Leaf morphogenesis and tillering behaviour in single plants and simulated swards of Guinea grass (*Panicum maximum* Jacq.) cultivars.

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I dedicate this thesis ‘in memoriam‘ of my parents,
Lygia and Paulo Américo.
I have made a good choice.

I also dedicate this thesis to my daughter Cintia
and my son Gabriel.
They have made a good choice.

And last but not least, I dedicate this thesis to
my grandson Eric.
My genetic contribution
to New Zealand.

The true role of science is to understand life and comprehend creation so we can participate in it and add to it. A scientist is meant to be a steward of life forms. He is charged not just to measure and quantify data and writing papers, but to get busy fostering the whole of creation.

Luther Burbank

ABSTRACT

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In a series of five experiments carried out in growth cabinet and glasshouse environment, potted plants of Guinea grass (*Panicum maximum* Jacq.) cultivars were subjected to different cutting heights and environmental conditions. Herbage accumulation, leaf and tiller morphogenesis, leaf tissue turnover and tiller dynamics were evaluated. In one study three cultivars, Aruana, Mombaça and Tanzânia were grown for 18 months in miniature swards where plants were subjected to two defoliation heights (150 and 300mm), and productivity and tiller dynamics were evaluated. Cultivar and defoliation intensity effects on herbage production, leaf morphogenesis and tiller population density were observed. Herbage DM harvested from Mombaça was 32.3 and 31.7% more than Tanzânia and Aruana, respectively. There were also seasonal effects on tiller appearance rate and tiller death rate associated with flowering. A greater proportion of tillers flowered in cv. Tanzânia than cv. Mombaça. Two further experiments quantitatively described leaf turnover and associated morphogenetic characters in potted plants of the same three cultivars. One of these carried out in a growth cabinet included three defoliation regimes (50 mm, 200 mm, or uncut) and leaf turnover and the distribution of various tiller categories within the plants were measured. The other, carried out in a glass house, examined leaf turnover and site filling responses in undefoliated established plants. Higher temperature in the growth cabinet increased LAR, LER, FLL, and senescence and reduced site filling, LLS and NLL, and these effects were greater than cultivar effects. Severe defoliation (50 mm) initially resulted in increased tiller number per plant in all cultivars, but later decreased tiller number per plant through tiller death. The next experiment was established to determine limits of plasticity in potted plants of cv. Mombaça and cv.

defoliation intensities (100, 200 and 400 mm height). Herbage growth and net accumulation declined progressively, and senescence increased with increasing defoliation height in both cultivars. Treatment effects on root mass and root development were similar to those on herbage production. There was evidence of serious decline in vigour of aging tillers in both cultivars, and of substantial differences in the contribution of individual tiller cohorts to production, independent of the age effect. A final experiment using ^{14}C showed that translocation of assimilates from primary tillers to daughter and secondary tillers was greater in cv. Tanzânia than cv. Mombaça. The implications of these studies to understanding of the morphogenetics and production potential of these cultivars, their relevance to management decisions, and requirements for further studies are discussed

Keywords: cv. Aruana, cv. Mombaça, cv. Tanzânia, defoliation intensity, Guinea grass morphogenesis, photoassimilate translocation.

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TABLE OF CONTENTS

CHAPTER 3: PRODUCTIVITY AND TILLER DYNAMICS IN GUINEA GRASS CULTIVARS UNDER TWO CUTTING HEIGHTS 21

LIST OF APPENDICES

LIST OF TABLES

CHAPTER 3.

CHAPTER 4.

CHAPTER 5.

CHAPTER 6.

LIST OF FIGURES

CHAPTER 2.

CHAPTER 3.

CHAPTER 4.

CHAPTER 5.

CHAPTER 6.

CHAPTER 7.

LIST OF PLATES

CHAPTER 3.

CHAPTER 5.

CHAPTER 6.

CHAPTER 1: Introduction

1.1 Introduction

Ruminant production in Brazil is largely grassland-based and according to some estimates there is an area of more than 105 million ha of cultivated pasture. Most of this grassland is located in the equatorial zone and pasture characteristics are typical of those in other tropical areas of the world. Of the tropical grasses introduced to Brazil last century, *Brachiaria* species (*B. brizantha* and *B. decumbens*) are most widely sown, while *Panicum maximum*, Guinea grass, is the second most widely used. This species is now found in both tropical and sub-tropical regions of Brazil because of its great adaptability and productivity. Historically, Brazilian pastures were utilized in extensive systems, with very low fertilizer input, but exploiting natural soil fertility following removal of forest. Early introductions of Guinea grass to Brazil were of the cultivar Colonião. More recently, other cultivars have been introduced from Australia and Africa, in the hope of improved tolerance to soils of low fertility, low pH and high aluminum content.

During the last 20 years, about nine new cultivars of *Panicum maximum* resulting from selection in Brazilian regional research centers have been released. For the most part, the selection goal has been high productivity under natural lower fertility conditions, and many trials were carried out from the 1960s to the present time, to compare one or more cultivars with other genera. Other breeding objectives have included forage quality, persistence and high animal performance. In the cultivar development to date, there has been very little attention to plant morphology and development, however.

Meanwhile, in the last decade, increase in land price and competitiveness on a global scale, have necessitated new and more efficient approaches to grassland farming. This need for improved performance of agricultural systems has led at the research level to release of Guinea grass cultivars Tanzânia (1990) and Mombaça (1993), selected for increased leaf dry matter production, higher leaf/stem ratio, faster regrowth after grazing, better seasonal distribution of dry matter and higher crude protein content, than the older cultivar Colonião.

To develop a full understanding required to efficiently manage any pasture, we have to consider not only adaptation to environment (Da Silva, 1995), which for tropical grasses has now been studied for many decades, but also aspects of shoot structure and phenology, shoot and leaf dynamics, light interception and carbon balance, tiller size/density compensation, tissue and nutrient fluxes, phenotypic plasticity and their response to variation in environment conditions and pasture management. Information of this type is now readily available for temperate pasture grasses, with a literature spanning more than 50 years. Some recent examples include Cruz & Boval, 2000; Gastal & Durand, 2000; Lemaire & Agnusdei, 2000; Matthew et al., 2000; and Nelson, 2000. As noted by Gomide J.A (1997), because of the contrasts between tropical and temperate grasses in pathways of C metabolism as well as greater variation in plant size and structure, generalization from the existing knowledge in temperate grasses will be difficult. Therefore the types of studies described above are now a major priority for research on tropical pasture species.

