.4.4.6 Conclusions

The results indicate that the life span of *T. leucothrix* tillers is approximately two years, with very few tillers reaching sexual maturity. Reproduction by seed therefore appears to be of little importance in this species.

In spite of its classification as an Increaser I species (Chapter 4), vegetative reproduction was higher in the annual winter burn than in the biennial spring burn treatment. The most intriguing aspect of the population dynamics of *T. leucothrix* is that the survivorship curves for the burning treatments were different, the death risk being higher in the annual winter burn than in the biennial spring burn treatment. This differential response to burning resulted in predictions of decreases in growth of tillers in annual winter burn treatments and increases in biennial spring burn treatments. It would appear therefore that a two year burning cycle would be the most appropriate for the maintenance of *T. leucothrix* in these montane grasslands.

5.4.5 *Harpechloa falx*

5.4.5.1 Primary tiller mass

Fig. 5.14 a illustrates the seasonal change in the dry mass of primary tillers of *H. falx*. Tillers increased in mass from December 1979, reach-

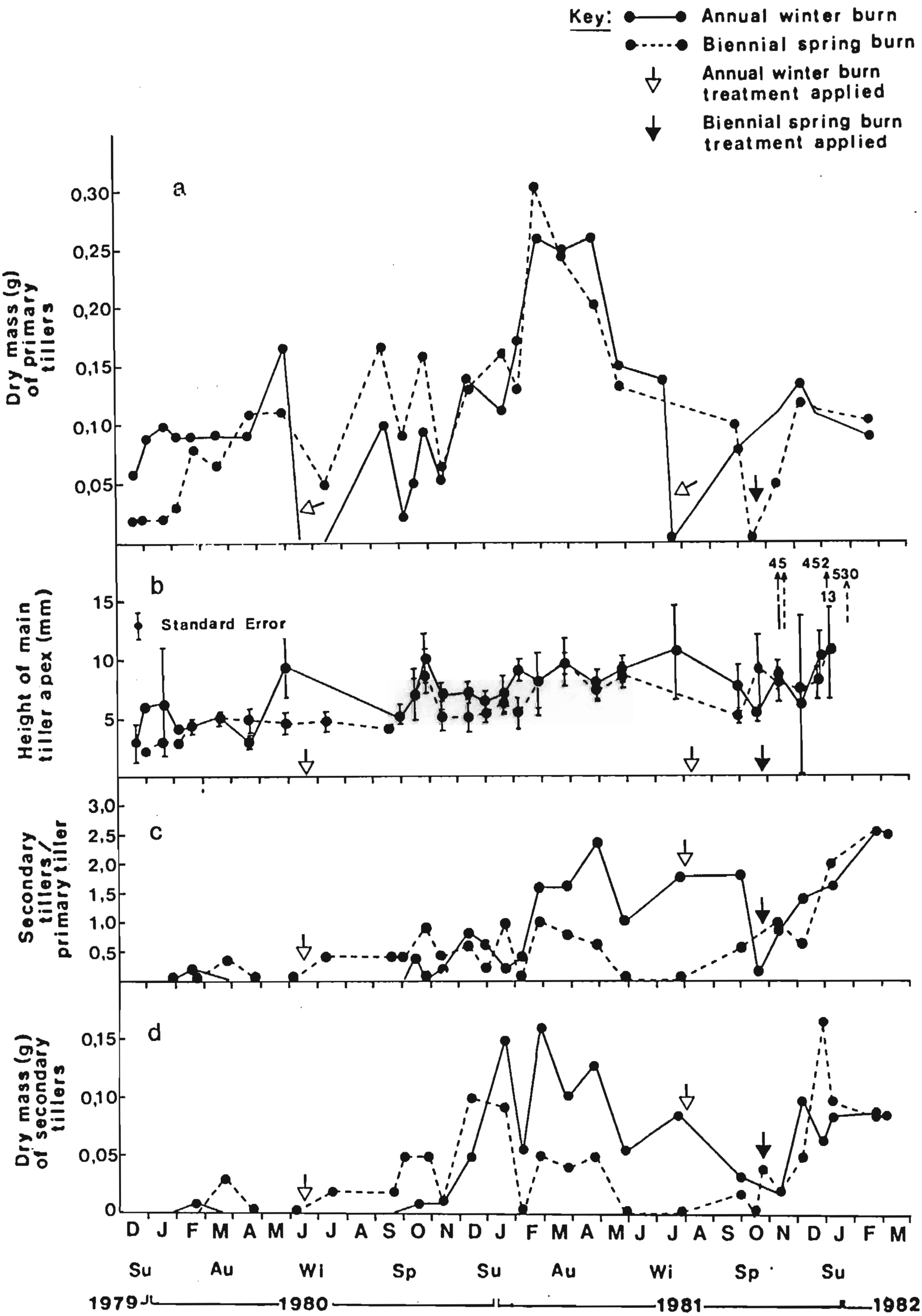


Figure 5.14 Seasonal variation in mean primary tiller mass (a), height of main shoot apex (b), number of secondary tillers per primary tiller (c) and mean mass of secondary tillers (d) of Harpechloa falx subjected to annual winter and biennial spring burn treatments.

ing maximum values of 0,11 and 0,17 g in the biennial spring and annual winter burn treatments respectively. In the next growing season (September - February, 1980), the dry mass of primary tillers in the annual winter burn treatment increased to 0,26 g, and to 0,31 g in the biennial spring burn treatment. The arrival of the frosts in May 1980, resulted in a decrease in tiller mass. Tiller mass in the 1981/82 growing season was low (<0,15 g) since only the basal portions remained. The results indicated that there was little difference in the dry mass of primary tillers burnt either annually in winter or biennially in spring.

5.4.5.2 Elevation of shoot apices

The apical buds of _H. falx_ showed no significant increase in height during the study period, remaining less than 10 mm above the soil surface in both treatments (Fig. 5.14 b). During this period only two marked tillers in the annual winter burn produced inflorescences. These results show that _H. falx_ is well adapted to frequent defoliation, the apical buds remaining safe from damage by fire during their entire life span.

5.4.5.3 Secondary tiller development

Initiation of secondary tillers from marked primary tillers commenced during February/March 1980 (Fig. 5.14 c). In the following 13 months initiation was sporadic, varying between 0,0 and 2,4 in the annual winter burn, and between 0,0 and 1,0 in the biennial spring burn treatment. During the 1981/82 growing season, maximum values for both burning treatments were 2,5 secondary tillers per primary. Perusal of the data (Fig. 5.14 c) shows that annual winter burning generally stimulated greater production of secondary tillers per primary tiller when compared with biennial spring burning.

5.4.5.4 Mass of secondary tillers

Fig. 5.14 d illustrates the change in dry mass of secondary tillers during the study period. In February/March secondary tillers were small, their average dry mass being less than 0,03 g in both treatments. In the following growing season (October 1980 to March 1981) the average dry mass increased in both the annual winter (0,16 g) and the biennial spring burn (0,01 g) treatments. The mass of secondary tillers in the annual winter burn was generally 0,05 g higher than in the biennial spring burn treatment during this period.

In the 1981/82 growing season, however, this situation was reversed when maximum values in the biennial spring burn were 0,16 g, when compared with 0,01 g in the annual winter burn treatment. The results indicate that frequency and season of burn may effect the mass of secondary tillers by stimulating their growth immediately after the application of the first treatment burn. The second annual burn applied in July 1981 did not, however, have this same effect.

5.4.5.5 Population dynamics of _H. falx_ subjected to annual winter and biennial spring burning

Life tables and survivorship curves of _H. falx_ subjected to the two different burning regimes are presented in Table 5.9 and Fig. 5.15 respectively. During the first growing season (day 0-151) there was no significant difference in the survivorship of H. falx in the two treatments. The average mortality rate (qx) was 0,146 and 0,086 tillers per day

TABLE 5.9 Life tables of populations of *Harpechloa falx* subjected to annual winter, biennial spring and summer burning treatments

Treatment	Days on which burn applied	Age interval (days) x-x[1]	Length of interval (days) Dx	No. surviving to day x Nx	Survivor-ship ℓ x	No. removed by sampling	No. remain-ing	No. dying during interval dx	Ave. mortality rate/day qx
annual	-	0-151	151	225	1,0000	35	190	22*a-	0,145
	198	151-305	154	199	0,8844	20	148	23 b-	0,149
winter	-	305-488	183	173	0,7689	50	75	11 c-	0,060
	490	488-700	211	155	0,6889	25	39	14 d-	0,066
burn	-	700+	-	132	0,5867	-	-	-	-
biennial	-	0-151	151	219	1,0000	30	189	13 a-	0,086
	-	151-305	154	204	0,9315	25	151	28 b-	0,182
spring	-	305-488	183	171	0,7808	50	73	11 c-	0,060
	660	488-700	211	153	0,6986	20	42	7 d-	0,033
burn	-	700+	-	143	0,6530	-	-	-	-

*Values sharing the same letter indicate comparisons between treatments (Standardized normal variate). - = Not significant
+ = Significant at the 1% probability level

in the annual winter and biennial spring burn treatments respectively. Between 88 and 93% of the original populations survived to the first winter, the mortality rate during this period remaining similar to that of the previous summer. The annual winter burn treatment applied during this period had no effect on the mortality rate.

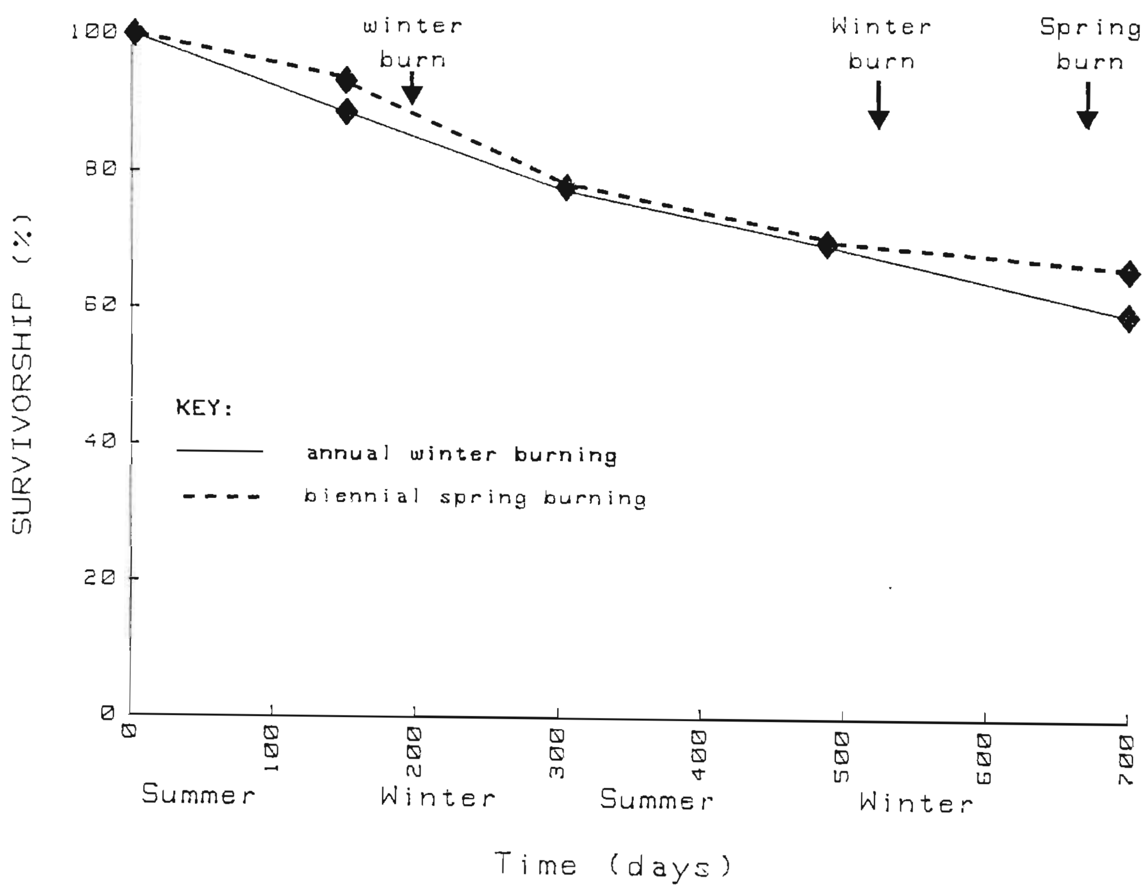


Figure 5.15 The survivorship curves of Harpechloa falx in Highland Sourveld grassland when subjected to annual winter and biennial spring burn treatments.

The second growing season (day 305-488) and winter period (day 488-700) were characterized by having a general decline in the mortality rate (qx = 0,060) when compared with the first year of the study (qx = 0,149). There were no significant differences in mortality between treatments. The treatment burns applied between days 488 and 700 therefore had no effect on the tillers which had survived to this period. By the end of the recording period approximately 60% of the original population were still surviving. Since the majority of individuals of H. falx in both treatments survived to an old age for the species, the survivorship curves for this species (Fig. 5.15) are characteristic of those described by Deevey (1947) as Type I.

The transition matrices used to predict the fate of successive cohorts of H. falx tillers are shown in Table 5.10. The results (Fig. 5.16) indicate that populations of H. falx tillers are capable of increasing with either annual winter or biennial spring burning. In Chapter 4, where the effects of 30 years of burning on species composition was examined, H. falx was found to represent 3,0% in veld burnt annually in winter and 6,6% in biennially spring burnt veld (Table 4.2). The population growth predicted in Fig. 5.16 a & b does not concur with these findings, since the predicted growth was similar in both treatments. They do however, illustrate that H. falx is capable of increasing under biennial spring burning, which may explain its classification as an Increaser I species.

5.4.5.6 Conclusions

Season and frequency of burn did not stimulate the elevation of shoot apices of H. falx, indicating that this species is well adapted to frequent defoliation. Furthermore, annual winter burning stimulated a greater number of ramets when compared with biennial burning.

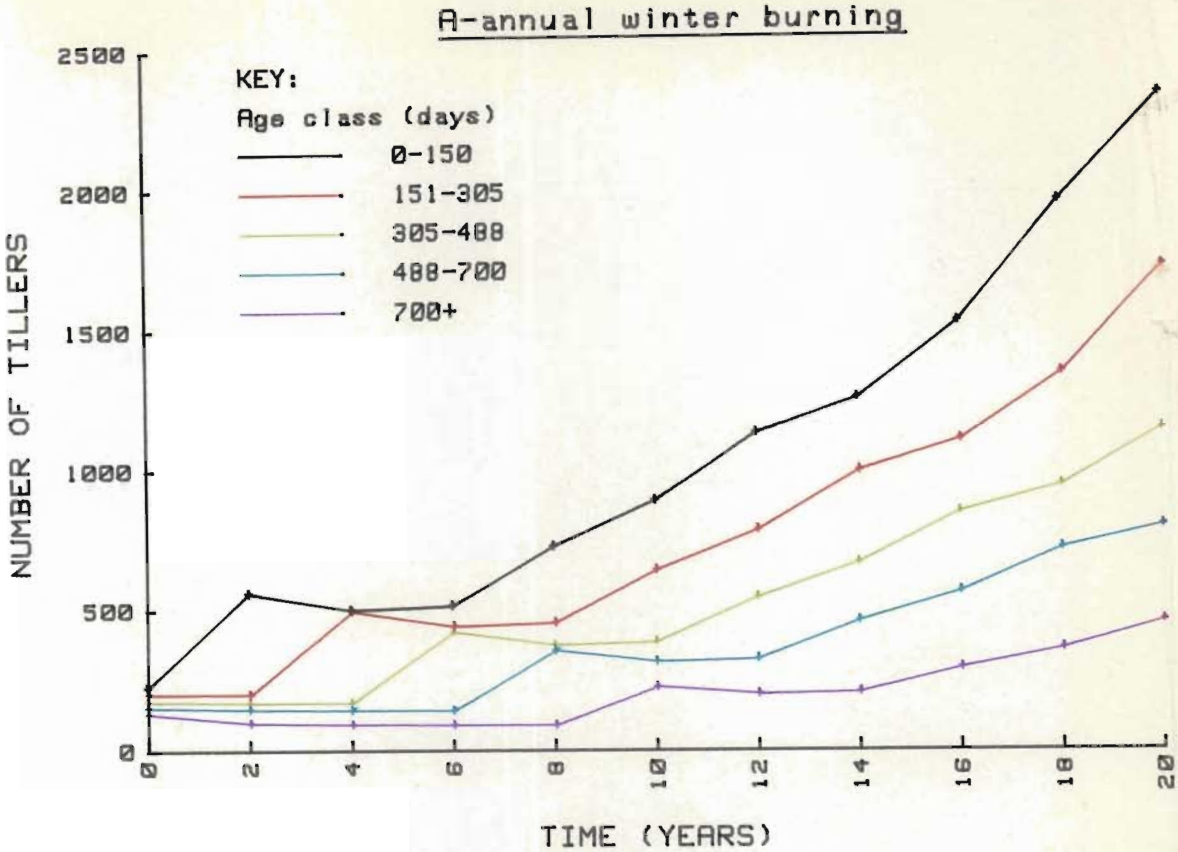
Tiller mortality was not affected by burning either in winter or in spring, while the number of individuals surviving to an old age for the species was high. The survivorship curves were therefore classed as Deevey Type I.

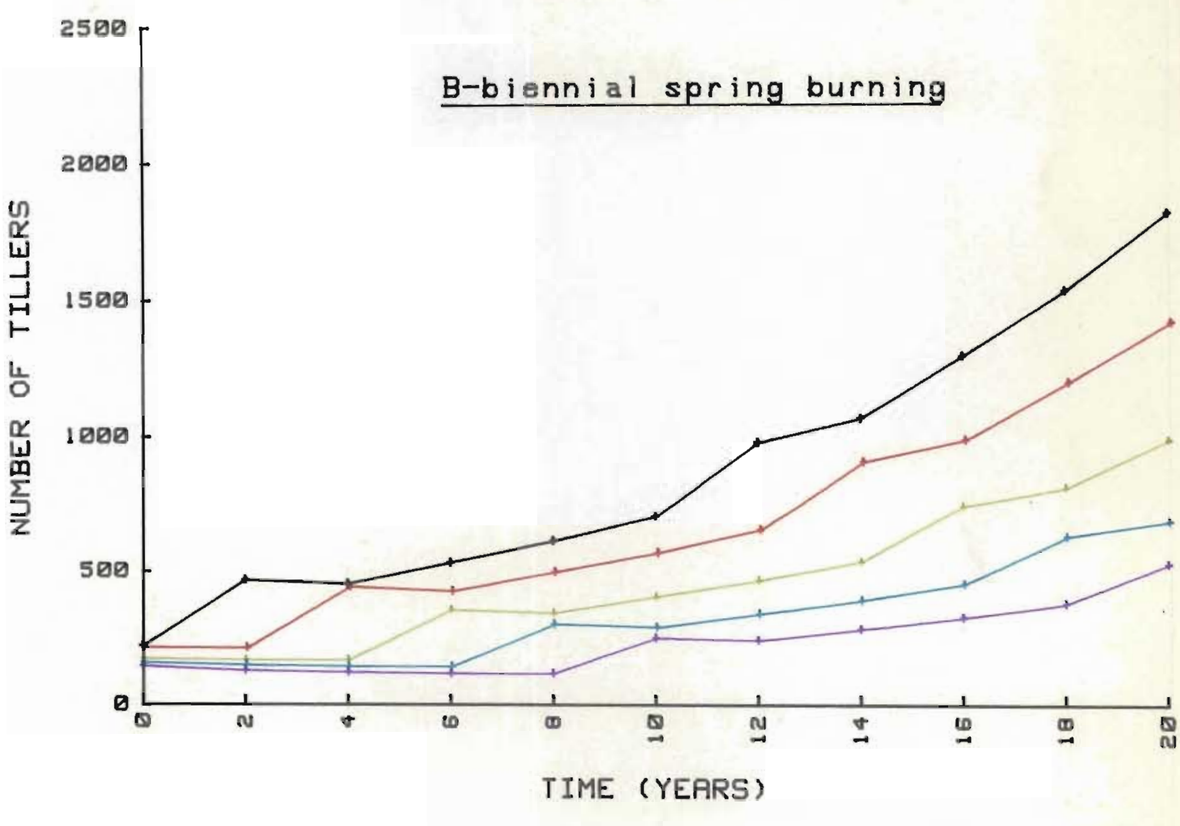
Predictions of population growth of H. falx tillers indicated that both annual winter and biennial spring burning would result in a population increase. It is concluded that either of these treatments would be suitable for the maintenance of H. falx in these Highland Sourveld grasslands.

TABLE 5.10 Transition matrices (A) and vectors (a) used to derive predicted values of population growth of *Harpechloa falx* populations in annual winter (i), and biennial spring burn treatments (ii).

$$\text{(i)}\quad \overset{A}{\begin{bmatrix} 0{,}03 & 0{,}10 & 0{,}88 & 0{,}92 & 1{,}80 \\ 0{,}88 & 0 & 0 & 0 & 0 \\ 0 & 0{,}85 & 0 & 0 & 0 \\ 0 & 0 & 0{,}85 & 0 & 0 \\ 0 & 0 & 0 & 0{,}64 & 0 \end{bmatrix}} \quad X \quad \overset{a}{\begin{bmatrix} 225 \\ 199 \\ 173 \\ 155 \\ 132 \end{bmatrix}}$$

$$\text{(ii)}\quad \begin{bmatrix} 0{,}07 & 0{,}40 & 0{,}46 & 0{,}40 & 1{,}60 \\ 0{,}93 & 0 & 0 & 0 & 0 \\ 0 & 0{,}82 & 0 & 0 & 0 \\ 0 & 0 & 0{,}85 & 0 & 0 \\ 0 & 0 & 0 & 0{,}83 & 0 \end{bmatrix} \quad X \quad \begin{bmatrix} 219 \\ 204 \\ 171 \\ 153 \\ 143 \end{bmatrix}$$


A-annual winter burning
KEY:
Age class (days)
0-150
151-305
305-488
488-700
700+
NUMBER OF TILLERS
2500
2000
1500
1000
500
0
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)


B-biennial spring burning
NUMBER OF TILLERS
2500
2000
1500
1000
500
0
0
2
4
6
8
10
12
14
16
18
20
TIME (YEARS)

5.5 General discussion

The results described in this chapter have revealed some unexpected generalities in the population dynamics of the perennial grasses studied (T. triandra, H. contortus, T. spicatus, T. leucothrix and H. falx). The most important of these are:

i) In all five species studied, the results suggest that flowering is of minimal importance for their propagation, the majority of tillers remaining vegetative until death. The extent of seed production is unclear as there have been no studies on the seedling dynamics of grasslands in South Africa. The role of seedling inputs should not be ignored, however, since although small seedling inputs contribute very little to maintaining the total size of the ramet population, they play a significant role in maintaining genetic diversity (Soane & Watkinson, 1979). The management of these montane grasslands needs to account for these factors, since a burning regime that results in a decline in the number of genets would result in a genetically impoverished population. If these patterns are to be determined, the demography of the genets must be studied, beginning with their initial colonization. Future research in these grasslands should therefore be directed at elucidating these factors.

ii) Coupled with (i) above, was the fact that in all the species studied shoot apices remained close to the soil surface, enabling them to survive frequent defoliation. These results were unexpected since observations at the Ukulinga Research Station near Pietermaritzburg (Tainton & Booysen, 1963) have shown that veld grasses differ widely in respect of their apical bud behaviour. As a result of such variation between grass species, management practices involving defoliation at different times during the year exert profoundly different effects on the grasses in the sward. Since this was not evident in this study, the implication is that the management of these Highland Sourveld Grasslands should be simpler than for the Southern Tall Grassveld in which Tainton and Booysen worked.

iii) In all examples described, recruitment of secondary tillers was stimulated by regular burning, the annual winter burn treatment producing on average more secondary tillers per primary tiller than the biennial spring treatment. Thus all species were well adapted to a regular fire regime.

iv) All species exhibited a remarkable smoothness of their survivorship curves. This suggests that climate and its variations as well as fire, have less impact on mortality than was expected. Fire, however, increased mortality when applied during the summer months when growth and recruitment were most active. Season of burn is therefore of little importance from the time of the first frosts in May until spring, but fires applied outside this period may be detrimental to the grass sward.

v) The predicted exponential increase in growth for the plant populations subjected to the various burning treatments was not demonstrated in the field, suggesting the occurence of density-dependent factors in the regulation of these populations. This implies that the most serious hazard in the life of these perennial grass plants may be overcrowding, especially too many neighbours of the same species.

The above generalizations do not explain the differential response of these five grass species to burning. This response is best explained by the combined effects of their different reproductive capacities (birth rates) and mortality rates. For example, the ability of _T. triandra_ and _H. contortus_ (both Decreaser species) to increase in regularly burnt veld, is a direct result of their higher birth rates when compared with the other species.

The decreaser character of _T. spicatus_ was, however, best explained by the high life expectancy (Deevey Type I curve) demonstrated in the cohort studied. Similar traits were shown by _H. falx_ (Increaser species) enabling it to increase in both annual winter and biennial spring burn treatments. _T. leucothrix_ (Increaser species) demonstrated the most interesting response to burning in that it had different survivorship curves for the annual winter and biennial spring burning regimes. The high life expectancy demonstrated with biennial spring burning enabled the population to increase, whereas a high mortality in annual winter burn treatment resulted in a decrease in the population.

The above discussion shows that it was not possible to group the Increaser and Decreaser species according to any one characteristic curve (i.e. Deevey Type I, II or III). In fact this was not even possible for the same species (e.g. _T. leucothrix_). According to Pianka (1970) and Solbrig & Solbrig (1979), such characterizations may be premature or inappropriate since they imply a greater knowledge of the history of a species than is generally available. In addition it suggests an inflexibility in population dynamics which most species do not display (Mack & Pyke, 1983).

The use of life tables and Leslie matrices should also be considered with caution, since they attempt to predict what will happen to members of the population, from what has happened. They may not do this very accurately for they assume that the future will repeat the past, that mortality will not change with time, and that there will be neither immigration nor emigration (Colinvaux, 1973).

This study, however, has demonstrated that a knowledge of the numbers and fates of individuals is fundamental to understanding the present status, as well as for predicting the future of a population. The single most important fact derived from this study is that a biennial burning regime would be the most suitable for maintaining these five important grass species at present levels of abundance in the Natal Drakensberg. Finally this study has shown that the scientific management of grasslands can be aided by a plant demographic approach.

5.6 Summary

i) Demographic studies were carried out to test the hypothesis that changes in the relative abundance of Decreaser and Increaser I species are brought about by changes in the birth and death rates of tillers as a direct result of fire or its absence.

ii) In all species investigated, flowering was found to be of minimal importance for their propagation, and the majority of tillers remained vegetative until death.

iii) Shoot apices remained close to the soil surface enabling all species to survive frequent defoliation.

iv) In all examples described, recruitment of secondary tillers was stimulated by regular burning, the annual winter burn treatment producing on average more secondary tillers per primary tiller than the biennial spring burn treatment.

v) All species exhibited smooth survivorship curves, suggesting that dramatic fluctuations in climate and severe defoliation, as by fire, have little impact on mortality.

vi) The results suggest the occurrence of density-dependent factors in the regulation of these populations.

vii) The differential responses of these five grass species to burning was best explained by the combined effects of their different reproductive capacities and mortality rates.

viii) A biennial burning regime was shown to be suitable for maintaining the most important grass species at present levels of abundance in the Natal Drakensberg.

CHAPTER 6

EFFECTS OF SHADING ON TILLER INITIATION IN SIX SELECTED GRASS SPECIES AT CATHEDRAL PEAK

6.1 Introduction

Tillering, the process by which lateral buds situated in the axils of the leaves at nodes of the grass stem develop into actively growing tillers, is vital to the production of grasses (Tainton, 1981). Different plants however, differ in their ability to produce tillers (Tainton, 1981).

In the present study it was observed that *T. triandra*, *H. contortus* and *T. spicatus* dominate grassland which is burnt regularly, while *H. falx*, *T. leucothrix* and *A. semialata* dominate veld which is burnt infrequently. It was established in Chapter 4 that these six princip~~le~~al grassland species of the Natal Drakensberg can be arranged along a successional axis, with defoliation frequency as the variable. This suggested that shading could have been implicated in controlling the relative competetive ability of these species, and that this may operate through the effect of shade on tillering.

Although the effect of shading on tiller initiation in agricultural crops has been extensively studied (Aspinall & Paleg, 1963; Friend, 1966; Fletcher & Dale, 1974) there has been little detailed investigation on the response in growth of indigenous grasses to shade. This may be important since Increaser species (which are most abundant in protected areas) generally tiller from below the ground, while Decreaser species (which are most abundant in regularly burnt areas) tiller from above the ground. This differential response to shading led Tainton & Mentis (1984) to hypothesize that Decreaser species are unable to produce tillers when the canopy remains dense for any length of time. Thus they attributed differences in tiller development to the intensity of shade at the crown level of the plant, rather than to any direct effect of burning.

In order to test the above hypothesis a nursery experiment was set up to determine the effects of intensity and height of artificial shade on the growth response of three Decreaser species (T. triandra, H. contortus and T. spicatus) and three Increaser species (H. falx, A. semialata and T. leucothrix).

6.2 Methods

Three hundred and seventy eight plants comprising sixty three whole tufts of T. triandra, T. spicatus, H. contortus, A. semialata, T. leucothrix and H. falx plants were collected in the field with roots intact to a depth of 200 mm. The plants were transplanted into black 200 mm diameter plastic bags filled with a 3 : 1 mixture of soil and sand. Plants were left to stabilize in the pots for 8 weeks, with dead plants being replaced with live until all plants were growing vigorously. During this period plants were irrigated to avoid water stress. Thereafter plants were exposed in an open nursery and were subjected to natural precipitation.

Plants were then randomly allocated to two groups for the examination of the following: i) the effect of intensity of shading on tiller initiation and ii) the effect of height of shading on tiller initiation.

6.2.1 Intensity of shading

Thirty six plants of each of the six species were randomly selected for each of the following treatments: 100%, 80%, 60% and 30% full sunlight. Each treatment was represented by nine replicates of each species. The bottoms of the plastic bags were removed to avoid limiting root volume. These bags were then buried in trenches so that plants were growing at normal ground level. Plants were widely spaced (0,25 X 1,00 m) to limit any possibility of interference between plants. Shadecloth, which does not alter the spectral quality of light (Gaskin, 1965), was used to provide artificial shade. The shadecloth was sewn onto cylindrical wire frames (diameter = 180 mm), set 200 mm above the ground. To obtain an estimate of growth all tillers were counted at the initiation of the experiment, and then recounted 12 months later. The results are expressed as the percentage increase in the number of tillers.

6.2.2 Height of shading

Shadecloth (representing 60% full sunlight) was sewn on to cylindrical wire frames (diameter = 180 mm), set 100 mm and 200 mm above the ground. The third treatment, the control, had no shading treatment. This experiment comprised three groups of 54 plants, each of the three treatments represented by 9 replicates of each species. The plants were set into trenches as described previously. Plant growth was estimated as described in the previous experiment.

6.2.3 Statistical procedures

An analysis of variance for a nested design was applied to the data. In order to obtain the normality requirement assumed by the analysis, it was necessary to transform the data. A plot of the variance against the mean gave a lognormal relationship, indicating that a logarithmic transformation was required. Since the data contained zeros it was necessary to adjust the transformation to $\log_e (x+1)$. The transformed relationship between the mean and variance is shown in Fig. 6.1 and Fig. 6.2. Since the ordinary treatment means of the original variate values are inefficient estimates of the true treatment means because of non-normality, and are prone to distortion when the data are log normally distributed (Rayner, 1967), the data were de-transformed after analysis. Although these means may be biased, they are considered to be more efficient estimates of the true mean (Rayner, 1967).

In order to determine which factor levels within the analysis of variance were significantly different from one another, a multiple comparisons procedure (Student-Newman-Keuls test, Snedecor & Cochran, 1971) was applied to the main effect means.

