

WATER USE OF PERENNIAL SUMMER GRASSES IN SOUTH AFRICA

by

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WATER USE OF PERENNIAL SUMMER GRASSES IN SOUTH AFRICA

by

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DEPARTMENT: Plant Production and Soil Science

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ABSTRACT

Five subtropical perennial grass species, *Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*, were subjected to four levels of water availability in a small plot trial under a rainshelter during the summer growing seasons of 1996/97 and 1997/98. This work was carried out on the Hatfield Experimental Farm of the University of Pretoria, Pretoria, South Africa.

The average yields for the tufted species (*C. ciliaris*, *D. eriantha* and *P. maximum*) were lower in the 1997/98 than the 1996/97 season. *C. ciliaris*, however, produced the highest average yields in both seasons. The average yields of the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) reacted differently, in that the average yields were higher in the 1997/98 than 1996/97 season.

The dry matter yields of all five grass species at slight water deficits, were not significantly different from yields under conditions of no water shortages, when the soil profile was brought to field capacity at the beginning of the growing season. The implication hereof is, that dry matter yields can be maintained, in conditions where slight water deficits occur, if there is some water stored in the soil profile.

C. ciliaris, a notable drought tolerant species, produced yields (11.7-20.0 t ha⁻¹) under non-control conditions (W1, W2 and W3) which were comparable to yields obtained from traditionally irrigated grasses such as the *Cynodon* hybrid (12.0-15.8 t ha⁻¹) and *P. clandestinum* (5.6-11.8 t ha⁻¹), under control conditions (W4). *P. clandestinum*, *D. eriantha* and *P. maximum* tended to be better adapted to wetter conditions, while the *Cynodon* hybrid was also able to produce good yields under both water limiting and non-limiting conditions.

Water use efficiency, regardless of the grass species, tended to be better under non-control conditions. Grasses were thus able to produce more dry matter per unit of water under conditions where water became scarce.

In vitro dry matter digestibility was not negatively affected by water scarcity, while crude protein content more often than not seemed to be better under control conditions. This could be due to the uptake mechanism of nutrients, in which water plays a vital role.

The number of stoma per unit area was more under control than water limiting conditions. The expression of the different structures on the leaf surfaces, were not

altered by the level of water availability.

In the absence of water shortages, the growth rates of *C. ciliaris*, *D. eriantha* and *P. maximum*, were almost twice those of the *Cynodon* hybrid and *P. clandestinum*, as measured at the end of two growth cycles in an irrigated field trial.

In a pot trial, under glasshouse conditions, with *C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum*, both the level of water availability, and the level of nitrogen were varied. Regardless of species and level of nitrogen, water was still used more efficiently under non-control conditions. Higher levels of nitrogen did, however, improve water use efficiency regardless of level of water available. As with higher levels of available water, higher levels of nitrogen also improved yields. In this trial, the *Cynodon* hybrid and *C. ciliaris* also out-yielded *P. clandestinum*.

In summary it can be said that *C. ciliaris* and the *Cynodon* hybrid are adapted to warm growing conditions in producing high yields regardless of the level of water available. *D. eriantha*, *P. maximum* and *P. clandestinum* would produce better in such growing conditions if water was not as limiting. Regardless of the species, the plants were able to use water more efficiently under non-control conditions, while *in vitro* digestibility was not negatively affected by water limiting conditions. Due to the uptake mechanism of nutrients, water limiting conditions may, however, decrease the crude protein content of the grass plants. Higher levels of nitrogen had a positive impact on dry matter yields and water use efficiency.

WATER GEBRUIK VAN MEERJARIGE SOMER-GRASSE IN SUID-AFRIKA

deur

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GRAAD: PhD - Weidingkunde

UITTREKSEL

Vyf subtropiese meerjarige grasspesies, *Cenchrus ciliaris*, 'n *Cynodon baster*, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* en *Pennisetum clandestinum*, is aan vier vlakke van waterbeskikbaarheid, in 'n klein perseel proef, onder 'n reënskerm, gedurende die 1996/97 en 1997/98 somer groeiseisoene blootgestel. Hierdie werk is uitgevoer op die Hatfield Proefplaas van die Universiteit van Pretoria, Pretoria, Suid-Afrika.

The gemiddelde opbrengste van die polgrasse (*C. ciliaris*, *D. eriantha* en *P. maximum*) was laer in die 1997/98 as in 1996/97 seisoen. *C. ciliaris* het egter die hoogste gemiddelde opbrengs in beide seisoene gelever. Die gemiddelde opbrengste van die *Cynodon baster* en *P. clandestinum* (kruipende-grasse) het die teenoorgestelde gereageer, met hoër opbrengste in die 1997/98 as in die 1996/97 seisoen.

Daar was geen betekenisvolle verskille tussen die droëmateriaal opbrengste van enige van die vyf grasspesies by geringe watertekorttoestande, in vergelyking met die geen watertekorte nie. Dit het geskied indien die grondprofiel aan die begin van die seisoen by veldkapasiteit was. Dit impliseer dat droëmateriaal opbrengste onderhou kan word in tye van geringe droogte, mits daar water in die grondprofiel gestoor is.

C. ciliaris, 'n bekende droogteverdraagsame spesie, het opbrengste ($11.7-20.0 \text{ t ha}^{-1}$) onder nie-kontrole toestande (W1, W2 en W3) geproduseer, wat vergelykbaar is met opbrengste wat onder kontrole water toestande (W4) vir tradisioneel besproeide grasses soos die *Cynodon baster* ($12.0-15.8 \text{ t ha}^{-1}$) en *P. clandestinum* ($5.6-11.8 \text{ t ha}^{-1}$) verkry is. *P. clandestinum*, *D. eriantha* en *P. maximum* was geneig om beter aangepas te wees by natter toestande, terwyl die *Cynodon baster* instaat was om goeie opbrengste onder beide waterbeperkende en nie-waterbeperkende toestande te produseer.

Waterverbruiksdoeeltreffendheid, ongeag die spesie, het geneig om beter by nie-kontrole toestande te wees. Die grasse was dus instaat om meer droëmateriaal te produseer per eenheid water verbruik, by toestande waar water beperk geraak het.

In vitro droëmateriaal verteerbaarheid was nie negatief deur watertekorte beïnvloed nie, terwyl ruproteïen inhoud meer dikwels, beter was by kontrole toestande. Dit kan toegeskryf word aan die opname meganisme van voedingstowwe waarby water 'n kern rol speel.

Die aantal stomas per eenheid oppervlakte was meer onder kontrole as by waterbeperkende toestande. Die voorkoms van die verskillende strukture op die blaaroppervlaktes, was nie deur die beskikbaarheid van water beïnvloed nie.

In die afwesigheid van watertekorte, was die groei van *C. ciliaris*, *D. eriantha* en *P. maximum*, bykans dubbel dié van die *Cynodon* baster en *P. clandestinum*, soos gemeet aan die einde van twee groeisiklusse.

In 'n potproef, onder glashuistoestande, met *C. ciliaris*, die *Cynodon* baster en *P. clandestinum*, is beide die vlak van waterbesikbaarheid en stikstof gevarieer. Onafhanklik van die spesie, en vlak van stikstof, is water meer doeltreffend verbruik onder nie-kontrole toestande. Hoër vlakke van stikstof het die waterverbruikdoeltreffendheid verbeter, onafhanklik van die vlak van waterbesikbaarheid. Soos met die toediening van meer water, het die toediening van meer stikstof ook tot 'n verhoging in droëmateriaalopbrengste aanleiding gegee. In hierdie proef het *C. ciliaris* en die *Cynodon* baster weer beter opbrengste as *P. clandestinum* gelewer.

Ter opsomming kan die gevolgtrekking gemaak word dat *C. ciliaris* en die *Cynodon* baster beter aangepas is by warm groeitoestande deur hoë opbrengste te lewer, onafhanklik van die vlak van water beskikbaar. *D. eriantha*, *P. maximum* en *P. clandestinum* kan ook goeie opbrengste lewer onder sulke wye water reeks groeitoestande, mits waterbesikbaarheid nie beperkend is nie. Onafhanklik van die grasspesie, het die plante water meer doeltreffend verbruik by nie-kontrole toestande, terwyl *in vitro* verteerbaarheid nie benadeel is deur watertekorte nie. As

gevolg van die opname meganisme van voedingstowwe, kan waterbeperkende toestande die ru-proteïen inhoud van grasplante wel benadeel. Hoër vlakke van stikstof het 'n positiewe invloed op beide droëmateriaal opbrengste en waterverbruiksdooeltreffendheid getoon.

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the above and below ground growth of *P. clandestinum*. 188

CHAPTER 1

GENERAL INTRODUCTION

In the mid 1980's the withdrawal of marginal arable land from maize production and the establishment of pastures instead was encouraged (Joubert, 1995). An estimated 1 million ha would in this way be planted to pastures, not only relieving pressure on the soil but also on the natural veld. To further encourage the switch to pasture crops, it was deemed necessary to investigate pasture crops in terms of their ability to produce under different growing conditions and also how these growing conditions can alter the quality of the pastures. With this information farmers will have a better idea what to expect from some grass species under conditions with and without adequate levels of water available.

Ensuring enough fodder for the animals is quite difficult under dryland conditions, due to rainfall uncertainty. However, some grasses can produce more mass per area with the same amount of water under the same growing conditions than others. However, research done in the past, in South Africa, involving water and grasses was restricted to only a few grass species, most of which were temperate. Lucerne (*Medicago sativa*), rye grass (*Lolium multiflorum*), kikuyu (*Pennisetum clandestinum*), weeping love grass (*Eragrostis curvula*) and oats (*Avena* sp.) received a lot of attention due to their popularity as planted pastures (Goodenough *et al.*, 1984; Steynberg *et al.*, 1993). Often the research was done with only one water regime to eliminate the influence of drought on the growth and production of the

grasses (Smith *et al.*, 1986; Van Heerden, 1986; Pieterse *et al.*, 1988; Le Roux *et al.*, 1991). In other studies the water use and water use efficiency of natural rain fed veld was determined with the aim to improve veld management (Opperman & Roberts, 1975; Opperman *et al.*, 1977; Snyman *et al.*, 1980; Moore *et al.*, 1988). The studies done by Mottram *et al.* (1977); Beukes & Weber (1981); Beukes & Barnard (1985) and Van Heerden & Tainton (1988) were aimed at irrigation scheduling. However, the only subtropical species which was included was kikuyu. In case studies involving irrigation and subtropical grasses, the effect of nitrogen on the yield and water use efficiency were investigated to advise farmers on the amounts of N that should be used (Rethman, 1987; Pieterse *et al.*, 1997; Pieterse & Rethman, 1999). Intensive studies on the effect of different levels of water availability on the growth, yield, water use, water use efficiency and quality of perennial subtropical grasses had not yet been done. It is these factors which will be addressed, with the specific aim to evaluate the grass species's ability to adapt to different levels of water availability.

The initial study was conducted over two summer growing seasons, using five perennial subtropical grass species, and four levels of water availability with the following aims:

- to determine the dry matter yield, water use efficiency and quality of the grass species when applying different amounts of water;

Further studies,

- to evaluate the effect of nitrogen on water use efficiency;
- to evaluate the growth pattern of the five grass species and

- to assess the affect of water availability on the grass' leaf morphology and number of stomata, were conducted in subsequent seasons.

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CHAPTER 2

WATER USE OF FIVE PERENNIAL SUB-TROPICAL GRASSES AT FOUR LEVELS OF WATER AVAILABILITY

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Abstract

The effect of four levels of water availability on the water use of five subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*) was evaluated in a small plot trial under a rain shelter at the University of Pretoria. The four treatments were: soil profile brought to 25 (W1), 50 (W2), 75 (W3) and 100% (W4 - the control) of field capacity on a weekly basis.

More water was used in the 1997/98 season in comparison with the 1996/97 season. This can be attributed to higher maximum temperatures during the 1997/98 season. Under the prevailing conditions, the *Cynodon* hybrid (1 000 mm) used the least amount of water followed by *C. ciliaris*, *P. clandestinum* and *D. eriantha* (1 100 mm), with *P. maximum* (1 200 mm) using the most water per season at the highest level of

water availability (W4). The results indicate that *P. maximum* tended to have a far greater luxury uptake of water than the other species, but especially the *Cynodon* hybrid, under conditions of unlimited water supply.

The W1, W2 and W3 treatments used more than the allocated water due to the fact that the soil profiles were brought to field capacity at the beginning of the season and the grass plants could then extract the extra water needed from the soil profile. This emphasizes the importance of good water management in drought prone areas. Water infiltration into the soil profile should be encouraged, while excessive runoff should be prevented.

Most of the roots (between 44% and 55% on a mass basis) were found in the top 42 cm of the soil profile, indicating the importance of keeping the top soil moist so as not to lose these roots. Despite the high proportion of roots in the top soil, significant amounts of root (14 - 20% on a mass basis) were found up to a depth of 1.05 m in the soil profile. Deeper soil samples could, however, not be taken due to the gravel layer starting at a depth of between 1.0 and 1.2 m in the soil profile. The soil profiles under *C. ciliaris*, the *Cynodon* hybrid and *P. maximum*, had a water deficit of between 10 and 20 mm at severe water limiting conditions at a depth of 1.6 to 1.8 m, while at the same depth *D. eriantha* and *P. clandestinum* only had a soil water deficit of between 10 and 15 mm. Despite the lack of physical evidence, the above water deficit measurements indicate that roots as deep as 1.8 m could be expected.

There were also minimal differences in the dry root mass under water limiting versus non-water limiting conditions. This is in contradiction to references in the literature, where root mass at deeper levels tended to be higher or lower, but never equal, under water limiting than non-water limiting conditions. During the first season (1995/96) the grasses were not differentially irrigated to encourage establishment. This might explain why there were little differences in the extraction depth, amounts and dry root mass. An important implication of this is that a new pasture, which is pampered in the first growing season, might be able to handle, or be better adapted to, stress conditions in the second and following seasons, than a planting which was stressed from the start.

Water use often impacts on the yield and quality of crops. Subsequent papers will, therefore, address the effect of this water use data on these aspects.

Keywords

Cenchrus ciliaris, a *Cynodon* hybrid, *Digitaria eriantha*, *Panicum maximum*, *Pennisetum clandestinum*, root mass, leaf area

2.1 Introduction

In South Africa, about 85% of the country is covered by natural veld. Of this about 65% receives less than 500 mm of rain per annum (Opperman & Roberts, 1975). A further 200 000 ha are planted to irrigated pastures (Steynberg *et al.*, 1993), but with initiatives to remove pressure from veld and marginal cropping areas (Joubert, 1995), more and more planted pastures are being established under both rainfed

and irrigated conditions. Information on the water use, yields and water use efficiency of grasses as influenced by different levels of water availability is, however, scarce.

Gathering information on the afore said situation can be approached from two angles. The one being water, and how it can be managed, and the other the grass itself and the water requirements thereof. The main aim of this study was not so much to schedule irrigation, as to evaluate grass species at different levels of water availability.

There are many environmental factors (especially climatic factors) that can affect the year to year variation of water use (Kramer, 1983). A comparison of species, receiving the same treatment, can, however, give an indication of their relative water use. However, the comparison of other research results of the same species, under different conditions, is not easy and misinterpretations can be made.

As a starting point for this study, the water use of five grasses was evaluated at four levels of water availability. The hypotheses being (1) that there will be differences in water use between species and (2) that species are more adaptable to different levels of water availability than is generally accepted.

2.2 Materials and Methods

Five subtropical perennial grasses were established under an automatic rain shelter on the Hatfield Experimental Farm, of the University of Pretoria in Pretoria, (25°45'S,

28°16'E), South Africa, during December 1995. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. Coastcross II (K11) (Coastcross bermudagrass), *Digitaria eriantha* subsp. *eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass).

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991) with 30% clay in the top soil (top 30 cm). The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon, which contains coarse gravel. The experimental plots were 2.5 x 2.0 m in size and separated by asbestos plates to a depth of 1.2 m.

During June 1995, seeds of *C. ciliaris*, *P. maximum*, *D. eriantha* and *P. clandestinum* were sown in seedling trays and kept in a greenhouse until December 1995. *C. ciliaris*, *P. maximum* and *D. eriantha*, which are tufted or bunch grasses, were established at a rate of 300 000 plants ha⁻¹, while the creeping grasses (the *Cynodon* hybrid & *P. clandestinum*) were established at 160 000 plants ha⁻¹. The *Cynodon* hybrid was established using vegetative material collected on the experimental farm. The initial germination rate of *D. eriantha* was less than adequate and additional seedlings had to be propagated. This delayed transplanting of this species from trays to the field site by ten weeks compared to the other species.

A neutron probe access tube was located in the centre of each plot. Neutron probe counts, using a Campbell neutron probe (503 DR), were taken at nine depths

increments, each of 200 mm, on a weekly basis for all plots. These counts, which are related to the volumetric water content, were then incorporated into a calibration equation to determine the water deficit for each layer. Just before the onset of each growing season, the soil profiles of all the plots were brought to field capacity. Only then were the plants subjected to four levels of water availability

The water availability levels used were:

- W1 - apply 25% of the amount given to W4.
- W2 - apply 50% of the amount given to W4
- W3 - apply 75% of the amount given to W4
- W4 - control, the soil profiles were brought to field capacity on a weekly basis

Water was applied by means of flood irrigation and the amounts of water applied were monitored using water flow meters.

During the establishment season (1995/96), the grasses were not subjected to differential irrigation treatments to ensure a good establishment as it has been found that some of these grasses only start to produce optimally during the second or third year. To ensure a fair comparison of the species, treatments were thus only imposed in the second (1996/97) and third seasons (1997/98).

According to soil analyses, the pH(H₂O) of the experimental soil was neutral. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top soil (30 mg kg⁻¹ P; 108 mg kg⁻¹ K) was much higher than that of the subsoil (8 mg kg⁻¹ P; 67 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and

potassium status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary.

As the plots were not grazed, but removed as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (1995/96 season), the plots received 75 kg N ha⁻¹, 40 kg P ha⁻¹ and 200 kg K ha⁻¹. Nitrogen and potassium were also applied to all plots as top dressings during the summer growing season, resulting in a total of 450 kg N ha⁻¹ a⁻¹, 40 kg P ha⁻¹ a⁻¹ and 400 kg K ha⁻¹ a⁻¹. In the subsequent seasons (1996/97 and 1997/98), nitrogen and potassium were applied to all plots as top dressings at rates of 225, 338, 394 and 450 kg N ha⁻¹ a⁻¹ and 200, 300, 350 and 400 kg K ha⁻¹ a⁻¹ for the W1, W2, W3 and W4 water availability levels respectively. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

The grasses were harvested at the 10% flowering stage, except for *P. clandestinum*, which was not allowed to grow taller than 40 cm. This resulted in an average of three to four cuts during each season. *C. ciliaris*, *D. eriantha* and *P. maximum* (tufted grasses) were cut to a height of 10 cm while the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) were cut to 5 cm. A sample plot of one square metre, in the middle of each plot, was harvested, after which the rest of the plot was also cut to the same height. The sample plots were permanently marked to ensure that the samples were taken from the same area at each harvest. The material was dried to constant mass for 48 hours at 65°C.

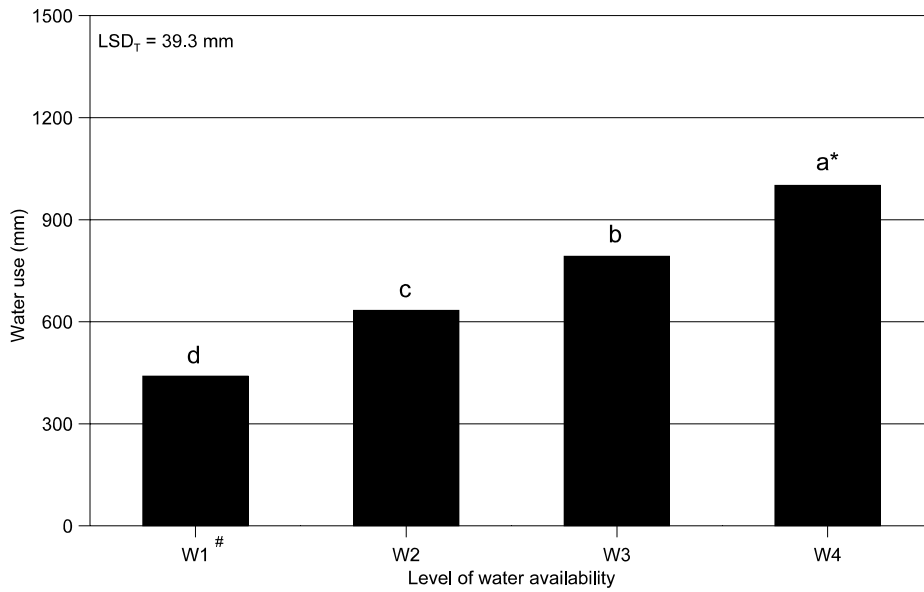
Root samples were collected in the summer of 1999. The soil cores were taken with a soil auger to a depth of 105 cm in 21 cm increments. The whole 1.8 meter soil profile was not investigated due to the presence of gravel from the 105 - 126 cm increment downwards. The gravel tended to either break the auger or was so coarse that a representative sample from these deeper layers was not achieved. After collecting the cores in the field, the soil was carefully washed away under running water. The roots were then left to dry at room temperature for seven days, before weighing it again.

A fully randomized block design with three replications was used. The statistical analysis was done using the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data are presented in the Appendix (Tables A 2.1 - A 2.10).

2.3 Results

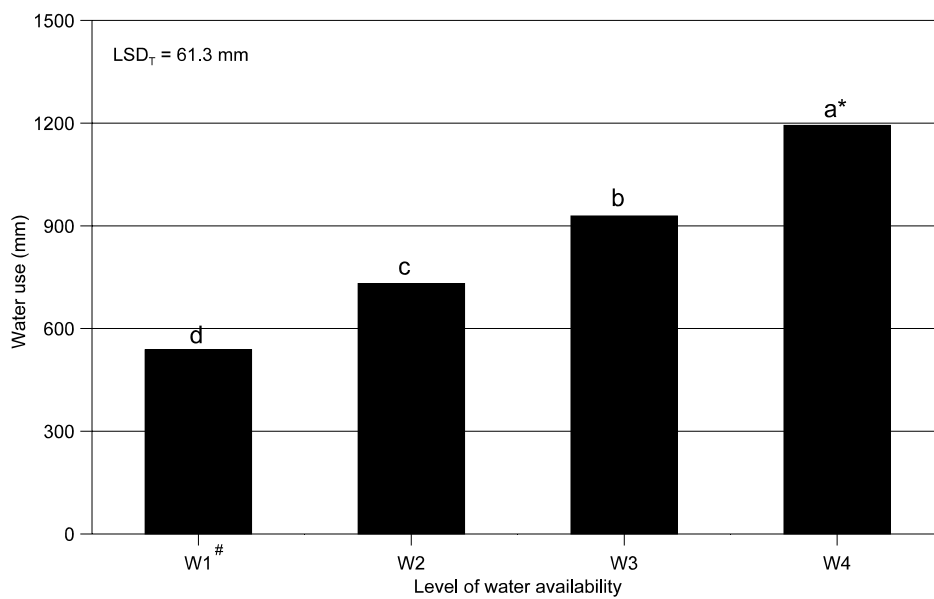
2.3.1 Water use

As stated earlier, the soil profiles were brought to field capacity at the beginning of the growing season. The deficit was measured weekly and water was applied according to the treatment. After the final harvest of the season, the soil water deficit was again measured. The water use was then calculated as the sum total of the amounts of water applied during the growing season and the soil water deficit at the end of the season. With the amounts used in this trial, four distinct treatments were established which differed significantly from each other (Figures 2.1 and 2.2).



* Treatments with the same letter do not differ significantly from each other ($P < 0.05$)
W1 - severely water stressed level, W4 - control

Figure 2.1 Average water use of grass species at four levels of water availability in the 1996/97 season.



* Treatments with the same letter do not differ significantly from each other ($P < 0.05$)
W1 - severely water stressed level, W4 - control

Figure 2.2 Average water use of grass species at four levels of water availability in the 1997/98 season.

The water use of the 1997/98 season was higher than in the previous season. The average minimum and maximum temperatures per month as registered for the period 1996 to 1998 are presented in Table 2.1. According to these data, the temperatures from August to February differed with a maximum of 2°C between the two seasons. During March and April 1998 the maximum temperatures were about 5°C higher than in 1997 over the same time period. With these higher temperatures, transpiration can be expected to be higher resulting in higher water use.

Apart from the obvious, it should be noted that although there was a 25% difference in amount of water applied between sequential treatments, this is not reflected in the water use (Table 2.2). This can be attributed to the uptake of stored water from the soil profile. This has important practical implications. Bringing the soil profile to field capacity at the beginning of the season can help the grasses to survive drought conditions. The severity of the drought that could be tolerated would depend on the water holding capacity of the soil (clay versus sand), the length and intensity of the drought, prevailing temperatures, the growth stage of the plants and the plants inherent ability to tolerate drought.

Table 2.1 Minimum and maximum temperatures recorded at the Hatfield Experimental Farm, Pretoria, during the trial period.

Month	Minimum temperature (°C)			Maximum temperature (°C)		
	1996	1997	1998	1996	1997	1998
January	16.5	17.0	16.7	27.1	27.1	27.4
February	15.2	15.0	15.1	23.4	26.1	25.8
March	13.4	15.2	16.1	25.2	23.5	28.3
April	10.4	9.7	12.1	21.6	21.2	26.0
May	8.3	6.6	5.8	20.5	19.2	21.6
June	4.5	3.4	2.6	18.5	18.2	15.9
July	3.4	4.8	5.1	17.2	18.7	20.1
August	6.7	7.4	6.6	20.3	22.7	21.9
September	10.1	11.5	10.9	24.8	23.2	24.5
October	14.3	12.7	11.0	27.5	25.4	19.8
November	14.3	14.0	13.4	25.0	26.1	24.6
December	15.8	16.0	15.4	26.7	27.8	25.5

Another interesting observation was made when determining the percentage water use of the W1, W2 and W3 treatments relative to that of the control. Despite higher water use in the 1997/98 than the 1996/97 season, there was only a one percent difference between the two seasons (Table 2.2 - values in brackets). From this two conclusions may be drawn: (1) it is not necessary to irrigate to field capacity when starting the season with a full profile; (2) when extrapolating from the values in Table 2.2, it seems as if the application of \pm 80-85% of the amount necessary to reach field capacity may make it unnecessary for the plants to also use some of the water stored in the soil profile. It is not, however, as simple as that, as temperatures and

other factors may also play a role.

Table 2.2 The percentage water use of the three treatments (W1, W2, W3) relative to that of the control (W4), over two seasons.

Season	Treatments			
	W1 = 25%	W2 = 50%	W3 = 75%	W4 = 100%
1996/97	44% (19%)*	63% (13%)	79% (4%)	100%
1997/98	45% (20%)	62% (12%)	78% (3%)	100%

*The values in brackets are the percentage deviation from the percentage applied.

Murtagh (1975) had already reported that *P. clandestinum* can grow well without bringing the soil profile back to field capacity, but that as soon as 50% or more of the plant available water has been depleted, one could expect *P. clandestinum* to perform poorly. When turfgrass growers in California were faced with water restrictions, they were forced to use less water, but together with Meyer and Gibeault (1986) they realized that a good turf quality could be maintained, even when less water was applied. Thus grasses can withstand a measure of drought, depending on the severity of the drought and grass species.

Garrot and Mancino (1994) found that with unrestricted water availability, grass plants tended to have a luxury uptake of water, but by making use of a “room for rain” strategy, it can improve water use, but then management is very important to keep the grasses in good production. Management in this case can include an appropriate cutting or grazing strategy. Julander (1945) observed a 60% die back in fields that were overgrazed during a drought, in comparison to the 20% die back in

ungrazed fields. The pastures that were not overgrazed during the drought also reacted faster, on drought relief, than the over-utilized counterparts. Masters and Britton (1990) confirmed this by saying that by applying the right clipping intensity and frequency, for a specific species and environmental conditions, the productivity of the grass can be improved or kept at desired production levels.

The observation made by the above scientists can be explained by the summary given by Nel and Annandale (1987), who stated that plants can easily extract water from the soil profile till a certain level (which differ from crop to crop and area to area), where-after extraction becomes more and more difficult, leading to yield losses due to the link between stomata closure, transpiration and photosynthesis (dry matter accumulation). Furthermore, plants will already have started to lose production long before it is visually noticeable. Thus, appropriate instruments/methods should be used to measure what the plant is experiencing.

Although this study is on fodder crops, where the yield is of great importance, visual acceptance has a higher value for turfgrass growers. However, to have as broad an application as possible for the results generated here, it should be kept in mind that different users (sheep, cattle, wildlife, turfgrass etc.) will have different needs. These needs will also determine how much water will be used, thereby adding an additional dimension to the severity of the drought that can be tolerated.

Thus far, the average water use over the two seasons has been discussed, but no attention has been given to as how the different levels of water availability affected

the individual grass species. In Figures 2.3 and 2.4 the amount of water used by the five species at four levels of water availability is illustrated.

Although the water use was higher in the 1997/98 than in the 1996/97 season, the amount by which it increased differed for the five grass species. Under the specific conditions of this trial, *C. ciliaris* used 2 mm and the *Cynodon* hybrid about 20 mm more water during the respective seasons under W4 conditions, while *P. clandestinum* used about 60 mm more. *D. eriantha* used about 340 mm and *P. maximum* 560 mm more water during the 1997/98 season. The average water use under W4 conditions, over two seasons, for *C. ciliaris* was 1 100 mm, that of the *Cynodon* hybrid 970 mm, *D. eriantha* 1 100 mm, *P. maximum* 1 200 mm and that of *P. clandestinum* 1 100 mm.

For the conditions applied in this trial, the *Cynodon* hybrid used the least amount of water followed by *C. ciliaris*, *P. clandestinum* and *D. eriantha*, with *P. maximum* using the most water per season under well watered conditions (W4 conditions). From well watered data alone one can, however, not say that the *Cynodon* hybrid is the most drought tolerant and *P. maximum* the least. It can at best provide information about the tendency of luxury uptake of water of different species with unlimited water.

The amounts of water applied to the W1, W2 and W3 treatments were derived from the amount applied to W4. Any increase in water use by the W4 treatment should, therefore, be automatically reflected by an increase in water use by the other three

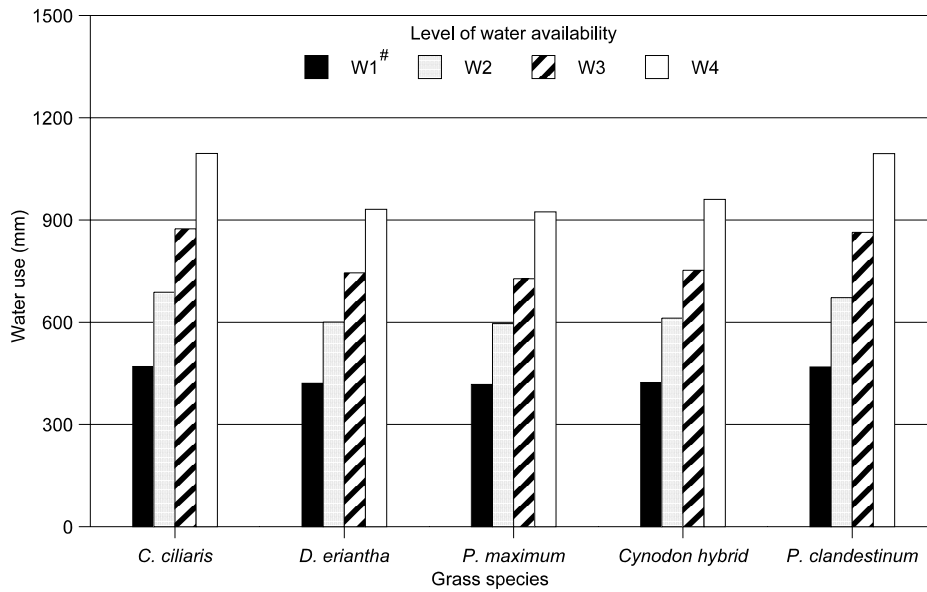
treatments. An examination of the data (Figures 2.3 and 2.4), however, showed that although this was true for most grass species and water treatment combinations, W3 *C. ciliaris* and W2 *P. clandestinum* used less water in the 1997/98 than 1996/97 seasons. These two water treatments used 17 and 29 mm less water respectively in the 1997/98 than in the 1996/97 season. The leaf area data (Figures 2.5 and 2.6) generally reflects higher leaf areas on those treatments using more water, and thus higher transpiration rates, in the 1997/98 than in the 1996/97 season. The lower water use of W3 *C. ciliaris* in 1997/98 could be explained by the smaller leaf area in 1997/98 (1.02 m²) in comparison to that of 1996/97 (1.13 m²). The same can, however, not be said about W2 *P. clandestinum* which had a far greater leaf area in 1997/98 (1.20 m²) than in 1996/97 (0.44 m²).

Although *P. maximum*, on average, tended to use far more water than *P. clandestinum* in the 1997/98 season, this was not reflected in the leaf area of the two species. *P. clandestinum* had a far greater leaf area, but used less water than *P. maximum* which had a lower leaf area. This may be explained by the growth habit of the two species, with *P. clandestinum* having a dense mat, covering the whole 5 m² of the experimental plot, and *P. maximum* plants forming individual tufts with open spaces visible between the tufts. This could have caused the *P. maximum* plots to lose more water through evaporation, especially with the slightly higher temperatures experienced in the 1997/98 season. With a poorer ground cover, raised soil temperatures might also damage the roots. Temperature differences as high as 10°C have been recorded in the top 25 mm of soil surfaces of overgrazed and protected grass plots (Julander, 1945). Such temperature differences, however, dropped to

about 2.5°C at a soil depth of 200 mm. The main root mass usually occurs in the top soil layers indicating that a large effect can be expected where there is a low basal cover.

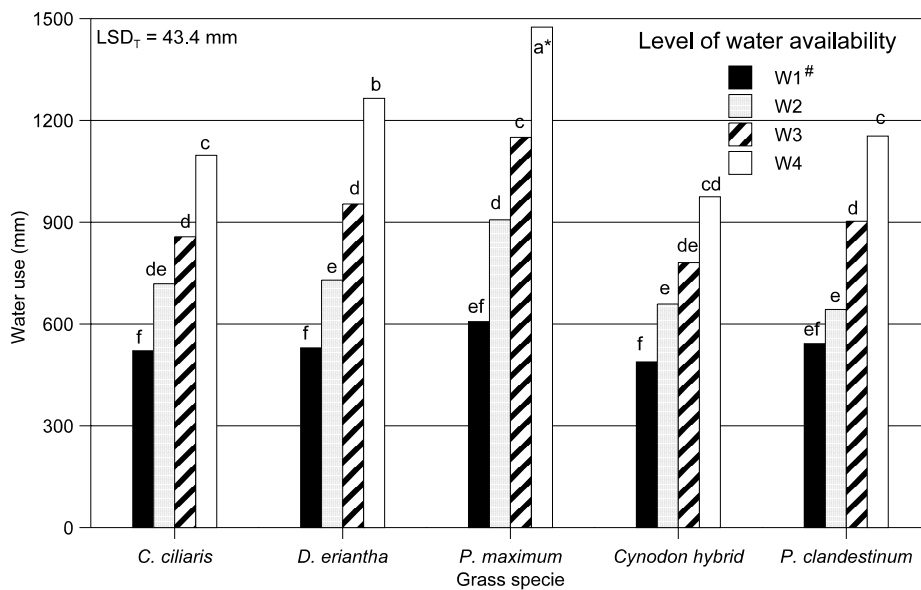
Stem density, amount of leaves per unit area and leaf orientation also contribute to resistance to water loss (Kim & Beard, 1988). Leaf width and vertical leaf extension rate influences total leaf area and thus evaporation area, indicating the importance of knowing the growth habit of the grass species being evaluated.

Although W2 *D. eriantha* had a smaller leaf area ($\pm 3\%$ less leaf area) in the 1997/98 than in the 1996/97 season, it was not reflected in lower water use, but this could be due to the very small difference in leaf area between the two seasons.



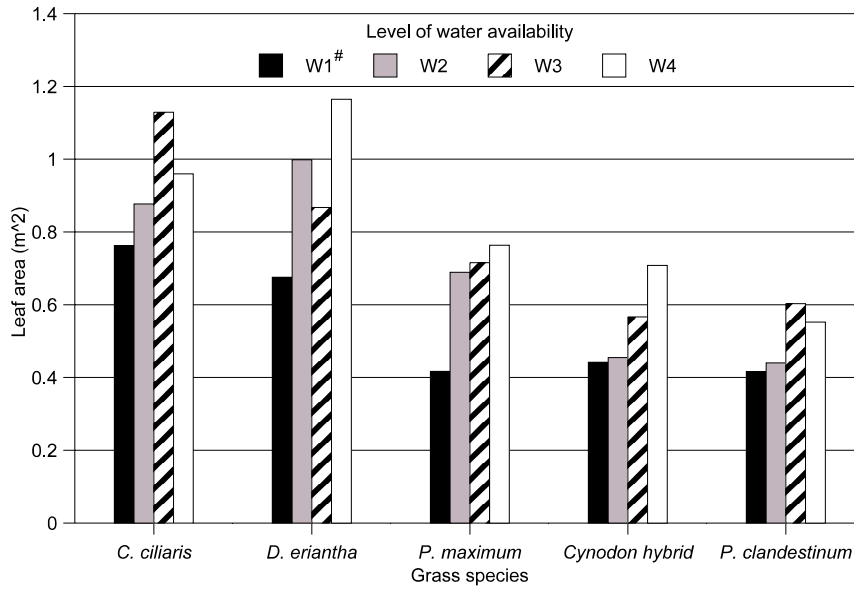
W1 - severely water stressed level, W4 - control
 No significant Grass species x Level of water availability interaction ($P < 0.05$)

Figure 2.3 Water use of five grass species at four levels of water availability, during the 1996/97 season.



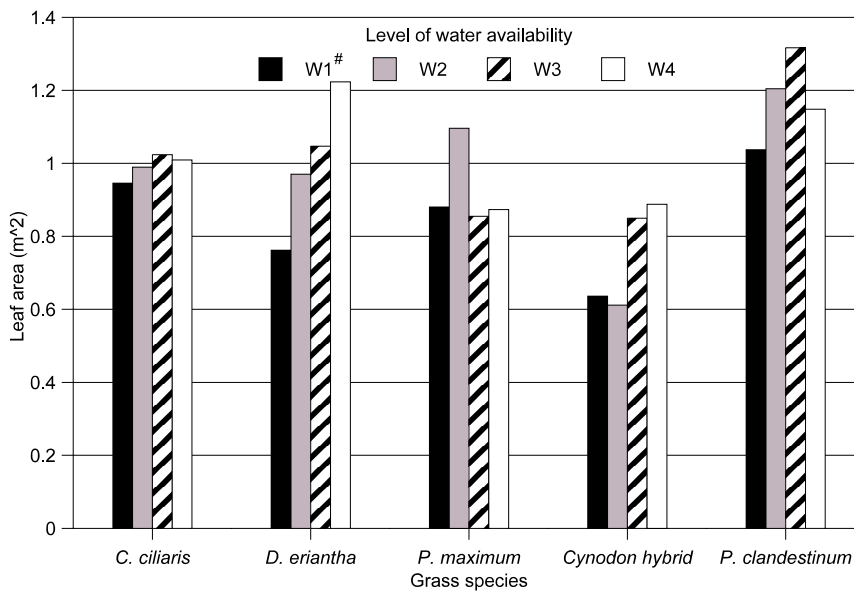
* Treatments with the same letter do not differ significantly from each other ($P < 0.05$)
 # W1 - severely water stressed level, W4 - control

Figure 2.4 Water use of five grass species at four levels of water availability, during the 1997/98 season.



W1 - severely water stressed level, W4 - control
 No significant Grass specie x Level of water availability interaction (P<0.05)

Figure 2.5 Leaf areas of five grass species at four levels of water availability in the 1996/97 season.



W1 - severely water stressed level, W4 - control
 No significant Grass specie x Level of water availability interaction (P<0.05)

Figure 2.6 Leaf areas of five grass species at four levels of water availability in the 1997/98 season.

2.3.2 Soil profile water loss

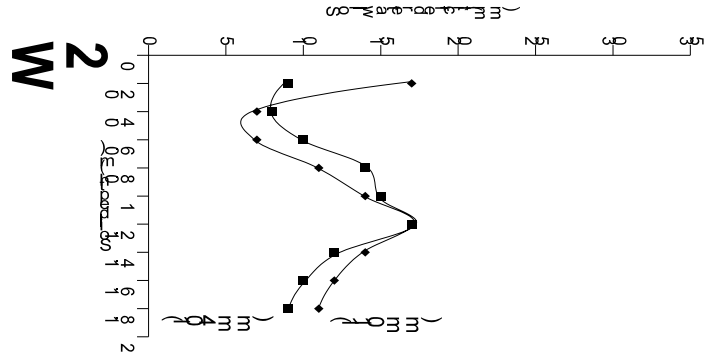
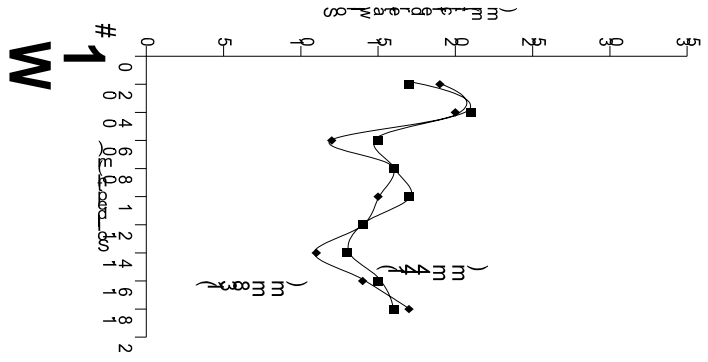
The water loss from different layers of the soil profile, for the five grass species at the four levels of water availability, are presented in Figures 2.7 - 2.11. These graphs represent the situation at the end each growing season.

The water loss from the soil profiles in both seasons differed for the five grass species. For the *Cynodon* hybrid (Figure 2.8), *P. maximum* (Figure 2.10) and *P. clandestinum* (Figure 2.11) losses from the soil profiles were greater in the 1997/98 than in the 1996/97 season. This was true for all water treatments. With *C. ciliaris* (Figure 2.7) soil profiles also tended to lose more water during the 1997/98 season, but only on the W2, 3 and 4 treatments. On W1 plots, *C. ciliaris* profiles tended to lose more water during the 1996/97 than the 1997/98 season. The difference between the two seasons was, however, only 6 mm and for all intents and purposes the water loss was approximately the same for the two seasons. The same could be said about the water loss of the W2 *C. ciliaris*, profiles where the difference between the two seasons was also 6 mm. The soil profiles of *D. eriantha* (Figure 2.9) tended to lose approximately the same amount of water in the two seasons.

When water was not limited (W3 and 4 treatments), the soil profiles tended to be quite wet at the end of the growing season, indicating a minimal water extraction by the grass roots, and thus strengthening the extrapolation made earlier that the application of less water than that necessary to reach field capacity, could result in minimal water extraction from the soil profile. The fact that the soil profile shows water loss at a depth of 1.8 m is an indication that very little, if any, water loss was

due to deep percolation. For *P. maximum* (W4 treatment) it even seems as if not enough water was applied, resulting in a dryer soil layer at 1.8 m than for the other grass species.

The high water loss of the soil profiles on the W1 treatments, emphasizes the contribution that a soil profile, filled to field capacity at the beginning of the season, can make if drought conditions develop later in the season. As with the W4 treatments, grass roots of the W1, 2 and 3 treatments made use of the whole soil profile to extract water.



Legend:
 ■ Pulse 1
 ◆ Pulse 2

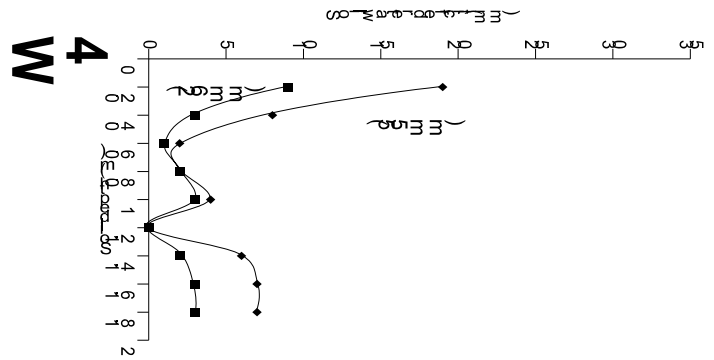
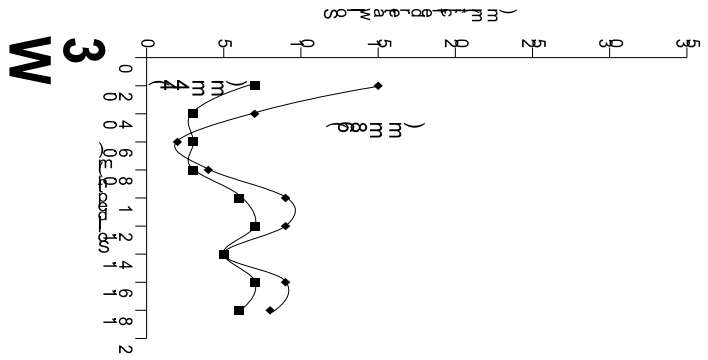
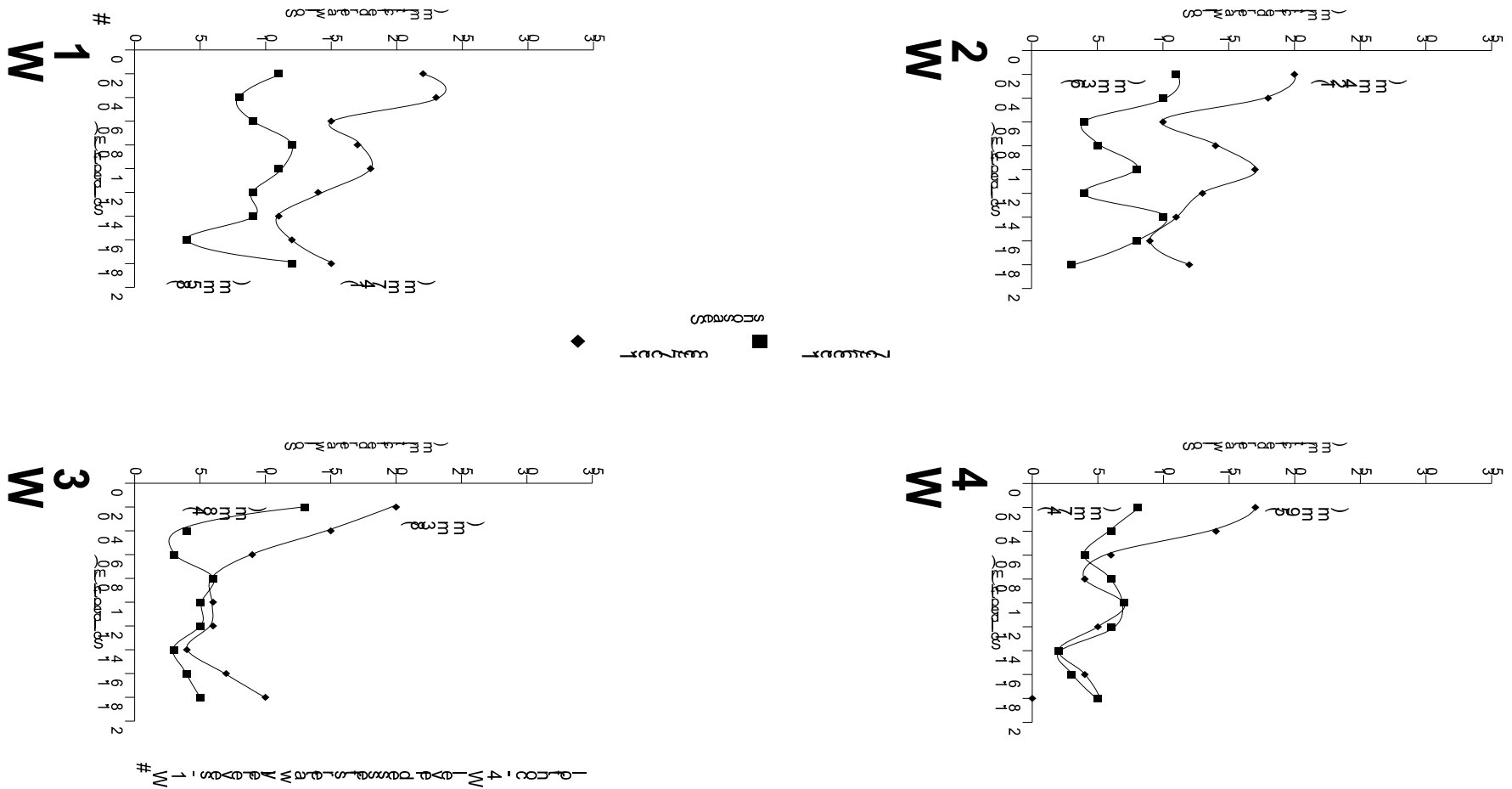


Figure 2: Fluorescence spectra of the samples.

The fluorescence spectra of the samples are shown in Figure 2. The x-axis represents the wavelength in nm, ranging from 200 to 400 nm. The y-axis represents the fluorescence intensity. The spectra show a characteristic peak around 280 nm, which is typical for nucleic acids. The intensity of the peak is higher for the sample labeled 'Pulse 1' compared to 'Pulse 2'.

TABLE 2. Seasonal variation in the abundance of *W. m. m.* in the water column of the Lake. The data were collected from the 1st to the 4th water column in the Lake. The data were collected from the 1st to the 4th water column in the Lake. The data were collected from the 1st to the 4th water column in the Lake.



