

Chapter 1 Introduction

1.1 background

The global increase in human population has increased the demand for plant and livestock products for food. This demand in turn is exerting enormous pressure on soil and water resources that are being degraded at alarming rates with the result that agriculture is being forced into drier areas (Esilaba *et al.* 2011; Qadir *et al.* 2013; Tilman *et al.* 2011) to meet the demand. Climate change, with its anticipated increases in ambient temperatures and carbon dioxide concentration (Wigley and Raper 2001; Dijkstra *et al.* 2010), poses environmental challenges that inevitably impact on plant species distribution and performance. Rainfall patterns are likely to be altered with the possibility of some areas receiving less than previously, thereby increasing the risk of crop failures. High yielding plant systems (cultivars or varieties matched with environment) have the potential to mitigate the food demand challenge (Tilman *et al.* 2011), but before they can be promoted in target areas, suitable plant systems need to be developed.

The importance of grasses worldwide in providing these high yielding plants cannot be over emphasized. There are more than 11,000 species of grasses (Clayton 2013), many of which play a critical role in the provision of food directly and indirectly through forage production. Important tropical forage grasses include Rhodes grass (*Chloris gayana* Kunth), Kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov) and Napier grass (*Pennisetum purpureum* Schumach). Grasses alone are estimated to comprise 20% of the earth's vegetation cover and make a profound contribution to the world economies and ecosystems that will continue into the future. The work detailed here focused on an important forage grass, Napier grass that could potentially support livestock in marginal

tropical areas where soil-water availability and high ambient temperatures are major constraints.

In east Africa and many other areas in tropical and subtropical regions of the world, Napier grass is one of the most important forage grasses for livestock (Tudsri *et al.* 2002; Tessema *et al.* 2010; Nyambati *et al.* 2011) but this is mainly in areas endowed with adequate soil moisture for most parts of the year. Napier grass, also known as elephant grass, is a perennial C₄ grass indigenous to tropical Africa (Boonman 1993). It is grown by over 70% of the smallholder dairy farmers in Kenya who are estimated to produce 80% of the nation's marketed milk (Staal *et al.* 1998) and it is likely that the cultivation of this grass will expand as livestock and dairy farming extends into drier areas. Although Napier grass is a well-adapted fodder plant for intensive dairy production, its performance is uncertain in drier environments. The problem is exacerbated by the increased frequency of extreme climatic conditions, especially high temperatures, and altered patterns and reduced amounts of precipitation (IFPRI 2010) that may constrain productivity. Napier grass yields have previously been closely associated with the amount of rainfall (Anindo and Potter 1994; Muia *et al.* 1999) and thus climate change is likely to impact on its productivity.

The ability of a plant to survive and be productive in marginal environments is dependent on its ability to maintain favourable plant-water relations to avoid desiccation and maintain transpiration with declining soil-water supply (Turner 1981). Stable plant-water relationships are achieved through stomatal control and/or osmotic adjustment that keeps tissue hydrated and physiologically active to fix carbon that in water-limited environments (Williams and Baruch 2000; Yunusa *et al.* 2005). Plant-water relationships have been used to assess drought tolerance for a wide range of crops and pasture species (Greenwood *et al.* 2008; Guenni *et al.* 2002; Colom and Vazzana, 2001;

Yunusa *et al.* 2005). Application of these techniques to Napier grass is almost non-existent. Although Napier grass is moderately drought tolerant (Butt *et al.* 1993; Tudsri *et al.* 2002; Tessema 2008; Yanxian *et al.* 2008), its regeneration and growth can be highly constrained by both prolonged water stress and a high degree of transient water stress (Yanxian *et al.* 2008).

There is limited physiological understanding of how Napier grass responds to variable water supply conditions in terms of tissue water relations, carbon assimilation and osmotic adjustment, especially when associated with elevated ambient temperature and/or carbon dioxide concentration. Whether these responses could be used to estimate production potential and shorten evaluation periods is a critical question. Given that there is a wide genetic base in Napier grass, it is possible that lines or cultivars may exhibit varied tolerance of water and temperature stress leading to different dry matter yields. Matching high yielding varieties to either wet or dry environments may contribute to fodder availability and hence improve livestock production in those areas. The work here entailed sequential studies on water relations and production of Napier grass cultivars in variable environments.

1.2 Research aims

- Establish whether water relations are associated with productivity potential and fodder quality in Napier grass that could hasten varietal evaluations for hot and dry environments.
- To investigate if water stress indices can be used as indicators of the productivity and forage quality of Napier grass accessions under contrasting climatic and soil conditions on lowland and highland tropical environments in Kenya

- Can these same indices be used to predict the impacts of short-term exposure to elevated ambient CO₂ and temperatures on the productivity of a C₃ (common reed) and a C₄ grass (Napier grass) subjected to limited water supply?

The study began with a literature review to provide background information on plant water relations, plant function and productivity, and the environmental context of this study (Chapter 2). Two Napier grass cultivars were then monitored for both physiologic and agronomic performance in temperature controlled glasshouse (Chapter 3). This was followed by field studies at two contrasting sites of a wet highland site and a semi-arid lowland site in tropical Kenya to explore field applications of plant water relations to predict productivity and forage quality differences amongst ascensions of Napier grass (Chapters 4 and 5). The likely impacts of elevated ambient carbon dioxide concentration and temperature on the plants' responses to reduced soil water supply were then compared for the C₃ common reed and the C₄ Napier grass (Chapter 6).