6.3 Results

6.3.1 Intensity of shading

The results in Table 6.1 showed that shading was significant at the 1% level. This is illustrated in Table 6.2 where the percentage increase in tillers decreased from 2808,6% under full sunlight to 12,1% under 30% sunlight. The multiple comparisons test (Table 6.2) showed that within each species there were no significant differences between the control (full sunlight) and 80% sunlight. Likewise for two of the Increaser species (*H. falx* and *T. leucothrix*) there were no significant differences between the control and 60% sunlight. However, at this level all the Decreaser species had a significant reduction in tiller numbers. This

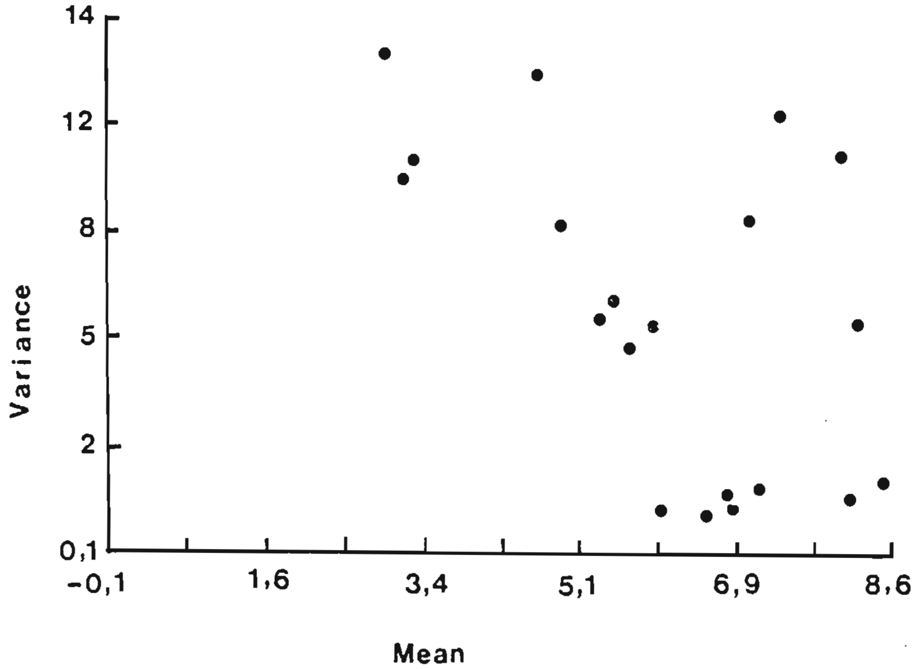


Figure 6.1 Relationship between treatment x (log x + 1) and variance (s^2) of transformed data from the intensity of shading experiment.

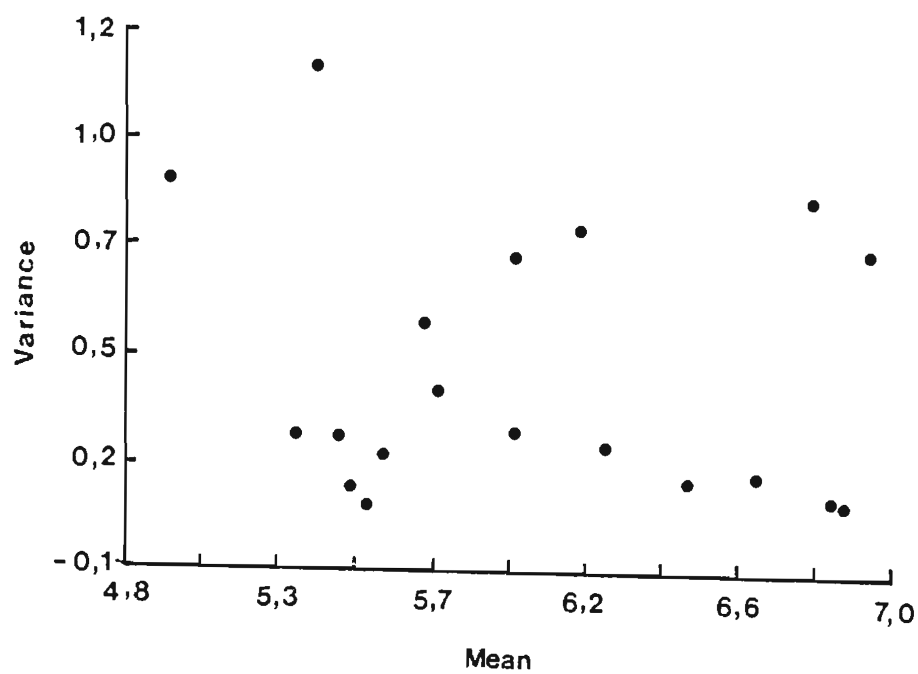


Figure 6.2 Relationship between treatment x (log x + 1) and variance (s^2) of transformed data from the height of shading experiment.

TABLE 6.1 Nested analysis of variance of transformed data to show the effect of shading intensity (A), Decreaser/Increaser effect (B) and species effect (C) on percentage increase in tillers

Source (Name)	df	Sums of Squares	Mean Square	F ratio	Significance
Total	215	1767,5971	8,2214	2,48	
A	3	858,0271	286,0090	86,28	***
B(A)	4	138,5859	34,6465	10,45	***
C(B(A))	16	134,5431	8,4089	2,54	***
Sampling error	192	636,4409	3,3148	–	–

TABLE 6.2 Effect of shade on the percentage increase in tillers subjected to different shade intensities between 2 March 1981 and 2 March 1982

Shade treatment (% full sunlight)	Mean shade effect	Species					
		Decreasers			Increasers		
		Tt	Hc	Ts	Hf	Tl	As
100% (control)	2808,6 a	c 1661,8 A	c 3103,2 A	c 3436,8 A	b 5010,5 A	b 1526,4 A	c 3619,6 A
80	684,6 b	bc 936,8 A	c 1142,0 A	c 911,8 A	ab 1235,3 A	b 408,8 A	bc 685,4 A
60	231,7 c	ab 209,7 A	b 141,3 A	b 157,5 A	ab 876,8 A	b 295;2 A	b 250,0 A
30	12,1 d	a 23,3 B	a 0,0 A	a 0,0 A	a 385,2 C	a 26,4 B	a 18,8 B
Mean species effect		298,0 A	148,9 A	134,8 A	1202,9 B	266,1 A	332,3 A
Mean decreaser/increaser effect		181,6 A			474,0 B		

Values sharing the same letter (Capitals for species data; lower case for shade effect) are not significantly different at the 1% level.

Tt = Themeda triandra
Hc = Heteropogon contortus
Ts = Trachypogon spicatus
Hf = Harpechloa falx
Tl = Tristachya leucothrix
As = Alloteropsis semialata

indicated that at 60% sunlight the Decreaser species were more sensitive to shade than the Increaser species. This was supported by the analysis of variance (Table 6.1) which showed that the comparison between the Decreaser and Increaser categories was significant at the 1% level.

The results showed that there were significant differences at the 1% level between species (Table 6.1). This mostly results from the death of two of the Decreaser species (H. contortus and T. spicatus) at the 30% sunlight level (Table 6.2). The multiple comparisons test showed that H. falx was best able to survive this low light intensity.

The results showed therefore that although reduced light intensities decreased tiller initiation in all species, the Decreaser species were more sensitive to shading than the Increaser species.

6.3.2 Height of shading

From the analysis of variance in Table 6.3 it was evident that height of shade had a significant effect ($p < 0,01$) on tiller initiation. There was a significant decrease in initiation of tillers from 592,8% under the control (no shade treatment) to 287,7% at the 20 cm height of shade level (Table 6.4). The multiple comparisons test (Table 6.4) showed that the 20 cm height of shade level was the most detrimental to tiller initiation.

In contrast to the shading intensity experiment, there was no significant difference between Decreasers and Increasers (Table 6.3). However differences between species were apparent with H. falx once again being less sensitive to shading than the other species.

TABLE 6.3 Nested analysis of variance of transformed data to show the effect of height of shade (A), Decreaser/Increaser effect (B) and species effect (C) on percentage increase in tillers

Source (Name)	df	Sums of Squares	Mean Square	F ratio	Significance
Total	161	115,4738	0,7172	1,76	
A	2	14,0475	7,0237	17,22	***
B(A)	3	2,9567	0,9856	2,42	NS
C(B(A))	12	39,7554	3,3130	8,13	***
Sampling error	144	58,7141	0,4077	-	-

TABLE 6.4 Effects of shade on the percentage increase in tillers subjected to different heights of shading between 14 March 1980 and 30 June 1981

Shade Treatment	Mean shade effect	Species					
		Decreasers			Increasers		
		Tt	Hc	Ts	Hf	Tl	As
No shade	592,8 c	a 223,0 A	b 933,1 B	b 757,2 B	a 1037,2 B	b 303,1 A	b 874,6 B
10 cm	400,3 b	a 213,1 A	a 501,6 A	a 315,6 A	a 968,3 B	ab 271,0 A	a 465,1 A
20 cm	287,7 a	a 249,7 AB	a 390,0 BC	a 259,9 SB	a 624,5 C	a 151,3 A	a 238,8 AB
Mean species effect		227,9 A	567,3 B	395,6 B	856,1 C	231,7 A	460,0 B
Mean decreaser/increaser effect		371,3 A			450,3 A		

Values sharing the same letter (Capitals for species data; lower case for shade effect) are not significantly different at the 1% level.

Tt = Themeda triandra
Hc = Heteropogon contortus
Ts = Trachypogon spicatus
Hf = Harpechloa falx
Tl = Tristachya leucothrix
As = Alloteropsis semialata

6.4 Discussion and conclusions

Although shading resulted in a marked reduction in tillering, all species showed outstanding growth capacities. All plants, apart from those subjected to the highest shading intensity treatment, had a percentage increase in tillers in excess of 140% (Table 6.2 and Table 6.3). This remarkable increase in the number of tillers is undoubtedly due to lack of competition. Caution should therefore be exercised when interpreting the results of potted plant experiments and extrapolating them to conditions in the field.

The results in Table 6.2 support the view expressed by Tainton & Mentis (1984), that Increaser species have a greater ability to survive shaded conditions than Decreaser species. These authors attribute this to the fact that new tillers of Decreaser species do not develop from heavily shaded basal nodes. Tainton & Mentis (1984) observed that Decreaser species respond to shade by the production of aerial tillers which lack roots and eventually die. The fact that two of the three Decreaser species in this study died at the highest shading intensity supports this view.

Tiller production also declined substantially with height of shade, especially at the 20 cm height level. The fact that height of shade was not significantly different between Decreasers and Increasers implies that it is the base of the plant that is the most sensitive to shade. This is supported by Deregibus, Sanchez, Casal & Trlica (1985), who attributed tillering rate and death of tillers to changes in red:far red light at the base of the plant. These authors found that increased shading brought about by higher leaf densities decreased incoming red light, resulting in reduced tillering rates. The authors suggest that the plant parts located at the base of the plant were most sensitive to changes in the spectral composition of light. The sensitivity of buds to changes in the quality and quantity of light has also been documented by Mor, Halevy & Porath (1980).

According to Deregibus et al. (1985) the red:far red ratio could serve as a signal to indicate canopy cover or leaf density. This signal is thought to interact with others related to the availability of various resources (water, assimilates, nutrients, etc.) to determine the rate of tiller formation or death. The distribution of carbon among different sinks may be controlled in this manner (Mor et al., 1980). It is interesting to note that there are morphological differences between Increasers and Decreasers (personal observation). Increasers have swollen bases and tiller from below ground, while Decreasers, which tiller above ground, have no such organs. It may be postulated that the swollen bases of Increasers are used as a sink for the storage of carbohydrates. Such a system may explain the differential response of Increasers and Decreasers to defoliation, and would confer a competitive advantage to Increasers at low light intensities.

It would appear that changes in canopy density together with concomitant changes in light quality, brought about by different fire regimes are an important mechanism in regulating grass vegetative reproduction through tillering. Thus with infrequent fire (i.e. low light interception) tillering is reduced, whereas frequent defoliation (i.e. high light interception) promotes tillering.

Although Increaser species were more tolerant of shade than Decreaser species, all species were detrimentally affected by low light intensities. Such conditions are most likely to occur in areas where fire has been absent for long periods. Examination of such areas (Westfall, Everson & Everson, 1983) indicate that eventually all grass species are replaced by woody species. Thus although certain species can survive shaded conditions better than others, none can survive long term protection without some form of defoliation.

The results of this study support those of Tainton (1981) who found that tillering patterns are not only a function of the species, but are dependent on the growing conditions which are provided. Thus by judicial management it is possible to provide conditions which favour one group of species and not the other.

6.5 Summary

i) Tiller initiation in all species decreased progressively with increasing shading intensity.

ii) Decreaser species were more sensitive to high shade intensities (30% full sunlight) than Increaser species.

iii) Decreaser and Increaser species did not differ significantly in their response to height of shading.

iv) Due to lack of competition tiller initiation in these potted plant experiments was considerably greater than that found in natural conditions.

CHAPTER 7

ABOVE GROUND DRY MATTER PRODUCTION AND QUALITY OF HIGHLAND SOURVELD

7.1 Introduction

In a recent review of the ecological effects of fire on grassland, Tainton & Mentis (1984) report that there is scant information specifically on the effect of fire on plant production and quality. This is supported by the fact that above-ground dry matter production data (standing dead and standing green material) measured at the Giant's Castle Game Reserve by Scotcher & Clarke (1981), are the only data of this kind for the Drakensberg. That there is so little data is surprising, as it is generally accepted that such information can contribute significantly to an understanding of the manner in which fire affects the functions of an ecosystem (Daubenmire, 1968). Since the techniques for estimating production are generally simple, this paucity of data probably reflects the tedious nature of these techniques.

The different fire treatments applied to the grassland at Cathedral Peak over the past 30 years provided an ideal opportunity for examining the long term effects of burning on herbage quantity and quality.

7.2 Procedure

7.2.1 Dry matter production (above ground)

The project consisted of two phases. The first was to compare the recovery growth rates of grass burnt annually in winter and biennially in spring.

The second was to compare the standing green material and the dry matter production of all treatments represented in the Cathedral Peak research catchments.

7.2.1.1 Phase 1

Time series harvests of biomass were used to form the basis of computing dry matter production. This was an intensive investigation and was confined to 3 pairs of replicated plots. Each pair consisted of a plot that had received 30 years of annual winter burning (referred to as 'a' plots) and 30 years of biennial spring burning (referred to as 'b' plots) The replicated plots were situated at ca 1 900 m on a north east, horizontal and westerly aspect and were referred to as plots 9, 10 and 11 respectively (Fig. 2.2). As grazing pressure by indigenous antelope was negligible in this study the plots, were not protected from grazing. The amount of material consumed by insects may be significant in grasslands (Coupland, 1979), but because of practical difficulties was not measured in this study.

The sampling unit was a 0,167 m^2 circle clipped to stubble height approximately 30 mm above ground level using electrically driven sheep shears. A portable generator was used to supply the electrical power. Five randomly located samples (considered to be the maximum practical number) were collected from each plot at the beginning of the growing season in 1978 and sampling continued at two weekly intervals until June 1979. In the following year samples were collected at approximately monthly intervals in the biennial spring burn plots only. In order to reduce the sampling load, standing biomass (all of which comprised green material) was estimated on annual winter burn plots during the second year using the pasture disc meter (Bransby & Tainton, 1977). Samples taken during the 1978/79 growing season were used to calibrate the disc pasture meter. The calibration equation was:

$$y = 2{,}014 + 0{,}041\ x \quad (r = 0{,}84; \quad n = 100)$$

where y = estimated standing green material (g/m^2)

x = mean disc height (mm).

Estimates of y were based on 50 disc meter readings per plot.

Standing green material was separated from standing dead material, oven-dried at 90°C, and weighed. The results are expressed as grams dry matter per square meter ($g\ DM/m^2$).

7.2.1.1.1 Calculations

Although the calculation of above ground dry matter production is usually based on time series harvests of biomass, no single standard technique of computation is available (Singh, Lauenroth & Steinhorst, 1975). A review of the various techniques was carried out by Singh et al. (1975). They concluded that trough peak analysis was the best method of calculating dry matter production (DMP). In this analysis only the positive increments and their corresponding clipping intervals are considered. The following advantages are gained from this approach: (1) it does not require biomass measurements for individual species; (2) more than one growth peak per season may be measured; and (3) it does not assume a zero starting point for standing live material, so that the method can be used for estimating DMP for any time interval. The main disadvantage of the method is the unaccounted loss of photosynthate, and losses due to translocation of metabolites to the unsampled below ground organs, resulting in an underestimation of production. Below ground respiration results in further loss of photosynthate, as do exudation and leaching (Grossman, 1982).

In this study standing green (B) refers to attached, live standing green material and standing dead (N) to attached standing dead material. The sum of B + N represents 'standing crop' which in this case applies only to above ground plant material. Since only B and N were measured in this study and litter decay was not measured, the methods 6a and 7 of Singh et al. (1975) appear to be most appropriate for calculating the mean rate of accumulation (A).

Method 6a may be mathematically expressed as:

$$A = (B_n - B_{n-1})^* \;/\; (t_k - t_0) \quad \ldots\ldots\ldots\ldots\ldots\ldots \;(1).$$

In this equation the harvests are at times t_0 to t_k, with positive values only (*) and their corresponding intervals being used.

Method 7 of Singh et al. (1975) attempts to correct for losses by death between clipping dates, which Williamson (1976) showed may be important. It may be written as:

$$A = [(B_n - 1) + (N_n - N_{n-1})]^{**} \;/\; (t_k - t_0) \quad \ldots\ldots\ldots(2).$$

Here ** indicates only those intervals during which the sum of the B and N differences are positive, and their corresponding clipping intervals are included. The calculation does not allow for loss by physical removal, decay or translocation of photosynthate below clipping height.

Another problem in calculating DMP is the amount of residual material carried over from a 'previous' to a 'current' growth season. Grossman

(1982) demonstrated that this carry over may be considerable. Because of this and other problems, which he considered produced an underestimate of the true value, he proposed a method for calculating DMP for perennial grass swards in Southern Africa. However, this method could not be used here since certain parameters required for the calculation were not measured (e.g. flow of standing dead to litter). Nevertheless in this trial, burning the experimental plots prior to the experiment, would have increased the accuracy of the DMP estimates (Grossman, 1982). Although the results are likely to be an underestimate of DMP, they are considered adequate for comparing the differences between the annual winter and biennial spring burn treatments.

Equations (1) and (2) give mean rates only. It is also of interest to examine the instantaneous rate, particularly that of standing green material (B). This was achieved by plotting the mass of standing green against time, and then differentiating. A number of different 'growth' functions were fitted in an attempt to model these data. These included 2nd degree and 3rd degree polynomials, and broken stick models using quadratic and linear equations. Splined functions (Hunt, 1982) were not considered suitable because of the variable nature of the data (Clarke, 1985, pers. comm.). The best fit was obtained using an exponential quadratic function. Standing green material (B) was then expressed as:

$$B = \exp\,(c + bx + ax^2) \;\ldots\ldots\ldots\ldots\ldots\ldots (3).$$

The rate of change of standing green can then be expressed as:

$$dB/dt = (bx + 2ax^2)\,[\exp\,(c + bx + ax^2)] \;\ldots\ldots\ldots\ldots (4),$$

where the term on the left represents the 'rate of change of standing green material', and that on the right the 'growth rate'. When dB/dt is positive it represents the 'standing green accumulation rate'.

7.2.1.2 Phase 2

The research catchments are protected by permanent fire breaks which have been burnt annually in winter for the last 30 years. This annual winter treatment was used as a control against which the other treatments within the catchments could be compared. This was achieved by demarcating 14 paired plots and 6 triplicate plots having a wide range of treatments, aspects, slopes and altitudes. Direct comparison of the various treatments was therefore possible. The harvesting of samples was identical to that described previously (see Phase 1).

In order to determine the mass of standing green, all the plots were sampled in the first week of January, a time when the maximum quantity of standing green material was expected. The standing green material was separated from the standing dead material and the oven-dry mass of each determined. In May, additional quadrats were harvested to provide total dry matter yield data. These samples, were however, not separated into standing green and dead components.

7.2.2 Dry matter production (below ground)

To obtain a complete appraisal of primary production it was necessary to gain some measure of the belowground dry matter production. Because of the inherent difficulties involved in sampling (San Jose, Berrade & Ramirez, 1982) and the laborious nature of the techniques, only one sample was possible. The sample was collected during March 1983 from an area with a history of biennial spring burning.

7.2.2.1 Procedure

A soil pit (0,75 m wide and 1,50 m deep) was excavated to obtain an estimate of maximum root dry matter production. A square meter quadrat was marked out on one side of the pit and all above ground vegetation removed from the soil surface. The soil from the area inside the quadrat was then excavated in 7 cm layers to a depth of 49 cm. Each soil layer was placed in a plastic bag and transported to the laboratory. The large clods of soil in each of these sub-samples were broken up before air drying the soil. After the bulk of the roots had been hand separated, the soil of each layer was submerged in a container filled with water. Once saturated, remaining roots were separated by flotation (McKell, Wilson & Jones, 1961). In this way loss of fine roots was minimized. Material (including other debris) collected in this manner was air-dried and any remaining roots removed by hand. The final root samples were then oven-dried at 105°C and the mass for each layer recorded.

7.2.3 Herbage nutritive value

Crude fibre (CF) and crude protein (CP) were used as an estimate of herbage quality. These two measures are still widely used by the Cedara Feed Analysis laboratory to estimate forage quality, and data are available which relate the CF and CP contents of forages to animal performance.

Samples analysed for herbage quality were those collected from plots 9, 10 and 11 of Phase 1, and plot 12c. The latter was included to obtain an estimate of the quality of grass protected from fire for 16 years. Samples were analysed by the proximate methods used by the Cedara Feed Analysis Laboratory, Department of Agriculture and Fisheries. In order to reduce costs, samples from each plot of the same treatment were bulked.

Samples were analysed for CP at approximately monthly intervals between September 1978 and June 1980 from the biennial spring burn plots; between September 1978 and June 1980 from the annual winter burn plots and between November 1979 and June 1980 from the protected plot.

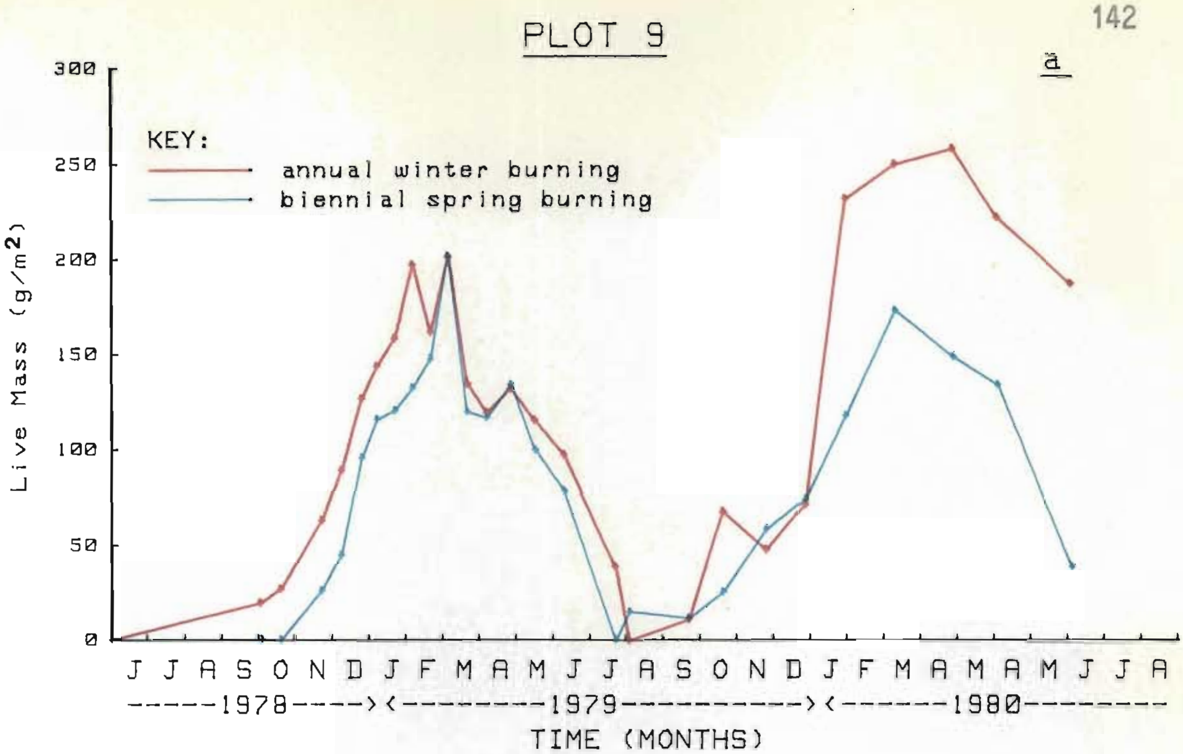
7.3 Results

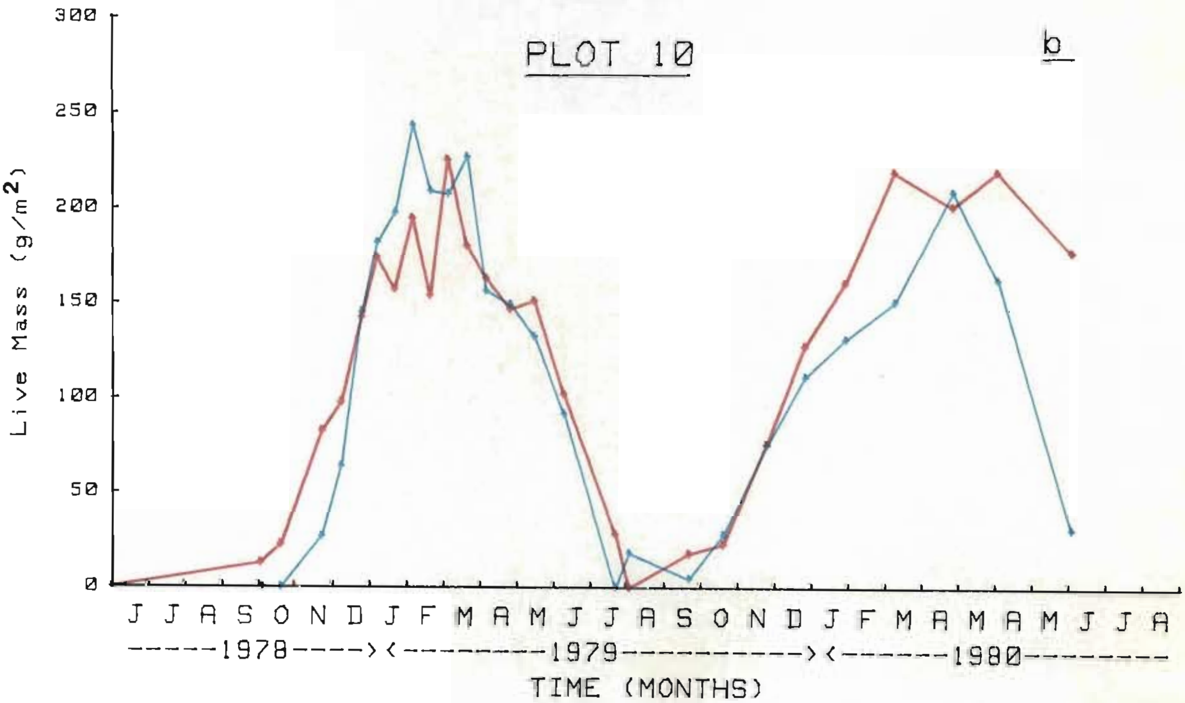
7.3.1 Dry matter production (above ground)

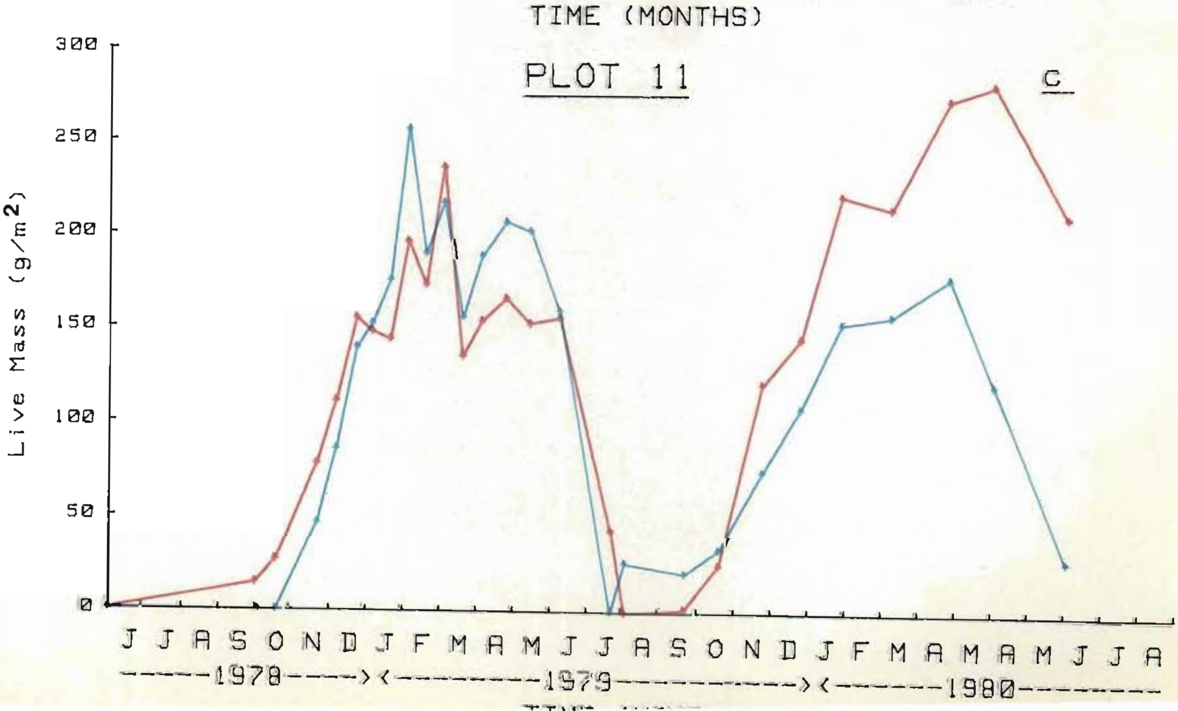
7.3.1.1 Phase 1

Summaries of all relevant data for each of the six plots are presented in Appendix B, Tables I to VI. Important differences between the treatments and seasonal rates of growth are best shown graphically (Fig. 7.1 a-c). In the first year following the burns (1978/79), the mass of standing green material is described by bell-shaped curves. As a result of the different seasons of burn, the biennial spring plots initially lagged behind the annual winter plots. By December these differences were no longer apparent. Maximum values were recorded between December and February, with peak values varying between 201 and 255 g/m². There were no noticeable differences between burning treatments. From March onwards there was a rapid decline in the amounts of standing green material. This was associated with death of the above ground parts due to the advent of winter and the arrival of the first frosts.

In the second year (1979/80) similar results were found (Fig. 7.1 a-c). During this period, however, maximum green standing mass was generally lower in the biennial spring burn plots (172-207 g/m²) than in the annual winter burn plots (218-280 g/m²). As there were no observable differences between the plots to which a particular burning treatment was applied,


PLOT 9
a
KEY:
annual winter burning
biennial spring burning
Live Mass (g/m2)
300
250
200
150
100
50
0
J J A S O N D J F M A M J J A S O N D J F M A M A M J J A
-----1978----><---------1979----------><-------1980--------
TIME (MONTHS)


PLOT 10
b
Live Mass (g/m2)
300
250
200
150
100
50
0
J J A S O N D J F M A M J J A S O N D J F M A M A M J J A
-----1978----><---------1979----------><-------1980--------
TIME (MONTHS)


PLOT 11
c
Live Mass (g/m2)
300
250
200
150
100
50
0
J J A S O N D J F M A M J J A S O N D J F M A M A M J J A
-----1978----><---------1979----------><-------1980--------

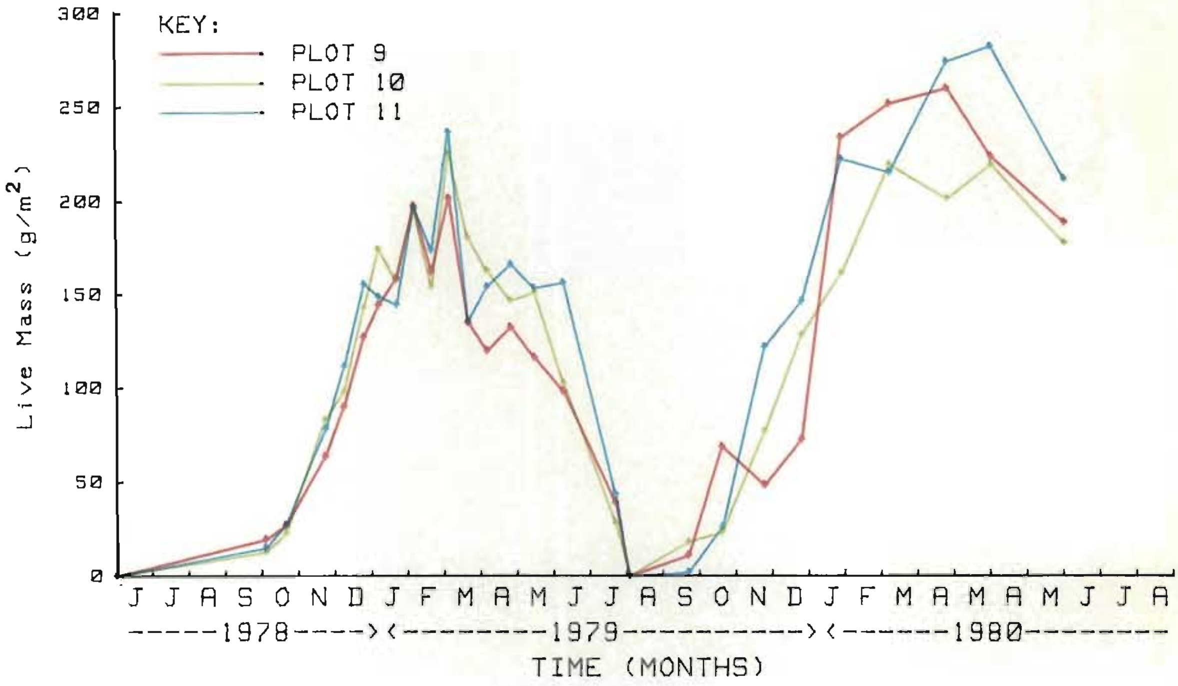
the data were pooled, and mean values calculated for each burning treatment (Figs. 7.2 a & b).