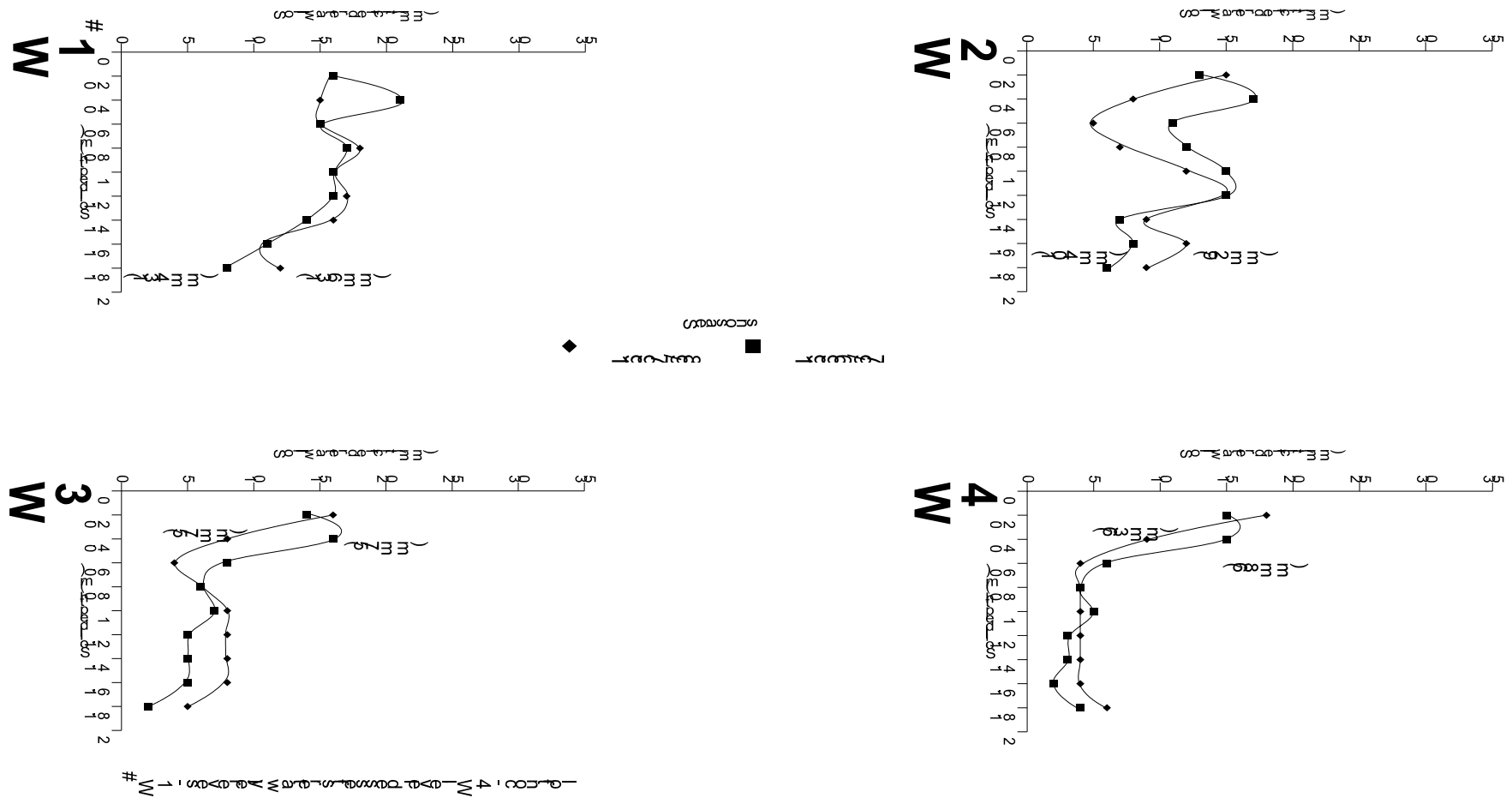


Figure 2.1: Comparison of the effective wavelength of the pulse and scatter series for the four different decomposition values. The pulse series is shown with squares and the scatter series with diamonds. The effective wavelength of the pulse series is consistently higher than that of the scatter series, and both series show a similar oscillatory pattern as the decomposition value increases.

TABLE 2: Comparison of the results of the four different models (M1, M2, M3, M4) for the four different scenarios (S1, S2, S3, S4) for the four different parameters (P1, P2, P3, P4). The results are presented in terms of the number of fish (N) and the number of fish per unit area (D).

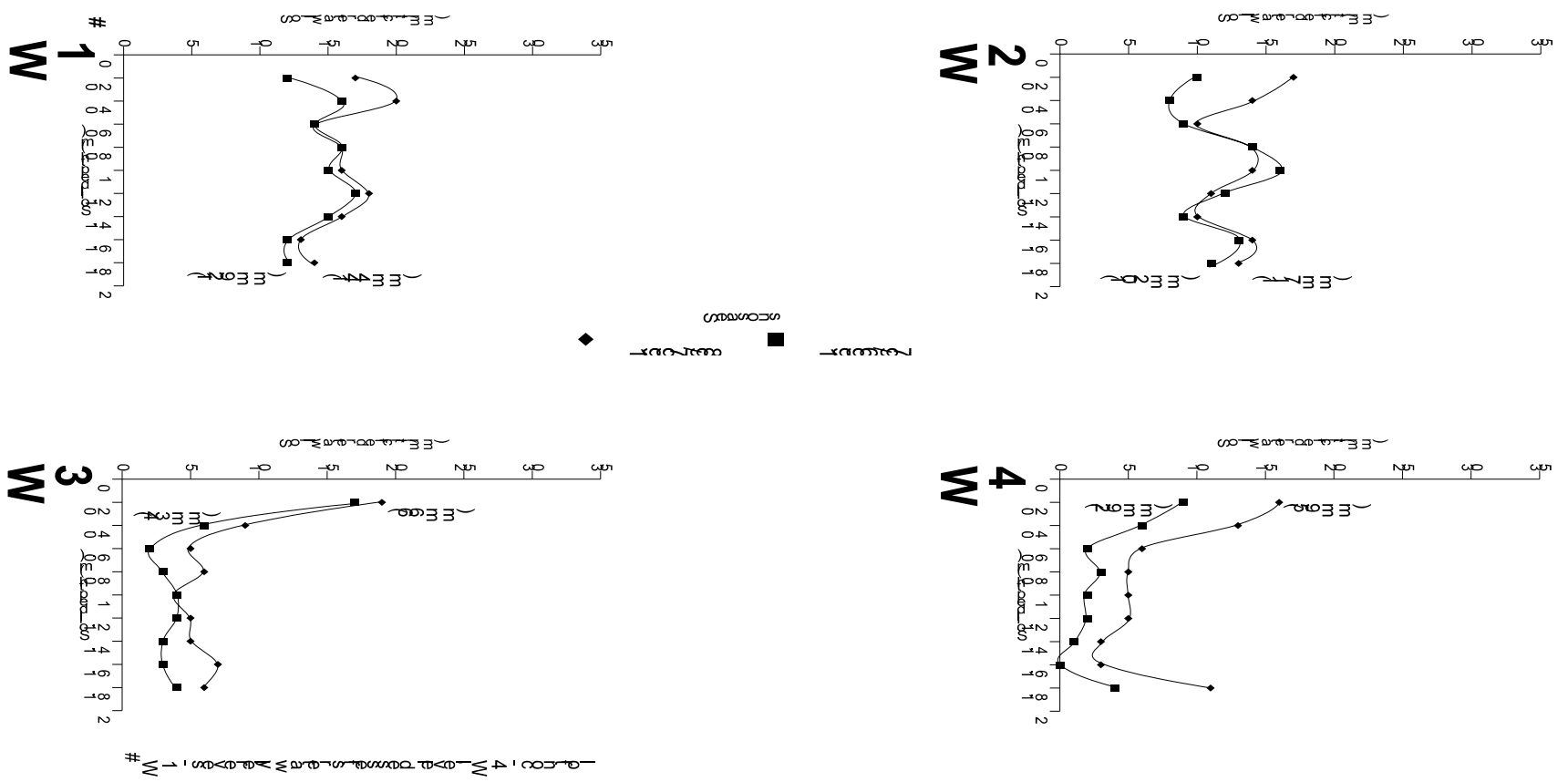
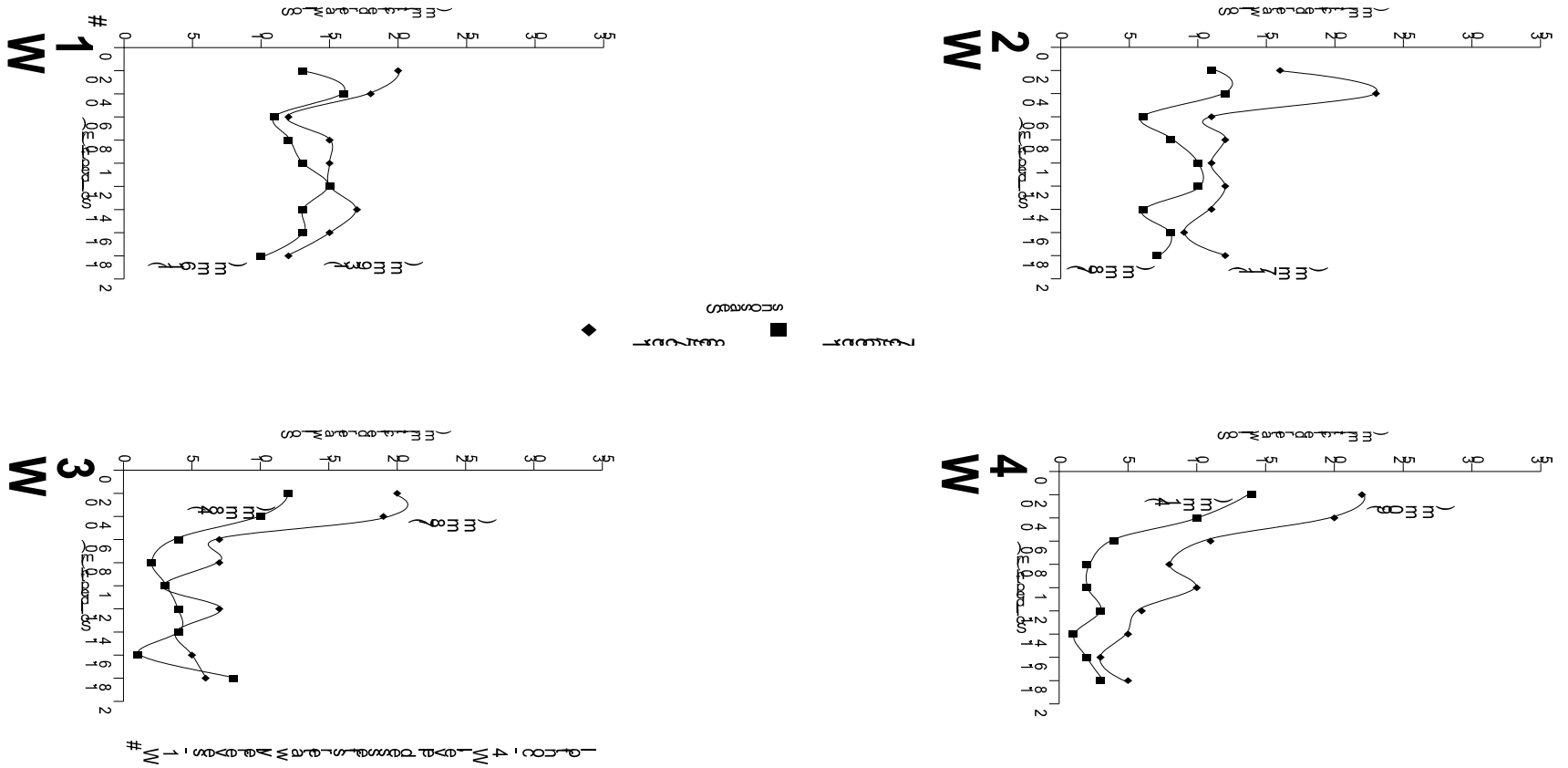


TABLE 2: 11 Sites where the first and second wave of the 2004-2005 influenza season were detected. The sites are numbered 1-11. The sites are numbered 1-11. The sites are numbered 1-11.



2.3.3 Root study

Root studies are often neglected, but without the development of a healthy root system, the above ground parts cannot produce optimally (Huang *et al.*, 1997) and it also affects the ability of the plant to withstand drought (Meyer & Green, 1980 & 1981).

Only *D. eriantha* and *P. clandestinum* tended to have a higher dry root mass under wet than under dry conditions (Figure 2.12). The dry root mass of *C. ciliaris*, the *Cynodon* hybrid and *P. maximum* tended to have a higher root dry mass under dry than under wet conditions.

With less water available, *D. eriantha* had the lowest root mass, followed by the *Cynodon* hybrid, *C. ciliaris* and *P. clandestinum*, with *P. maximum* having the highest root mass. With unlimited water available the picture changed with the *Cynodon* hybrid having the lowest root mass, followed by *P. maximum*, *C. ciliaris* and *D. eriantha*, with *P. clandestinum* having the highest root mass. With unlimited water the two creeping species, the *Cynodon* hybrid and *P. clandestinum*, tended to have the lowest and highest root masses respectively with the tufted species having intermediate root masses. This is in line with the findings of Rodel and Boulwood (1981) who reported lower root masses for stoloniferous grass species in comparison to those of rhizomatous species, which had the highest root mass, and tufted species having intermediate root masses.

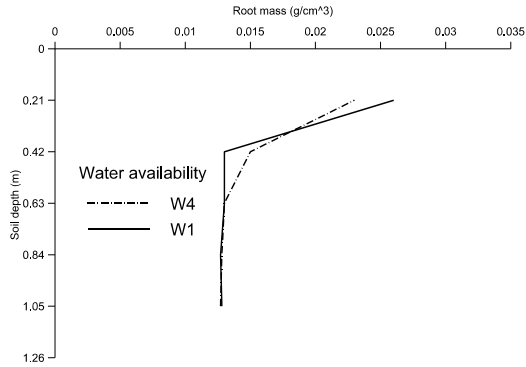
On a dry root mass basis, the grasses tended to have between 44 - 55% of the roots in the top 42 cm of soil (Figure 2.12). There were, however, differences between the

species in terms of wet and dry conditions. *C. ciliaris*, the *Cynodon* hybrid and *P. maximum* dry root mass tended to be higher under low (W1) than high (W4) water availability levels, while the dry root mass *D. eriantha* and *P. clandestinum* exhibited the opposite tendency.

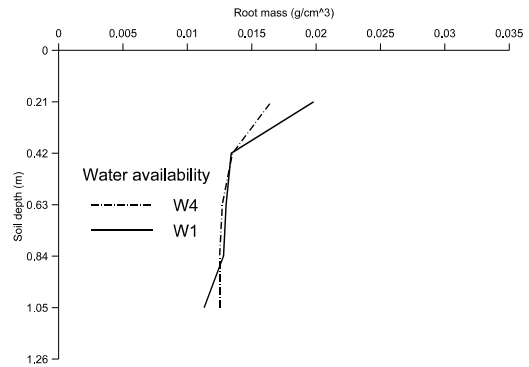
Christie (1978) found 75% of the roots of both native and introduced *C. ciliaris* plants in the top 40 cm of the soil profile in a sandy red soil in Charleville (Australia), receiving between 647 - 664 mm rainfall. Horowitz (1972) found the below ground dry mass of the *Cynodon* hybrid to be 62%, 26% and 12% for the 0 -15 cm, 15 - 30 cm and 30 - 45 cm soil increments respectively

Rethman *et.al.* (1997) found 49 - 62% of grass roots (*C. ciliaris*, *D. eriantha*, *P. maximum*) in the top 40 cm. For *C. ciliaris* it was 50% in the top 40 cm and 50% deeper as 40cm; 49% and 51% for *D. eriantha* for the two depths and 62% and 38% for *P. maximum* at the two depths. The different species all exhibited a reduction in root mass with increased drought stress. *C. ciliaris* showed a reduction of 0.38 g, while *D. eriantha* only showed a difference of 0.15 g but the root mass of *P. maximum* decreased by 0.78 g. Despite lower root masses, *C. ciliaris* and *D. eriantha* produced better yields than *P. maximum*. There was, however, not a good relation between the above and below ground dry mass and it is suggested that this could be due to only taking vertical cores, which did not cater for horizontal root spread.

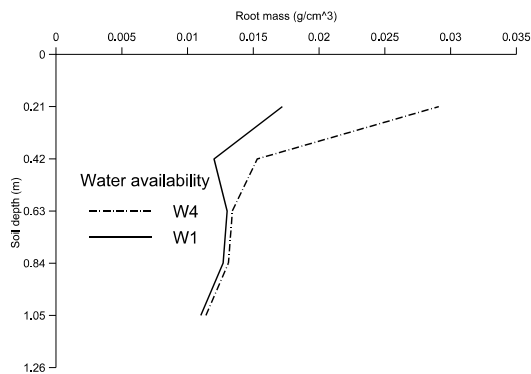
C. ciliaris



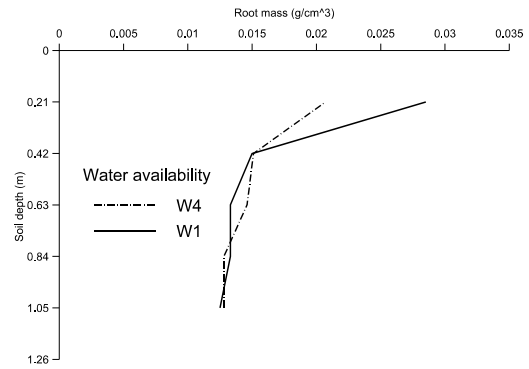
Cynodon hybrid



D. eriantha



P. maximum



P. clandestinum

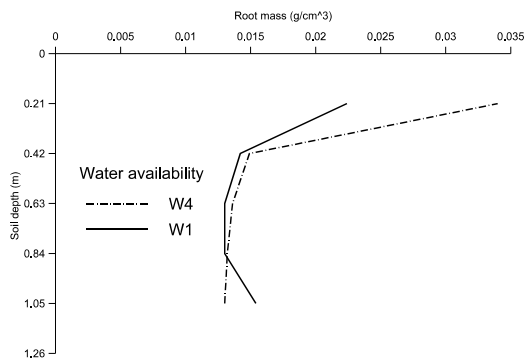


Figure 2.12 Dry mass of roots in the well watered control (W4) and the most water limited treatment (W1) of five grass species.

2.4 Discussion and Conclusions

The grasses did react differently to the four levels of water availability, confirming the first hypothesis, but the amount of water used is not an indication of a grasses ability to withstand drought. To confirm the latter, the above ground production (yield), quality (dry matter digestibility and crude protein content) and water use efficiency could be used as indicators of drought tolerance. The hypothesis on species being more drought tolerant, than is commonly acknowledged, could not, however, be confirmed at this stage.

An examination of water use, however, did highlight the following:

- it is 'n good practice to start the growing season with a wet profile, or in other words a profile brought to field capacity, where possible;
- it is not necessary to bring the soil profile back to field capacity every time water is applied, if the season started with a wet profile. Leaving at least 10% room for rain, could lead to water savings in the long term;
- following the aforesaid watering regime, even the grasses with unlimited water would develop a deep root system;
- most of the roots (on a dry mass basis) were found in the top 42 cm of the soil profiles. With poor soil cover, leading to increased soil temperatures, a strong effect on survival and production can be expected;
- development of a good canopy/basal cover, not only prevents excessive water loss from the soil profile, but also prevents high soil temperatures which can result in the death of the shallow roots;
- in conducting such studies, root studies together with soil temperature data

and canopy structure, are invaluable, as these play an important role in the water loss and production ability of the grass plants under different water regimes.

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CHAPTER 3

DRY MATTER YIELDS OF FIVE SUB-TROPICAL PERENNIAL GRASS SPECIES AT FOUR LEVELS OF WATER AVAILABILITY

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Abstract

The effect of four levels of water availability on the yield of five subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*) was evaluated in a small plot trial under a rain shelter at the University of Pretoria. The four treatments were: soil profile brought to 25 (W1), 50 (W2), 75 (W3) and 100% (W4 - the control) of field capacity on a weekly basis.

Under W4 (control) and W3 conditions, yields did not differ significantly ($P \geq 0.05$). Where, however, less water was available (W2 and W1), yields were significantly ($P \leq 0.05$) reduced in comparison with the control (W4). By bringing the soil profiles to field capacity at the beginning of the season, a water reservoir was established in the soil which buffered the effect of induced drought, leading to non-significant ($P \geq 0.05$) differences in yield. The capacity of the reservoir, together with the factors affecting

water loss, will thus determine the level of water depletion which can be tolerated before yields will significantly be affected. Due to the large number of variables, no single recipe for success can be advocated, while basic principles should not be overlooked. These include a basic knowledge of soil, and how to improve water infiltration and decrease excessive water loss, climate, and how it affects water loss and fodder species and how they react to different management strategies. Then only can a fodder production system be improved and maintained.

C. ciliaris, a notable drought tolerant species, produced yields ($11.7-20.0 \text{ t ha}^{-1}$) under non-control conditions (W1, W2 and W3) which were comparable to yields obtained under control conditions (W4) for traditionally irrigated grasses such as the *Cynodon* hybrid ($12.0-15.8 \text{ t ha}^{-1}$) and *P. clandestinum* ($5.6-11.8 \text{ t ha}^{-1}$). *P. clandestinum*, *D. eriantha* and *P. maximum* tended to be better adapted to wetter conditions.

These results also indicated that traditionally drought tolerant grass species (for example *C. ciliaris*) should not be overlooked when identifying species for use under irrigation. By choosing a grass species that can produce the same or higher yields with less water, than another species, water can automatically be used more efficiently.

When production of perennial grasses is investigated, long term trials are the only way to obtain accurate results. Two growing seasons are not enough, especially if the pastures have just been planted, since plants need at least one season to establish. With two growing seasons, after the establishment season,, the variation is just enough to increase the number of uncertainties as to what caused these differences. In future, at least three season's data, excluding the establishment

season, should be collected, while five year's data would be ideal. If similar trials were, however, to be conducted in more extensive (drier) conditions, the number of growing seasons should even be higher.

Keywords

Cenchrus ciliaris, a *Cynodon* hybrid, *Digitaria eriantha*, *Panicum maximum*, *Pennisetum clandestinum*, drought, dry matter partitioning

3.1 Introduction

Pastures, planted or natural, will always be part of the South African landscape. They grow, not only as dryland crops, but can often be found in areas where supplementary irrigation is available. Due to the nature of the rainfall in South Africa, even grasses in the latter areas can be subjected to drought, and knowledge of the impact of different levels of water availability on the yield and nutritive value thereof is, therefore, very important. Information on the water usage (Chapter 1) and resultant yields of planted pastures, as well as of natural veld, are, however, very scarce, making decision making, in terms of the best grass species for an area, very difficult.

It was, therefore, the aim of this trial to compare the yield potential of five grass species which can be found as planted pastures and /or as veld grasses in South Africa, at different levels of water availability. The hypotheses are that:

- the grasses will differ in their ability to produce with different amounts of water available;

- and that they will be able to produce good yields, even when subjected to mild water stress.

3.2 Materials and Methods

Five subtropical perennial grasses were established under an automatic rain shelter on the Hatfield Experimental Farm, of the University of Pretoria in Pretoria, (25°45'S, 28°16'E), South Africa, during December 1995. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. Coastcross II (K11) (Coastcross bermudagrass), *Digitaria eriantha* subsp. *eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass).

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991) with 30% clay in the top soil. The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon, which contains coarse gravel. The experimental plots were 2.5 x 2.0 m in size and separated by asbestos plates to a depth of 1.2 m.

During June 1995, seeds of *C. ciliaris*, *P. maximum*, *D. eriantha* and *P. clandestinum* were sown in seedling trays and kept in a greenhouse until December 1995. *C. ciliaris*, *P. maximum* and *D. eriantha* which are tufted or bunch grasses, were established at a rate of 300 000 plants ha⁻¹, while the creeping grasses (the *Cynodon* hybrid & *P. clandestinum*) were established at 160 000 plants ha⁻¹. The *Cynodon* hybrid was established using vegetative material collected on the experimental farm. The initial germination rate of *D. eriantha* was less than adequate and additional

seedlings had to be propagated. This delayed transplanting of this species from trays to the field site by ten weeks compared to the other species.

A neutron probe access tube was located in the centre of each plot. Neutron probe counts, using a Campbell neutron probe (503 DR), were taken at nine depth increments, each of 200 mm, on a weekly basis for all plots. These counts, which are related to the volumetric water content, were then incorporated into a calibration equation to determine the water deficit for each layer. Just before the onset of each growing season, the soil profiles of all the plots were brought to field capacity. Only then were the plants subjected to four levels of water availability

The water availability levels used were:

- W1 - apply 25% of the amount given to W4.
- W2 - apply 50% of the amount given to W4
- W3 - apply 75% of the amount given to W4
- W4 - control, the soil profiles were brought to field capacity on a weekly basis

Water was applied by means of flood irrigation and the amounts of water applied were monitored using water flow metres.

During the establishment season (1995/96), the grasses were not subjected to differential irrigation treatments to ensure a good establishment as it has been found that some of these grasses only start to produce optimally during the second or third year . To ensure a fair comparison of the species, treatments were thus only imposed in the second (1996/97) and third seasons (1997/98).

According to soil analyses, the pH(H₂O) of the experimental soil was neutral. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top soil (30 mg kg⁻¹ P; 108 mg kg⁻¹ K) was much higher than that of the subsoil (8 mg kg⁻¹ P; 67 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and potassium status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary. As the plots were not grazed, but removed as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (1995/96 season), the plots received 75 kg N ha⁻¹, 40 kg P ha⁻¹ and 200 kg K ha⁻¹. Nitrogen and potassium were also applied to all plots as top dressings during the summer growing season, resulting in a total of 450 kg N ha⁻¹ a⁻¹, 40 kg P ha⁻¹ a⁻¹ and 400 kg K ha⁻¹ a⁻¹. In the subsequent seasons (1996/97 and 1997/98), nitrogen and potassium were applied to all plots as top dressings at rates of 225, 338, 394 and 450 kg N ha⁻¹ a⁻¹ and 200, 300, 350 and 400 kg K ha⁻¹ a⁻¹ for the W1, W2, W3 and W4 water availability levels respectively. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

The grasses were harvested at the 10% flowering stage, except for *P. clandestinum*, which was not allowed to grow taller than 40 cm. This resulted in an average of three to four cuts during each season. *C. ciliaris*, *D. eriantha* and *P. maximum* (tufted grasses) were cut to a height of 10 cm while the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) were cut to 5 cm. A sample plot of one square metre, in the middle of each plot, was harvested, after which the rest of the plot was

also cut to the same height. The sample plots were permanently marked to ensure that the samples were taken from the same area at each harvest. The material was dried to constant mass for 48 hours at 65°C.

During the harvesting process, sub-samples of 0.25 x 0.25 m were taken of the creeping grasses, while tufts were regarded as sub-samples of the tufted grasses. These samples were sorted into leaves, stems and inflorescences. A direct comparison between these two sub-samples could thus not be made. To make comparison possible, the dry matter contribution per unit area was determined.

A fully randomized block design with three replications was used. The statistical analysis was done using the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data is presented in the Appendix (Tables A 3.1 - A 3.14).

3.3 Results

3.3.1 Dry matter yield

The yields reported in the literature (Table 3.1) sometimes correspond well with the results (Figures 3.1, 3.2 and Table 3.2) obtained in this trial, but sometimes they differ widely. This is not due to good or bad research practices, but rather the variety of growing conditions that makes extrapolation from one situation to another very difficult. Results of other researchers are, however, not useless because more often than not, similar trends are observed even if the yield *per se* is not comparable.

The findings in the literature (Table 3.1) can be summarized as follows: *C. ciliaris* is said to produce well under extreme drought conditions (<300 mm annual rainfall) (Fianu and Winch, 1983; Anonymous, 1989 (b)), while *P. clandestinum* is said to fare far better when growing with 700 mm or more water per year (Dale and Read, 1975; Dannhauser, 1988; Anonymous, 1989 (a)). *D. eriantha*, *P. maximum* and the *Cynodon* hybrid fall in a group between these two extremes, needing between 400 - 500 mm water per year (Anonymous, 1989 (a) & (b), 1995), and can be found under both irrigation and dryland cultivation (Theron and Arnott, 1977; Burton *et al.*, 1987; Oosthuizen, 1987; Dannhauser, 1988; Cilliers, 1989; Nel, 1989; Gouws, 1990). Being a drought tolerant species, *C. ciliaris* is seldom found under irrigated conditions, despite the fact that it still produces good yields under higher rainfall conditions (Anonymous, 1989 (b)). *P. clandestinum* is, however, not to be found in low rainfall areas without supplemental irrigation.

Table 3.1 Yield data obtained from literature for *C. ciliaris*, the *Cynodon* hybrid, *D. eriantha*, *P. maximum* and *P. clandestinum*.

Grass specie	Growing conditions	Yield (t dry material ha ⁻¹)	Reference
<i>C. ciliaris</i>	Dryland (Malawi, Tanzania) Dryland (Ghana) KwaZulu-Natal - 714 - 1190 mm rain (South Africa) Dryland (South Africa)	2.0 - 8.0 5.4 - 6.0 6.2 - 8.1 2.5 - 6.9	Bogdan, 1977 Fianu and Winch, 1983 Brockett and Gray, 1984 Anonymous, 1989 (b)
<i>D. eriantha</i>	KwaZulu-Natal - 714 - 1190 mm rain (South Africa) Dryland and irrigation (South Africa) Highveld - dryland (South Africa) Potchefstroom- dryland (South Africa) Potchefstroom - 478 and 803 mm rain (South Africa)	9.3 - 10.8 4.0 16.0 7.1 - 12.0 4.0 - 11.0 4.5 and 13.1	Brockett and Gray, 1984 Oosthuizen, 1987 Pieterse <i>et al.</i> 1988 Dannhauser, 1991 Dannhauser, 1991
<i>Cynodon</i> hybrid	KwaZulu-Natal, dryland (South Africa) KwaZulu-Natal, irrigation, 500 kg N ha ⁻¹ (South Africa) KwaZulu-Natal (South Africa) Dryland and irrigation with fertilizers (South East, USA) Highveld + irrigation + 300 kg N ha ⁻¹ (South Africa) Eastern Transvaal (South Africa) 600 - > 1 000 mm (South Africa) 360 kg N ha ⁻¹ (Kentucky, USA)	7.6 - 13.0 26.0 7.4 - 7.7 13.1 - 14.4 17.6 - 20.0 4.0 - 9.1 3 - 30 3 - 8	Theron and Arnott, 1977 Theron and Arnott, 1977 Brockett and Gray, 1984 Burton <i>et al.</i> , 1987 & 1988 Pieterse <i>et al.</i> 1988 Rethman and De Witt, 1988 Nel, 1989 Belesky <i>et al.</i> , 1991
<i>P. maximum</i>	French Guiana Venda, > 750 mm rain Different cutting regimes (Malaysia) Potchefstroom - dryland (South Africa) Potchefstroom - 478 and 803 mm rain (South Africa) 550 - 750 mm rain (South Africa)	14.4 15.0 - 30.0 1.7 - 44.5 7.0 - 11.0 6.0 and 12.0 4 - 12	Bogdan, 1977 Cilliers, 1989 Wan Hassan <i>et al.</i> , 1990 Dannhauser, 1991 Dannhauser, 1991 Nel, 1994 (a) & (b)
<i>P. clandestinum</i>	Hawaii with different N applications KwaZulu-Natal, dryland (South Africa) Queensland, Australia KwaZulu-Natal with 40 - 80 kg N ha ⁻¹ , 714 - 1190 mm rain (South Africa) Irrigation with fertilizers and different cutting regimes (Western Cape, South Africa) Eastern Transvaal (South Africa)	4.8 - 35.3 8.2 - 12.2 Max of 12.0 4.3 - 13.1 12 - 22 4.0 - 5.7	Whitney, 1974 Theron and Arnott, 1977 Bogdan, 1977 Brockett and Gray, 1984 Van Heerden, 1986 Rethman and De Witt, 1988

The dry matter yields presented in Figures 3.1 and 3.2, represent the total above ground yields for each season. There was no significant ($P \geq 0.05$) grass species x level of water availability interaction in either the 1996/97 nor the 1997/98 season. The average yields at the four levels of water availability, however, differed from each other in both seasons. In the 1996/97 season (Figure 3.1(a)) only the W1 level resulted in a significantly ($P \leq 0.05$) lower yield than the remaining three levels. In the following season (Figure 3.2(a)) both the W1 and W2 levels resulted in significantly ($P \leq 0.05$) lower yields than under control conditions (W4). It is important to note that although grasses at the W1 level received 75% less water than the control plots (W4), the same reduction in yield was not experienced. The same is true for the W2 and W3 levels, which received 50 and 25% less water respectively than the control (W4). In the 1996/97 season the W3 plants even produced higher yields than the control with 25% less water. Burton *et al.* (1987 & 1988) (Table 3.1) also harvested the same or higher yields from the *Cynodon* hybrid without than with supplementary irrigation. Beukes and Weber (1981) reported luxury water uptake by *Medicago sativa*, resulting in non-significant differences in yield with and without adequate amounts of water. This implies that by bringing a profile back to field capacity on a weekly basis, where the profile was at field capacity at the beginning of the season, might not result in greater yields, which in turn would make the extra inputs (water, electricity, labour, time, fertilizers) non-profitable.

In 1996/97 (Figure 3.1(b)) *C. ciliaris* produced significantly ($P \leq 0.05$) the highest yield followed by *D. eriantha* and the *Cynodon* hybrid which did not differ significantly ($P \geq 0.05$) from each other. *P. maximum* produced significantly ($P \leq 0.05$) lower yields

than the two highest producing grasses, but significantly ($P \leq 0.05$) more than *P. clandestinum*. During 1997/98 (Figure 3.2(b)) *C. ciliaris* and the *Cynodon* hybrid produced significantly ($P \leq 0.05$) higher yields than the other three grass species. The yields of *D. eriantha*, *P. maximum* and *P. clandestinum* did not differ significantly ($P \geq 0.05$) from each other. On average over the two seasons *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* produced more dry material than *P. maximum* and *P. clandestinum*.

In a long term trial (5 - 7 years) conducted in KwaZulu-Natal by Brockett and Gray (1984), *D. eriantha* (9 - 11 t ha⁻¹) had the highest yields, followed by the *Cynodon* hybrid (7 - 8 t ha⁻¹), *C. ciliaris* (6 - 8 t ha⁻¹) and *P. clandestinum* (4 - 8 t ha⁻¹). Where *P. maximum* and *C. ciliaris* were compared in terms of drought tolerance, *C. ciliaris* plants were able to survive a drought that led to 50% die-back of *P. maximum* plants (Anonymous, 1978).

In the 1996/97 season (Figure 3.1(b)) the yields of the two creeping grasses were quite low in comparison to the yields reported in the literature (Van Heerden, 1986; Burton *et al.*, 1987; Pieterse, *et al.*, 1988 & 1989). Despite these initial low yields *P. clandestinum* and the *Cynodon* hybrid did quite well in the 1997/98 season (Figure 3.2(b)), with the *Cynodon* hybrid producing higher yields than *P. clandestinum*. The same trend was found in Pietermaritzburg (KwaZulu-Natal) (Hefer & Tainton, 1990) where the *Cynodon* hybrid yielded about 3.5 to 4.5 t ha⁻¹ in comparison with the 3.0 to 4.3 t ha⁻¹ of *P. clandestinum* in the same trial.

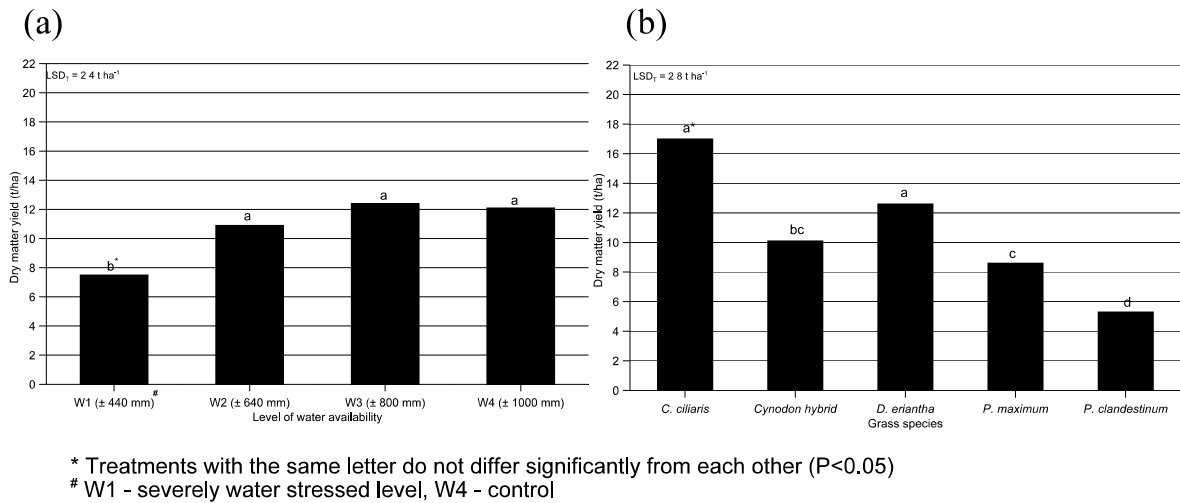


Figure 3.1(a) Average dry matter yield at four levels of water availability in the 1996/97 season

Figure 3.1(b) Average dry matter yield of five subtropical perennial grasses in the 1996/97 season.

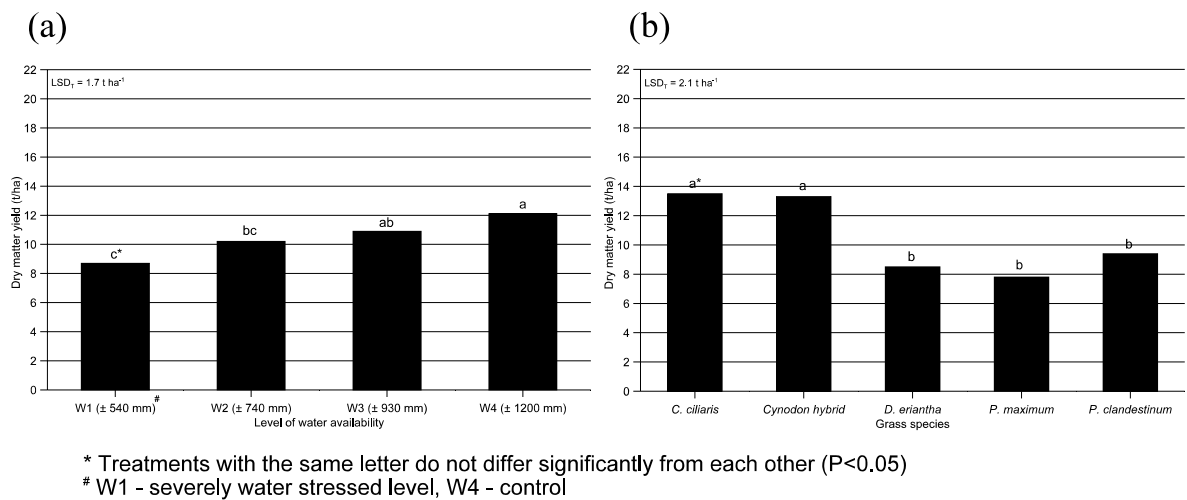


Figure 3.2(a) Average dry matter yield at four levels of water availability in the 1997/98 season

Figure 3.2(b) Average dry matter yield of five subtropical perennial grasses in the 1997/98 season.

Although there was no significant ($P \geq 0.05$) water availability x grass species interaction, it is important to note the yield differences of the five grasses for the four levels (Table 3.2). Some grass species like *C. ciliaris* produced higher yields under non-control conditions (W1, W2 and W3) than *D. eriantha*, *P. maximum* and *P. clandestinum* produced under control conditions (W4). This was true for both seasons. The same was true for *D. eriantha* in the 1996/97 season which produced higher yields under W2 and W3 conditions than the *Cynodon* hybrid, *P. maximum* and *P. clandestinum*. During 1996/97 the *Cynodon* hybrid and *P. maximum* also produced higher yields under non-control conditions (W1, W2 and W3) than *P. clandestinum* under control conditions.

In 1997/98 the *Cynodon* hybrid produced higher yields under W2 and W3 conditions than *D. eriantha*, *P. maximum* and *P. clandestinum* under control conditions. By choosing a grass species that can produce the same or higher yields with less water, than another specie, water can automatically be used more efficiently.

According to the literature *P. maximum* is better adapted to drought conditions than *D. eriantha*, while *D. eriantha* grew better than *P. maximum* and *C. ciliaris* with higher amounts of water available (Dannhauser, 1991; Snyman, 1994). In the two seasons of the trial, however, it was *D. eriantha* which produced higher yields than *P. maximum* under drought conditions, and it did not correlate with the trend indicated by the literature. *D. eriantha* although, producing better than *P. maximum* under wet conditions could not outyield *C. ciliaris* under these conditions.

The *Cynodon* hybrid can produce good yields under both irrigated and dryland

conditions. This was confirmed by the results of the second season (Table 3.2). In comparison to *P. clandestinum*, the *Cynodon* hybrid used less water and is more drought tolerant (Theron and Arnott, 1977; Rethman and De Witt, 1988; Nel, 1989). This was confirmed in the current study.

Table 3.2 Influence of level of water availability on the dry matter yield (t ha^{-1}) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	11.7	17.0	20.0	19.2	17.0
<i>Cynodon</i> hybrid	7.4	8.8	12.1	12.0	10.1
<i>D. eriantha</i>	8.2	14.9	14.1	13.2	12.6
<i>P. maximum</i>	6.2	8.7	9.2	10.4	8.6
<i>P. clandestinum</i>	4.0	5.1	6.3	5.6	5.3
Mean	7.5	10.9	12.4	12.1	
LSD _T (G) = 2.8					
LSD _T (I) = 2.4					
1997/98 season					
<i>C. ciliaris</i>	12.4	13.9	13.9	13.7	13.5
<i>Cynodon</i> hybrid	9.7	13.2	14.7	15.8	13.3
<i>D. eriantha</i>	6.9	8.2	9.0	9.9	8.5
<i>P. maximum</i>	7.0	7.0	7.7	9.4	7.8
<i>P. clandestinum</i>	7.7	8.7	9.3	11.8	9.4
Mean	8.7	10.2	10.9	12.1	
LSD _T (G) = 2.1					
LSD _T (I) = 1.7					

* W1 -severely water stressed level, W4 - control

The *Cynodon* hybrid regularly produced better yields than *D. eriantha* under highveld conditions in Gauteng (Pieterse *et al.*, 1988 & 1989), correlating well with the trend

in Table 3.2. According to Rethman and De Witt (1988) *Cynodon* is less well adapted to the high rainfall, but cool conditions of the eastern highveld of Mpumalanga, while *P. clandestinum* was able to produce well under those conditions. Dannhauser (1988) confirms this by stating that *P. clandestinum* is recommended for high rainfall cooler areas, while *D. eriantha*, *Cynodon* and *P. maximum* could be used under high and low water availability conditions, which correlates well with the findings in Table 3.2. Snyman (1994) confirmed that *D. eriantha* and *C. ciliaris* did better than *P. maximum* under drought conditions, but also stated that *D. eriantha* did better than *C. ciliaris* under dryland conditions in the Free State Province, which is in contrast with the present results.

The results of Taylor *et al.*, (1976) (New Zealand) are quite different than those reported in the current study. According to them, the yields of *C. ciliaris* and *P. clandestinum* were similar under dryland conditions, while *P. clandestinum* produced almost 10 t ha⁻¹ more dry material under irrigation conditions than *C. ciliaris*.

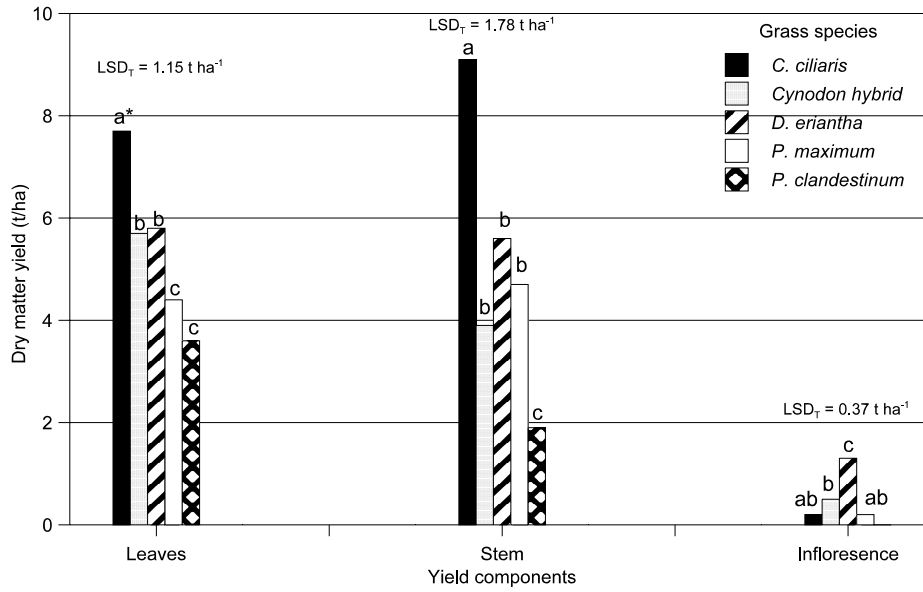
In the 1997/98 season the yields of *P. clandestinum* practically doubled for all the levels of water availability in comparison to the previous season. In 1997/98 *P. clandestinum* and *P. maximum* yields under control conditions (W4) were much higher than under the other levels. These two species appear to be better adapted to cooler and more moist conditions, and water stress resulted in large yield decreases. Snyman (1994) also stated that *P. maximum* was not adapted to drought conditions and had a better potential under better water supply conditions.

3.3.2 Contribution of the yield components to the above-ground dry matter yield

Due to the cutting regime followed, the reproductive component made up only a very small proportion of the above-ground dry matter yield (Figures 3.3 and 3.4), which consisted mainly of leaves and stem.

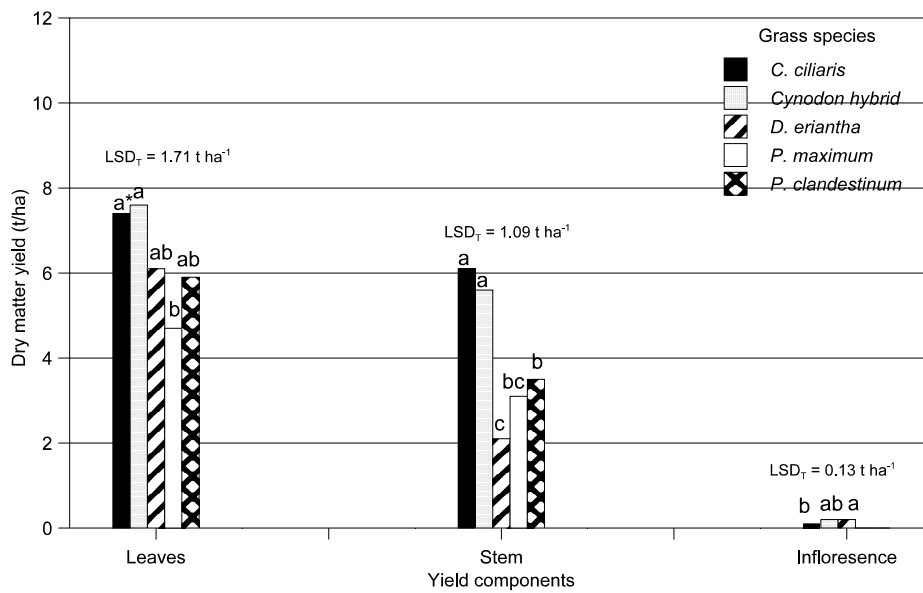
The *Cynodon* hybrid, *D. eriantha* and *P. clandestinum* followed the same trend in terms of leaf and stem material. These grasses had more leaf than stem in both seasons. Dannhauser (1991) also mentions a high leaf : stem ratio for the *Cynodon* hybrid as well as a large amount of leaf material being produced by *D. eriantha*. From the literature it is also evident that *P. clandestinum* produces an abundance of leaves (Gibbs-Russel *et al.*, 1991) while *D. eriantha* can easily be ensiled due to its leafiness (Dickinson *et al.*, 1990).

P. maximum and *C. ciliaris* were not consistent in the two seasons. In the 1996/97 season the stem dry matter yields of the two species were 0.9 and 1.3 t ha⁻¹ respectively more than for the leaves. In the following season, however, the leaf dry matter yields were 1.0 and 1.2 t ha⁻¹ respectively more than the stem dry matter yields for *P. maximum* and *C. ciliaris* respectively. In the 1996/97 season, *P. maximum* was only cut twice and *C. ciliaris* three times, while in the 1997/98 season three cuttings were taken from *P. maximum* and four cuttings from *C. ciliaris*, resulting in shorter regrowth periods, with less accumulation of stem material, thus explaining the higher leaf dry matter yields relative to the stem yields in the 1997/98 than in the 1996/97 season.



* Treatments with the same letter do not differ significantly from each other (P<0.05)

Figure 3.3 The contribution of different plant components to the production of five perennial grasses in the 1996/97 season.



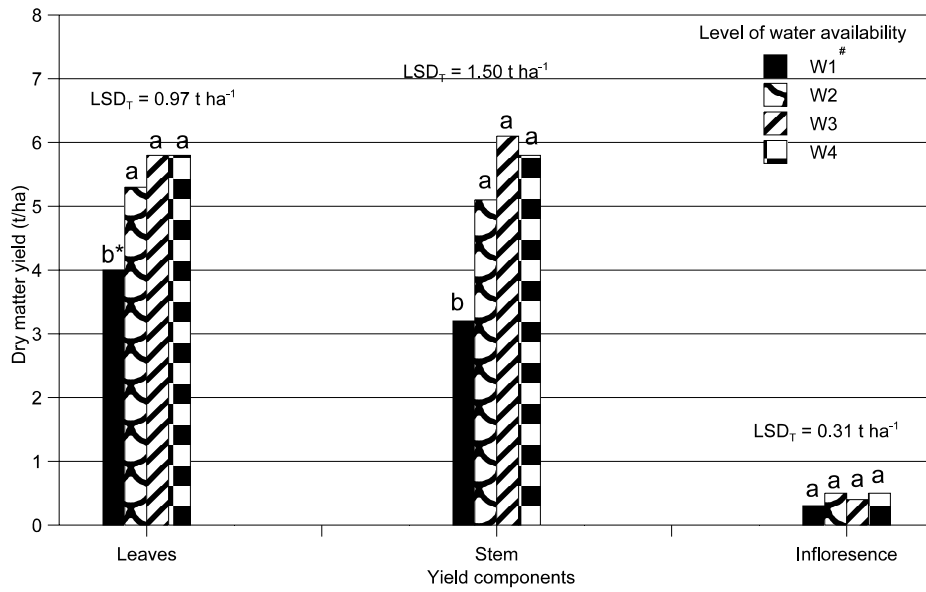
* Treatments with the same letter do not differ significantly from each other (P<0.05)

Figure 3.4 The contribution of different plant components to the production of five perennial grasses in the 1997/98 season.