References

- Anindo DO, Potter HL (1994) Seasonal variation in productivity and nutritive value of Napier grass at Muguga, Kenya. *East Africa Agriculture and Forestry Journal* **59**,177–185.
- Boonman JG (1993) East Africa's grasses and fodders, their ecology and husbandry (Kluwer Academic Publisher: The Netherlands).
- Butt MN, Donart GB, Southward MG, Pieper RD, Mohammand N (1993) Effect of defoliation on plant growth of Napier grass. *Tropical Science* **33**, 111–120.
- Clayton WD, Vorontsova MS, Harman KT, Williamson H (2013) GrassBase - The Online World Grass Flora. <http://www.kew.org/data/grasses-db.html>. [accessed 16 April 2013]

- Colom MR, Vazzana C (2001) Drought stress effects on three cultivars of *Eragrostis curvula*. *Plant Growth Regulation* **34**,195–202.
- Dijkstra FA, Blumental D, Morgan JA, LeCain DR, Follett RF (2010) Elevated CO₂ effects on semi-arid grassland plants in relation to water availability and competition. *Functional Ecology* **24**, 1152–1161.
- Esilaba AO, Muturi GM, Cheruiyot HK, Okoti M, Nyariki DM, Keya GA, Miriti JM, Kigomo JN, Olukoye G, Wekesa L (2011) The desert margins programme approaches in upscaling best-bet technologies in arid and semi-arid lands in Kenya. *In: Innovations as key to the green revolution in Africa*; eds Bationo, A, Waswa, B, Okeyo, Jeremiah M, Maina, F pp 1177–1191. (Springer Science: New York).
- Greenwood KL, Mundy GN, Kelly KB (2008) On-farm measurement of the water use and productivity of maize. *Australian Journal of Experimental Agriculture* **48**, 274–284. doi:10.1071/EA06094
- Guenni O, Marin D, Baruch Z (2002) Responses to drought of five *Brachiaria* species. Biomass production, leaf growth, root distribution, water use and forage quality. *Plant and Soil* **243**, 229–241. doi:10.1023/A:1019956719475
- IFPRI (2010) Food security farming and climate change to 2050 (International Food Policy Research Institute: Washington DC, USA).
- Muia JMK, Tamminga S, Mbugua PN, Kariuki JN (1999) Optimal stage of maturity for feeding Napier grass (*Pennisetum purpureum*) to dairy cattle in Kenya. *Tropical Grasslands* **33**, 182–190.
- Nyambati EM, Lusweti CM, Muyekho FN, Mureithi JG (2011) Up-scaling Napier grass (*Pennisetum purpureum* Schumach) production using “Tumbukiza” method in

smallholder farming systems in Northwestern Kenya. *Journal of Agricultural Extension and Rural Development* **3**, 1–7.

Qadir M, Noble AD, Chartres C (2013) Adapting to climate change by improving water productivity of soils in dry areas. *Land Degradation Development* **24**, 12–21. doi: 10.1002/ldr.1091

Staal SJ, Chege L, Kenyanjui M, Kimari A, Lukuyu B, Njubi D, Owango M, Tanner J, Thorpe W, Wambugu M (1998) Characterisation of dairy systems supplying the Nairobi milk market: A pilot survey in Kiambu district for the identification of target producers. KARI/MoA/ILRI Collaborative Research Project Report. Available at: www.reading.ac.uk/ssc/media/ILRI_2006Nov/Publication/Full%20Text/Staal.pdf (accessed 14 August 2013).

Tessema ZK, Mihret J, Solomon M (2010) Effect of defoliation frequency and cutting height on growth, dry matter yield and nutritive value of Napier grass (*Pennisetum purpureum* (L.) Schumach). *Grass and Forage Science* **65**, 421–430.

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America*. **108**, 20260–20264.

Tudsri S, Jorgensen ST, Riddach P, Pookpakdi A (2002) Effects of cutting height and dry season closing date on yield and quality of five Napier grass cultivars in Thailand. *Tropical Grasslands* **36**, 248–252.

Turner NC (1981) Techniques and experimental approaches for the measurement of plant water status. *Plant Soil* **58**, 339–366.

Wigley TML, Raper SCB (2001) Interpretation of high projections for global-mean warming. *Science* **293**, 451–454.

- Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions* **2**, 123–140.
- Yanxian Y, Chengfei L, Yucang S, Zhixizn P, Guangheng F, Zhonghua J (2008) Photosynthesis characteristics of three species of forages in the arid-hot valleys. *Journal of Natural Sciences* **13**, 309–316.
- Yunusa IAM, Thomson SE, Pollock KP, Youwei L, Mead DJ (2005) Water potential and gas exchange did not reflect performance of *Pinus radiata* D. Don in an agroforestry system under conditions of soil-water deficit in a temperate environment. *Plant and Soil* **275**, 195–206.

Chapter 2 Literature Review

2.1 Plant water relations

Water is crucial for plant growth and development. The ability of plants to maintain favourable tissue water status is critical for survival and continuous photosynthesis and water uptake. The study of plant-water relations is concerned with how plants maintain tissue hydration involving water extraction from the soil, its transportation within the plant and eventual loss through the stomata. The status of water in plants is usually expressed in terms of water potential (Ψ_w) and has negative units of pressure (Passioura 2010). The total water potential of the plant is the sum of osmotic potential (Ψ_π), hydrostatic pressure (Ψ_p) and water potential by gravity (Ψ_g). Osmotic potential constitutes the presence of solutes e.g. sucrose molecules that attract water and thus decrease their tendency to diffuse elsewhere. Hydrostatic pressure or pressure potential refers to pressure exerted on the plant cell membrane against the rigid cell wall as water moves in to the cell while gravity causes water to move downwards and thus potential for water movement is dependent on height (Lambers *et al.* 1998; Larcher 2003).