In view of the lack of knowledge on these issues in tropical forage grasses, this thesis will focus on plant morphogenesis of Guinea grass, with emphasis on two main plant processes: leaf tissue turnover, and tiller dynamics under different defoliation heights. However, some measurements of physiological characteristics, such as photosynthetic rate and photoassimilate translocation, are also included. The two cultivars Tanzânia and Mombaça are compared, with some experiments including a third cultivar, Aruana.

1.2 Objectives

From the general objectives above, the following more specific objectives were developed:

- to explore patterns of tiller turnover in swards of different Guinea grass cultivars, and the effect, if any, of defoliation intensity on tiller turnover;
- to quantitatively describe leaf turnover and associated morphogenetic characters in Guinea grass;
- to determine limits of plasticity in response to increasing defoliation intensity, and defoliation intensity effects on root stem development;

- to evaluate the life history and contribution to yield of different generations of tillers in Guinea grass plants;
- to determine whether observed morphogenetic differences between cultivars could be explained by differences in photosynthetic rate or photoassimilate translocation.

1.3 Thesis structure

This thesis is presented in 7 chapters. The present introductory chapter is followed by a literature review in Chapter 2. Chapter 3 describes a glasshouse experiment which monitored miniature swards of three Guinea grass cultivars, Aruana, Mombaça and Tanzânia, over an 18 month period. The miniature swards were subject to two defoliation heights, 150 and 300 mm, and productivity and tiller dynamics were evaluated. Chapter 4 reports results from two short-term experiments describing leaf turnover. One of these experiments was conducted in growth cabinets, the other in a glasshouse. Chapter 5 describes a follow-up experiment designed to obtain more detailed information throughout a growing season, about the components of yield at the tiller level and their variation with cutting height, for the two cultivars Mombaça and Tanzânia. Chapter 6 reports a short-term experiment carried out with cultivars Mombaça and Tanzânia, in which particular categories of tiller were labeled with $^{14}CO_2$ and radiocarbon translocation to other parts of the plant determined. In conclusion, Chapter 7 provides general discussion of results and suggestions for further field research.

CHAPTER 2: Literature Review

2.1. Introduction

Brazil, with its 8.5 million km^2 land area, is located in South America between latitude 5° North and latitude 34° South and from 35° to 75° longitude West. It has at least six major ecosystems (tropical humid, semi-arid, cerrado, pantanal, Atlantic Forest and subtropical) which present different climatic characteristics, soils and vegetation, and where the production systems vary greatly as a function of the local conditions, infrastructure, input contribution and patterns of commercialisation (Zimmer & Euclides-Filho, 1997). Ruminant production in Brazil (with a estimated 160 million cattle) is based on grassland systems, and there is an estimated area of 105 million ha in cultivated pastures. Among the most important grass species used in sown pastures in Brazil are *Brachiaria* (*B. decumbens* and *B. brizantha*), *Paspalum notatum*, and *Cynodon dactylon* with the bunch grasses *Panicum maximum* (Guinea grass) and *Pennisetum purpureum* (elephant grass) also widely used. *P. maximum* ranks second after *Brachiaria* species in terms of area sown and its use is increasing due to its high DM productivity resulting. A recent estimate is that there is now an area of 5.5 million ha sown with Guinea grass cultivars in Central Brazil (Bono et al., 2000).

2.2. *Panicum maximum*

2.2.1. Species description

The genus *Panicum* belongs to the family Poaceae (formerly called *Gramineae*), sub family *Panicoide*, tribe *Paniceae* and includes perennial and annual species, with various growth habits. *Panicum* is a large genus with more than 500 species occurring mainly in tropical areas around the world (Bogdan, 1977). In this genus there are many species potentially useful for grazing, however, only a few of these are widely used for animal production. The most important species is *P. maximum* followed by *P. coloratum*. *P. maximum* is a very variable species and numerous distinct types occur naturally in Africa, mainly in East Africa. The plants differ in habit, height, stem thickness, degrees of branching, and other characteristics. *P. maximum* requires a warm and frost-free tropical environment. It tolerates shade and can be grown under tree plantations. *Panicum* sp. may be established either by seed or vegetatively, by splitting mature plants into component tillers. *P. maximum* responds well to N fertilization, with responses expressed in both DM yield and animal production.

2.2.2. History

As mentioned above, *P. maximum* Jacq. originated in tropical Africa (Bogdan 1977). The species is believed to have been introduced to Brazil during the 18th century, probably coming from western Africa to Central America, and then later to Brazil (Parsons, 1972). It is so long-established and well adapted to local conditions that it is considered a native grass in some regions. Historically, this species, with cv. Colonião the original cultivar, was used for new pastures on soils with high natural fertility, following deforestation. Later, in the sixties, the cultivar Colonião was substituted by others less demanding of high soil fertility such as Australian and African cultivars Makueni, Green panic, Gatton panic, Hamil, Guiné and Sempre verde (Aguiar, 2000). Some of the cultivars listed above are still in use, but only in restricted areas (Aronovich, 1995; Zimmer & Euclides-Filho, 1997). *Brachiaria* species were introduced in the seventies and because these grasses were tolerant of low fertility soils and less demanding in terms of management, they were quickly accepted by farmers and are now widely used. Meanwhile an international agreement was established between ORSTOM (Institut Francais de Recherche Scientifique pour le Development en Cooperation) and EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) in the eighties under which transfer to Brazil of a French germplasm collection of *Panicum* took place, supervised by Dr Yves Savidan (Jank, 1994). This collection was one of the most representative of *P. maximum* variability, with 426 apomictic accessions and 417 sexual plants (Savidan et al., 1985) collected mainly in eastern Africa (Tanzania and Kenya). The availability of this new material led to new interest among researchers and farmers in *P. maximum* as a forage grass.