As with whole plant dry matter yields, the yields of the different yield components tended to increase with greater water availability (Figures 3.5 and 3.6).

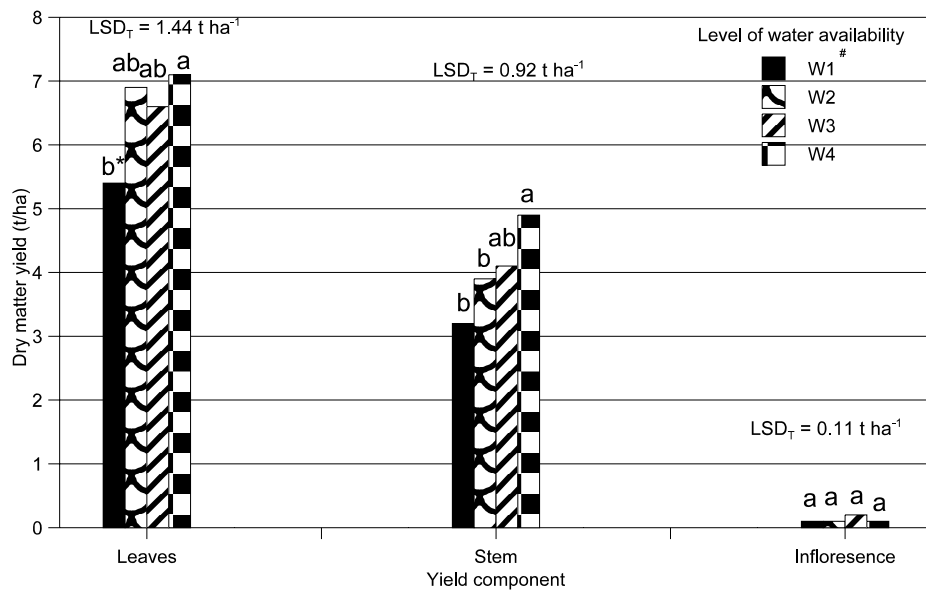
In both seasons there were no significant ($P \geq 0.05$) differences between the yield contributions of the leaf and stem material at the W2, W3 and W4 levels (Figures 3.5 and 3.6). Significantly ($P \leq 0.05$) lower stem and leaf material yields were, however, produced at the W1 level of water availability in both seasons.

In both seasons more leaf than stem material was produced at level W1. For the other levels it differed in the two seasons. In 1996/97 (Figure 3.5) more leaf material at W2, less at W3 and the same at W 4 was produced, while in the 1997/98 season (Figure 3.6), more leaf material was produced at all four levels of water availability. Overman and Wilkinson (1989) found that, regardless of the amount of N applied, the leaves made out the biggest proportion of the bermudagrass dry matter produced. In a dry season the final yield of *C. ciliaris* was 5.36 t ha^{-1} and in a wet season 6.04 t ha^{-1} . For the latter results, the stem : leaf ratio was initially 50:50 during the dry season but the proportion of stem increased over time. In the wet season the proportion of leaf was initially higher but later settled to a 50:50 leaf : stem ratio (Fianu and Winch, 1983).



* Treatments with the same letter do not differ significantly from each other (P<0.05)
 # W1 - severely water stressed level, W4 - control

Figure 3.5 The contribution of different plant components to production as affected by four levels of water availability in the 1996/97 season.



* Treatments with the same letter do not differ significantly from each other (P<0.05)
 # W1 - severely water stressed level, W4 - control

Figure 3.6 The contribution of different plant components to production as affected by four levels of water availability in the 1997/98 season.

3.4 Discussion and Conclusions

When the grass species were subjected to different levels of water availability, they were able to keep on producing well under mild water stress. When the soil profiles were brought back to field capacity on a weekly basis, the grasses sometimes even produced lower yields than plants receiving 25% less water. These disappointing yields on the W4 plots may be attributed to luxury water uptake without contributing to yield, nutrient deficiencies and/or nutrient leaching.

As expected, the five grass species differed in terms of their production ability when treated alike. Over a two year period, *C. ciliaris* (15.3 t ha⁻¹), the *Cynodon* hybrid (11.7 t ha⁻¹) and *D. eriantha* (10.6 t ha⁻¹) produced the highest average yields, while *P. maximum* (8.2 t ha⁻¹) and *P. clandestinum* (7.4 t ha⁻¹) produced the least.

The growth of the creeping grasses (the *Cynodon* hybrid and *P. clandestinum*), were lower than expected in the 1996/97 season, but caught up in the 1997/98 season. According to literature, some grasses take longer to establish and that is why long term trials are advisable when growing and evaluating perennial crops.

Some grass species, like *C. ciliaris*, produced higher yields under non-control conditions (W1, W2 and W3) than *D. eriantha*, *P. maximum* and *P. clandestinum* produced under control conditions (W4). By choosing a grass species that can produce the same or higher yields with less water, than another species, water can automatically be used more efficiently.

It is, however, not only the availability of water that affects the success of a species in a specific area. Several authors have emphasized the importance of temperature tolerance for the success of a species. In line with this, Brockett and Gray (1984) found that *C. ciliaris* could produce acceptable yields in the high rainfall areas of the Highland sourveld of KwaZulu-Natal, but due to its lack of tolerance of cold temperatures, better adapted weeds and grasses invaded and dominated the *C. ciliaris* stand. *Cynodon* (Theron and Arnott, 1977; Rethman and De Witt, 1988; Coetsee, 1993) and *P. maximum* (Snyman, 1994) can also not tolerate severe frost conditions. *P. clandestinum* can, conversely, not tolerate high temperatures (Nel, 1989), while *P. maximum* proved to be better adapted to such temperature conditions (Nel, 1994(a) and 1994(b)). *C. ciliaris* is said to be adapted to growing under high temperature conditions, and can keep on producing at 35°C, when the leaves of other grasses start to become necrotic (Christie, 1975).

The partitioning of dry matter between the yield components often influences the acceptability of the forage for animals. Grazers prefer softer material, with less lignin, which is more easily digested. The *Cynodon* hybrid, *D. eriantha* and *P. clandestinum* had more leaf than stem material in both seasons. The leaf contribution for *P. maximum* and *C. ciliaris* was lower than that of the stem in the first season, but with a change in cutting regime in the second season it changed. In the second season *P. maximum* and *C. ciliaris* were cut more frequently, resulting in the accumulation of proportionately less stem material. By adjusting the cutting frequency, grasses can still produce well and at the same time accumulate less stem material, which is difficult to digest. The optimum cutting frequencies were not tested in this trial, but

from the literature it can be deduced that a single harvest per growing season is too little while six cuts or more can have a negative effect on the profitability of the system (Whitney, 1974; Singh et al., 1995).

3.5. References

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CHAPTER 4

NUTRITIVE VALUE OF FIVE PERENNIAL SUB-TROPICAL GRASSES UNDER DIFFERENT LEVELS OF WATER AVAILABILITY

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Abstract

The effect of four levels of water availability on the nutritive value, in terms of *in vitro* dry matter digestibility and crude protein content (CP), of five subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*) was evaluated in a small plot trial under a rain shelter at the University of Pretoria. The four treatments were: soil profile brought to 25% (W1), 50% (W2), 75% (W3) and 100% (W4 - the control) of field capacity on a weekly basis.

With respect to digestibility, no single species was consistently more digestible than the others. It was only the digestibility of *D. eriantha* that stayed relatively constant over the two seasons. The digestibilities varied from 50 - 61% for *C. ciliaris*; 54 - 61% for the *Cynodon* hybrid; 56 - 63% for *D. eriantha*; 50 - 69% for *P. maximum* and 36 - 66% for *P. clandestinum*. Care should, however, be taken when comparing these

digestibilities with results obtained by other researchers, since different analytical methods and diet of the donor sheep could have had a strong effect.

The availability of water did not have any apparent influence on the digestibility of the grasses, which was surprising as it might have been expected that with more vigorous growth (in good conditions) an increase in fibre might have depressed digestibility.

The level of water availability did, however, have an effect on the crude protein content of the whole plant, leaves and stem material. The whole plant CP content of *P. maximum* tended to be higher under water stressed (W1) than well watered conditions (W4) while the plants of *D. eriantha* and the *Cynodon* hybrid with very little or no water stress (W3 and W4) had a higher CP content than the other irrigation levels. Although there was very little difference in crude protein content between the four irrigation treatments of *C. ciliaris* and *P. clandestinum* plants in the 1996/97 season, in the following season (1997/98) the crude protein contents under water limiting conditions (W1) were slightly higher than those of the well watered control plants (W4).

The *Cynodon* hybrid and *P. clandestinum* had consistently the highest CP content of the five grasses in both seasons. The *Cynodon* hybrid and *P. clandestinum*, contained on average (8.5% CP) much more crude protein than the three tufted grasses (average of 5.5%). The crude protein content of the latter species did not differ significantly ($P \geq 0.05$) from each other. As with agricultural crops, grass species with higher crude protein contents, often have lower yields, due to the higher energy

cost of protein assimilation.

Keywords

Cenchrus ciliaris, *Cynodon* hybrid, *Digitaria eriantha*, *Panicum maximum*,
Pennisetum clandestinum, digestibility, crude protein

4.1 Introduction

Although the amount of forage, feed or fodder available to an animal is important, the quality thereof will determine if the animal is taking in enough nutrients to maintain health, growth and reproduction. The lower the digestibility of grass, the more the animal has to take in to achieve the same results as with more digestible grass. The animal can, however, only consume a limited amount of bulk feed each day and if this has a low digestibility the animal won't be able to obtain all the energy it needs. The same applies to crude protein content. Each class of animal has a specific crude protein requirement per day. If this requirement is not met, growth and hence production can be seriously affected.

Protein shortages are of major concern to rumen production systems. Protein sources are, however, expensive to buy, and the farmer would like to get as much as possible crude protein from the pasture itself (Van Niekerk, 1997).

Despite differences in yield and quality over species and time, one should identify species with a natural higher fodder quality and or somehow improve the fodder quality of low quality species (Van Niekerk, 1997). Theron and Harwin (1976) confirmed the importance of high quality fodder by achieving a 38% increase in live

weight of animals by replacing veld with improved pastures.

The aim of this trial was to determine the effect of four levels of water availability on the nutritive value of different grass species.

The hypotheses are:

1. that the grass species will have different digestibilities and crude protein contents;
2. that the level of water availability will affect digestibility and crude protein content of the grasses, and
3. that there will be a negative correlation between stem material content and digestibility and crude protein content of the forage.

4.2 Materials and Methods

Five subtropical perennial grasses were established under an automatic rain shelter on the Hatfield Experimental Farm, of the University of Pretoria in Pretoria, (25°45'S, 28°16'E), South Africa, during December 1995. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. Coastcross II (K11) (Coastcross bermudagrass), *Digitaria eriantha subsp. eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass).

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991) with 30% clay in the top soil. The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon, which contains coarse gravel. The experimental plots

were 2.5 x 2.0 m in size and separated by asbestos plates to a depth of 1.2 m.

During June 1995, seeds of *C. ciliaris*, *P. maximum*, *D. eriantha* and *P. clandestinum* were sown in seedling trays and kept in a greenhouse until December 1995. *C. ciliaris*, *P. maximum* and *D. eriantha* which are tufted or bunch grasses, were established at a rate of 300 000 plants ha⁻¹, while the creeping grasses (the *Cynodon* hybrid & *P. clandestinum*) were established at 160 000 plants ha⁻¹. The *Cynodon* hybrid was established using vegetative material collected on the experimental farm. The initial germination rate of *D. eriantha* was less than adequate and additional seedlings had to be propagated. This delayed transplanting of this species from trays to the field site by ten weeks compared to the other species.

A neutron probe access tube was located in the centre of each plot. Neutron probe counts, using a Campbell neutron probe (503 DR), were taken at nine depth increments, each of 200 mm, on a weekly basis in all plots. These counts, which are related to the volumetric water content, were then incorporated into a calibration equation to determine the water deficit for each layer. Just before the onset of each growing season, the soil profiles of all the plots were brought to field capacity. Only then were the plants subjected to four levels of water availability

The water availability levels used were:

- W1 - apply 25% of the amount given to W4.
- W2 - apply 50% of the amount given to W4
- W3 - apply 75% of the amount given to W4
- W4 - control, the soil profiles were brought to field capacity on a

weekly basis

Water was applied by means of flood irrigation and the amounts of water applied were monitored using water flow meters.

During the establishment season (1995/96), the grasses were not subjected to differential irrigation treatments to ensure a good establishment as it has been found that some of these grasses only start to produce optimally during the second or third year. To ensure a fair comparison of the species, treatments were thus only imposed in the second (1996/97) and third seasons (1997/98).

According to soil analyses, the pH(H₂O) of the experimental soil was neutral. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top soil (30 mg kg⁻¹ P; 108 mg kg⁻¹ K) was much higher than that of the subsoil (8 mg kg⁻¹ P; 67 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and potassium status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary. As the plots were not grazed, but removed as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (1995/96 season), the plots received 75 kg N ha⁻¹, 40 kg P ha⁻¹ and 200 kg K ha⁻¹. Nitrogen and potassium were also applied to all plots as top dressings during the summer growing season, resulting in a total of 450 kg N ha⁻¹ a⁻¹, 40 kg P ha⁻¹ a⁻¹ and 400 kg K ha⁻¹ a⁻¹. In the subsequent seasons (1996/97 and 1997/98), nitrogen and potassium were applied to all plots as top dressings at rates of 225, 338, 394

and 450 kg N ha⁻¹ a⁻¹ and 200, 300, 350 and 400 kg K ha⁻¹ a⁻¹ for the W1, W2, W3 and W4 water availability levels respectively. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

The grasses were harvested at the 10% flowering stage, except for *P. clandestinum*, which was not allowed to grow taller than 40 cm. This resulted in an average of three to four cuts during each season. *C. ciliaris*, *D. eriantha* and *P. maximum* (tufted grasses) were cut to a height of 10 cm while the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) were cut to 5 cm. A sample plot of one square metre, in the middle of each plot, was harvested, after which the rest of the plot was also cut to the same height. The sample plots were permanently marked to ensure that the samples were taken from the same area at each harvest. The material was dried to constant mass for 48 hours at 65°C.

Intact plants, as well as the different yield components, were milled after drying. A Wiley no. 3 mill, with a 1 mm sieve was used. The milled product was then used to determine the *in vitro* dry matter digestibility and crude protein content of the crops.

In vitro dry matter digestibility

The dry matter, organic matter and ash contents of the samples were determined by drying 2 g or each milled sample for 24 hours at 60°C (dry matter content), before incinerating at 600°C for 4 hours (ash content). The organic matter content was calculated as the difference between the dry matter and ash contents. For the *in vitro*

digestibility of the crops, 0.2 g plant material was used for the analysis using the method proposed by Tilley and Terry (1963).

Crude protein content

The milled plant samples were analysed for nitrogen content using the Kjeldahl technique (Association of Official Analytical Chemists, 1984). The analyses were done by the Soil Science Laboratory of the Department of Plant Production and Soil Science, University of Pretoria. The values were multiplied by 6.25 (Van der Merwe and Smith, 1991) to express the results in terms of crude protein content.

A fully randomized block design with three replications was used. The statistical analysis was done using the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data is presented in the Appendix (Tables A4.1 - A4.28).

4.3 Results

4.3.1 In vitro dry matter digestibility

There is some controversy over the comparability of quality analyses done by different researchers. Quality data from other researchers will, therefore, only be included to illustrate the variation that exists in the literature.

Inflorescence material was not taken into account, due to the very limited amount of material produced before harvesting. The dry matter digestibility of the whole plant,

stem and leaf material (Figure 4.1) was significantly ($P \leq 0.05$) better in 1996/97 than in 1997/98. It was speculated that the lower whole plant digestibility could possibly be attributed to the amount of stem relative to leaf material in the two seasons. There was, however, no significant ($P \geq 0.05$) correlation between the leaf:stem ratio in the material harvested and the whole plant digestibility (Appendix Tables A4.1 - A4.4). t'Mannetje (1975) also found no correlation between leaf percentage and digestibility. He did, however, report a negative correlation between dry matter yield and digestibility and a positive correlation between N percentage and digestibility. According to Singh *et al.* (1995), however, there was a significant positive correlation between the number of leaves and the leaf:stem ratio and digestibility, while an increase in the number of tillers per plant was significantly correlated with a reduction in digestibility. O'Reagain and Mentis (1989) also concluded that leafy grass species with few stems were more highly acceptable to cattle. Leaf material digestibility was better than that of the stem material in both seasons. This was also confirmed by t'Mannetje (1975); Fianu and Winch (1984) and Marais (1990).

The fact that leaf and stem digestibility was lower than that of the whole plant was totally unexpected. It have been influence by the age of the plants. This is, however, unlikely, because the plants were cut back after each harvest and it was the regrowth which was analysed at a similar physiological growth stage. The only significant ($P \leq 0.05$) correlations were between the stem and whole plant digestibilities in the 1996/97 season (Appendix Table A4.1). When the stem material was more digestible so too was the digestibility of the whole plant.

Almost no similarities were found in terms of the whole plant digestibilities in the two seasons (Figures 4.2 and 4.3). In the 1996/97 season *C. ciliaris* and the *Cynodon* hybrid were the least digestible (Figure 4.2), while in the following season (1997/98) they tended to be the most digestible (Figure 4.3), with the trend being reversed in the case of *P. clandestinum* (Figures 4.2 and 4.3). *D. eriantha* tended to be more digestible than the *Cynodon* hybrid (Figure 4.2) in 1996/97, while this difference was not evident in 1997/98 (Figure 4.3). In digestibility studies reported by Dannhauser (1991(a)); Grunow and Rabie (1985) and Theron and Arnott (1977) the authors respectively found that *P. maximum* was more digestible than *D. eriantha*; *C. ciliaris* more digestible than *D. eriantha*; and *P. clandestinum* more digestible than the *Cynodon* hybrid.

The whole plant digestibilities of *C. ciliaris*, *D. eriantha* and *P. clandestinum* tended to increase with higher amounts of water applied, while those of the *Cynodon* hybrid and *P. maximum* tended to decrease with more water applied in the 1996/97 season (Figure 4.2). In the 1997/98 season (Figure 4.3) three of the grass species (*D. eriantha*, *P. maximum* and the *Cynodon* hybrid) tended to become less digestible with more water supplied. It was only *C. ciliaris* that exhibited a higher digestibility with more water added. *P. clandestinum* did not exhibit a clear tendency. Fianu and Winch (1984) observed better digestibilities in a wet than in a dry season.

The leaves of *C. ciliaris* and *D. eriantha* tended to be the most digestible in both seasons with those of *P. clandestinum* being the least digestible (Figures 4.4 and 4.5).

The stems of *C. ciliaris*, *D. eriantha*, *P. maximum* and the *Cynodon* hybrid were less digestible than the leaves, while the digestibility *P. clandestinum* stem material tended to be better than that of the leaves in both seasons (Figures 4.4, 4.5, 4.6 and 4.7). There was then also a positive correlation ($r^2 = +0.60$) between the whole plant digestibility and that of the stem material of the *P. clandestinum* plants in the 1996/97 season only.

As with the whole plant digestibilities, there were no clear reactions of the digestibility of the leaves and stems when water availability was manipulated (Figures 4.4, 4.5, 4.6 and 4.7).

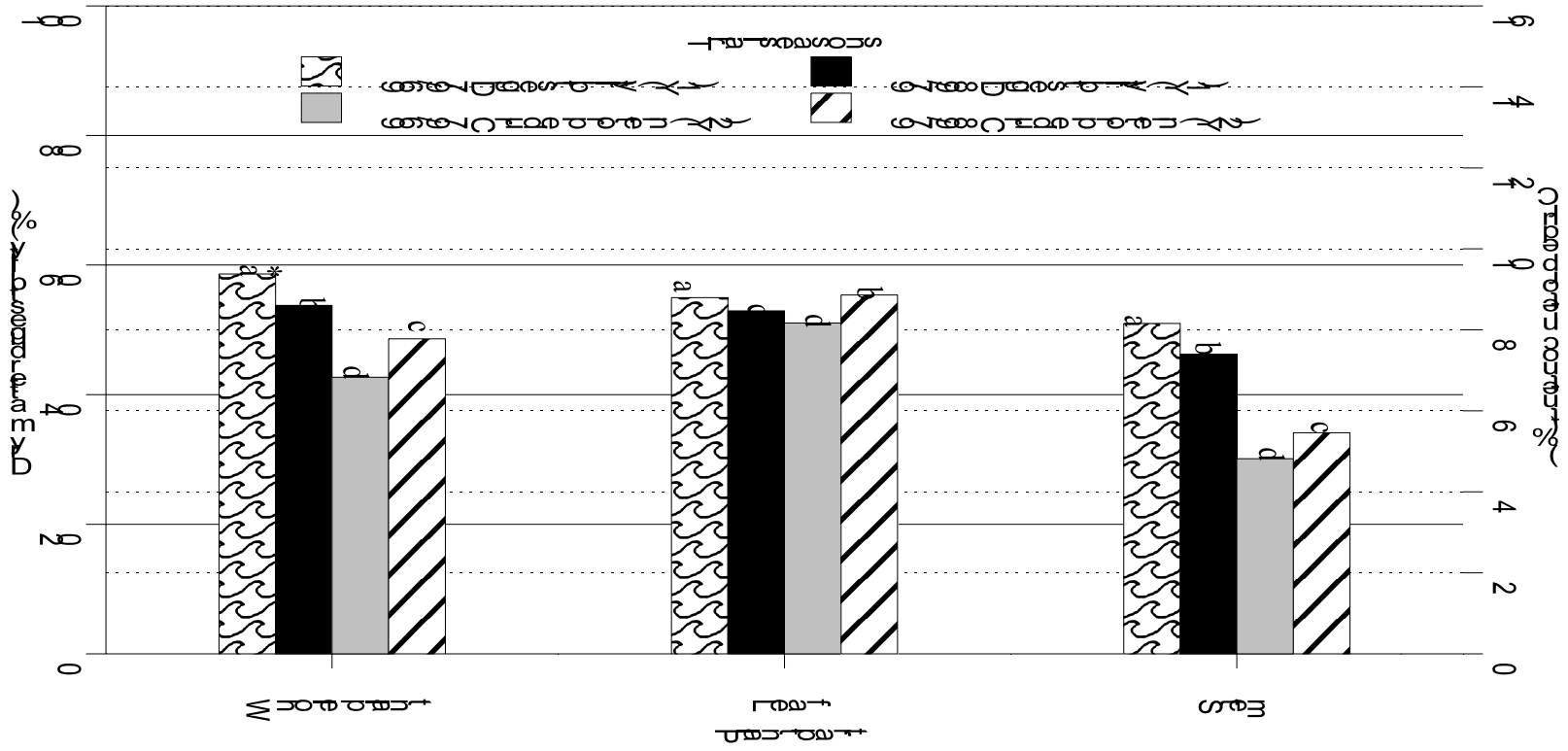
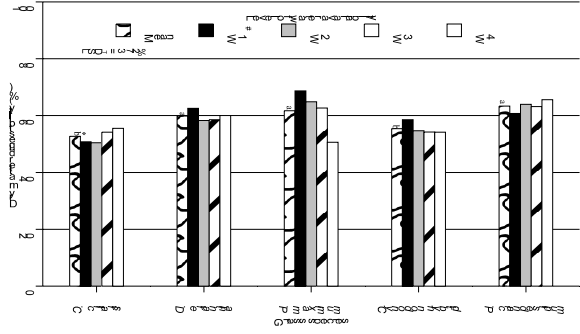
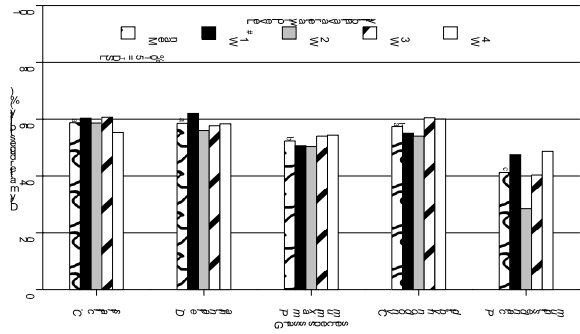


Figure 14: The effect of Fes, FesL and FesL + FesL on the intake of dry matter (DMI) by sheep. The bars represent the mean DMI (g/kg live weight) of sheep offered the different treatments. Error bars represent the standard error of the mean (SEM). Different letters indicate significant differences (P < 0.05) between treatments.

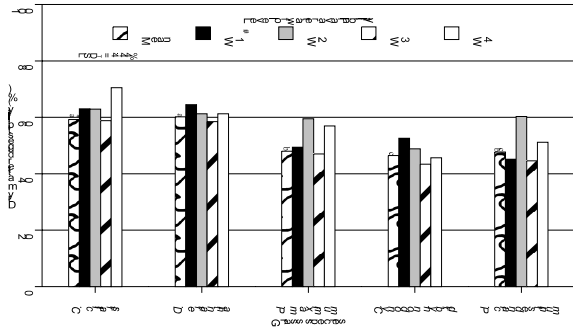
TABLE 14: The effect of Fes, FesL and FesL + FesL on the intake of dry matter (DMI) by sheep. The bars represent the mean DMI (g/kg live weight) of sheep offered the different treatments. Error bars represent the standard error of the mean (SEM). Different letters indicate significant differences (P < 0.05) between treatments.



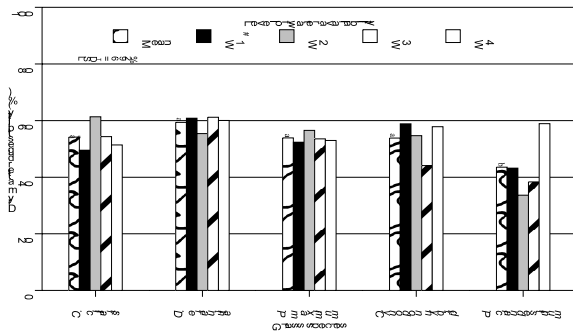
24 EPHF
 The W to S over time series
 and S to W over time series
 are shown in the figure.



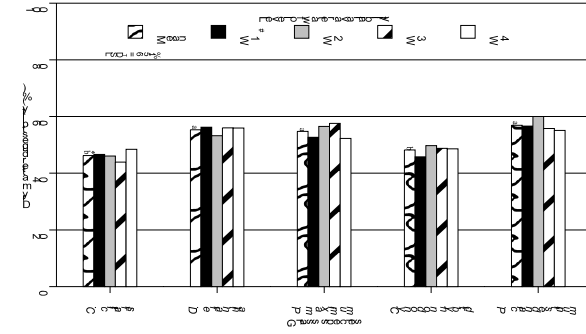
34 EPHF
 The W to S over time series
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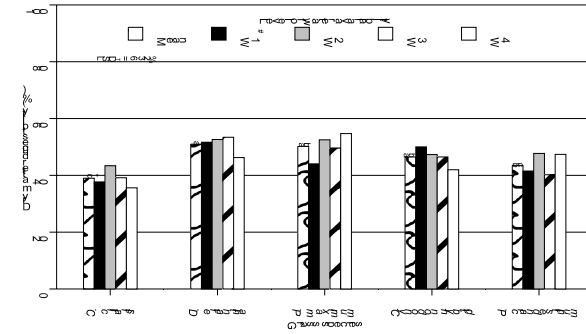
44 EPHF
 The W to S over time series
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 are shown in the figure.



54 EPHF
 The W to S over time series
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64 EPHF
 The W to S over time series
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74 EPHF
 The W to S over time series
 and S to W over time series
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4.3.2 Crude protein content

The crude protein (CP) content followed the opposite trend over the two seasons to that of digestibility (Figure 4.1), with plants tending to have a higher CP content in the 1997/98 than 1996/97 season, leading to the question on the possibility of a negative correlation between CP content and digestibility. While t'Mannetje (1975) reported a strong positive correlation between N% in the plant material and digestibility, Minson (1973) reported a poor correlation between the two parameters which agrees with the present results of no correlation (data not shown).

The leaf material tended to have a higher CP content than the stem material in both seasons (Figure 4.1). The same trend was reported by Fianu and Winch (1984) and t'Mannetje (1975). There was also a strong positive correlation between stem and leaf CP content and that of the whole plant. The whole plant CP content correlated with the CP of the leaves ($r^2 = +0.75$ to $+0.95$) and that of the stems ($r^2 = +0.55$ to 0.95).

A comparison of the whole plant CP content (Figures 4.8 and 4.9) indicates slightly higher CP contents in 1997/98 than in 1996/97 for *C. ciliaris*, *P. maximum* and the *Cynodon* hybrid, while that of *D. eriantha* was almost the same in the two seasons and that of *P. clandestinum* was slightly lower in 1997/98. In both seasons (Figures 4.8 and 4.9) the whole plant CP contents of the *Cynodon* hybrid and *P. clandestinum* were higher than those of the other three grasses. High CP contents for the *Cynodon* hybrid and *P. clandestinum* were also observed by Rethman and De Witt (1988). Theron and Arnott (1977) also recorded CP contents of over 12% for

both the *Cynodon* hybrid and *P. clandestinum*.

In a trial reported by Snyman (1994) *C. ciliaris* had the lowest CP content when compared to *P. maximum* and *D. eriantha*, but *C. ciliaris* was able to maintain the CP content over the season while the other two grasses showed a $\pm 4\%$ reduction in CP over the same period. Dannhauser (1991(a), (b)) concluded that the CP content of grass species is influenced by soil type. Nutrient content of the soil can thus play a significant role in the CP content of species and the CP content of a species can thus vary from one location to the next.

The whole plant CP content of *P. maximum* tended to be higher under water stressed (W1) than under well watered conditions (W4) while the plants with very little or no water stress (W3 and W4) of *D. eriantha* and the *Cynodon* hybrid had a higher CP content than the other irrigation levels (Figure 4.8). In the 1996/97 season there was very little difference in crude protein content between the four irrigation treatments of *C. ciliaris* and *P. clandestinum* plants (Figure 4.8). In the following season (Figure 4.9), however, the crude protein contents under water limiting conditions (W1) were slightly higher than those in the well watered control plants (W4).

The leaves (Figures 4.10 and 4.11) in both seasons, for all the species, had more crude protein than the stems (Figures 4.12 and 4.13). Leaves and stems of the *Cynodon* hybrid and *P. clandestinum* had the highest crude protein content in both seasons (Figures 4.10, 4.11, 4.12 and 4.13).

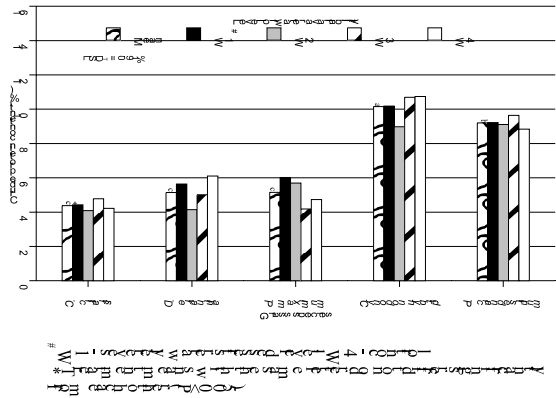


Figure 1: Percentage of total dry weight of various plant parts in Experiment 1.

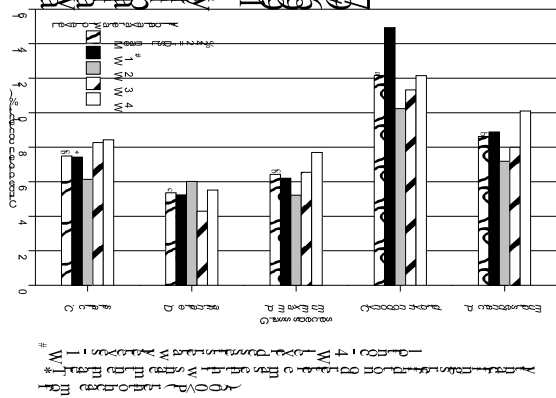


Figure 2: Percentage of total dry weight of various plant parts in Experiment 2.

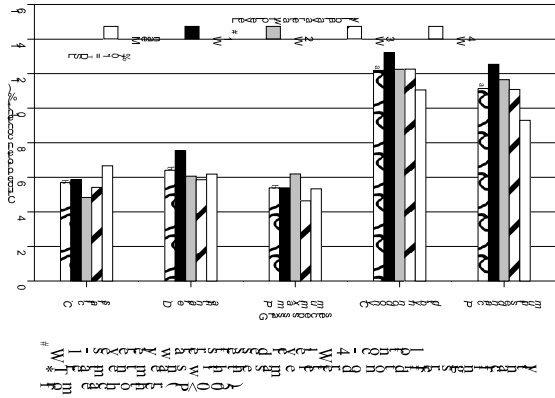


Figure 3: Percentage of total dry weight of various plant parts in Experiment 3.

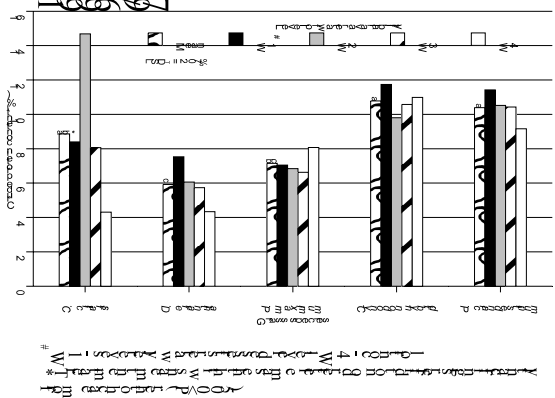


Figure 4: Percentage of total dry weight of various plant parts in Experiment 4.

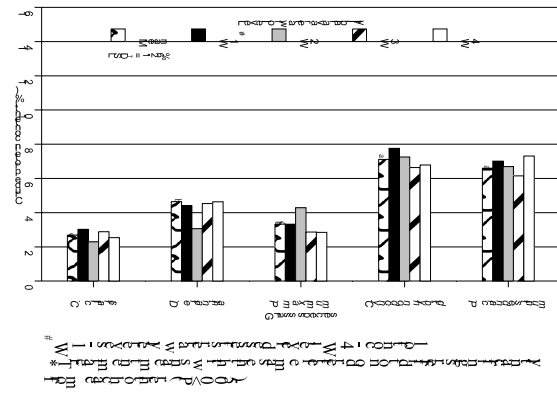


Figure 5: Percentage of total dry weight of various plant parts in Experiment 5.

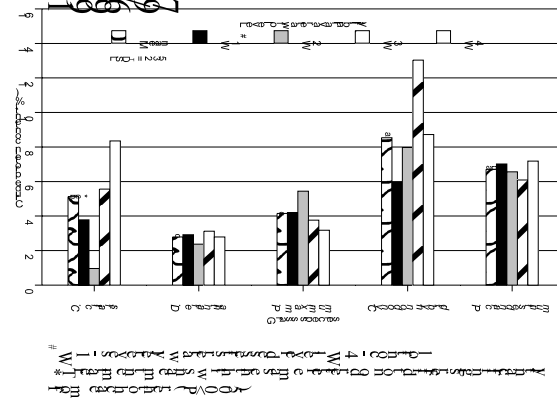


Figure 6: Percentage of total dry weight of various plant parts in Experiment 6.

4.4 Discussion and Conclusions

Differences in the dry material digestibility of the different grasses, under different water regimes, over the two seasons, made it difficult to draw definite conclusions. However, it was evident that the digestibility of the grass species evaluated was quite low and varied between 40 and 70% with a mean digestibility of about 55%. This is not uncommon, as other scientists have also recorded digestibilities ranging between 39 - 70% for *C. ciliaris* (Fianu and Winch, 1984; Grunow and Rabie, 1985; Dannhauser, 1991(a), (b); Moolman, 1993) and 54 - 70% for *P. clandestinum* (Theron and Arnott, 1977; Dugmore *et al.*, 1985; Van Heerden, 1986; Dugmore and Du Toit, 1988; Tainton, 1988; Dickinson *et al.*, 1990; Dannhauser, 1991(a), (b)). Digestibilities of 49 - 88% for *P. maximum* (WanHassan *et al.*, 1990; Dannhauser, 1991(a), (b); Nel, 1994; Singh *et al.*, 1995; Pieterse *et al.*, 1997), 51 - 65% for *Cynodon* (Theron and Arnott, 1977; Nel, 1989; Dannhauser, 1991(a), (b); Viljoen, 1994) and 40 - 65% for *D. eriantha* have also been reported (Grunow and Rabie, 1985; Dannhauser, 1991(a), (b)).

The absence of significant ($P \geq 0.05$) differences in digestibility, due to level of water availability, should not be seen as a lack of results, but as good news as it seems as if water, or the lack thereof, does not affect the digestibility of the grass plants. Data quoted by Thompson *et al.* (1989), however, stated that better digestibilities were recorded under water stressed than under non-stressed conditions. Increased temperatures, however, did decrease the cell wall digestibility (Thompson *et al.*, 1989).

The age of plants at harvest has a more profound effect on the digestibility as noted by Dannhauser (1991(a), (b)). He reported that the dry matter digestibility of *Cynodon* declined from 65% in the beginning of the growing season (spring) to 40% at the end of the growing season (autumn/winter). Due to the harvesting regime followed in this trial, where new regrowth was harvested, it was not possible to compare digestibilities at the beginning and end of the season. *In vitro* digestibility from hand harvesting, is, however, only an indication of the potential digestibility and could be different from what the animal consumes due to selective grazing (Van Niekerk, 1997).

There were no significant ($P \geq 0.05$) correlations between the digestibility or CP content of stem material and that of the whole plant. This can be attributed to the relatively young stage at which the grasses were harvested. If it had been delayed until after flowering, there might have been a significant affect on the nutritive values of the grasses.

The crude protein content of the grasses tended to be more affected by the amount of water available than was digestibility. This may be due to the mode of uptake of nitrogen, where water plays an important role. With respect to CP there were clear differences between grass species, with the two creeping grasses, the *Cynodon* hybrid and *P. clandestinum*, containing much more crude protein (average of 8.5%) than the three tufted grasses (average of 5.5%). Hefer and Tainton (1990) found that *P. clandestinum* had a higher CP content than *Cynodon* under growing conditions in Natal. The opposite was, however, found in this trial. According to Tainton (1988) CP

contents of as high as 32% have been reported for *P. clandestinum*. Crude protein content values for *P. clandestinum* in other literature ranged from 7.6 to 23.3% (Theron and Arnott, 1977; Dugmore and Du Toit, 1988; Rethman and De Witt, 1988), while CP of *Cynodon* ranged from 7.3 to 20.8% (Olsen, 1974; Theron and Arnott, 1977; Dugmore *et al.*, 1985; Rethman and De Witt, 1988; Nel, 1989). Van Niekerk (1997) indicated that grasses high in CP, often produce lower yields. This might explain the relatively low yields of *P. clandestinum* (Marais *et al.*, unpublished). The CP content of the other grasses ranged from high (15 - 25%) to low (3 - 5%) (Olsen, 1972; Rodel and Boulwood, 1981; Grunow and Rabie, 1985; Pieterse *et al.*, 1989; Dickinson *et al.*, 1990; WanHassan *et al.*, 1990; Dannhauser, 1991(a), (b); Nel, 1994; Snyman, 1994; Singh *et al.*, 1995; Pieterse *et al.*, 1997).

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CHAPTER 5

WATER USE EFFICIENCY OF FIVE PERENNIAL SUB-TROPICAL GRASS SPECIES AT FOUR LEVELS OF WATER AVAILABILITY

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Abstract

The effect of four levels of water availability on the water use efficiency of five subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*) was evaluated in a small plot trial under a rain shelter at the University of Pretoria. The four treatments were: soil profile brought to 25 (W1), 50 (W2), 75 (W3) and 100% (W4 - the control) of field capacity on a weekly basis.

The grasses differed from each other in terms of water use efficiency, regardless of whether it was expressed as dry matter yield (WUE_{DM}), digestible dry matter yield (WUE_{DDM}) or crude protein yield (WUE_{CP}). As could be expected, WUE_{DM} (10.7 - 17.2 kg ha mm) was higher than that of WUE_{DDM} (5.9 - 9.9 kg ha mm) with WUE_{CP} (0.9 - 1.6 kg ha mm) the lowest for all the grass species.

In both seasons *C. ciliaris* was one of the more efficient water users. The relative

water use efficiency of the other grasses varied from season to season. Where WUE_{CP} is of particular importance (for example in dairy enterprises), the *Cynodon* hybrid should be kept in mind, since it had the highest value over the two year period.

The WUE (WUE_{DM} , WUE_{DDM} and WUE_{CP}) of the grasses tended to be better under non-control conditions. Good management is, however, important under these conditions to ensure not only a high WUE, but also satisfactory yields.

Keywords

Cenchrus ciliaris, *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum*, *Pennisetum clandestinum*, water use efficiency

5.1 Introduction

Water use efficiency (WUE) is a way to evaluate plant species in terms of their ability to produce with a certain amount of water available. There are many factors affecting WUE, including the type of plant/plant community, soil type, soil depth, climatic conditions, frequency and intensity of watering and utilization practices. To be able to evaluate a plant's WUE, as many of these factors as possible should be kept constant to ensure a fair comparison between the grass species. From there, plant species that are able to produce more with less water should be favoured in areas with limited water resources.

Water-use efficiency (WUE) can be expressed in a hydrological and physiological context. In a purely hydrological context, WUE has been defined as "the ratio of the

volume of water used productively, i.e., transpired and in some cases also evaporated, from the area under study, to the volume of water potentially available for that purpose, i.e., that reaching the crop growing region via rainfall and irrigation plus that available from the soil” (Stanhill, 1986).

Physiologically it can be defined as “the ratio of the weight of crop water loss to the atmosphere, to that of its yield or total dry matter production” (Stanhill, 1986). Most often the hydrological and physiological definitions are combined and WUE is expressed as the amount of dry material (kg) being produced per area (ha) per mm water. The latter can be defined as water transpired/evapotranspired/ irrigated etc. and should, therefore, be clearly defined.

In this report, WUE is given in terms of dry matter yield, digestible dry matter yield or crude protein dry matter yield (kg) per area (ha) per amount of water (mm) evapotranspired. The amount of water was calculated as the sum total of water applied throughout the trial period together with the water deficit at the end of the season (Marais *et al.*, unpublished (a)).

The hypotheses for this report are:

- that the grass species will differ in their ability to use water efficiently and
- that the grasses will use water more efficiently under water limiting than non-limiting conditions.

5.2 Materials and Methods

Five subtropical perennial grasses were established under an automatic rain shelter

on the Hatfield Experimental Farm, of the University of Pretoria in Pretoria, (25°45'S, 28°16'E), South Africa, during December 1995. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. Coastcross II (K11) (Coastcross bermudagrass), *Digitaria eriantha* subsp. *eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass).

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991) with 30% clay in the top soil. The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon, which contains coarse gravel. The experimental plots were 2.5 x 2.0 m in size and separated by asbestos plates to a depth of 1.2 m.

During June 1995, seeds of *C. ciliaris*, *P. maximum*, *D. eriantha* and *P. clandestinum* were sown in seedling trays and kept in a greenhouse until December 1995. *C. ciliaris*, *P. maximum* and *D. eriantha* which are tufted or bunch grasses, were established at a rate of 300 000 plants ha⁻¹, while the creeping grasses (the *Cynodon* hybrid & *P. clandestinum*) were established at 160 000 plants ha⁻¹. The *Cynodon* hybrid was established using vegetative material collected on the experimental farm. The initial germination rate of *D. eriantha* was less than adequate and additional seedlings had to be propagated. This delayed transplanting of this species from trays to the field site by ten weeks compared to the other species.

A neutron probe access tube was located in the centre of each plot. Neutron probe counts, using a Campbell neutron probe (503 DR), were taken at nine depths

increments, each of 200 mm, on a weekly basis for all plots. These counts, which are related to the volumetric water content, were then incorporated into a calibration equation to determine the water deficit for each layer. Just before the onset of each growing season, the soil profiles of all the plots were brought to field capacity. Only then were the plants subjected to four levels of water availability.

The water availability levels used were:

- W1 - apply 25% of the amount given to W4.
- W2 - apply 50% of the amount given to W4
- W3 - apply 75% of the amount given to W4
- W4 - control, the soil profiles were brought to field capacity on a weekly basis

Water was applied by means of flood irrigation and the amounts of water applied were monitored using water flow meters.

During the establishment season (1995/96), the grasses were not subjected to differential irrigation treatments to ensure a good establishment as it has been found that some of these grasses only start to produce optimally during the second or third year. To ensure a fair comparison of the species, treatments were thus only imposed in the second (1996/97) and third seasons (1997/98).

According to soil analyses, the pH(H₂O) of the experimental soil was neutral. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top soil (30 mg kg⁻¹ P; 108 mg kg⁻¹ K) was much higher than that of the subsoil (8 mg kg⁻¹ P; 67 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and potassium

status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary. As the plots were not grazed, but removed as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (1995/96 season), the plots received 75 kg N ha⁻¹, 40 kg P ha⁻¹ and 200 kg K ha⁻¹. Nitrogen and potassium were also applied to all plots as top dressings during the summer growing season, resulting in a total of 450 kg N ha⁻¹ a⁻¹, 40 kg P ha⁻¹ a⁻¹ and 400 kg K ha⁻¹ a⁻¹. In the subsequent seasons (1996/97 and 1997/98), nitrogen and potassium were applied to all plots as top dressings at rates of 225, 338, 394 and 450 kg N ha⁻¹ a⁻¹ and 200, 300, 350 and 400 kg K ha⁻¹ a⁻¹ for the W1, W2, W3 and W4 water availability levels respectively. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

The grasses were harvested at the 10% flowering stage, except for *P. clandestinum*, which was not allowed to grow taller than 40 cm. This resulted in an average of three to four cuts during each season. *C. ciliaris*, *D. eriantha* and *P. maximum* (tufted grasses) were cut to a height of 10 cm while the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) were cut to 5 cm. A sample plot of one square metre, in the middle of each plot, was harvested, after which the rest of the plot was also cut to the same height. The sample plots were permanently marked to ensure that the samples were taken from the same area at each harvest. The material was dried to constant mass for 48 hours at 65°C.

Intact plants, as well as the different yield components, were milled after drying. A Wiley no. 3 mill, with a 1 mm sieve was used. The milled product was then used to determine the *in vitro* dry matter digestibility and crude protein content of the crops.

In vitro dry matter digestibility

The dry matter, organic matter and ash content of the samples were determined by drying 2 g or each milled sample for 24 hours at 60°C (dry matter content), before incinerating at 600°C for 4 hours (ash content). The organic matter content was calculated as the difference between the dry matter and ash contents. For the *in vitro* digestibility of the crops, 0.2 g plant material was used for the analysis using the method proposed by Tilley and Terry (1963).

Crude protein content

The milled plant samples were analysed for nitrogen content using the Kjeldahl technique (Association of Official Analytical Chemists, 1984). The analysis were done by the Soil Science Laboratory of the Department of Plant Production and Soil Science. The values were multiplied by 6.25 (Van der Merwe and Smith, 1991) to express the results in terms of crude protein content.

A fully randomized block design with three replications was used. The statistical analysis was done using the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data is presented in the Appendix (Tables A5.1 - A5.10).

5.3 Results

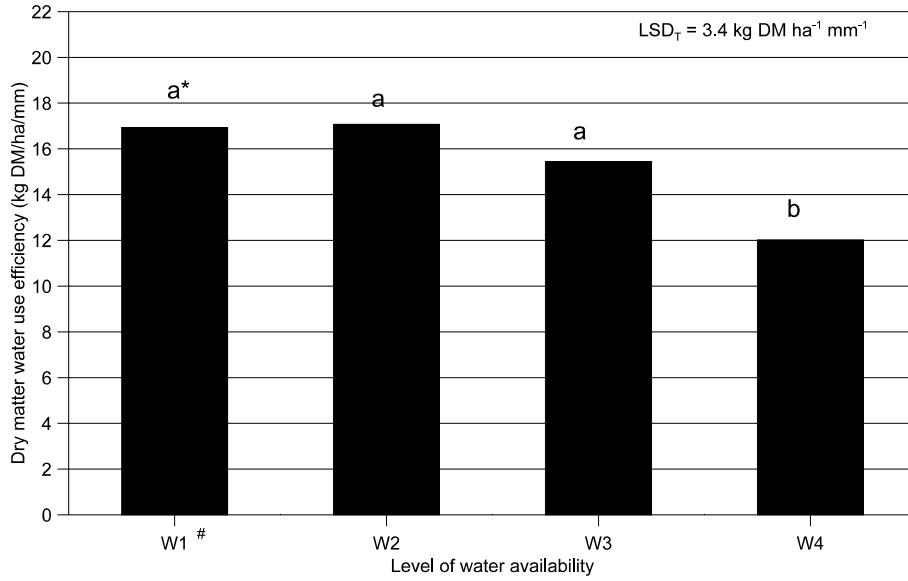
5.3.1 Water use efficiency in terms of dry matter yield (WUE_{DM})

In both seasons there were significant ($P \leq 0.05$) differences in the WUE_{DM} of the different irrigation levels. Water was used more efficiently under “non-control” conditions (Figures 5.1 and 5.2). In the 1996/97 season (Figure 5.1) it was only the control (W4) treatment that used water less efficiently than the other three treatments (W1, W2 & W3), while in the following season (Figure 5.2) both the well watered treatments (W3 and W4) used water less efficiently than under severe water limiting conditions (W1). Bielorai (1982) and Aggarwal and Sinha (1983) also observed better WUE under water stress than under non-limiting conditions. There was, however, a poor correlation between water use and WUE due to many factors contributing to water losses that do not necessarily contribute to yield.

The grasses tended to differ from each other in terms of water use efficiency. In both seasons *C. ciliaris* was one of the more efficient water users. The relative water use efficiency of the other grasses varied from season to season.