$$\Psi_w = \Psi_\pi + \Psi_p + \Psi_g$$

The gravitational term is mostly ignored (Lambers *et al.* 1998) because it only becomes important in water columns more than 10 m high that do not occur in forage plants (Woodruff *et al.* 2004) hence;

$$\Psi_w = \Psi_\pi + \Psi_p \dots\dots\dots 1$$

Water and temperature stress could affect the water potential status by altering osmotic potential and/or hydrostatic pressure. Studies on different plant species have shown how water potential can vary within the same species in different environments or different species within the same environment. Toft *et al.* (1987) worked on *Eustachys paspaloides*,

a perennial C₄ grass, and found osmotic adjustment occurred in water stressed *E. paspaloides*, 0.20 and 0.29 MPa for clipped and unclipped plants respectively. They concluded osmotic adjustment was an acclimation response to short-term drought rather than a mechanism for reducing the effects of water stress. The delay in permanent wilting afforded by lowered osmotic potential was about one day. A study on sorghum and sunflower reported an osmotic potential decrease of approximately 0.6 MPa for each mega-pascal decrease in leaf water potential (Turner *et al.* 1978). Both sorghum and sunflower adjusted osmotically in response to water deficits at a rate of at least 0.1 MPa per day. Similar observations were reported on eucalyptus seedlings that had been wilted twice, once and watered daily (Myers and Neales 1986). There was an increase in osmotic potential -2.02, -1.86 and -1.66 MPa respectively. The general trend is, with limited water availability, the osmotic potential becomes less negative. Osmotic adjustment as a response to water stress is species specific rather than an attribute possessed by all plants. A study on *Setaria sphacelata* var. *splendia*, a C₄ perennial grass (Silva and Arrabaca 2004) did not find significant osmotic adjustment to either rapidly or slowly induced water stress. Osmotic adjustment in buffel grass (*Cenchrus ciliaris* cv *Biloela*), green panic (*Panicum maximum* var. *trichoglume*) and black speargrass (*Heteropogon contortus*, Woolooga strain) ranged from 0.84 to 1.0 MPa from chemical analyses of solutes and 0.5 to 0.7 MPa from pressure/volume curves. The osmotic adjustment reached a plateau 22 days after watering ceased and its inverse relationship with leaf water potential was the same for the three species. Osmotic adjustment delayed the onset of permanent wilting in water stressed leaves by only 4 days. Therefore its contribution to maintenance of leaf growth during water stress was small for the three grasses (Wilson and Ludlow 1983). Therefore, a combination of different mechanisms by different plant species under water stress could probably result in their survival.

Movement of water declines as the soil dries out and the matric forces holding it to the soil particles increases (Larcher 2003). Water uptake by the roots is estimated by an equation as given by Lambers *et al* (2008).

$$d\theta'/dt = D(\theta' - \theta_a)/2b^2 \dots\dots\dots 2$$

where $d\theta'/dt$ is rate of fall of mean soil water content with time t ; D , diffusivity of soil water, θ_a is the soil water content at the surface of the root and b is the radius of the putative cylinder of soil surrounding the root.

Well-watered plants are turgid and cells are distended by an internal pressure that may be as high as 1 MPa. Plants perform best when they are turgid and many of the structures of higher plants serve to maintain cells sufficiently hydrated in order to grow, photosynthesize and respire (Passioura 2010).

Water has high latent heats of evaporation and freezing (heat energy required to convert a unit of water from liquid to vapour or ice to liquid) which helps plants to cope with frosts and heat loads. It has high cohesive strengths which enable it to withstand large tensions that develop in the xylem and maintain continuity of liquid water throughout the plant (Passioura 2010). Also, water is the major medium for transporting metabolites that include carbohydrates, nutrients and phytohormones required for growth and development. Therefore, plants depend on water for their structure and support, cooling and metabolic processes (Nobel 2005).

Water relationships in Napier grass cultivars have not been explored to estimate how their water integrity is maintained under water and temperature stresses. These relationships are likely to provide a basis upon which to select cultivars for dry areas for improved forage production.

2.2 Carbon assimilation

The exchange of CO₂ and O₂ in plants occur through the stomata on the leaves by which plants synthesise the metabolites, mainly carbohydrates, necessary for growth. This process (photosynthesis), utilizes atmospheric CO₂ and water to synthesise the metabolites, and O₂, a by-product of the process, is released from the plant via the same route. The rate of photosynthesis is a function of many factors including the species involved, light intensity, water availability and temperature. Water deficit will decrease photosynthesis because of both stomatal and non-stomatal limitations (Lambers *et al.* 1998). Stomatal response is the most important factor controlling carbon fixation. Stomates closure is usually the first response to desiccation and occurs more quickly than other changes such as increased root growth, reduced leaf area and changes in pigment proteins (Yordanov *et al.* 2000).

Plant species differ in their responses to water stress. Evaluation of Lehmann lovegrass (*Eragrostis lehmanniana*) versus bush muhly (*Muhlenbergia porteri*) in a semi-arid savannah showed higher leaf-level photosynthesis and stomatal conductance in *E. lehmanniana*. Net ecosystem CO₂ exchange (NEE) was more negative in *E. lehmanniana* (-0.69 to -3.00 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than *M. porteri* (+1.75 to -1.55 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Hamerlynck *et al.* 2010). An evaluation of two perennial grasses, *Corynephorus canescens* (L.) Beauv. and *Agrostis vinealis* Schreber (Boot and Dubbelden 1990), found higher net photosynthesis per unit plant weight in *A. vinealis*. This was attributed to differences in leaf area ratio (LAR) that was 8.5 and 12.3 respectively and *A. vinealis* had higher transpiration 0.051 versus 0.036 $\text{mmol H}_2\text{O g}^{-1} \text{s}^{-1}$. These data demonstrate differences among species in water use and perhaps if the measurements were conducted when species were subjected to water or temperature stress the results may have been different.