In the last 20 years, nine new cultivars have been released as a result of selection programs in different research institutions: IZ-1 (1979), Tobiatã (1982), Centenário (1986), Centauro (1988), Aruana (1989), Vencedor (1990), Tanzânia (1990) and Mombaça (1993) (Jank, 1995), and recently Massai (Euclides et al., 2000)

2.2.3. Cultivars

The literature is rich in reports on DM yield of Guinea grass cultivars (Bogdan, 1977; Jank & Savidan, 1985; Corsi, 1988; Savidan et al., 1990; Jank et al., 1994; Corsi & Santos, 1995; Jank, 1995). DM accumulation ranged from 3 to 53 tonnes/ha/year in a two-year evaluation of 156 *Panicum maximum* accessions in Campo Grande, Brazil (Savidan et al., 1990; Jank et al., 1994)

The most studied cultivar in the past was cv. Colonião, used since the beginning of the last century. After becoming disappointed with the low productivity of this cultivar in low fertility soils and its sensitivity to mismanagement, farmers and researchers started to look for cultivars more tolerant to acid and low fertility soils and soils with high aluminium content. Recent selections were produced from the CNPGC (Centro Nacional de Pesquisa de Gado de Corte) collection, including the two most recent releases, Tanzânia and Mombaça. Both cultivars showed improved productivity in total and leaf DM, high seed yield and better distribution in DM yield through the year than cv. Colonião during two years evaluation (Jank & Costa, 1990). Aruana yielded less than cv. Colonião in separate trials (Ghisi et al., 1989; Cecato et al., 1996) but presented better annual DM distribution. Details of the three cultivars used in this research project follow:

cv. **Aruana:** Seeds of this cultivar were brought from Africa in the 1970s and after years of evaluation under clipping systems, the cultivar was officially released by the Institute of Animal Production (IZ - Instituto de Zootecnia) in 1989. It is a bunch grass with an average 80 cm height and develops a good ground cover compared with other cultivars, due to its thin and flexible stems that, when in contact with soil, produce roots. It is considered a stoloniferous grass and grows well under shade. This cultivar produced 15-20 ton DM/ha/year with 37.5 % of the annual yield in winter (IZ, 1989). Aruana shows a high persistency under hard grazing, and fast recovery after defoliation, attributed to numerous basal buds. Aruana has higher palatability for sheep. This cultivar has been used successfully since 1995 in sheep grazing systems (Santos et al., 2001) cv. **Mombaça:** This cultivar is a direct selection from the ORSTOM collection and was released in 1993 by CNPGC. It is a bunch grass, with an average 165 cm height with erect leaves, averaging 30mm width. It has high productivity (approximately 40.2 tonnes DM/ha/year). This cultivar produces only 11% of the annual yield in winter and flowers once a year, in autumn (April to June). Crude protein content in leaves and stem is 13.4 and 9.7%, respectively (Jank, 1995).

cv. **Tanzânia:** Also a direct selection from the ORSTOM collection, released in 1990 by CNPGC. It is a bunch grass with an average 130 cm height, with leaves becoming decumbent in later stages of regrowth and averaging 26mm width, and productivity measured at approximately 32.1 tonnes DM/ha/year. Tanzânia produces 10.5% of the annual yield in winter and flowering occurs in autumn. Its crude protein content is 12.7 and 9.1% in leaves and stem, respectively (Jank, 1995).

2.2.4. Industry management practices

As a consequence of recent research in developed areas in central southwest and southeast Brazil, *P. maximum* cultivars have been used, mainly intensively, in rotational systems for beef and dairy cattle. In general terms, beef cattle grazing areas average around 80 ha in area, this being divided into 13 to 16 paddocks with two to three days grazing in each paddock during a grazing rotation, and a post grazing height between 30 and 50 cm. During the growing season (September to April) the stocking rate is around 5 to 10 AU/ha (AU = animal unit, 450kg live weight) but can decrease to 2 AU/ha in the cooler dry season (May to August). In some regions, where the temperature is not a limiting factor, irrigation systems have been used.

In intensive dairy systems, the typical farm area is smaller (~10 ha) with more paddocks, (around 30) but only one to two days grazing in each paddock during a grazing round. The herd is usually divided into groups of animals, according to production. The stocking rate is usually about 8.5 AU/ha in the growing season, reducing to around 2.0 in dry season (Aguiar, 2000).

2.2.5. Current knowledge of *Panicum*

P. maximum was a successful species in newly developed pastures and usually performed well in Brazil's tropical environment, even without regular fertilizer application. An entire Symposium held in Brazil in 1995 was devoted to the theme Colonião Grass, the term Colonião Grass used in this context to denote the species, *P. maximum*, rather than the original cultivar used in Brazil last century. This symposium collected together the most up to date research results for this species (Peixoto et al., 1995). The most commonly reported results were total annual DM production, green leaf production, leaf/stem ratio (Leaf/stem ratio is of interest because tropical grasses usually form elongated internodes during vegetative growth. Stem formation is not confined to the flowering period, as it commonly is in temperate grasses). Other papers reported aspects of environmental adaptation including tolerance to drought and frost, aluminium toxicity, low soil nutrient levels, and to pests and diseases. A third category of papers considered forage quality (crude protein content, fibre content, and DM digestibility).

In those papers reporting DM yield, sources and levels of nutrients (mainly nitrogen, phosphorus and potassium) were commonly evaluated, or alternatively, the effect of frequency, intensity and timing of defoliation. The goal of such research has been to find the best combination, of frequency (changing from 3 to 8 weeks in summer to 9 to 14 weeks in winter) and intensity of defoliation (15 to 80 cm grazing or cutting height), for each grass species or cultivar, in each region.