The fitted curves and the rate of change of standing green (dB/dt), are given in Figs. 7.3 a & b). These figures summarize the standing green dynamics in the annual winter and biennial spring burn treatments. The integral of the positive part of the growth rate curve approximates the dry matter production of these treatments. It does not, however, take losses due to physical removal, death between clipping dates, decay or translocation of photosynthate to tiller bases and roots into consideration.

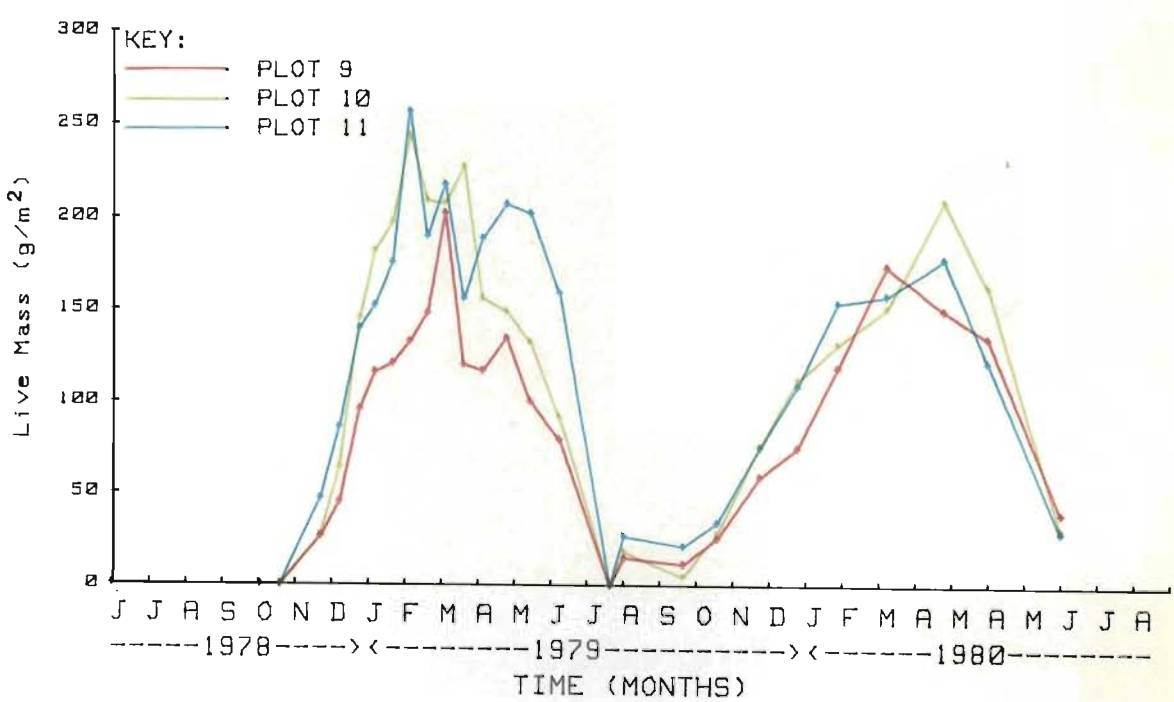
The rate of biomass accumulation in the first year was 13,2 and 14,1 g/m²/wk in the annual winter (Fig. 7.3a) and biennial spring (Fig. 7.3 b) burn plots respectively. On an annual basis (i.e. the integral of the growth rate curve) net productivity was 233,4g/m²/yr and 225,6 g/m²/yr in the two treatments. This represents a difference of only 3%.

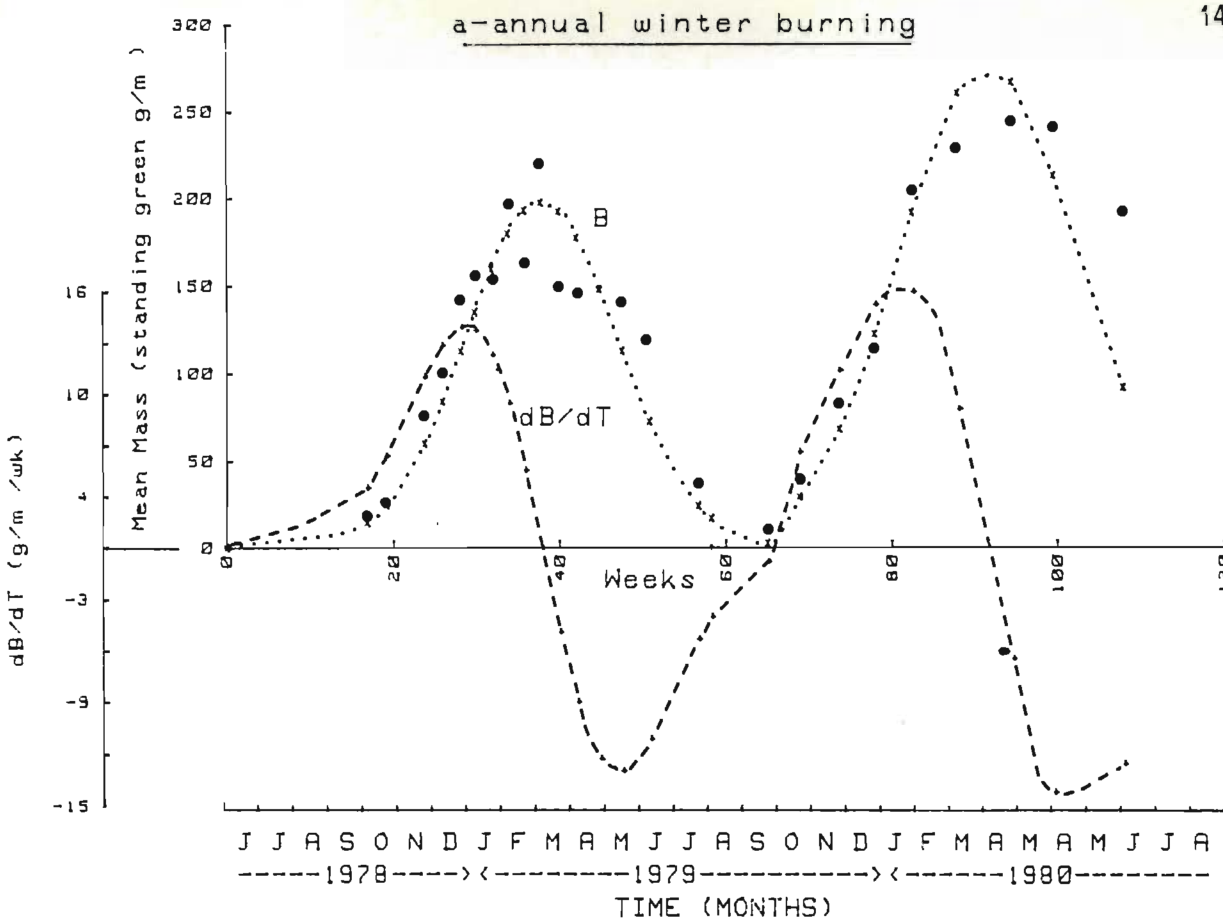
In the second growing season maximum accumulation in the annual winter burn plots was 15,8 g/m²/wk (Fig. 7.3 a). This was 5,65 g/m²/wk higher than that recorded in the biennial spring burn plots (Fig. 7.3 b). Also noticeable was the fact that maximum net primary productivity in the biennial spring burn plots was 4,0 g/m²/wk lower in the second season than in the first. On an annual basis, net productivity in the second year was higher in the annual winter burn plot (310,95 g/m²) than in the biennial spring burn plot 170,20 g/m²). The higher production in this second year than in the first year on annual winter burnt plots may have been due either to more favourable growing conditions in the second year, or to an overestimation of the standing green material by the disc pasture meter.

a-annual winter burning



b-biennial spring burning





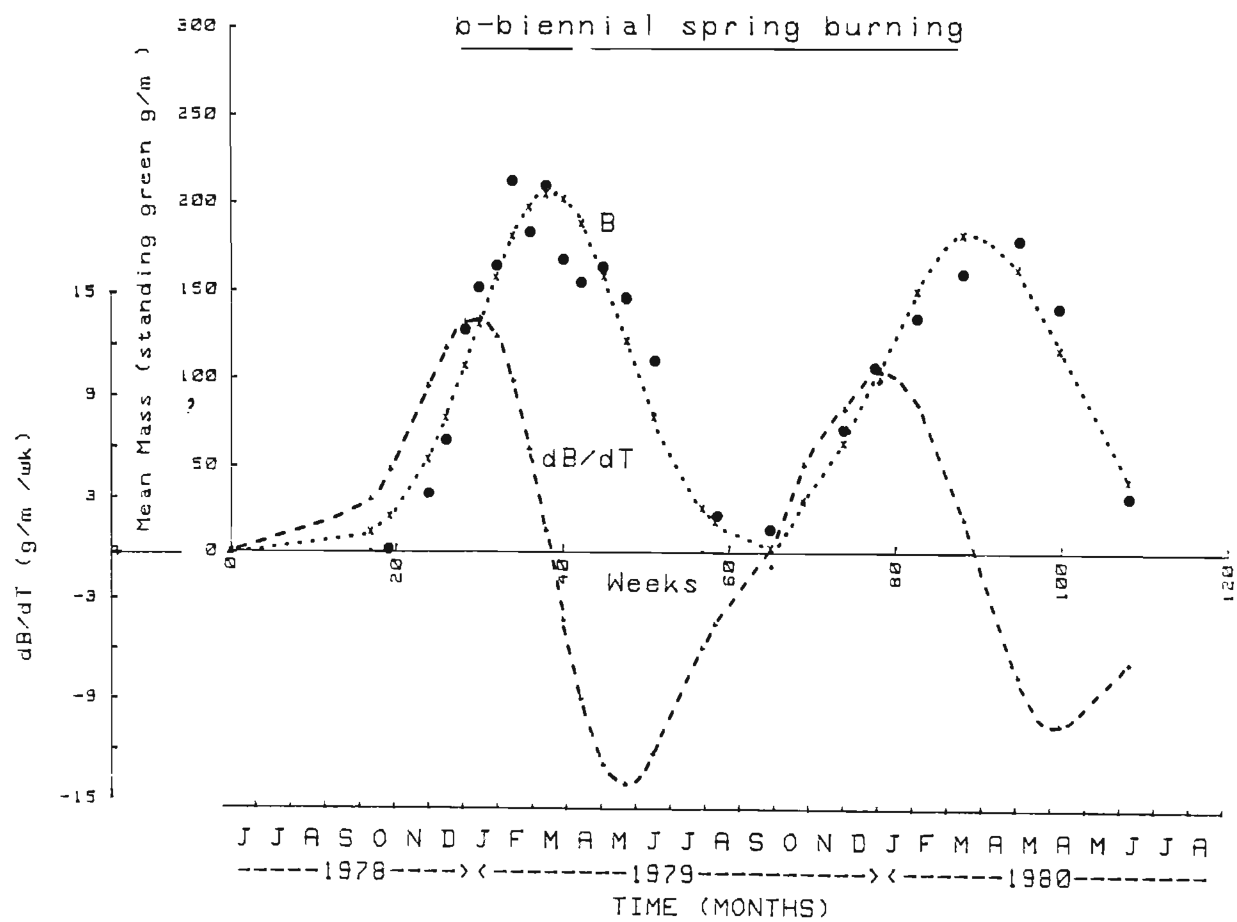


Figure 7.3 a-b. Comparisons of monthly changes in the standing green material (g/m^2) of plots 9, 10 and 11 (closed circles) and the rate of change of standing green material (dB/dT) of Highland Sourveld burnt annually in winter (a) and biennially in spring (b). The curve B is the best fit of equation (3) to the field results. Its parameters are

The maximum net primary productivity rate in both burning treatments was reached at the end of December, and the maximum live biomass at the end of March in both the 1978/79 and 1979/80 growing seasons (Figs. 7.3 a & b).

Dry mass of green grass stems and inflorescences was 22,3; 22,8 and 15,4 g/m^2 for plots 9b, 10b and 11b respectively. This represented approximately 10% of the net productivity in the second growing season (Appendix B). No flowering material was collected in the annual winter plots.

Standing dead material was recorded in both the annual winter and biennial spring burn treatments from the end of April 1979, immediately after the first frosts (Appendix B). By the end of June standing dead material represented approximately 95% of the total dry matter yield. The annual winter burns, applied in July, resulted in the removal of the above ground material in these plots. Standing dead material in the biennial spring burn plots was carried over into the next growing season, increasing steadily until February and rising sharply with the advent of frosts in May 1980. At the end of this two year period total dry matter yield had approximately doubled to 476, 638 and 518 g/m^2 in plots 9b, 10b and 11b respectively.

The mean rates of accumulation (A) calculated using equations (1) and (2) are shown in Table 7.1. The methods produced similar estimates for each season of the annual winter burn treatment (9 $g/m^2/wk$), and for the first season of the biennial spring burn treatment (13,08 & 14,71 $g/m^2/wk$ for equations (1) and (2) respectively). However higher results were recorded by equation 2 (11,37 $g/m^2/wk$) in the second season of the biennial spring burn treatment when compared with equation 1 (7,87 g/m²/wk). This higher value is due to the fact that losses by death between clipping dates are accounted for in equation (2). Irrespective of which equation is used to calculate mean accumulation, it is apparent that growth in the second season of the biennial spring burn treatment was lower than in the first growing season.

TABLE 7.1 Mean rates of accumulation (g/m² / wk) calculated using equations (1) and (2). Values are the means of plot 9, 10 and 11.

Equation	Season	Annual Winter Burn	Biennial Spring Burn
1	first	8,11	13,08
1	second	9,42	7,87
2	first	9,90	14,71
2	second	9,42	11,37

7.3.1.2 Phase 2

Least squares analysis in which the standing green and total dry mass values were adjusted to remove the effects of slope, altitude and aspect are shown in Tables 7.2 and 7.3. The biennial spring and biennial spring with light summer grazing plots included both one year and two year post-fire age grasslands. In the analysis these age classes were separated.

Results of the standing green material collected during January 1979

TABLE 7.2 Comparisons of standing green mass (g/m^2) between treatments

Treatment	Mean	Versus Annual Winter Burning			Versus Biennial Spring Burning + Grazing (1st season)			Biennial Spring Burning + Grazing (2nd season)			Biennial Spring Burning (1st season)			Biennial Spring Burning (2nd season)		
	$\bar{x}$	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Annual winter burning	144,7		–													
Biennial spring burning + grazing (1st season)	154,5	7,7	±27,9	NS		–										
Biennial spring burning + grazing (2nd season)	99,1	-18,4	±22,6	NS	25,5	±36,0	NS		–							
Biennial spring burning (1st season)	154,4	12,6	±15,2	NS	4,9	±31,8	NS	-31,0	±27,4			–				
Biennial spring burning (2nd season)	135,1	- 0,1	±18,2	NS	7,8	±33,3	NS	-18,3	±29,2	NS	12,7	±21,7	NS		–	
Protection	118,2	-28,4	±13,2	+	36,1	±30,8	NS	10,0	±26,3	NS	41,0	±17,3	+	28,3	±20,0	NS

+ = $p < 0.05$

++ = $p < 0.001$

Est. = Estimate

SE = Standard error

Sig. = Significant

TABLE 7.3 Total Dry Matter yield (g/m²)

Treatment	Mean	Versus Annual Winter Burning			Versus Biennial Spring Burning + Grazing (1st season)			Biennial Spring Burning + Grazing (2nd season)			Biennial Spring Burning (1st season)			Biennial Spring Burning (2nd season)		
	$\bar{x}$	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.	Est.	SE	Sig.
Annual winter burning	190		–													
Biennial spring burning + grazing (1st season)	365	180,8	±92,6	+		–										
Biennial spring burning + grazing (2nd season)	164	- 9,6	±75,6	NS	190,4	±119,5	+		–							
Biennial spring burning (1st season)	202	8,4	±50,4	NS	172,4	±105,4	NS	-18,0	±90,8	NS		–				
Biennial spring burning (2nd season)	471	247,1	±60,4	+++	-66,3	±110,5	NS	-256,7	±96,8	++	-238,7	±72,2	++		–	
Protection	609	410,6	±43,7	+++	-229,8	±102,4	+++	-420,2	±87,3	+++	-402,2	±57,4	+++	-163,5	±66,2	++

p < 0.01
+ p < 0.05
++ p < 0.01
+++ p < 0.001

Est. = Estimate
SE = Standard error
Sig. = Significance

(Table 7.2) showed that the only significant comparisons were protection ($\overline{x}$ = 118,2 g/m²) versus annual winter burning ($\overline{x}$ = 144,47 g/m²) and protection versus the biennial spring burning in one year post-fire age grassland ($\overline{x}$ = 154,5 g/m²). Mean values of standing green varied between 99,1 and 154,5 g/m² and were considerably lower than maximum standing green values recorded in Phase 1 (approximately 220 g/m²). These lower values (recorded in January) are underestimates of the maximum standing green since peak values were only reached at the end of February (see results, Phase 1), nearly two months later than was predicted.

Comparisons of total dry matter (TDM) yield data are presented in Table 7.3. These results showed that TDM yield values in grassland protected from fire ($\overline{x}$ = 609 g/m²) were significantly higher than all the other treatments. In the first season following a fire there were no significant differences between the annual winter burn ($\overline{x}$ = 190 g/m²), the biennial spring burn ($\overline{x}$ = 202 g/m²) and the biennial spring burn with grazing ($\overline{x}$ = 164 g/m²) treatments. Likewise there were no significant differences between the second season of the biennial spring burn ($\overline{x}$ = 471 g/m²) and the biennial spring burn with grazing ($\overline{x}$ = 365 g/m²) treatments. Results from the biennial spring burn treatment (Table 7.3) showed that the TDM production doubled from 202 g/m² in the first season to 471 g/m² in the second. This indicates little decay or loss of material by grazing or other means during this two year period. Similar results were found in the biennial spring burn with grazing treatment, where the mean TDM yield increased from 164 to 365 g/m² from the first to the second season. Although these values were lower than those in the other treatments, differences were not significant, implying that the grazing was very light.

7.3.2 Dry matter production (below ground)

The results presented in Table 7.4 showed that at the time of maximum dry matter production (February), roots extended at least to a depth of 49 cm. Sixty four per cent (585 g/m²) of the roots occurred in the top 14 cm, while 25,4% (222 g/m²) occurred in the following 14 cm. This biomass decreased with depth so that only 1,33% of the roots were present between 42 and 49 cms. Thus, although roots extended to a depth of at least 49 cm, approximately 65% of the total root dry matter (903 g/m²) was confined to the top 14 cm of soil, and approximately 90% to the top 28 cm.

TABLE 7.4 Distribution of roots in the top 50 cm of the soil

Soil depth (cm)	0-7	7-14	14-21	21-28	28-35	35-42	42-49	Total
Dry mass (g/m^2)	306	279	126	96	64	20	12	903
Percentage of roots present in each layer	33,89	30,90	13,95	10,09	7,09	2,21	1,33	100

7.3.3 Herbage nutritive value

Monthly changes in the crude protein (CP) and crude fibre (CF) of the standing green material are illustrated in Fig. 7.4. During the 1978/79 growing season CP in the annual winter burn plots declined from a maximum of 8,5% in early spring (September) to a minimum of 3,7% in winter (July). In the biennial spring burn plots the trend was similar, although the maximum value (9,4%)was recorded in November. This delay was probably due to the difference in the time of application of the treatment burns. By the end of December these differences were no longer apparent. The minimum value in the biennial spring burn treatment was recorded at the end of winter (early September) just prior to the start of the next spring flush.

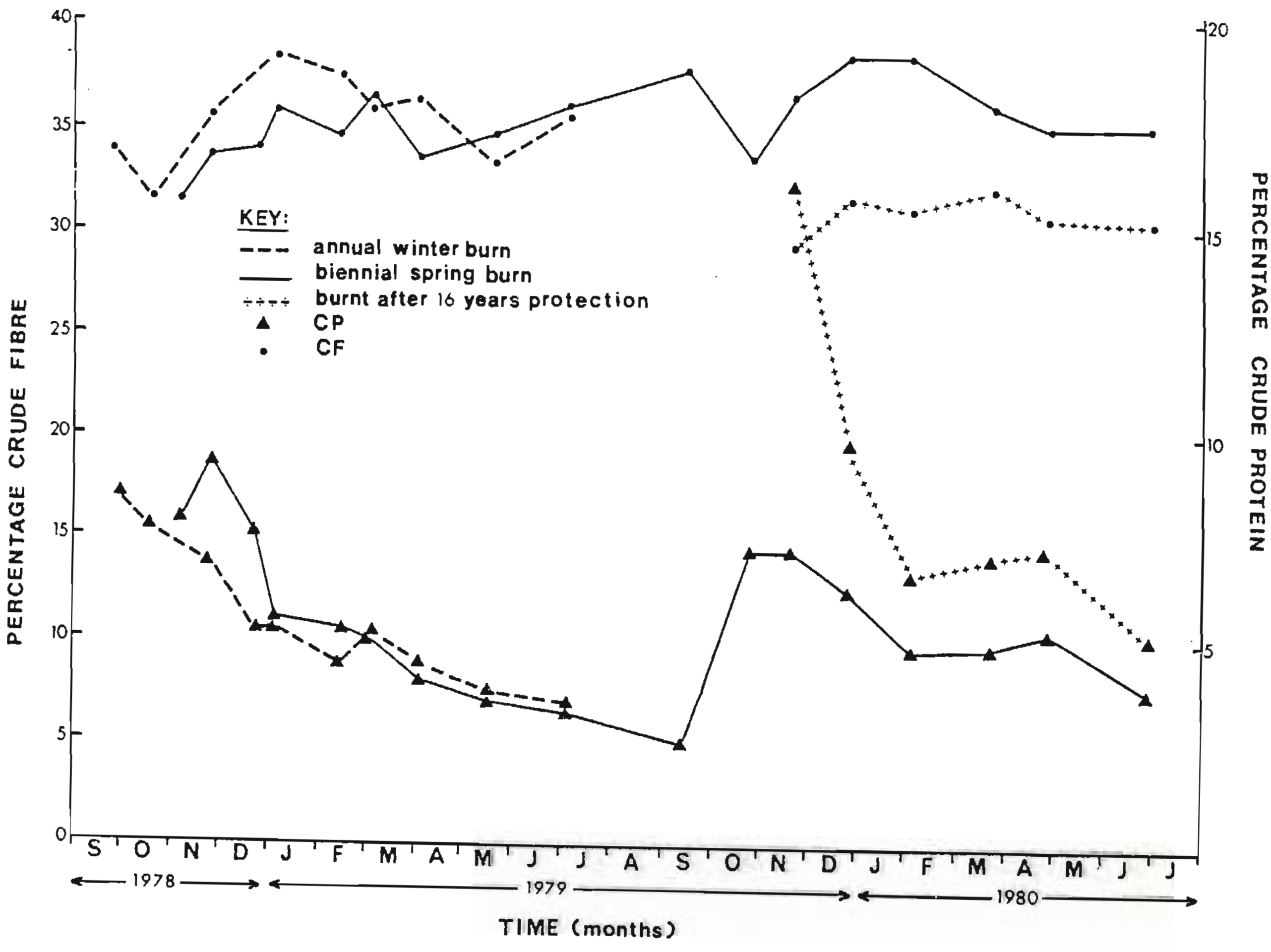


Figure 7.4 Crude protein and fibre content of standing green material of Highland Sourveld burnt annually in winter, biennially in spring and after 16 years protection.

In the following season (1979/80) crude protein increased to a maximum of 7,1% in October. Thereafter values declined to 3,9% at the end of June. This maximum value was approximately 2% lower than that recorded in the previous growing season.

The maximum value attained in the plot which had been protected from fire for 16 years and then burnt (plot 12c) was considerably higher (16,1%) than the values recorded in the annual winter and biennial spring burn treatments. This value declined sharply after November to approximately 6% at the beginning of February. Between February and April CP values remained essentially constant and then declined to 4,9% in June.

Using mean values of standing green from Phase 1, it is possible to show the amounts of CP available per hectare for each treatment (Fig. 7,5). The mass of CP per hectare increased sharply between October and December 1978 in both the annual winter and biennial spring burn treatments. Although the maximum for the biennial spring burn treatments (113 kg CP/ha) was higher than for the annual winter burn treatments (95 kg CP/ha), there was little difference between the two treatments. In spite of the high CP levels found in plot 12c, the maximum value recorded per hectare was only 45 kg. This low value is a result of the decrease in standing green material (Appendix D, Table 1) brought about by the prolonged period of protection.

In contrast to CP, CF levels (Fig. 7.5) tended to increase during the initial part of the growing season (October to December) and then decrease towards winter. The CF ranged between 31% and 38%. Values from the annual winter burn plots were initially about 2% higher than those in the biennial spring burn plots. In the second season of the biennial spring burn the pattern was similar although values tended to be higher than those of the previous season.

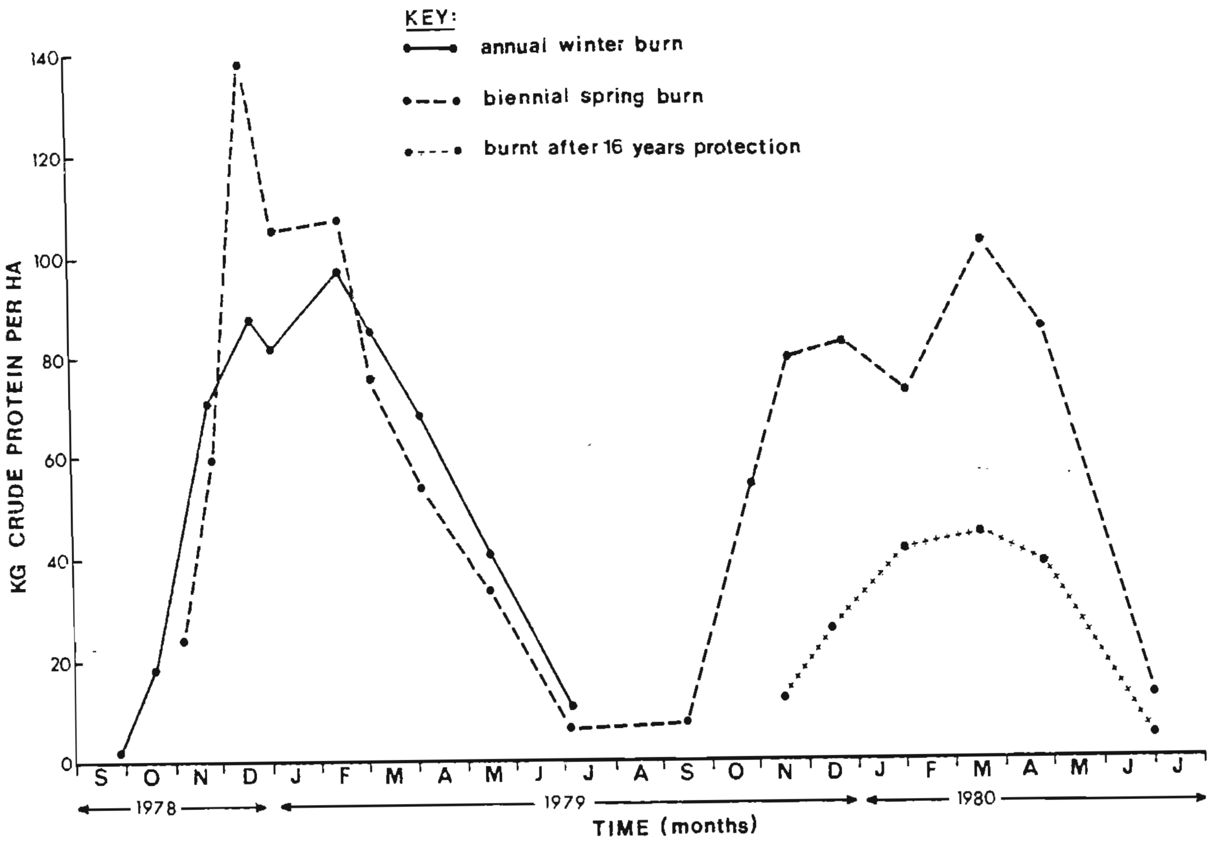


Figure 7.5 Crude protein yield (kg CP/ha) in plots burnt annually in winter, biennially in spring and after 16 years protection.

7.4 Discussion and conclusions

The results of this study showed that differences in the effects of burning the veld, either in winter or in spring, were largely short term. Although growth was stimulated earlier in the season by burning in winter, the maximum net productivity was approximately 230 g/m² for both treatment burns (determined by the integral of the growth curve). Tainton *et al*. (1977) also found that the recovery growth rate of Tall Grassveld burnt in winter and in early spring was very similar. Values recorded in this study were similar to those of Scotcher (1982) who found that the maximum net productivity of one year-old grassland was approximately 200 g/m²/yr. However, the veld during the non-burning season of the biennial spring burn treatment showed a marked decrease in productivity (ca 60 g/m²/yr). Similarly, protected treatments where fire had been excluded for a number of years also had significantly lower values of standing green material.

Production estimates from other areas of the grassland biome (Rutherford, 1978) range from 63 g/m²/yr for grasslands around Bloemfontein receiving 500 mm mean annual rainfall, to 390 g/m²/yr in the higher rainfall grasslands near Pietermaritzburg. The values recorded for Highland Sourveld in this study (230 g/m²/yr) would therefore place these grasslands amongst the more productive areas of Southern Africa.

In the lower rainfall areas of Southern Africa rainfall generally has a significant positive effect on the productivity of grasslands (Huntley, 1984). The 1978 growing season of this study was characterised by having 25% more precipitation than normal (Fig. 2.2). That yields were not affected by this above average rainfall suggests that moisture is generally not a limiting factor in the growth of these grass plants.

Estimates of the below ground dry matter were 903 g/m². Unfortunately it was not possible to distinguish between living and dead material, limiting the use of these data. It is interesting to note, however, that the below ground dry matter mass of veld burnt biennially in spring was approximately 300 g/m² greater than the above ground material after 2 years of growth.

The CP and CF values found in this study did not differ markedly from those of previous workers (Weinmann, 1955; Scotcher, 1982). Summer levels ranged between 5 and 10%, while winter levels dropped to approximately 3%. If 7% CP is considered to be the minimum level for animal maintenance (N.R.C., 1970), then the stimulation of fresh green shoots high in CP on burnt grassland early in the season, may be an important factor for the survival of antelope in these areas.

Various techniques were used to estimate the production of the grassveld in this study. The limitations of these methods have already been discussed. However, in areas where grazing is minimal and decay slow (as was the case in this study) the selection of a particular technique is probably not as important as in areas where this is not the case. Perhaps what is important is the number of samples taken at the time when maximum values are expected. Thus it is recommended that sampling intensity should be increased at this time, since the calculation of A in equations (1) and (2) is based on the peak value.

The calculation of net productivity using fitted mathematical functions avoids the problems just discussed and allows the calculation of the instantaneous growth rate. It does however, smooth the data, which may result in the loss of real fluctuations in the data.

The data presented in this study illustrate the beneficial effect of fire on the growth and quality of these montane grasslands. The most important aspect of these results is that there were no significant differences in the production of grasslands which had received either 30 years of annual winter or biennial spring burning. From a management point of view it would appear that the veld can be burnt at any time between winter (May/June) and spring (September/October) without adversely affecting productivity.