Cochard (2002) reported reduced transpiration of maize by 90% caused by stomatal closure when xylem pressures reached -1.6 MPa. Xylem embolism remained low (10 per cent loss conductivity- hydraulic conductance) in leaf veins when plants exhibited water stress symptoms. This suggested that stomatal closure during drought helps to mitigate xylem embolism in maize. If water supply from the roots does not match the loss from leaves, leaf water status must decline and this reduces photosynthesis (Lambers *et al.* 1998). Stomatal adjustments can occur so that stomatal conductance and photosynthetic rate are less sensitive to decline in water potential. Ludlow *et al.* (1985) working with three grasses (*Panicum maximum*, *Heteropogon contortus* and *Cenchrus ciliaris*) monitored stomatal conductance and leaf photosynthetic rate under water stress. They observed that the water potential at which photosynthetic rate approached zero, became more negative from -1.9, -2.0 and -2.4 MPa to -4.0, -4.0 and -3.3 MPa for the three grasses respectively. It could be inferred from this that there is a minimum water potential that each of the species would require to remain photosynthetically active.

The carbon dioxide compensation point (point at which rate of photosynthesis equals that of respiration) of C₄ plants ranges from 0 to 0.5 Pa compared with 4 to 5 in C₃ plants. In addition, C₄ plants have higher photosynthetic rates per unit of leaf nitrogen than C₃ plants especially at high temperatures. This partially explains why Napier grass produces such large biomass compared with many grasses (Relwani *et al.* 1982). Most authors have not found a CO₂ genotype interaction on biomass productivity. Of the approximately 4,000 CO₂ plant science-papers published during the last decade, only 30 reported genotype responses. For total plant biomass, a significant CO₂ genotype interaction was in seven out of 21 species studied (Roumet *et al.* 2002) suggesting the importance of species specific studies. For example, Roumet *et al.* (2002) reported no differences in two perennial grasses (*Bromus erectus* and *Dactylis glomerata*) in biomass response to elevated CO₂. This was

in contrast to Moya *et al.* (1998) who reported increased total dry weight at elevated CO₂ (110%) in *Oryza sativa*, from 1892 to 2386 g/m². Carbon dioxide demand is determined by the rate of processing CO₂ in the chloroplast which is governed by the structure and biochemistry of the chloroplasts and environmental factors such as irradiance (Lambers *et al.* 1998).

2.3 Water use efficiency

Water use efficiency (WUE) can be described at two levels according to water use during C gain or biomass accumulation (Larcher, 2003). The first is the instantaneous WUE at the leaf level that expresses the ratio of carbon fixed versus the water lost through transpiration when that carbon was being fixed and is usually referred to as the photosynthetic WUE. The other is the productivity WUE that expresses the above ground dry matter production against the amount of water utilised by the plant/crop over a period of time (days-years), and this often include water lost through evaporation from the soil that supported the growth (Lambers *et al.* 1998).

$$\text{Instantaneous WUE} = A/E = g_c/g_w \dots\dots\dots 4$$

where *A* = carbon gain in photosynthesis, *E* = water loss in transpiration, *g_c* = leaf conductance for CO₂ (mmol.m²s⁻¹) and *g_w* = water vapour (mol.m²s⁻¹).

$$\begin{aligned} \text{Productivity WUE} &= \text{dry matter produced/water utilised} \dots\dots\dots 5 \\ &= \text{kg DM/kg H}_2\text{O} \\ &= \text{kg DM ha}^{-1} \text{ mm}^{-1} \end{aligned}$$

High water use efficiency would be an important attribute in Napier grass cultivars as it may suggest which lines could thrive better during dry spells. Lelievre *et al.* (2011) working with temperate perennial grasses (*Dactylis glomerata* L. and *Lolium arundinaceum* Schreb.) under Mediterranean conditions found productivity WUE ranging

from 0.7–2.8 kg DM/kg H₂O for different accessions of the two perennials. Water use efficiency during rains was highly correlated with sward recovery after drought and perhaps this response would be apparent in Napier grass. Zhang *et al.* (2005) working with three ecotypes of *Populus davidiana* reported significant differences for both productivity and instantaneous WUE at soil moisture levels of 100% down to 20%. The WUEs ranged from 1.72–2.96 kg DM/kg H₂O and 1.93–3.58 mmol mol⁻¹ respectively. Most WUE studies have concentrated on annuals (Condon *et al.* 2002; Richards *et al.* 2002) probably because most of the food crops are annuals. Perennials, which do not require planting seasonally, may have an advantage as they prolong utilizing available soil moisture. Plant traits related to improved water use and nutrient uptake under drought include low shoot:root ratio, high root density, deep root penetration and high root hair density (Boot 1989; Hochman and Heiyar 1989). Grasses may have deep roots that reach moisture lower in the soil profile. *Chloris gayana*, a perennial, is known to have roots reaching 4.7 metres below the soil surface (Skerman and Riveros 1990) thus enabling the species to produce during drought conditions. Information on Napier grass root density down the soil profile versus the DM yield is limited. Assessing Napier grass cultivars with respect to these attributes could explain help different Napier grass yields under different soil water stress conditions and could therefore prove useful information when selecting cultivars for specific purposes.