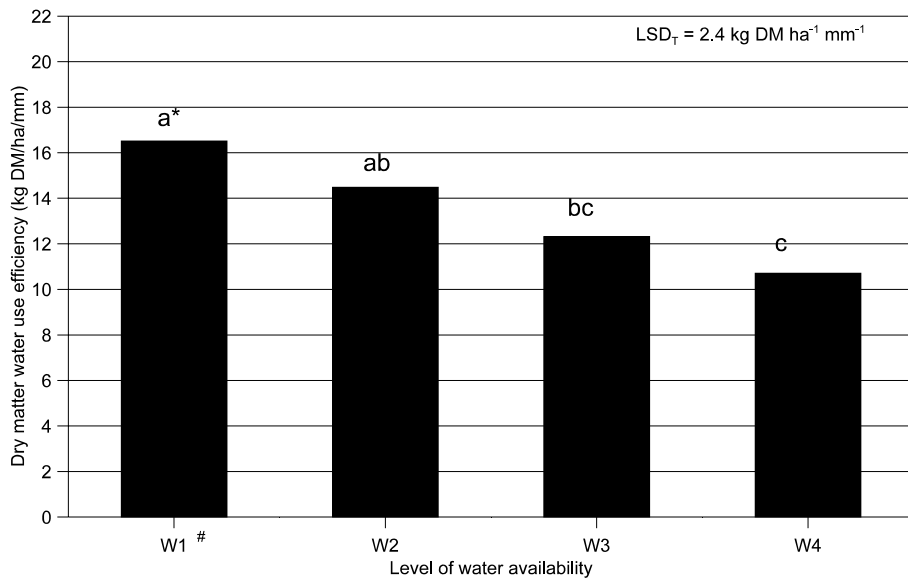
In both seasons *C. ciliaris*, *P. maximum* and *P. clandestinum* used water most efficiently under W1 conditions, while the *Cynodon* hybrid and *D. eriantha* used water most efficiently under W1, W2 and W3 conditions (Table 5.1). All five grasses, however, used water the least efficiently when water was not limiting (W4). This is contrary to the findings of Dobrenz *et al.* (1969) who reported a decrease in WUE for *P. maximum antidotale* when soil moisture stress increased.

In this trial *C. ciliaris* and the *Cynodon* hybrid were the most efficient water users. The use of these grasses under a wide range of moisture conditions can, therefore, be recommended. The same can not, however, be said for *P. maximum* and *P. clandestinum* which were the least efficient water users in this trial. From this trial, no definite conclusions can be drawn about *D. eriantha*, except that water was more efficiently used under water limiting (W1) than control conditions (W4).



* Treatments with the same letter do not differ significantly from each other ($P < 0.05$)
 # W1 - severely water stressed level, W4 - control

Figure 5.1 The average dry matter water use efficiency of five grass species for four levels of water availability in the 1996/97 season.



* Treatments with the same letter do not differ significantly from each other ($P < 0.05$)
 # W1 - severely water stressed level, W4 - control

Figure 5.2 The average dry matter water use efficiency of five grass species for four levels of water availability in the 1997/98 season.

Table 5.1 Influence of level of water availability on the WUE_{DM} ($\text{kg DM ha}^{-1} \text{mm}^{-1}$) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	24.9	24.7	22.8	17.6	22.5
<i>Cynodon</i> hybrid	17.4	14.3	16.2	12.4	15.1
<i>D. eriantha</i>	19.4	24.9	19.0	14.3	19.4
<i>P. maximum</i>	14.9	14.6	12.7	11.4	13.4
<i>P. clandestinum</i>	8.6	7.5	7.3	5.2	7.2
Mean	17.0	17.2	15.6	12.1	
LSD _T (G) = 4.0					
LSD _T (I) = 3.4					
1997/98 season					
<i>C. ciliaris</i>	23.9	19.3	16.3	12.7	18.0
<i>Cynodon</i> hybrid	19.9	20.0	18.8	16.3	18.7
<i>D. eriantha</i>	13.0	11.3	9.5	7.9	10.4
<i>P. maximum</i>	11.6	8.5	6.7	6.4	8.3
<i>P. clandestinum</i>	14.2	13.4	10.4	10.4	12.1
Mean	16.5	14.5	12.3	10.7	
LSD _T (G) = 2.9					
LSD _T (I) = 2.4					

* W1 -severely water stressed level, W4 - control

5.3.2 Water use efficiency in terms of digestible dry matter yield (WUE_{DDM})

The digestible dry matter yields of *C. ciliaris*, *P. maximum* and *D. eriantha*, were higher in the 1996/97 than the 1997/98 season (Table 5.2). This is in accordance with the dry matter yields (Marais *et al.*, unpublished (b)), where the *Cynodon* hybrid and *P. clandestinum* were the only grasses which produced higher yields in the 1997/98 than the 1996/97 season. In the 1996/97 season only *C. ciliaris* produced significantly ($P \leq 0.05$) higher digestible dry matter yields than the other grasses

(Table 5.2). In the following season (1997/98 season), the *Cynodon* hybrid also (in addition to *C. ciliaris*) produced significantly ($P \leq 0.05$) higher digestible dry matter yields than *D. eriantha*, *P. maximum* and *P. clandestinum*. In terms of the level of water availability (Table 5.2), the digestible dry matter yields were significantly ($P \leq 0.05$) higher under W3 and W4 than under W1 conditions, in both seasons. This was also true for the dry matter yields reported by Marais *et al.* (unpublished (b)).

There was a significant ($P \leq 0.05$) interaction between water availability and grass species in the 1997/98 season (Table 5.3) for WUE_{DDM} . During that season, *C. ciliaris* and *D. eriantha* used water most efficiently with an increase in water deficit. For *P. maximum*, the *Cynodon* hybrid and *P. clandestinum* water was used more efficiently under W1, and sometimes W3 conditions, than under control conditions (W4). The differences in WUE_{DDM} between W2, W3 and W4 were not, however, always significant ($P \leq 0.05$) for the latter three grasses. As with WUE_{DM} , WUE_{DDM} was again better under water stressed than under control conditions (Table 5.3). In both seasons, *P. maximum* and *P. clandestinum* used water the least efficiently.

Table 5.2 Influence of level of water availability on the digestible dry matter yield (t DDM ha⁻¹) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	5.9	8.5	10.8	10.6	9.0
<i>Cynodon</i> hybrid	4.3	4.8	6.6	6.5	5.6
<i>D. eriantha</i>	3.1	5.6	5.5	7.9	5.6
<i>P. maximum</i>	4.3	5.7	5.8	5.1	5.2
<i>P. clandestinum</i>	2.5	3.3	4.0	3.7	3.4
Mean	4.0	5.6	6.5	6.8	
LSD _T (G) = 2.4					
LSD _T (I) = 2.0					
1997/98 season					
<i>C. ciliaris</i>	7.5	8.1	8.4	7.6	7.9
<i>Cynodon</i> hybrid	5.3	6.7	8.6	9.4	7.5
<i>D. eriantha</i>	4.0	4.6	5.2	5.8	4.9
<i>P. maximum</i>	3.6	3.5	4.2	5.1	4.1
<i>P. clandestinum</i>	3.3	2.8	3.8	5.7	3.9
Mean	4.7	5.2	6.0	6.7	
LSD _T (G) = 1.2					
LSD _T (I) = 1.0					

* W1 -severely water stressed level, W4 - control

Table 5.3 Influence of level of water availability on the WUE_{DDM} ($\text{kg DDM ha}^{-1} \text{mm}^{-1}$) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	12.6	12.4	12.3	9.7	11.8
<i>Cynodon</i> hybrid	10.2	7.8	8.8	6.7	8.4
<i>D. eriantha</i>	12.1	14.5	11.1	8.5	11.6
<i>P. maximum</i>	9.1	9.3	7.9	7.4	8.4
<i>P. clandestinum</i>	5.3	4.8	4.7	3.4	4.5
Mean	9.9	9.8	9.0	7.1	
LSD _T (G) = 2.2					
LSD _T (I) = 1.9					
1997/98 season					
<i>C. ciliaris</i>	14.4	11.3	9.8	6.9	10.6
<i>Cynodon</i> hybrid	11.0	10.1	11.3	9.7	10.5
<i>D. eriantha</i>	7.8	6.3	5.4	4.6	6.0
<i>P. maximum</i>	5.9	3.9	3.6	3.5	4.2
<i>P. clandestinum</i>	6.0	4.5	4.2	5.0	4.9
Mean	9.0	7.2	6.9	5.9	
LSD _T (G) = 1.7					
LSD _T (I) = 1.4					
LSD _T (GxI) = 0.7					

* W1 -severely water stressed level, W4 - control

5.3.3 Water use efficiency in terms of crude protein yield (WUE_{CP})

The crude protein yield of all the grasses, except that of *D. eriantha*, tended to be higher in the 1997/98 than 1996/97 season (Table 5.4). In both seasons, *C. ciliaris* and the *Cynodon* hybrid produced higher crude protein yields than the other grasses. The crude protein yields tended to be higher under control (W4) than severely water stressed (W1) conditions in both seasons.

As with WUE_{DM} and WUE_{DDM} , water use efficiency in terms of crude protein yield was considerably better under severe water limiting (W1) than under control conditions (W4) (Table 5.5). The *Cynodon* hybrid, *C. ciliaris* and *D. eriantha* used water the most efficiently in the 1996/97 season while the WUE_{CP} of the *Cynodon* hybrid and *C. ciliaris* were the best in the following season. *P. maximum* and *P. clandestinum* were highly variable in this respect.

Table 5.4 Influence of level of water availability on the crude protein yield (t CP ha⁻¹) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	0.5	0.7	1.0	0.9	0.8
<i>Cynodon</i> hybrid	0.8	0.8	1.3	1.3	1.0
<i>D. eriantha</i>	0.3	0.4	0.5	0.8	0.5
<i>P. maximum</i>	0.4	0.5	0.4	0.5	0.4
<i>P. clandestinum</i>	0.4	0.5	0.6	0.5	0.5
Mean	0.5	0.6	0.7	0.8	
LSD _T (G) = 0.3					
LSD _T (I) = 0.2					
1997/98 season					
<i>C. ciliaris</i>	1.1	1.6	0.9	1.0	1.1
<i>Cynodon</i> hybrid	1.3	1.4	1.4	2.2	1.6
<i>D. eriantha</i>	0.4	0.4	0.5	0.5	0.5
<i>P. maximum</i>	0.5	0.5	0.4	0.6	0.5
<i>P. clandestinum</i>	0.8	0.7	0.7	1.0	0.8
Mean	0.8	0.9	0.8	1.1	
LSD _T (G) = 0.3					
LSD _T (I) = 0.2					
LSD _T (GxI) = 0.1					

* W1 -severely water stressed level, W4 - control

Table 5.5 Influence of level of water availability on the WUE_{CP} ($kg\ CP\ ha^{-1}\ mm^{-1}$) of five perennial grasses.

Grass	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
1996/97 season					
<i>C. ciliaris</i>	1.1	1.0	1.1	0.9	1.0
<i>Cynodon</i> hybrid	1.8	1.3	1.7	1.3	1.5
<i>D. eriantha</i>	1.1	1.0	1.0	0.9	1.0
<i>P. maximum</i>	1.4	1.3	1.2	1.0	1.2
<i>P. clandestinum</i>	0.8	0.7	0.7	0.5	0.7
Mean	1.2	1.1	1.1	0.9	
LSD _T (G) = 0.3					
LSD _T (I) = 0.3					
1997/98 season					
<i>C. ciliaris</i>	2.2	2.2	1.0	1.0	1.6
<i>Cynodon</i> hybrid	2.7	2.1	1.8	2.3	2.2
<i>D. eriantha</i>	0.7	0.5	0.6	0.4	0.6
<i>P. maximum</i>	0.9	0.5	0.3	0.4	0.5
<i>P. clandestinum</i>	1.4	1.1	0.7	0.9	1.0
Mean	1.6	1.3	0.9	1.0	
LSD _T (G) = 0.3					
LSD _T (GxI) = 0.3					
LSD _T (GxI) = 0.1					

* W1 -severely water stressed level, W4 - control

5.4 Discussion and Conclusions

The grasses did differ from each other in terms of water use efficiency, regardless of whether this was expressed as dry matter yield (WUE_{DM}), digestible dry matter yield (WUE_{DDM}) or crude protein yield (WUE_{CP}). As could be expected, WUE_{DM} ($10.7 - 17.2\ kg\ ha^{-1}\ mm^{-1}$) was higher than that of WUE_{DDM} ($5.9 - 9.9\ kg\ ha^{-1}\ mm^{-1}$) with WUE_{CP} ($0.9 - 1.6\ kg\ ha^{-1}\ mm^{-1}$) the lowest for all the grass species.

In both seasons *C. ciliaris* was one of the more efficient water users. The relative water use efficiency of the other grasses varied from season to season. Where WUE_{CP} is of particular importance (for example in dairy enterprises), the *Cynodon* hybrid should be kept in mind, since it had the highest value over the two year period.

In the literature a few WUE_{DM} values have been reported, but these are far lower (3 - 9 kg DM ha⁻¹ mm⁻¹ for *D. eriantha*; 2 - 6 kg DM ha⁻¹ mm⁻¹ for *P. maximum* and 2.5 - 7 kg DM ha⁻¹ mm⁻¹ for *C. ciliaris* (Snyman *et al.*, 1987; Snyman, 1989; 1994) than the values reported for this trial (7.9 - 24.9 kg ha⁻¹ mm⁻¹ for *D. eriantha*; 6.4 - 14.9 kg ha⁻¹ mm⁻¹ for *P. maximum*; 5.2 - 24.9 kg ha⁻¹ mm⁻¹ and 12.7 - 24.9 kg ha⁻¹ mm⁻¹ for *Cenchrus*). The reasons being that:

- some of the grasses reported on were rangeland species (Snyman *et al.*, 1987; Snyman, 1989; 1994) where the growing conditions were not ideal (seed quality, fertilizer, crop protection etc.)
- evaporation and transpiration are influenced by the vapour pressure deficit, which differs from area to area (for example low at the coastal areas and higher in the dry Karoo) and season to season. For correct comparisons, the WUE should first of all be corrected for the vapour deficit in that area for the specific time the trial was conducted
- the type of plant/plant community, soil type, soil depth, climatic conditions, frequency and intensity of watering and utilization practices may differ for each situation and thus have an affect on the results (Opperman *et al.*, 1977; Snyman *et al.*, 1980 and 1987; Stanhill, 1986; Stout, 1992; Saeed and El-Nadi, 1997).

It was only Stout (1992) who reported comparable WUE values (of 4.4 - 25.0 kg DM ha⁻¹ mm⁻¹) for *Dactylis glomerata* and *Panicum virgatum*.

The WUE (WUE_{DM}, WUE_{DDM} and WUE_{CP}) of the grasses tended to be better under non-control conditions. Beukes and Barnard (1985); Devitt *et al.*, (1992); Moolman (1993) and Garrot and Mancino (1994) also reported better WUE under conditions where the soil profiles were not brought back to field capacity with each watering. There is, however, a threshold of tolerance and when water deficits become too severe it can lead to not only poor WUE but also to poor dry matter production. This implies a higher management input to ensure optimum production and WUE.

Although no C₃ grass species were used in this particular trial, it is of value to mention that C₄ grass species were found to be far more WUE than C₃ grass species (Ng *et al.*, 1975; Forde *et al.*, 1976; Christie, 1978; Brown and Simmons, 1979; Frean *et al.*, 1980; Kramer, 1983; Feldhake and Boyer, 1995). Due to a better WUE of C₄ than C₃ grass species, the introduction of C₄ grass species into a new system should not have a negative effect on the ecosystem (Feldhake and Boyer, 1995) and under South African conditions where drought often occurs, the use of C₄ grasses could mean more fodder with less water.

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CHAPTER 6

THE GROWTH AND PRODUCTIVITY OF FIVE PERENNIAL SUB-TROPICAL GRASS SPECIES UNDER IRRIGATION IN PRETORIA, SOUTH AFRICA.

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Abstract

Five subtropical grass species, *Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*, were cultivated in 15 m² plots with non-limiting water and nutrients. The growth patterns and productivity of the five grasses were studied to facilitate management and utilization recommendations.

With adequate water and nutrients, all five grass species were able to produce green material throughout the summer growing season. Under the conditions on the Hatfield Experimental Farm of the University of Pretoria, *C. ciliaris*, *D. eriantha* and *P. maximum* produced the highest growth rate and production during the 1997/98 growing season. During the first part of each growing cycle, the growth rate and production of *P. clandestinum* and the *Cynodon* hybrid were similar. Towards the

end of the cycles, however, this changed with the growth of the *Cynodon* hybrid surpassing that of *P. clandestinum*. *P. clandestinum*, despite a low growth rate, had a reliable leaf production throughout the growing season. This was different from the other four grasses, which started to flower at the end of each growth cycle, resulting in an increase in the amount and proportion of stem material.

It should also be kept in mind that these grasses were subjected to a light to medium defoliation, resulting in a high growth rate during the second growth cycle. This might not have been the case if heavy grazing, which could reduce the photosynthetic leaf area, had been applied.

Due to the lower yields of *P. clandestinum* it is , however, necessary to adjust animal numbers and period of stay in each paddock very carefully. *P. clandestinum* is also prone to lodging if left to grow too tall, causing the lower leaves to senesce and thus reduce the productivity. The periods of absence should not, therefore, be too long.

The *Cynodon* hybrid, *C. ciliaris*, *D. eriantha* and *P. maximum* tended to reach full bloom within one to two weeks of each other. The utilization of these species, for grazing, hay or foggage, and the impact of such flowering on quality (because of the increase in the proportion of stem/fibre) will, therefore, influence harvest/management decisions.

Keywords

Cenchrus ciliaris, *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum*

maximum, *Pennisetum clandestinum*, growth rate, leaf area

6.1 Introduction

The growth patterns of a grass can provide information on the availability of that species at a given time of the year. This can help with fodder flow planning (Smith *et al.*, 1986; Pieterse *et al.*, 1988) and identifying grass species for specific purposes in a specific area. This information can also play an important role in making management decisions that will ensure optimum utilization of the grass species without impacting upon growth in the subsequent season.

In this study the growth patterns of the five grasses under non-limiting growth conditions were determined. The hypothesis being that there will be differences in growth patterns leading to different management and utilization strategies.

6.2 Materials and Methods

Five subtropical perennial grasses were established in 15 m² plots on the Hatfield Experimental Farm, Pretoria, (25°45'S, 28°16'E), South Africa, during October 1996. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. K11 (Coach-grass), *Digitaria eriantha* subsp. *eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass). A fully randomized design with three replications was used.

The grasses were established using seedlings produced during the winter of 1996 and transplanted after the last cold snap in October of that year. Seedlings were produced for all the grasses except the *Cynodon* hybrid, which was established from vegetative sprigs collected on the experimental farm. The creeping grasses (the *Cynodon* hybrid and *P. clandestinum*) were established at a rate of 160 000 plants ha⁻¹ while the tufted grasses (*C. ciliaris*, *D. eriantha* and *P. maximum*) were planted at a rate of 300 000 plants ha⁻¹. After establishment in 1996, the grasses were irrigated on a weekly basis. An overhead irrigation system was used and individual plots were not differentially irrigated. In the first week of September 1997 all the plots received 50 mm irrigation. The irrigation/rainfall information for the period September 1997 - April 1998 is set out in table 6.1.

Table 6.1 Irrigation applied and rainfall recorded on the experimental farm during September 1997 till April 1998.

Month	Irrigation (mm)	Rainfall (mm)	Total (mm)
September 1997	85	42	127
October	125	23.4	148.4
November	50	127.6	177.6
December	60	98.6	158.6
January 1998	25	135.2	160.2
February	50	120.5	170.5
March	70	69.4	139.4
Till 20 April 1998	30	1.5	31.5
Total (mm)	505	618.2	1 113.2

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991)

with 30% clay in the top soil. The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon that contains coarse gravel. According to soil analyses, the pH(H₂O) of the experimental soil was on average 6.02. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top (0 - 30 cm) soil (24 mg kg⁻¹ P; 76 mg kg⁻¹ K) was much higher than that of the sub (30 - 60 cm) soil (1 mg kg⁻¹ P; 19 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and potassium status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary. As the plots were not grazed, but removed as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (October 1996), the plots received 50 kg N ha⁻¹, 40 kg P ha⁻¹ and 25 kg K ha⁻¹. After planting each plot received 75 kg N ha⁻¹ and 200 kg K ha⁻¹ during January 1997 and March 1997 as top dressing. During the autumn and winter of 1997 the plots received neither irrigation nor fertilizers. At the beginning of October 1997 every plot received a top dressing of 75 kg N ha⁻¹ and 200 kg K ha⁻¹. The grasses were cut back during January 1998, after which each plot received another top dressing of 75 kg N ha⁻¹ and 200 kg K ha⁻¹. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

In June 1997, the grasses on all the plots were cut back to a height of 5 cm for the creeping grasses, while the tufted grasses were cut back to a height of 10 cm. During the winter neither water nor fertilizer were applied and the growth was negligible till late in September 1997. Starting from the second week in October 1997

in 20 day intervals, sample plots of 1 m² in each main plot were harvested. The grasses in a sample plot were cut back to a height of 5 (creeping grasses) or 10 cm (tufted grasses), while the rest of the main plot were left undisturbed. At the end of December 1997, *C. ciliaris*, the *Cynodon* hybrid, *D. eriantha* and *P. maximum* reached full bloom and all the main plots were cut back to the relevant heights. For *P. clandestinum* the main plots were cut back as soon as the grasses reached a height of 40 cm. The materials of the sequential harvests were divided into leaf and stem material after which the leaf area were measured before all the material was dried for 48 h at 65°C. The dry matter yields were determined subsequently.

6.3 Results

6.3.1 Growth rate and cumulative dry matter production

In the study area, September is characterised by relative cool nights, resulting in new growth being delayed until the end of September / beginning of October. During the 20 days of the first growth cycle (20 October 1997), there were very little differences in the growth rate of the five species (Figure 6.1). During the following three weeks, slight differences in growth rates could be discerned. At the beginning of December 1997, some differences in the growth rates of the five grasses are evident, with these becoming stronger in mid December. At this stage, *C. ciliaris* and *D. eriantha* had higher growth rates followed by *P. maximum*, with the *Cynodon* hybrid and *P. clandestinum* having almost the same growth rate (Figure 6.1). At the end of the first growth cycle (8 January 1998), the *Cynodon* hybrid exhibited a higher growth rate than that of *P. clandestinum*, but this was still not as high as that of the other three grass species.

In the first growth cycle, there were no differences in growth rate between *D. eriantha* and *C. ciliaris*, which had the highest yields (Figure 6.2), before they were cut back for the second growth cycle. The two creeping grasses, especially *P. clandestinum*, produced the lowest yields over the same growth period (Figure 6.2), with the growth rate and yield of *P. maximum* being lower than those of the other two tufted grasses, but higher than those of the two creeping grasses for the first growth cycle (Figure 6.1 and 6.2).

The yields in the second growth cycle were much higher than in the first growth cycle for all the grass species (Figure 6.2). The three tufted grass species again produced higher yields than the two creeping grasses. The yields of the three tufted species, at the end of the season did not differ much, but the yield of the *Cynodon* hybrid was much better than that of *P. clandestinum*.

As with the growth rate during the first growth cycle, the growth rate of the *Cynodon* hybrid was initially slow but during March and April (1998) it surpassed the growth of *P. clandestinum* (Figure 6.1). The growth rates of the three tufted grass species were essentially similar up until the end of March (1998), when the growth rate of *C. ciliaris* increased slightly and remained as such until the end of the trial (20 April 1998). The growth rate of *D. eriantha* and *P. maximum* only began to separate at the end of the trial (20 April 1998) with *D. eriantha* exhibiting a slightly higher growth rate than *P. maximum* (Figure 6.1).

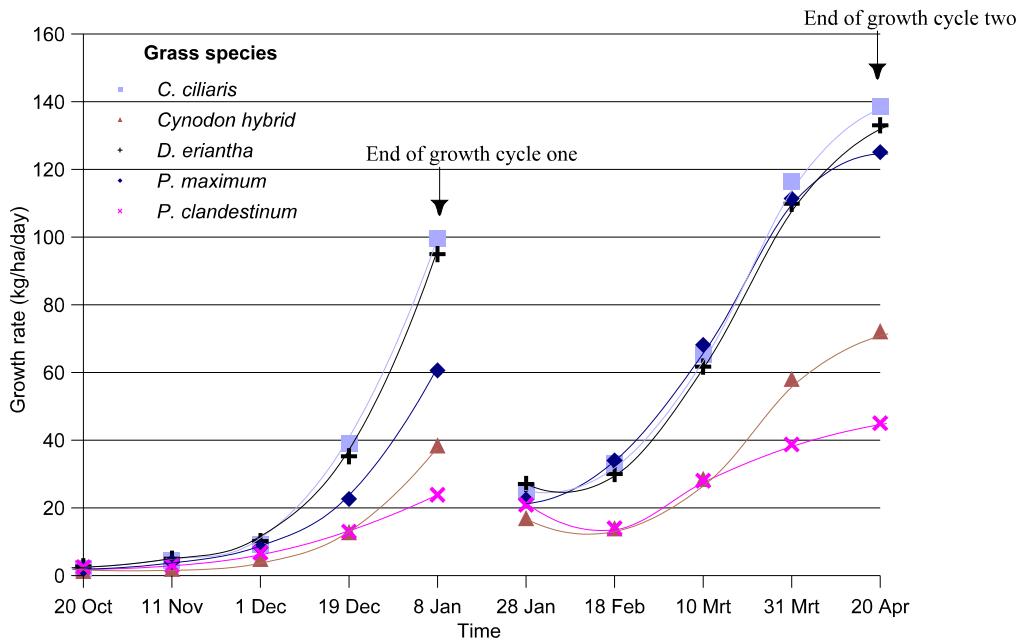


Figure 6.1 Relative growth rates of sub-tropical grasses over two growth cycles under irrigation.

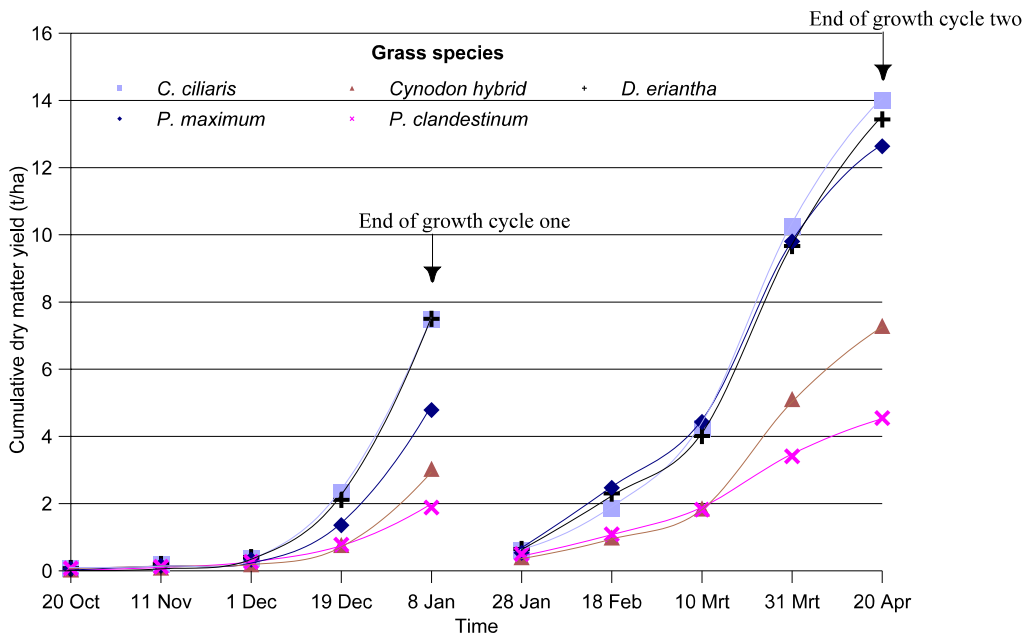


Figure 6.2 Cumulative dry matter yields of five grass species over two growth cycles, under irrigation.

6.3.2 Cumulative leaf area

The cumulative leaf area per sample plot (1 m²) (Figure 6.3) of all five grass species followed the same trend as the growth rate (Figure 6.1) and dry matter yield (Figure 6.2). There was, however, a clearer distinction between the species with *D. eriantha* maintaining the highest leaf area and *P. clandestinum* the lowest (Figure 6.3) during the first growth cycle.

In the second growth cycle the leaf area of the *Cynodon* hybrid was almost equal to that of *P. maximum*, but the leaf areas of all these grasses were lower than that of *C. ciliaris* and *D. eriantha* (Figure 6.3). The leaf area of *P. clandestinum* was once again the lowest of all the grass species.

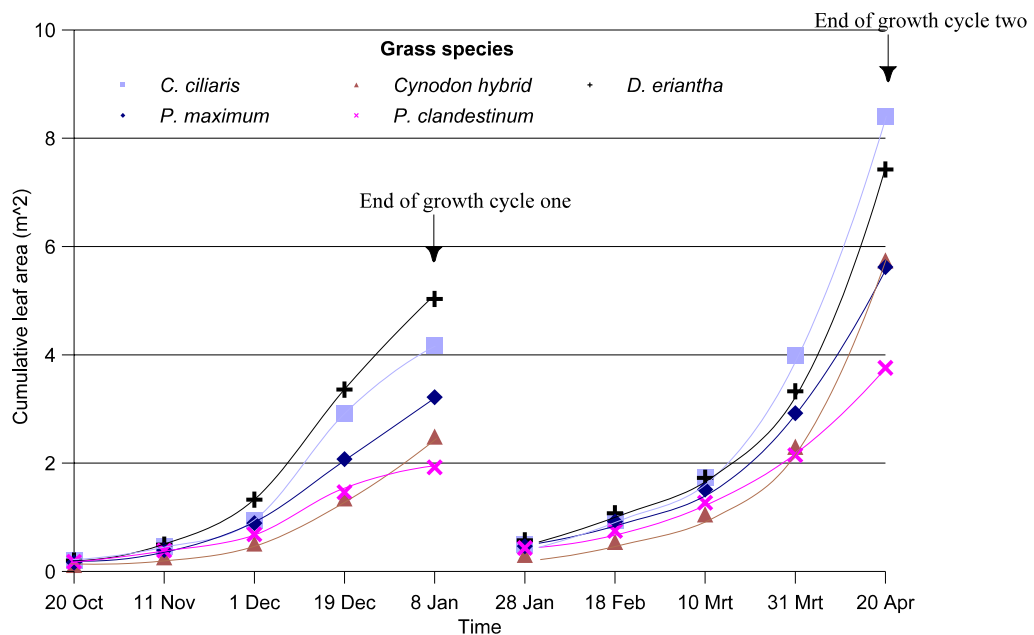


Figure 6.3 Cumulative leaf area of five grass species over each of two growth cycles.

6.3.3 Partitioning of assimilates to leaf, stem and inflorescence

The percentage leaf in the whole plant (Figure 6.4) was the highest in *P. clandestinum*, followed by *C. ciliaris* and the *Cynodon* hybrid. *D. eriantha* and *P. maximum* have the highest percentage stem, and the lowest proportion of leaf of these grasses.

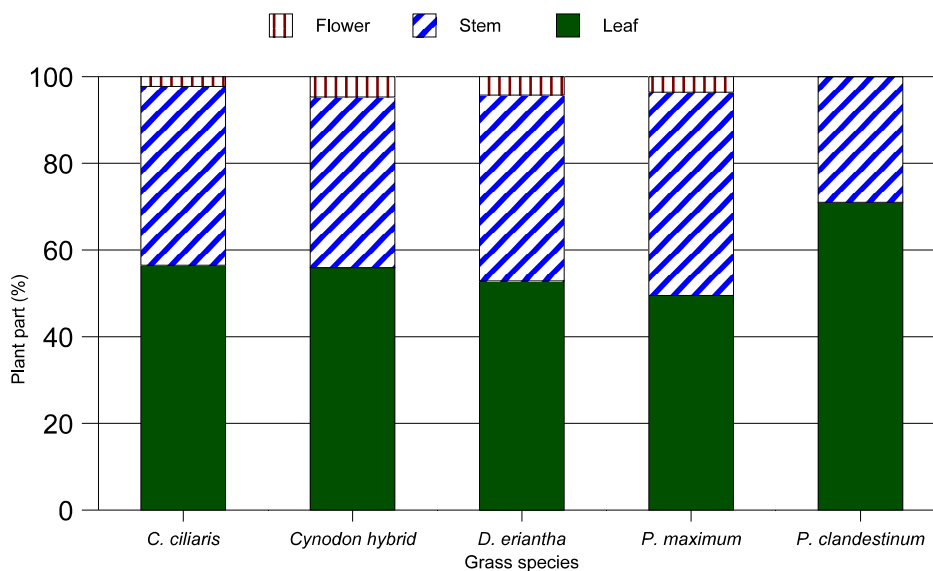


Figure 6.4 Partitioning of assimilates to leaf, stem and inflorescence of five sub-tropical grass species

6.4 Discussion and Conclusions

The growth patterns for the five grass species differed from each other. The tufted grass species (*C. ciliaris*, *D. eriantha* and *P. maximum*) tended to accumulate dry mass earlier in the season, compared to the creeping grass species (the *Cynodon* hybrid and *P. clandestinum*). From the point of view of utilization, *C. ciliaris*, *D. eriantha* and *P. maximum* are able to supply fodder sooner than the *Cynodon*

hybrid and *P. clandestinum* after cutting, possibly as a result of the higher stubble height and hence greater residual leaf area. These first three grasses, however, also reach maturity a lot faster with the creeping grasses which comparatively produce less stem and inflorescence.

P. clandestinum, for example, exhibits less fluctuation in growth rate over the season than the widely fluctuating tufted species. For future reference, one should take note that different cultivars may also have different growth rates and yield potentials (Goodenough *et al.*, 1984). Thus after identifying the best species for a specific purpose, the next step is to identify the best cultivar for that situation.

Due to the lower yields of *P. clandestinum* it is, however, necessary to adjust animal numbers and period of stay in each paddock very carefully. *P. clandestinum* is also prone to lodging if left to grow too tall, causing the lower leaves to senesce and thus reduce the productivity. The periods of absence should not, therefore, be too long.

C. ciliaris, the *Cynodon* hybrid, *D. eriantha* and *P. maximum* usually do not have a problem with lodging. These species can thus be left to grow out during the growing season to be used as standing hay in the winter months with the addition of supplementary licks, although it must be remembered that extended periods of stockpiling result in a higher proportion of stem in the standing hay with a corresponding decline in quality, because of the increase in percentage stem.

It must also be kept in mind that these grasses were subjected to a light to medium defoliation, resulting in a high growth rate during the second growth cycle. This might

not have been the case if heavy grazing, which could reduce the photosynthetic leaf area, had been applied. The grasses were also grown without water stress, ensuring green material throughout the season (Taylor *et al.*, 1976; Pieterse *et al.*, 1988), which might not have been the case under dryland or rainfed conditions.

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CHAPTER 7

MORPHOLOGICAL STUDY OF THE LEAVES OF FIVE SUB-TROPICAL PERENNIAL GRASS SPECIES

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Abstract

The effect of four levels of water availability on the leaf morphology of five subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum* and *Pennisetum clandestinum*) was evaluated in a small plot trial under a rain shelter at the University of Pretoria. The four treatments were: soil profile brought to 25 (W1), 50 (W2), 75 (W3) and 100% (W4 - the control) of field capacity on a weekly basis.

C. ciliaris and the *Cynodon* hybrid tended to have a large number of trichomes on the leaf surfaces, while the stomata were well protected from the environment by the veins. This may explain the adaptation of these species to drought conditions. In contrast *P. clandestinum* leaves had few trichomes and the stomata were much more exposed, which may result in poor water use efficiency and in-ability to grow under drought conditions. *P. maximum* also has the characteristics which should

have made it very productive and adaptive to drought conditions, but it did not fare very well under such conditions. *D. eriantha* had more stomata on the abaxial than adaxial leaf surface and the epidermis was covered by large wax crystals, it was however not enough to ensure the yields and water use efficiency of *C. ciliaris* and the *Cynodon* hybrid, although it was better than both *P. maximum* and *P. clandestinum*.

The availability of water and species interaction was significant ($P \leq 0.05$) with *C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum* tending to have more stomata with more water when looking at the adaxial leaf surface, while *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* also exhibited this tendency on the abaxial surface of leaves. No tendencies were observed for the other species. Overall, it may be concluded that water had very little effect on the number of stomata when compared with species differences, which had a much stronger effect.

Keywords

Cenchrus ciliaris, *Cynodon* hybrid, *Digitaria eriantha* subsp. *eriantha*, *Panicum maximum*, *Pennisetum clandestinum*, trichome, stomata, epidermis, wax crystals

7.1 Introduction

In a series of papers by Marais *et al.* (unpublished), it had become apparent that certain grass species were better adapted to drought conditions than others. The reasons for this may be genetic and the genetic make-up of a plant is reflected in its morphology. Of particular importance are the stomata and cuticle layers on the leaf surface, which could affect water loss and thus photosynthesis. Many authors have

found not only morphological but also anatomical changes in water stressed plants (Sullivan, 1972; Bleckmann *et al.*, 1980; Traore *et al.*, 1989). According to them, these changes could be linked to better water use and productivity under drought conditions.

In this paper the leaf surface morphology of the five grass species under non water limiting conditions are described, as different levels of water did not have an effect on the morphology of the species. The effect of water availability on the number of stomata was also evaluated.

7.2 Materials and Methods

Five subtropical perennial grasses were established under an automatic rain shelter on the Hatfield Experimental Farm, of the University of Pretoria in Pretoria, (25°45'S, 28°16'E), South Africa, during December 1995. The trial ended in June 1998. The five grasses were *Cenchrus ciliaris* cv. Molopo (Blue buffel-grass), a *Cynodon* hybrid cv. K11 (Coach-grass), *Digitaria eriantha* subsp. *eriantha* cv. Irene (Smuts finger-grass), *Panicum maximum* cv. Gatton (Guinea grass) and *Pennisetum clandestinum* cv. Whittet (Kikuyu grass).

The soil at the site is a Shorrocks series of the Hutton form (MacVicar *et al.*, 1991) with 30% clay in the top soil. The A-horizon of the soil is uniform to a depth of 1.2 m, before reaching the B-horizon, which contains coarse gravel. The experimental plots were 2.5 x 2.0 m in size and separated by asbestos plates to a depth of 1.2 m.

During June 1995, seeds of *C. ciliaris*, *P. maximum*, *D. eriantha* and *P. clandestinum*

were sown in seedling trays and kept in a greenhouse until December 1995. *C. ciliaris*, *P. maximum* and *D. eriantha*, which are tufted or bunch grasses, were established at a rate of 300 000 plants ha⁻¹, while the creeping grasses (the *Cynodon* hybrid & *P. clandestinum*) were established at 160 000 plants ha⁻¹. The *Cynodon* hybrid was established using vegetative material collected on the experimental farm. The initial germination rate of *D. eriantha* was less than adequate and additional seedlings had to be propagated. This delayed transplanting of this species from trays to the field site by ten weeks compared to the other species.

A neutron probe access tube was located in the centre of each plot. Neutron probe counts in all the plots were taken at nine depth increments, each of 200 mm, on a weekly basis. These counts, which are related to the volumetric water content, were then incorporated into a calibration equation to determine the water deficit for each layer. Just before the onset of each growing season, the soil profiles of all the plots were brought to field capacity. Only then were the plants subjected to four levels of water availability

The water availability levels used were:

- W1 - apply 25% of the amount given to W4.
- W2 - apply 50% of the amount given to W4
- W3 - apply 75% of the amount given to W4
- W4 - control, the soil profiles were brought to field capacity on a weekly basis

Water was applied by means of flood irrigation and the amounts of water applied were monitored using water flow meters.

During the establishment season (1995/96), the grasses were not subjected to differential irrigation treatments to ensure a good establishment as it has been found that some of these grasses only start to produce optimally during the second or third year. To ensure a fair comparison of the species, treatments were thus only imposed in the second (1996/97) and third seasons (1997/98).

According to soil analyses, the pH(H₂O) of the experimental soil was neutral. The phosphorus (Bray II) and potassium (Ammonium acetate extractable cations) status in the top soil (30 mg kg⁻¹ P; 108 mg kg⁻¹ K) was much higher than that of the subsoil (8 mg kg⁻¹ P; 67 mg kg⁻¹ K). To achieve a non-limiting soil phosphorus and potassium status of 40 mg kg⁻¹ P and 150 mg kg⁻¹ K, which would ensure that these nutrients were not limiting, annual applications of these nutrients were necessary. As the plots were not grazed, but harvested as hay, N, P and K were lost from the soil and the fertilizer regime was designed to replace these losses. At planting (1995/96 season), the plots received 75 kg N ha⁻¹, 40 kg P ha⁻¹ and 200 kg K ha⁻¹. Nitrogen and potassium were also applied to all plots as top dressings during the summer growing season, resulting in a total of 450 kg N ha⁻¹ a⁻¹, 40 kg P ha⁻¹ a⁻¹ and 400 kg K ha⁻¹ a⁻¹. In the subsequent seasons (1996/97 and 1997/98), nitrogen and potassium were applied to all plots as top dressings at rates of 225, 338, 394 and 450 kg N ha⁻¹ a⁻¹ and 200, 300, 350 and 400 kg K ha⁻¹ a⁻¹ for the W1, W2, W3 and W4 water availability levels respectively. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

The grasses were harvested at the 10% flowering stage, except for *P. clandestinum*, which was not allowed to grow taller than 40 cm. This resulted in an average of three to four cuts during each season. *C. ciliaris*, *D. eriantha* and *P. maximum* (tufted grasses) were cut to a height of 10 cm while the *Cynodon* hybrid and *P. clandestinum* (creeping grasses) were cut to 5 cm. A sample plot of one square metre, in the middle of each plot, was harvested, after which the rest of the plot was also cut to the same height. The sample plots were permanently marked to ensure that the samples were taken from the same area at each harvest. The material was dried to constant mass for 48 hours at 65°C.

During the last harvest in 1998, leaf samples were collected for use in a microscopy study. The oldest, actively growing, leaves were sampled as younger leaves can have a higher stomata density due to cells which have not yet fully expanded (Shearman & Beard, 1972). A sub-sample from the middle of the leaf blade was taken to describe the leaf surface morphology of the five grass species and for evaluating the effect of water availability on stomata number and appearance. The sub-samples were always taken from the middle of the leaf blade, for all the treatment combinations, as it has been found that the morphology may differ on different parts of the same leaf blade (Pazourek, 1969; Shearman & Beard, 1972). A JEOL, JSM840 scanning microscope was used to study the leaf surfaces. Before the leaf samples could, however, be placed into the scanning microscope, they had to be prepared according to the method set out by Hayat (1981). During this preparation, the leaf materials were fixed and dried under controlled conditions before being placed on a button and coated with a thin layer of gold.

A fully randomized block design with three replications was used. The statistical analysis was done using the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data is presented in the Appendix (Tables A7.1 - A7.4).

7.3 Results

7.3.1 Terminology

Before the presentation of results, it is meaning-full to define the terminology used in this paper.

The leaf can be divided into two zones. The costal zone above the veins and the intercostal zone between veins (Metcalf, 1960). Two types of epidermis cells are present namely long and short cells, where long cells are horizontally elongated and vertically narrow, while short cells are almost the same size horizontally and vertically.

Short cells often contain silica and/or cork bodies (Metcalf, 1960; Prat, 1967; Dahlgren & Clifford, 1982; Fahn, 1982) and can be exodermic, bearing salient prolongations *it est* hooks, spikes, hairs, setae, spines or papillae (Prat, 1967). The epidermis layer of some species may have no short cells (Prat, 1967). In a surface view the silica cells can have a circular, elliptic, dumb-bell, acutely angled, cross shaped, crenate or saddle shape (Figure 7.1).

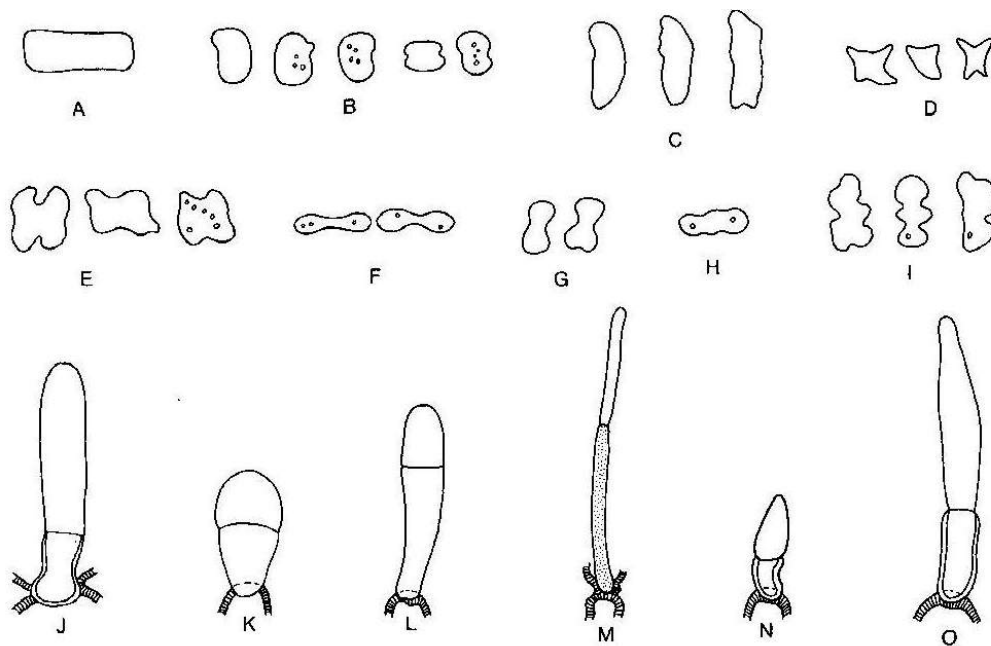


Figure 7.1 Illustration of silica bodies and (A - I) and microhairs (J - O) generally found on the epidermis of grasses.

Silica bodies: A - rectangular, B - saddle shaped, C - large narrow, D - acutely angled, E - cross shaped, F - dumbbell shaped, G - transversely dumbbell shaped, H - crenate, I - transversely crenate.

Microhairs: J - L with inflated distal cell, M - O with non-inflated distal cell. (Dahlgren *et al.*, 1985)

The waxy layer above the epidermis of the leaf forms part of the cuticle (Coombe & Bell, 1965). The wax can be in the form of granules, rods or scales and restricts the movement of water into or out of the leaf. Epicuticular wax structures can have different patterns and differ between species, age of leaf, etc. (Traore, *et al.*, 1989; Webb & Almeida, 1990; Balok & St. Hilaire, 2002).

The stomata are situated in the epidermis layer of the leaf and consist of two guard cells and an opening (cleft or pore) between them (Coombe & Bell, 1965; Fahn, 1982). Stomata, together with subsidiary or accessory cells which border the guard cells, are called the stomatal apparatus or the stomatal complex (Paliwal, 1969). The guard cells can be flush with the interstomatal cells or overlap them (Watson & Johnston, 1978).

In the grasses, the stomata are most often found in intercostal zones. In dry conditions they might also be restricted to the sides or bases of furrows and grooves on the leaf surface (Metcalf, 1960). Sometimes the grooves can be protected by prickles, or stomata can be covered by overlaying papillae. The stomata are usually in well defined horizontal bands, but Shearman and Beard (1972) noted that the stomata were in parallel rows on the adaxial side of *Agrostis* species, while scattered throughout the abaxial surface.

The guard cells may be level, sunken or raised relative to the other epidermal cells. The guard cells, of members of the Poaceae, are usually dumb-bell shaped in comparison to the kidney shaped guard cells of most other plants. Stomata are distributed more or less equal distances from each other and are specific to the species and leaf side. Different shapes of subsidiary cells are to be found and can differ not only between species but even on a single leaf blade. In the current study the stomata were not classified according to the shape of the subsidiary cells, since it can be so variable.

The number of stomata, per square millimetre of leaf surface, differs among plants (24 for *Avena sativa* and *Triticum sativum* to 1 198 for *Quercus lyrata*), between the adaxial and abaxial side of the leaf (Gray, 1881; Coombe & Bell, 1965; Martin & Juniper, 1970; Fahn, 1982, Gardner *et al.*, 1990; Balok & St Hilaire, 2002) as well as between cultivars of the same species (Shearman & Beard, 1972; Joubert, 1981; Traore, *et al.*, 1989). External factors such as light (Pazourek, 1970; Onwueme & Johnston, 2000), temperature (Bleckmann *et al.*, 1980), water (Shearman & Beard, 1972; Dreyer & Human, 1974; Joubert, 1981; Balok & St. Hilaire, 2002), cultivation practices (Teare *et al.*, 1971; Dreyer & Human, 1974) etc., can also have an influence on the number of stomata per unit area.

Trichomes are classified as all the uni- and multicellular appendages of the epidermis (Fahn, 1982). Trichomes are widely used to distinguish between plant families and genera. There are several shapes of trichomes and in grasses they are classified as macro-hairs, micro-hairs, prickle hairs and papillae (Metcalfe, 1960). A trichome consists of a foot (the part inserted in the epidermis) and body (the part projecting from the epidermis).

Macro-hairs are usually unicellular and can easily be seen with the naked eye. When the foot of a macro hair is surrounded by epidermal cells which are large and inflated and raised above the surface level it is called a cushion hair. Macro-hairs can often be confused with prickles. Macro-hairs are to be found in the intercostal zones or are common over the veins or at the leaf margins. Intercostal macro-hairs are often cushion hairs or have a sunken base/foot.

Micro-hairs are almost always two celled. The distal cell is usually thin walled and can be damaged or destroyed easily, while the basal cell is more durable due to a thicker cell wall. It is also believed that the distal cell could be filled with material that is secreted and therefore looks damaged or is totally absent. The micro-hairs can not be seen with the naked eye. The micro-hairs occur in the stomatal bands, or in the intercostal zones between the stomatal bands and veins.

Prickle hairs are robust, sharply but shortly pointed structures with swollen bases. Associated with short cells, they arise directly from the epidermis and the swollen bases form an integral part of the epidermis. The sharp point is usually directed towards the apex of the leaf, but exceptions can occur. They have thick lignified walls. Two sizes of prickle hairs, namely large size or prickles and small size or hooks, can be recognized. The latter have a more rounded base which can best be seen when studied from above. None, one or both types can be found on the leaves. The prickles/hooks can be found above or between veins with prickles above the veins and hooks between them. Angular, strongly pointed prickles are common at leaf margins.