7.5 Summary

i) In this chapter the long term effects of burning on herbage quantity and quality were examined.

ii) The results indicated that differences in the effects of burning veld, either in winter or in spring were largely short term.

iii) Maximum net productivity was approximately 230 g/m^2 in both annual winter and biennial spring burning.

iv) Standing green material in protected areas was ca 20% lower than regularly burnt veld.

v) There was little difference in the amount of CP available per hectare between annual winter (113 kg CP/ha) and biennial spring burning (95 kg CP/ha). However, burning after 16 years of protection from fire resulted in a marked decrease (45 kg CP/ha).

vi) Winter burning stimulated fresh green shoots high in CP in early spring. This was considered an important factor for the survival of antelope in these areas.

vii) The results showed that Highland Sourveld grassland can be burnt at any time between May and October without adversely affecting productivity.

CHAPTER 8

THE EFFECT OF VELD BURNING ON CANOPY COVER AND SEDIMENT YIELD

8.1 Introduction

The catchment areas of the Natal Drakensberg are characterized by deeply dissected valleys and steep slopes. Falling within the region of very high rainfall energy ($>$ 10 000 J/m²/annum - Schulze, 1980) of South Africa the potential for soil erosion in these areas in considerable. Garland, Chisholm & Christian (1977) described the area as "... a high energy geomorphological system that is in a state of imbalance with climatic and hydrological conditions". They concluded that "erosion and denudation rates are quite rapid, since significant quantities of soil and rock are transported over fairly short time spans of only 10 to 20 years". Thus modifications of existing land use may result in a serious increase in rates of denudation. Management of the area should therefore take into account the effect of these geomorphological processes resulting in rapid rates of erosion (Garland et al., 1977).

In the early days of European settlement of these areas, farmers practised extensive burning together with heavy grazing (Nanni, 1969). This resulted in rapid degradation of the veld and accelerated soil erosion. As a result a commission of enquiry was held in 1923 which issued a report condemning burning in Catchment Areas (Levyns, 1929). This was re-emphasized in the Governments' investigation report following the severe droughts during 1932 and 1933 (Scott, 1951; 1955).

However, by the early 1960's seral development to woody plant species, reduction of grass basal cover, accumulation of dead fuels and concomitant increases in fire hazard and reduced water yields, illustrated the need for controlled burning treatments (Wicht, 1959; Le Roux, 1966; Duffey et al., 1974; Bands, 1977). It was apparent that the only means by which catchment areas could be managed for the production of high quality water and preservation of the soil mantle was by regular burning. Thus complete protection of these grasslands from fire was replaced by a policy of burning the veld every second year in spring (Bainbridge & Scott, 1981). This policy was still in practice at the commencement of this study.

Despite the controversy surrounding the use of fire and its effect on the water and sediment yield of catchments, there has been little research on these aspects in South Africa (Garland, 1982). At Cathedral Peak the hydrological effects of biennial burning in grassland catchments have been monitored since 1949. The results of these experiments (Nanni, 1960; Bosch, 1979) have suggested that fire has little effect on streamflow. The only measurements of erosion in the Drakensberg have been made by Watson (1981), who attempted to estimate the effects of veld burning on sediment yield from catchment XI at Cathedral Peak. Her results indicated, from measured run-off from firebreaks that had been burnt annually in early winter for 30 years, that regular fire had not resulted in accelerated soil losses. As this is the only work of this nature in the Drakensberg, it is apparent that further research on the effects of fire on the quality of water flowing from mountain catchments is required.

The aims of this study were to determine firstly the effect of veld burning on vegetal cover, and secondly to predict soil loss using the canopy data derived from the different veld burning treatments.

8.2 Methods

8.2.1 Canopy cover

8.2.1.1 Apparatus - Levy Bridge

The original Levy Bridge design detailed by Levy & Madden (1933) was adapted for this study following Granger's observations (in Watson, 1981) that the mean basal diameter of this type of tussock grassland is approximately 130 mm. The interval between the holes in the horizontal bar through which the striking pin is directed was therefore increased from 50 mm to 150 mm. This necessitated lengthening the horizontal bar from the standard 0,5 m to 1,5 m. Furthermore, 15 mm X 65 mm long brass sleeves were inserted into the holes to minimize lateral movement of the pin, and the diameter of the pin was increased to 12 mm to prevent bending. A sharpened point (ca 1 mm) was attached to the end of this pin.

8.2.1.2 Sampling technique

A preliminary assessment was carried out to determine the required sampling intensity. The Levy bridge was placed randomly 100 times in a 25 X 25 m plot to obtain a total of 1000 point positions. The measurements were carried out when the canopy cover was low (September) since variability is highest at this time and sample size should be greatest. On the basis of running mean calculations, 40 point positions were considered adequate. However, at a later date these data were reanalysed to check whether this was enough to give a standard error within 10% of the mean. As it is possible for only integral values to occur in this type of enumeration, a discrete or discontinuous distribution was expected. However, a plot of the frequency distribution of the data (Fig. 8.1) and a Chi-squared test (Table 8.1) showed that this was not the case. A Chi-

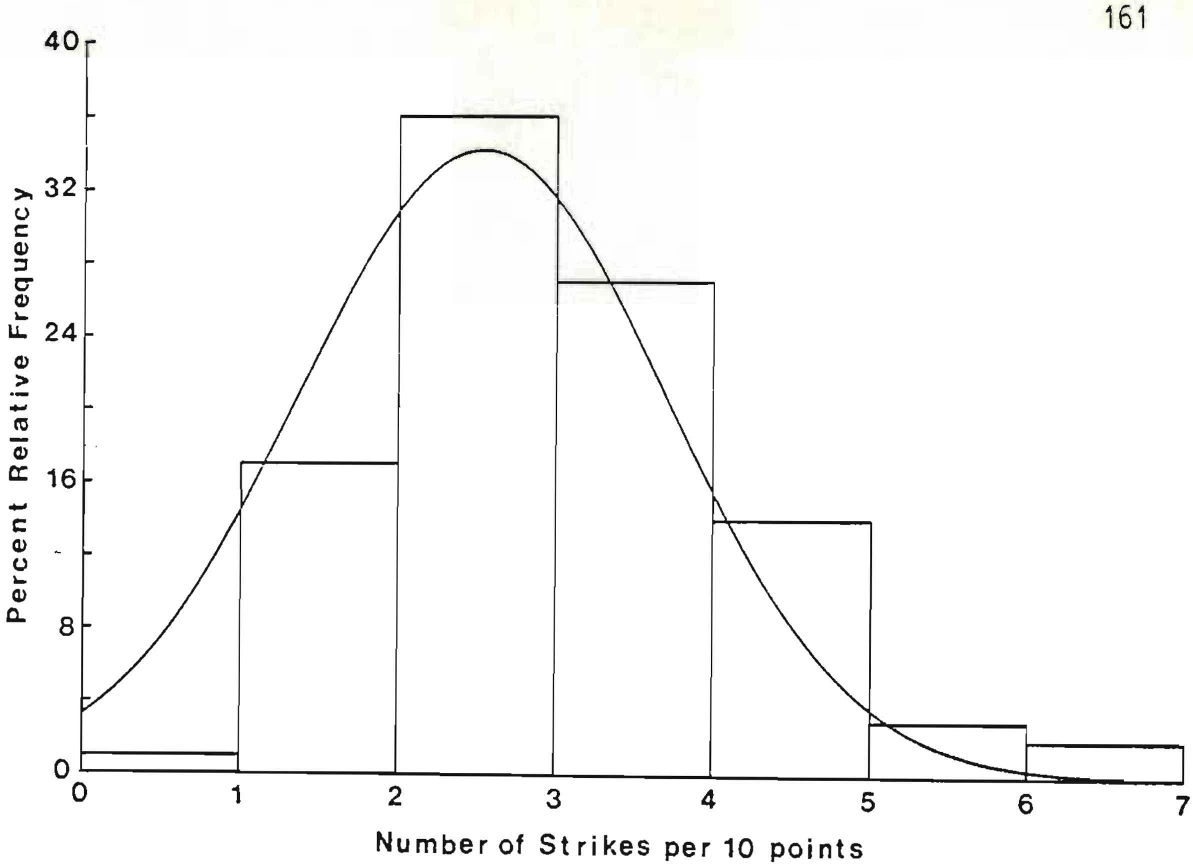


Figure 8.1 Frequency distribution (percent) of canopy cover data and normal curve overlay for 100 emplacements of the Levy bridge.

TABLE 8.1 Distribution of canopy cover data collected from 100 placements of the Levy bridge. Fitted Poisson distribution.

No. of strikes per bridge placement (10 points)	Observed Frequency	Expected Frequency	Contribution to Chi-square
0	1	9,499	7,604
1	17	22,992	1,562
2	36	33,148	0,245
3	27	23,964	0,384
4	14	8,679	7,119
5	3	1,570	
6	2	0,148	

Chi-square value = 16,91; Degrees of freedom = 3

$0.01 > p > 0.001$

squared test for normal goodness of fit (Table 8.2) was therefore applied and showed that the data were normally distributed. The standard error of the mean (Parker, 1973) was therefore calculated as:

$$\frac{\overline{x} + s}{n} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

and the standard deviation (s) as the square root of the variance. The number of samples required to give a standard error within 10% of the mean could be calculated by substitution in the formula:

$$n = \frac{(s)^2}{(0,1\overline{x})} \quad \ldots\ldots\ldots\ldots\ldots\ldots (2).$$

TABLE 8.2 Distribution of canopy cover data collected from 100 placements of the Levy brige. Chi-square goodness-of-fit for normality.

No. of strikes per bridge placement (10 points)	Lower Limit	Observed No. of Obs.	Expected No. of Obs.
1	1,0000	17	18,03
2	1,8333	36	27,13
3	2,6667	27	25,04
4	3,5000	14	14,18
5	4,3334	3	4,92
6	5,1667	2	1,05

Chi-square value = 4,735; Degrees of freedom = 3

$0{,}10 > p > 0{,}05$

The $\bar{x}$ and s of the data collected in this experiment were 2,53 and 1,17 respectively. The minimal number of required placements of the bridge was calculated as 21,24. Thus, the sampling intensity of 40 used in this study was greater than the actual intensity required.

During the early stages of this study it was envisaged that SLEMSA (the Soil Loss Estimator Model for Southern Africa, Dept. of Agricultural Technical Services, 1976) would be used for predicting soil losses. In this model aerial canopy cover is the only vegetation parameter required as an input into the model. Thus initial measurements included this parameter only. However, it later became apparent that MUSLE (Modified Universal Soil Loss Equation, Williams & Berndt, 1977) would be the more appropriate model for predicting sediment yield from catchments. In this model canopy includes mulch and close growing vegetation in addition to cover. Thus the initial results were later complemented with combined estimates of canopy and mulch cover (see later discussion).

8.2.1.3 Study Sites

Comparisons of canopy cover from annual winter and biennial spring burning treatments were obtained from the three replicated plots 9 a & b, 10 a & b, and 11 a & b (described previously in Chapter 7). Plot 12c was included in this study to examine recovery growth rate of veld burnt after 16 years protection. Canopy cover was also estimated in an annual winter (plot 12 a), biennial spring (plot 12 b) and summer burn treatment (plot

12 d).

Canopy cover estimates were taken in the above treatments at approximately two weekly intervals during the 1978 and 1979 growing seasons. Additional estimates of combined canopy and mulch data were recorded from the annual winter and biennial spring burning treatment during 1984 and 1985.

In order to assess the possible effect of altitude on canopy recovery additional canopy cover estimates were taken in a high altitude plot (1 900 m) and a low altitude plot (1 400 m), both which had received long term annual winter burn treatments.

8.2.2 Soil loss modelling

8.2.2.1 During the period 1976 - 1979

Modelling of soil loss enables management with foresight, and not only after damage has occurred (Schulze, 1979). In Southern Africa both the Universal Soil Loss Equation (Wischmeier & Smith, 1978) and the SLEMSA equations have been used to model soil erosion.

Schulze (1979) applied SLEMSA to the Drakensberg Key Area, and later used a modified version of USLE (MUSLE) for use in entire catchments (Schulze, 1981). Sensitivity tests run on SLEMSA indicated that slight variations in some parameters caused soil loss estimates to vary, in some cases by hundreds of percent. This led the author to conclude that at present SLEMSA can at best give only comparative results. The MUSLE, developed from more than 10 000 plot years of data, was therefore considered to be the better corroborated of the two models. Since prediction from a whole catchment was required, the MUSLE was adopted in this study.

8.2.2.2 Description of the Modified Universal Soil Loss Equation

Traditionally soil loss has been predicted on an average annual basis with equations including a rainfall energy component (Musgrave, 1947; Wischmeier & Smith, 1965). Because this approach is neither suited to modelling sediment yield (as opposed to soil loss) from catchments (as opposed to runoff plots), nor to applications where shorter time intervals are required (e.g. for water quality modelling), the USLE was modified (MUSLE, Williams, 1975 in Williams & Berndt, 1977) by replacing the rainfall energy factor with a run-off factor. According to Williams & Berndt (1977) the MUSLE increases sediment yield prediction accuracy and is applicable to individual storms on catchments. These authors found that in 60 catchments, MUSLE generally explained 80% or more of the variation in individual storm sediment yield for each catchment.

The MUSLE is expressed as:

$$Y = 11{,}8\ (Q \times qp)^{0{,}56}\ K.C.P.LS \ldots\ldots\ldots\ldots\ldots\ldots(1)$$

where Y = the sediment yield from an individual storm in metric tons,

Q = storm runoff volume in m^3,

qp = peak runoff rate in m^3/s,

K = the soil erodibility factor,

C = cover factor,

P = the erosion-control-practice factor, and

LS = the slope length and gradient factor.

In this study, values of Q and qp were obtained from measured runoff from Catchment IV (area = 0,947 ha) at Cathedral Peak. Although Q and qp are highly intercorrelated, Q is more related to the detachment process, while qp describes sediment transport processes (Williams & Berndt, 1977). Values for K and LS for Catchment IV were obtained from Schulze, 1979. The C factor of the model is divided into three types:

Type I - Canopy cover: This is defined as the percentage of the total surface area of ground that cannot be hit by vertically falling raindrops because of interception by leaves and stems which do not directly contact the soil surface.

$$* \text{ Type I} = 1,0 - 0,008\ x$$

where x = percentage canopy cover.

Type II - Mulch and close growing vegetation: This includes all plant material in direct contact with the soil surface, and is expressed as the percentage of ground surface it occupies. Mulch intercepts raindrops, impedes overland flow of water and promotes infiltration.

$$* \text{ Type II} = 1{,}078 - 0{,}107 \sqrt{y}$$

where y = percentage mulch.

Type III - Residual effect: Land use affects soil structure, density, porosity, surface roughness, organic matter content and rooting, all of which influence erodibility at a site. All these effects are specified as "residual". Values for the residual effect on natural areas were obtained from Wischmeier (1975).

* Type III = 0,2 (residual effect on natural areas).

* These equations are based on Figs. 1, 2 and 3 in Wischmeier (1975).

The C factor was calculated for the annual winter and biennial spring burning treatments in the following manner:

$$C = \text{Type I} \times \text{Type II} \times \text{Type III} \quad \ldots\ldots\ldots\ldots\ldots (2).$$

If cover includes both canopy and surface mulch, the canopy and mulch factors overlap and cannot both be fully credited. The mulch factor is taken at full value and the canopy factor is reduced to apply only to the percentage of the surface not covered by mulch. Thus the effective canopy cover

$$a = x \times (100 - y)/100 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3).$$

Then Type I = 1,0 - 0,008 a.

In making this adjustment it was assumed that canopy and mulch cover were distributed independently. It is unlikely that this assumption is valid, but it probably suffices as an approximation, except when mulch cover is low (Mentis, 1982). The product of the three types (C) is non-dimensional and ranges from 0 - 1. Daily values of C were computed for the four-year period between 1976 and 1979. This period was chosen since values of measured runoff were readily available for this period. Four years were used to obtain two cycles of a biennial spring burn. Sediment loss was predicted by substiuting the above data for catchment IV into the MUSLE for the period 1976 to 1979.

It is more important to note that the cover value was the only factor which varied in the comparison of the sediment yield from annual winter and biennial spring burn treatments.

8.2.2.3 Modelling long term effects of veld burning on sediment loss

In order to estimate long term effects of annual winter and biennial spring burn treatments, the MUSLE was used to predict daily values of sediment loss for a 20-year period from 1951 to 1970. To enable easy handling of the large data sets required for these analyses, the MUSLE was added as an option into the ACRU model (Schulze, 1981) by W. George, Assistant Research Fellow in the Dept. of Agricultural Engineering, University of Pietermaritzburg. For the period 1976 to 1979 observed values of Q and qp were used. However, between 1950 and 1970 only daily streamflow was available. For this period the ACRU model was used to derive the daily Q and qp values.

8.3 Results

8.3.1 Canopy cover

Estimates of canopy cover (from October to December 1975) for veld burnt annually in winter (plots 9a, 10a & 11a) and biennially in spring (plots 9b, 10b & 11b) are shown in Fig. 8.2 a-c. It is apparent from these diagrams that the biennial spring plots initially lagged behind the annual winter burn plots as a result of the different seasons of burn. At the beginning of the recording period these differences were approximately 20%. By the end of November these differences were no longer significant. Maximum values at the end of the growing season varied between 60 and 80% in both treatments. Initially, lower percentage canopy cover values were also recorded in the biennial spring burn treatment in the beginning of the 1979/80 growing season (Fig. 8.2 d). Canopy cover in Plot 12 c, which had been protected for 16 years and then burnt, was however, significantly lower than the corresponding winter and spring burns throughout the growing season (Fig. 8.2 d). This difference was greatest in January, when estimates were approximately 40% lower than those from the annual winter and biennial spring burn treatments. By the end of March 1980 this difference had decreased to approximately 15%.

Fig. 8.2 e illustrates the canopy recovery of plots burnt in the previous summer, autumn and winter. There was little difference between the recovery of the autumn and winter plots, maximum values being 62 and 73% respectively. The summer burn however, resulted in significantly lower canopy cover values, with the maximum value (47%) being approximately 15 - 20% lower than the autumn and winter burn treatments.

Estimates of canopy cover recorded in the low and high altitude plots during the 1981 growing season are shown in Fig. 8.2 f. The results show that there were no significant differences in the canopy recovery between the two sites.

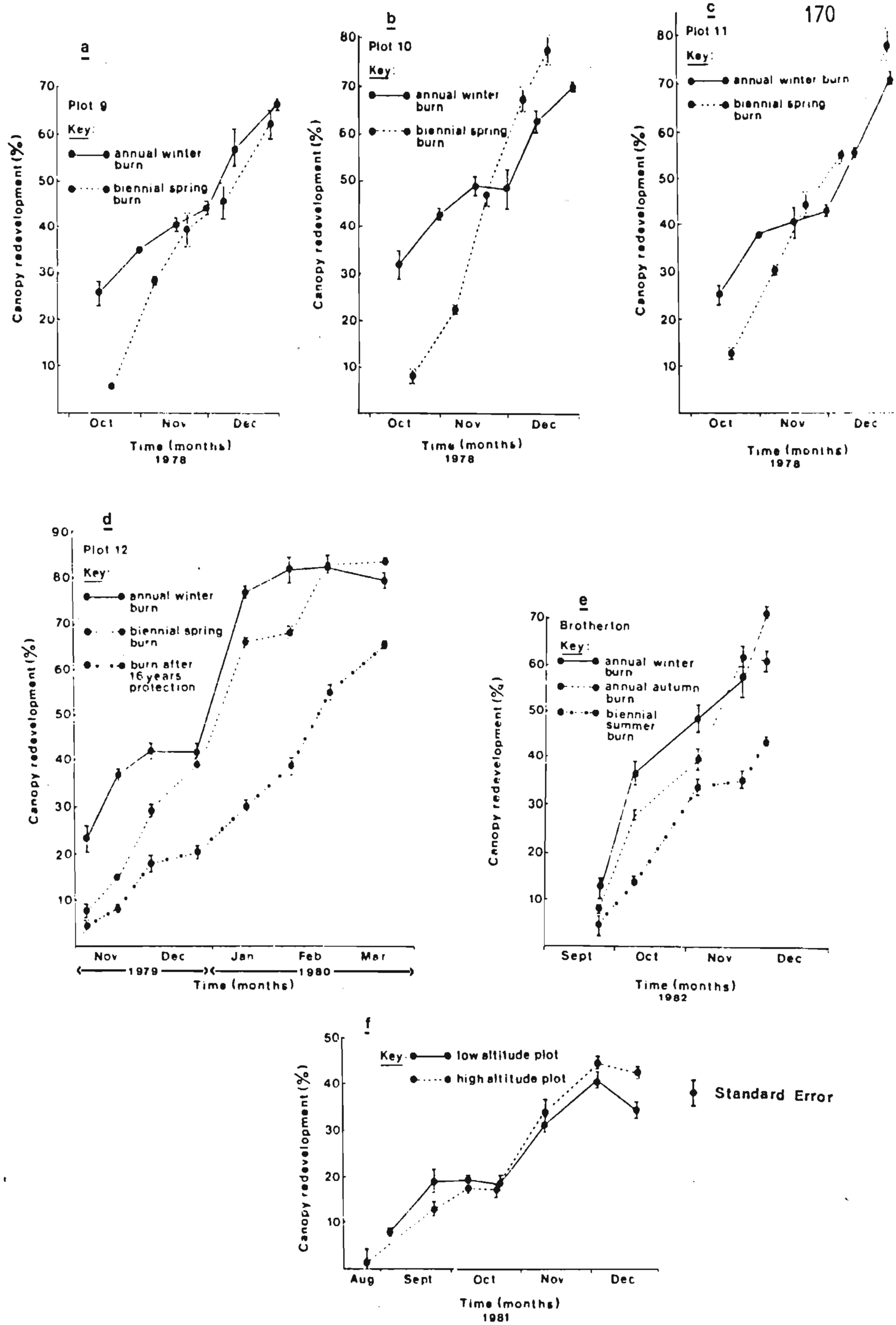


Figure 8.2 a-f Percentage canopy cover in plots burnt annually in winter, biennially in spring (a-d), after 16 years protection (d) and after autumn and summer burning treatments (e). Altitudinal comparisons are shown in (f).

8.3.2 Soil loss modelling

Generalized curves of percentage cover for annual winter and biennial spring burn treatments (Fig. 8.3 a & b) were developed from canopy data from the previous section, and additional measurements of canopy and mulch estimated during 1984 and 1985.

In the annual winter burn treatment (Fig. 8.3 a), canopy cover reached a maximum of 80% and mulch cover reached 62%. Canopy cover dropped to 0% in May after the annual winter fire treatment removed the aerial canopy. Mulch cover, represented by stubble or tuft after the fire, dropped to 30%. These values remained constant throughout the rest of the winter period until growth resumed in August. Thereafter canopy recovery growth was rapid with both canopy and mulch cover reaching pre-burn values by the end of December.

Although mulch values in the biennial spring burn treatment were similar to those of the annual winter burn treatment, maximum canopy cover values were approximately 20% higher than the winter burn values (Fig. 8.3 b). These values were attained in September of the second year after a burn. The fire treatment in early October removed the canopy, while mulch values approximated those of the annual winter burn treatment (30%). By early November growth had recommenced and canopy and mulch cover increased rapidly until January.

Seasonal trends in the C factor over a two-year period, derived from Fig. 8.3 a & b), are shown in Fig. 8.4 for both annual winter and biennial spring burning. Since the C factor in the MUSLE is directly proportional to soil loss, low values of C (i.e. high cover), represent low values of soil loss.

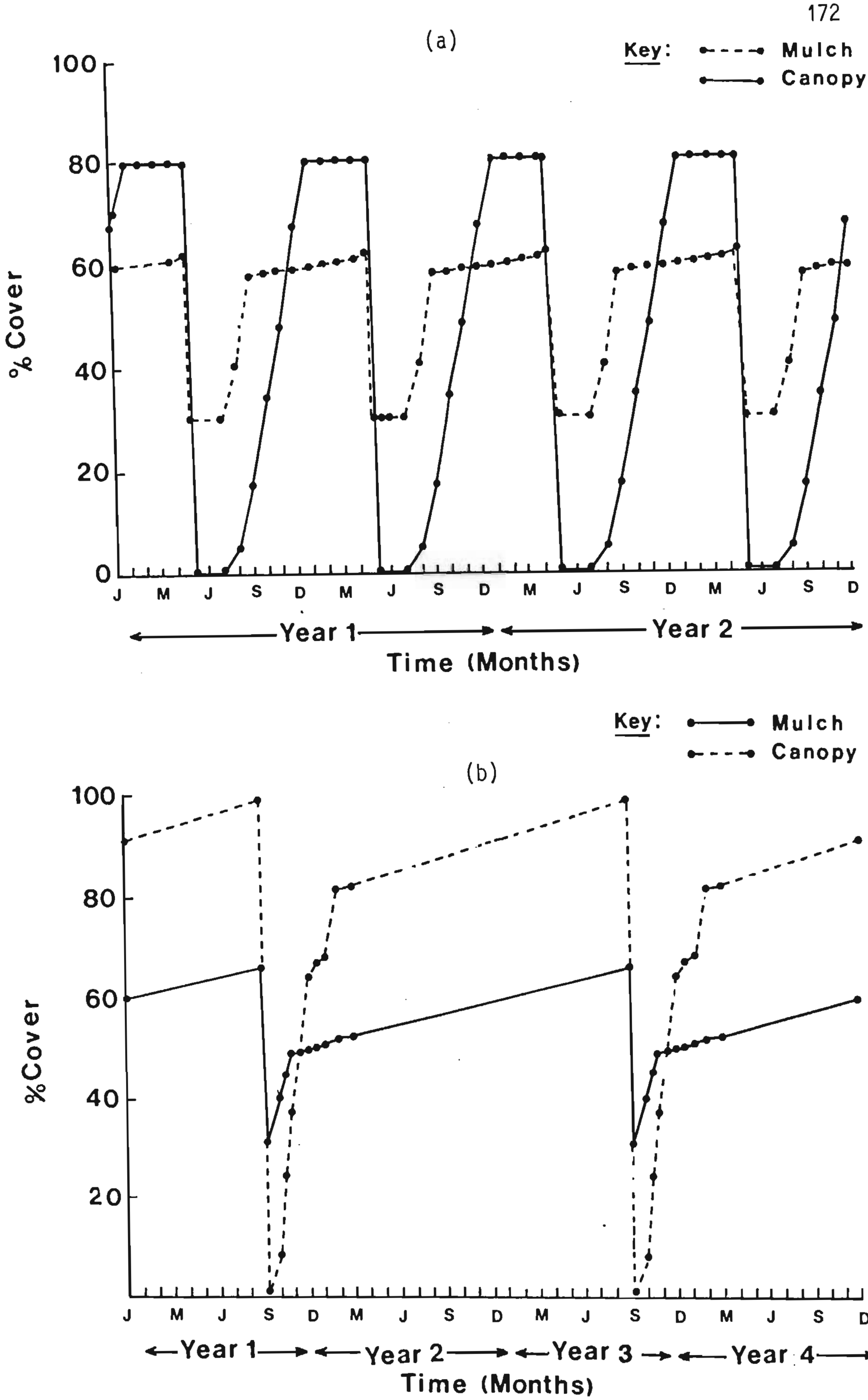


Figure 8.3 a&b — Generalized curves of percentage cover and mulch cover for annual winter (a) and biennial spring burning (b) over a 48 month period.

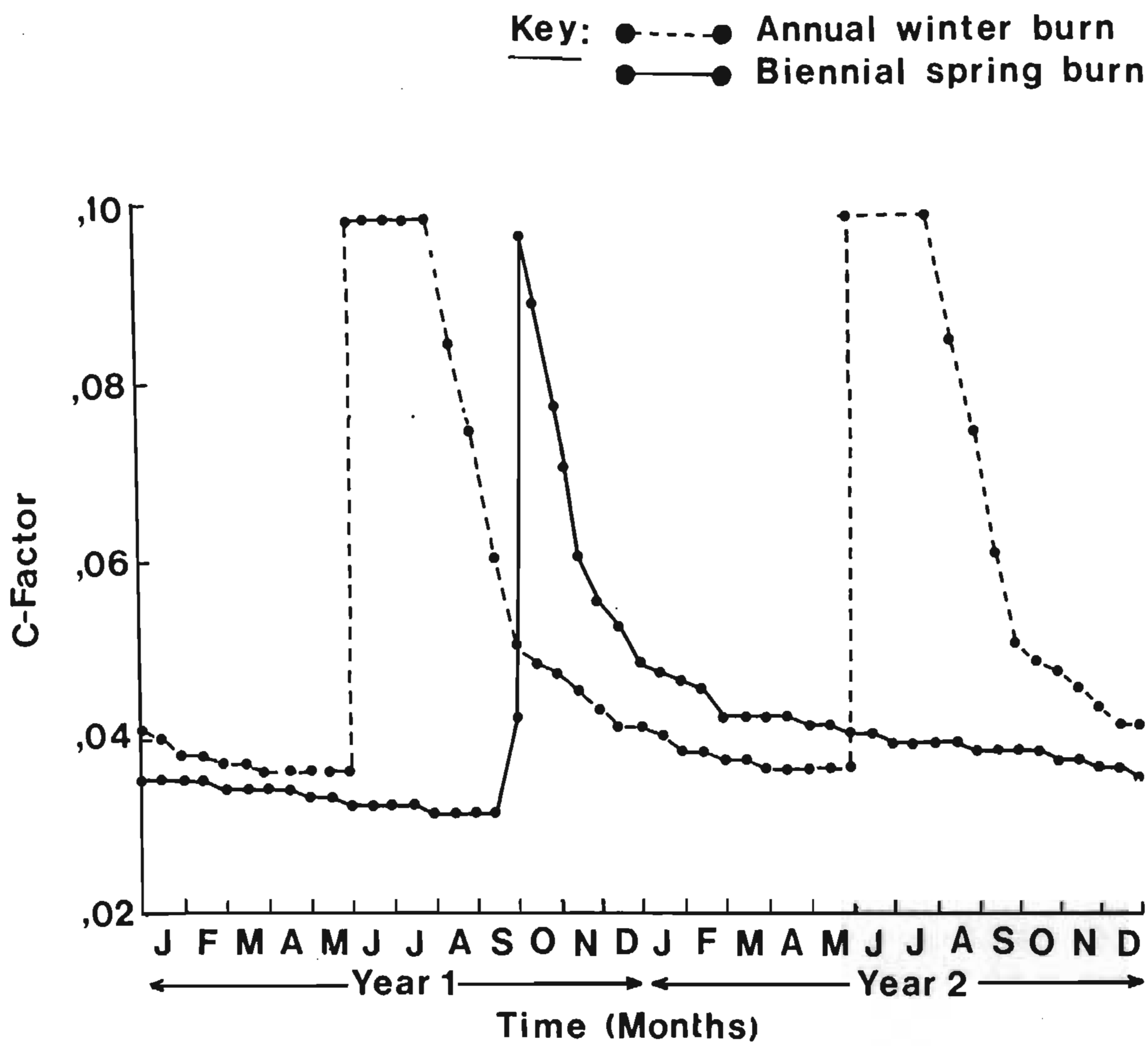


Figure 8.4 Monthly changes in the cover-factor (C) for annual winter and biennial spring burning over a two year period.

At the end of the annual winter and biennial spring burning cycles (March/ April - year 1, Fig. 8.4), C factor values were low (<0,04) with little differences between treatments (< 10%). The application of the winter burn in May resulted in a sharp increase in the C factor from 0,036 to 0,098. These high levels persisted until growth was initiated two months later in September. During this period the C factor in the biennial spring burn treatment remained low. However, values increased rapidly to 0,096 following the treatment burn in September. In spite of the immediate commencement of growth in this treatment, the C factor was consistently higher than that of the annual winter burn treatment until the following June (a period of approximately seven months). At this stage the annual winter burn cycle was repeated, increasing the C factor to 0,096 as in the previous year.

The C factor values for both burning treatments were substituted into the MUSLE to obtain estimates of predicted sediment loss (Fig. 8.5). The results showed a distinct seasonal trend with maximum predicted sediment loss (up to 185 tons) during the wet summer periods, and minimum predicted sediment loss during the dry winter periods (<2 tons).

Differences between the annual winter and biennial spring burn treatments were generally small. Predicted losses were lower in the annual winter burn when the burning of the two treatments coincided every second year, but were higher in the alternate years.

The long term effect of these two burning treatments on predicted sediment yield are shown in Fig. 8.6. Differences in the mean monthly sediment yield (20 years data) between treatments were generally small between January and July. In August and September predicted losses were greater in the annual winter burn treatment. From October to December, however, losses were greatest from the biennial spring burn treatment.