However, twenty years ago, Ludlow & Charles-Edwards (1980) commented that few general principles have emerged from these experiments and felt this unfortunate. More recently, Humphreys (1997) criticized this general approach, because the morphological characteristics of the remaining material after grazing/harvest were not recorded. He also commented that the seasonal record of harvest for different treatments was confounded in an unidentifiable way with different residual stubble and did not necessarily reflect accurately, treatment effects on growth. Also, differences in plant response to cutting and grazing (respectively, non selective and potentially selective removal of herbage) may give rise to seasonally restricted growth in grazing systems, not observed in research experiments. Commonly, the only morphological character evaluated was tiller number per plant, but without any appreciation of the issue of size/density compensation (see Section 2.4.3 below), or of the dynamic process of tiller appearance and death in a sward, over time.

Another indication of the lack of morphogenetic information for *P. maximum* is obtained from collating statistics on published papers. In a recent literature search by the author in CAB Abstracts (September 2001) about 3000 references to *P. maximum* were located, yet only three were concerned with morphogenesis and none with tiller dynamics. In the most recent International Grassland Congress in Brazil in 2001, only two papers dealt with tiller dynamics in Guinea grass. One of these refers to cv. Mombaça (Coelho et al., 2001) and other to cv. Tanzânia (Barbosa et al., 2001). Both provide data for only a single regrowth period following defoliation.

Another concept that has been widely promoted as a management criterion in tropical pastures is the need to avoid physical removal of elevated growing points during grazing, and to keep intact growing points in order to achieve faster regrowth after defoliation (Gomide et al., 1979; Gomide & Zago, 1980, Favoretto et al.; 1987, Alcântara et al., 1991). More recently, regulation of tillering by apical dominance was reviewed by Murphy & Briske (1992). Those authors concluded that environmental variables might be equally or more important than physiological processes of apical dominance in determining tiller initiation.

In the 1990s in Brazil, with the economic pressure and increase in land price, animal production based on pasture had to be economically reliable and competitive with other agricultural land uses. This requirement, together with the release of new cultivars, Tanzânia and Mombaça (Jank, 1995) and some research suggesting benefit from a more intensive use of the species as in rotational systems (Corsi, 1984, 1988), changed the approach to pasture management. With this change in emphasis, researchers are now interested to know more about basic physiological determinants of plant regrowth after defoliation (Aguiar, 2000). For instance, tillering ability and leaf growth and development, are now of major interest, with a view to developing new cultivars that are both agronomically persistent, as well as providing high quantities of quality herbage to support the needs of grazing animals.

Despite this change in emphasis, we are still far from attaining the knowledge and understanding necessary to manage with confidence, the response of grasses to defoliation in tropical pasture (Humphreys, 1991, 1997). Many authorities (Da Silva, 1995; Faria et al., 1996; Gomide, J.A., 1997; Maraschin, 2000; Aguiar, 2000; Corsi et al., 2001) have questioned the basis of our management techniques and have emphasised the need for more objective information on plant growth and morphogenesis of tropical plants, including *P. maximum*.

2.3. Environmental factors and plant productivity

Pasture productivity is influenced by major environmental factors such as light, temperature, soil moisture availability and soil nutrients, and intrinsic factors of the plant (morphology, physiology and adaptability). Another external factor, management, includes all practices imposed by man and animals utilizing forage plants interfering with plant productivity and persistency.

Temperature affects the growth rate of plants through the cumulative effect on each separate process of development and on the rates and directions of metabolic pathways associated with growth (Pearson & Ison, 1997). One important trait that distinguishes tropical (C_4) from temperate (C_3) grasses is the higher temperature range for growth and development in the former. As a group, tropical grasses have a 35°C optimum temperature compared with 25°C for temperate grasses (McWilliam, 1978; Humphreys, 1981), but stop growing or grow extremely slowly below 15°C (Cooper & Tainton, 1968). The productivity of plant communities depends basically on the incoming light energy, captured by the green parts (mainly leaves) of the plants. However, there are many factors involved in the determination of productivity, through effects on the quantity and quality of the light and the photosynthesis process itself (season of the year, weather conditions, slope of the ground, latitude). Tropical and subtropical plants are, potentially, more productive than temperate grasses, due to the higher efficiency of the C_4 photosynthetic pathway, as well as the higher irradiance in the tropics (Holmes, 1981). It was observed by Deinum et al. (1996) that light intensity stimulated growth, tillering and yield per tiller and increased stem proportion in two tropical grasses (*B. brizantha* and *P. maximum*).

Jones (1969) observed that nil to 6 % of Guinea grass plants survived a winter with a minimum temperature of –10°C. The response of plants to temperature is complex because most growth processes are influenced simultaneously by other factors such as light, stage of development (flowering or vegetative growth) and management. Basically, high temperature tends to increase the rate of leaf appearance and leaf area expansion (McWilliam, 1978; Ivory & Whiteman, 1978), while low temperature normally increases tillering (McWilliam, 1978; Kobayashi et al., 1977). In contrast, Ivory (1975) obtained a decrease of tillering in *P. maximum* var trichoglume with a reduction in temperature.

As with other components of climate, water plays a very important role in growth and development of grasses (Turner & Begg, 1978). Periods of water deficit could be considered one of the most limiting climatic factors to grasses in tropical environments, and different species react differently to water deficit (Humphreys, 1991). In general, severe or prolonged water deficit always decreases yield in grasses. Ng et al. (1975) observed an increase in leaf death and reduction in leaf elongation and development in *P. maximum* var. trichoglume. Those same authors (Ludlow & Ng, 1976) showed an 80% reduction in leaf elongation rate of that same cultivar when the leaf water potential fell from -4 to-7 bars and elongation ceased at -10 bars. Dias Filho et al. (1989) working with *P. maximum* cv. Tobiatã, noticed a decrease in total biomass (roots and shoots) and in leaf elongation rate, resulting in low number of leaves per tiller in plants subject to water deficit.

Among the environmental factors that affect plant growth and development, nutrients and water in the soil can be manipulated by man within certain economic limits. From the sixteen essential elements for plant growth, nitrogen and potassium are the most abundant (after carbon) and, as a result, the most needed. Nitrogen is the largest fertilizer input in forage systems (Sanderson et al., 1997), and affects DM productivity in pastures mainly through increase in tiller number (Barbosa et al., 1997; Colozza et al., 2000), leaf elongation rate, and leaf size (Cruz & Boval, 2000), but only slightly affects leaf appearance rate (Lemaire & Chapman, 1996).