Papillae are variously shaped protrusions from the outer walls of epidermal cells. They are dome shaped structures over veins but are found most often in the intercostal zone. There can be one or more papillae per long cell. The papillae of the epidermis next to a stomata, often overarch to protect the stomatal pores.

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7.3.7 Number of stomata

On average, the *Cynodon* hybrid and *P. maximum* tended to have the highest number of stomata in total (adaxial and abaxial), followed by *D. eriantha* and *C. ciliaris* with *P. clandestinum* having the least number of stomata (Figure 7.42). When the adaxial and abaxial sides of the leaves of the different species are compared, the *Cynodon* hybrid tended to have significantly ($P \leq 0.05$) the highest number of stomata on the adaxial surface. *P. maximum* had the second highest number, followed by *D. eriantha*. *D. eriantha*, however, had 15 to 20 stomata per unit area less than *P. maximum* and the *Cynodon* hybrid. There was not much of a difference in number of stomata on the adaxial surface between *C. ciliaris*, *D. eriantha* and *P. clandestinum*, but *P. clandestinum* still had the lowest number and had significantly ($P \leq 0.05$) less than *D. eriantha* (Figure 7.42).

On the abaxial surface, *D. eriantha* tended to have the highest number of stomata, but it did not differ significantly ($P \geq 0.05$) from either the *Cynodon* hybrid or *P. maximum*. *C. ciliaris* had about 10 stomata per unit area less than this group, with *P. clandestinum* having an even lower number of stomata, and significantly ($P \leq 0.05$) so (Figure 7.42). Despite the low number of stomata in *P. clandestinum*, this species had the biggest stomata (36 - 41 μm) followed by *C. ciliaris* (30 - 32 μm), and *D. eriantha* (25 - 27 μm). The two species with the largest number of stomata, the *Cynodon* hybrid and *P. maximum* had correspondingly the smallest stomata, of 17 - 19 μm and 17 - 24 μm respectively.

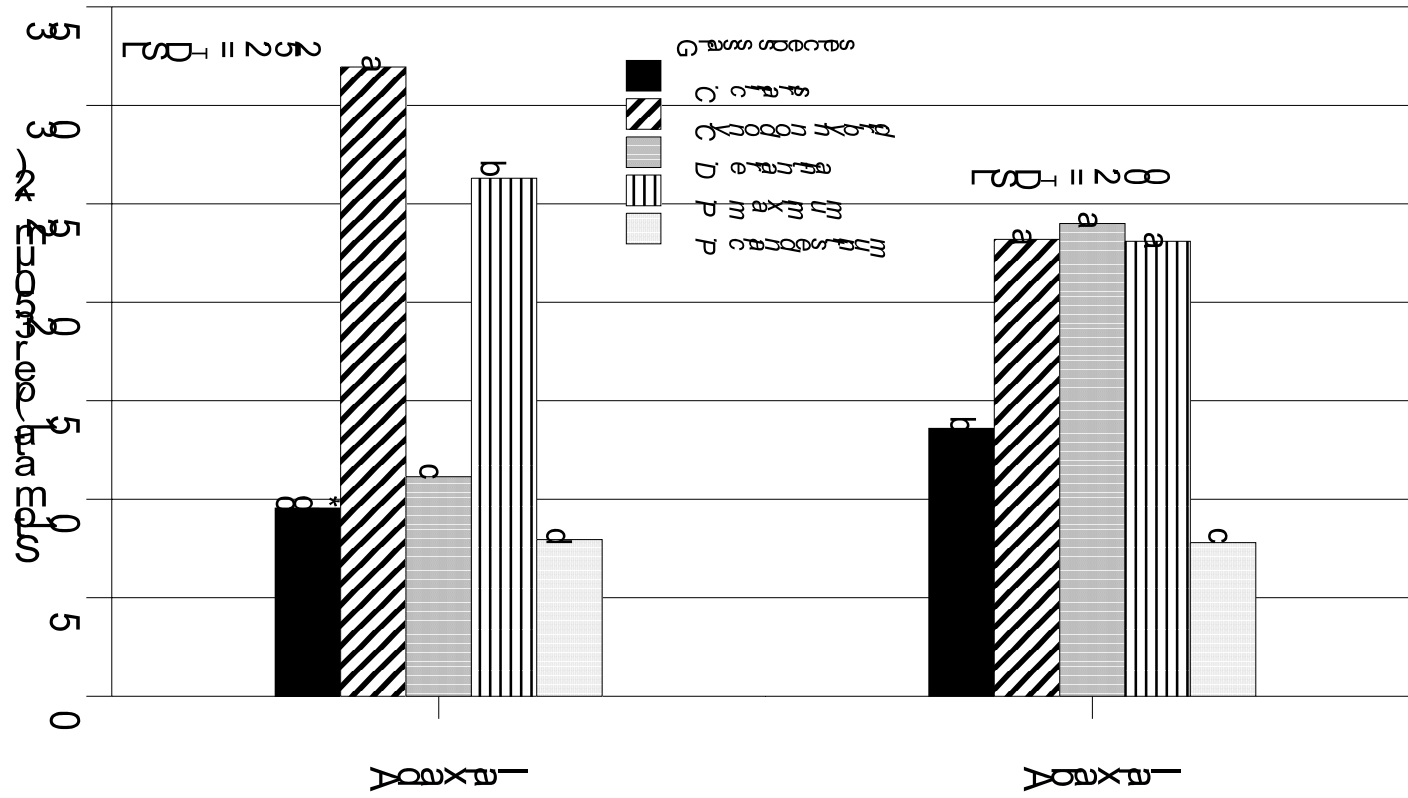


Figure 1. Effect of different treatments on the number of eggs per female.

Figure 1. Effect of different treatments on the number of eggs per female. The Y-axis represents the number of eggs per female, ranging from 0 to 15. The X-axis shows two groups: Control and Treated. Each group has five bars representing different treatments: Control (black), Dose 1 (diagonal lines), Dose 2 (horizontal lines), Dose 3 (vertical lines), and Dose 4 (checkered). Error bars and significance letters (a, b, c) are present on each bar.

There was no significant ($P \geq 0.05$) main effect of water availability on the number of stomata on the adaxial surfaces of the leaves of the five grass species (Table 7.1). The only significant ($P \leq 0.05$) differences were recorded between the abaxial leaf surfaces of W2 and W4 plants (Table 7.1), with W4 plants having significantly ($P \leq 0.05$) more stomata than the W2 plants.

Table 7.1 Effect of the availability of water on the average number of stomata on the adaxial and abaxial leaf surfaces of five grass species.

	W1*	W2	W3	W4
<i>Adaxial surface</i>	17 a [#]	18 a	17 a	19 a
<i>Abaxial surface</i>	19 ab	17 b	18 ab	20 a

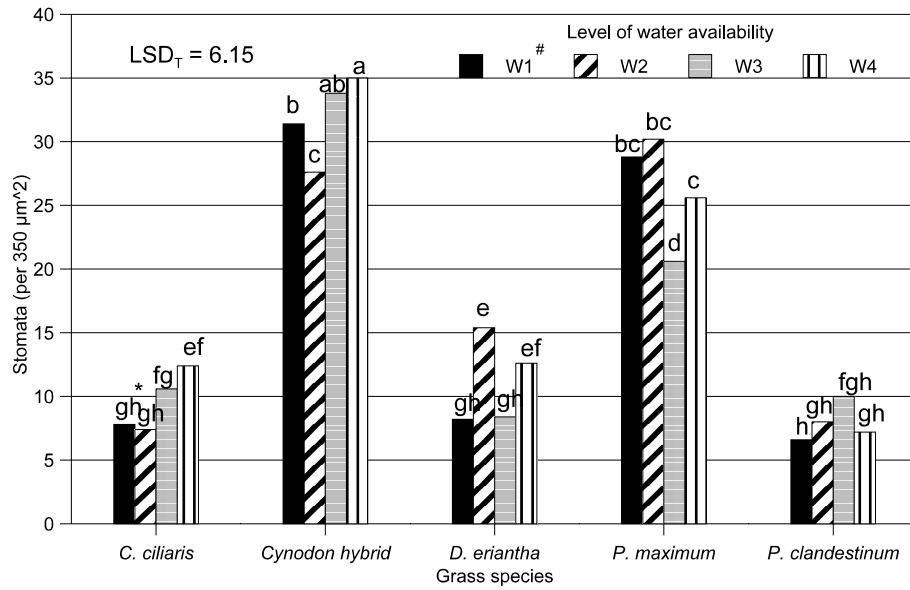
* W1 - severe water limiting conditions, W4 - control.

[#] Values in a row with the same alphabetical letter, do not differ significantly from each other ($P \leq 0.05$).

There was, however, a significant ($P \leq 0.05$) species x water availability interaction (Figures 43 and 44). While *C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum* tended to have an increased number of stomata on the adaxial leaf surfaces with an increase in the amount of water available (Figure 43), there was no clear tendency for *D. eriantha* and *P. maximum*.

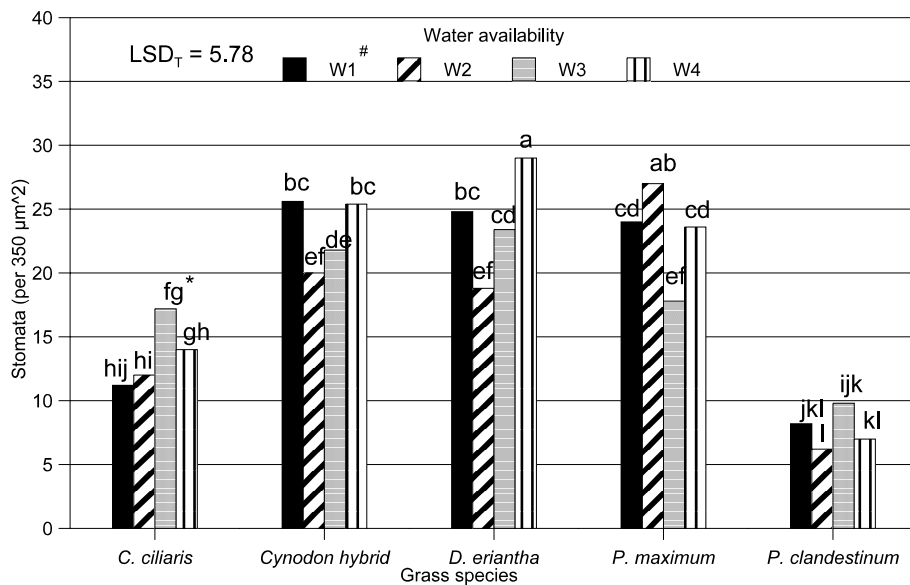
On the abaxial leaf surfaces, *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* tended to have a higher number of stomata with an increase in the amount of water available (Figure 44). For *P. maximum* and *P. clandestinum* there was no clear tendency on

the abaxial leaf surface.



W1 - severe water limiting conditions, W4 - control - non water limiting conditions
 * Bars with the same letter do not differ significantly (P<0,05) from each other.

Figure 7.43 Number of stomata on the adaxial leaf surface of five grass species as influenced by water availability.



W1 - severe water limiting conditions, W4 - control - non water limiting conditions
 * Bars with the same letter do not differ significantly (P<0,05) from each other.

Figure 7.44 Number of stomata on the abaxial leaf surface of five grass species as influenced by water availability.

7.4 Discussion and Conclusions

From the leaf surface descriptions of the grasses the following important features, in terms of adaptations that may reduce water loss, were noted:

Both leaf surfaces (adaxial and abaxial) of *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* and the adaxial leaf surface of *P. maximum* tended to have a wax deposit. In the case of the *Cynodon* hybrid and *D. eriantha* it even covered the stomatal openings. The wax layer did then not only restrict water loss from the epidermal cells, but also from the main structures for water loss, namely the stomata. This could explain the good water use of the *Cynodon* hybrid.

In the *Cynodon* hybrid some of the papillae sculpted over an adjacent stoma, further restricting excessive water loss from the stomatal aperture. In *D. eriantha* (especially abaxial) and *C. ciliaris* (adaxial and more so abaxial) the stomata are located in deep grooves between the veins, or tucked away below the veins to create the same restriction barrier for water loss as the papillae in the *Cynodon* hybrid. The stomata of *P. maximum* and *P. clandestinum* were not as protected as in the previous three grass species. The stomata were, however, a little lower than the surrounding epidermis cells, which could also be seen as a type of protection. This was, unfortunately not enough, especially in the case of *P. maximum*, and resulted in disappointing yields and water use efficiency values.

Another strategy to combat excessive water loss from the leaves, is to reduce the number, and/or size, of the stomatal aperture on the leaf as a whole or on one side of the leaf. On the adaxial leaf surfaces the *Cynodon* hybrid had significantly ($P \leq 0.05$) the highest number of stoma, followed by *P. maximum*. The wax layer and protecting papillae might explain why the *Cynodon* hybrid had better yields and water use

efficiency values than *P. maximum* despite this high potential water loss due to the number of stomata. The same holds true for the lower side where there was no significant ($P \geq 0.05$) difference in the number of stoma for the *Cynodon* hybrid, *D. eriantha* and *P. maximum*. Here not only the *Cynodon* hybrid, but also *D. eriantha* had extra protection against water loss, which *P. maximum* did not have.

P. clandestinum had significantly ($P \leq 0.05$) the lowest number of stomata on both leaf surfaces, followed by *C. ciliaris*. This might be the way, or additional way for *C. ciliaris*, in which these two species combat excessive water loss, despite the bigger size of the individual stoma.

Plant species adapted to dry conditions often have fewer stoma on the adaxial than abaxial side of the leaf. If that holds true, it can explain why it is reflected in *C. ciliaris* and *D. eriantha*. The *Cynodon* hybrid and *P. maximum* had more stomata on the adaxial than abaxial leaf surface and can explain why the stomata are that much smaller and are adapted in other ways to combat water loss. *P. clandestinum* had almost the same number of stomata on either side of the leaf.

Shearman & Beard (1972), Van de Roovaart & Fuller (1935) and others noted less stomata per area for well watered than for water stressed grass plants. This can be explained by the larger size of the epidermis cells under optimal conditions resulting in a greater distance between stomata and a lower stomatal frequency as compared to plants growing under adverse conditions. This was not the case in this trial. Some of the grasses (*C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum* adaxial and *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* abaxial) tended to have less stomata with less water available. The other species had no clear tendency.

Although the number of trichomes per leaf area was not determined, *P. clandestinum* clearly had the least trichomes. The *Cynodon* hybrid and *P. maximum* leaves were densely covered with macrohairs, while *C. ciliaris* and *D. eriantha* were covered by prickles and hooks. Traore, *et al.*, (1989) concluded that plants with a higher trichome density are better adapted to stressful environments than their hairless counterparts. Trichomes increase the leaf boundary layer resistance to air flow and increase radiation reflectance. As with stomata number, the number of trichomes per leaf, and between species (Balok & St. Hilaire, 2002) and cultivars can also differ. The low number of trichomes might explain why *P. clandestinum* did not do as well under drought conditions as the other grass species, but cannot fully explain the poor performance of *P. maximum*.

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7.3.2 *Cenchrus ciliaris*

There were no significant differences in the leaf surface appearance at the different levels of water availability, and it was, therefore, decided only to describe the leaf surfaces of the control (W4) plants. Photos of the leaves as affected by the other levels of water availability are included in the appendix (Figures A7.1 - A7.5). There were, however, differences between species.

The adaxial leaf surface of *C. ciliaris* consists of well defined costal (over vein) and intercostal (between veins) zones (Figures 7.2 (x50) and 7.3 (x300)). At the summit of the costal zone a single row of prickles can be found with two rows of prickles at the lower edges of the veins. Numerous hooks can be found in the intercostal zone. Stomata can also be found in the same area as the hooks, and sometimes the hooks and stomata alternate with each other. At the summit of the veins, silica bodies in the shape of dumbbell, cross shaped or nodular forms can be found alongside and between the prickles. Micro-hairs with two distinct cells are situated closely beside the vein. The distal cells of the micro-hairs have collapsed as has been found in many grass species (Metcalf, 1960). No macro-hairs were present.

In a closer view (x2500) (Figure 7.4) one can clearly see wax deposits on the surface in the form of rods. In some instances the wax crystals have merged to form a solid structure. In this view one can also clearly see the dumbbell shaped guard cells with two subsidiaries, one at each side of the guard cells of the stoma. The leaf edge consists of a single row of prickles (Figure 7.5). The points of these prickles are rather blunt in comparison to those on the abaxial side of the leaf (Figure 7.9).

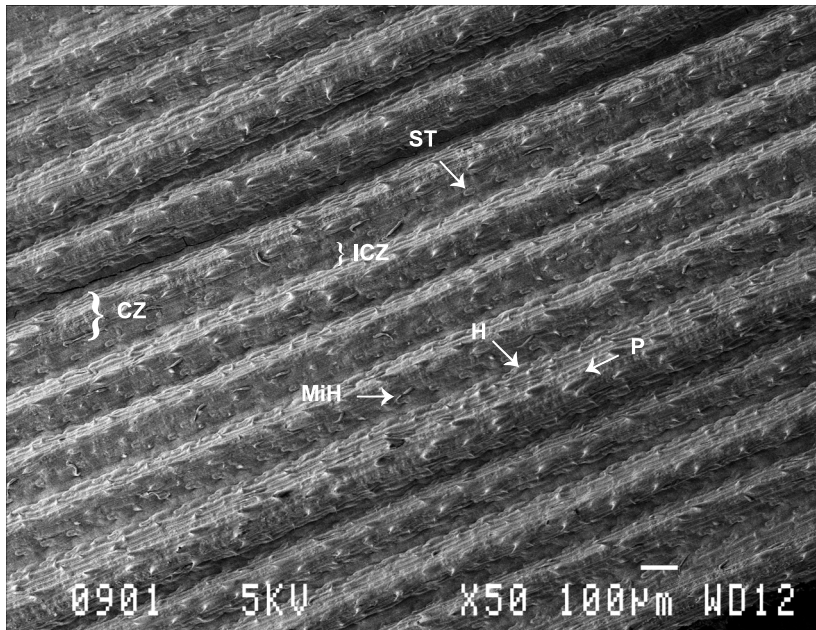


Figure 7.2 Surface of the adaxial side of a *C. ciliaris* leaf grown without any water stress (W4). MiH -Micro-hair, CZ - Costal zone, ST - Stoma, H - Hook, ICZ -Intercostal zone, P -Prickle.

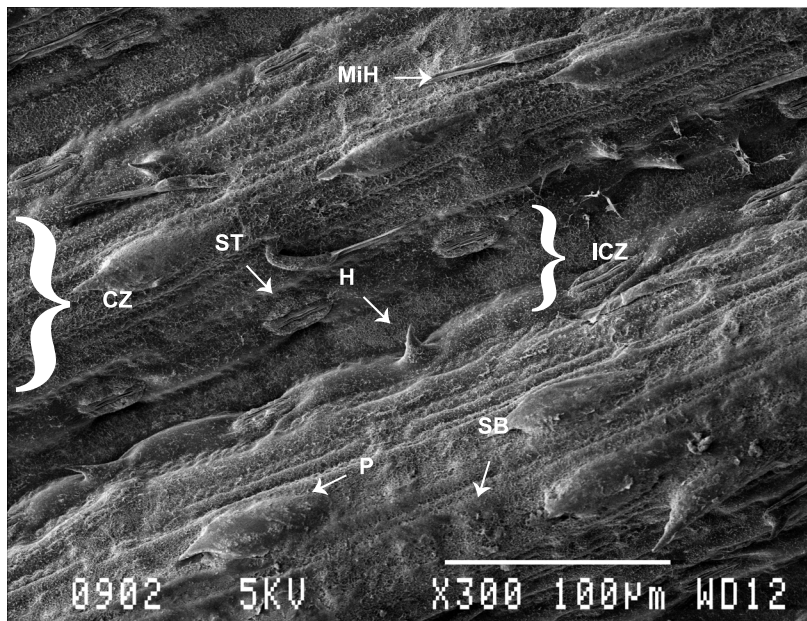


Figure 7.3 Surface of the adaxial side of a *C. ciliaris* leaf grown without any water stress (W4). MiH - Micro-hair, CZ - Costal zone, ST - Stoma, H - Hook, ICZ -Intercostal zone, P -Prickle, SB - Silica body.

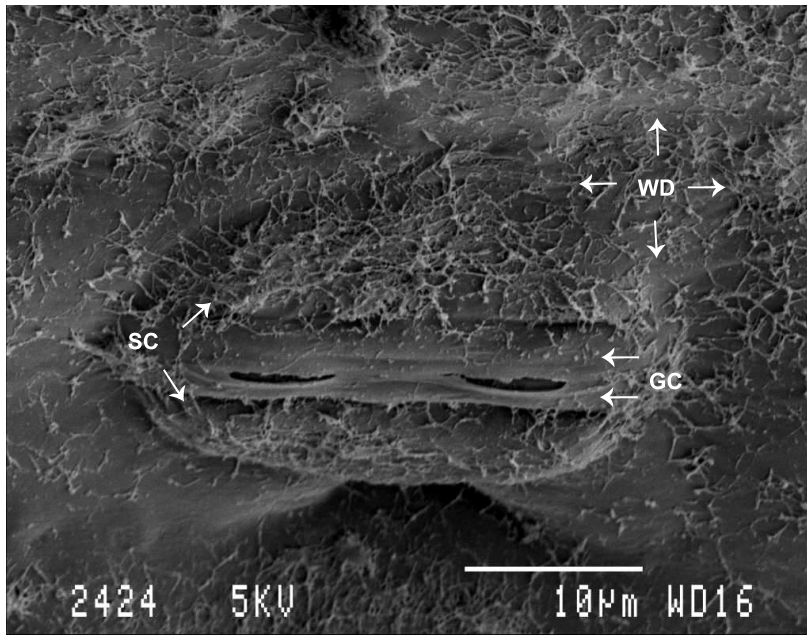


Figure 7.4 A stoma found on the adaxial side of a *C. ciliaris* leaf grown without any water stress (W4) (x2500). GC - Guard cell, SC - Subsidiary cell, WD - Wax deposit.

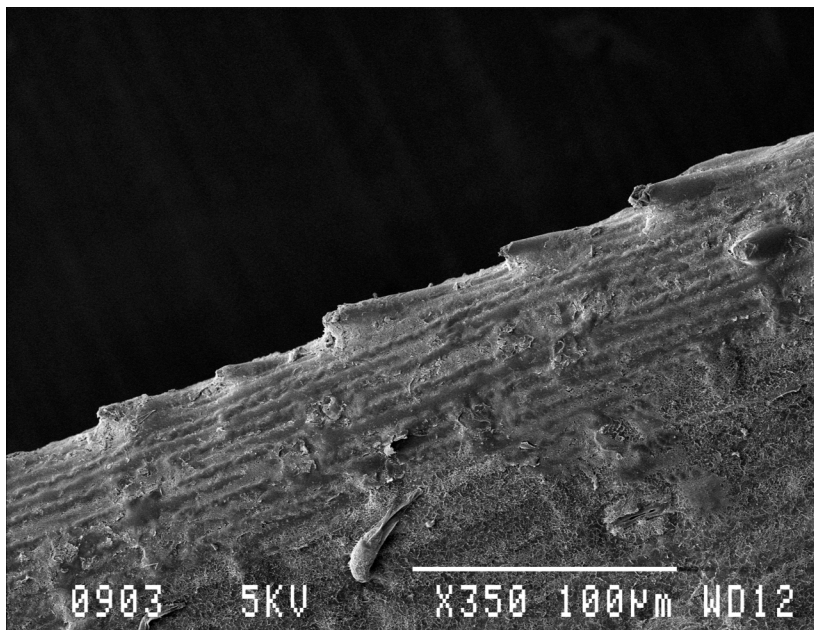


Figure 7.5 Leaf edge of the adaxial side of a *C. ciliaris* leaf grown without any water stress (W4).

On the abaxial side of the leaf surface of *C. ciliaris*, the costal and intercostal zones are much more pronounced (Figures 7.6 and 7.7). The micro-hairs are closely situated beside the veins with prickles at the summit and edges of the vein and numerous hooks between the veins. Once again no macro-hairs were found. The silica bodies are similar to those found on the adaxial leaf surface. The stomata are to be found in the valley between the veins and are similar to the ones found on the adaxial side (Figure 7.8). The leaf edge consists out of three rows of pointed prickles (Figure 7.9).

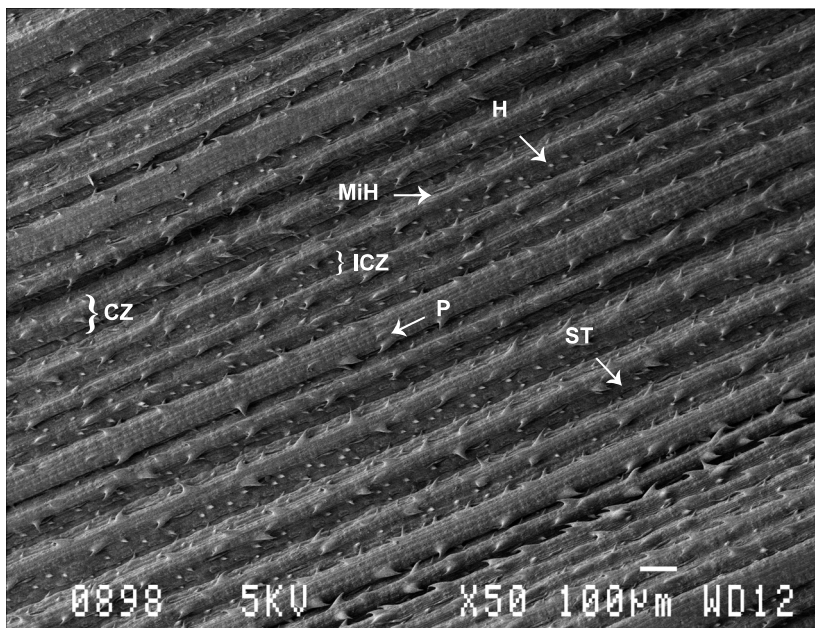


Figure 7.6 Abaxial Surface of a *C. ciliaris* leaf grown without any water stress (W4). MiH - Micro-hair, CZ - Costal zone, ST - Stoma, H - Hook, ICZ - Intercostal zone, P - Prickle.

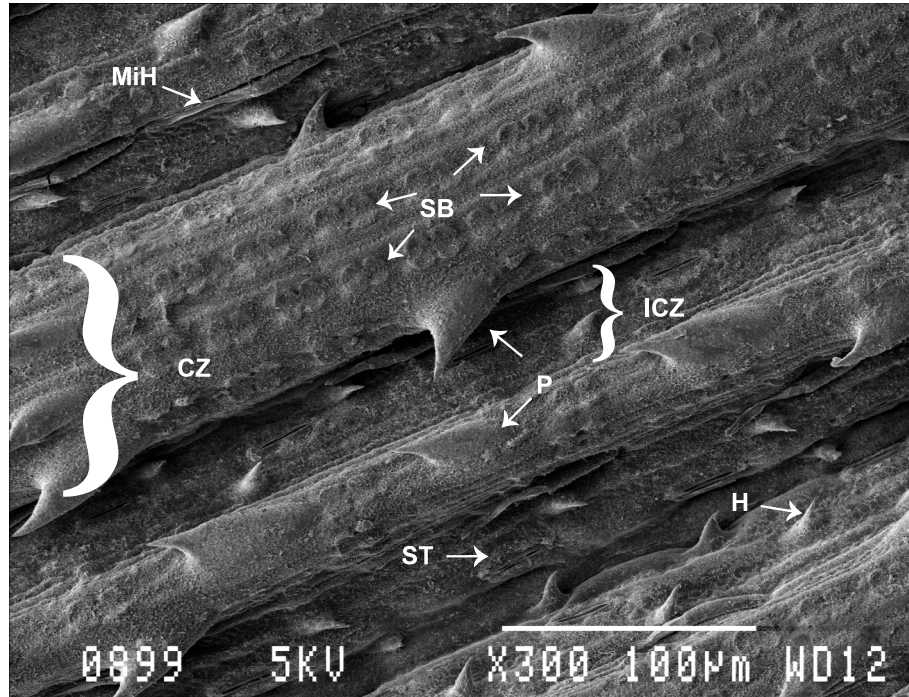


Figure 7.7 Abaxial surface of a *C. ciliaris* leaf grown without any water stress (W4). MiH - Micro-hair, CZ - Costal zone, ST -Stoma, H - Hook, ICZ - Intercostal zone, P - Prickle, SB - Silica body.

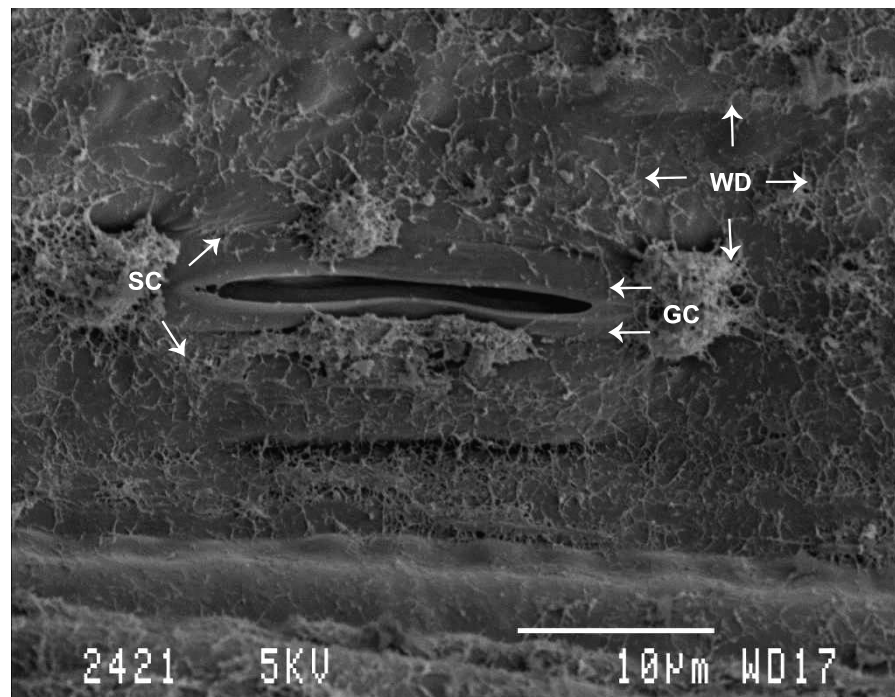


Figure 7.8 A stoma found on the abaxial side of a *C. ciliaris* leaf grown without any water stress (W4) (x2500). GC - Guard cell, SC - Subsidiary cell, WD - Wax deposit.

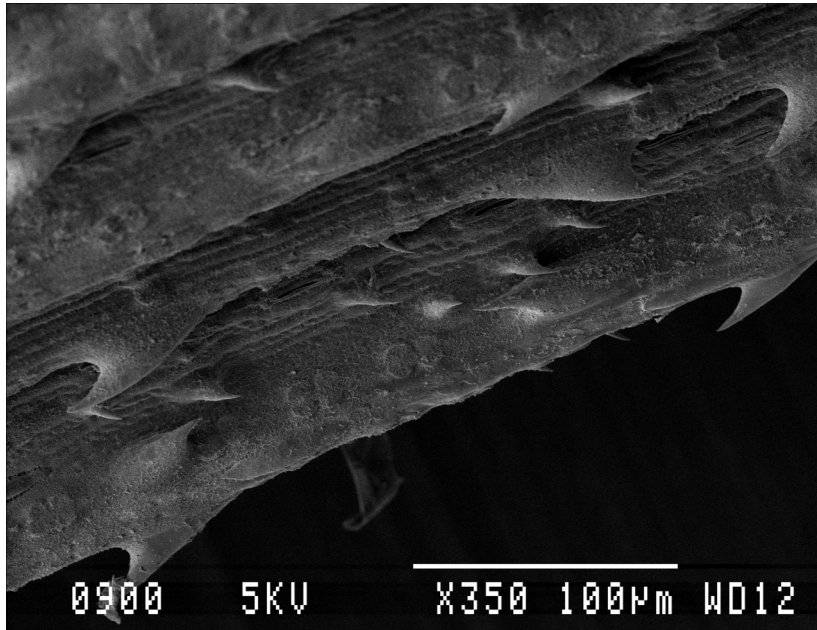


Figure 7.9 Leaf edge of the abaxial side of a *C. ciliaris* leaf grown without any water stress (W4).

7.3.3 *Cynodon* hybrid

The adaxial side of the *Cynodon* hybrid leaf has fairly long and numerous macro-hairs with sunken bases (foots) in the intercostal zone and prickles spread throughout the surface (Figure 7.10). Micro-hairs with inflated distal cells, sunken into pits can be found in the intercostal zone. The prickles are found in rows, but are further apart than those of *C. ciliaris*, with some of the prickles appearing in pairs. The costal and intercostal zones are not as pronounced (Figure 7.11) as found for *C. ciliaris* (Figure 7.3). In this closer view (Figure 7.11) numerous nodule like papillae can also be observed.

As with the leaf surface of *C. ciliaris*, the leaf surfaces of the *Cynodon* hybrid leaves are covered by a rod like wax layer. The rods sometimes merge to form a solid structure which protrudes over or even covers some of the stomata (Figures 7.12). The stomata are flush with, or sometimes lower than, the surrounding epidermis cells and papillae sculpting over a stoma will sometimes be found (Figures 7.11 and 7.12). The leaf edge consists out of a single row of sharp pointed prickles (Figure 7.13).

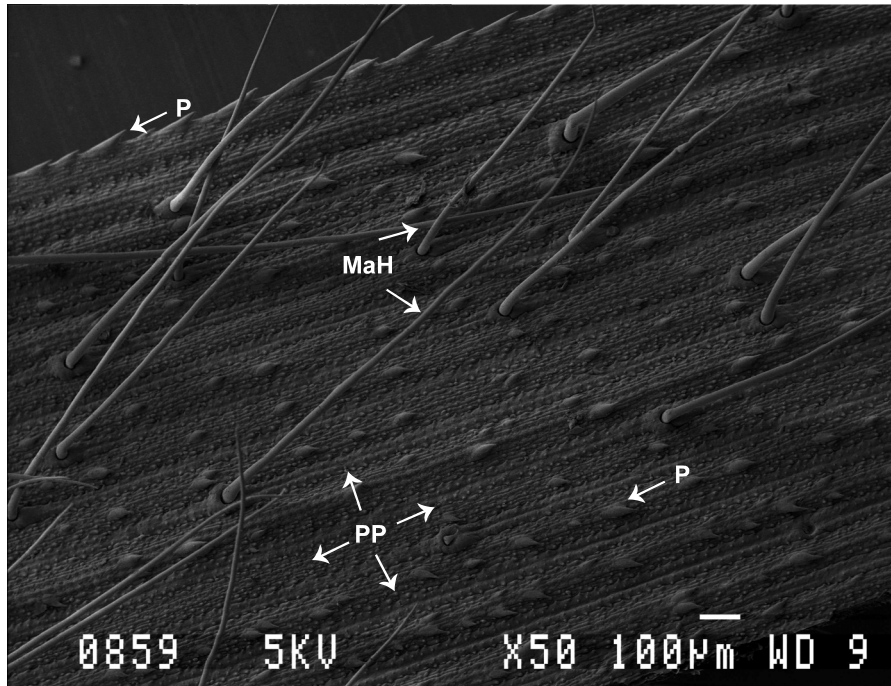


Figure 7.10 Adaxial surface of a *Cynodon* hybrid leaf grown without any water stress (W4). MaH - Macro-hair, P - Prickle. PP - Papillae.

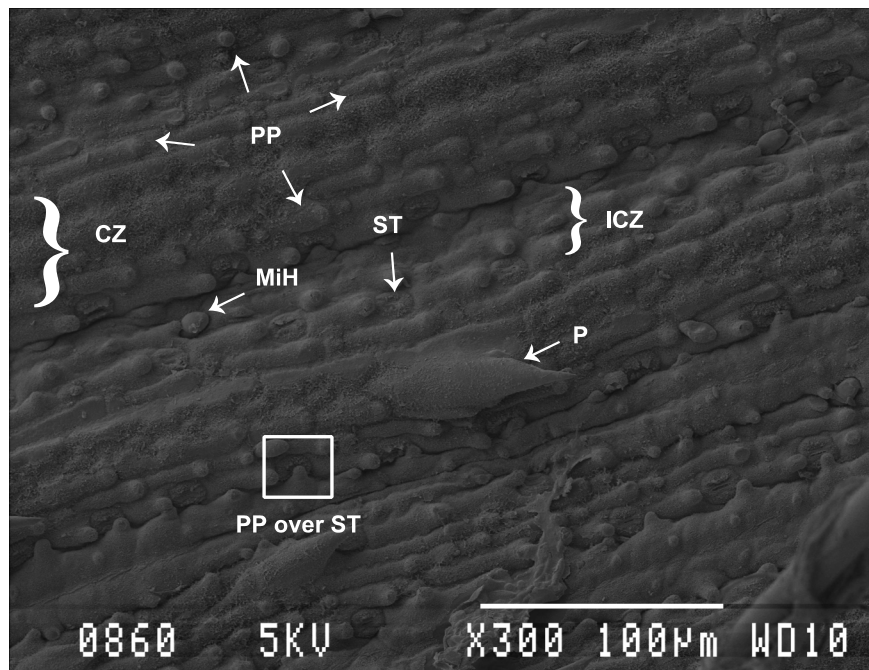


Figure 7.11 Adaxial surface of a *Cynodon* hybrid leaf grown without any water stress (W4). CZ - costal zone, ICZ - Intercostal zone, ST - Stoma, PP - Papillae, P - Prickle, MiH - Micro-hair, PP over ST - Papillae overlying a stoma.

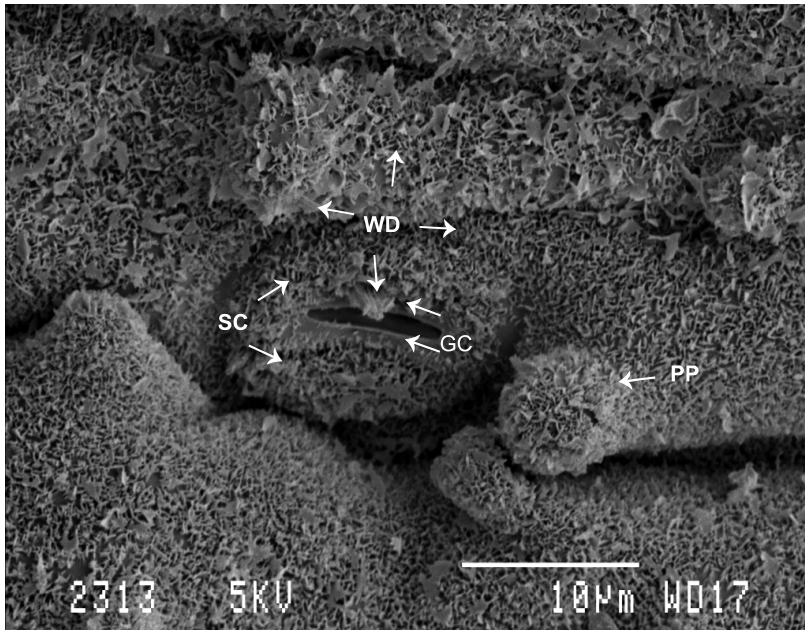


Figure 7.12 A stoma found on the adaxial side of a *Cynodon* hybrid leaf grown without any water stress (W4) (x2500). GC - Guard cell, SC - Subsidiary cell, WD - Wax deposit, PP - Papillae.

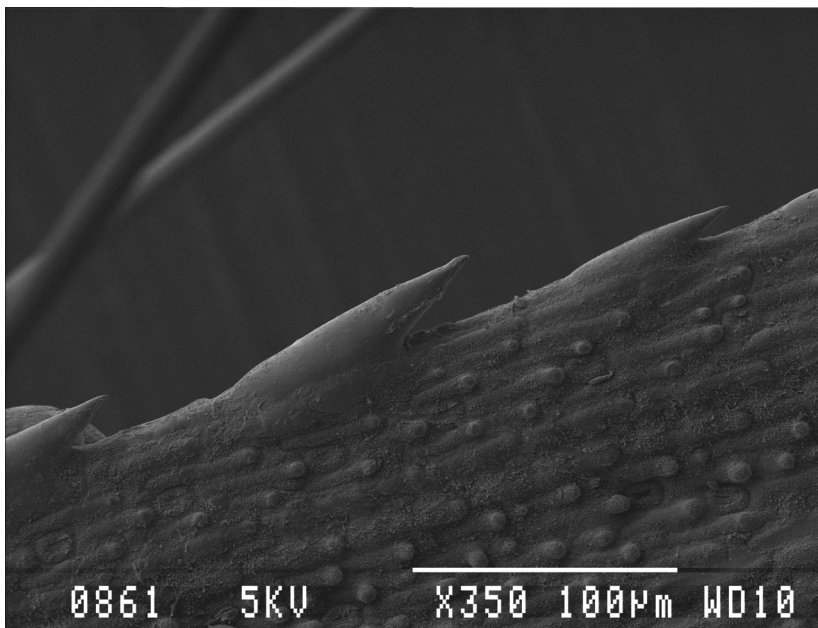


Figure 7.13 Leaf edge of the adaxial side of a *Cynodon* hybrid leaf grown without any water stress (W4).

Compared to the adaxial side (Figure 7.10) of a *Cynodon* hybrid leaf, the macro-hairs are more numerous on the abaxial side (Figure 7.14), but no prickles were observed at this magnification (x50). The macro-hairs on the abaxial side (Figure 7.14) are also shorter than those on the adaxial side (Figure 7.10), but are further the same. At higher magnification (x300) (Figure 7.15), still no prickles were observed, but micro-hairs of the same sort found on die adaxial side were observed. The leaf surface was again covered by a wax deposit with some of the wax crystals protruding over the stomatal openings (Figure 7.16). Some of the papillae adjacent to a stoma, also protrude over the stoma (Figure 7.16), as was found on the adaxial side of the *Cynodon* hybrid leaf. A single row of pointed prickles were to be found on the leaf edge (Figure 7.17).

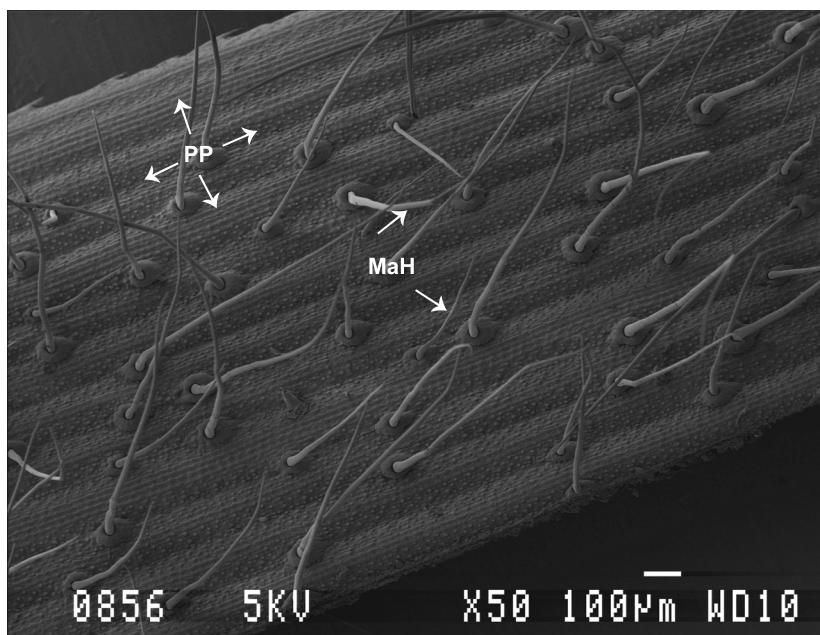


Figure 7.14 Abaxial surface of a *Cynodon* hybrid leaf grown without any water stress (W4). MaH - Macro-hair, PP - Papillae.

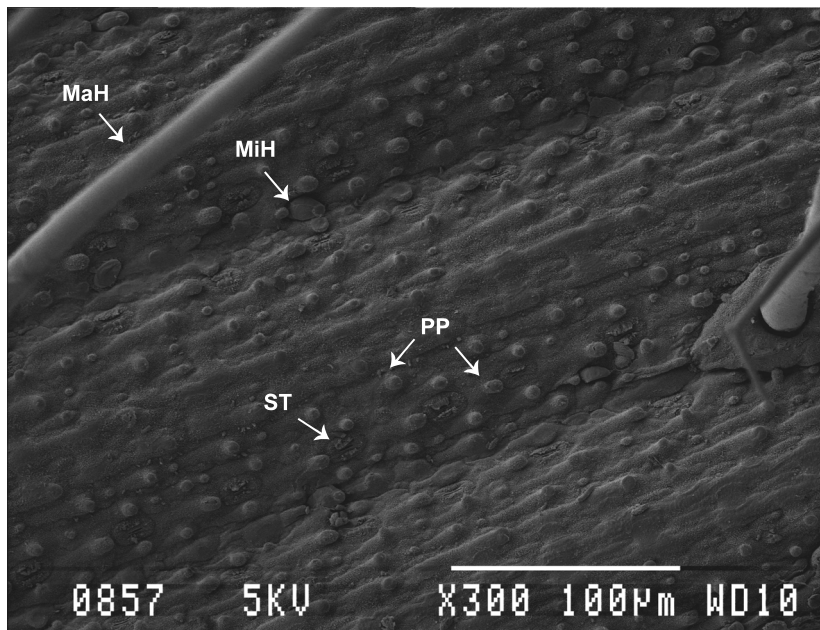


Figure 7.15 Abaxial surface of a *Cynodon* hybrid leaf grown without any water stress (W4). MaH - Macro-hair, MiH - Micro-hair, ST - Stoma, PP - Papillae.

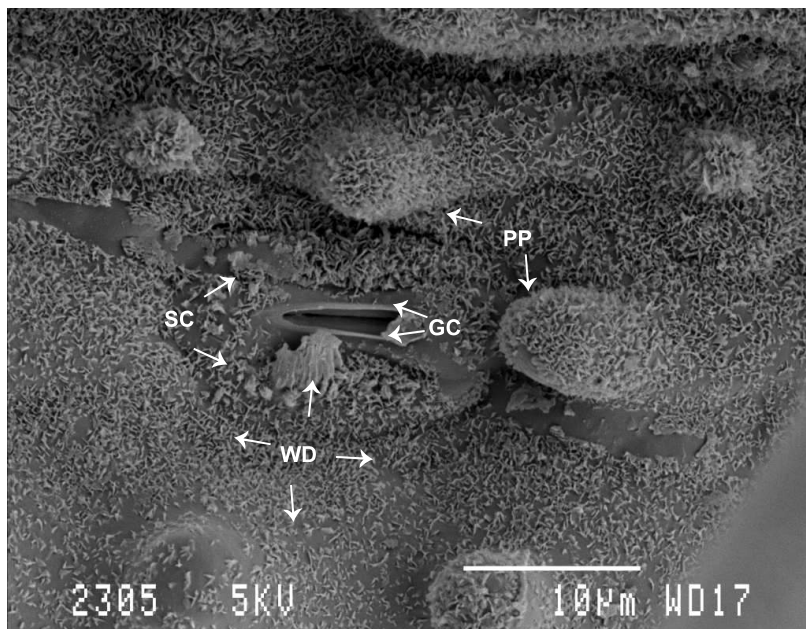


Figure 7.16 A stoma found on the abaxial side of a *Cynodon* hybrid leaf grown without any water stress (W4) (x2500). GC - Guard cell, SC - Subsidiary cell, WD - Wax deposit, PP - Papillae.

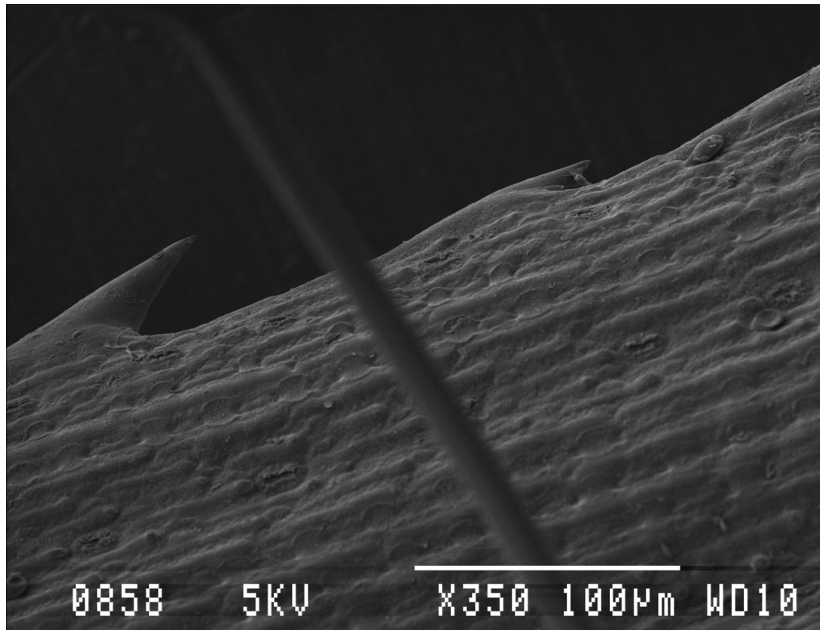


Figure 7.17 Leaf edge of the abaxial side of a *Cynodon* hybrid leaf grown without any water stress (W4).

7.3.4 *Digitaria eriantha* subsp. *eriantha*

Well defined costal and intercostal zones can be observed on the adaxial surface of a *D. eriantha* leaf (Figures 7.18 and 7.19). There are only micro-hairs (Figure 7.19), as is the case with *C. ciliaris* (Figure 7.3). The micro-hairs are in two adjacent rows parallel to the vein with prickles (sometimes paired) over the veins (Figure 7.19). A row of hooks can be found in approximately the middle of the intercostal zone (Figure 7.19). Silica bodies with cross or butterfly shapes were found over the veins. The stomata borders both sides of a vein (Figure 7.19) and are covered with wax crystals (Figure 7.20), making it difficult to identify the guard and subsidiary cells. There are prickles present on the leaf edges (Figure 7.21).