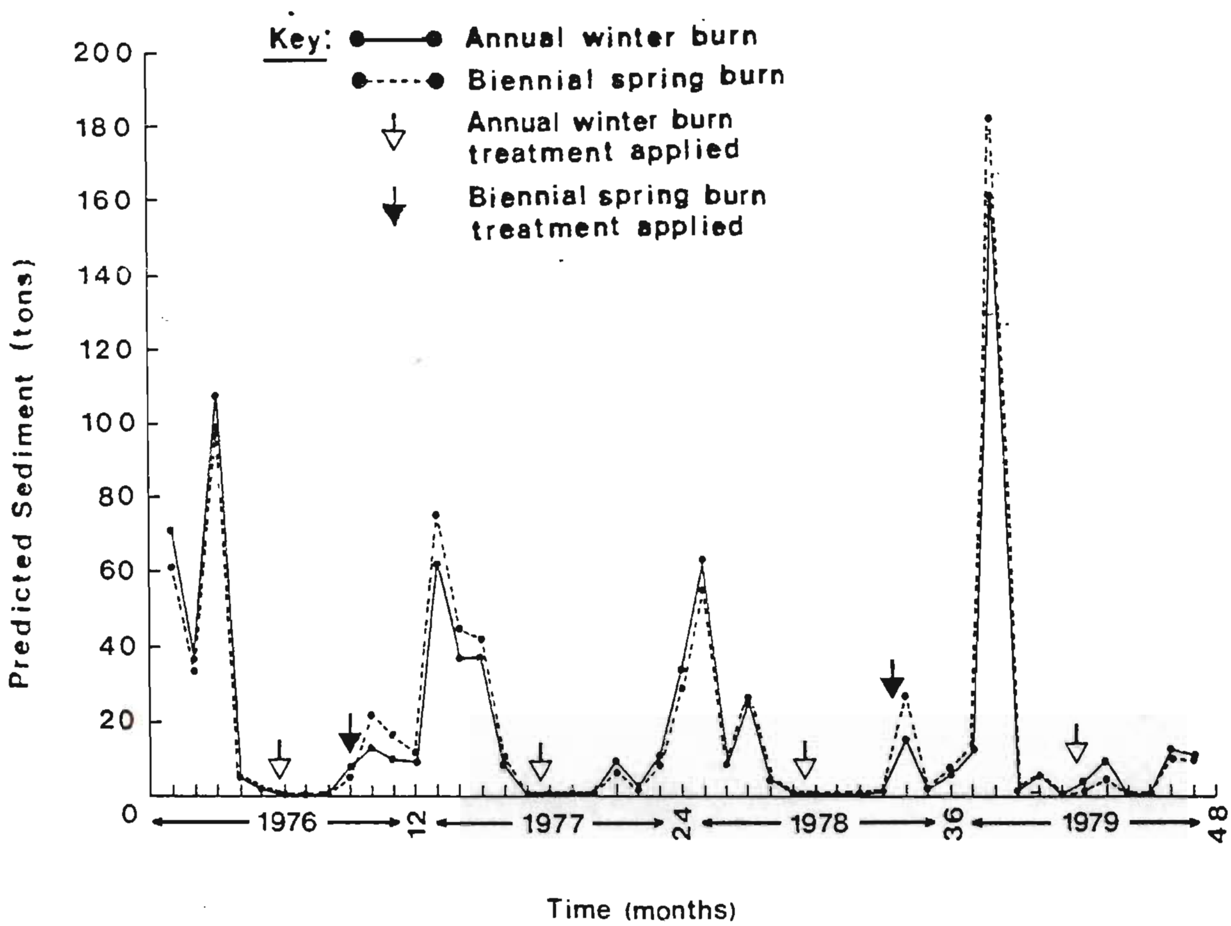


Figure 8.5 Estimates of predicted sediment loss using the MUSLE for the period 1976-1979 in annual winter and biennial spring burning.

8.3.3 Corroboration of the MUSLE

Corroboration is the procedure by which the model is assessed to determine the degree to which it meets expectation. In terms of the objectives of this study interest is focussed on the relative difference between burning treatments. Thus the predictive ability of the model in absolute terms was of little concern. However, since this is the only data of this kind available in Southern Africa, some attempt at corroboration is made.

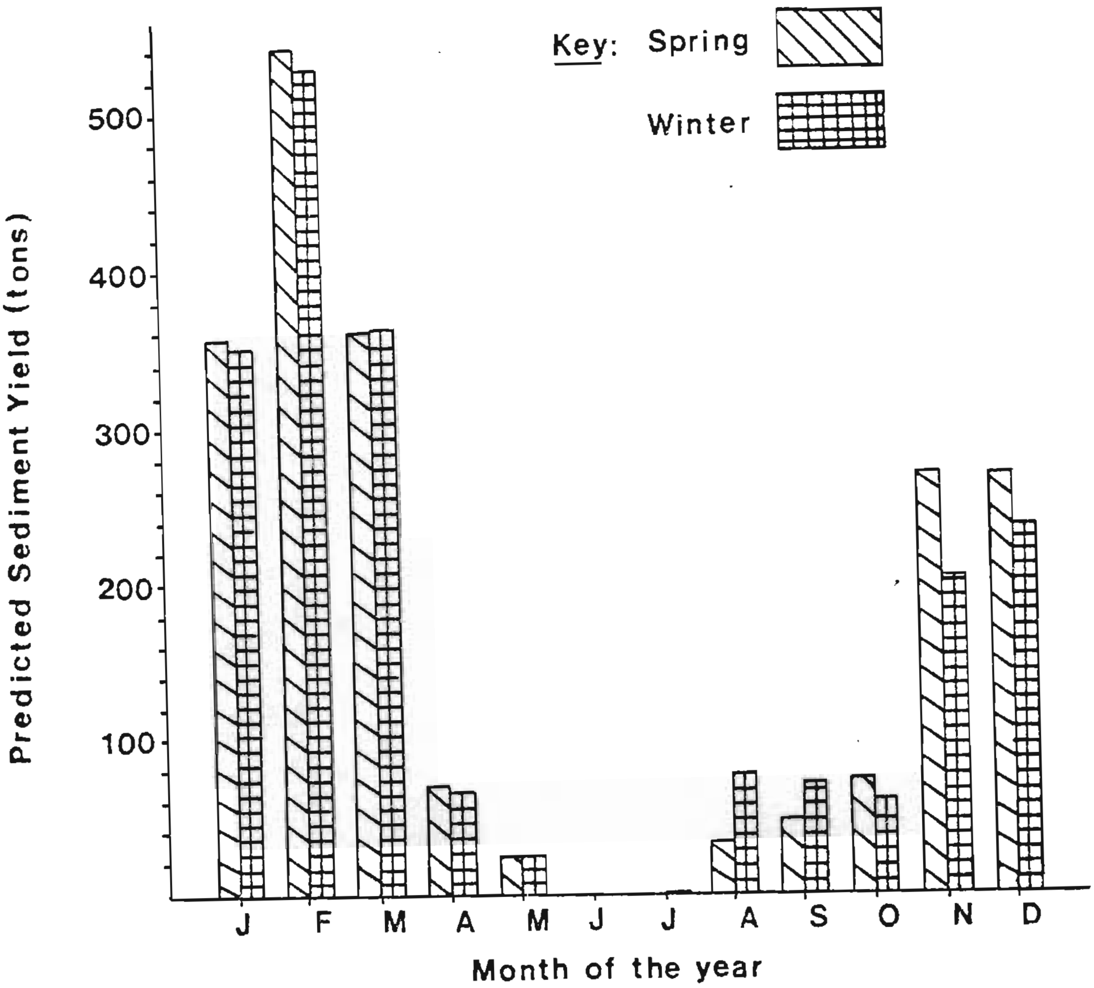


Figure 8.6 Long term monthly means (20 years data) of sediment yield predicted for annual winter and biennial spring burning in catchment IV.

To test the MUSLE, observed sediment yield data from C IV (van Wyk, 1985, unpublished report) were compared against predicted sediment yield by examining their relationship with observed monthly stormflow (Fig. 8.7). Stormflow was selected as the independent variable as it was considered to be the variable most closely associated with sediment loss. Unfortunately the measurements of observed sediment (1981-1984) did not coincide with observations of predicted sediment in this study (1976-1979). Thus direct comparisons for individual storm events could not be made. The period 1981-1984 could not be modelled for soil loss since observed stormflow and peak discharge data were not available. Nevertheless the data in Fig. 8.6 should provide some measure of the magnitude between observed and predicted sediment losses from catchment IV.

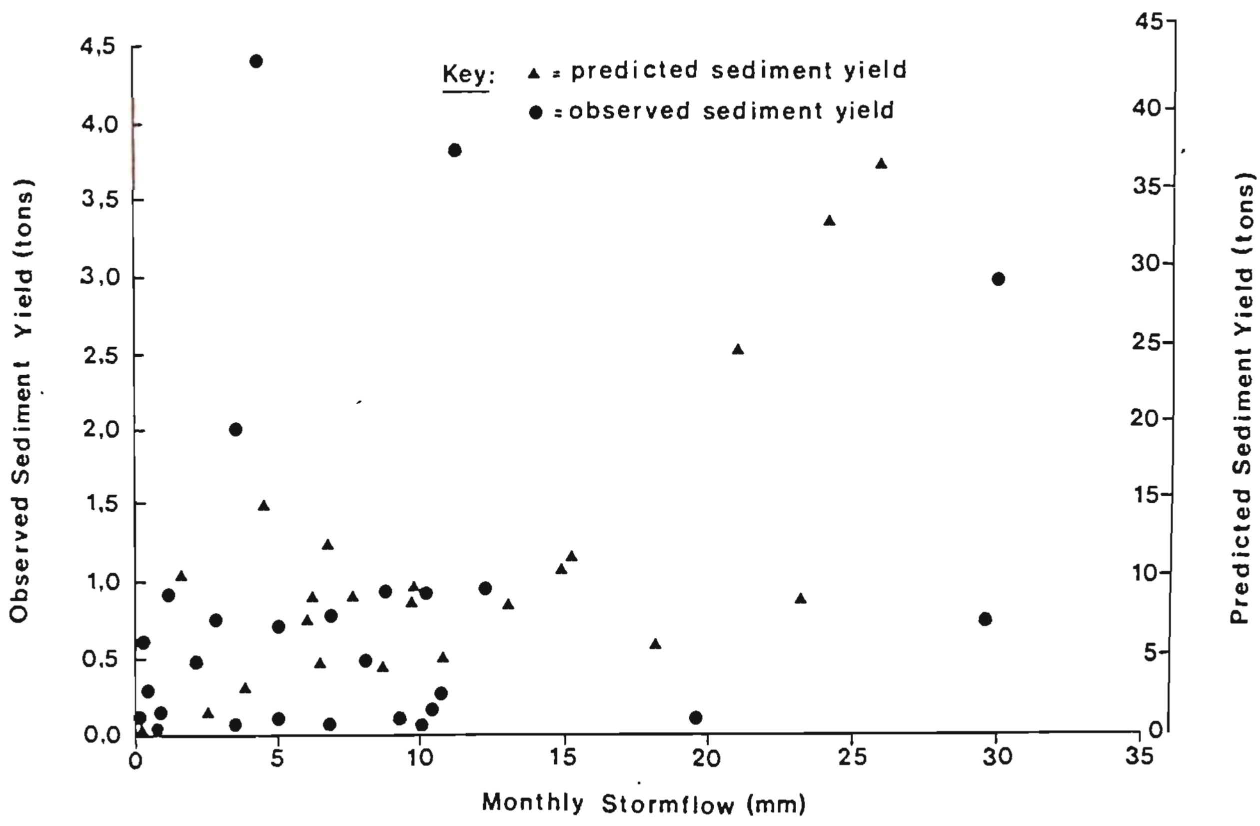


Figure 8.7 Comparisons between monthly stormflow (mm) and observed sediment (tons), and monthly stormflow and predicted sediment for catchment IV.

The results show that measured sediment loss was generally less than 1 ton/month for the catchment, while the maximum was 4,5 tons/month. Predicted losses, on the other hand, were generally ten times higher than the observed estimates. The data show that predicted losses were better correlated with monthly stormflow than the observed data which were more scattered. The better correlation between predicted losses and monthly stormflow might be expected, since the MUSLE uses a runoff factor to predict soil losses. The poor relationship between observed sediment and monthly stormflow needs further investigation before comment can be made. This would best be achieved by using daily streamflow and sediment values since monthly totals are difficult to relate to individual storm events.

8.4 Discussion and conclusion

The results of the experiment have shown that there is little difference in the percentage canopy cover at the end of the growing season between veld which had received 30 years of annual winter burning, and veld which had been burnt biennially in spring. However, differences in season of burn resulted in exposure to erosive forces at different times of the year. Thus early winter burning exposes the soil for an extended period during the dry season, but allows for immediate recovery in spring. In contrast, spring burning exposes the soil to the first summer rains and results in higher predicted sediment losses than does annual winter burning.

This study has not quantified the effects of frost and wind erosion. Coetzee (1942) noted, however, that autumn burning, which leaves a substantial portion of the soil exposed before regeneration of the cover in spring, considerably increased the susceptibility to wind erosion. Loss of soil by wind following burning was, however, found to be of minor significance in the Tall grassveld of Natal (Edwards, 1961).

The results of this study concur with those of Watson (1981), who found that annual winter burning did not result in accelerated soil losses. It would appear then that the optimum time of burning is mid-August (late winter), when the effects of exposure to wind and rainfall erosion would be minimized. Scott (1952), however, reported that soil losses from a veld burning trial at Estcourt were highest from annual August and triennial spring burnt veld. However, in this study both summer burnt areas and an area protected from fire for 16 years, showed significantly reduced canopy cover. These treatments might therefore be expected to result in increased runoff and erosion. Summer burning and protection from fire should therefore be used with caution since they would conflict with the primary management objective of the prevention of accelerated erosion.

The fact that there was little difference in the recovery of the canopy over an altitudinal range of 500 m was surprising, as temperature decreases with increasing altitude. One would therefore have expected the canopy to have been initiated earlier at the lower altitude. There appears to be no explanation for this apparent anomaly. The implication of this result is that the area between 1 400 m and 1 900 m (i.e. the approximate range of Highland Sourveld), can be managed as a single unit.

As far as the author is aware, there are no published accounts of attempts to apply MUSLE to veld in Southern Africa using observed stormflow and peak runoff rates. Mentis (1982) used the USLE to predict soil losses with changes in canopy cover due to burning and grazing. According to Garland (1982) there is a tacit acceptance among investigators that USLE will provide the basis of future South African research on soil loss modelling. The results of this study have shown that while the MUSLE is useful for comparative studies, its predictive ability is poor. This may be attributable to the fact that other variables controlling soil loss may be dominant in different regions. Alternatively, variables may interact in different ways in regions of dissimilar terrain and environmental characteristics (Garland, 1982). However, the fact that agreement between observed and predicted values was poor does not necessarily mean poor prediction by the model. There are two reasons why the model may appear to be overpredicting sediment loss in the present study. Firstly, since the MUSLE is not a sediment routing model, the location of deposition cannot be determined. This may explain the lack of agreement between the observed sediment and predicted values from the catchment IV weir. Secondly, the collection of observed sediment data is fraught with difficulties and measurements are most likely to underestimate sediment losses, because larger sediment particles are often not sampled.

It is obvious from this discussion that thorough tests of validation should be carried out on the MUSLE before it is either accepted or rejected for use in South Africa. Until further research is carried out in this field, the MUSLE does, however, remain useful for comparative purposes.

8.5 Summary

i) This chapter examined the effects of various veld management practices on vegetal cover and soil loss.

ii) There was little difference in the percentage canopy cover at the end of the growing season between veld which had received 30 years of annual winter burning and 30 years of biennial spring burning.

iii) Differences in season of burn resulted in exposure to erosive forces at different times of the year.

iv) Winter burning did not result in accelerated soil losses.

v) The optimum time for burning is mid-August, when the effects of exposure to wind and rainfall erosion are minimized.

vi) Both summer burning and protection from fire significantly reduced canopy cover.

vii) Estimates of predicted sediment loss showed a distinct seasonal trend with maximum losses (185 tons) occurring during the wet summer periods, and minimum losses occurring during the dry winter periods ($<$ 2 tons).

viii) Differences in predicted sediment loss between annual winter and biennial spring burning were generally small.

ix) The results showed that while the MUSLE is useful for comparative studies, its predictive ability is poor.

CHAPTER 9

FACTORS AFFECTING THE TIMING OF GRASSLAND REGROWTH AFTER FIRE

9.1 Introduction

Burning in late spring and early summer, after active growth has commenced, has been shown in this study (Chapter 5) and in the Tall Grassveld of Natal (Dillon, 1979) to lead to severe damage to the grass cover and to T. triandra in particular (Tainton & Mentis, 1984). Other trials at Underberg showed that the closer the time of the burn is to the start of active spring growth, the more rapid is the recovery of the grassveld (Tainton, Groves & Nash, 1977). The design of a burning policy would therefore be greatly improved by an insight into the factors controlling the initiation of grass growth in the spring, thereby enabling the end of the fire season to be more accurately determined.

Growth essentially comprises the conversion by solar energy of atmospheric carbon dioxide, soil nutrients and water into herbage. The basic climatic factor limiting growth is the seasonal input of solar energy, but in practice the utilization of solar energy may be limited by other climatic factors such as low temperature and water stress (Cooper & Tainton, 1968). In the Natal Drakensberg, the dormant winter period is characterized by long periods of drought and low temperatures. An experiment was therefore designed to test the hypothesis that early rainfall (i.e. increased soil moisture) is responsible for stimulating growth. The experimental design together with the parameters studied are presented as a flow diagram in Fig. 9.1.

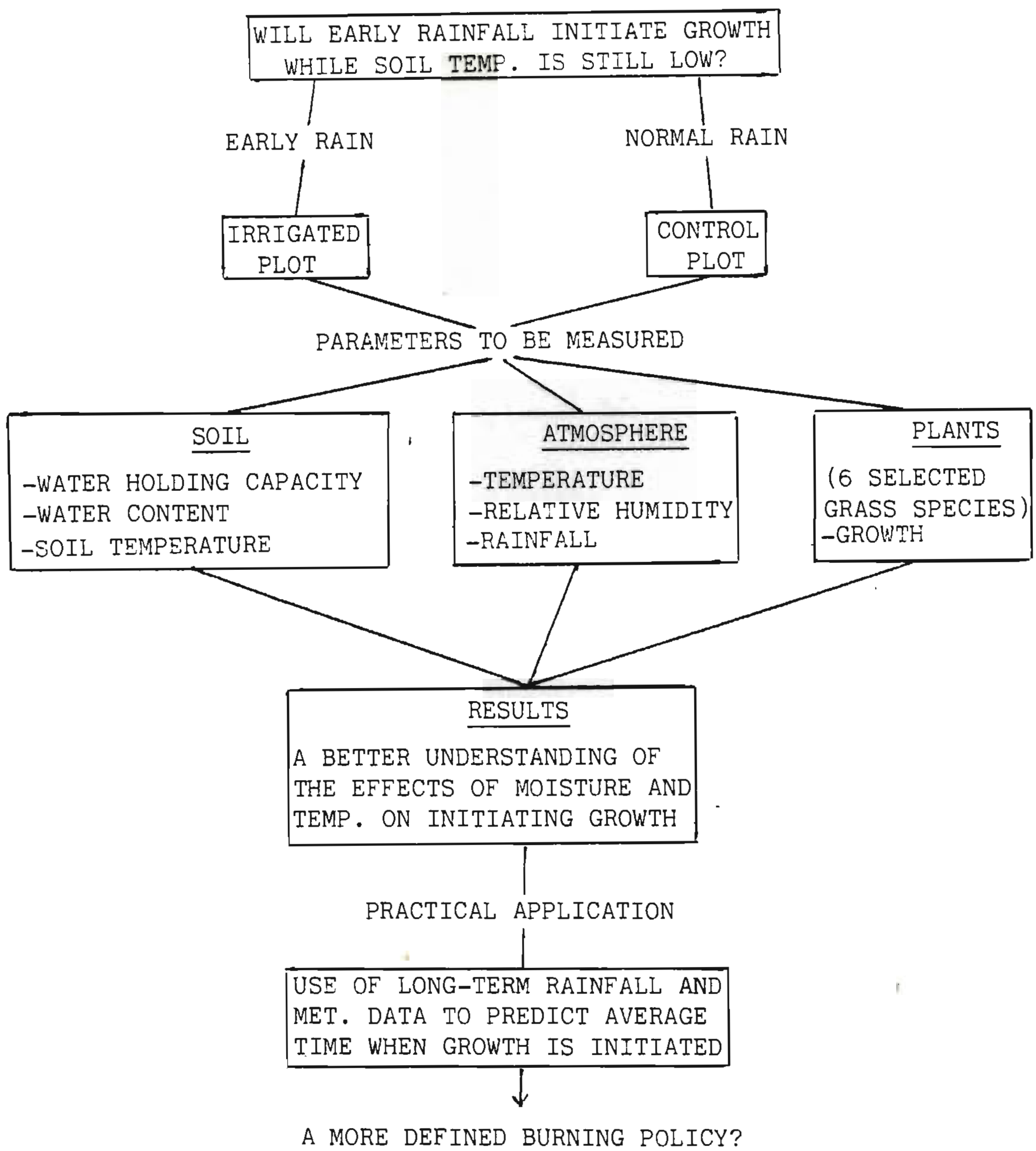


Figure 9.1 Flow diagram of the experimental design and parameters measured in the investigation of the factors affecting the initiation of grassland regrowth.

9.2 Study site

Two adjacent plots (15 x 15 m) were located at an altitude of 1 800 m in veld which had previously received a biennial spring burn treatment. The site was situated on level ground ca 500 m from the meteorological station at Cathedral Peak. A nearby stream provided water for irrigation purposes. Both plots were burnt in early July so that new growth could be easily measured.

One of these plots received additional moisture by irrigation (referred to as the irrigated plot) to simulate early rain, while the other (the control) received natural precipitation only.

9.3 Methods

9.3.1 Irrigation

The irrigated plot received water by gentle spray from 10 microjets situated 33 mm apart on a 3,0 m long portable horizontal bar. This system was used so that the whole apparatus could be pushed through the plot at a constant rate to obtain an even distribution of water. This was essential as preliminary investigations revealed very uneven water distribution from stationary microjects. For example, the coefficients of variation from stationary microjets and from the portable apparatus were 68,0 and 28,5% respectively. These values were obtained by measuring the amount of water delivered for each technique over a 3 X 4 m area at a grid interval of 1 X 1 m (i.e. 20 grid positions). Calibration of the portable apparatus indicated that at a speed of the apparatus of 1 m per minute across the plot, an equivalent of 7 mm of rainfall was delivered.

In practice the plot was divided into four lanes through which the apparatus was pushed at a rate of approximately 1 m per minute. Ten containers were randomly placed in each row and the amount of water delivered in each was measured. In this way the mean amount of water applied by each irrigation event could be calculated. This was checked against a standard raingauge placed at ground level in the irrigated plot. Differences between the mean obtained from the containers and the values for the raingauge were generally less than 1 mm. Irrigation continued at weekly intervals from 26 August 1982 to 29 September 1982.

9.3.2 Rainfall

Rainfall was measured after each rainfall event from an on site rain gauge.

9.3.3 Ambient air temperature

A continuous record of ambient air temperature was obtained from a thermograph at the Cathedral Peak meteorological station. Temperature was expressed as "total daily temperature", that is, the integrated area under the diurnal curve. It was felt that this would provide the most meaningful index of the temperature conditions during the trial.

9.3.4 Soil temperature

This was recorded at three depths (30 mm, 60 mm and 90 mm) in each plot from temperature probes (wax type), and a continuous recorder during the study period. As the curves for the three depths were very similar, only data from the 30 mm depth are presented here. Total daily temperature was calculated in a similar manner to that described for air temperature.

9.3.5 Soil moisture

Five randomly selected soil cores within each plot were collected at 0-30, 30-60 and 60-90 mm depths. Samples were collected before and immediately after each irrigation event and after each rainfall event between 19 August 1982 and 30 September 1982. In the event of no rain falling the samples were taken every 7 days. Soil moisture was determined gravimetrically (98°C for 24 hours).

Although an estimate of percentage soil moisture is useful, it provides little information about the amount of water available to the plants. Soil moisture characteristics were therefore estimated from undisturbed soil samples (i.e. cores in which the natural structure of the soil is preserved as far as possible) taken from the study site. These soil cores were used to determine field capacity (i.e. the moist end) and permanent wilting percentage (i.e. the dry end). Estimates of water potential were made from the gravimetric measurements of water content by drawing the calibration curve relating matric potential to water content.

Two replicates of undisturbed cores were taken from both the irrigated and control site at a depth of 30 - 60 mm. Matric potentials of - 12,2 kPa (field capacity) to - 69,0 kPa were determined using Tempe cells and successive weighings in desorption from saturation by application of air pressure. Matric potentials of - 98,3 kPa and - 1 462 kPa (permanent wilting point) were determined by use of pressure chambers and ceramic plates. These measurements were carried out in the soil science laboratory at the Agricultural Faculty of the University of Natal.

9.3.6 Growth

Growth was estimated in six selected grass species (*T. triandra*, *H. contortus*, *T. spicatus*, *H. falx*, *T. leucothrix* and *A. semialata*) at weekly intervals throughout the study period. Twenty plants of each species in each plot were chosen at random and the longest leaf measured.

9.4 Results

The time and amount of rainfall in relation to the irrigation that was applied is shown in Fig. 9.2 d. Both plots received 67 mm rain, and an additional 47 mm water was applied to the irrigated plot. Thus a total of 114 mm was received by the irrigated plot, an amount of 24 mm above the average rainfall for this period (90 mm).

The field capacity (FC) of the dry mass of the soil at the control and irrigated sites was estimated to be 71,1% and 73,8% respectively (Table 9.1 & Fig. 9.3). Permanent wilting point (PWP) (-1 462 kPa) occurred at ca 43% of the dry mass of the soil (Table 9.1 & Fig. 9.3). The relationship between matric potential and soil moisture content was similar at both sites, although the irrigated site tended to have slightly higher moisture contents at the -12,2; -34,5; -69,0 and -98,3 kPa matric potentials (Fig. 9.3).

Additions and losses of water from the soil are usually measured in inches or centimetres, and may be readily converted to volumes. It is useful to convert the water content, expressed per unit mass, into water content per unit volume. This conversion is achieved by multiplying the percentage soil moisture by the bulk density of the soil. Thus the percentage available soil moisture (FC - PWP) may, for any depth of soil,

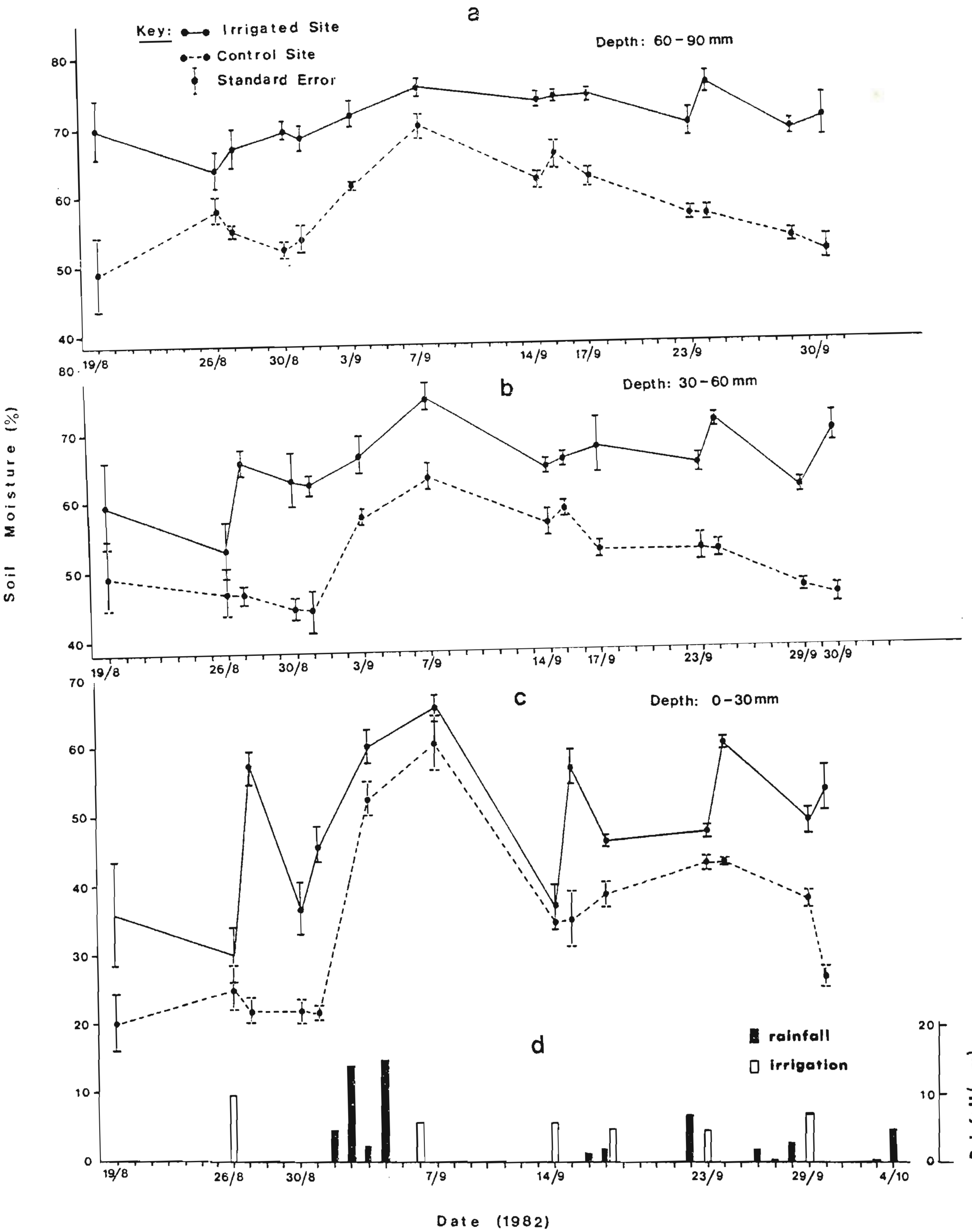


Figure 9.2 a-d Comparisons of soil moisture (%) at three depths (a-c) at the control and irrigated sites. Rainfall and irrigation amounts (mm) are also presented (d).

be expressed as millimeters per unit of soil depth. From these calculations it is evident that if the soil was at FC, there would be ca 43 mm of available soil moisture to the plants.

TABLE 9.1 Soil water retention data from the control and irrigated sites (Soil form - Griffin).

Matric Potential (k Pa)	% Water Content					
	Control Site			Irrigated Site		
	Rep 1	Rep 2	$\bar{x}$	Rep 1	Rep 2	$\bar{x}$
- 12,2	69,2	78,4	73,8	69,4	72,8	7,1
- 34,5	60,4	69,2	64,8	63,2	63,5	63,4
- 69,0	57,5	67,0	62,0	61,0	61,7	61,4
- 98,3	61,1	63,4	62,3	60,7	51,1	55,9
- 1462,0	42,1	42,5	42,3	42,1	43,4	42,8
Estimated saturated water content	84,7	104,5	94,6	91,7	101,7	96,7
Bulk density	1,48	1,41	1,45	1,45	1,42	1,44

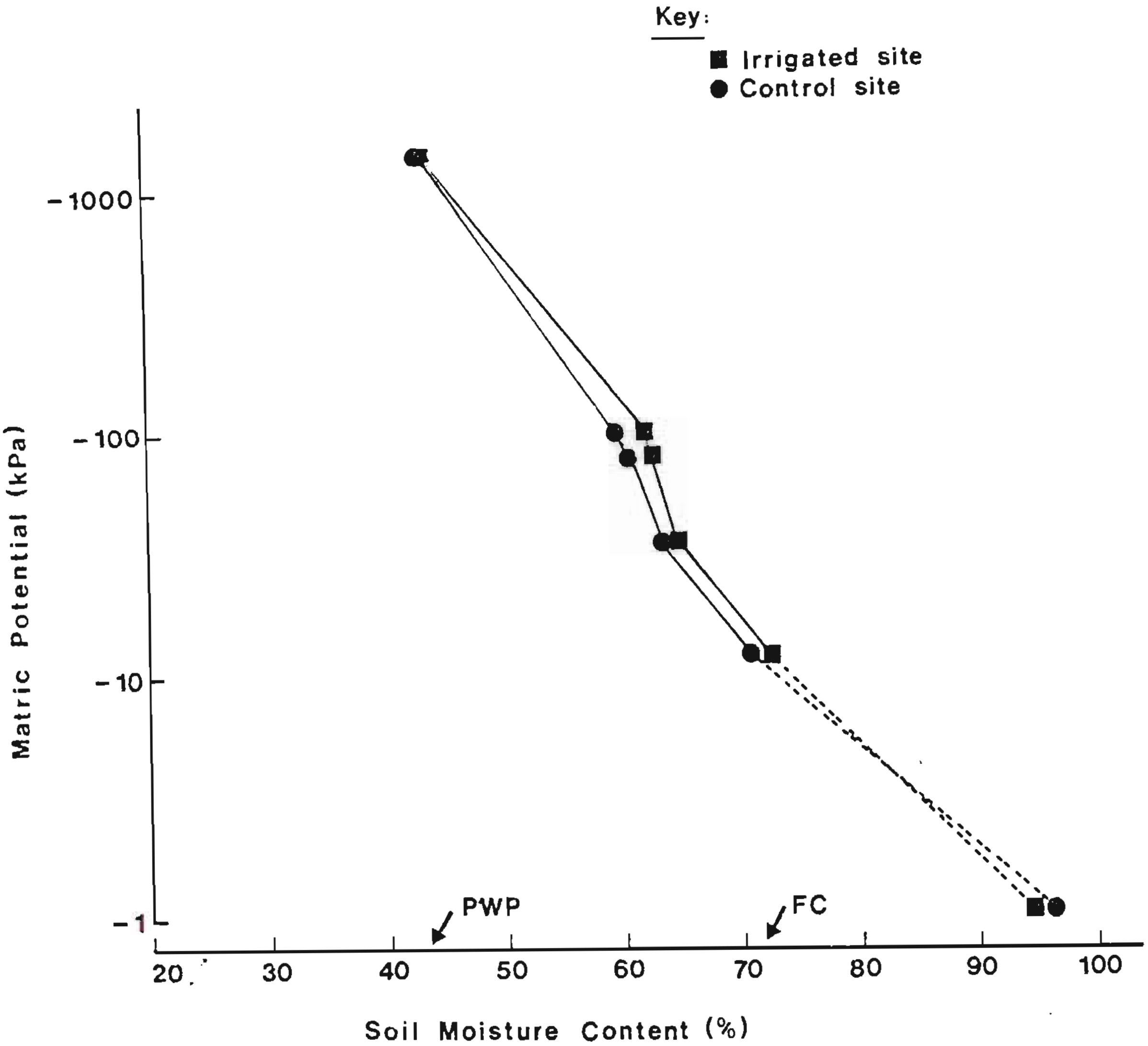


Figure 9.3 Moisture characteristic curve (matric potential) plotted over water content) at a depth of 30-60 mm at the control and irrigated sites. Each point is the mean of two replicates. Soil form - Griffin. (PWP = permanent wilting point; FC = field capacity).