2.4 Heat and water stress

Favourable temperatures for plant performance depend on plant adaptations. Cold-adapted plants can photosynthesize without harm between 0 and 30°C (Larcher 2003), while warm season crops operate safely between 7 and 40°C. Plants in hot tropical environments can go even higher between 15 and 45°C with no apparent problem (Downton *et al.* 1984). Heat stress in plants therefore, constitutes temperatures above

these limits. Increased water uptake by plants during heat stress assists in cooling off the plant during transpiration. Under field conditions, temperature and water stress often occur concurrently (Xu and Zhou 2005) inevitably intensifying the stress. Numerous studies on impact of heat and water stresses have been done in a diverse range of plant species. Water stress resistance or drought resistance, which varies amongst species, refers to the ability to maintain favourable water balance and turgidity when under drought conditions (Schrader *et al.* 2005; Lambers *et al.* 2008). Guenni *et al.* (2002) working with five *Brachiaria* perennial grasses reported varied water use. *Brachiaria brizantha*, *B. decumbens* and *B. mutica* had highest water use of 0.25 litres day⁻¹ while *B. humidicola* and *B. dictyoneura* had lowest of 0.13 litres day⁻¹. A study on three cultivars of *Eragrostis curvula* (Tanganyika, Consol and Ermelo) showed reduced photosynthesis as a result of water stress for six days (Colom and Vazzana 2001). This was 52, 35 and 55% respectively in relation to control treatments that were well watered. The Consol cultivar was found to be more resistant to water stress.

A comparison of two C₄ grasses in Venezuela found *Hyparrhenia rufa* drought evasive compared with *Trachypogon plumosus* that showed drought resistance. The former had higher net photosynthesis during the rainy season but the two species were similar during drought. This was reflected in leaf conductance (g_s) that was 30% higher during that period as well as transpiration rate (E) in the range of 20–40%. *Hyparrhenia rufa* had higher stomatal sensitivity to leaf water potential with the lowest leaf conductance occurring near -2.0 MPa in contrast to *T. plumosus* in the range of -2.5 to -3.0 MPa (Baruch and Fernandez 1993). A study on *Leymus chinensis*, a C₃ perennial forage grass, showed that when severely water stressed (25–30% of field capacity), it increased dry mass allocation to the below ground roots (Xu and Zhou 2005), most likely to enhance water exploration and extraction. Similar studies on these aspects in Napier grass cultivars

have not been undertaken such that there is a limited understanding of their performance under limited soil-water conditions.

Reports suggest that plant hormones contribute to heat stress signalling (Kotak *et al.* 2007). A sudden increase in temperature is characterized by elevated synthesis of a set of proteins called heat shock proteins (hsps) which have been associated with the development of thermotolerance. Heat shock proteins help cells to cope with heat-induced damage to cellular proteins (Krishna 2004; Lambers *et al.* 1998). A study by Xu *et al.* (2008) showed that heat-inducible genes were only expressed when *Agrostis scabra* (C₃) was subjected to heat stress and may contribute to its superior ability to survive in chronically high-temperature soils. Similar observations were made in *Sorghum bicolor* (C₄) when subjected to heat stress (Clarke and Critchley 1990). These diverse highly-specialised processes reveal the extent to which some grass species can cope with temperature stress.

Although Yanxian *et al.* (2008) showed that Napier grass had higher photosynthetic rate and adaptability to arid-hot climates than the two legumes they compared it with, their study gave no indication of whether these features would vary or not among Napier grass provenances, which have been shown to have substantial genetical and morphological variation (Nyambati, *et al* 2007; Van de wouw *et al* 1999). Root biomass may be critical for drought tolerance (Orians and Solbrig 1977; Lambers *et al.* 1998) and is likely to be important in making future varietal recommendations in Napier grass.

Plants also have various other mechanisms to deal with water stress. Corbin *et al.* (2005) showed that certain perennial grasses during drought can utilize 28–60% of the water available in fog. Furthermore, Carmo-silva *et al.* (2009) reported production of an unusual amino acid (2-Amino-5-hydroxypentanoic acid) that increased with increasing water

stress in two C₄ grasses (*Cynodon dactylon* and *Zoysia japonica*). However, the benefit of this amino acid remains unknown. Increases in proline levels by up to five fold have been recorded in three perennial grasses (Bawa and Sen 1993) subjected to moisture stress whereas 11 annuals in the same study only doubled the level. Leaf senescence also occurs during dry periods to help plants reduce water loss and avoid drought (Blum 1996). Leaf senescence is a highly regulated and active process, contributing to plant survival (Gepstein 2004). As a management option, harvesting Napier grass just before the beginning of the dry season, regardless of the recommended harvesting height, may assist in two ways. Firstly, it would act like leaf senescence to avoid water loss, and secondly, avoid deterioration of forage quality that has been generally shown to decline, both in crude protein and digestibility, during the dry season (Anindo and Potter 1994).

2.5 Elevated atmospheric CO₂ concentration and impact on plant performance

Predictions of a rise in temperatures ascribed to 'climate change' are expected to be coupled with elevated atmospheric CO₂ concentrations. The atmospheric CO₂ concentration was stable at ~270 µmol mol⁻¹ for at least 1000 years prior to the start of the industrial revolution. Carbon dioxide concentrations have been accelerating since then and by the year 2009 stood at 384 µmol mol⁻¹, estimated to be about 40% higher than any time in the last 20 million years (Leaky *et al.* 2009). By the middle of the current century the concentration is projected to reach 550 µmol mol⁻¹ and 700 µmol mol⁻¹ by the end of the century (Prentice *et al.* 2001). These increases are likely to affect plants that have adapted to considerably lower levels of CO₂ concentration. Plants of different species exposed to elevated CO₂ levels have shown diverse responses (Dijkstra *et al.* 2010; Morgan *et al.* 2007) including increased biomass while others have shown no response. *Hesperostipa comata* and *Pascopyrum smithii* were found to increase biomass production when grown under 780 ppm. However, *Artemisia frigida* and *Linaria daimatica* showed

no effect in the same study (Dijkstra *et al.* 2010). Elevated CO₂ stimulates photosynthetic carbon gain and improves nitrogen use efficiency and decreases water use at leaf and canopy scale (Leaky *et al.* 2009). There have been presumed benefit in plants stomatal conductance, transpiration, water use efficiency and leaf water potential under elevated CO₂ (Wullschleger *et al.* 2002). However, under limited soil-water conditions, there have been increases in root:shoot ratio characterized by fine-root proliferation (Wullschleger *et al.* 2002) that likely promotes water extraction from the soil. The effect of elevated CO₂ on Napier grass tissue water relations, water use efficiency or growth has not been reported and could assist in understanding the possible effects of climate change on this grass into the future.