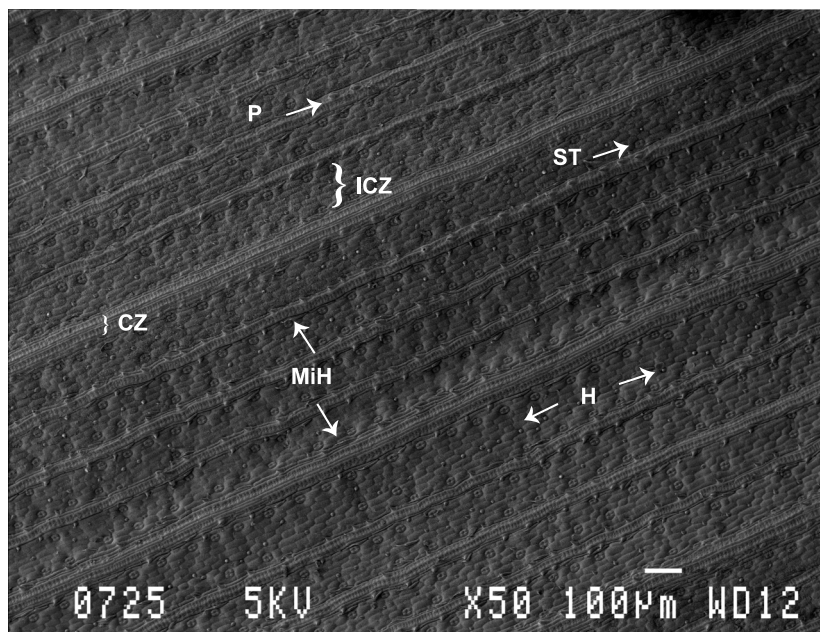


Figure 7.18 Adaxial surface of a *D. eriantha* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MiH - Micro-hair, P - Prickle. H -Hook, ST - Stoma.

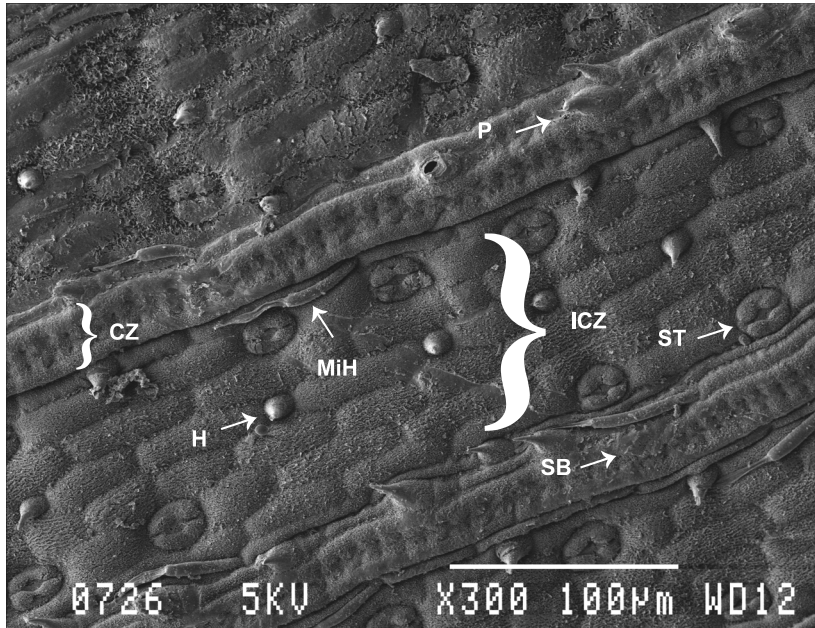


Figure 7.19 Adaxial surface of a *D. eriantha* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MiH - Micro-hair, P - Prickle, H - Hook, ST - Stoma, SB - Silica bodies.

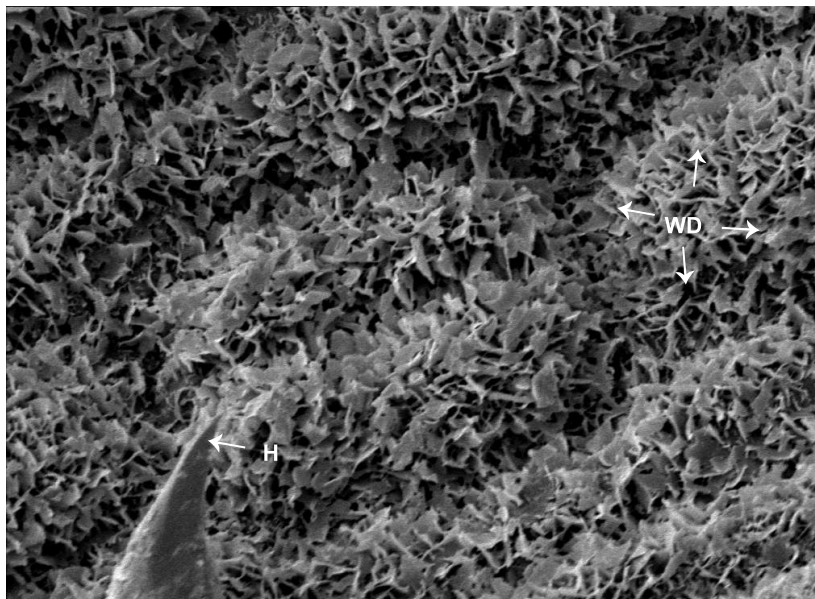


Figure 7.20 A stoma found on the adaxial side of a *D. eriantha* leaf grown without any water stress (W4) (x2500). WD - Wax deposit, H -Hook.

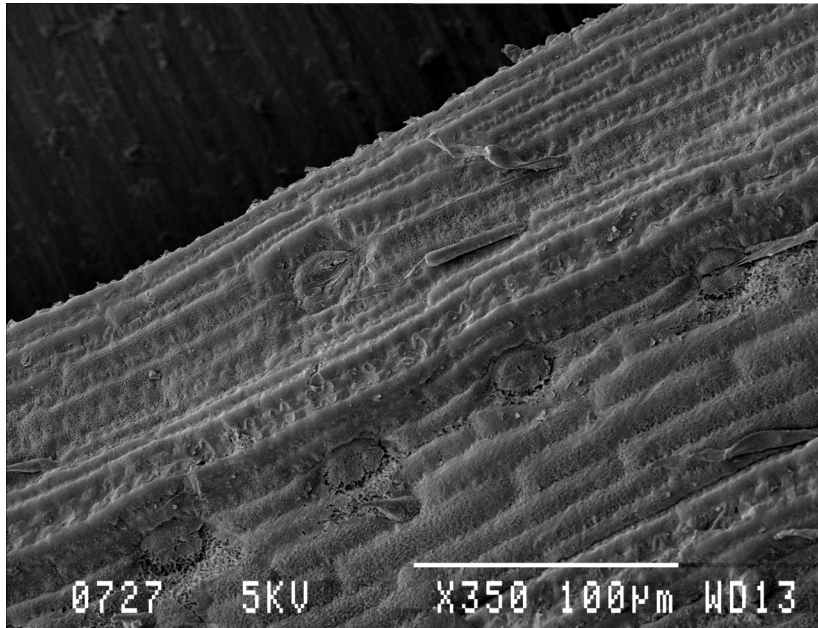


Figure 7.21 Leaf edge of the adaxial side of a *D. eriantha* leaf grown without any water stress (W4).

Costal and intercostal zones are also clearly visible on the abaxial side of the *D. eriantha* leaf (Figures 7.22 and 7.23). The same type of micro-hairs, although fewer, were found on the abaxial (Figures 7.22 and 7.23), than on the adaxial (Figures 7.18 and 7.19), side of the leaf. The abaxial leaf surface was also covered with prickles (costal zone) and hooks (intercostal zone) (Figure 7.23). As on the adaxial side, silica bodies of the same shape can be found on the abaxial side of the leaf. The stomata are to be found in the intercostal zone (Figure 7.23) and are covered by wax crystals (Figure 7.24). Some of the stomata are overshadowed by the adjacent veins (Figure 7.23). A three rowed prickle covered leaf edge can be observed on the abaxial side of the leaves (Figure 7.25).

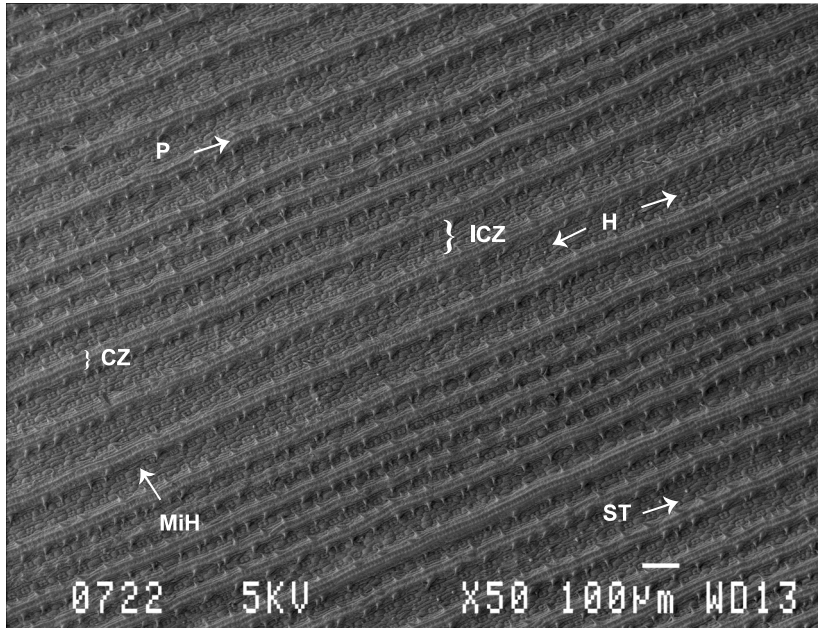


Figure 7.22 Abaxial surface of a *D. eriantha* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MiH - Micro-hair, P - Prickle. H - Hook, ST - Stoma.

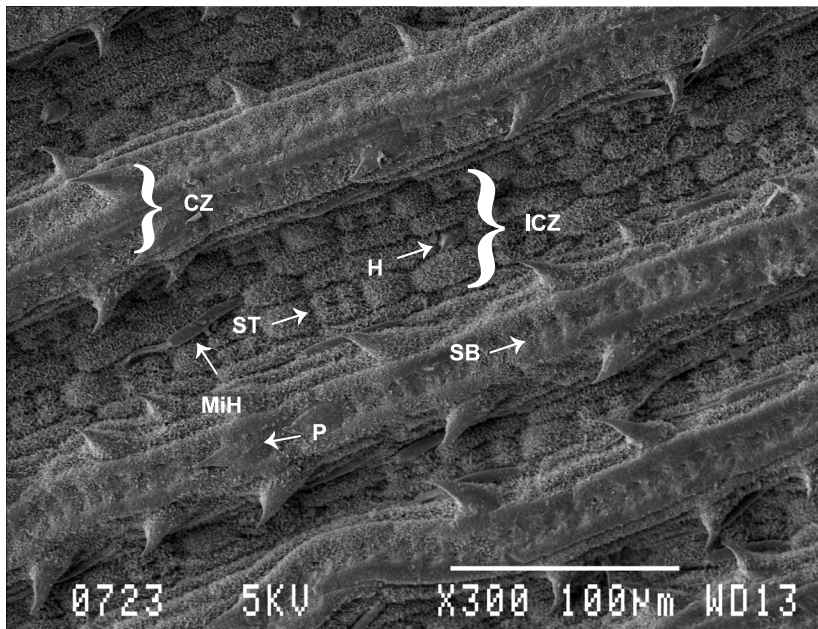


Figure 7.23 Abaxial surface of a *D. eriantha* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MiH - Micro-hair, P - Prickle, H - Hook, ST - Stoma, SB - Silica bodies.

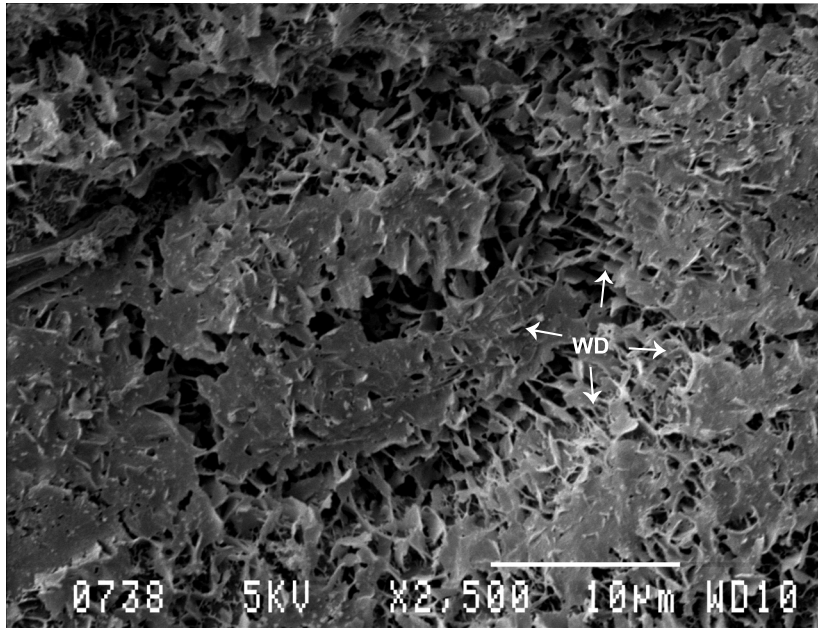


Figure 7.24 A stoma found on the abaxial side of a *D. eriantha* leaf grown without any water stress (W4) (x2500). WD - Wax deposit.

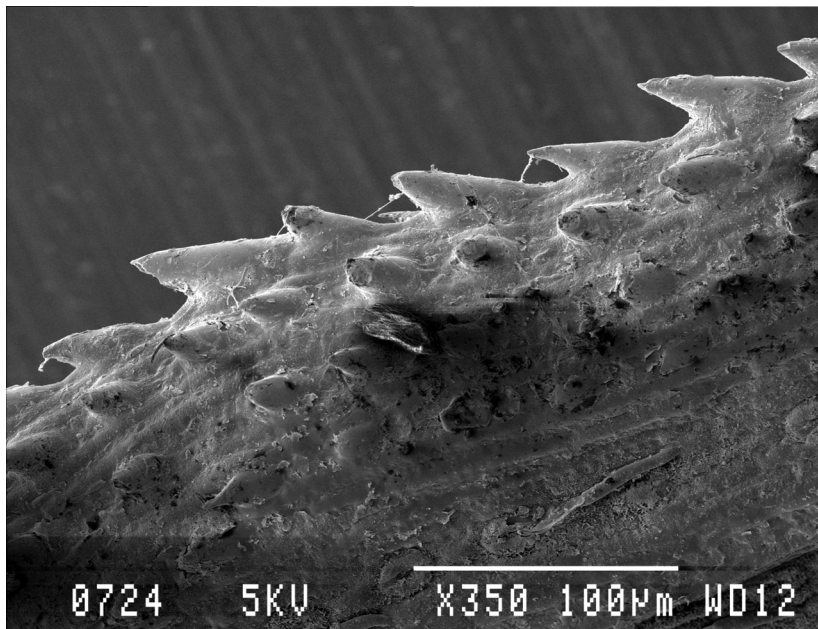


Figure 7.25 Leaf edge of the abaxial side of a *D. eriantha* leaf grown without any water stress (W4).

7.3.5 *Panicum maximum*

Numerous prickles and short macro-hairs (Figure 7.26) are to be found in the intercostal zone on the adaxial side of a *P. maximum* leaf. Micro-hairs, similar to the ones found on *C. ciliaris* (Figure 7.3) and *D. eriantha* (Figure 7.19), are also present, but are less abundant (Figure 7.27). Costal and intercostal zones can be identified, but are less pronounced than those in *D. eriantha* and *C. ciliaris*. Silica bodies, in the form of dumbbells or nodules, are associated with the veins (Figure 7.27). As in *D. eriantha*, the stomata border the veins (Figure 7.27) and are seldom, if ever, found in the middle of the intercostal zone. The leaf surface is once again covered by a wax deposit (Figure 7.28), but it does not cover the guard cells as was the case for *D. eriantha*. Two to three rows of prickles can be found on the leaf edge (Figure 7.29).

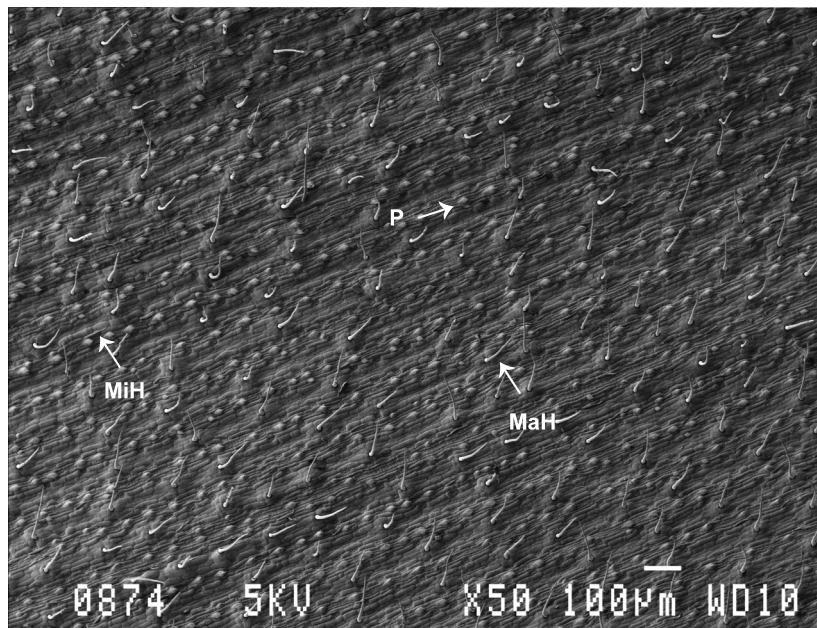


Figure 7.26 Adaxial surface of a *P. maximum* leaf grown without any water stress (W4). MaH - Macro-hair, MiH - Micro-hair, P - Prickle.

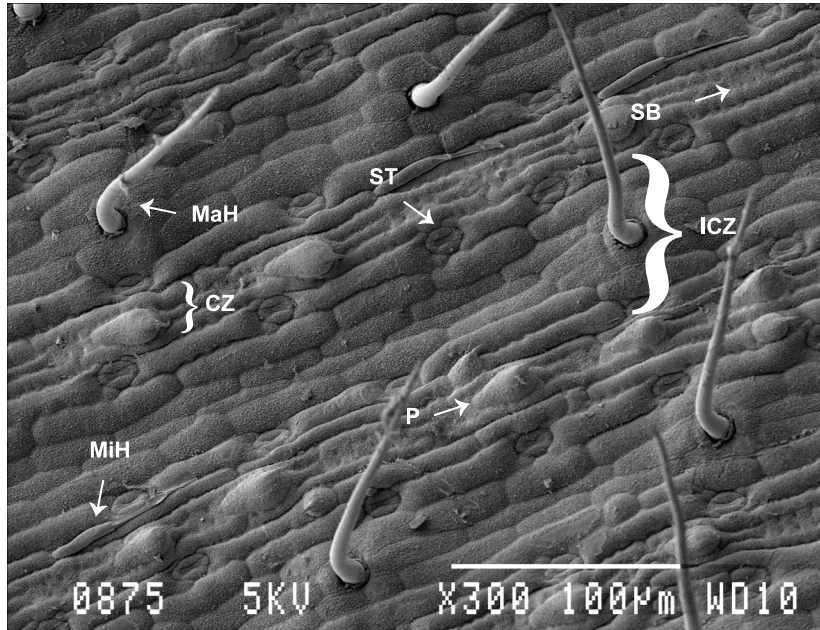


Figure 7.27 Adaxial surface of a *P. maximum* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MaH - Macro-hair, MiH - Micro-hair, P - Prickle, ST - Stoma, SB - Silica body.

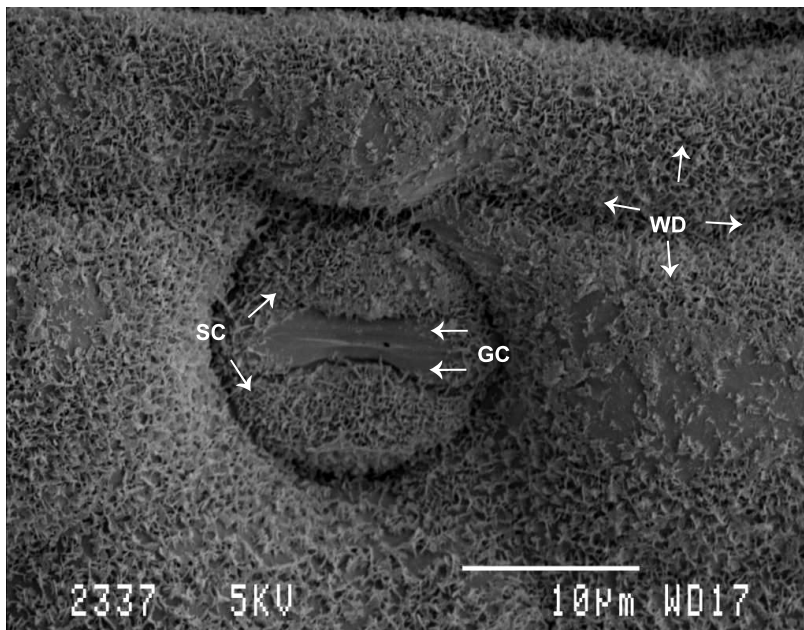


Figure 7.28 A stoma found on the adaxial side of a *P. maximum* leaf grown without any water stress (W4) (x2500). WD - Wax deposit, SC - Subsidiary cell, GC - Guard cell.

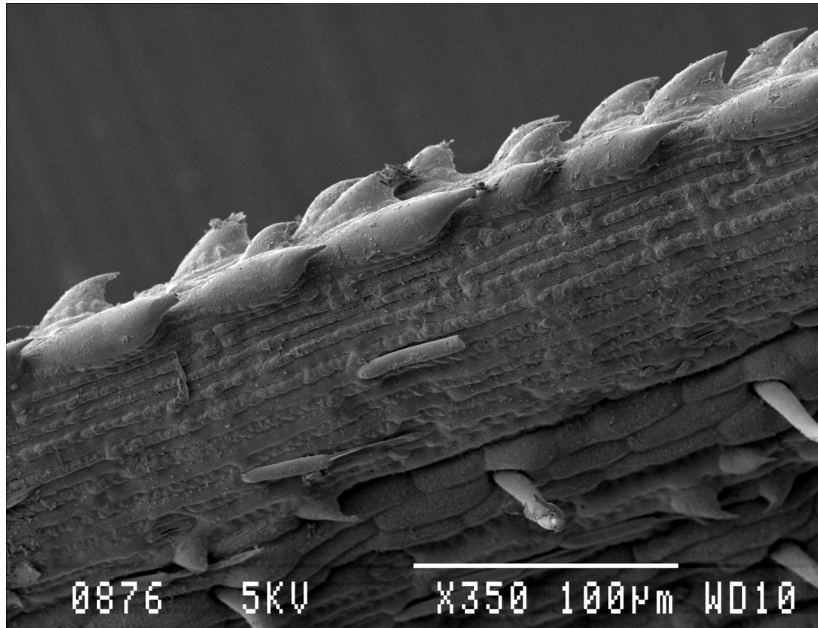


Figure 7.29 Leaf edge of the adaxial side of a *P. maximum* leaf grown without any water stress (W4).

The abaxial (Figure 7.30) leaf surface has the same components as the adaxial side, but the position of some of these components differ between the two surfaces. The difference being that the prickles can be found on the border of the costal and intercostal zones on the abaxial surface (Figure 7.31), while it is in the middle of the costal zone on the adaxial surface (Figure 7.27). The macro-hairs are in straight rows in the intercostal zone (Figure 7.31). The micro-hairs are in the same row, adjacent to the macro-hairs. The surface is smoother and the costal silica bodies are clearly dumbbell to saddle shaped. The stomata are found close to a row of macro- and micro-hairs, or prickles, and little wax deposit is evident (Figure 7.32). Prickles can be found in two to three rows on the leaf edge (Figure 7.33).

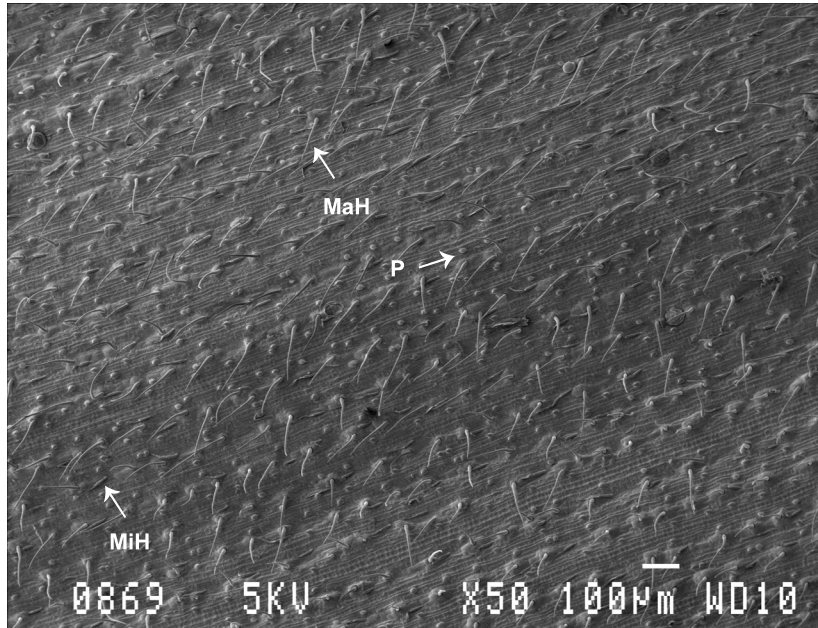


Figure 7.30 Abaxial surface of a *P. maximum* leaf grown without any water stress (W4). MaH - Macro-hair, MiH - Micro-hair, P - Prickle.

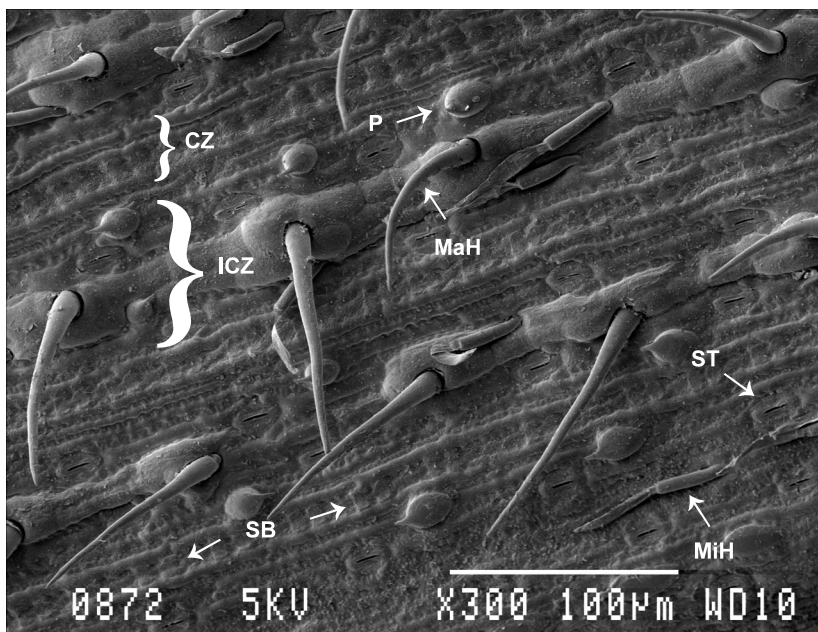


Figure 7.31 Abaxial surface of a *P. maximum* leaf grown without any water stress (W4). CZ - Costal zone, ICZ - Intercostal zone, MaH - Macro-hair, MiH - Micro-hair, P - Prickle, ST - Stoma, SB - Silica body.

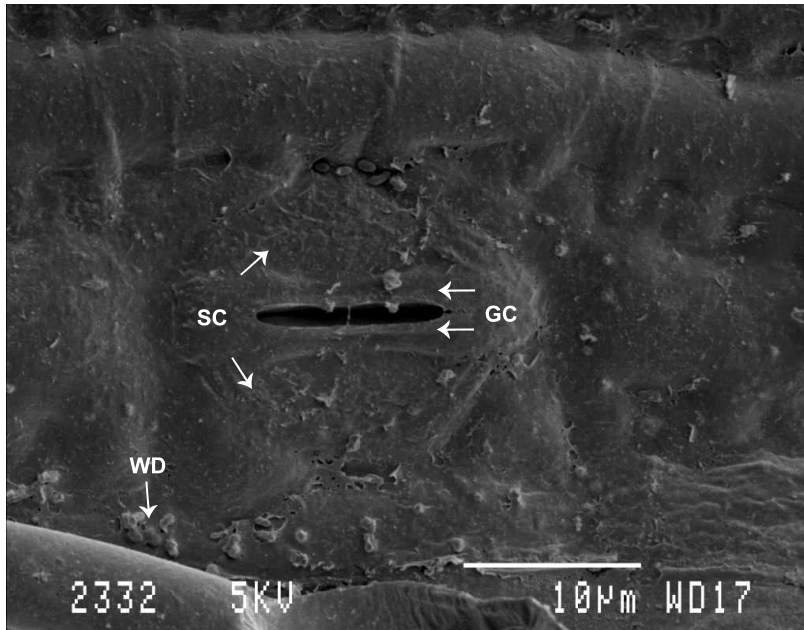


Figure 7.32 A stoma found on the abaxial side of a *P. maximum* leaf grown without any water stress (W4) (x2500). WD - Wax deposit, SC - Subsidiary cell, GC -Guard cell.

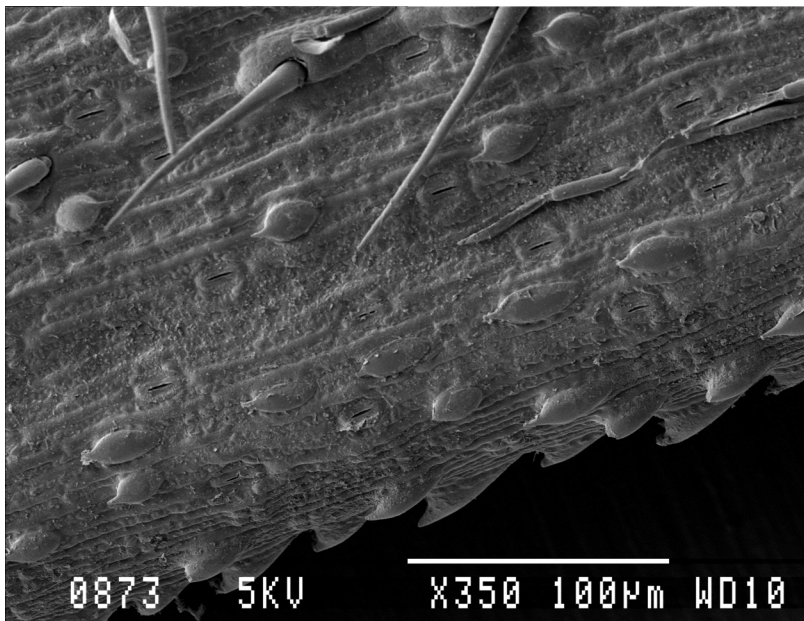


Figure 7.33 Leaf edge of the abaxial side of a *P. maximum* leaf grown without any water stress (W4).

7.3.6 *Pennisetum clandestinum*

The adaxial leaf surface of a *P. clandestinum* plant had infrequent macro- and micro-hairs (Figure 7.34). The micro-hairs differed somewhat from the previous four grass species, in that the distal cell had not collapsed (Figure 7.35), and more closely relates to the prickles of the other species. Silica bodies in the shape of dumbbells and prickles are to be found. The stomata are clearly visible and not covered with wax crystals (Figure 7.36), while a single row of prickles exists on the leaf edge (Figure 7.37).

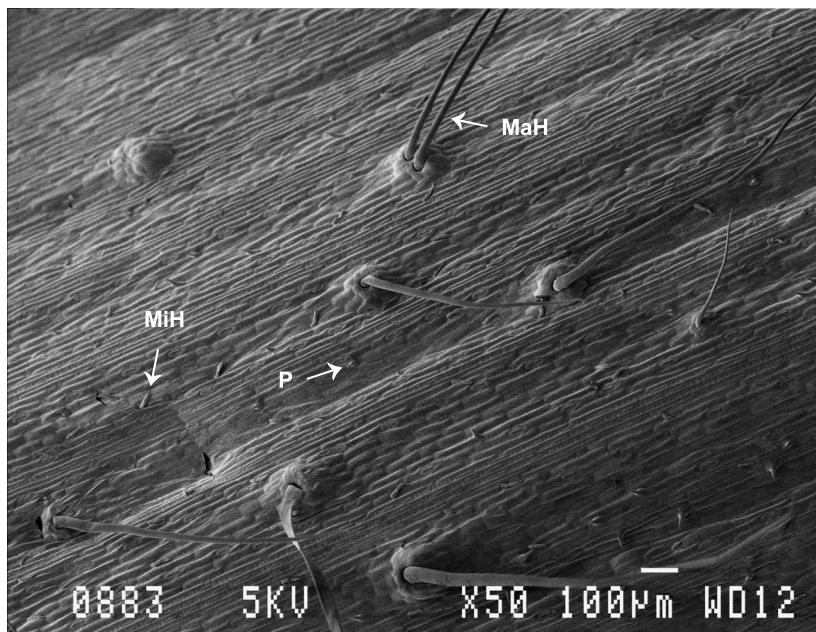


Figure 7.34 Adaxial surface of a *P. clandestinum* leaf grown without any water stress (W4). MaH - Macro-hair, MiH - Micro-hair, P - Prickle.

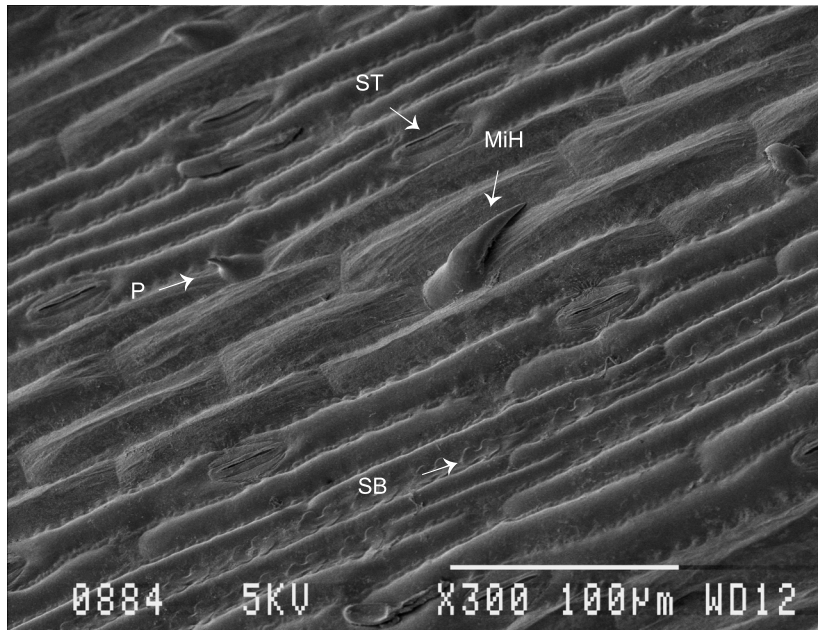


Figure 7.35 Adaxial surface of a *P. clandestinum* leaf grown without any water stress (W4). MiH - Micro-hair, P - Prickle, ST - Stoma, SB - Silica body.

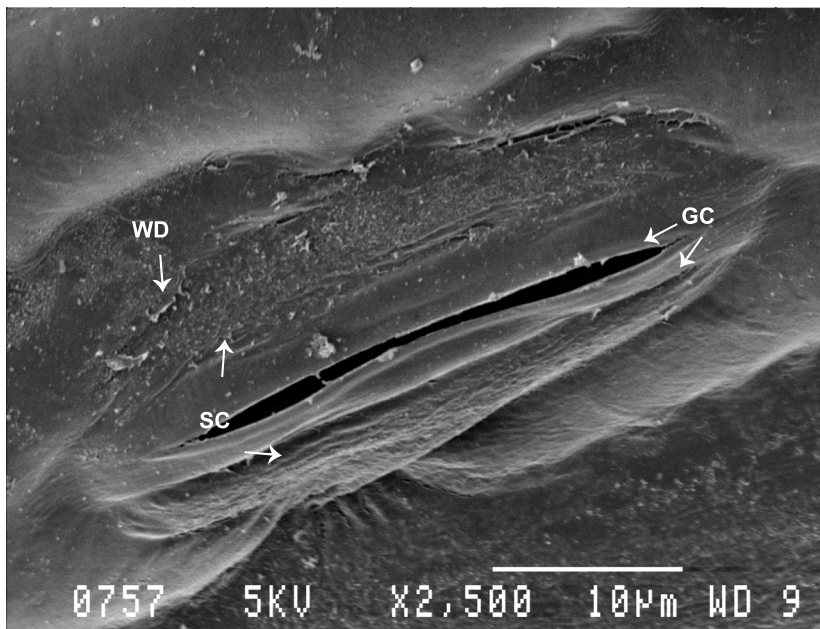


Figure 7.36 A stoma found on the adaxial side of a *P. clandestinum* leaf grown without any water stress (W4) (x2500). WD - Wax deposit, SC - Subsidiary cell, GC -Guard cell.

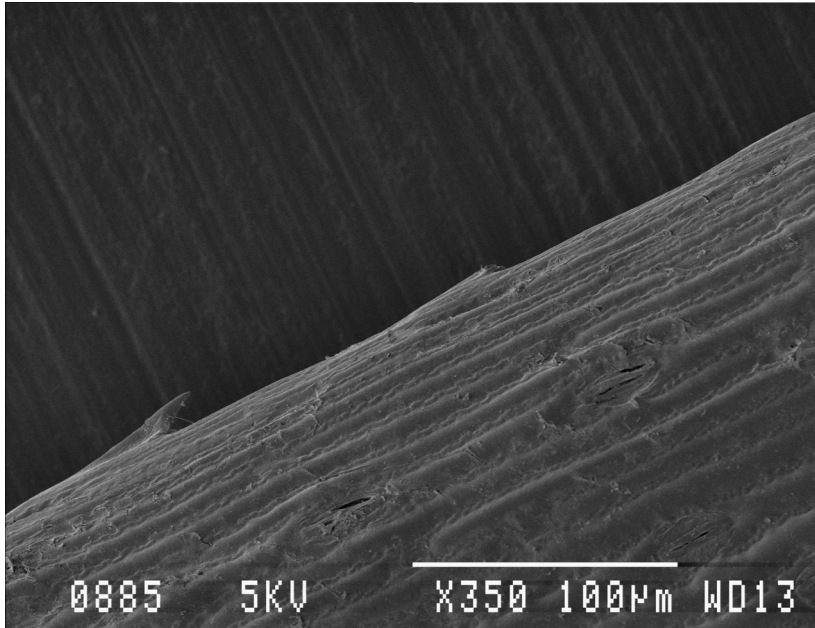


Figure 7.37 Leaf edge of the adaxial side of a *P. clandestinum* leaf grown without any water stress (W4).

Infrequent macro- and micro-hairs are found on the abaxial leaf surface of *P. clandestinum* (Figure 7.38). The long cells are not as angular (Figure 7.39) as on the adaxial side of the leaf. The leaf surface is smooth without any prickles, while the stomata are clearly visible (Figure 7.40). The leaf edge consists out of a single row of prickles (Figure 7.41).

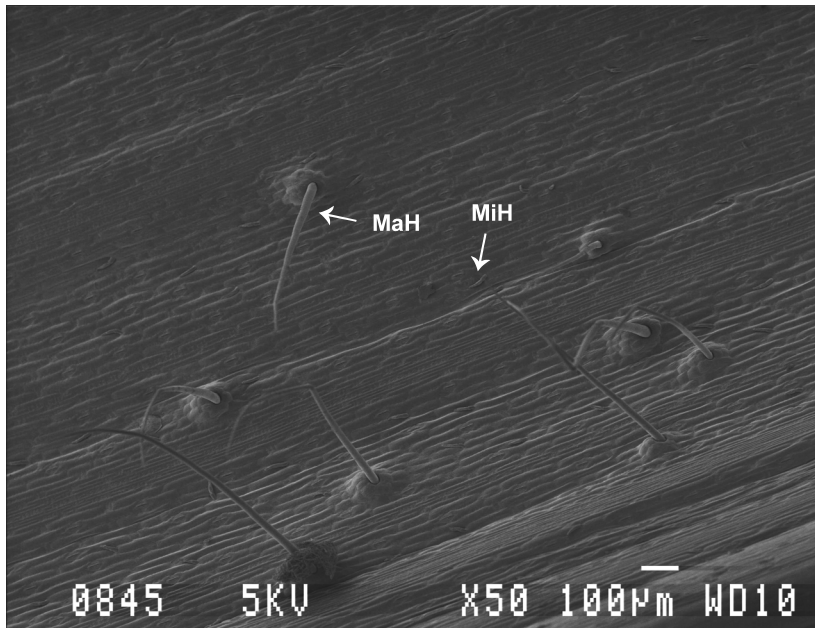


Figure 7.38 Abaxial surface of a *P. clandestinum* leaf grown without any water stress (W4). MaH - Macro-hair, MiH - Micro-hair.

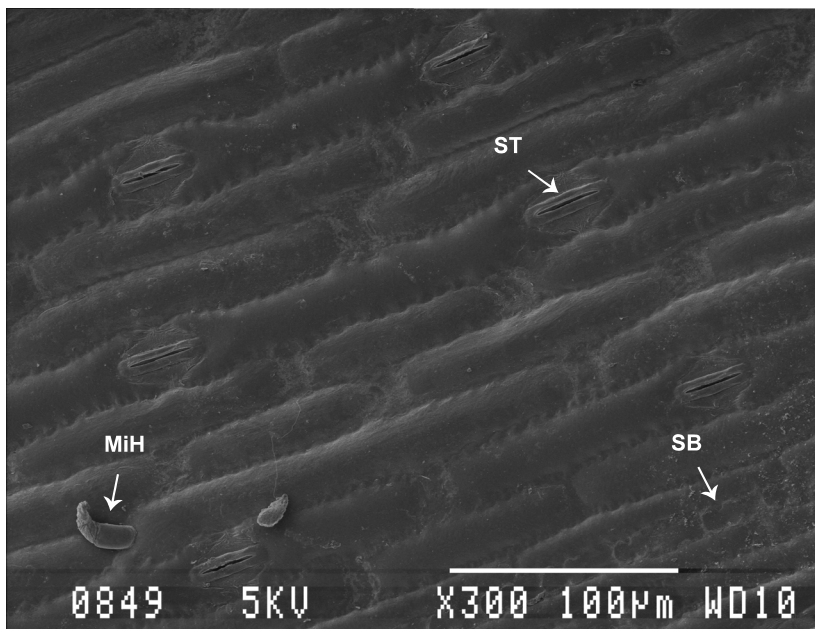


Figure 7.39 Abaxial surface of a *P. clandestinum* leaf grown without any water stress (W4). MiH - Micro-hair, ST - Stoma, SB - Silica body.

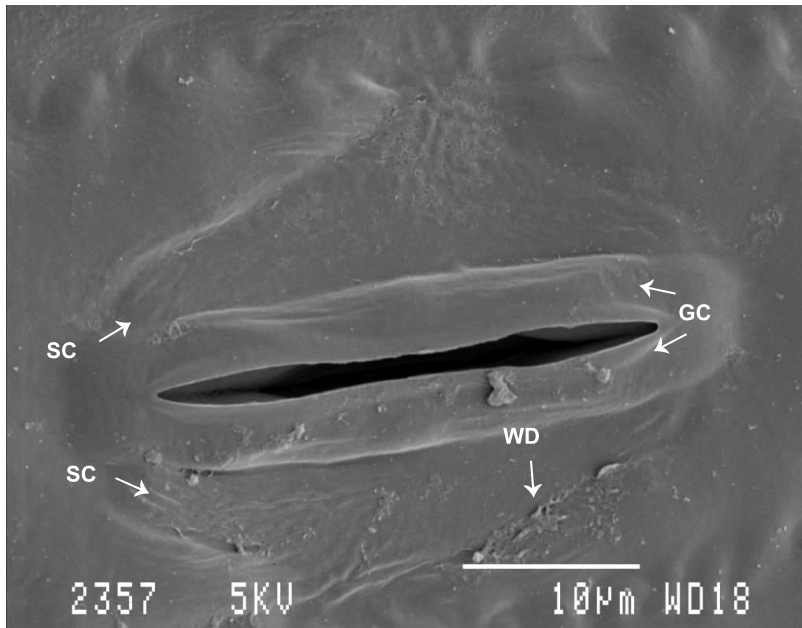


Figure 7.40 A stoma found on the abaxial side of a *P. clandestinum* leaf grown without any water stress (W4) (x2500). WD - Wax deposit, SC - Subsidiary cell, GC -Guard cell.

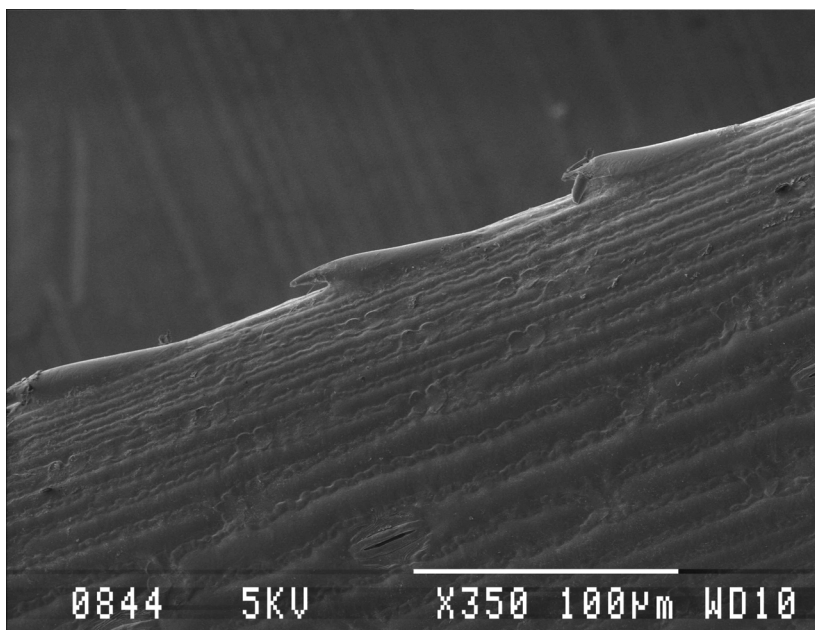


Figure 7.41 Leaf edge of the abaxial side of a *P. clandestinum* leaf grown without any water stress (W4).

CHAPTER 8

THE EFFECT OF WATER AND NITROGEN AVAILABILITY ON THE YIELD AND WATER USE EFFICIENCY OF THREE SUB-TROPICAL PERENNIAL GRASS SPECIES

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Abstract

The effect of three levels of water availability and four levels of nitrogen on the yield and water use efficiency of three subtropical perennial grasses (*Cenchrus ciliaris*, a *Cynodon* hybrid and *Pennisetum clandestinum*) was evaluated in a pot trial in a greenhouse at the University of Pretoria. The three levels of water availability were: soil profile brought to 33 (W1), 66 (W2) and 100% (W3) of field capacity twice per week. The grasses also received four levels of nitrogen namely: N0 = 10 kg N ha⁻¹, N1 = 80 kg N ha⁻¹, N2 = 160 kg N ha⁻¹ and N3 = 280 kg N ha⁻¹.

The *Cynodon* hybrid used significantly ($P \leq 0.05$) less water than *C. ciliaris*, but was able to produce significantly ($P \leq 0.05$) the highest yields in this trial. As was expected, the grasses tended to use more water and produce higher yields as the level of nitrogen was increased. All three grasses tended to produce higher yields at

the N3 level than at the N0 level, despite restricted water supply. Where water availability is thus restricted, nitrogen should still be applied. The amount of nitrogen will, however, be determined by the economic return. The economics are emphasized when comparing the yields at W2 and W3, regardless of the amount of nitrogen applied. The yields at these two levels of water availability were similar and diminishing increases in yield may lead to a drop in profit.

Water use efficiency was improved with increased amounts of nitrogen, but was not significantly ($P \leq 0.05$) different at the N2 and N3 levels of nitrogen. This demonstrates that even a little nitrogen can increase the WUE, while WUE may not be negatively affected if a high level of nitrogen availability is not maintained.

The root systems of all three grass species tended to be weaker under W1 than W2 and W3 conditions, with that of the *Cynodon* hybrid being the poorest. The root systems also tended to be stronger with N2 and N3 than with N0 and N1 levels of nitrogen, regardless of the amount of water applied.

Keywords

Cenchrus ciliaris, *Cynodon* hybrid, *Pennisetum clandestinum*, nitrogen, water, water use efficiency

8.1. Introduction

In a field trial with small plots under a rainshelter (Marais *et al.*, unpublished (b)), it was found that grasses receiving adequate amounts of water (100% of field capacity) (W4) on a weekly basis often produced less dry matter than the grasses receiving 25% less water (75% of field capacity) (W3). It was speculated that the

grasses with adequate amounts of water, were not receiving enough nitrogen to satisfy the N demand under these ideal growing conditions. To verify this, a pot trial was conducted where combinations of water availability and nitrogen supply were applied to three of the grass species.

The hypotheses for this investigation were that:

- the grasses would produce the highest yields at the highest level of water and nitrogen availability;
- the grasses would have better water use efficiencies under water limiting than non-limiting conditions and
- the grasses would have better water use efficiencies under non nitrogen limiting than nitrogen limiting conditions.

8.2. Materials and Methods

Three subtropical perennial grasses were established in 5ℓ pots filled with soil from the experimental farm (Red Hutton) (MacVicar *et al.*, 1991) and placed in a glasshouse situated on the Hatfield Experimental Farm, Pretoria, (25°45'S, 28°16'E), South Africa, during the 2002/2003 growing season. The trial ended in June 2003. The grass species used in this trial were *Cenchrus ciliaris* (Blue buffel-grass, cv. Molopo), a *Cynodon* hybrid cv. Coastcross II (K11) (Coastcross bermudagrass), and *Pennisetum clandestinum* (Kikuyu, cv. Whittet).