The effects of irrigation and rainfall on soil moisture are illustrated in Fig. 9.2 a-c. At the time of irrigation (26/8/82) there was no significant difference between sites. Soil moisture at this time was approximately 25, 50 and 60% in the 0-30, 30-60 and 60-90 mm regions respectively. The 10 mm of additional water added to the irrigated plot increased soil moisture by ca 27% in the 0-30 mm region. Similar patterns were noted in the 30-60 mm zone, although the magnitude (ca 15% increase) was much less. In the 60-90 mm region the effect was not immediately apparent, there being no significant difference between the plots at this time. In the following five days, however, during which time no water was received by either plot (Fig. 9.2), the moisture content in the irrigated plot tended to increase in the 60-90 mm region, while in the control it decreased. This would indicate that there is a time lag of 1-2 days for moisture to infiltrate to the 60-90 mm region. By the 30/8/82 the moisture in the 0-30 mm region had decreased by 20% and estimates were similar to those prior to irrigation. In contrast, estimates of soil moisture in the 30-60 mm region did not decrease significantly during this period. This pattern, whereby moisture fluctuated widely in the 0-30 mm region (between 20 and 65%), and not in the deeper regions, was evident throughout the study period.

Between the 1/9/82 and 4/9/82 approximately 38 mm of natural rainfall was recorded. This resulted in soil moisture increasing to a maximum of 65, 70 and 75% in the irrigated plot and 60, 63 and 70% in the control for the 0-30, 30-60 and 60-90 mm regions respectively. Differences between sites were therefore small at this time. The occurrence of this natural rainfall was unfortunate as it was hoped that the soil moisture potential in the irrigated plot could be maintained above that of the control. In any event, by the 14/9/82 the soil moisture in the 0-30 mm zone had returned to approximately 35% in both treatments.

For the remainder of the study period (14 to 30/9/82) the additional water applied to the irrigated plot maintained soil moisture at a significantly higher level than in the control.

An interesting feature of these soil moisture data was that the irrigated plot always had higher moisture values (even before irrigation commenced) than in the control plot. This may be due to the slight difference in the moisture characteristics between sites discussed previously (pg. 189). It was fortunate that it was the irrigated site that was wetter as the trial was designed to investigate the effect of increased moisture on plant growth.

Soil moisture in the 60-90 mm zone of the irrigated site (ca 70%) approximated that of FC (71%). In addition the moisture contents of both sites in the 30-60 and 60-90 mm region did not drop below the PWP (43%). Thus at both sites moisture was always freely available below a depth of 30mm.

Tne daily trends in the total daily air temperature and soil temperatures are shown in Fig. 9.4 and Fig. 9.5 respectively. Immediately apparent from these figures is the effect of the cooler cloudy conditions (Fig. 9.2 d) experienced between the 2-5/9/82 and again on the 23/9/82, which resulted in a sharp decrease in both ambient and soil temperatures. Both air and soil temperature followed very similar trends and surprisingly the maximum values attained (ca 400°C) were the same for both parameters.

The results of the growth measurements of the six grass species (Fig. 9.6) showed that there were generally no significant differences in growth between plants in the control and irrigated plots. In all species growth followed the typical sigmoid curve, starting at some or other low value on the 30/9/82 and increasing to a maximum by the beginning of October. The maximum length attained by the longest leaf during the study varied from 90 mm in *H. contortus* to 210 mm for *H. falx*.

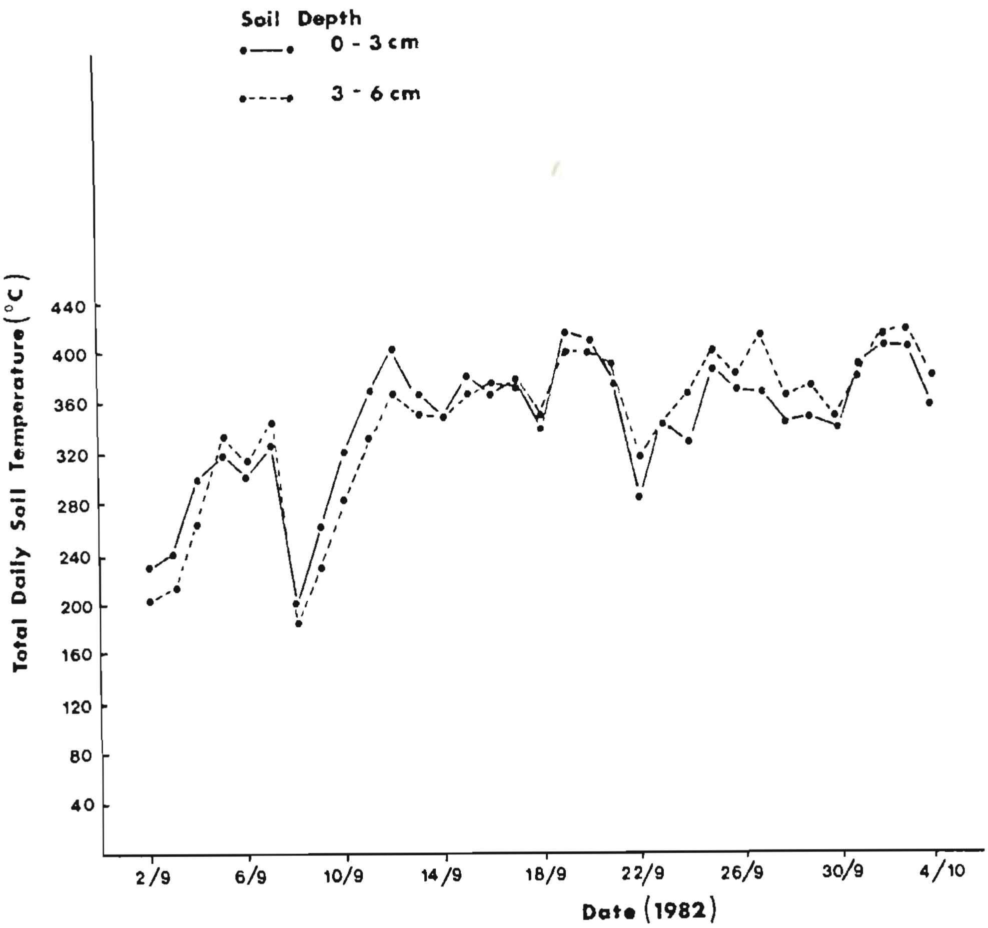


Figure 9.4 Daily trends in total daily soil temperature.

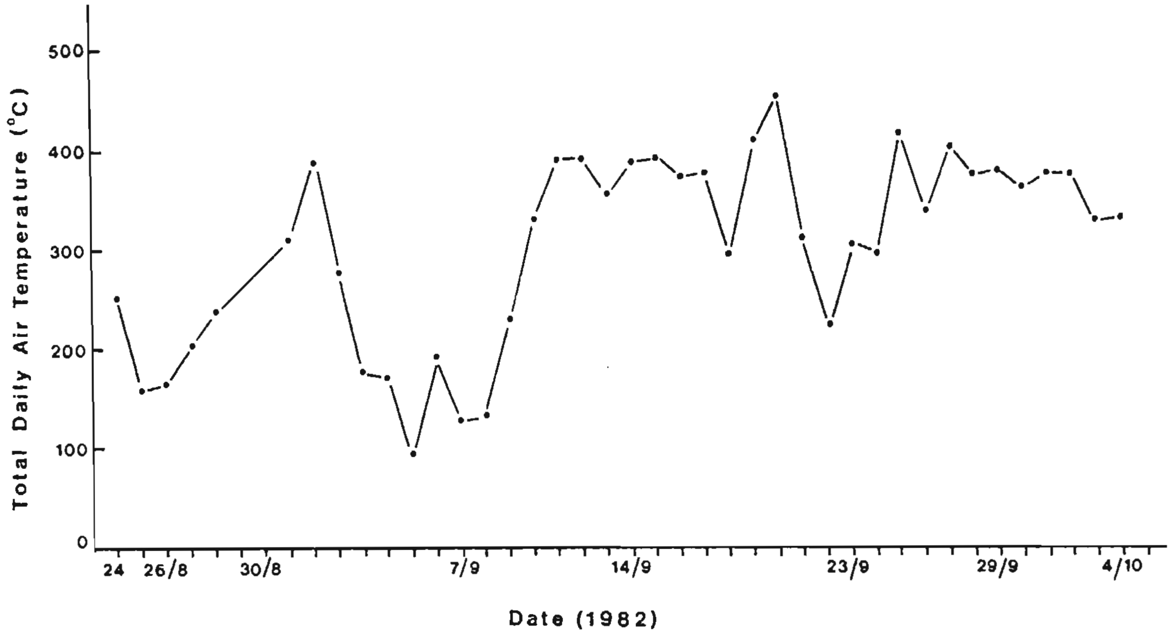


Figure 9.5 Daily trends in total daily air temperature.

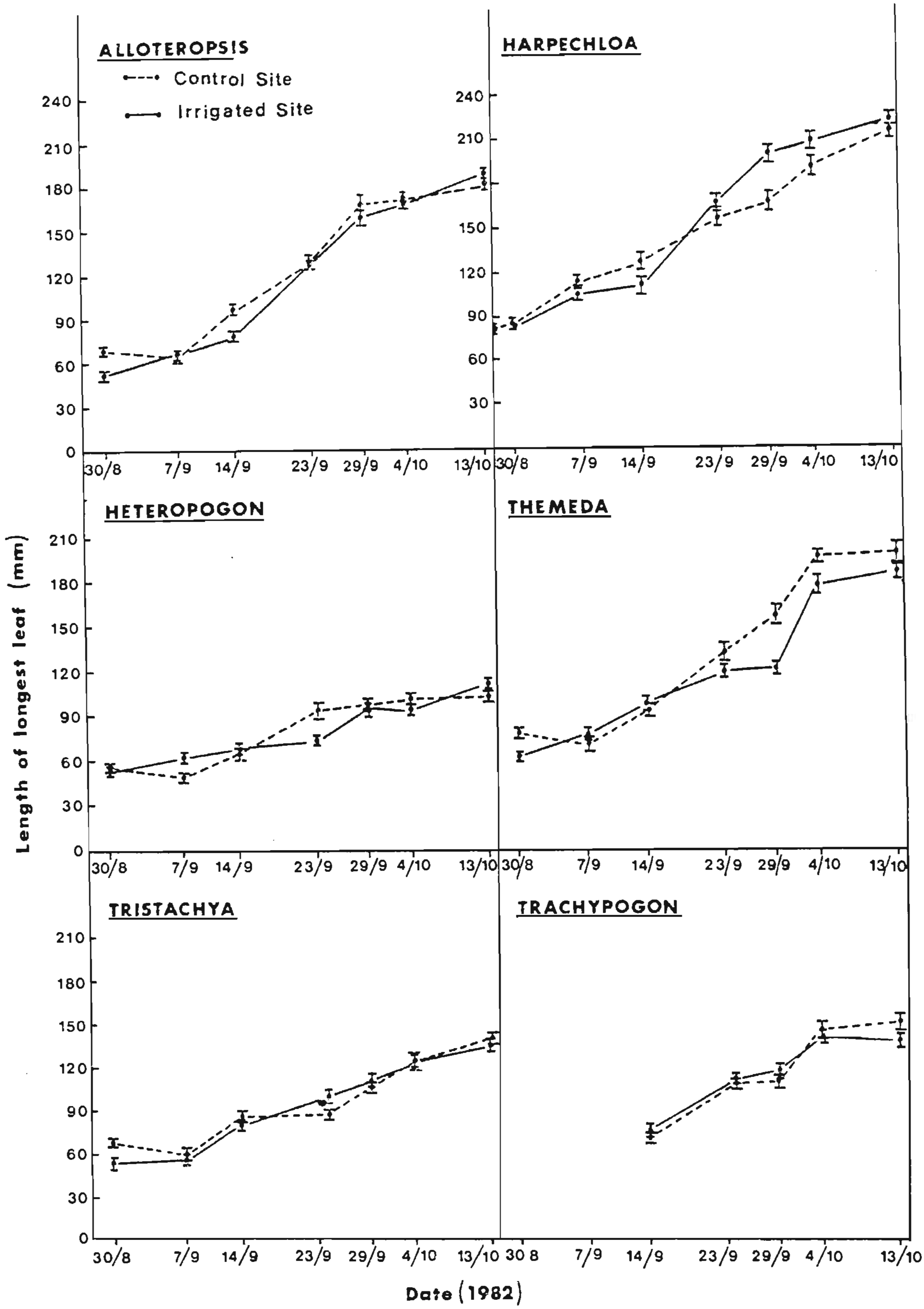


Figure 9.6 Mean weekly leaf lengths (mm) of Alloteropsis semialata, Harpechloa falx, Heteropogon contortus, Themeda triandra, Tristachya leucothrix and Trachypogon spicatus in the control and irrigated sites during spring, 1982. Vertical bars represent standard errors.

The correlation coefficients between the various parameters are presented in Table 9.2. There was a high correlation between soil temperature and air temperature. This is also reflected in the correlation between growth and air temperature and between growth and soil temperature, both of which were significant at the 1% level. There was however no significant correlation between growth and soil moisture in either the control or irrigated plots.

TABLE 9.2 Correlation coefficients (r) for various parameters measured at the control and irrigated plots.
(NS = not significant; * = $p < 0.1$; ** = $p < 0.01$)

FACTORS			r	Sig.
Growth	vs	Soil Temp.	0,88	*
Growth	vs	Air Temp.	0,89	**
Growth	vs	Soil Moisture (Control)	0,10	NS
Growth	vs	Soil Moisture (Irrigated)	0,10	NS
Soil Temp. (0 - 30 mm)	vs	Air Temp.	0,94	**
Soil Temp. (30 - 60 mm)	vs	Air Temp.	0,90	**

9.5 Discussion

The values for FC and PWP are unusually high when compared with soils from other areas, a fact best explained by their high organic matter contents (Cass, 1985, pers. comm.). Similar results for soils at Cathedral Peak were found by Everson, 1979.

In the False Thornveld of the Eastern Cape, Danckwerts (1984) found that an important determinant of herbage production is the time of onset of the first effective rains. In this study, however, the results showed that even after a long drought period, such as that which occurred prior to the study, soil moisture was high (average = 60%) at a depth of 90 mm. Since a proportion of the grass roots penetrate to at least a depth of 500 mm (see results, Chapter 7), water is likely to be available to the plants throughout the year. This is contrary to the results of Sharrow & Wright (1977), who showed that in Texas soil moisture was the limiting factor in dry years in *Hilaria mutica*.

The extension of the rainy season by early spring irrigation had no significant effect on initiation or increase in growth. In contrast, studies by Parrot & Donald (1970) showed that an 18-day difference in the date of the first rains had a marked influence on the commencement of growth. This indicates that in the present study, some factor other than moisture was limiting growth. This is supported by the fact that there was no correlation between growth and soil moisture (Table 9.2). The results, although preliminary, demonstrate that early rainfall is not responsible for stimulating growth. The high correlation between growth and soil and air temperature (Table 9.2) suggest that temperature may be one of the limiting plant growth factors in this environment.

These results have important implications for management, as previously in dry years (when foresters were unable to complete their burning programmes) the burning period was extended later into spring. The rationale for this was that growth was delayed in years of drought. This study has shown, however, that the initiation of growth in these years is probably not influenced by rainfall.

The results of this st[...] are for one season only, and will need to be repeated before th[...]act time of commencement of growth can be predicted with co[...]ce. They have indicated, however, that significant growth has [...]ace by the end of September. If the veld is to be mainta[...]s present condition then burning should not be permitted fr[...]onwards.

[...]ary

Soil moisture in the study area was high (even after a long period drought), with values of approximately 60% being recorded at a depth of 90 mm.

ii) At both sites moisture was always freely available below a depth of 30 mm.

iii) There was no correlation between growth and soil moisture.

iv) High correlations were found between growth and soi[l] temperature.

v) It is concluded that soil moisture is [...] initiating grass growth in spring in the [...]

Th[...]

1) [...]

s[...]

2) to [...]

obje[...]

The wor[...] where [...] Levy bri[...] & Haydock [...] methods wer[...] differences a[...] quency distribu[...] ods showed that [...] point. It is conc[...] ing grassland speci[...]

bridge & Scott, 1981). The blocks in turn are divided into compartments in which the appropriate burning treatment for the predominant vegetation is applied. Burning prescriptions prior to 1981 required that grasslands be burnt biennially in spring, after the first rains. In the event of no rainfall, they were to be burnt dry before the end of November. The 'ideal' burning period is in late winter (August - September) while the grasses are still dormant (Scott, 1971; Tainton, Groves & Nash, 1977; Dillon, 1979; Scotcher & Clarke, 1981). Thus there is a relatively short period over which managers should implement burns. This period is further restricted by prevailing weather conditions which are seldom suitable for burning. It is apparent then, that some compromise must be reached that is also practical for managers.

Evidence from this study (Chapter 5) has shown that burning once growth has been initiated can have detrimental effects on these grass swards. For example, summer burning (December) resulted in a 95% mortality rate of tagged Themeda triandra tillers, and a marked reduction in recovery growth rates. The only alternative for managers of large areas would therefore be to burn earlier in the season, that is during early winter.

In this study it was shown that there were no significant differences in mean veld condition scores between plots which had received over 30 years of annual winter and biennial spring burning. Similarly, there were no significant differences in the yield of above ground living material between these treatments (Chapter 7). Plots burnt in early October (spring) had significantly lower percentage canopy cover values than the winter burnt plots in the early growing season (Chapter 8). Thus areas burnt at this time have little protection during the November/ December high intensity rains. However, areas burnt in winter (June and July) are also subjected to long periods of soil exposure. These results suggest that burning should be allowed earlier in the season (from May onwards) rather than later in the year, that is into spring. Because significant growth has taken place by the end of September (Chapters 5, 7 & 9), burning should not be permitted from October onwards. In dry years this period should not be extended (as has previously been permitted), as growth may be initiated prior to the first rains (Chapter 9). The most suitable season for burning Highland Sourveld is therefore from the time of the first frosts in May until the end of October.

In this study it was shown that the absence of fire results in a decrease in both veld condition (Chapter 3) and yield (Chapter 7). A regular fire regime was shown to be essential for maintaining these grasslands. Annual and biennial burning were not significantly different in their ability to maintain veld condition, productivity and canopy cover, and so provide protection for the soil. A biennial burning regime maintained the dominant grass species at their present levels of abundance (Chapter 5). This, together with the fact that biennial burning is cheaper to apply, suggests that a biennial burning regime would be most suitable for these grasslands.

According to Nanni (1969) the best form of veld management would be a combination of different burning seasons and different frequencies. In this manner no species would be favoured at the expense of others. Such a burning programme would, however, be complicated and difficult to apply. The results of this study have been incorporated into a revised management burning programme which is also a compromise of Nanni's proposal. The burning season is now divided into three periods: 1) May (early winter), 2) June-July (winter) and 3) August-September (early spring).

This is aimed at encouraging ecological resiliance, since burning biennially ensures that a management compartment is burnt in a different period once every six years. An added advantage of such a policy is that there is a phased reduction in fuels loads and so provides some protection against wildfires.

This raises the question of how such a burning policy would affect the fauna of these areas. Although not part of this study, it is obviously a question which must be considered. Rowe-Rowe (1982) has made observations on the five most abundant antelopes (eland, grey rhebuck, mountain reedbuck, oribi and blesbok), in the Natal Drakensberg. All of these antelopes showed positive responses to fire, feeding on recently-burnt veld in preference to unburnt veld. Early burning (May and, to a lesser extent June and July), would provide a green flush of high quality food for the winter period. Rowe-Rowe (1982) recommended biennial burning as this provides equal areas of burnt and unburnt veld. Unburnt veld was considered important to provide cover for grey rhebuck, mountain reedbuck and oribi, as lying out behaviour is practised by these antelopes for at least six weeks after the young are born.

Biennial burning has also been found satisfactory for maintaining small-mammal communities (Rowe-Rowe & Lowry, 1982). These small mammal populations are considered to be important in contributing to the abundance and species richness of avian and terrestrial predators.

Mentis & Bigalke (1979), who examined grassland francolins in these montane grasslands, found that these birds flourished in biennial burns and that populations declined in the absence of fire. Annual burning was not advocated in this study as important food plants do not flower under this burning regime.

An avifaunal survey of the Natal Drakensberg (Little & Bainbridge, in press.) has shown that most grassland bird species are ecologically adapted to the presence of fires during the dormant period. Since most bird species begin breeding in early spring, these authors recommended that late spring burns (after September) be avoided. The burning regime proposed for the grass vegetation is therefore also the most suitable for the local fauna.

From the preceding discussion it is obvious that fires and Highland Sourveld grassland (including the fauna dependent on them) are inseparable. Management plans for these montane grassland areas that do not consider this inherent relationship are bound to fail, as the only way of achieving the stated objectives, is through the regular use of fire in the dormant period.

ACKNOWLEDGEMENTS

I would like to thank the Director-General of the Directorate of Forestry and Environmental Conservation for permission to undertake the study as an official project and for financial support.

There have been many people who have encouraged, advised and assisted me in this study.

Firstly, Terry my wife, professional colleague, technical assistant, typist and editor, for her assistance and companionship throughout the study.

I am grateful to Professor N.M. Tainton for his supervision of the study, his valuable suggestions in the field work and for critically reading the draft of the thesis.

I wish to express my sincere appreciation to Professor G.P.Y. Clarke of the Dept. of Statistics and Biometry, University of Natal, for his keen interest and assistance. His guidance and endless patience through the many complex statistical analyses have been invaluable.

I wish to thank Professor R. Schulze and W. George of the Dept. of Agricultural Engineering, University of Natal, for their assistance with the soil loss modelling.

Part of this work was financed by a C.S.I.R grant from the SCOPE programme on "The Ecological Effects of Fire".

Valuable discussions were held with many people, in particular M.T. Mentis, M. Savage, F.R. Smith and P. Manders. I also thank F.J. Kruger for his useful criticisms of some of the chapters of the thesis, and Prof. E. Granger for help in the initiation of the project.

Special appreciation is expressed to P. Hallot, C. Coetser and S. Hardy for field assistance, to K. Carter and G. Ruddock for implementing and supervising treatment burns at Cathedral Peak and R. Walker for his help in the processing of data of the techniques experiment.

The Cedara College of Agriculture undertook all the chemical analyses of the vegetation samples. I am grateful to A. Cass for help with the analysis of soil samples.

Finally, thanks are due to Miss. J. Scott for preparation of the figures, Mrs. C. R. du Plessis for typing of the tables and Mrs. E. Hardy for proof reading the final draft.

APPENDIX A Results of the analysis of variance using wheel point adjusted data

Becium

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	12,808	2,562	0,280	N.S.
OP	5	39,003	7,801	0,852	N.S.
ME	5	43,481	8,696	0,949	N.S.
DA.OP	25	170,905	6,836	0,746	N.S.
DA.ME	25	119,554	4,782	0,522	N.S.
OP.ME	25	177,426	7,097	0,775	N.S.
RESIDUAL	125	1144,871	9,159		
TOTAL	215	1708,047	7,944		
GRAND TOTAL	215	1708,047			

GRAND MEAN 2,38
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 2,38

DA	1	2	3	4	5	6
	2,24	2,55	2,55	2,39	1,92	2,64

OP	1	2	3	4	5	6
	1,81	2,27	3,06	2,72	2,46	1,98

ME	1	2	3	4	5	6
	2,84	1,93	3,04	2,16	2,49	1,84

OP DA	1	2	3	4	5	6
1	1,97	1,03	1,88	2,32	4,60	1,66
2	3,15	1,36	3,36	2,63	3,25	1,54
3	1,43	2,60	4,76	2,71	2,19	1,62
4	1,68	4,13	2,75	3,32	1,13	1,34
5	1,45	1,93	1,70	1,33	2,30	2,81
6	1,18	2,58	3,92	3,99	1,28	2,90

ME DA	1	2	3	4	5	6
1	2,74	1,80	2,11	3,04	1,95	1,82
2	2,14	1,86	4,14	2,53	2,25	2,38
3	4,01	1,66	2,43	2,01	3,52	1,67
4	3,77	2,10	3,39	1,85	1,95	1,30
5	2,07	2,71	0,91	1,10	3,15	1,58
6	2,30	1,45	5,28	2,43	2,12	2,28

ME OP	1	2	3	4	5	6
1	2,24	1,14	3,33	1,04	1,88	1,23
2	3,01	1,91	2,73	1,86	1,07	3,05
3	4,01	3,03	4,51	2,31	3,65	0,86
4	0,83	1,93	4,38	3,62	3,70	1,84
5	2,72	1,23	2,90	1,88	2,92	3,10
6	4,23	2,35	0,41	2,24	1,72	0,94

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,713	0,713	0,713	0,747	0,747	0,747

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	3,026	127,0

APPENDIX A (Continued) Diheteropogon

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	3,51	0,70	0,030	N.S.
OP	5	55,38	11,08	0,472	N.S.
ME	5	432,82	86,56	3,691	***
DA.OP	25	318,73	12,75	0,544	N.S.
DA.ME	25	205,80	8,23	0,351	N.S.
OP.ME	25	577,79	23,11	0,986	N.S.
RESIDUAL	125	2931,35	23,45		
TOTAL	215	4525,38	21,05		
GRAND TOTAL	215	4525,38			

GRAND MEAN 8,03
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 8,03

DA	1	2	3	4	5	6
	7,97	7,93	8,20	8,05	7,85	8,19

OP	1	2	3	4	5	6
	8,52	7,83	7,17	8,39	7,71	8,57

ME	1	2	3	4	5	6
	6,62	6,35	10,08	7,78	7,66	9,71

OP	1	2	3	4	5	6
DA						
1	6,55	6,65	7,68	10,53	8,81	7,61
2	5,99	9,96	6,57	7,50	7,74	9,83
3	11,06	7,45	7,14	6,50	8,57	8,46
4	10,19	7,81	6,94	8,00	6,60	8,79
5	9,53	8,74	5,98	7,72	7,23	7,93
6	7,80	6,39	8,73	10,10	7,31	8,81

ME	1	2	3	4	5	6
DA						
1	6,25	5,71	10.93	8,03	6,78	10,13
2	6,64	6,85	6,76	8,82	7,45	11,07
3	6,68	7,43	12,10	7,06	7,40	8,50
4	6,87	5,33	10,90	7,18	8,12	9,91
5	7,38	5,37	9,27	8,39	6,95	9,72
6	5,89	7,40	10,53	7,18	9,28	8,85

ME	1	2	3	4	5	6
OP						
1	5,48	7,61	6,62	10,84	9,98	10,59
2	7,73	3,12	11,34	6,30	8,92	9,59
3	5,72	5,56	8,74	7,70	5,48	9,83
4	7,37	7,51	13,89	5,76	7,28	8,55
5	3,96	7,48	8,33	8,93	6,48	11,08
6	9,46	6,82	11,55	7,15	7,83	8,59

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	1,141	1,141	1,141	2,796	2,796	2,796

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	4,803	60,3

APPENDIX A (Continued)

Harpechloa

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	5,170	1,034	0,385	N.S.
OP	5	17,919	3,584	0,385	N.S.
ME	5	125,696	25,139	9,354	***
DA.OP	25	87,372	3,515	1,308	N.S.
DA.ME	25	40,056	1,602	0,596	N.S.
OP.ME	25	77,133	3,085	1,148	N.S.
RESIDUAL	125	335,927	2,687		
TOTAL	215	689,773	3,208		
GRAND TOTAL	215	689,773			

GRAND MEAN 1,77
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 1,77

DA	1	2	3	4	5	6
	1,91	1,54	1,91	1,70	1,92	1,62

OP	1	2	3	4	5	6
	1,73	1,98	1,69	1,61	2,25	1,33

ME	1	2	3	4	5	6
	2,43	2,23	0,95	1,77	2,64	0,58

OP	1	2	3	4	5	6
DA						
1	3,12	1,22	1,09	2,47	2,67	0,91
2	1,52	2,49	1,40	1,18	1,93	0,70
3	1,55	2,34	2,70	1,23	2,44	1,24
4	2,11	1,90	1,31	1,89	2,00	1,00
5	0,96	1,86	0,74	1,72	2,95	3,29
6	1,15	2,05	2,91	1,20	1,53	0,89

ME	1	2	3	4	5	6
DA						
1	3,20	2,05	0,89	1,91	3,42	0,00
2	1,72	2,04	1,40	1,70	1,63	0,73
3	2,70	2,29	0,67	1,91	2,98	0,92
4	1,46	2,94	0,51	1,77	3,20	0,34
5	2,77	1,70	1,57	1,74	2,78	0,94
6	2,72	2,35	8,69	1,56	1,85	0,56

ME	1	2	3	4	5	6
OP						
1	3,14	1,53	1,04	1,47	2,90	0,05
2	1,35	3,39	0,85	2,16	2,40	1,72
3	2,96	2,05	1,55	0,78	2,52	0,28
4	2,39	1,61	0,41	2,95	2,13	0,20
5	2,54	2,84	1,00	2,22	4,57	0,54
6	1,94	1,94	0,88	1,01	1,55	0,69

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,386	0,386	0,386	0,946	0,946	0,946

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	1,639	92,8

APPENDIX A (Continued)

<u>Helichrysum</u>

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	3,05	0,61	0,037	N.S.
OP	5	19,48	3,90	0,236	N.S.
ME	5	88,18	17,64	1,066	N.S.
DA.OP	25	500,49	20,02	1,211	N.S.
DA.ME	25	174,35	6,97	0,422	N.S.
OP.ME	25	527,72	21,11	1,276	N.S.
RESIDUAL	125	2067,13	16,54		
TOTAL	215	3380,40	15,72		
GRAND TOTAL	215	3380,40			

GRAND MEAN 2,03
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 2,03

DA	1	2	3	4	5	6
	1,96	1,94	2,13	2,20	1,85	2,08

OP	1	2	3	4	5	6
	2,15	2,06	1,77	2,54	2,04	1,59

ME	1	2	3	4	5	6
	2,33	2,20	1,02	2,22	2,97	1.41

OP / DA	1	2	3	4	5	6
1	0,38	0,72	3,05	5,32	2,06	0,22
2	3,98	3,44	1,69	0,61	0,51	1,41
3	0,74	0,60	0,44	3,03	5,49	2,48
4	5,21	2,68	0,15	1,78	1,18	2,18
5	0,24	0,30	2,02	3,56	2,70	2,30
6	2,37	4,61	3,28	0,94	0,33	0,92