2.4. Plant morphogenesis

Plant morphogenesis can be defined as the dynamic expression of processes of generation and expansion of plant form in space (Chapman & Lemaire, 1993). Characters of interest when studying plant morphogenesis include the rate of appearance and growth in size and number of plant parts and also the corresponding death (senescence) rates. At the sward level, productivity and perenniality depends on the ability of the population of grass plants to recover new leaf area after defoliation (Gomide, J.A., 1997). It follows that information about leaf and tiller growth and development is a basic tool to improve techniques in pasture management.

The growth and development of grass plants has been studied for many years as a primary tool for developing pasture management strategies in temperate countries (Mitchell, 1953, 1954; Brougham, 1956, 1960). Contrasting with this approach, in tropical countries, in general, pasture management strategies are developed (Carvalho, 1997) from consideration of two main system variables - stocking rate (and associated factors) and grazing methods (i.e. continuous or rotational grazing). These approaches result in a descriptive catalogue of alternative outcomes, without understanding of the mechanisms and components of those systems outcomes, such as animal weight gain. Thus it can be argued that the lack of component research on tropical grass production has inhibited development of improved pasture management strategies in tropical areas.

Since there is little information about plant morphogenesis and sward dynamics in tropical grasses, the remainder of this literature review will focus on information available for and concepts developed with temperate grasses (Richards, 1993; Lemaire & Chapman, 1996; Matthew et al., 2000, 2001; Lemaire & Agnusdei, 2000; Nelson, 2000; Cruz & Boval, 2000; Lemaire, 2001) showing how parallel research might be applied in tropical grass pastures.

2.4.1. Plant structure – phytomers and tillers

The morphology of grasses has been described by Silsbury (1970). The basic unit of production is the tiller, which consists of a chain of small units called phytomers. Phytomers are produced in sequence in the meristematic zone in the apex of a primary shoot. Each phytomer comprises a leaf (blade and sheath), internode and node, a bud on the opposite side to the leaf in the shoot axis, and one or more adventitious roots. The production of new leaves on an individual grass tiller is a continuous process (Lemaire & Agnusdei, 2000), but production of new leaves is impossible after elimination of the meristematic tissue in the apex of the shoot by grazing or cutting. In a vegetative state, generally, temperate grasses do not show internode elongation and the meristematic tissue or growing point is always near the ground level. On the other hand, tropical bunch grasses can elongate internodes very early in the vegetative stage of development resulting in generally taller tillers (Bogdan, 1977; Humphreys, 1981).

For many years research in tropical forage grasses has concentrated on means of avoiding damage to apical meristem in order to maintain high growth rate (Gomide et al., 1979; Corsi, 1984; Alcântara et al., 1985, 1991; Coelho et al., 2000). However this approach inevitably allows stem elongation and loss of nutritive value as stem matures (Dovrat et al., 1980). It is generally recognized that in temperate grasses the maintenance of balance between herbage productivity and nutritive value includes a compromise between tiller development and tiller dynamics associated with grazing control (Hodgson, 1990), and there is a need for better understanding of the scope for manipulating tiller potential in tropical species as a feasible mean for increasing sward productivity and persistence (Corsi & Santos, 1995)

2.4.2. Leaf tissue turnover

Each grass leaf consists of a blade or lamina connected at an angle to a sheath, the junction being identified by a membranous ligule. There are five stages in the growth of a grass leaf, namely: initiation, pre-appearance, post-appearance, maturity and senescence. The leaf primordia initiate as lateral appendages on the apex in acropetal succession. The interval between two successive units is called plastochron. At first, the leaf primordium grows as a diffuse meristem and increases in size mainly by cell division. Lamina growth is due to cell extension in the meristematic region above the ligule, while sheath growth is due to extension in the other meristematic region at the leaf base (Silsbury, 1970). After the ligule emerges the leaf stops elongating. During vegetative growth stages, cool-season grasses like tall fescue and perennial ryegrass generally have two leaves elongating at the same time (Nelson, 2000). The same author noted that comparable information is not available yet for C4 grasses. In a vegetative grass sward (Chapman & Lemaire, 1993) where only leaves are produced, morphogenesis (dynamics of generating and expanding organs in space) is a function of three main traits below.

Leaf Appearance Rate (LAR) expresses the number of leaves appearing per day or per degree-days (Gomide, J.A., 1997). This appearance of leaves at the tiller apex can be expressed also as the leaf appearance interval or phyllochron (1/LAR), defined as the time interval between the appearance of two successive leaves and is expressed in days or degree days/leaf. LAR plays a central role in shoot morphogenesis and potential tiller production (Chapman & Lemaire, 1993) and has a close relationship with temperature in grasses (Anslow, 1966).

Leaf Elongation Rate (LER) is the cumulative effect of cell elongation (Durand et al., 1999) and is expressed in cm or mm per leaf/day or per tiller/day. LER is strongly affected by N nutrition (Gastal et al., 1992).

Leaf Life-Span (LLS) measures the period of time during which newly appeared leaf tissue remains green and is expressed in days or degree-days.

Each of these three traits is determined genetically, but can be modified by external factors such as temperature, light, water and nutrient status. As illustrated in Figure 2.1, interaction between these basic morphogenetic variables determines four main structural aspects of the sward.

Final leaf length (FLL) is the product of LER and the duration of the elongation period for a single leaf (LED). LED increases with the leaf insertion level in the grass shoot (Wilson, 1976a, Gomide, J.A., 1997).

Number of leaves per tiller is the product of LLS and LAR. In seedlings LAR is higher in the first leaves than in following leaves (Gomide, J.A., 1997) and leads to a high number of leaves per tiller. With time this number falls to an almost constant number, but different for species and cultivars, determined by the synchronism of leaf appearance and death. The stabilization of leaf number per tiller constitutes an objective index to advise pasture management in order to avoid leaf losses through senescence and death, so as to maximize harvest/grazing efficiency (Gomide, J.A., 1997).