Before the start of the trial, the water holding capacity of the soil was determined after the plastic pots were filled with 5kg of air dry soil. Small pieces of shade cloth

were placed over the holes in the pots to prevent the soil from spilling, but did allow for drainage. After weighing, the pots were watered with enough water to saturate the soil, before covering it with plastic bags to prevent evaporation. The pots were then left for two days, weighed again, left for another 12 hours and weighed again to ensure that field capacity had been reached. The difference in weight then represented the amount of water that would be needed to bring the soil to field capacity.

During June 2002, seeds of *C. ciliaris* and *P. clandestinum* were sown in seedling trays and kept in the glasshouse till October 2002. The *Cynodon* hybrid was established from vegetative material collected on the experimental farm.

During October 2002 the seedlings were transplanted (1 plant per pot) to 5l pots with the soil brought to field capacity. For the first month the plants were irrigated on a regular basis to ensure good establishment. From November 2002, the pots were differentially watered, twice a week, as follows:

- W1 - received 33% of the amount needed to restore field capacity
- W2 - received 66% of the amount needed to restore field capacity
- W3 - was brought back to field capacity

The plants were cut back to a height of 10 cm for *C. ciliaris* and 5 cm for the *Cynodon* hybrid and *P. clandestinum*, as soon as they started to flower (*C. ciliaris* and the *Cynodon* hybrid) or when they reached a height of 25 cm (*P. clandestinum*). This resulted in harvests every four to five weeks. The harvested material was dried

to a constant mass for 48 hours at 65°C.

At planting, during October 2002, each pot received N , P (75mg P per pot) and K (250mg K per pot). The amount of P and K were based on advice from a ¹Plant Nutritionist. The amounts of N applied were 10 kg N ha⁻¹ for N0 and N1 treatments, 20 kg N ha⁻¹ for the N2 and 40 kg N ha⁻¹ for the N3 treatments respectively. After each cut, nitrogen was applied at the following rates:

- N0 - control - received no nitrogen, apart from the initial application of 10 kg N ha⁻¹ at planting
- N1 - received 10 kg N ha⁻¹ at planting and after each cut
- N2 - received 20 kg N ha⁻¹ at planting and after each cut
- N3 - received 40 kg N ha⁻¹ at planting and after each cut

The grasses were cut seven times during the trial period resulting in total applications of 10 kg N ha⁻¹, 80 kg N ha⁻¹, 160 kg N ha⁻¹ and 280 kg N ha⁻¹ respectively for the N0, N1, N2 and N3 treatments over the growing season. The fertilizers used were limestone ammonium nitrate (LAN) (28.0% N), superphosphate (8.3% P) and potassium chloride (KCl) (50.0% K).

A fully randomized block design with 10 replications was used. The statistical analysis was done with the Statistical Analysis System (SAS, 1996). Tukey's least significant difference at the 5% level of probability was used to determine significant differences between treatment means. Relevant statistical analysis data is

¹ Personal communication: Prof AS Claassens, Department of Plant Production and Soil Science, University of Pretoria, Pretoria, South Africa.

presented in the Appendix (Tables A8.1 - A8.6).

8.3. Results

8.3.1. Water use

The water use for this trial represented the total amount of water evapotranspired over the experimental period expressed as ℓ per pot (Figures 8.1 - 8.3).

The treatments received and used significantly ($P \leq 0.05$) different amounts of water, with treatment W1 using the least and W3 using the most water (Figure 1). As with the earlier rainshelter trial (Marais *et al.*, unpublished (b)), the W1 and W2 treatments lost respectively more than the 33 and 66% water allocated to them, by tapping into water reserve created at the beginning of the trial when the soil in all pots was brought to field capacity. This higher water loss may be attributed to higher evaporation losses due to smaller plants in these two treatments.

More water was used with higher rates of nitrogen fertilization (Figure 8.2), with N0 and N1 using the least and N3 the most water. The water use of N0 plants did not differ significantly ($P \geq 0.05$) from that of N2 plants. This may again be attributed to higher water loss through evaporation due to smaller plants.

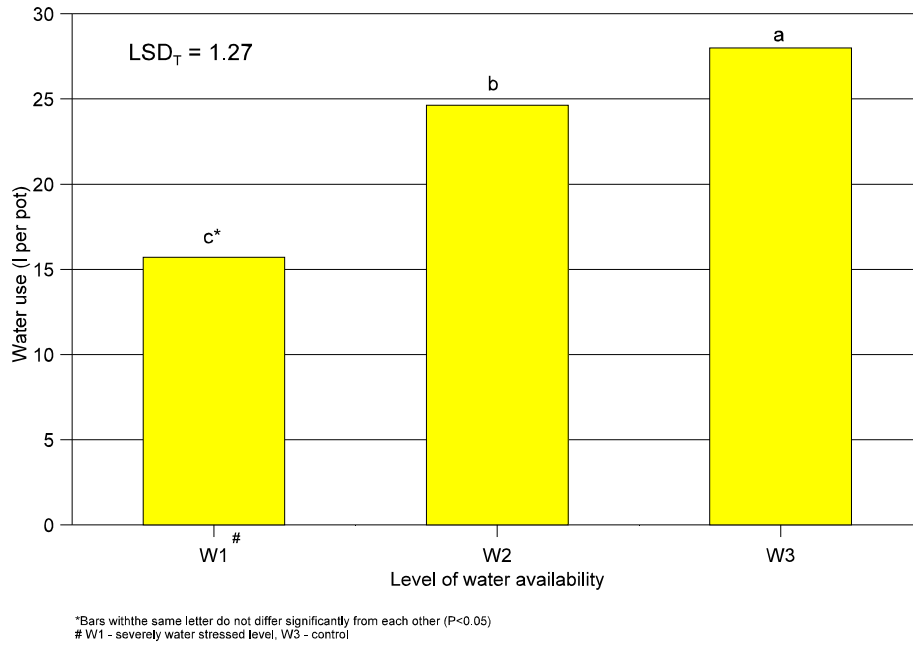


Figure 8.1 Average water used at three levels of water availability.

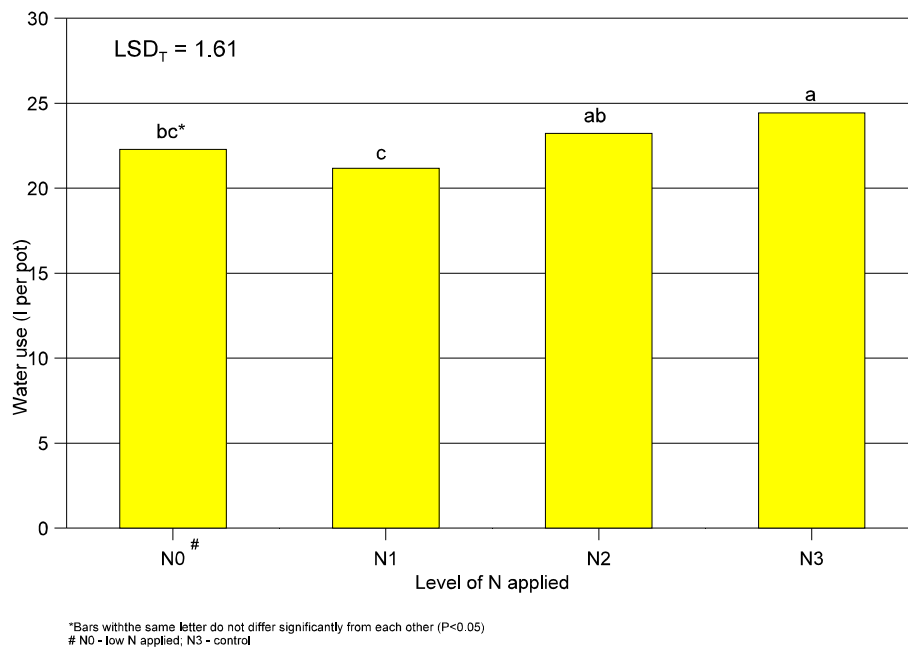


Figure 8.2 Average water use at four levels of nitrogen fertilization.

Only the average water use of *C. ciliaris* and the *Cynodon* hybrid differed significantly ($P \leq 0.05$) from each other with the *Cynodon* hybrid using the least and *C. ciliaris* the most water (Figure 8.3). These results are similar to the results reported in an unpublished article by Marais *et al.*, (a) in a rainshelter trial. There was a significant ($P \leq 0.05$) species x nitrogen interaction with *C. ciliaris* and *P. clandestinum* tending to use more water at higher applications of nitrogen (Figure 8.3). For the *Cynodon* hybrid there was, however, no clear tendency.

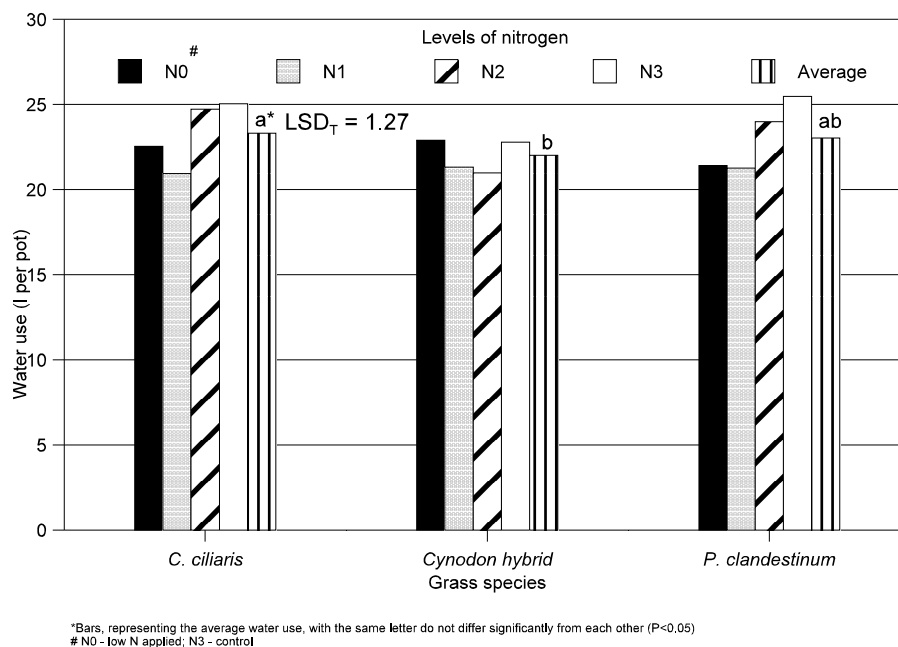


Figure 8.3 The average water use of three grass species over all levels of water and nitrogen, as well as the water use of three grass species at four levels of nitrogen.

8.3.2. Dry matter yield

The dry matter yield is the cumulative yield of seven cuttings taken over the 2002/2003 growing season and is presented as dry matter yield per plant in Figures

8.4 - 8.7.

As also reported by Marais *et al.*, (unpublished (a)) the two treatments receiving the most water (W2 and W3), produced yields which were not significantly ($P \geq 0.05$) different from each other (Figure 8.4), but which were significantly ($P \leq 0.05$) higher than the treatment receiving the least water (W1).

When the dry matter yields are presented as averages of the different levels of nitrogen applied (Figure 8.5), the grasses receiving the most nitrogen (N3) produced significantly ($P \leq 0.05$) more dry material than the other three nitrogen treatments. Treatment N0, receiving the least amount of nitrogen, produced significantly ($P \leq 0.05$) the least dry matter with no significant ($P \geq 0.05$) difference in the dry matter yields produced at the N1 and N2 levels.

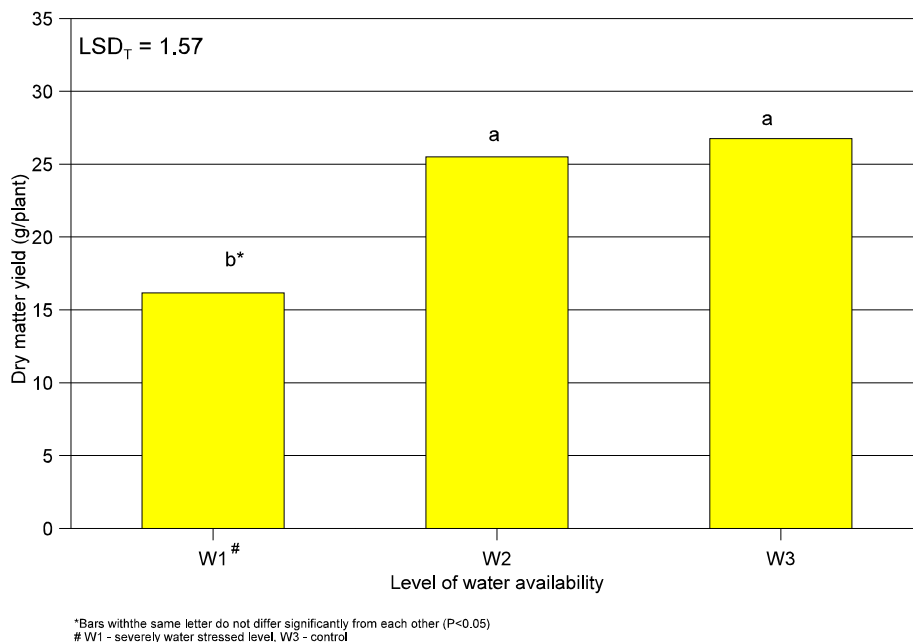


Figure 8.4 Average dry matter yield per plant as affected by three levels of water availability.

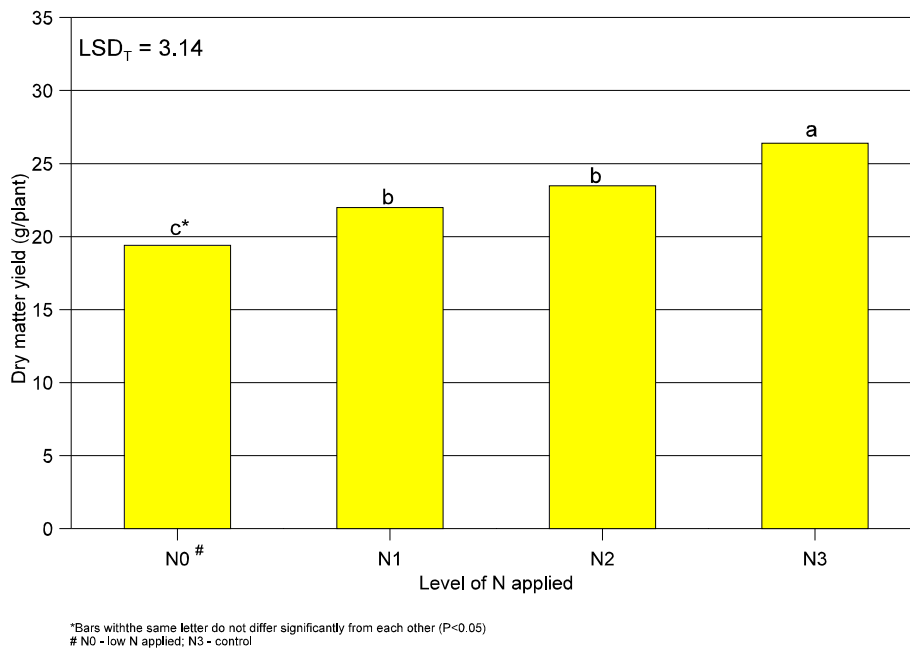


Figure 8.5 Average dry matter yield per plant as affected by four levels of nitrogen.

The average dry matter yield of the three grass species over three levels of water availability and four levels of nitrogen, differed significantly ($P \leq 0.05$) from each other (Figure 8.6). The *Cynodon* hybrid produced significantly ($P \leq 0.05$) the highest and *P. clandestinum* significantly ($P \leq 0.05$) the lowest yields in this trial. In the rainshelter trial, reported by Marais et al. (unpublished (a)) *P. clandestinum* also produced significantly ($P \leq 0.05$) the lowest yields in both seasons, but the ranking order of the *Cynodon* hybrid and *C. ciliaris* differed in the two experimental seasons.

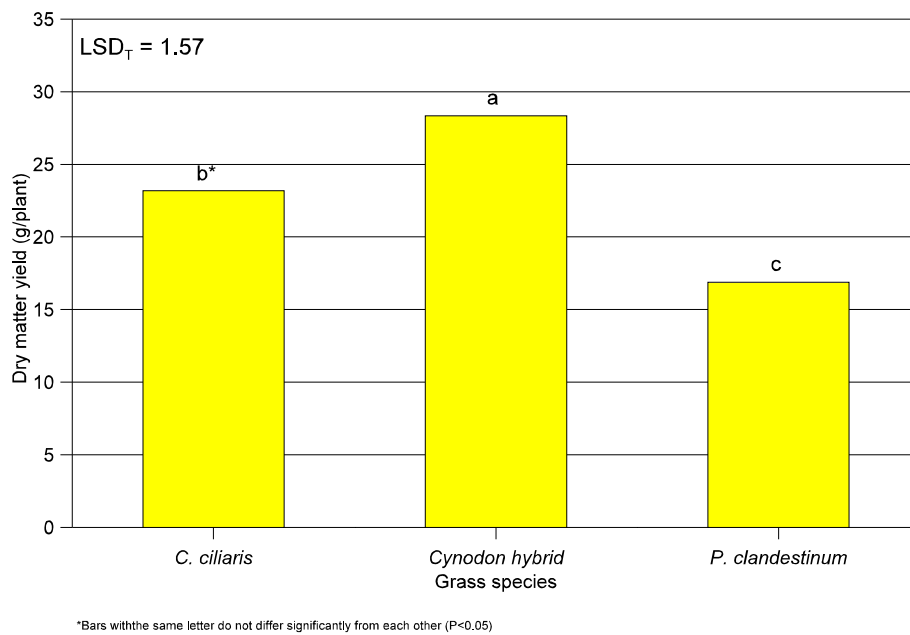


Figure 8.6 Average dry matter yield of three grass species over all levels of water availability and nitrogen.

There was a significant ($P \leq 0.05$) water x nitrogen x species interaction (Figure 8.7), which can be summarised as follows:

- For *C. ciliaris* there was a tendency for higher yields with increased amounts of nitrogen where the grasses received the lowest amount of water (W1) during the season. There was, however, no such tendency for the *Cynodon* hybrid and *P. clandestinum*, although these grasses did produce higher yields at the highest levels of applied nitrogen (N3), as compared with plants receiving the least (N0) nitrogen, when subjected to low levels of water (W1).
- The dry matter yields of the *Cynodon* hybrid at the W2 and W3 treatments, regardless of amount of nitrogen applied, were quite similar. This was also true for

C. ciliaris and *P. clandestinum*, with the exception of *C. ciliaris* N2 and *P. clandestinum* N0 and N1.

- *P. clandestinum* tended to produce the lowest, while the *Cynodon* hybrid tended to produce the highest yields, regardless of the amount of water or nitrogen applied.

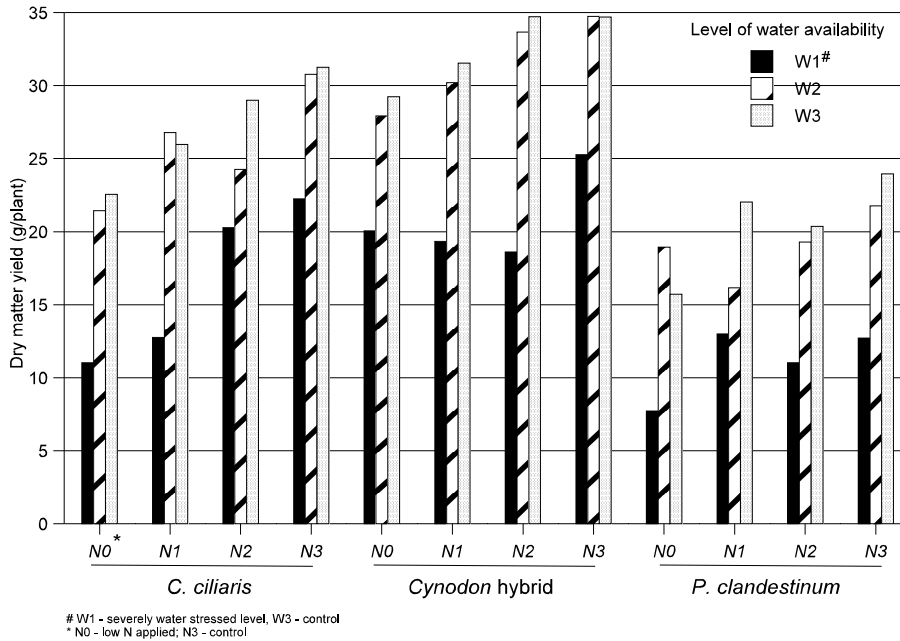


Figure 8.7 Dry matter yield of three grass species as affected by three levels of water availability and four levels of nitrogen.

8.3.3. Water use efficiency (WUE)

The water use efficiencies (WUE) of the grasses are presented as the amount of dry matter produced per litre of water used (Figures 8.8 - 8.10).

The average WUE, as effected by nitrogen level (Figure 8.8), tended to increase

with the more nitrogen applied. Despite this, the WUE of the grasses at the N1, N2 and N3 levels did not differ significantly ($P \geq 0.05$) from each other, although they differed significantly ($P \leq 0.05$) from the N0 treatment.

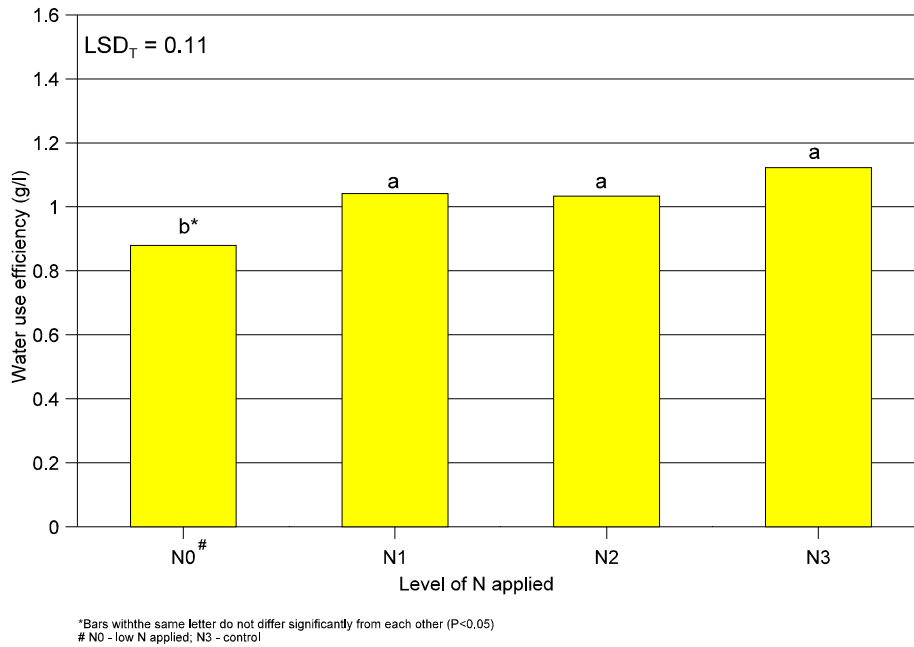


Figure 8.8 Average water use efficiency as affected by four levels of nitrogen.

The *Cynodon* hybrid used water significantly ($P \leq 0.05$) more efficiently than the other grasses, followed by *C. ciliaris* and *P. clandestinum* (Figure 8.9). The WUE of *P. clandestinum* was particularly low in comparison to that of the *Cynodon* hybrid, which was also true for the rainshelter trial (Marais *et al.*, unpublished (c)).

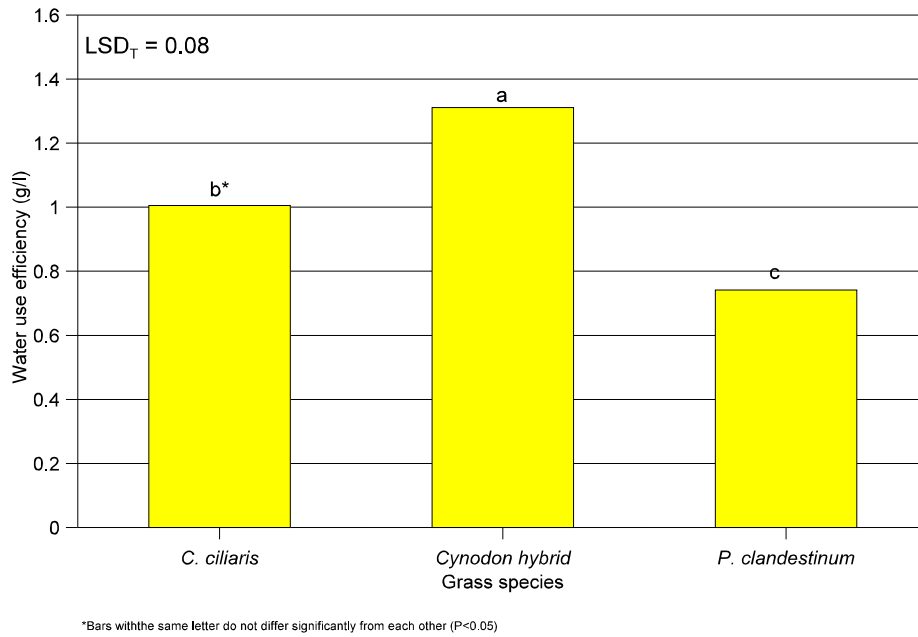


Figure 8.9 Average water use efficiency of three grass species as affected by water availability and nitrogen.

The grasses (especially the *Cynodon* hybrid) tended to use water more efficiently at lower levels of water availability (W1 and W2) regardless of the amount of nitrogen applied (Figure 8.10). The exception to this trend being the *P. clandestinum* N1 treatment.

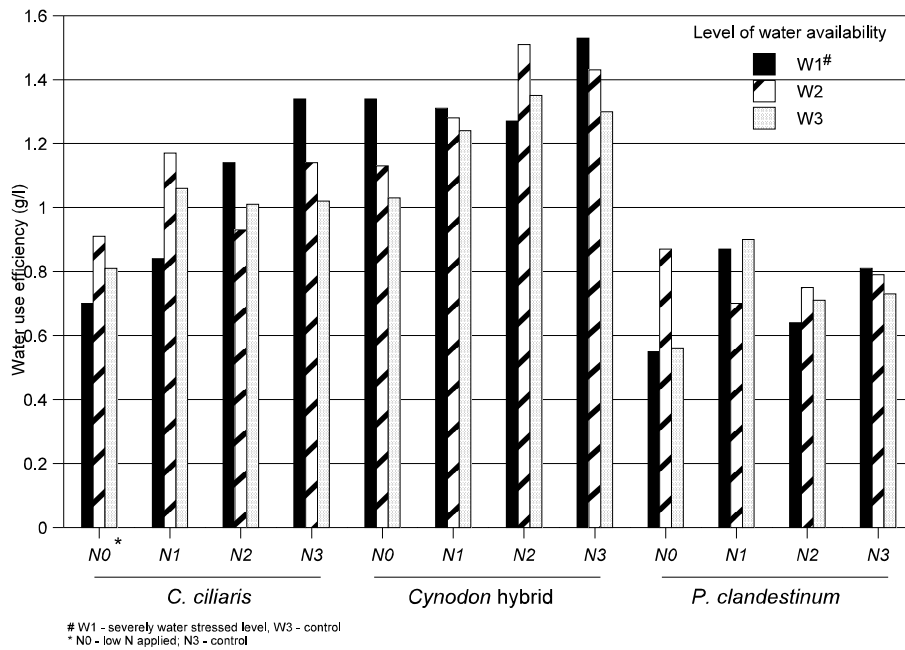


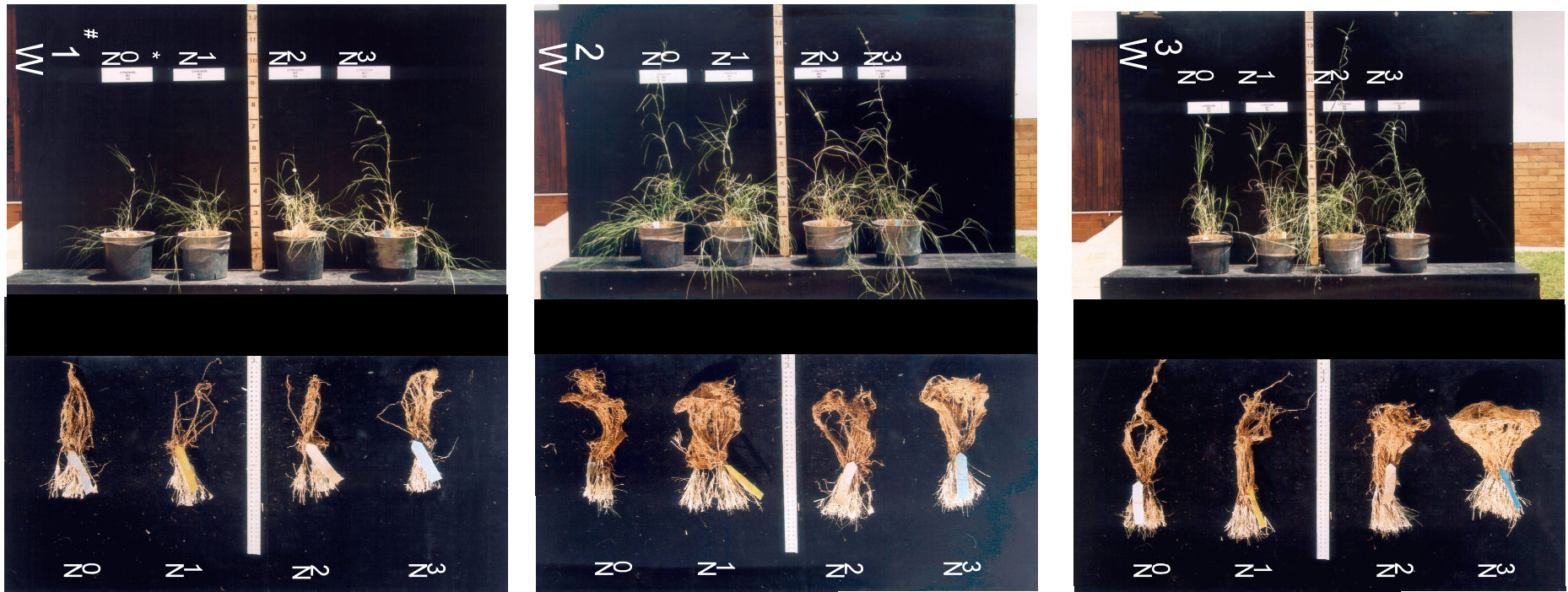
Figure 8.10 Water use efficiency of three grass species as affected by three levels of water availability and four levels of nitrogen.

8.3.4. Above and below ground production

Visually there was little difference between the W2 and W3 plants of all three grass species (Figures 8.11 - 8.13), with W2 plant often looking better than the W3 plants. The W1 plants, however, were notably smaller.

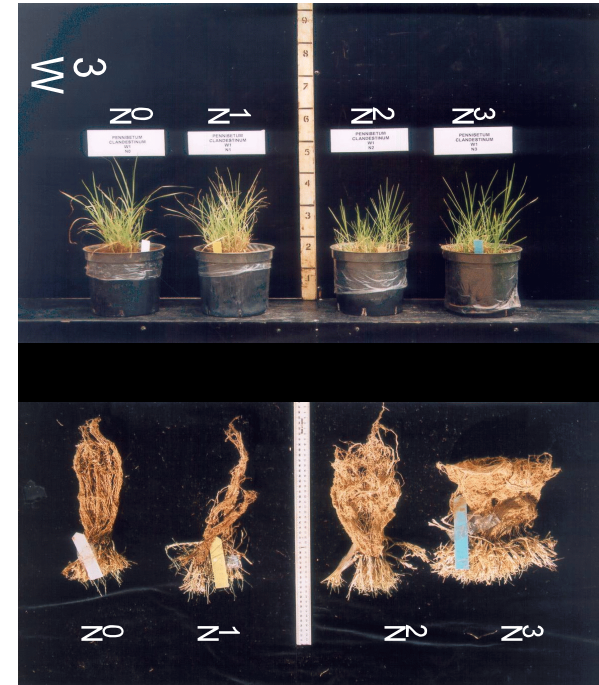
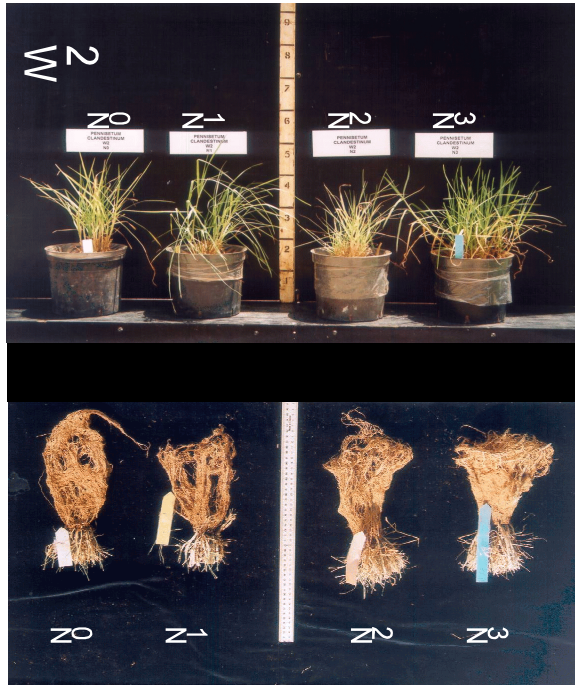
The same trend was evident in the root systems (Figures 8.11 - 8.13). W2 and W3 root systems did not differ much, with W2 root systems often appearing better than those of W3 plants. The W1 root systems was notably poorer than those of the other two levels of water availability. The root system of the *Cynodon hybrid* at W1 was the poorest of the three grass species.

With respect to the above ground components it was not always clear what the effect of the nitrogen was, but for the root systems it was clearer. The roots tended to become much more branched with N2 and N3 than with N0 and N1 levels of nitrogen. This was, furthermore, more pronounced at the W1 and W3 than the W2 treatments.



1 W - 3 W
 - 3 W - 1 W
 - 3 W - 1 W

W 3 W 2 W 1 W
 Z 0 Z 1 Z 2 Z 3



1
W
Z0
Z1
Z2
Z3

W
Z0
Z1
Z2
Z3

8.4. Discussion and Conclusions

The beneficial effect of nitrogen on dry matter production is well documented (Olsen, 1972; 1974; Mathias *et al.*, 1973; Whitney, 1974(a); 1974(b); Kathju *et al.*, 1979; Monson & Burton, 1982; Cook & Mulder, 1984; Miles, 1991; 1997; Pieterse *et al.*, 1997; Pieterse & Rethman, 1999). In this trial the highest yields were most often recorded with the highest amounts of water and nitrogen applied, but did not differ significantly ($P \geq 0.05$) from plants receiving a little less water and nitrogen. This has significant applications when determining the economic feasibility of production systems.

These results also shed some light on the yields obtained in the rainshelter trial (Marais *et al.*, unpublished(a)). The yields under the rainshelter tended to be higher under slight water limitations than under non-water limiting conditions. It was speculated that a nitrogen deficiency could have been the cause for this lower than expected yields. In the pot trial, the same trend was followed, non-significant ($P \geq 0.05$) differences between the yields at slight and non-water limiting conditions, receiving the highest amount of nitrogen. This might imply that under these conditions the grasses have reached their optimum production potential where not even the addition of more water and or nitrogen could increase it. Another explanation might be the lack of other limiting growth factors which are not as obvious to detect.

Water use efficiency is usually improved by adding nitrogen to the system (Mathias *et al.*, 1973; Pieterse *et al.*, 1997). Seven out of the twelve treatment combinations

showed better WUE under water limiting than with adequate amounts of water available. In this trial the addition of nitrogen, thus had a positive effect on the WUE, but above a certain level, the increase became insignificant.

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CHAPTER 9

SUMMARY

Ruminant animal production enterprises rely heavily on planted pastures and natural veld for production. To make a profit from these enterprises, input costs must be optimized. One way of achieving this is to select grass species adapted to the specific production environment (mainly climatic conditions), which can not only produce high yields but also feed of a high quality.

With the implementation of a government initiative, in which a shift from annual monocropping systems to more sustainable perennial grass and legume systems, from which animals can be produced, was encouraged, the opportunity to intensify the knowledge on some annual and perennial fodder species arose. The aims of these studies were to produce the different species under different levels of water availability, to evaluate the water use efficiency of the different species and the ability of such species to adapt to different scenarios.

1. *C. ciliaris*, a notable drought tolerant species, produced yields (11.7-20.0 t ha⁻¹) under non-control conditions (W1, W2 and W3) which were comparable to yields obtained under control conditions (W4) for traditionally irrigated grasses such as the *Cynodon* hybrid (12.0-15.8 t ha⁻¹) and *P. clandestinum* (5.6-11.8 t ha⁻¹).

These results also indicated that a traditionally drought tolerant grass species,

such as *C. ciliaris*, should not be overlooked when identifying species for use under irrigation.

In both seasons *C. ciliaris* was one of the more efficient water users with water use efficiencies ranging from 12.7 - 24.9 kg DM ha⁻¹ mm⁻¹; 6.9 - 14.4 kg DDM ha⁻¹ mm⁻¹ and 0.9 - 2.2 kg CP ha⁻¹ mm⁻¹ for W4 and Control (W1) conditions respectively.

The relatively good yields and water use efficiencies of *C. ciliaris* could be attributed to having a large number of trichomes on the leaf surfaces while the stomata were well protected from the environment by the veins. In this way excessive water loss from the leaf surfaces could be limited.

The dry matter digestibility of *C. ciliaris* ranged from 50.44 to 60.66 from W1 to W3 conditions while the crude protein content ranged from 4.09 to 8.43 from W2 to W4 conditions.

In a growth analysis, *C. ciliaris* grew at a rate of 100 to 140 kg ha⁻¹ day⁻¹ at the end of two consecutive growth cycles during the summer growing period.

In a trial with only *C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum*, the yield and dry matter water use efficiency as affected by different levels of water and nitrogen were evaluated. This was done after yields in the rainshelter trial were sometimes higher at W2 than control conditions, and it was speculated that a nitrogen deficiency could have caused this. At high levels of nitrogen, the level of water available became less important as the yield at W2 and W3 levels did not differ significantly.

2. The *Cynodon* hybrid initially produced relatively poor yields in the 1996/97

season, but produced similar yields to *C. ciliaris* in the 1997/98 season. A few researchers have argued that some perennial grass species take one to two growing seasons to become well established. In this time the true yield potential of the species is not realized. The water use efficiencies varied from 12.4 to 20.0 kg DM ha⁻¹ mm⁻¹, 6.7 to 11.0 kg DDM ha⁻¹ mm⁻¹ and 1.3 to 2.7 kg CP ha⁻¹ mm⁻¹ for W4 and W1 conditions respectively.

The relatively good yields and water use efficiencies of the *Cynodon* hybrid, as in the case with *C. ciliaris*, could be attributed to having a large number of trichomes on the leaf surfaces while the stomata were well protected from the environment by the veins. In this way excessive water loss from the leaf surfaces could be limited.

The dry matter digestibility of the *Cynodon* hybrid ranged from 54.0 to 60.2% and the crude protein content from 8.98 to 10.74% for W1 and W4 conditions respectively. The crude protein content of the *Cynodon* hybrid was the highest of the five grass species. Combined with good yields, this is a grass species with a lot of different potential applications.

The growth rate of the *Cynodon* hybrid was, however, far lower than that of the tufted species reaching a maximum of 40 to 70 kg ha⁻¹ day⁻¹ for two growth cycles.

3. *D. eriantha* tended to be better adapted to wetter conditions. Despite this tendency, it still produced yields of 6.9 and 13.2 t ha⁻¹ under W1 and W4 conditions respectively which is in the same yield order recorded by other South

African researchers. In terms of dry matter and digestible dry matter water use efficiency, *D. eriantha* were also good, ranging from 7.9 to 19.4 kg DM ha⁻¹ mm⁻¹ and 4.6 to 14.5 kg DDM ha⁻¹ mm⁻¹, while the crude protein water use efficiency was rather low (0.4 to 1.1 kg CP ha⁻¹ mm⁻¹) due to the low crude protein content of the plants.

D. eriantha had more stomata on the abaxial than adaxial leaf surface and the epidermis was covered by large wax crystals, it was however not enough to ensure the yields and water use efficiency of *C. ciliaris* and the *Cynodon* hybrid, but it was better than both *P. maximum* and *P. clandestinum*.

The dry matter digestibility ranged from 56 to 62.75% and the crude protein content ranged from 4.15 to 6.11%.

The growth rate of *D. eriantha* at the end of two growth cycles were about 5 kg ha⁻¹ day⁻¹ less than that of *C. ciliaris*.

4. *P. maximum* also tended to be better adapted to wetter conditions. The yields over the two summer growing seasons were disappointingly low ranging from 6.2 to 10.4 kg ha⁻¹ at the W1 and W4 water availability levels respectively. The water use efficiencies in terms of dry matter yield and digestible dry matter were, therefore, also low at 6.4 and 14.9 kg DM ha⁻¹ mm⁻¹ and 3.5 to 9.1 kg DDM ha⁻¹ mm⁻¹ at the W1 and W4 levels respectively, while the crude protein water use efficiencies were not as bad at 0.3 to 1.4 kg CP ha⁻¹ mm⁻¹ for levels W1 and W4, respectively.

Digestible dry matter content at W1 and W4 were 50. and 68.71% respectively ,

while the crude protein contents for the same treatments were 4.18 to 7.7%.

As in *D. eriantha*, the stomata border the veins and are seldom, if ever, found in the middle of the intercostal zone. The leaf surface is once again covered by a wax deposit, but it does not cover the guard cells as was the case for *D. eriantha*.

Although the leaf surfaces of *P. maximum* thus possess some of the characteristics to prevent excessive water loss, these were not as extensive as those found in *C. ciliaris*, for example. This might explain why *P. maximum* was not able to produce yields and use water as efficiently as those grass species with the better water loss prevention from the leaves.

The maximum growth rate of *P. maximum* at the end of two growth cycles were 60 and 110 kg ha⁻¹ day⁻¹ respectively, placing it's growth rate between that of *C. ciliaris* and *D. eriantha* on the one end and the *Cynodon* hybrid and *P. clandestinum* on the other end. Despite the growth rate of *P. maximum* being lower than that of *C. ciliaris* and *D. eriantha*, it was much higher than that of the *Cynodon* hybrid and *P. clandestinum*.

5. *P. clandestinum* also tended to be better adapted to wetter conditions. As with the *Cynodon* hybrid, it produced much better yields in the 1997/98 (7.7 and 11.8 t ha⁻¹ at W1 and W4) than 1996/97 (4.0 and 5.6 t ha⁻¹ at W1 and W4) season. This resulted in rather low water use efficiencies in the 1996/97 season of 5.2 and 8.6 kg DM ha⁻¹ mm⁻¹, 3.4 and 5.3 kg DDM ha⁻¹ mm⁻¹ and 0.5 and 0.8 kg CP ha⁻¹ mm⁻¹, while the water use efficiencies in 1997/98 were 10.4 and 14.2 kg DM ha⁻¹ mm⁻¹, 5.0 to 6.0 kg DDM ha⁻¹ mm⁻¹ and 0.9 and 1.4 kg CP ha⁻¹ mm⁻¹,

respectively.

Dry matter digestibility for the 1996/97 season was 60.77 and 65.61% while it was quite low in the following season at only 28.5 and 48.66%. *P. clandestinum* plants, however, contained a much higher crude protein content (7.19 and 10.11%) in both seasons than *C. ciliaris*, *D. eriantha* and *P. maximum*, but not the *Cynodon* hybrid.

The leaf surfaces of *P. clandestinum* were characterised by big but few stomata. These stomata was also not protected in the same way as any of the other grass species, while the epidermis was protected by a smooth waxy layer. This was, however, not enough to prevent excessive water loss from the leaf surfaces and might explain the low water use efficiencies for this species.

The growth rate of *P. clandestinum* were the lowest for the five grass species tested, reaching a maximum of 25 and 45 kg ha⁻¹ day⁻¹ at the end of the two growth cycles.

6. As water became less available, less photosynthesis could take place resulting in lower yields. Although there was a significant reduction in yields between the highest and lowest levels of water availability, the yields in between these extremes were not significantly different. This absence of significance can be explained by the plant's ability to use water stored in the soil profile. If the soil profiles were not filled to field capacity at the beginning of the season, significant differences could have been expected.

The water use efficiency at lower levels of water availability (17.0 kg ha⁻¹ mm⁻¹)

were often better than under control (non-water limiting) conditions ($10.7 \text{ kg ha}^{-1} \text{ mm}^{-1}$). This means that plants were able to adapt to the lower levels of water available by using less water to produce the same amount of dry matter than would have been the case under control conditions. This would imply that less water could be used per unit area or that more hectares of a certain crop can be produced, with the assumption that the soil profiles were at field capacity at the start of the season.

Dry matter digestibility was not as affected by the level of water availability as was crude protein content. Whereas dry matter digestibility was improved by higher levels of water available in some cases, it was often the case for crude protein content. This better crude protein content could have been the result of higher levels of nitrogen applied at higher levels of water availability. This was done to prevent nitrogen deficiencies at the higher levels of water availability.

In a morphological study on the grass leaves, few differences could be found in terms of level of water availability. The most clear cut effect of the level of water was on the number of stoma per area. For *C. ciliaris*, the *Cynodon* hybrid and *P. clandestinum* there was a tendency of fewer stoma per area, with less water available, on the adaxial leaf surfaces, while the abaxial leaf surfaces of *C. ciliaris*, the *Cynodon* hybrid and *D. eriantha* also tended to have fewer stoma with less water available. The level of water availability did not alter the number of stoma per leaf surface.

7. In a glasshouse trial where the effect of different levels of water and nitrogen

availability were tested for *C. ciliaris*, the *Cynodon* hybrid and *P. maximum* the following results were obtained. The *Cynodon* hybrid used significantly less water than *C. ciliaris*, but produced significantly the highest yields in this trial. As was expected, the grasses tended to use more water and also produce higher yields as the level of nitrogen applied was increased.

All three grasses tend to produce higher yields at the N3 level, compared with the N0 level of nitrogen, despite receiving less water. Where water availability is thus restricted, one should still apply nitrogen. The amount of nitrogen will, however, be determined by how much the economic return is increased. The economics are emphasized when comparing the yields at W2 and W3, regardless of the amount of nitrogen applied. The yields at these two levels of water availability were similar and diminishing increases in yield may lead to a drop in profit, if this is not taken into consideration.

Water use efficiencies were increased by increased amounts of nitrogen applied, but were not significantly different from each other at the N2 - N3 level of nitrogen. Even a little bit of nitrogen increased the WUE, while not maintaining a high level of nitrogen, it might not have a negative effect on WUE.

The root systems of all three grass species tended to be poorer at W1 than W2 and W3 conditions, with that of the *Cynodon* hybrid being the poorest. The root systems also tend to be better with N2 and N3 than with N0 and N1 levels of nitrogen, regardless of the amount of water applied.

APPENDIX

Data and statistical analysis of data presented in **Chapter 2**.

Table A2.1 Influence of level of water availability on the water use (mm) of five perennial grasses in 1996/97.

Grass species (G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	470.0	688.0	874.0	1095.3	781.8
<i>Cynodon</i> hybrid	423.0	612.0	752.3	960.3	686.9
<i>D. eriantha</i>	421.0	600.3	745.0	931.3	674.4
<i>P. maximum</i>	417.3	596.0	727.7	923.7	666.2
<i>P. clandestinum</i>	468.7	672.3	863.7	1094.7	774.8
Mean	440.0	633.7	792.5	1001.1	
LSD _T (G) = 46.8					
LSD _T (I) = 39.3					

* W1 -severely water stressed level, W4 - control

Table A2.2 Shortened ANOVA for the water use (mm) of five perennial grasses at four levels of water availability in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	23.91	< 0.0001
Level of water availability (I)	3	527.47	<0.0001
GxI	12	1.38	0.2176
Mean Square Error	1612.05		
CV %	5.6		
R ²	0.98		

Table A2.3 Influence of level of water availability on the water use (mm) of five perennial grasses in 1997/98.

Grass species (G)	Irrigation level (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	521.2	719.5	856.6	1096.9	798.6
<i>Cynodon hybrid</i>	488.1	659.5	781.1	975.3	726.0
<i>D. eriantha</i>	530.4	729.1	953.8	1265.1	869.6
<i>P. maximum</i>	606.8	906.7	1149.8	1475.2	1034.6
<i>P. clandestinum</i>	542.0	643.2	902.8	1154.0	810.5
Mean	537.7	731.6	928.8	1193.3	
LSD _T (G x I) = 43.4					

* W1 -severely water stressed level, W4 - control

Table A2.4 Shortened ANOVA for the water use (mm) of five perennial grasses at four levels of water availability in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	41.28	< 0.0001
Level of water availability (I)	3	299.99	<0.0001
GxI	12	3.53	0.0013
Mean Square Error	3927.031		
CV %	7.4		
R ²	0.97		

Table A2.5 Influence of level of water availability on the leaf areas (m²) of five perennial grasses in 1996/97.

Grass species (G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	0.76	0.88	1.13	0.96	0.93
<i>Cynodon</i> hybrid	0.44	0.45	0.57	0.71	0.54
<i>D. eriantha</i>	0.38	1.00	0.87	1.16	0.93
<i>P. maximum</i>	0.42	0.69	0.72	0.76	0.65
<i>P. clandestinum</i>	0.42	0.44	0.60	0.55	0.50
Mean	0.54	0.69	0.78	0.83	
LSD _T (G) = 0.18					
LSD _T (I) = 0.15					

* W1 -severely water stressed level, W4 - control

Table A2.6 Shortened ANOVA for the leaf areas (m²) of five perennial grasses at four levels of water availability in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	22.65	< 0.0001
Level of water availability (I)	3	10.37	<0.0001
GxI	12	1.18	0.3282
Mean Square Error	0.02265987		
CV %	21.2		
R ²	0.77		

Table A2.7 Influence of level of water availability on the leaf areas (m²) of five perennial grasses in 1997/98.

Grass species (G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	0.95	0.99	1.02	1.01	0.99
<i>Cynodon</i> hybrid	0.64	0.61	0.85	0.89	0.75
<i>D. eriantha</i>	0.76	0.97	1.05	1.22	1.00
<i>P. maximum</i>	0.88	1.10	0.86	0.87	0.93
<i>P. clandestinum</i>	1.04	1.20	1.32	1.15	1.18
Mean	0.85	0.97	1.02	1.02	
LSD _T (G) = 0.22					
LSD _T (I) = 0.18					

* W1 -severely water stressed level, W4 - control

Table A2.8 Shortened ANOVA for the leaf areas (m²) of five perennial grasses at four levels of water availability in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	8.31	< 0.0001
Level of water availability (I)	3	2.83	0.0505
GxI	12	1.12	0.3711
Mean Square Error		0.034688	
CV %		19.2	
R ²		0.58	

Table A2.9 Influence of level of water availability on the root mass (g) of five perennial grasses in 1999.