ME / DA	1	2	3	4	5	6
1	1,13	2,67	0,07	2,63	4,85	0,40
2	2,83	2,92	2,06	0,92	2,07	0,84
3	4,45	0,82	0,61	1,32	3,88	1,69
4	2,86	1,94	1,17	2,13	3,07	2,00
5	0,73	1,85	1,04	2,77	2,55	2,18
6	2,00	2,98	1,17	3,53	1,43	1,35

ME / OP	1	2	3	4	5	6
1	5,08	1,58	2,39	0,68	3,13	0,05
2	0,15	4,94	0,35	3,44	0,92	2,54
3	2,49	0,03	1,44	1,61	4,85	0,21
4	0,55	3,55	0,81	5,31	3,22	1,81
5	5,07	0,71	0,88	0,68	4,93	0,00
6	0,66	2,37	0,25	1,59	0,80	3,84

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,959	0,959	0,959	2,348	2,348	2,348

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	4,067	200,8

APPENDIX A (Continued)

Hypoxis

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	207,808	41,562	4,666	***
OP	5	296,979	59,396	6,668	***
ME	5	1154,725	230,945	25,927	***
DA.OP	25	375,110	15,004	1,684	**
DA.ME	25	203,706	8,148	0,915	N.S.
OP.ME	25	405,972	16,239	1,823	**
RESIDUAL	125	1113,437	8,907		
TOTAL	215	3757,739	17,478		
GRAND TOTAL	215	3757,739			

GRAND MEAN 3,35
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 3,35

DA	1	2	3	4	5	6
	4,92	4,34	3,32	2,76	2,15	2,61

OP	1	2	3	4	5	6
	2,50	5,66	2,06	3,72	3,39	2,76

ME	1	2	3	4	5	6
	7,00	4,92	0,44	2,76	4,20	0,76

OP DA	1	2	3	4	5	6
1	4,67	9,54	2,87	7,26	3,08	2,09
2	0,63	8,06	3,05	3,58	6,84	3,86
3	3,05	6,36	1,65	4,17	2,25	2,44
4	1,57	5,32	1,66	2,94	3,22	1,84
5	1,53	3,05	1,92	1,42	1,61	3,36
6	3,54	1,66	1,19	2,98	3,34	2,95

ME DA	1	2	3	4	5	6
1	9,80	5,73	0,98	6,97	5,88	0,14
2	9,99	5,03	0,59	2,68	4,27	3,45
3	5,91	5,97	0,17	2,18	4,82	0,86
4	5,54	4,92	0,17	1,95	3,87	0,09
5	4,46	3,93	0,15	1,49	2,87	0,00
6	6,32	3,96	0,58	1,29	3,52	0,00

ME OP	1	2	3	4	5	6
1	5,29	4,29	0,46	0,93	3,60	0,41
2	9,38	8,63	0,16	6,79	8,43	0,59
3	3,04	4,36	0,77	1,23	2,38	0,55
4	11,83	4,50	0,50	2,40	3,07	0,05
5	6,42	3,82	0,52	2,75	3,90	2,95
6	6,03	3,95	0,24	2,45	3,83	0,00

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,703	0,703	0,703	1,723	1,723	1,723

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	2,985	89,1

Oxalis

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	21.429	4.286	0.541	N.S.
OP	5	20,942	4,188	0,529	N.S.
ME	5	278,862	55,772	7,045	***
DA.OP	25	228,813	9,154	1,156	N.S.
DA.ME	25	155,680	6,227	0,787	N.S.
OP.ME	25	278,180	11,127	1,405	N.S.
RESIDUAL	125	989,629	7,917		
TOTAL	215	1973,565	9,179		
GRAND TOTAL	215	1973,565			

GRAND MEAN 1,45
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 1,54

	1	2	3	4	5	6
DA	1,98	1,48	1,78	1,69	1,21	1,09

	1	2	3	4	5	6
OP	1,23	1,58	1,21	1,33	1,93	1,96

	1	2	3	4	5	6
ME	3,04	2,33	0,14	1,46	2,27	0,00

OP / DA	1	2	3	4	5	6
1	0,43	0,98	1,98	2,80	4,21	1,47
2	0,38	3,51	1,70	1,14	0,37	1,80
3	2,14	0,15	0,65	1,71	4,12	1,92
4	2,16	3,71	0,50	0,26	0,64	2,90
5	0,74	0,32	0,76	0,83	2,22	2,39
6	1,51	0,79	1,66	1,26	0,00	1,30

ME / DA	1	2	3	4	5	6
1	3,60	2,38	0,08	2,16	3,65	0,00
2	1,71	4,09	0,08	0,63	2,40	0,00
3	6,26	0,95	0,07	0,89	2,53	0,00
4	3,49	2,84	0,00	1,97	1,87	0,00
5	1,03	2,11	0,21	1,55	2,35	0,00
6	2,12	1,61	0,37	1,58	0,83	0,00

ME / OP	1	2	3	4	5	6
1	3,67	2,21	0,31	0,00	1,17	0,00
2	0,83	4,81	0,17	2,74	0,92	0,00
3	1,94	1,18	0,11	1,22	2,80	0,00
4	0,66	1,48	0,03	2,95	2,88	0,00
5	6,10	0,90	0,17	0,56	3,83	0,00
6	5,00	3,39	0,03	1,32	2,03	0,00

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,663	0,663	0,663	1,625	1,625	1,625

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	2,814	182,8

APPENDIX A (Continued)

Rendlia

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	137,14	27,43	0,301	N.S.
OP	5	95,25	19,05	0,264	N.S.
ME	5	1335,63	267,12	3,707	***
DA.OP	25	508,23	20,33	0,282	N.S.
DA.ME	25	345,32	13,81	0,192	N.S.
RESIDUAL	25	750,72	30,03	0,417	N.S.
TOTAL	125	9008,43	72,07		
	215	12180,70	56,65		
GRAND TOTAL	215	12180,70			

GRAND MEAN 10,88
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 10,88

	1	2	3	4	5	6
DA	9,93	9,90	11,17	11,38	12,15	10,75

	1	2	3	4	5	6
OP	11,42	11,10	11,05	9,43	11,29	11,00

	1	2	3	4	5	6
ME	8,86	8,48	15,71	10,32	9,61	12,30

OP / DA	1	2	3	4	5	6
1	9,85	9,77	9,35	10,40	8,84	11,37
2	9,70	10,93	9,01	12,07	9,19	8,54
3	10,69	12,83	9,23	9,10	13,17	11,98
4	12,58	12,55	12,79	8,87	9,69	11,82
5	14,41	11,65	15,27	8,30	13,13	10,12
6	11,27	8,89	10,63	7,84	13,70	12,15

ME / DA	1	2	3	4	5	6
1	7,48	8,79	13,86	7,82	8,87	12,78
2	9,11	4,32	12,10	11,98	10,40	11,51
3	9,73	9,50	16,57	9,68	9,08	12,44
4	7,00	9,33	18,88	10,78	9,57	12,73
5	10,50	10,10	17,92	10,52	10,48	13,36
6	9,35	8,85	14,93	11,14	9,23	10,97

ME / OP	1	2	3	4	5	6
1	6,99	6,38	16,86	13,66	10,65	13,96
2	10,37	7,45	16,10	11,00	13,15	8,55
3	7,39	10,21	16,10	8,00	8,78	15,79
4	10,04	9,71	14,12	5,55	5,23	11,93
5	10,10	8,55	15,27	13,00	8,47	12,25
6	8,28	8,60	15,81	10,63	11,35	11,31

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	2,001	2,001	2,001	4,901	4,901	4,901

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	8,489	78,0

Scilla

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	13,804	2,761	0,862	N.S.
OP	5	109,887	21,977	6,863	***
ME	5	472,072	94,414	29,483	***
DA.OP	25	104,692	4,188	1,308	N.S.
DA.ME	25	37,986	1,519	0,474	N.S.
OP.ME	25	168,558	6,742	2,105	***
RESIDUAL	125	400,298	3,202		
TOTAL	215	1307,297	6,080		
GRAND TOTAL	215	1307,297			

GRAND MEAN 1,97
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 1,97

DA	1	2	3	4	5	6
	1,51	2,12	1,77	2,02	2,10	2,27

OP	1	2	3	4	5	6
	2,22	0,65	1,40	2,31	2,64	2,57

ME	1	2	3	4	5	6
	4,05	3,34	0,39	1,36	2,61	0,05

OP / DA	1	2	3	4	5	6
1	3,31	0,12	0,18	1,07	1,82	2,55
2	1,57	0,18	0,81	2,21	4,62	3,35
3	2,26	0,04	2,22	1,85	1,61	2,64
4	1,82	0,44	1,64	3,47	2,84	1,92
5	2,33	2,01	2,00	2,13	1,65	2,46
6	2,00	1,10	1,57	3,14	3,30	2,51

ME / DA	1	2	3	4	5	6
1	2,55	2,48	0,77	1,04	2,22	0,00
2	4,58	4,09	0,11	1,38	2,58	0,00
3	3,71	2,29	0,28	1,73	2,62	0,00
4	4,63	3,38	0,41	1,34	2,27	0,11
5	3,69	4,21	0,36	1,34	2,78	0,21
6	5,13	3,57	0,43	1,32	3,17	0,00

ME / OP	1	2	3	4	5	6
1	5,77	3,27	0,59	0,87	2,80	0,00
2	0,80	1,26	0,12	0,50	1,15	0,07
3	1,77	3,01	0,12	1,01	2,37	0,14
4	6,02	3,17	0,24	1,85	2,58	0,00
5	3,87	6,36	0,53	1,92	3,05	0,11
6	6,05	2,94	0,76	2,00	3,68	0,00

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,422	0,422	0,422	1,033	1,033	1,033

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	1,790	91,1

APPENDIX A (Continued)

Senecio

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	25,466	5,093	0,871	N.S.
OP	5	25,693	5,139	0,879	N.S.
ME	5	299,234	59,847	10,234	***
DA.OP	25	115,210	4,608	0,788	N.S.
DA.ME	25	65,191	2,608	0,446	N.S.
OP.ME	25	220,630	8,825	1,509	***
RESIDUAL	125	730,985	5,848		
TOTAL	215	1482,409	6,895		
GRAND TOTAL	215	1482,409			

GRAND MEAN 1,67
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 1,67

	1	2	3	4	5	6
DA	1,45	2,35	1,87	1,51	1,51	1,34

	1	2	3	4	5	6
OP	1,35	2,41	1,64	1,51	1,59	1,52

	1	2	3	4	5	6
ME	3,91	2,01	0,54	1,42	1,82	0,33

OP / DA	1	2	3	4	5	6
1	1,24	1,58	1,68	2,51	0,70	1,00
2	2,72	3,32	1,28	0,79	2,94	3,03
3	0,76	4,49	1,96	1,93	0,77	1,31
4	0,68	1,12	1,63	1,91	1,63	2,09
5	1,21	1,29	2,54	0,89	2,20	0,92
6	1,49	2,70	0,76	1,02	1,28	0,78

ME / DA	1	2	3	4	5	6
1	3,79	1,61	0,35	1,64	1,32	0,00
2	3,33	4,09	1,77	1,56	1,53	1,80
3	4,83	2,54	0,17	2,22	1,45	0,00
4	3,65	1,75	0,52	1,32	1,82	0,00
5	4,16	1,04	0,29	0,86	2,53	0,18
6	3,74	1,03	0,12	0,90	2,25	0,00

ME / OP	1	2	3	4	5	6
1	2,33	3,54	0,19	0,81	1,23	0,00
2	8,58	1,52	0,23	1,53	2,63	0,00
3	3,87	2,23	0,32	1,41	2,03	0,00
4	4,26	1,56	0,00	1,43	1,80	0,00
5	2,39	1,77	0,72	1,64	1,03	1,98
6	2,05	1,45	1,77	1,68	2,17	0,00

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,570	0,570	0,570	1,396	1,396	1,396

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	2,418	144,8

APPENDIX A (continued)

Themeda

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	144,95	28,99	1,265	N.S.
OP	5	129,18	25,84	1,127	N.S.
ME	5	1965,63	393,13	17,149	***
DA.OP	25	799,02	31,96	1,394	N.S.
DA.ME	25	544,88	21,80	0,951	N.S.
OP.ME	25	547,43	21,90	0,955	N.S.
RESIDUAL	125	2865,52	22,92		
TOTAL	215	6996,61	32,54		
GRAND TOTAL	215	6996,61			

GRAND MEAN 14,06
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 14,06

	1	2	3	4	5	6
DA	15,18	13,10	14,74	12,92	14,01	14,38

	1	2	3	4	5	6
OP	13,54	14,34	14,25	15,06	14,49	12,64

	1	2	3	4	5	6
ME	18,11	15,68	10,66	14,08	16,17	9,64

OP	1	2	3	4	5	6
DA						
1	14,35	15,16	13,41	14,61	17,08	16,46
2	11,70	10,56	17,59	18,00	10,92	9,86
3	14,14	17,90	13,78	14,17	16,71	11,72
4	12,08	16,13	13,82	12,97	11,02	10,70
5	15,91	11,65	12,54	13,91	14,21	15,84
6	13,06	14,66	14,37	16,72	16,20	11,28

ME	1	2	3	4	5	6
DA						
1	19,34	18,51	9,60	13,60	18,50	11,52
2	16,53	10,42	14,20	13,89	15,40	8,19
3	19,79	16,21	10,01	15,14	17,87	9,40
4	13,60	17,36	8,14	13,57	15,90	8,96
5	19,15	15,66	11,44	14,01	14,55	9,25
6	22,24	15,92	10,56	14,25	14,82	10,50

ME	1	2	3	4	5	6
OP						
1	16,94	16,07	8,50	15,57	16,12	8,05
2	15,12	17,22	10,81	15,41	16,87	10,63
3	16,20	15,91	12,92	13,35	16,68	10,45
4	22,56	15,21	9,09	14,49	16,38	12,65
5	19,69	17,31	13,24	14,05	16,45	6,20
6	18,14	12,36	9,40	11,59	14,53	9,84

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	1,129	1,129	1,129	2,764	2,764	2,764

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	4,788	34,1

Trachypogon

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	95,59	19,12	1,506	N.S.
OP	5	102,65	20,53	1,617	N.S.
ME	5	122,78	24,56	1,934	*
DA.OP	25	233,62	9,34	0,736	N.S.
DA.ME	25	287,04	11,48	0,904	N.S.
OP.ME	25	253,65	10,15	0,799	N.S.
RESIDUAL	125	1587,07	12,70		
TOTAL	215	2682,39	12,48		
GRAND TOTAL	215	2682,39			

GRAND MEAN 1,95
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 1,95

	1	2	3	4	5	6
DA	1,66	3,36	1,55	2,07	1,36	1,72

	1	2	3	4	5	6
OP	2,44	0,83	2,07	1,24	2,40	2,74

	1	2	3	4	5	6
ME	1,39	3,04	2,85	1,36	1,99	1,08

OP / DA	1	2	3	4	5	6
1	1,96	1,17	1,45	0,90	2,70	1,78
2	6,10	0,17	1,98	1,11	3,21	7,60
3	1,25	0,10	1,93	1,37	1,94	2,69
4	2,37	1,95	3,34	1,05	2,07	1,63
5	1,64	0,28	1,97	1,10	1,40	1,77
6	1,32	1,29	1,76	1,89	3,08	0,98

ME / DA	1	2	3	4	5	6
1	0,86	1,97	1,66	1,53	2,88	1,05
2	1,19	7,15	7,65	1,16	2,17	0,85
3	1,97	2,78	1,39	1,20	1,37	0,58
4	1,16	2,68	4,77	1,11	1,92	0,77
5	1,24	1,42	0,76	1,55	1,62	1,55
6	1,91	2,24	0,84	1,62	2,02	1,69

ME / OP	1	2	3	4	5	6
1	1,07	6,55	2,81	1,31	1,35	1,54
2	0,40	0,41	1,83	0,09	0,80	1.45
3	1,02	3,47	1,77	1,79	2,70	1,66
4	1,89	1,63	1,02	0,83	1,70	0,35
5	1,79	4,25	2,44	2,31	2,57	1,05
6	2,16	1,94	7,21	1,85	2,85	1,44

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,840	0,840	0,840	2,057	2,057	2,057

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	3,563	182,5

APPENDIX A (Continued)

Tristachya

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	508,88	101,78	3,816	***
OP	5	130,53	26,11	0,979	N.S.
ME	5	1069,87	213,97	8,024	***
DA.OP	25	1289,76	51,59	1,935	***
DA.ME	25	849,31	33,97	1,274	N.S.
OP.ME	25	826,57	33,06	1,240	N.S.
RESIDUAL	125	3333,41	26,67		
TOTAL	215	8008,36	37,25		
GRAND TOTAL	215	8008,36			

GRAND MEAN 18,55
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 18,55

DA	1	2	3	4	5	6
	18,86	15,36	18,43	18,97	20,29	19,38

OP	1	2	3	4	5	6
	19,26	18,84	18,99	19,03	16,97	18,19

ME	1	2	3	4	5	6
	19,62	18,38	18,02	19,72	21,35	14,19

OP / DA	1	2	3	4	5	6
1	22,92	18,34	18,40	17,79	17,31	18,40
2	14,61	17,87	14,82	16,22	12,24	16,43
3	19,43	17,28	21,77	19,47	15,70	16,93
4	15,23	13,09	21,12	21,14	20,30	20,32
5	20,18	25,81	20,50	22,02	17,08	16,13
6	23,18	20,66	17,34	15,46	19,21	20,34

ME / DA	1	2	3	4	5	6
1	24,33	19,59	18,04	18,17	19,45	13,57
2	14,99	13,07	12,30	18,10	23,98	9,75
3	16,75	18,07	20,27	20,62	18,92	15,95
4	20,89	18,48	15,59	22,17	21,10	15,56
5	20,71	21,39	22,14	20,04	23,87	13,57
6	20,05	19,68	19,80	19,24	20,80	16,72

ME / OP	1	2	3	4	5	6
1	17,44	17,69	22,76	20,34	22,05	15,26
2	18,43	18,31	19,41	20,05	21,55	15,31
3	18,41	21,61	14,65	23,40	21,03	14,84
4	21,14	17,30	22,80	16,17	22,57	14,22
5	21,12	16,38	13,20	18,87	20,18	11,98
6	21,19	18,99	15,32	19,40	20,73	13,52

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	1,217	1,217	1,217	2,981	2,981	2,981

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	5,164	27,8

APPENDIX A (Continued) Vernonia

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	7,201	1,440	0,298	N.S.
OP	5	17,934	3,587	0,742	N.S.
ME	5	56,288	11.258	2,328	**
DA.OP	25	107,363	4,295	0,888	N.S.
DA.ME	25	155,820	6,233	1,289	N.S.
OP.ME	25	150,495	6,020	1,245	N.S.
RESIDUAL	125	604,512	4,836		
TOTAL	215	1099,613	5,114		
GRAND TOTAL	215	1099,613			

GRAND MEAN 2,22
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 2,22

DA	1	2	3	4	5	6
	2,28	2,55	2,30	2,01	2,14	2,06

OP	1	2	3	4	5	6
	1,72	2,01	2,51	2,54	2,19	2,36

ME	1	2	3	4	5	6
	1,82	2,10	2,58	1,91	1,74	3,18

OP	1	2	3	4	5	6
DA						
1	2,76	2,65	2,11	3,02	1,36	1,77
2	1,61	2,03	2,90	1,66	5,17	1,95
3	1,99	1,62	2,85	3,02	1,62	2,71
4	1,08	1,82	1,91	2,38	2,21	2,62
5	0,92	1,77	2,11	2,96	1,87	3,18
6	1,98	2,18	3,15	2,21	0,90	1,93

ME	1	2	3	4	5	6
DA						
1	0,99	1,44	3,70	2,59	1,80	3,15
2	2,48	5,81	1,26	1,88	1,88	2,01
3	2,17	1,03	3,21	1,62	1,67	4,13
4	0,99	1,61	2,10	1,97	2,02	3,35
5	1,96	1,03	2,70	1,34	2,13	3,65
6	2,30	1,72	2,51	2,09	0,92	2,82

ME	1	2	3	4	5	6
OP						
1	1,80	1,47	1,08	1,74	1,30	2,94
2	1,74	1,74	3,09	1,32	1,78	2,40
3	1,64	1,66	4,18	2,75	0,98	3,83
4	1,83	1,06	2,04	2,25	2,27	5,82
5	1,50	4,59	1,98	1,25	1,93	1,87
6	2,38	2,11	3,12	2,16	2,15	2,25

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	0,518	0,518	0,518	1,270	1,270	1,270

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	2,199	98,9

***** ANALYSIS OF VARIANCE *****

SOURCE OF VARIATION	DF	SS	MS	VR	Sig.
UNITS STRATUM					
DA	5	61,20	12,24	0,386	N.S.
OP	5	151,47	30,29	0,954	N.S.
ME	5	446,78	89,36	2,815	**
DA.OP	25	291,32	11,65	0,367	N.S.
DA.ME	25	411,21	16,45	0,518	N.S.
OP.ME	25	425,13	17,01	0,536	N.S.
RESIDUAL	125	3968,19	31,75		
TOTAL	215	5755,30	26,77		
GRAND TOTAL	215	5755,30			

GRAND MEAN 11,52
TOTAL NUMBER OR OBSERVATIONS 216

***** TABLES OF MEANS *****

GRAND MEAN 11,52

	1	2	3	4	5	6
DA	10,76	10,88	11,67	11,83	12,27	11,70

	1	2	3	4	5	6
OP	12,04	11,21	10,44	11,10	11,24	13,07

	1	2	3	4	5	6
ME	13,11	9,05	12,63	11,65	10,21	12,45

OP	1	2	3	4	5	6
DA						
1	11,19	12,10	10,12	7,59	10,76	12,78
2	12,79	10,55	11,24	9,06	8,72	12,91
3	13,53	10,92	9,55	11,96	10,60	13,48
4	10,44	11,29	10,83	13,98	11,98	12,54
5	12,64	12,86	11,35	11,07	12,19	13,49
6	11,66	9,55	9,53	12,94	13,27	13,24

ME	1	2	3	4	5	6
DA						
1	11,39	7,97	14,00	10,40	8,70	12,00
2	15,75	6,49	8,33	11,83	10,92	11,96
3	13,35	10,37	13,02	12,58	9,02	11,70
4	11,33	10,01	13,50	10,37	12,98	12,78
5	12,15	9,72	15,31	12,60	10,72	13,10
6	14,67	9,77	11,53	12,14	8,95	13,13

ME	1	2	3	4	5	6
OP						
1	14,38	9,17	14,56	13,54	7,87	12,75
2	11,85	10,19	13,33	10,61	8,18	13,13
3	10,08	8,60	10,35	12,25	9,23	12,10
4	11,76	6,77	10,72	12,49	12,85	12,01
5	15,45	8,25	12,89	9,77	11,30	9,77
6	15,12	11,35	13,93	11,26	11,85	14,92

***** STANDARD ERRORS OF DIFFERENCES OF MEANS *****

TABLE	DA	OP	ME	DA OP	DA ME	OP ME
REP	36	36	36	6	6	6
SED	1,328	1,328	1,328	3,253	3,253	3,253

***** STRATUM STANDARD ERRORS AND COEFFICIENTS OF VARIATION *****

STRATUM	DF	SE	CV%
UNITS	125	5,634	48,9

APPENDIX B:TABLE 1
BIOMASS DATA (g/m2):PLOT 09A ANNUAL WINTER BURN

DATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
1/06/78	0.00	0.00	0.00	-	0.00	0.00	0	0.00	0.00	0
7/09/78	19.63	2.25	0.00	-	0.00	0.00	118	16.86	16.86	19.63
3/10/78	27.00	3.13	0.00	-	0.00	0.00	16	2.28	19.14	27.01
7/11/78	63.38	4.25	0.00	-	0.00	0.00	32	4.57	23.71	63.38
2/11/78	89.63	10.38	0.00	-	0.00	0.00	15	2.14	25.85	89.63
8/12/78	127.00	8.88	0.00	-	0.00	0.00	16	2.29	28.14	127.00
0/12/78	144.00	14.69	0.00	-	0.00	0.00	12	1.71	29.85	144.00
3/01/79	158.38	15.63	0.00	-	0.00	0.00	14	2.00	31.85	158.38
7/01/79	197.13	8.25	0.00	-	0.00	0.00	14	2.00	33.85	197.13
1/01/79	161.63	5.25	0.00	-	0.00	0.00	14	2.00	35.85	161.63
4/02/79	210.13	7.31	0.00	-	0.00	0.00	14	2.00	37.85	210.13
1/03/79	134.50	12.44	0.00	-	0.00	0.00	15	2.14	39.99	134.51
6/03/79	119.63	8.25	0.00	-	0.00	0.00	15	2.14	42.13	119.63
4/04/79	132.13	13.37	0.00	-	0.00	0.00	19	2.71	44.84	132.13
3/04/79	115.50	9.19	0.00	-	0.00	0.00	19	2.71	47.55	115.50
6/05/79	97.50	14.44	92.30	10.75	0.00	0.00	23	3.29	50.84	189.80
6/06/79	38.88	5.63	182.00	13.75	0.00	0.00	41	5.86	56.70	220.88
3/08/79	11.00	P	0.00	-	0.00	0.00	58	8.29	64.99	11.00
9/09/79	68.00	R	0.00	-	0.00	0.00	27	3.86	68.85	68.00
3/10/79	48.00	E	0.00	-	0.00	0.00	34	4.86	73.71	48.00
2/11/79	72.00	D	0.00	-	0.00	0.00	30	4.29	78.00	72.00
4/12/79	232.00	I	0.00	-	0.00	0.00	32	4.57	82.57	232.00
1/02/80	250.00	C	0.00	-	0.00	0.00	39	5.57	88.14	250.00
8/03/80	258.00	T	0.00	-	0.00	0.00	46	6.57	94.71	258.00
2/04/80	222.00	E	0.00	-	0.00	0.00	35	5.00	99.71	222.00
9/06/80	187.00	D	0.00	-	0.00	0.00	58	8.28	107.99	187.00

Summary statistics-live material

1st growing season (6/10/78-17/1/79)		2nd growing season (23/8/79-18/3/80)	
$Sum(B_n - B_{n-1})$ =	197.13g/m^2	$Sum(B_n - B_{n-1})$ =	247.01g/m^2
No.weeks =	33.85	No.weeks =	29.72
Rate =	5.82g/m^2/wk	Rate =	8.31g/m^2/wk

Mean rate of accumulation (A) =8.31 g/m^2/wk

PPENDIX B:TABLE 2
IOMASS DATA :PLOT 09B

BIENNIAL SPRING BURN

DATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
6/10/78	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00
7/11/78	26.00	2.44	0.00	0.00	0.00	0.00	32	4.57	4.57	26.00
2/11/78	44.88	6.19	0.00	0.00	0.00	0.00	15	2.14	6.71	44.88
8/12/78	95.75	13.00	0.00	0.00	0.00	0.00	16	2.29	9.00	95.75
0/12/78	115.88	8.63	0.00	0.00	0.00	0.00	12	1.71	10.71	115.88
3/01/79	120.63	9.50	0.00	0.00	0.00	0.00	14	2.00	12.71	120.63
7/01/79	132.50	15.50	0.00	0.00	0.00	0.00	14	2.00	14.71	132.50
1/01/79	147.75	11.69	0.00	0.00	0.00	0.00	14	2.00	16.71	147.75
4/02/79	201.75	16.19	0.00	0.00	0.00	0.00	14	2.00	18.71	201.75
1/03/79	119.81	12.94	0.00	0.00	0.00	0.00	15	2.14	20.85	119.81
5/03/79	116.63	13.69	0.00	0.00	0.00	0.00	15	2.14	22.99	116.63
4/04/79	134.13	15.25	0.00	0.00	0.00	0.00	19	2.71	25.70	134.13
5/04/79	99.81	7.75	0.00	0.00	0.00	0.00	19	2.71	28.41	99.81
6/05/79	78.63	8.13	79.63	4.63	0.00	0.00	23	3.29	31.70	158.26
5/07/79	14.75	3.75	132.75	14.88	0.00	0.00	50	7.14	38.84	147.50
5/08/79	11.38	4.44	164.88	8.56	0.00	0.00	49	7.00	45.84	176.26
/09/79	25.30	5.70	132.10	16.90	9.90	0.00	27	3.86	49.70	167.30
5/10/79	58.60	5.20	191.30	21.60	2.10	0.00	34	4.86	54.56	252.00
2/11/79	74.40	9.30	142.00	17.30	7.00	0.00	30	4.29	58.85	223.40
6/12/79	117.90	19.80	377.40	53.40	23.30	0.00	32	4.57	63.42	518.60
/02/80	172.90	23.20	243.50	27.20	0.00	10.30	39	5.57	68.99	416.40
/03/80	148.60	20.80	259.30	30.90	0.00	2.50	46	6.57	75.56	407.90
/04/80	133.90	11.60	256.70	21.30	0.00	6.40	35	5.00	80.56	390.60
/06/80	39.10	6.10	437.80	37.80	0.00	9.10	70	10.00	90.56	476.90

Summary statistics -live material

1st growing season (6/10/78-17/1/79)		2nd growing season (23/8/79-18/3/80)	
Sum($B_n - B_{n-1}$) =	132.5g/m^2	Sum($B_n - B_{n-1}$) =	179.52g/m^2
No.weeks =	14.71	No.weeks =	29.72
Rate =	9.01g/m^2/wk	Rate =	6.04g/m^2/wk

Mean rate of accumulation (A) =15.16 g/m^2/wk

PPENDIX B:TABLE 3

IOMASS DATA (g/m2):PLOT 10A ANNUAL WINTER BURN

ATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
1/06/78	0.00	0.00	0.00	-	0.00	0.00	0	0.00	0.00	0.00
7/09/78	79.25	5.38	0.00	-	0.00	0.00	118	16.86	16.86	79.25
3/10/78	22.56	2.69	0.00	-	0.00	0.00	16	2.28	19.14	22.56
7/11/78	82.63	8.38	0.00	-	0.00	0.00	32	4.57	23.71	82.63
2/11/78	97.63	6.56	0.00	-	0.00	0.00	15	2.14	25.85	97.63
8/12/78	142.13	5.00	0.00	-	0.00	0.00	16	2.29	28.14	142.13
0/12/78	173.63	14.63	0.00	-	0.00	0.00	12	1.71	29.85	173.63
3/01/79	156.75	13.94	0.00	-	0.00	0.00	14	2.00	31.85	156.75
7/01/79	194.25	13.25	0.00	-	0.00	0.00	14	2.00	33.85	194.25
1/01/79	153.38	8.31	0.00	-	0.00	0.00	14	2.00	35.85	153.38
4/02/79	224.75	8.75	0.00	-	0.00	0.00	14	2.00	37.85	224.75
1/03/79	179.63	14.19	0.00	-	0.00	0.00	15	2.14	39.99	179.63
/03/79	162.25	21.75	0.00	-	0.00	0.00	15	2.14	42.13	162.25
5/04/79	146.00	13.75	0.00	-	0.00	0.00	19	2.71	44.84	146.00
/04/79	150.38	13.31	0.00	-	0.00	0.00	19	2.71	47.55	150.38
/05/79	101.75	10.75	107.13	10.75	0.00	0.00	23	3.29	50.84	208.88
/06/79	28.00	3.75	145.00	7.75	0.00	0.00	41	5.86	56.70	173.00
/08/79	18.00	P	0.00	-	0.00	0.00	58	8.29	64.99	18.00
/09/79	23.00	R	0.00	-	0.00	0.00	27	3.86	68.85	23.00
/10/79	76.00	E	0.00	-	0.00	0.00	34	4.86	73.71	76.00
/11/79	127.00	D	0.00	-	0.00	0.00	30	4.29	78.00	127.00
/12/79	160.00	I	0.00	-	0.00	0.00	32	4.57	82.57	160.00
/02/80	218.00	C	0.00	-	0.00	0.00	39	5.57	88.14	218.00
/03/80	200.00	T	0.00	-	0.00	0.00	46	6.57	94.71	200.00
/04/80	218.00	E	0.00	-	0.00	0.00	35	5.00	99.71	218.00
/06/80	176.00	D	0.00	-	0.00	0.00	58	8.28	107.99	176.00

Summary statistics-live material

1st growing season (6/18/78-17/179)
$Sum(B_n - B_{n-1}) =$ 194.25 g/m^2
No.weeks = 33.85
Rate = 5.74 g/m^2/wk

2nd growing season (23/8/79-18/3/80)
$Sum(B_n - B_{n-1}) =$ 182.01 g/m^2
No.weeks = 29.72
Rate = 6.12 g/m^2/wkk