Tiller density, is indirectly linked to the LAR, since there is one axillary bud, capable of developing into a new tiller, associated with every leaf. However, initiation of axillary buds is subject to physiological signals within the plant and varies greatly according to environmental conditions, especially light level. The proportion of axillary buds developing is known variously as the site filling ratio (Davies, 1974) or the site usage (Skinner & Nelson, 1992) and defines tiller appearance rate (TAR). The dynamic equilibrium between tiller appearance and tiller death determines the tiller population density of grazed swards.

Leaf Area Index, LAI, was defined by Watson (1947) as the green leaf area supported by unit ground surface. It is determined by the product of mean leaf area of individual leaves, leaf number per tiller and tiller population density. More than 90% of the dry weight of plants comes from photosynthetic assimilation of carbon (Gardner et al., 1985). Canopy cover or LAI determines light capture and therefore plays an important role in sward productivity and is a useful variable describing interaction between grasses and their environment (Bahmani, 1999).

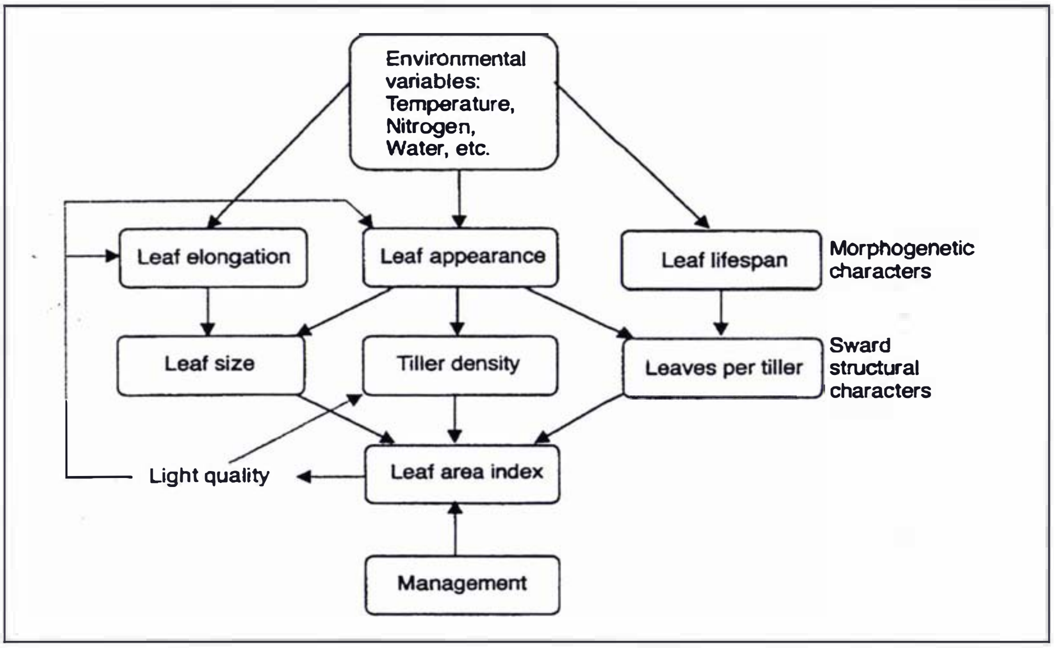


Figure 2.1. Diagram of relationship between morphogenetic variables and sward structural traits. (Chapman & Lemaire, 1993)

2.4.3. Tillering behaviour

As described above, in the base of each new leaf produced there is always a bud, with potential to form a future new tiller. Therefore tiller number is indirectly related to the number of leaves produced on each tiller axis. Tiller production seems to be synchronized with leaf development on the main stem, tillers normally appearing during the life of their subtending leaf, and resulting in a very predictable pattern of tiller appearance (Klepper et al., 1982). Site filling was originally defined as the ratio of new tillers to new leaves appearing (Davies, 1974). Because of delay between leaf and tiller appearance on the tiller axis, there are always more new leaves than tillers, resulting in a theoretical maximum site filling ratio of 0.41 (Davies, 1974) or 0.69 if prophyll buds are considered (Neuteboom & Lantinga, 1989). More recently, there has been a tendency to develop statistics which focus the fate of particular buds, at stated positions on the tiller axis (Skinner & Nelson, 1992; Bos & Neuteboom, 1998), rather than on the whole plant average for number of new tillers per tiller per leaf appearance interval. The value of site-specific statistics is that transient surges of tiller production can be recorded in precise detail.

Maintenance of productivity and high LAI of a sward are determined by two main components, leaf and tiller production. Tiller dynamics studies based on evaluation of rates of appearance, death and survival, play a meaningful role in determining whether the dynamics of these processes impose limitations on pasture productivity at certain times of the year.

The equilibrium between tiller appearance and death, which determines the tiller population in the canopy, is dependent on the LAI of a sward. LAI varies according to the defoliation regime. According to Matthew et al. (2000) there are three separate but related considerations in defining tiller dynamics in a grass sward: tiller morphology, canopy leaf area optimisation and persistence. The first of these considers the inter-relationship and feedback between leaf, root and tiller formation and provides insights to carbon allocation. It can be considered the first level of complexity, because we are dealing with the tiller as a unit of study. The second, canopy leaf area optimisation, recognises that increase and decrease in tiller population density is an important mechanism for adjustment and optimisation of sward leaf area, for example in response to a change in defoliation height. Canopy leaf area optimisation, then, deals with a higher level of complexity, and includes the interaction of individual plants that may or may not be from the same species. The third consideration is the survival of the plant population. Persistence, or perenniality in grass swards is determined by the net balance of seasonal patterns of tiller appearance and death.