Grass species (G)	Level of water availability (I)*	Soil depth increment (m) (D)				
		0 - 0.21	0.21 - 0.42	0.42 - 0.63	0.63 - 0.84	0.84 - 1.05
<i>C. ciliaris</i>	W1	2.50	0.59	0.32	0.27	0.25
	W4	2.21	0.74	0.37	0.28	0.29
<i>Cynodon hybrid</i>	W1	1.84	0.86	0.43	0.56	0.55
	W4	1.33	0.42	0.30	0.26	0.27
<i>D. eriantha</i>	W1	1.40	0.40	0.30	0.27	0.21
	W4	3.72	1.00	0.57	0.49	0.42
<i>P. maximum</i>	W1	2.95	0.70	0.53	0.39	0.28
	W4	2.15	0.62	0.51	0.33	0.23
<i>P. clandestinum</i>	W1	2.61	0.85	0.42	0.45	0.41
	W4	3.33	0.79	0.53	0.46	0.45

LSD_T(G x I x D) = 0.57

* W1 -severely water stressed level, W4 - control

Table A2.10 Shortened ANOVA for the root mass (g) of five perennial grasses at four levels of water availability in 1999.

Source	df	F value	Pr > F
Grass species (G)	4	5.40	0.0006
Level of water availability (I)	1	1.96	0.1648
GxI	4	13.79	< 0.0001
Depth (D)	4	253.31	< 0.0001
GxD	16	3.24	0.0002
IxD	4	1.30	0.2746
GxIxD	16	4.10	< 0.0001
Mean Square Error	0.091968		
CV %	35.8		
R ²	0.92		

Data and statistical analysis of data presented in Chapter 3.

Table A.3.1 Shortened ANOVA for the dry matter yield (t ha^{-1}) of five perennial grasses at four levels of water availability in 1996/97

Source	df	F value	Pr > F
Grass species (G)	4	28.31	< 0.0001
Level of water availability (I)	3	9.64	< 0.0001
GxI	12	0.86	0.5933
Mean Square Error	5.917824		
CV %	16.8		
R ²	0.79		

Table A3.2 Shortened ANOVA for the dry matter yield (t ha^{-1}) of five perennial grasses at four levels of water availability in 1997/98

Source	df	F value	Pr > F
Grass species (G)	4	39.15	< 0.0001
Level of water availability (I)	3	12.61	< 0.0001
GxI	12	1.00	0.4642
Mean Square Error	3124003.6		
CV %	22.7		
R ²	0.84		

Table A3.3 Influence of level of water availability on the contribution of the leaf (tha^{-1}) component to the production of five perennial grasses in 1996/97.

Grass species (G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	5.66	7.58	8.88	8.61	7.68
<i>Cynodon</i> hybrid	4.23	5.07	6.71	6.55	5.64
<i>D. eriantha</i>	4.26	6.72	6.14	5.97	5.77
<i>P. maximum</i>	3.07	4.18	3.57	4.36	3.80
<i>P. clandestinum</i>	2.73	3.17	3.90	3.56	3.34
Mean	3.99	5.34	5.84	5.81	
LSD _T (G) = 1.15					
LSD _T (I) = 0.97					

* W1 -severely water stressed level, W4 - control

Table A3.4 Shortened ANOVA for the contribution of the leaf (t ha^{-1}) component to the production of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	37.18	< 0.0001
Level of water availability (I)	3	11.57	< 0.0001
GxI	12	1.17	0.3366
Mean Square Error	0.9773167		
CV %	18.84		
R ²	0.83		

Table A3.5 Influence of level of water availability on the contribution of the stem (t ha⁻¹) component to the production of five perennial grasses in 1996/97.

Grass species (G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	5.92	9.15	11.09	10.33	9.12
<i>Cynodon</i> hybrid	2.65	3.03	5.05	4.92	3.91
<i>D. eriantha</i>	3.24	6.95	6.43	5.66	5.57
<i>P. maximum</i>	3.10	4.36	5.42	5.86	4.69
<i>P. clandestinum</i>	0.79	0.37	1.10	1.19	1.92
Mean	3.24	5.08	6.09	5.76	
LSD _T (G) = 1.78					
LSD _T (I) = 1.47					

* W1 -severely water stressed level, W4 - control

Table A3.6 Shortened ANOVA for the contribution of the stem (t ha⁻¹) component to the production of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	36.06	< 0.0001
Level of water availability (I)	3	10.37	< 0.0001
GxI	12	1.00	0.4678
Mean Square Error	2.3374617		
CV %	30.33		
R ²	0.82		

Table A3.7 Influence of level of water availability on the contribution of the inflorescence (t ha^{-1}) component to the production of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	0.11	0.27	0.00	0.23	0.15
<i>Cynodon</i> hybrid	0.47	0.66	0.37	0.52	0.51
<i>D. eriantha</i>	1.07	0.93	0.32	0.81	1.26
<i>P. maximum</i>	0.70	1.66	1.32	2.02	0.14
<i>P. clandestinum</i>	none	none	none	none	none
Mean	0.26	0.46	0.43	0.49	

LSD_T(G) = 0.37

* W1 -severely water stressed level, W4 - control

Table A3.8 Shortened ANOVA for the contribution of the inflorescence (t ha^{-1}) component to the production of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	31.30	< 0.0001
Level of water availability (I)	3	1.60	0.2050
GxI	12	1.15	0.3527
Mean Square Error	0.10022333		
CV %	76.68		
R ²	0.78		

Table A3.9 Influence of level of water availability on the contribution of the leaf (t ha^{-1}) component to the production of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	7.49	7.20	8.20	6.47	7.34
<i>Cynodon</i> hybrid	5.10	7.12	9.26	8.90	7.59
<i>D. eriantha</i>	4.72	6.25	6.44	7.18	6.15
<i>P. maximum</i>	4.36	3.94	4.40	6.16	4.72
<i>P. clandestinum</i>	5.38	6.44	4.83	7.02	5.92
Mean	5.41	6.19	6.63	7.15	
LSD _T (G) = 1.71					
LSD _T (I) = 1.44					

* W1 -severely water stressed level, W4 - control

Table A3.10 Shortened ANOVA for the contribution of the leaf (t ha^{-1}) component to the production of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	7.54	0.0001
Level of water availability (I)	3	3.76	0.0181
GxI	12	1.56	0.1451
Mean Square Error	2.1589725		
CV %	23.17		
R ²	0.60		

Table A3.11 Influence of level of water availability on the contribution of the stem (t ha⁻¹) component to the production of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	4.83	6.48	5.69	7.22	6.05
<i>Cynodon</i> hybrid	4.54	5.90	4.90	6.85	5.55
<i>D. eriantha</i>	2.01	1.84	2.34	2.44	2.16
<i>P. maximum</i>	2.64	3.08	3.27	3.25	3.06
<i>P. clandestinum</i>	2.30	2.23	4.51	4.81	3.46
Mean	3.27	3.91	4.14	4.91	
LSD _T (G) = 1.09					
LSD _T (I) = 0.92					

* W1 -severely water stressed level, W4 - control

Table A3.12 Shortened ANOVA for the contribution of the stem (t ha⁻¹) component to the production of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	38.08	< 0.0001
Level of water availability (I)	3	7.90	0.0003
GxI	12	1.62	0.1245
Mean Square Error	0.8800839		
CV %	23.13		
R ²	0.83		

Table A3.13 Influence of level of water availability on the contribution of the inflorescence ($t\ ha^{-1}$) component to the production of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	0.07	0.21	0.003	0.00	0.07
<i>Cynodon</i> hybrid	0.05	0.17	0.49	0.08	0.20
<i>D. eriantha</i>	1.00	0.62	0.34	0.00	0.22
<i>P. maximum</i>	none	none	none	none	none
<i>P. clandestinum</i>	none	none	none	none	none
Mean	0.06	0.10	0.15	0.07	

LSD_T(G) = 0.13

* W1 -severely water stressed level, W4 - control

Table A3.14 Shortened ANOVA for the contribution of the inflorescence ($t\ ha^{-1}$) component to the production of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	10.94	< 0.0001
Level of water availability (I)	3	2.18	0.1059
GxI	12	2.80	0.0072
Mean Square Error		0.01194776	
CV %		112.81	
R ²		0.68	

Data and statistical analysis of data presented in **Chapter 4**.

Table A4.1 Correlation (r^2) between plant yield components and *in vitro* dry matter digestibility of five annual fodder crops in 1996/97.

Yield component	<i>In vitro</i> dry matter digestibility of				
	<i>C. ciliaris</i>	<i>Cynodon</i> hybrid	<i>D. eriantha</i>	<i>P. maximum</i>	<i>P. clandestinum</i>
Leaf	0.1	- 0.3	- 0.4	- 0.7	0.6
Stem	0.2	- 0.3	- 0.6	- 0.6	0.5
Inflorescence	- 0.2	0.3	- 0.3	- 0.2	-

Table A4.2 Correlation (r^2) between plant yield components and *in vitro* dry matter digestibility of five annual fodder crops in 1997/98.

Yield component	<i>In vitro</i> dry matter digestibility of				
	<i>C. ciliaris</i>	<i>Cynodon</i> hybrid	<i>D. eriantha</i>	<i>P. maximum</i>	<i>P. clandestinum</i>
Leaf	- 0.01	0.4	0.1	0.2	- 0.03
Stem	- 0.6	0.1	- 0.2	0.4	0.4
Inflorescence	0.03	0.3	0.7	-	-

Table A4.3 Correlation (r^2) between plant yield components and crude protein content of five annual fodder crops in 1996/97.

Yield component	Crude protein content of				
	<i>C. ciliaris</i>	<i>Cynodon</i> hybrid	<i>D. eriantha</i>	<i>P. maximum</i>	<i>P. clandestinum</i>
Leaf	0.3	0.1	- 0.6	0	0.4
Stem	0.4	0.4	- 0.6	- 0.5	0.5
Inflorescence	- 0.2	- 0.5	- 0.1	- 0.1	-

Table A4.4 Correlation (r^2) between plant yield components and crude protein content of five annual fodder crops in 1997/98.

Yield component	Crude protein content of				
	<i>C. ciliaris</i>	<i>Cynodon</i> hybrid	<i>D. eriantha</i>	<i>P. maximum</i>	<i>P. clandestinum</i>
Leaf	0.5	0.4	0.1	0.1	0.03
Stem	0.6	0.1	- 0.2	- 0.6	- 0.3
Inflorescence	- 0.1	0.3	0.7	-	-

Table A4.5 Influence of level of water availability on the whole plant digestible dry matter (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	50.81	50.44	54.19	55.51	52.74
<i>Cynodon</i> hybrid	58.60	54.68	54.25	54.18	55.43
<i>D. eriantha</i>	62.57	58.32	58.58	60.00	59.87
<i>P. maximum</i>	68.71	64.89	62.68	50.63	61.73
<i>P. clandestinum</i>	60.77	63.99	63.17	65.61	63.38
Mean	60.29	58.46	58.58	57.19	
LSD _T (G) = 3.72					
LSD _T (GxI) = 6.86					

* W1 -severely water stressed level, W4 - control

Table A4.6 Shortened ANOVA for the whole plant digestible dry matter (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	23.17	< 0.0001
Level of water availability (I)	3	2.39	0.0827
GxI	12	5.26	< 0.0001
Mean Square Error	10.196358		
CV %	5.45		
R ²	0.80		

Table A4.7 Influence of level of water availability on the whole plant digestible dry matter (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	60.33	58.67	60.67	55.33	58.75
<i>Cynodon</i> hybrid	55.0	54.0	60.5	60	57.38
<i>D. eriantha</i>	62.0	56.0	57.67	58.33	58.50
<i>P. maximum</i>	50.67	50.33	54.0	54.33	52.33
<i>P. clandestinum</i>	47.5	28.5	40.33	48.67	41.25
Mean	55.10	49.50	54.63	55.33	
LSD _T (G) = 5.10					
LSD _T (I) = 4.28					
LSD _T (GxI) = 9.57					

* W1 -severely water stressed level, W4 - control

Table A4.8 Shortened ANOVA for the whole plant digestible dry matter (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	26.87	< 0.0001
Level of water availability (I)	3	3.84	0.0180
GxI	12	2.44	0.0205
Mean Square Error	18.848039		
CV %	8.07		
R ²	0.81		

Table A4.9 Influence of level of water availability on the leaf digestible dry matter (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	63.02	62.89	58.82	70.50	63.81
<i>Cynodon</i> hybrid	52.57	48.82	43.40	45.65	47.61
<i>D. eriantha</i>	64.50	61.24	58.45	61.24	61.36
<i>P. maximum</i>	49.42	59.49	47.06	56.96	53.23
<i>P. clandestinum</i>	45.18	60.33	44.57	51.20	50.32
Mean	54.94	58.55	50.46	57.11	
LSD _T (G) = 4.44					
LSD _T (I) = 3.72					

* W1 -severely water stressed level, W4 - control

Table A4.10 Shortened ANOVA for the leaf digestible dry matter (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	37.22	< 0.0001
Level of water availability (I)	3	10.74	< 0.0001
GxI	12	3.39	0.0027
Mean Square Error	14.187361		
CV %	6.86		
R ²	0.87		

Table A4.11 Influence of level of water availability on the leaf digestible dry matter (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	49.51	61.36	54.34	51.39	54.15
<i>Cynodon</i> hybrid	58.84	54.65	44.07	57.82	53.84
<i>D. eriantha</i>	60.82	55.38	61.15	60.04	59.35
<i>P. maximum</i>	52.37	56.56	53.52	52.95	53.85
<i>P. clandestinum</i>	43.20	33.62	38.36	58.9	43.52
Mean	52.95	52.32	50.29	56.22	
LSD _T (G) = 6.92					
LSD _T (GxI) = 19.91					

* W1 -severely water stressed level, W4 - control

Table A4.12 Shortened ANOVA for the leaf digestible dry matter (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	11.32	< 0.0001
Level of water availability (I)	3	2.58	0.0668
GxI	12	3.69	0.0009
Mean Square Error	35.228052		
CV %	11.21		
R ²	0.71		

Table A4.13 Influence of level of water availability on the stem digestible dry matter (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	46.62	46.10	43.94	48.47	46.28
<i>Cynodon hybrid</i>	45.78	49.72	48.78	48.65	48.23
<i>D. eriantha</i>	56.25	63.26	55.99	55.93	55.35
<i>P. maximum</i>	52.70	56.52	57.58	52.27	54.77
<i>P. clandestinum</i>	56.61	60.03	55.79	55.09	56.88
Mean	51.59	53.13	52.42	52.08	
LSD _T (G) = 6.51					

* W1 -severely water stressed level, W4 - control

Table A4.14 Shortened ANOVA for the stem digestible dry matter (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	8.34	< 0.0001
Level of water availability (I)	3	0.21	0.8865
GxI	12	0.44	0.9382
Mean Square Error	31.078630		
CV %	10.64		
R ²	0.50		

Table A4.15 Influence of level of water availability on the stem digestible dry matter (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	37.72	43.40	39.20	35.62	38.98
<i>Cynodon hybrid</i>	50.02	47.34	46.47	41.99	46.46
<i>D. eriantha</i>	51.67	52.65	53.59	46.25	51.04
<i>P. maximum</i>	44.06	52.51	49.59	54.71	50.22
<i>P. clandestinum</i>	41.52	47.71	40.27	47.39	44.22
Mean	45.00	48.72	45.83	45.19	
LSD _T (G) = 6.32					

* W1 -severely water stressed level, W4 - control

Table A4.16 Shortened ANOVA for the stem digestible dry matter (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	10.00	< 0.0001
Level of water availability (I)	3	1.32	0.2833
GxI	12	1.30	0.2627
Mean Square Error		29.034992	
CV %		11.66	
R ²		0.62	

Table A4.17 Influence of level of water availability on the whole plant crude protein content (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	4.43	4.09	4.78	4.22	4.38
<i>Cynodon</i> hybrid	10.18	8.98	10.70	10.74	10.15
<i>D. eriantha</i>	5.64	4.15	5.01	6.11	5.23
<i>P. maximum</i>	6.02	5.69	4.18	4.73	5.15
<i>P. clandestinum</i>	9.22	9.11	9.64	8.84	9.20
Mean	7.10	6.41	6.86	6.93	
LSD _T (G) = 0.91					
LSD _T (GxI) = 1.82					

* W1 -severely water stressed level, W4 - control

Table A4.18 Shortened ANOVA for the whole plant crude protein content (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	137.89	< 0.0001
Level of water availability (I)	3	2.06	0.1211
GxI	12	2.21	0.0310
Mean Square Error	0.6102936		
CV %	11.43		
R ²	0.94		

Table A4.19 Influence of level of water availability on the whole plant crude protein content (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	8.44	8.27	6.14	7.43	7.57
<i>Cynodon</i> hybrid	12.15	11.32	10.24	14.94	12.16
<i>D. eriantha</i>	5.54	4.29	6.03	5.24	5.27
<i>P. maximum</i>	7.70	6.55	5.22	6.21	6.42
<i>P. clandestinum</i>	10.10	7.99	7.19	8.89	8.55
Mean	8.87	7.69	6.97	8.54	
LSD _T (G) = 2.42					

* W1 -severely water stressed level, W4 - control

Table A4.20 Shortened ANOVA for the whole plant crude protein content (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	14.59	< 0.0001
Level of water availability (I)	3	2.07	0.1241
GxI	12	0.68	0.7578
Mean Square Error	4.2032972		
CV %	26.32		
R ²	0.70		

Table A4.21 Influence of level of water availability on the leaf crude protein content (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	5.88	4.84	5.43	6.68	5.71
<i>Cynodon</i> hybrid	13.22	12.26	12.26	11.06	12.20
<i>D. eriantha</i>	7.54	6.07	5.87	6.19	6.42
<i>P. maximum</i>	5.39	6.21	4.64	5.33	5.40
<i>P. clandestinum</i>	12.54	11.66	11.09	9.30	11.15
Mean	8.91	8.21	7.86	7.71	
LSD _T (G) = 1.07					
LSD _T (I) = 0.90					
LSD _T (GxI) = 2.14					

* W1 -severely water stressed level, W4 - control

Table A4.22 Shortened ANOVA for the leaf crude protein content (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	149.57	< 0.0001
Level of water availability (I)	3	5.10	0.0044
GxI	12	2.50	0.0148
Mean Square Error		0.8415367	
CV %		11.22	
R ²		0.94	

Table A4.23 Influence of level of water availability on the leaf crude protein content (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	8.40	14.68	8.06	4.31	8.86
<i>Cynodon</i> hybrid	11.74	9.80	10.58	10.99	10.78
<i>D. eriantha</i>	7.53	6.06	5.73	4.34	5.92
<i>P. maximum</i>	7.05	6.84	6.63	8.07	7.15
<i>P. clandestinum</i>	11.42	10.52	10.43	9.16	10.39
Mean	9.23	9.58	8.27	7.38	
LSD _T (G) = 2.07					
LSD _T (GxI) = 3.88					

* W1 -severely water stressed level, W4 - control

Table A4.24 Shortened ANOVA for the leaf crude protein content (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	14.71	< 0.0001
Level of water availability (I)	3	1.91	0.1481
GxI	12	2.70	0.0123
Mean Square Error	3.0715849		
CV %	19.78		
R ²	0.75		

Table A4.25 Influence of level of water availability on the stem crude protein content (%) of five perennial grasses in 1996/97.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	3.04	2.31	2.88	2.55	2.69
<i>Cynodon</i> hybrid	7.77	7.26	6.64	6.78	7.11
<i>D. eriantha</i>	4.41	3.06	4.53	4.64	4.16
<i>P. maximum</i>	3.32	4.29	2.88	2.85	3.34
<i>P. clandestinum</i>	7.01	6.69	6.15	7.31	6.79
Mean	5.11	4.72	4.62	4.83	
LSD _T (G) = 1.26					

* W1 -severely water stressed level, W4 - control

Table A4.26 Shortened ANOVA for the stem crude protein content (%) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	41.82	< 0.0001
Level of water availability (I)	3	0.56	0.6477
GxI	12	0.89	0.5620
Mean Square Error		1.16795	
CV %		22.40	
R ²		0.82	

Table A4.27 Influence of level of water availability on the stem crude protein content (%) of five perennial grasses in 1997/98.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	3.78	0.97	5.56	8.35	4.66
<i>Cynodon</i> hybrid	5.94	7.97	13.03	8.72	8.92
<i>D. eriantha</i>	2.92	2.37	3.12	2.79	2.80
<i>P. maximum</i>	4.21	5.44	3.76	3.18	4.15
<i>P. clandestinum</i>	7.02	6.56	6.09	7.18	6.71
Mean	4.77	4.66	6.31	6.04	
LSD _T (G) = 2.35					
LSD _T (GxI) = 4.70					

* W1 -severely water stressed level, W4 - control

Table A4.28 Shortened ANOVA for the stem crude protein content (%) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	13.87	< 0.0001
Level of water availability (I)	3	1.74	0.1769
GxI	12	2.52	0.0160
Mean Square Error	4.0285389		
CV %	36.72		
R ²	0.72		

Data and statistical analysis of data presented in **Chapter 5**.

Table A5.1 Shortened ANOVA for the dry matter water use efficiency (WUE_{DM}) ($\text{kg DM ha}^{-1} \text{mm}^{-1}$) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	35.17	< 0.0001
Level of water availability (I)	3	6.97	0.0007
Gxl	12	0.81	0.6374
Mean Square Error	11.781191		
CV %	22.14		
R^2	0.81		

Table A5.2 Shortened ANOVA for the dry matter water use efficiency (WUE_{DM}) ($\text{kg DM ha}^{-1} \text{mm}^{-1}$) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	42.23	< 0.0001
Level of water availability (I)	3	15.61	< 0.0001
Gxl	12	0.99	0.4734
Mean Square Error	6.159307		
CV %	18.38		
R^2	0.85		

Table A5.3 Shortened ANOVA for the digestible dry matter yield (t DDM ha⁻¹) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	11.34	< 0.0001
Level of water availability (I)	3	5.36	0.0034
Gxl	12	0.58	0.8414
Mean Square Error	4.3392803		
CV %	36.36		
R ²	0.63		

Table A5.4 Shortened ANOVA for the digestible dry matter yield (t DDM ha⁻¹) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	36.69	< 0.0001
Level of water availability (I)	3	10.28	< 0.0001
Gxl	12	1.70	0.1116
Mean Square Error	0.9957435		
CV %	17.30		
R ²	0.85		

Table A5.5 Shortened ANOVA for the digestible dry matter water use efficiency (WUE_{DDM}) (kg DDM ha⁻¹ mm⁻¹) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	28.10	< 0.0001
Level of water availability (I)	3	6.40	< 0.0001
Gxl	12	0.77	0.4734
Mean Square Error	3.7083796		
CV %	21.52		

R² 0.78

Table A5.6 Shortened ANOVA for the digestible dry matter water use efficiency (WUE_{DDM}) (kg DDM ha⁻¹ mm⁻¹) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	52.74	< 0.0001
Level of water availability (I)	3	11.98	< 0.0001
Gxl	12	2.06	0.0492
Mean Square Error	1.9820199		
CV %	19.41		
R ²	0.89		

Table A5.7 Shortened ANOVA for the crude protein yield (t CP ha⁻¹) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	14.53	< 0.0001
Level of water availability (I)	3	5.62	0.0029
Gxl	12	1.04	0.4352
Mean Square Error	0.05314635		
CV %	36.28		
R ²	0.71		

Table A5.8 Shortened ANOVA for the crude protein yield (t CP ha⁻¹) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	41.21	< 0.0001
Level of water availability (I)	3	3.63	0.0237
Gxl	12	2.75	0.0115
Mean Square Error	0.04862742		

CV %	25.93
R ²	0.88

Table A5.9 Shortened ANOVA for the crude protein yield water use efficiency (WUE_{CP}) (kg CP ha⁻¹ mm⁻¹) of five perennial grasses in 1996/97.

Source	df	F value	Pr > F
Grass species (G)	4	14.17	< 0.0001
Level of water availability (I)	3	2.88	0.0495
GxI	12	0.37	0.9668
Mean Square Error		0.08521261	
CV %		26.51	
R ²		0.66	

Table A5.10 Shortened ANOVA for the crude protein yield water use efficiency (WUE_{CP}) (kg CP ha⁻¹ mm⁻¹) of five perennial grasses in 1997/98.

Source	df	F value	Pr > F
Grass species (G)	4	52.77	< 0.0001
Level of water availability (I)	3	15.36	< 0.0001
GxI	12	2.21	0.0374
Mean Square Error		0.08086769	
CV %		23.93	
R ²		0.90	

Data and statistical analysis of data presented in **Chapter 7**.

Table A7.1 Influence of level of water availability on the number of stomata on the adaxial leaf sides of five perennial grass species.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	7.80	7.40	10.60	12.40	9.55
<i>Cynodon</i> hybrid	31.40	27.60	33.80	35.00	31.95
<i>D. eriantha</i>	8.20	15.40	8.40	12.60	11.15
<i>P. maximum</i>	28.80	30.20	20.60	25.60	26.30
<i>P. clandestinum</i>	6.60	8.00	10.00	7.20	7.95
Mean	16.56	16.68	17.7	18.56	
LSD _T (G) = 2.52					
LSD _T (GxI) = 6.15					

* W1 -severely water stressed level, W4 - control

Table A7.2 Shortened ANOVA for the number of stomata on the adaxial leaf sides of five perennial grass species.

Source	df	F value	Pr > F
Grass species (G)	4	295.03	< 0.0001
Level of water availability (I)	3	2.73	0.0493
GxI	12	6.80	< 0.0001
Mean Square Error		8.15000	
CV %		16.43	
R ²		0.94	

Table A7.3 Influence of level of water availability on the number of stomata on the abaxial leaf sides of five perennial grass species.

Grass species(G)	Level of water availability (I)*				Mean
	W1	W2	W3	W4	
<i>C. ciliaris</i>	11.20	12.00	17.20	14.00	13.60
<i>Cynodon</i> hybrid	25.60	20.00	21.80	25.40	23.20
<i>D. eriantha</i>	24.80	18.80	23.40	29.00	24.00
<i>P. maximum</i>	24.00	27.00	17.80	23.60	23.10
<i>P. clandestinum</i>	8.20	6.20	9.80	7.00	7.80
Mean	18.76	16.80	18.00	19.80	
LSD _T (G) = 2.38					
LSD _T (I) = 2.00					
LSD _T (GxI) = 5.78					

* W1 -severely water stressed level, W4 - control

Table A7.4 Shortened ANOVA for the number of stomata on the abaxial leaf sides of five perennial grass species.

Source	df	F value	Pr > F
Grass species (G)	4	145.62	< 0.0001
Level of water availability (I)	3	5.49	0.0018
GxI	12	7.16	< 0.0001
Mean Square Error	7.275000		
CV %	14.71		
R ²	0.90		

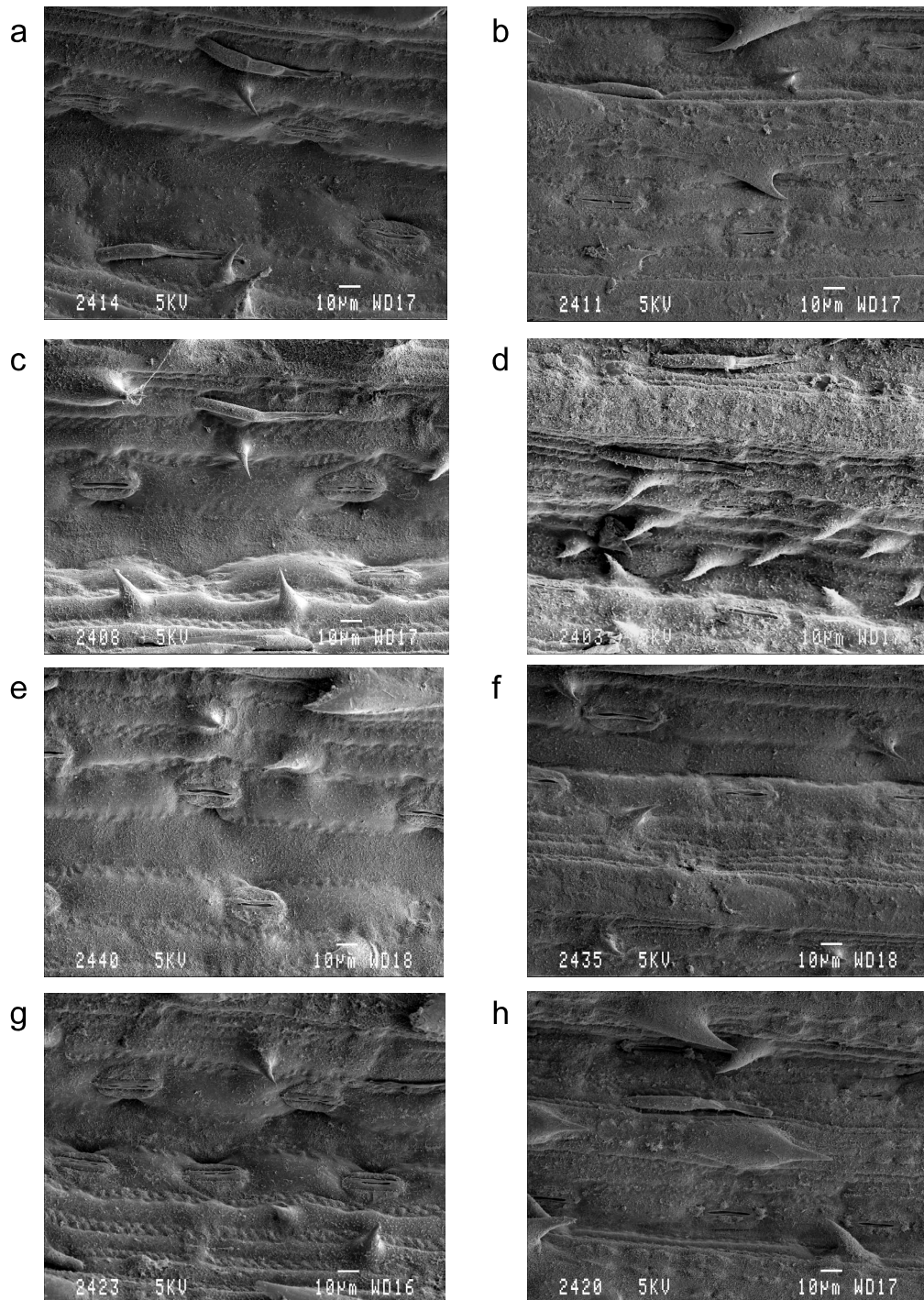


Figure A7.1 Adaxial (left) and abaxial (right) leaf surfaces of *C. ciliaris* as affected by different levels of water availability (x600). a & b - W1; c & d - W2; e & f - W3; g & h - W4

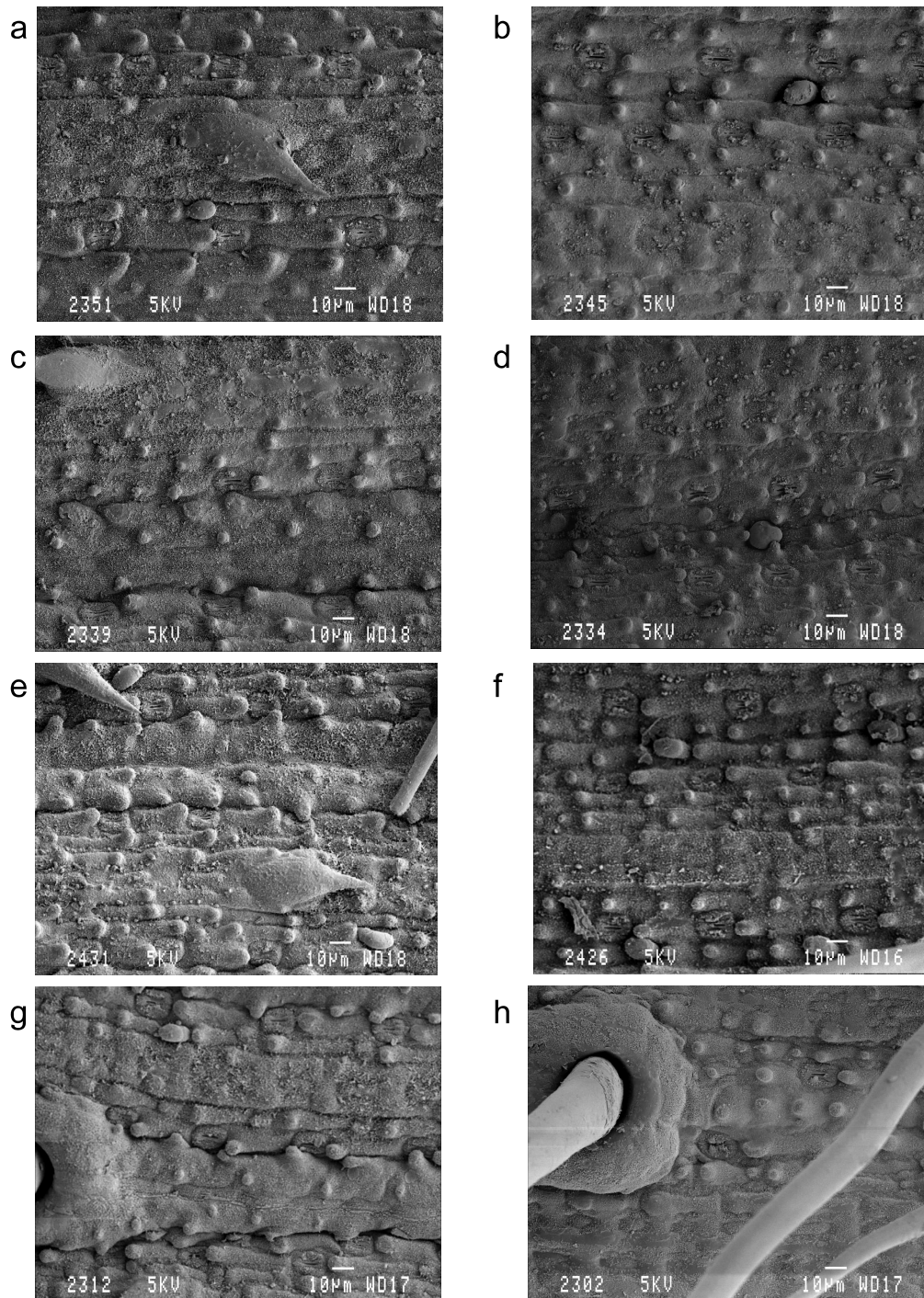


Figure A7.2 Adaxial (left) and abaxial (right) leaf surfaces of *Cynodon* hybrid as affected by different levels of water availability (x600). a & b -W1; c & d -W2; e & f - W3; g & h - W4

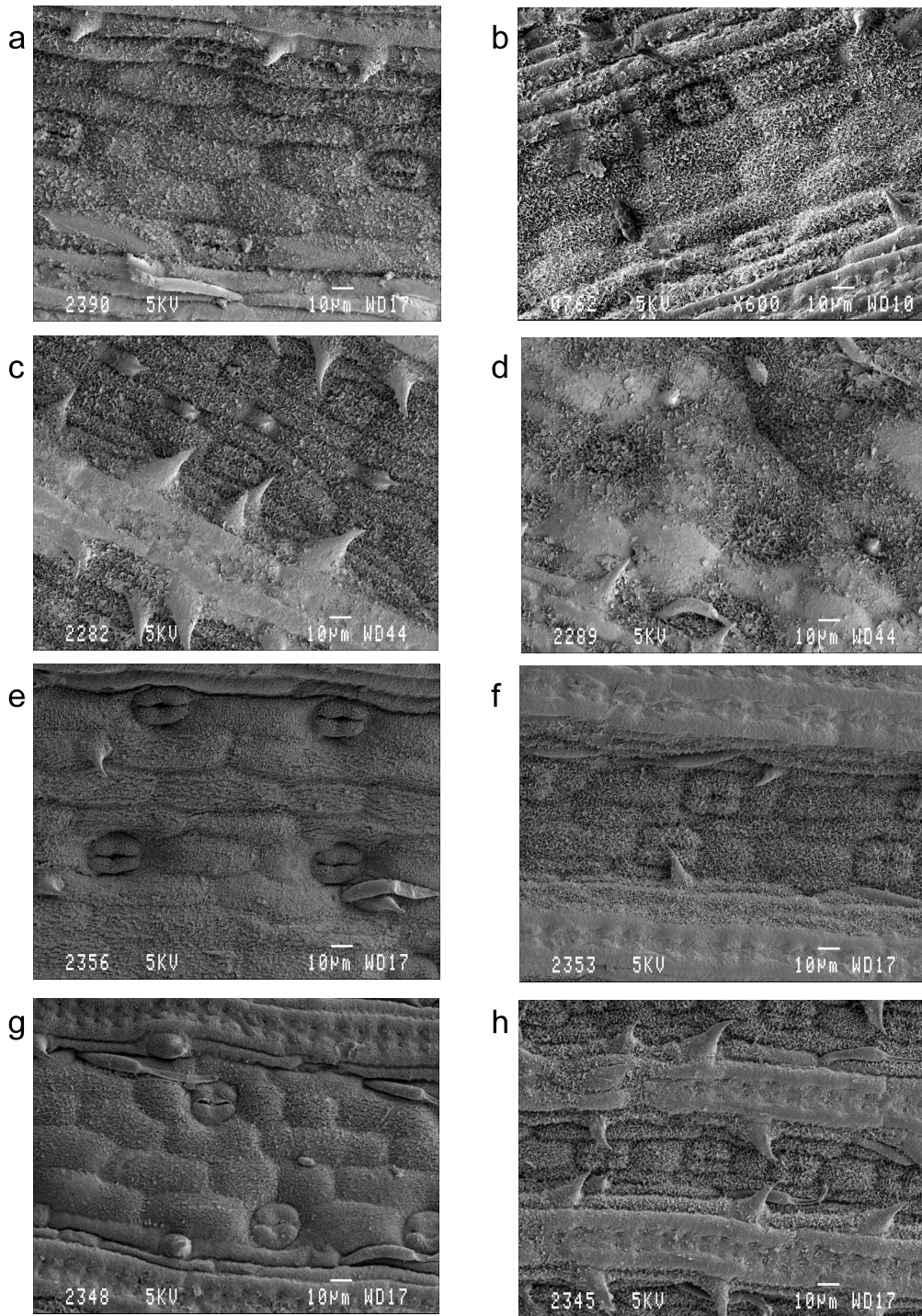


Figure A7.3 Adaxial (left) and abaxial (right) leaf surfaces of *D. eriantha* as affected by different levels of water availability (x600). a & b -W1; c & d -W2; e & f - W3; g & h - W4

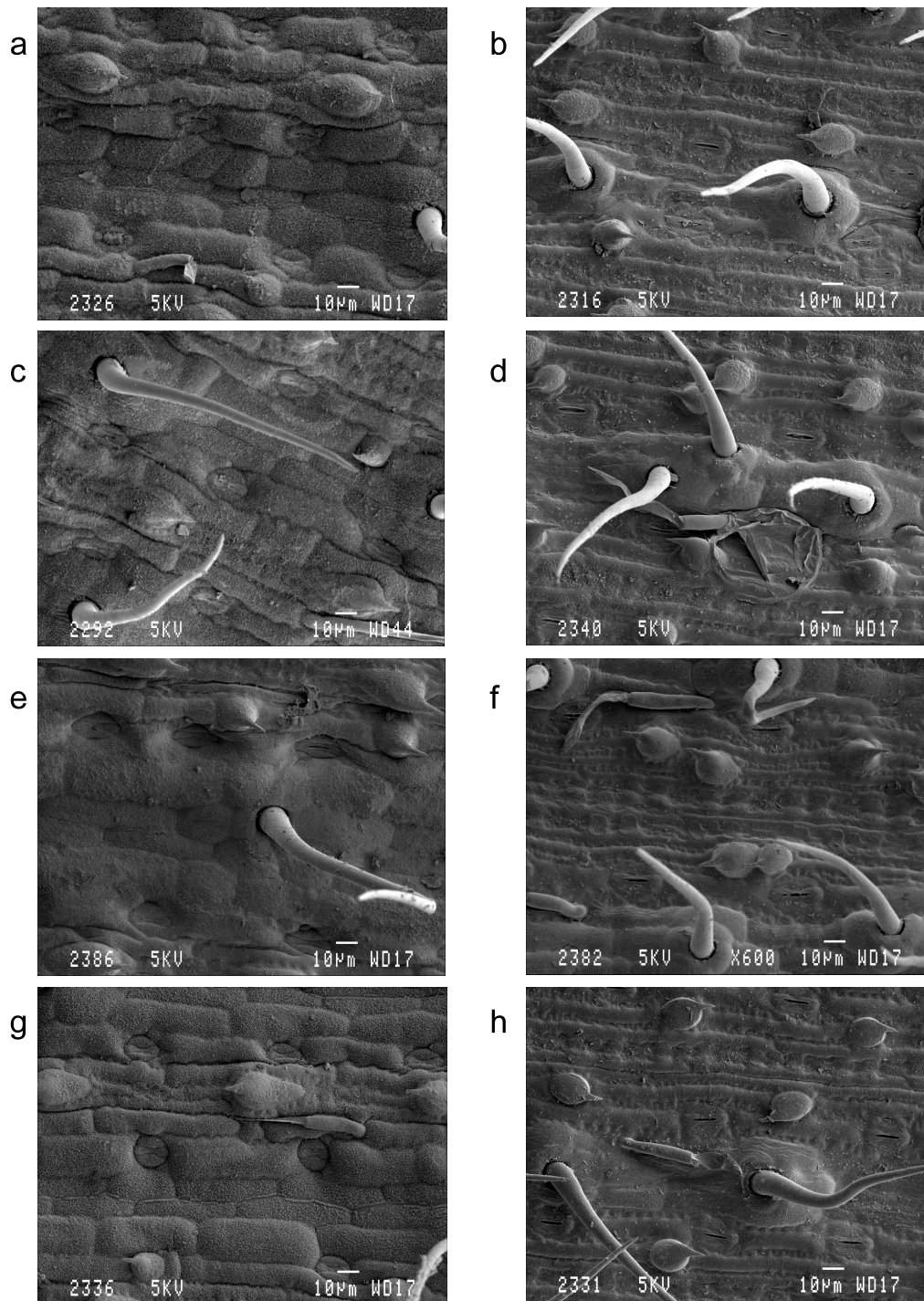


Figure A7.4 Adaxial (left) and abaxial (right) leaf surfaces of *P. maximum* as affected by different levels of water availability (x600). a & b -W1; c & d -W2; e & f - W3; g & h - W4

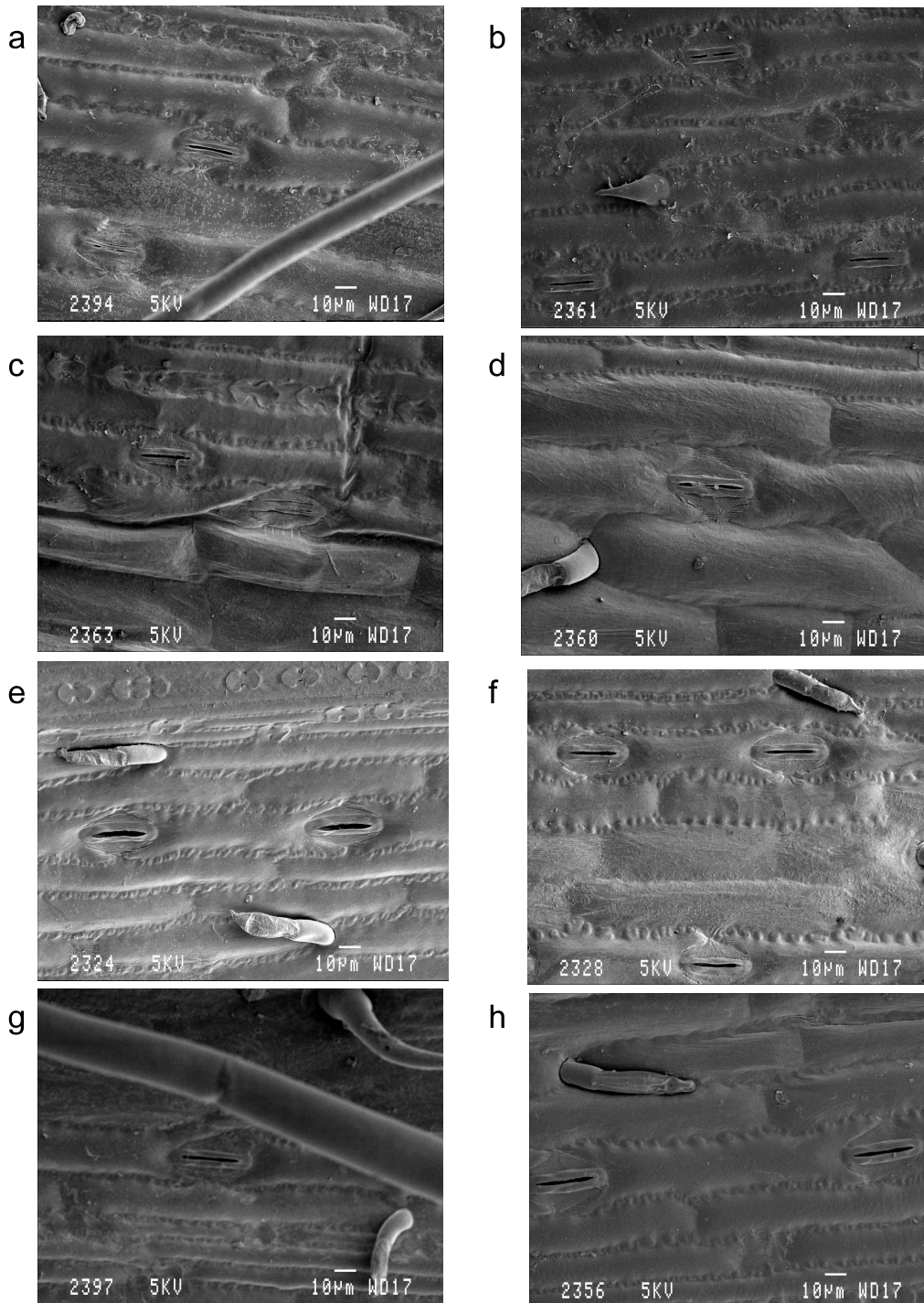


Figure A7.5 Adaxial (left) and abaxial (right) leaf surfaces of *P. clandestinum* as affected by different levels of water availability (x600). a & b - W1; c & d -W2; e & f - W3; g & h - W4

Data and statistical analysis of data presented in **Chapter 8**.

Table A8.1 Influence of level of water availability and nitrogen applied on the water use (l) of three perennial grass species.

Grass species(G)	Level of water availability (I)*			Mean
	W1	W2	W3	
<i>C. ciliaris</i>	16.32	25.25	28.37	23.31
<i>Cynodon</i> hybrid	15.21	23.93	26.86	22.00
<i>P. clandestinum</i>	15.62	24.72	28.77	23.04
Mean	15.72	24.63	28.00	
LSD _T (G) = 1.27				
LSD _T (I) = 1.27				
LSD _T (N) = 1.61				
LSD _T (GxN) = 4.39				

* W1 -severely water stressed level, W3 - control

Table A8.2 Shortened ANOVA for the water use of three perennial grass species.

Source	df	F value	Pr > F
Grass species (G)	2	3.36	0.0382
Level of water availability (I)	2	283.21	< 0.0001
GxI	4	0.39	0.8152
Level of N applied (N)	3	10.12	< 0.0001
GxN	6	2.78	0.0150
IxN	6	1.70	0.1284
GxIxN	12	0.60	0.8388
Mean Square Error	6.828818		
CV %	11.47		
R ²	0.86		

Table A8.3 Influence of level of water availability and nitrogen applied on the dry matter yield (g pot⁻¹) of three perennial grass species.

Grass species(G)	Level of water availability (I)*			Mean
	W1	W2	W3	
<i>C. ciliaris</i>	16.57	25.82	27.19	23.19
<i>Cynodon hybrid</i>	20.82	31.63	32.55	28.33
<i>P. clandestinum</i>	11.11	19.04	20.51	16.89
Mean	16.17	25.49	26.75	

LSD_T(G) = 1.57
LSD_T(GxI) = 1.57
LSD_T(N) = 3.14
LSD_T(GxIxN) = 5.43

* W1 -severely water stressed level, W3 - control

Table A8.4 Shortened ANOVA for the dry matter yield of three perennial grass species.

Source	df	F value	Pr > F
Grass species (G)	2	150.91	< 0.0001
Level of water availability (I)	2	153.53	< 0.0001
GxI	4	0.90	0.4653
Level of N applied (N)	3	29.30	< 0.0001
GxN	6	1.59	0.1559
IxN	6	0.48	0.8183
GxIxN	12	2.16	0.0186
Mean Square Error		10.453183	
CV %		14.18	
R ²		0.87	

Table A8.5 Influence of level of water availability and nitrogen applied on the water use efficiency ($\text{g } \ell^{-1}$) of three perennial grass species.

Grass species(G)	Level of water availability (I)*			Mean
	W1	W2	W3	
<i>C. ciliaris</i>	1.01	1.04	0.97	1.01
<i>Cynodon</i> hybrid	1.37	1.34	1.23	1.31
<i>P. clandestinum</i>	0.72	0.78	0.73	0.74
Mean	1.03	1.05	0.98	

LSD_T(G) = 0.08
LSD_T(GxN) = 0.29
LSD_T(GxIxN) = 0.29

* W1 -severely water stressed level, W3 - control

Table A8.6 Shortened ANOVA for the water use efficiency of three perennial grass species.

Source	df	F value	Pr > F
Grass species (G)	2	130.58	< 0.0001
Level of water availability (I)	2	2.26	0.1096
GxI	4	0.76	0.5540
Level of N applied (N)	3	12.32	< 0.0001
GxN	6	1.79	0.1081
IxN	6	1.87	0.0926
GxIxN	12	2.50	0.0062
Mean Square Error		0.03008258	
CV %		17.02	
R ²		0.77	