Mean rate of accumulation (A) =8.23 g/m^2/wk

APPENDIX B:TABLE 4
BIOMASS DATA :PLOT 10B

BIENNIAL SPRING BURN

DATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MASS LIVE FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
6/10/78	0.00	7.25	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00
7/11/78	26.69	8.06	0.00	0.00	0.00	0.00	32	4.57	4.57	26.69
2/11/78	63.81	17.06	0.00	0.00	0.00	0.00	15	2.14	6.71	63.81
8/12/78	145.00	12.51	0.00	0.00	0.00	0.00	16	2.29	9.00	145.00
0/12/78	181.60	14.56	0.00	0.00	0.00	0.00	12	1.71	10.71	181.60
3/01/79	197.13	44.19	0.00	0.00	0.00	0.00	14	2.00	12.71	197.13
7/01/79	242.90	16.56	0.00	0.00	0.00	0.00	14	2.00	14.71	242.90
1/01/79	208.40	17.06	0.00	0.00	0.00	0.00	14	2.00	16.71	208.40
4/02/79	206.80	25.69	0.00	0.00	0.00	0.00	14	2.00	18.71	206.80
1/03/79	226.10	7.56	0.00	0.00	0.00	0.00	15	2.14	20.85	226.10
6/03/79	155.50	25.31	0.00	0.00	0.00	0.00	15	2.14	22.99	206.50
4/04/79	148.40	17.75	0.00	0.00	0.00	0.00	19	2.71	25.70	206.00
3/04/79	131.60	12.61	0.00	0.00	0.00	0.00	19	2.71	28.41	206.00
6/05/79	91.30	3.88	115.90	14.88	0.00	0.00	23	3.29	31.70	207.20
5/07/79	18.13	2.69	155.00	11.50	0.00	0.00	50	7.14	38.84	173.13
3/08/79	4.80	4.13	229.60	44.44	0.00	0.00	49	7.00	45.84	234.40
9/09/79	27.90	5.19	251.10	24.75	8.00	0.00	27	3.86	49.70	287.00
3/10/79	75.40	5.69	316.10	18.81	2.63	0.00	34	4.86	54.56	394.13
2/11/79	111.20	7.38	298.50	11.69	22.81	0.00	30	4.29	58.85	432.51
4/12/79	130.60	10.51	323.80	39.75	7.81	0.00	32	4.57	63.42	462.21
1/02/80	150.00	11.13	341.30	37.63	0.00	24.25	39	5.57	68.99	491.30
8/03/80	207.56	18.06	347.94	53.94	0.00	19.88	46	6.57	75.56	555.50
2/04/80	161.38	7.31	441.63	14.19	0.00	23.88	35	5.00	80.56	603.01
1/06/80	30.81	6.88	607.25	41.38	0.00	14.00	70	10.00	90.56	638.06

Summary statistics-live material

1st growing season (6/10/78-17/1/79)		2nd growing season (23/8/79-18/3/80)	
$Sum(B_n - B_{n-1}) =$	242.91g/m^2	$Sum(B_n - B_{n-1}) =$	244.01g/m^2
No.weeks =	14.71	No.weeks =	29.72
Rate =	16.51g/m^2/wk	Rate =	8.21g/m^2/wk

Mean rate of accumulation = 10.33 g/m^2/wk

PPENDIX B:TABLE 5

IOMASS DATA (g/m2):PLOT 11A ANNUAL WINTER BURN

ATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
1/06/78	0.00	0.00	0.00	-	0.00	0.00	0	0.00	0.00	0.00
7/09/78	15	1.44	0.00	-	0.00	0.00	118	16.86	16.86	15.00
3/10/78	27.44	1.56	0.00	-	0.00	0.00	16	2.28	19.14	27.44
7/11/78	78.00	7.38	0.00	-	0.00	0.00	32	4.57	23.71	78.00
2/11/78	111.38	9.00	0.00	-	0.00	0.00	15	2.14	25.85	111.38
3/12/78	155.13	7.81	0.00	-	0.00	0.00	16	2.29	28.14	155.13
0/12/78	148.25	9.94	0.00	-	0.00	0.00	12	1.71	29.85	148.25
3/01/79	144.13	13.31	0.00	-	0.00	0.00	14	2.00	31.85	144.13
7/01/79	196.00	18.38	0.00	-	0.00	0.00	14	2.00	33.85	196.00
1/01/79	173.13	15.50	0.00	-	0.00	0.00	14	2.00	35.85	173.13
4/02/79	235.88	8.56	0.00	-	0.00	0.00	14	2.00	37.85	235.88
1/03/79	135.13	7.69	0.00	-	0.00	0.00	15	2.14	39.99	135.13
5/03/79	153.63	10.19	0.00	-	0.00	0.00	15	2.14	42.13	153.63
4/04/79	165.63	16.25	0.00	-	0.00	0.00	19	2.71	44.84	165.63
3/04/79	152.38	19.75	0.00	-	0.00	0.00	19	2.71	47.55	152.38
5/05/79	155.38	13.19	155.75	13.38	0.00	0.00	23	3.29	50.84	311.13
5/06/79	43.38	6.10	181.63	27.31	0.00	0.00	41	5.86	56.70	225.01
5/08/79	2.00	P	0.00	-	0.00	0.00	58	8.29	64.99	2.00
/09/79	26.00	R	0.00	-	0.00	0.00	27	3.86	68.85	26.00
/10/79	121.00	E	0.00	-	0.00	0.00	34	4.86	73.71	121.00
/11/79	145.00	D	0.00	-	0.00	0.00	30	4.29	78.00	145.00
/12/79	221.00	I	0.00	-	0.00	0.00	32	4.57	82.57	221.00
/02/80	214.00	C	0.00	-	0.00	0.00	39	5.57	88.14	214.00
/03/80	272.00	T	0.00	-	0.00	0.00	46	6.57	94.71	272.00
/04/80	280.00	E	0.00	-	0.00	0.00	35	5.00	99.71	280.00
/06/80	210.00	D	0.00	-	0.00	0.00	58	8.28	107.99	210.00

Summary statistics-live material

1st growing season (6/10/78-17/1/79		2nd growing season (23/8/79-188/3/80)	
$Sum(B_n - B_{n-1})$ =	196.01g/m²	$Sum(B_n - B_{n-1})$ =	270.01g/m²
No.weeks =	33.85	No.weeks =	29.72
Rate =	5.79g/m²/wk	Rate =	9.08g/m²/wk

Mean rate of accumulation (A) =10.32 g/m²/wk

PPENDIX B:TABLE 6
IOMASS DATA :PLOT 11B   BIENNIAL SPRING BURN

ATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	No. DAYS	No. WEEKS	ACCUM. TIME (WEEKS)	TOTAL MASS
6/10/78	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00
7/11/78	46.81	3.25	0.00	0.00	0.00	0.00	32	4.57	4.57	46.81
2/11/78	85.69	5.69	0.00	0.00	0.00	0.00	15	2.14	6.71	85.69
8/12/78	139.50	12.06	0.00	0.00	0.00	0.00	16	2.29	9.00	139.50
0/12/78	151.88	12.06	0.00	0.00	0.00	0.00	12	1.71	10.71	151.88
3/01/79	175.25	22.69	0.00	0.00	0.00	0.00	14	2.00	12.71	175.25
7/01/79	255.88	20.75	0.00	0.00	0.00	0.00	14	2.00	14.71	255.88
1/01/79	189.38	15.38	0.00	0.00	0.00	0.00	14	2.00	16.71	189.38
4/02/79	216.75	15.06	0.00	0.00	0.00	0.00	14	2.00	18.71	216.75
1/03/79	155.38	15.25	0.00	0.00	0.00	0.00	15	2.14	20.85	155.38
5/03/79	188.13	30.88	0.00	0.00	0.00	0.00	15	2.14	22.99	188.13
4/04/79	206.38	20.88	0.00	0.00	0.00	0.00	19	2.71	25.70	206.38
3/04/79	201.38	24.69	0.00	0.00	0.00	0.00	19	2.71	28.41	201.38
6/05/79	158.88	9.75	237.37	33.88	0.00	0.00	23	3.29	31.70	396.25
5/07/79	26.43	5.69	203.00	26.56	0.00	0.00	50	7.14	38.84	229.43
3/08/79	21.00	3.31	191.88	32.19	0.00	0.00	49	7.00	45.84	212.88
9/09/79	33.88	1.75	236.50	30.25	8.44	0.00	27	3.86	49.70	278.82
5/10/79	74.50	8.00	340.81	48.19	3.25	0.00	34	4.86	54.56	418.56
2/11/79	108.00	1.69	255.12	32.69	10.06	0.00	30	4.29	58.85	373.18
6/12/79	152.69	18.44	274.06	55.38	15.38	0.00	32	4.57	63.42	442.13
/02/80	156.69	15.38	303.38	25.63	0.00	15.50	39	5.57	68.99	460.07
/03/80	176.88	11.06	393.13	30.63	0.00	15.43	46	6.57	75.56	570.01
/04/80	120.63	9.34	380.81	48.95	0.00	16.13	35	5.00	80.56	501.44
/06/80	28.88	3.56	489.69	26.81	0.00	12.06	70	10.00	90.56	518.57

Summary statistics -live material

1st growing season (6/10/78-17/1/79)
$Sum(B_n-B_{n-1}) =$ 255.88g/m²
No.weeks = 14.71
Rate = 17.39g/m²/wk

1stgrowing season (23/8/79-18/3/80)
$Sum(B_n-B_{n-1}) =$ 193.01g/m²
No.weeks = 29.72
Rate = 6.49g/m²/wk

Mean rate of accumulation (A)=15.93 g/m²/wk

APPENDIX C

Parameters of curves in Fig. 7.3 a & b.

The equations are of the form:

$$y = \exp\,(P1 + P2x + P3x^2)$$

where: y = standing green biomass (g/m^2),

P1, P2 and P3 are the parameter coefficients

Fig. 7.3 a 1978-79 (first season - annual winter burn):

$$y = \exp\,(-\,4{,}57941 + 0{,}52712x - 0{,}00702x^2)$$

Fig. 7.3 a 1979-80 (second season - annual winter burn):

$$y = \exp\,(-\,3{,}32271 + 0{,}45516x - 0{,}00601x^2)$$

Fig. 7.3 b 1978-79 (first season - biennial spring burn):

$$y = \exp\,(2{,}77284 + 0{,}26207x - 0{,}00671x^2)$$

Fig. 7.3 b 1979-80 (second season - biennial spring burn):

$$y = \exp\,(-\,29{,}18000 + 0{,}76498x - 0{,}00425x^2)$$

APPENDIX D:TABLE 1
BIOMASS DATA :PLOT 12C BURNT AFTER 16 YEARS PROTECTION

DATE	MEAN LIVE MASS	STD. ERROR	MEAN DEAD MASS	STD. ERROR	MEAN LIVE MASS FLOWERS	MASS DEAD FLOWERS	TOTAL MASS
22/11/79	7.69	1.19	7.06	3.56	0.00	0.00	14.75
24/12/79	26.25	5.38	40.51	7.38	0.00	0.00	66.76
01/02/80	62.75	6.63	16.75	4.81	0.00	0.00	79.5
18/03/80	64.06	9.88	55.56	9.13	0.00	0.00	119.62
22/04/80	54.38	13.44	48.31	17.56	7.94	0.00	110.63
19/06/80	7.81	3.25	134.56	18.13	0.00	3.00	142.37

REFERENCES

Acocks, J.P.H., 1953. Veld types on South Africa. Bot. Surv. S. Afr. Mem. No. 28. Govt. Printer, Pretoria.

Aspinall, D. & Paleg, L.G., 1963. Effects of day length and light intensity on growth of barley. I. Growth and development of apex with a fluorescent light source. Bot. Gaz. 124: 429-437.

Bainbridge, W.R. & Scott, D.F., 1981. Policy memorandum for the Drakensberg State Forests. Departmental report, Dept. of Environment Affairs, Pietermaritzburg.

Bands, D.P., 1977. Prescribed burning in Cape fynbos. Proceedings of the symposium on environmental consequences of fire and fuel management in Mediterranean ecosystems. USDA Forest Service General Technical Report WO-3, 245-256.

Bayer, A.W., 1955. The ecology of grasslands. The grasses and pastures of South Africa. Ed. D. Meredith. Central News Agency, Johannesburg.

Becker, D.A. & Brockett, J.J., 1973. Evaluation of sampling techniques on tall-grass prairies. J. Range Mgmt., 26: 61-65.

Bosch, J.M., 1979. Treatment effects on annual and dry period streamflow at Cathedral Peak. S. Afr. For. J. 108: 29-38.

Booysen, P. De V., Tainton, N.M. & Scott, J.D., 1963. Shoot-apex development in grasses and its importance in grassland management. Herb. Abstr. 33(4): 209-213.

Bransby, D.I. & Tainton, N.M., 1977. The disc pasture meter: possible application in grazing management. Proc. Grassld. Soc. Sth. Afr. 12: 115-118.

Brown, D., 1954. Methods of surveying and measuring vegetation. Commonwealth Bureau of Pastures and Field Crops, Hurley, Berkshire, Bulletin 42.

Bryant, A.T., 1929. Olden times in Natal and Zululand. Longmans Green & Co., London.

Cable, J.H.C., Scott, K. & Carter, P.L., 1980. Excavations at Good Hope Shelter, Underberg District, Natal. Ann. Natal Mus. 24(1): 1-34.

Canfield, R.H., 1957. Reproduction and life span of some perennial grasses of Southern Arizona. J. Range Mgmt. 10: 199-203.

Cass, A., 1985. Personal communication. Armidale: Dept. of Agronomy and Soil Science, University of New England, Australia.

Clarke, G.P.Y., 1985. Personal communication. Pietermaritzburg: Dept. of Statistics and Biometry, University of Natal.

Clements, F.E., 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Coetzee, P.J.S., 1942. Fire and veld management. Veld burning as an agent in the "ngongoni" sourveld. Farming in S. Afr. 17: 107-116.

Colinvaux, P.A., 1973. Introduction to ecology. John Wiley & Sons, New York.

Cooper, J.P. & Tainton, N.M., 1968. Light and temperature requirements for the growth of tropical and temperate grasses. Herb. Abstr. 38(3): 167-176.

Coupland, R.T., 1979. Problems in studying grassland ecosystems. In: Grassland ecosystems of the world: analysis of grasslands and their uses. Ed. R.T. Coupland. Cambridge University Press, London.

Danckwerts, J.E., 1984. Towards improved livestock production off sweet grassveld. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Danckwerts, J.E., Aucamp, A.J. & Du Toit, L.P., 1984. Ontogeny of Themeda triandra in the False Thornveld of the Easter Cape. J. Grassl. Soc. Sth. Afr. 1: 9-14.

Daubenmire, R., 1968. Ecology of fire in grasslands. Adv. Ecol. Res. 5: 209-266.

Deevey, E.S., 1947. Life tables for natural populations of animals. Q. Rev. Biol. 22: 283-314.

Department of Agricultural Technical Services - Natal Region, 1976. Soil loss estimator for Southern Africa. Natal Agric. Res. Bull., No. 7. 64 pp and Appendices.

Deregibus, V.A., Sanchez, R.A., Casal, J.J. & Trlica, M.J., 1985. Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. J. Appl. Ecol. 22: 199-206.

Dillon, R.F., 1979. Research reports of the Department of Pasture Science, University of Natal.

Duffey, E., Morris, M.G., Sheail, J., Ward, L.K., Wells, D.A. & Wells, T.C.E., 1974. Grassland ecology and wildlife. Chapman & Hall Ltd., London.

Dyer, R.A., 1963. Preface to: An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Ed. D.J.B. Killick. Bot. Surv. S. Afr. Mem. No. 34. Govt. Printer, Pretoria.

Dyksterhuis, E.J., 1949. Condition and management of rangeland bases on quantitative ecology. J. Range Mgmt. 2: 104-114.

Edwards, P.J., 1961. Studies in veld burning and mowing in the Tall Grassveld of Natal. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Edwards, P.J., 1969. Veld burning in the Giant's Castle Game Reserve. Lammergeyer 10: 64-67.

Egler, F.E., 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4: 412-417.

Everson, C.S., 1979. Autecological studies on Philippia evansii N.E.Br. with particular reference to water relations. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Everson, C.S. & Tainton, N.M., 1984. The effect of thirty years of burning on the Highland Sourveld of Natal. J. Grassl. Soc. Sth. Afr. 1: 15-20.

Fletcher, G.M. & Dale, J.E., 1974. Growth of tiller buds in barley: effects of shade treatment and mineral nutrition. Ann. Bot. 38: 63-76.

Foran, D.B., Tainton, N.M. & Booysen, P. De V., 1978. The development of a method for assessing veld condition in three grassveld types in Natal. Proc. Grassld. Soc. Sth. Afr., 13: 27-33.

Friend, D.J.C., 1966. The effects of light and temperature on the growth of cereals. In: Growth of cereals and grasses. Eds. F.L. Milthorpe & J.D. Ivins. Butterworths, London, 181-199.

Garland, G.C., 1982. An appraisal of South African research into runoff erosion. S. Afr. Geog. J. 64(2): 138-143.

Garland, G.C., Chisolm, J.P. & Christian, C.R., 1977. Reconnaissance mapping for land-use planning in the Natal Drakensberg, South Africa. Environmental Conservation, 4(2): 103-108.

Gaskin, T.A., 1965. Light quality under Sarlon shade cloth. Agron. J. 57: 313-314.

Gaugh, H.G., 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.

Gower, J.C., 1971. A general coefficient of similarity. Biometrics 27: 857-874.

Gower, J.C., 1974. Maximal predictive classification. Biometrics 30: 643-654.

Granger, J.E., 1976. The plant succession and some associated factors in Catchment IX, Cathedral Peak Research Station. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Grieg-Smith, P., 1983. Quantitative plant ecology. 3rd Edition. Blackwell Scientific Publications, Oxford.

Grossman, D., 1982. Primary production of rangeland: Practical and interpretive problems. Proc. Grassld. Soc. Sth. Afr. 17: 76-78.

Harper, J.L., 1977. Population biology of plants. Academic Press, London.

Harper, J.L. & White, J., 1974. The demography of plants. A. Rev. Ecol. Syst. 5: 419-463.

Hunt, R., 1982. Plant growth curves. Edward Arnold, London.

Huntley, B.J., 1984. Characteristics of South African biomes. In: Ecological effects of fire in South African ecosystems. Eds. P. De V. Booysen & N.M. Tainton. Springer-Verlag, Berlin.

Hyder, D.N., Bement, R.E., Remmenga, E.E. & Terwilliger, C., 1966. Vegetation - soils and vegetation grazing relations from frequency data. J. Range Mgmt. 19: 11-17.

Jain, S., 1979. Adaptive strategies: polymorphism, plasticity and homeostasis. In: Topics in plant population biology. Eds. O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven. Macmillan Press Ltd., London.

Johnston, A., 1957. A comparison of the line interception, vertical point quadrat, and loop methods as used in measuring basal area of grassland vegetation. Can. J. Plant Sci. 37: 34-42.

Killick, D.J.B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Bot. Surv. S. Afr. Mem. No. 34. Govt. Printer, Pretoria.

Le Roux, H.H., 1966. Veldbestuur in die water-opvanggebied van die winterreenstreek van Suidwes-Kaapland. For. in S. Afr. 6: 1-32.

Leslie, P.H., 1945. On the use of matrices in certain population mathematics. Biometrika 33(3): 183-212.

Leslie, P.H., 1948. Some further notes on the use of matrices in population mathematics. Biometrika 34(3 & 4): 213-245.

Levy, E.B. & Madden, E.A., 1933. The point method of pasture analysis. N.Z. J. Agric. 46: 267-279.

Levyns, M.R., 1929. Veld burning experiments at Ida's Valley, Stellenbosch. Trans. Royal Soc. S. Afr. 17: 61-92.

Little, R.M. & Bainbridge, W.R., in press. Avifaunal conservation in the state forests of the Natal Drakensberg. Proceedings of the Sixth Pan-African Ornithological Congress, 1985, Francistown, Botswana.

Mack, R.N. & Pyke, D.A., 1983. The demography of Bromus tectorum: variation in time and space. J. Ecol. 71: 69-93.

Manry, D.E., 1983. Ecology of the Bald Ibis Geronticus calvus and fire in the South African Grassland Biome. M.Sc. Thesis, University of Cape Town.

McKell, C.M., Wilson, A.M. & Jones, M.B., 1961. A flotation method for easy separation of roots from soil samples. Agron. J. 53: 56-57.

Mentis, M.T., 1980. Towards objective veld condition assessment. Proc. Grassld. Soc. Sth. Afr. 18: 77-80.

Mentis, M.T., 1981. Evaluation of the wheel-point and step-point methods of veld condition assessment. Proc. Grassld. Soc. Sth. Afr. 16: 89-94.

Mentis, M.T., 1982. A simulation of the grazing of sour grassveld. Ph.D. Thesis, University of Natal, Pietermaritzburg.

Mentis, M.T., 1984. Monitoring in South African grasslands. South African National Scientific Programmes Report No. 91. 55 pp.

Mentis, M.T. & Bigalke, R.C., 1979. Some effects of fire on two grassland francolins in the Natal Drakensberg. S. Afr. J. Wildl. Res. 9: 1-8.

Mentis, M.T. & Collinson, R.F.H., 1979. Management goals for wildlife reserves in grassveld and bushveld. Proc. Grassld. Soc. Sth. Afr. 14: 71-74.

Mentis, M.T., Collinson, R.F.H. & Wright, M.G., 1980. The precision of assessing components of the condition of moist tall grassveld. Proc. Grassld. Soc. Sth. Afr. 15: 43-46.

Mentis, M.T. Meiklejohn, M.J. & Scotcher, J.S.B., 1974. Veld burning in Giant's Castle Game Reserve, Natal Drakensberg. Proc. Grassld. Soc. Sth. Afr. 9: 26-31.

Mor, Y., Halvey, A.G. & Porath, D., 1980. Characterization of the light reaction in promoting the mobilizing ability of the rose shoot tips. Plant Physiol. 66: 996-1000.

Mueller-Dombois, D. & Ellenberg, H., 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Musgrave, G.W., 1947. The quantitative evaluation of factors in water erosion, a first approximation. J. Soil and Water Conservation 2: 133-138.

Nanni, U.W., 1956. Forest hydrological research at Cathedral Peak Research Station. J. S. Afr. For. Assoc. 27: 2-35.

Nanni, U.W., 1960. The immediate effects of veld burning on streamflow in Cathedral Peak catchments. J. S. Afr. For. Assoc. 34: 7-12.

Nanni, U.W., 1969. Veld management in the Natal Drakensberg. J. S. Afr. For. Assoc. 28: 5-15.

Nanni, U.W., 1970. The effect of afforestation on streamflow at Cathedral Peak: Report No. 1. S. Afr. For. J. 74: 6-12.

Nanni, U.W., 1972. Water use by riparian vegetation at Cathedral Peak. S. Afr. For. J. 80: 1-10.

N.R.C., 1970. Nutrient requirements of domestic animals, No. 4. Nutrient requirements of beef cattle, National Research Council, Washington, D.C.

Parker, R.E., 1973. Introductory statistics for biology. Edward Arnold, London.

Parrot, R.T. & Donald, C.M., 1970. I. Effect of length of season and of defoliation on the growth, water content and desiccation of annual pastures. Aust. J. of Exp. Agr. Anim. Husb. 10: 67-75.

Phillips, J.F.V., 1965. Fire - as master and servant: its influence in the bioclimatic regions of trans-Saharan Africa. Proceedings of the Tall Timbers Fire Ecology Conference 11: 1-17.

Pianka, E.R., 1970. On r- and K- selection. Am. Nat. 104: 592-597.

Poissonet, P.S., Poissonet, J.A., Gordon, M.P. & Long, G.A., 1973. A comparison of sampling methods in dense herbaceous pasture. J. Range Mgmt. 26: 65-67.

Rayner, A.A., 1967. A first course in biometry for agriculture students. University of Natal Press, Pietermaritzburg.

Rethman, N.F.G., 1971. Elevation of shoot-apices of two ecotypes of Themeda triandra on the Transvaal Highland. Proc. Grassld. Soc. Sth. Afr. 6: 86-92.

Rowe-Rowe, D.T., 1982. Influence of fire on antelope distribution and abundance in the Natal Drakensberg. S. Afr. J. Wildl. Res. 12(4): 124-129.

Rowe-Rowe, D.T. & Lowry, P.B., 1982. Influence of fire on small-mammal populations in the Natal Drakensberg. S. Afr. J. Wildl. Res. 12(4): 130-139.

Rutherford, M.C., 1978. Changes in biomass of some perennial grass species. Proc. Grassld. Soc. Sth. Afr. 11: 43-46.

San Jose, J.J., Berrade, F. & Ramirez, J., 1982. Seasonal changes of growth, mortality and disappearance of belowground root biomass in the Trachypogon savanna grass. Oecol. Plant. 3(17): 347-358.

Sarukhan, J. & Harper, J.L., 1973. Studies on plant demography: Ranunculus repens L., R. bulbosus L. and R. acris. I. Population flux and survivorship. J. Ecol. 61: 675-716.

Schmutz, E.M., Reese, M.E., Freeman, B.N. & Weaver, L.C., 1982. Metric belt transect system for measuring cover, composition, and production of plants. Rangelands 4: 162-164.

Schulze, R.E., 1974. Catchment evapotranspiration in the Natal Drakensberg. Ph. D. Thesis, University of Natal, Pietermaritzburg.

Schulze, R.E., 1979. Soil loss in the key area of the Drakensberg. Ag. Eng. in South Africa. 13: 22-33.

Schulze, R.E., 1980. The distribution of kinetic energy of rainfall in South Africa - a first assessment. Water S.A. 6(2): 49-58.

Schulze, R.E., 1981. Estimation of storm runoff and sediment yield for selected small dam sites in Kwa Zulu. Agricultural catchments research unit report No. 12. University of Natal, Pietermaritzburg.

Scotcher, J.S.B., 1982. Interrelations of vegetation and eland (Taurotragus Oryx Pallus) in Giant's Castle Game Reserve, Natal. Ph.D. Thesis, University of the Witwatersrand, Johannesburg.

Scotcher, J.S.B. & Clarke, J.C., 1981. Effects of certain burning treatments on veld condition in Giant's Castle Game Reserve. Proc. Grassld. Soc. Sth. Afr. 16: 121-127.

Scott, J.D., 1951. Conservation of vegetation in South Africa. Management and conservation of vegetation in Africa, Commonwealth Bureau of Pastures and Field Crops Bull. 41: 9-27.

Scott, J.D., 1952. A contribution to the study of the problems of the Drakensberg Conservation Area. Sci. Bull. 324, Dept. of Agric., Union of S. Afr.

Scott, J.D., 1955. Principles in pasture management. The grasses and pastures of South Africa. Ed. D. Meredith. Central News Agency, Johannesburg.

Scott, J.D., 1970. Pros and cons of eliminating veld burning. Proc. Grassld. Soc. Sth. Afr. 5: 23-26.

Scott, J.D., 1971. Veld burning in Natal. Proceedings of the Tall Timbers Fire Ecology Conference 11: 35-51.

Scott, J.D., 1984. An historical review of research on fire in South Africa. In: Ecological effects of fire in South African ecosystems. Eds. P. de V. Booysen & N.M. Tainton. Springer-Verlag, Berlin.

Sharrow, S.H. & Wright, 1977. Effects of fire, ash and litter on soil nitrate, temperature, moisture and Tobosa grass production in the rolling plains. J. Range Mgmt. 30(4): 266-270.

Silvertown, J.W., 1982. Introduction to plant population ecology. Longmans Group Ltd., New York.

Singh, J.S., Lauenroth, W.K. & Steinhorst, R.K., 1975. Review and assessment of various techniques for estimating net aerial primary production in grassland from harvest data. Bot. Rev. 41: 181-232.

Snedecor, G. & Cochran, W., 1971. Statistical methods. Iowa State University Press, Ames, Iowa.

Soane, I.D. & Watkinson, A.R., 1979. Clonal variation in populations of Ranunculus repens. New Phytol. 82: 557-573.

Solbrig, O.T. & Solbrig, D.J., 1979. Introduction to population biology and evolution. Addison-Wesley, Reading, Massachusetts.

Tainton, N.M., 1964. Developmental morphology of the apical meristem of Themeda triandra Forsk. S. Afr. J. Afr. Sci. 7: 93-100.

Tainton, N.M., 1981. The ecology of the main grazing lands of South Africa. In: Veld and pasture management in South Africa. Ed. N.M. Tainton. Shuter & Shooter, Pietermaritzburg.

Tainton, N.M. & Booysen, P. De V., 1963. The effects of management on apical bud development and seeding in Themeda triandra and Tristachya hispida. S. Afr. J. Agric. Sci. 6: 21-30.

Tainton, N.M. & Booysen, P. De V., 1965. Growth and development in perennial veld grasses. 1. Themeda triandra tillers under various systems of defoliation. S. Afr. J. Agric. Sci. 8: 93-110.

Tainton, N.M., Edwards, P.J. & Mentis, M.T., 1980. A revised method for assessing veld conditions. Proc. Grassld. Soc. Sth. Afr. 15: 37-42.

Tainton, N.M., Groves, R.H. & Nash, R., 1977. Time of mowing and burning veld: short term effects on production and tiller development. Proc. Grassld. Soc. Sth. Afr. 12: 59-64.

Tainton, N.M. & Mentis, M.T., 1984. Fire in grassland. In: Ecological effects of fire in South African ecosystems. Eds. P. De V. Booysen & N.M. Tainton. Springer-Verlag, Berlin.

Tiedman, J.A. & Weiland, R.G., 1983. The use of microplots to sample grassveld in Lesotho. Proc. Grassld. Soc. Sth. Afr. 18: 143-146.

't Mannetje, L. & Haydock, K.P., 1963. The dry-weight-rank method for the botanical analysis of pasture. J. Br. Grassl. Soc. 18: 268-275.

Tidmarsh, C.E.M. & Havenga, C.M., 1954. The wheel point method of survey and measurement of semi-open grasslands and Karoo vegetation in South Africa. Bot. Surv. S. Afr. Mem., No. 29. Govt. Printer, Pretoria.

Tothill, J.C., 1978. Measuring botanical composition. In: Measurement of grassland vegetation and animal production. Ed. E.L. 't Mannetje. Commonwealth Agricultural Bureaux Farnham Royal, Bucks, England, 22-63.

Tyson, P.D., Preston-Whyte, R.A. & Schulze, R.E., 1976. The climate of the Drakensberg. Natal Town and Regional Planning Reports. Vol. 31. 82 pp.

Van Wyk, D.B., 1985. The influence of catchment management on erosion and subsequent sediment and nutrient loads in South African mountain streams. Unpublished report. Department of Environment Affairs, Jonkershoek.

Walker, B.H., 1970. An evaluation of eight methods of botanical analysis on grasslands in Rhodesia. Jnl. Appl. Ecol. 7: 403-416.

Walter, H., 1971. Ecology of tropical and subtropical vegetation. Van Rostrand, New York. 539 pp. x581.52 623

Watson, H.K., 1981. Firebreak treatment and sediment yield from small catchments at Cathedral Peak. M.Sc. Thesis, University of Natal, Pietermaritzburg.

Weinmann, H., 1955. The chemistry and physiology of grasses. In: The grasses and pastures of South Africa. Ed. D. Meredith. Central News Agency, Johannesburg.

West, O., 1951. The vegetation of Weenen County, Natal. Bot. Surv. S. Afr. Mem. No. 23. Govt. Printer, Pretoria.

Westfall, R.H., Everson, C.S. & Everson, T.M., 1983. The vegetation of the protected plots at Thabamhlope Research Station. S. Afr. J. Bot. 2(1): 15-25.

Westoby, M., 1980. Relations between genet and tiller population dynamics: survival of *Phalaris tubersosa* tillers after clipping. J. Ecol. 68: 863-869.

Wicht, C.L., 1959. The management of water catchments. Afr. Soils. 4(3): 20-51.

Williams, J.R. & Berndt, H.D., 1977. Sediment yield prediction based on watershed hydrology. Trans. ASAE. 20: 1100-1104.

Williamson, P., 1976. Above-ground primary production of chalk grassland allowing for leaf death. J. Ecol. 64: 1059-1075.

Wischmeir, W.J., 1975. Estimating the soil loss equation's cover and management factor for undisturbed areas. In: Present and prospective technology for predicting sediment yield and sourees: Proceedings of the sediment-yield workshop, USDA Sedimentation Lab., Oxford, MS, November 28-30, 1972. ARS-S-40.

Wischmeir, W.H. & Smith, D.D., 1965. Predicting rainfall erosion losses from cropland east of the Rocky Mountains. Agricultural Handbook 282. USDA-ARS.

Wischmeir, W.H. & Smith, D.D., 1978. Predicting rainfall erosion losses - a guide to conservation planning. Agricultural Handbook 537. USDA-ARS.