In a continuously grazed *Cynodon* sp. sward, Fagundes et al. (1999) recorded a range in LAI of 0.9 to 2.8 for a sward surface height range of 50 to 200 mm in swards maintained at different steady states. There was no significant difference between sward surface heights for herbage accumulation rate averaged over the entire experimental period of approximately one year. In the same experiment Carvalho et al. (1999) observed a higher tiller turnover and higher tiller population density under hard than under lax grazing. Tiller density decreased with increasing sward surface height (14300 to 6800 tillers/m^2) and tiller weight increased (18 to 70 mg/tiller) (Sbrissia et al., 1999). This principle of size/density compensation (SDC) in grass swards has been identified in many studies with temperate species (Bircham & Hodgson, 1983; Matthew et al., 1996; Hernández-Garay et al., 1999). Yoda et al. (1963) found for several plant species that plotting the logarithm of weight against logarithm of plant density showed a -3/2 slope, which has been since called the self-thinning law of ecology, though recently less supported as a concept than previously. Mathew et al. (1996), showed that size density compensation in grass swards, observed to follow slopes steeper than –3/2, conformed or nearly conformed to –3/2 compensation when correction was made for change in LAI and tiller shape with sward height. From this we understand that the –3/2 size/density relationship can be used to determine LAI-neutral combinations of herbage mass and shoot density.

Tiller population dynamics has been studied for a long time, as presented in Langer's review (1963). According to Matthew et al. (2000) all studies of tillering are laborious and demand time and patience and can be categorised in four groups. Firstly, the simplest studies count changes in population over time. A second level is monitoring tagged tillers and observing tiller appearance and death as components of population density. Still more accurate understanding can be gained through monitoring tiller survival within successive cohorts during a period of time, to find whether particular categories of tillers within a population are more prone to death. The most complete demographic analysis requires, in addition to monitoring survival, categorisation of new tillers according to the cohort that originated them.

An up to date review of previous studies and statistical techniques applied for analysis of the resulting data is presented by Bahmani (1999). In this study, seasonal episodes of tiller birth and death explained the majority of variation, with comparatively small differences between two ryegrass cultivars, or in response to addition of N fertilizer or irrigation.

2.4.4. Flowering

Flowering of a grass tiller follows a transition at the apex from leaf production to initiation of flower primordia. This transition occurs in response to environmental signals such as day length, and details differ between grass species. Ryegrass and many other temperate grasses, for instance, flower following exposure to cold in winter (vernalisation) and in response to increasing day length in spring. *P. maximum* has a range of flowering period, but the present cultivars normally flower in autumn, as day length decreases. It is not clearly understood which agents cause the morphological changes that occur during reproduction (Robson et al., 1988). There is a synchronism between the processes of stem elongation, inflorescence formation, and expansion of the last formed leaves, culminating in the emergence of the inflorescence from the sheath of the flag leaf. (Robson et al., 1988). Since flowering results reduction of forage quality, and later tiller death, variation between cultivars for, or management effects on percentage of tillers flowering are important considerations in developing forage grass management strategies.

2.4.5. Root development

Root formation on the tiller axis is nodally organised and occurs in a synchronised sequence. At a particular node or phytomer on the tiller axis, the developmental sequence is: leaf formation, tiller bud initiation, root initiation. Root growth rate follows a seasonal pattern similar to pasture growth rate, but root growth being 15 to 20 % of the shoot growth (Matthew, 1992). Evans (1976) found that in ryegrass, new root production initiates in the autumn after soil cools and becomes moist. Production continues through winter and spring but ceases or is reduced during summer drought. Suarez & Hernandez (1980) found the same proportion of shoot and root growth (kg/ha) when evaluating seedlings of *P. maximum* during the establishment period (60 days).

In an up to date review, Matthew et al. (2001) emphasises the need to understand that root and shoot development in grasses are inter-related as much through sequencing of events on the tiller axis, as through any hormonal control the plant may exert in a physiological sense. There are few studies relating defoliation height and frequency and root production in grazed swards. For perennial ryegrass, Matthew (1992) found little difference in root production between hard and laxly grazed field swards. Even so, where time allows there must always be interest in measuring both root and shoot growth, especially where considerations of carbon supply may be limiting shoot growth, and whole-plant understanding is desired.

2.5. Application of morphogenetic information to modify industry practice.

The primary objective of management is to maximise the intake of nutrients by the animals from the pastures on a sustained basis (Humphreys, 1991). So the problem faced by pasture manager is to reconcile the conflicting requirements for daily forage supply for grazing animal and to maintain a satisfactory canopy leaf area in order to intercept and utilise current radiation. To use pasture profitably, it is necessary to develop defoliation strategies, which maximise quality and quantity of forage grown. This, in turn requires understanding of component processes.

Management based on plant morphogenesis and sward structure has been used in some temperate countries, and research centres have been working in this area for more than 50 years. The challenge for this study will be develop an understanding of sward processes at the component level, to complement existing understanding of tropical pastures based mainly in rest intervals, stocking rate and intensity of grazing with fixed periods, rarely taking into account the physiology of the plant and without any control of the structural characteristics of the sward such as LAI. As Hodgson (1985) commented, research with temperate pastures suggests that stocking rate should not be considered as a primary determinant of either herbage production or animal performance because its influence is mediated via effects upon a range of sward traits, which collectively define the state of the sward.

2.6. Conclusion

More analytical studies to elucidate component factors affecting productivity and persistence at the sward level in tropical pastures are needed. Such studies may help towards a better interpretation of results in other tropical pasture experiments and may also be useful in determining reasons for poor persistence of introduced species in tropical and subtropical areas (Chapman & Lemaire, 1993). This thesis reports a series of experiments designed to provide previously unavailable sward-component-level information on production of a tropical grass widely used in Brazil, Guinea Grass (*P. maximum*).

CHAPTER 3: Productivity and tiller dynamics in Guinea grass cultivars under two cutting heights.

3.1. Introduction

As noted in Chapter 2, Guinea grass is considered one of the most productive grasses and has been used for a long time in Brazil (Aronovich, 1995), however, the high productivity of tropical grasses for pastures has not been reflected in high animal performance, (Faria et al., 1996). Despite active selection programs and release of new cultivars limitations to animal performance and pasture persistency are still a common problem (Vieira & Kichel, 1995).