2.6 Nutritional quality

Fodder has been reported to decline in digestibility during reduced soil moisture availability. The dry matter digestibility coefficient (percentage digestibility at most 1 when totally digestible) of Napier grass decreased from 0.72 in the dry season to 0.56 in the wet season and neutral detergent fibre increased from 687 g/kg DM in the wet season to 705 g/kg DM in the dry season (Anindo and Potter 1994). These changes in the dry season could be due to increased lignification and in hemicelluloses that are not readily digestible. Thus elevated temperatures and water stress may inevitably lower the quality of fodder, however the performance of Napier grass lines with respect to this attribute has not been well explored.

In five *Brachiaria species*, water stress up to wilting point improved nutrient content and digestibility in five *Brachiaria species*. The species *Brachiaria brizantha*, *B. decumbens*, *B. mutica*, *B. humidicola* and *B. dictyoneura* had nitrogen percentages in the order of 0.89, 0.86, 1.64, 1.11 and 0.75 respectively. When grown under drought treatments, these

values went up to 1.01, 1.09, 1.86, 1.53 and 1.29 respectively (Guenni *et al.* 2002). The increases were attributed to delayed leaf ontogeny. Similar observations were made by Wilson (1983) working with *Panicum maximum* var. trichoglume and *Cenchrus ciliaris* cv Biloela with treatments of irrigation twice weekly and dry treatments (12–14 weeks dry period). Percentage dry matter digestibility was high for green leaf, dead leaf and stem fractions for both grasses. *Panicum maximum* fractions from wet treatments had digestibility percentages of 61.6, 57.3 and 41.7 respectively. These were significantly lower than the same fractions from dry treatments, 62.6, 62.5 and 48.2 respectively. The same trend was observed in *Cenchrus ciliaris*. Wet fractions had 60.6, 55.6 and 45.8 while dry fractions had 63.3, 61.9 and 48.4 respectively. These observations were attributed to delayed leaf ontogeny and changes in leaf chemistry with fractions from dry treatments having better digestibility and thus better nutritional quality. This is in contrast to Anindo and Potter (1994) who reported crude protein decline from 141 g/kg DM in the wet season to 110 g/kg DM in the dry season in Napier grass but these data were based on a single cultivar. A similar observation was reported by Craine *et al.* (2010) in grazing lands where increasing temperature and declining precipitation decreased dietary forage protein at the rate of 2.8 mg g⁻¹ °C⁻¹ and digestible organic matter at -1.72 mg g⁻¹ °C⁻¹. In view of these contrasting findings, there is a need to understand how different Napier grass cultivars would respond to water stress and increased temperature in both production and forage quality to allow informed recommendations for the more rapid screening of cultivars in the future.

2.7 Conclusion

Napier grass is generally regarded as drought resistant, but there has been limited or no research to understand the mechanisms by which different provenances respond to drought and/or temperature stress and whether simple stress indices such as RWC, LWP

and WUE can provide a basis for varietal recommendations. Whilst plant physiologists have concentrated most of their work on food crops, forage experts have concentrated on biomass, characterisation and quality. There is therefore a gap about the physiology and below ground traits with regard to the effects of water stress on important fodders, especially Napier grass. Some authors reported that increasing temperature reduces forage quality while others reported improvements in quality. As such, studies on Napier grass responses to water stress and high temperatures on both below and above ground could provide vital information for the management of the grass for improved productivity. In addition, the influence of elevated CO₂ on responses to water stress in Napier grass will help in understanding likely scenarios as global warming takes effect. The main factors that affect Napier grass productivity are summarized in Figure 2.1

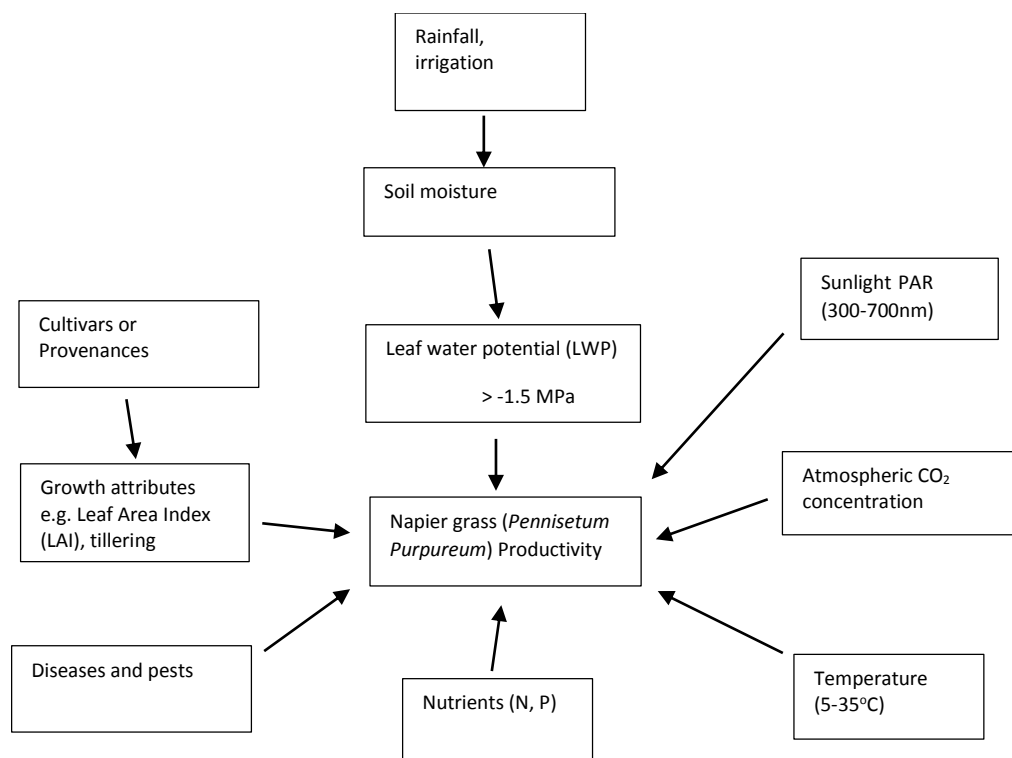


Figure 2.1 Conceptual model of the main factors that influence Napier grass productivity.

2.8 Research questions

- Can tissue water status be used to predict production and forage quality potential in Napier grass accessions?
- Are there differences in yield and quality in Napier grass accessions when grown under lowland or highland tropical environmental conditions?
- Are there differences among Napier grass accessions in water stress indices, water use and water use efficiency in response to drought and increased temperatures in tropical environments?
- What is the impact of elevated CO₂ concentrations at different temperatures on Napier grass water relations and productivity compared to a grass with the C₃ photosynthetic pathway?

References

- Anindo DO, Potter HL (1994) Seasonal variation in productivity and nutritive value of Napier grass at Muguga, Kenya. *East Africa Agriculture and Forestry Journal* **59**,177–185.
- Baruch Z, Fernandez DS (1993) Water relations of native and introduced C₄ grass in a neotropical savanna. *Oecologia* **96**, 179 –185.
- Bawa AK, Sen DN (1993) Moisture stress-induced proline accumulation in ephemeral grasses from arid zone of India. *Journal of Arid Environments* **24**,135–137.
- Blum A (1996) Crop responses to drought and the interpretation of adaptation. *Plant Growth Regulation* **20**, 135–148.
- Boot RGA (1989) The significance of size and morphology of root systems for nutrient acquisition and competition. In: Causes and consequences of variation in growth rate

- and productivity in higher plants, (eds) H Lambers, ML Cambridge, H Konings and TL Pons pp 299–312 (SPB Academic Publishing, The Hague Netherlands).
- Boot RGA, Dubbelden KCD (1990) Effects of nitrogen supply on growth, allocation and gas exchange characteristics of two perennial grasses from inland dunes. *Oecologia* **85**, 115–121.
- Carmo-silva AE, Keys AJ, Beale MH, Ward JL, Baker JM, Hawkins ND, Arrabaca MC, Parry MAJ (2009) Drought stress increases the production of 5-hydroxynorvaline in two C4 grasses. *Phytochemistry* **70**, 664–671.
- Clarke AK, Critchley (1990) Synthesis of early heat shock proteins in young leaves of barley and sorghum. *Plant Physiology* **94**, 567–576.
- Cochard H (2002) Xylem embolism and drought-induced stomatal closure in maize. *Planta* **215**, 466–471.
- Colom MR, Vazzana C (2001) Drought stress effects on three cultivars of *Eragrostis curvula*. *Plant Growth Regulation* **34**, 195–202.
- Condon AG, Richards RA, Rebetze GJ, Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. *Crop Science* **42**, 122–131.
- Corbin JD, Thomsen MA, Dawson TE, D’Antonio CM (2005) Summer water use by California coastal prairie grasses: fog, drought, and community composition, *Oecologia* **145**, 511–521.
- Crane JM, Elmore AJ, Olson KC, Tollesons D (2010) Climate change and cattle nutritional stress. *Global Change Biology* **16**, 2901–2911.
- Dijkstra FA, Blumenthal D, Morgan JA, LeCain DR, Follett R (2010) Elevated CO₂ effects on semi-arid grassland plants in relation to water availability and competition. *Functional Ecology* **24**, 1152–1161. doi: 10.1111/j.1365-2435.2010.01717.x.

- Downton WJS, Berry JA, Seemann JR (1984) Tolerance of photosynthesis to high temperature in desert plants. *Plant Physiology* **74**, 786–790
- Gepstein S (2004) Leaf senescence-not just a “wear and tear” phenomenon. *Genome Biology* **5**, 112–114.
- Guenni O, Marin D, Baruch Z (2002) Responses to drought of five *Brachiaria* species. Biomass production, leaf growth, root distribution, water use and forage quality. *Plant and Soil* **243**, 229–241.
- Hamerlynck EP, Sott RL, Moran MS, Keefer TO, Huxman TE (2010) Growing season ecosystem and leaf-level gas exchange of an exotic native semiarid bunch grass. *Oecologia* **163**, 561–570.
- Hochman Z, Helyar KR (1989) Climatic and edaphic constraints to the persistence of legumes in pastures. *In: Persistence of forage legumes* (eds) GC Marten, AG Matches, RF Barnes, RW Brougham, RJ Clements and GW Sheath pp 177–204 (ASA-CSSA, Madison, WI, USA).
- Kotak S, Larkindale J, Lee U, Koskull-Döring PV, Vierling E, Scharf K (2007) Complexity of the heat stress response in plants. *Plant Biology* **10**, 310–316.
- Krishna P (2004) Plant responses to heat stress. *In: Plant responses to abiotic stress* pp 73–101. (Springer Berlin / Heidelberg: Germany).
- Lambers H, Chapin FS, Pons TH (1998) *Plant physiological ecology*. (Springer-Verlag: New York).
- Lambers H, Chapin FS, Pons TL (2008) *Plant physiological ecology*. (Springer Science: New York).
- Larcher W (2003) *Physiological plant ecology*. (Springer-Verlag: Berlin, Heidelberg).
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009) Elevated CO₂ effects on plants carbon, nitrogen, and water relations: six important lessons

- from FACE. *Journal of Experimental Botany* **60**, 2859–2876. doi: 10.1093/jxb.erp096.
- Lelievre F, Seddaiu G, Ledda L, Porqueddu C, Volaire F (2011) Water use efficiency and drought survival in Mediterranean perennial forage grasses. *Field Crops Research* **121**, 333–342.
- Ludlow MM, Fisher MJ, Wilson JR (1985) Stomatal adjustment to water deficits in three tropical grasses and a tropical legume in controlled conditions and in the field. *Journal of Plant Physiology* **12**, 131–149.
- Morgan JA, Milchunas DG, Lecain DR, West M, Mosier AR (2007) Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the short steppe. *Proceedings of the National Academy of Sciences of the USA*, **104**, 14724–14729.
- Moya TB, Ziska LH, Namuco OS, Olszyk D (1998) Growth dynamics and genotypic variation in tropical, field grown paddy rice (*Oryza sativa*. L) in response to increasing carbon dioxide and temperature. *Global Change Biology* **4**, 645–656.
- Myers BA, Neales TF (1986) Osmotic adjustment, induced by drought in seedlings of three *Eucalyptus* species. *Australian Journal of Plant Physiology* **13**, 597–603.
- Nobel PS (2005) *Plant Physiology* third edition. (Elsevier academic press: Burlington, MA, USA).
- Nyambati EM, Muyekho FN, Lusweti CM, Onginjo E (2007) Production, characterisation and nutritional quality of Napier grass (*Pennisetum purpureum* Schum.) cultivars in western Kenya. *Africa Crop Science Proceedings* **8**, 185–188.
- Orians GH, Solbrig OT (1977) A cost-income model of leaves and roots with special reference to arid and semiarid areas. *American Naturalist* **111**, 677–690.

- Passioura JB (2010) Plant-water relations. *In: Encyclopedia of life sciences (ELS)*. (John Wiley and Sons, Ltd: Chichester). DOI: 1002/97804470015902.a0001299.pub2
- Prentice IC, Fraquhar GD, Fasham MJR (2001) The carbon cycle and the atmospheric carbon dioxide. *In: Climate change 2001: the scientific basis*. Contribution of working group 1 to the third Assessment Report of the Intergovernmental Panel on Climate Change Eds Houghton JT, Ding Y, Griggs DJ, Noguer M, Van der Linden PJ, Xiaosu D, pp183–239 (Cambridge University Press: New York).
- Relwani LL, Nakat RV, Kandale DY (1982) Intercropping of four leuceana cultivars with three grasses. *Leuceana Research Reports* **3**, 41.
- Richards RA, Rebetzke GJ, Condon AG, VanHarwaar-den AF (2002) Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* **42**, 111–121.
- Roumet C, Laurent G, Canivenc G, Roy J (2002) Genotypic variation in the response of two perennial grass species to elevated carbon dioxide. *Oecologia*, **133**, 342–348.
- Schrader JA, Gardner SJ, Graves WR (2005) Resistance to water stress of *Alnus maritima*: intraspecific variation and comparisons to others. *Environmental and Experimental Botany* **53**, 281–298.
- Silva JMD, Arrabaca MC (2004) Contributions of soluble carbohydrates to the osmotic adjustment in the C4 grass *Setaria sphacelata*: A comparison between rapidly and slowly imposed water stress. *Journal of Plant Physiology* **161**, 551–555.
- Skerman PJ, Riveros F, (1990) Tropical grasses (FAO Plant Production and Protection series No. 23. FAO: Rome, Italy).
- Toft NL, McNaughton SJ, Georgiadis NJ (1987) Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. *Australian Journal of Plant Physiology* **14**, 211–226.

- Turner NC, Begg JE, Tonnet ML (1978) Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. *Australian Journal of Plant Physiology* **5**, 597–608.
- Van de wouw M, Hanson J, Luethi S (1999) Morphological and agronomic characterisation of a collection of Napier grass (*Pennisetum purpureum* x *P. glaucum*). *Tropical Grasslands* **33**, 150–158.
- Wilson JR (1983) Effects of water stress on invitro dry matter digestibility and chemical composition of herbage of tropical pasture species, *Australian Journal of Agricultural Resources* **34**, 377–390.
- Wilson JR, Ludlow MM (1983) Time trends of solute accumulation and influence of potassium fertilizer on osmotic adjustment of water-stressed leaves of three tropical grasses. *Australian Journal of Plant Physiology* **10**, 523–537.
- Woodruff DR, Bond BJ, Meinzer FC (2004) Does turgor limit growth in tall trees? *Plant, Cell and Environment* **27**, 229–236.
- Wullschlegel SD, Tschapliski TJ, Norby RJ (2002) Plant water relations at elevated CO₂-implications for water-limited environments. *Plant, Cell and Environment* **25**, 319–331.
- Xu J, Belanger F, Huang B (2008) Differential gene expression in shoots and roots under heat stress for a geothermal and non-thermal *Agrostis* grass species contrasting in heat tolerance. *Environmental and Experimental Botany* **63**, 240–247.
- Xu Z, Zhou G (2005) Effects of water stress and nocturnal temperature on carbon allocation in the perennial grass, *Leymus chinensis*. *Physiologia Plantarum* **123**, 271–280.

Yanxian Y, Chengfei L, Yucang S, Zhixizn P, Guangheng F, Zhonghua J (2008)

Photosynthesis characteristics of three species of forages in the arid-hot valleys.

Journal of Natural Sciences **13**, 309–316.

Yordanov I, Velikova V, Tsonev T (2000) Plant responses to drought, acclimation, and

stress tolerance. *Photosynthetica* **38**, 171–186.