Researchers in temperate areas know that pasture management encompasses factors in addition to frequency and severity of defoliation, and have a different approach to understanding and managing components of the pasture system (Hodgson & Da Silva, 2000). In recent years, there has been an increased interest in using ecophysiological research to provide information for better management of tropical pastures (Gomide J.A., 1997; Humphreys, 1997; Maraschin, 2000). In particular, such research aims to have more information at the component level of the sward (tillers and leaves). This component understanding of the biological processes of the plant, and of the periodic events related to yield such as leaf and tiller birth and death and limits of plasticity can then be harmonized, as far as possible, with management practices. Chapman & Lemaire (1993) commented that such information could be helpful in identifying reasons for poor persistence of species in tropical/subtropical areas and consequently defining management regimes for the utilisation of forage resources in those environments.

The present experiment was undertaken to provide systematic information about tiller dynamics in Guinea grass swards with the following objectives:

- to test a proposed methodology for evaluating tiller dynamics in tropical bunch grasses;

- to evaluate strategies of regrowth and persistency in Guinea grass cultivars with different morphological traits under two defoliation levels through processes of leaf and tiller dynamics.

3. 2. Materials and Methods

3.2.1. Plant material management and experimental layout

The experiment was carried out in a glasshouse, located at the Plant Growth Unit, Massey University, Palmerston North (40°16'S, 175°17'E) from October 1998 to August 2000. It comprised three Guinea grass cultivars, Aruana, Mombaça and Tanzânia, subjected to two defoliation levels, 150 mm above soil level (Low Cut, LC) and 300 mm above soil level (High Cut, HC).

Each block was planted in a timber box (Fig. 3.1, Plate 3.1a) of size 5 x 0.6 x 0.30 m, filled with a mixture of soil and washed sand (1:1) and fertilized with 3 kg/m^3 dolomite, 3 kg/m^3 agriculture lime and 3 kg/m^3 of a slow release fertilizer (Osmocote brand) with 16%N, 3.5%P, 10%K, 2.4% S and micro elements (Mg, Bo, Cu, Fe, Mn, Mo and Zn). Seeds were sown in trays on 20 October 1998 and after two weeks, seedling plants were transplanted to plots of 24 plants in a 4 x 6 distribution within the boxes (Fig 3.2) with a density of 70 plants/m^2. The total area for each plot was 0.48m^2 (0.8 x 0.6 m)

Plants were watered daily with tap water and after each harvest plots were fertilized with the equivalent of 50 kg N/ha as urea and 30 kg K/ha as potassium chloride. In the second year, (November 1999) in addition to the use of N and K fertilizer, plots were fertilized weekly to run off by irrigation with a commercial water soluble fertilizer with: 20% N, 8.7% P, 16.6% K, 0.065% S, 0.05% Mg, 0.007% B, 0.004% Cu, 0.05% Fe, 0.025% Mn, 0.001% Mo and 0.003%Zn in a approx. concentration of .5%.

Plants were cut at approximately monthly intervals in Spring/Summer and at longer intervals in Autumn/Winter for two years (Table 3.1). Reproductive development occurred after the April harvest, (i.e., H5 and H15 in years one and year two, respectively) and lasted until the end of July/August, in both years (Table 3.1)

Table 3.1. Schedule of harvests and activities during the experimental period:

Date		Season	Weeks (days) between harvests
20/10/98	Sowing seeds in a tray	Spring 1	
4-5/11/98	Transplanted to the box	Spring 1	
16/12/98	Initial cut (200 mm high) (Hi)	Spring 1	8 (57)
13/01/99	Harvest 1(treatments started) (H1)	Summer 1	4 (28)
10/02/99	Harvest 2 (H2)	Summer 1	4 (28)
10/03/99	Harvest 3 (H3)	Summer 1	4 (28)
14/04/99	Harvest 4 (H4)	Autumn 1	5 (35)
20/05/99	Harvest 5 (H5)	Autumn 1	5 (36)
21/07/99	Harvest 6 (H6)	Winter 1	9 (62)
08/09/99	Harvest 7 (H7)	Winter 1	7 (49)
13/10/99	Harvest 8 (H8)	Spring 2	5 (35)
10/11/99	Harvest 9 (H9)	Spring 2	4 (28)
07/12/99	Harvest 10 (H10)	Spring 2	4 (27)
04/01/00	Harvest 11 (H11)	Summer 2	4 (28)
02/02/00	Harvest 12 (H12)	Summer 2	4 (29)
01/03/00	Harvest 13 (H13)	Summer 2	4 (28)
04/04/00	Harvest 14 (H140	Autumn 2	5 (34)
23/05/00	Harvest 15 (H15)	Autumn 2	7 (49)
15/08/00	Destructive Harvest (H16)	Winter 2	12 (84)

3.2.2. Measurements:

Temperature records were obtained from a maximum-minimum thermometer suspended 1.7 m above ground level, and from two Skye SKH 2021 'thermistor' sensors located within the sward and connected to a data logger. Light measurements were made using two Skye SKP 1110/1 'pyranometer' sensors placed just above the sward level

3.2.2.1. Herbage accumulation and specific leaf area

All plants were cut with scissors and a sheet of cardboard was used as a reference guide to achieve uniform cutting height. Border plants were harvested and this herbage discarded, while material from all central plants was retained for yield determination. (The area so harvested was 0.40 x 0.24m = 0,096m^2). Green herbage collected was weighed and separated into lamina and stem (leaf sheath and true stem) fractions and oven dried for 48h at 60°C.There was no senescent leaf material in any harvest. Samples of complete leaves from harvested material of each plot were selected to evaluate leaf area with a portable Leaf Area Meter (LI-COR model LI-3000), and then specific leaf area (SLA) was calculated.

3.2.2.2. Tiller population dynamics

From the eight plants in the central area of each plot, four alternate plants (Figure 3.2) were selected for tiller counting throughout the study, resulting in 16 plants for each treatment. After the first regular cut (Table 3.1) the main tiller in each sample plant was labeled with a colored wire ring, and all others with a second color. After each harvest (Table 3.1) new tillers were counted and labeled with a unique colour. Tillers were considered dead when completely dried and senescent, and in this case the ring was discarded, although lost or broken tillers were counted as dead. Estimates were made of the components of tiller dynamics, as follows:

- Relative Tiller Appearance Rate (TAR) was calculated as the number of new tillers recorded at each new harvest divided by the total number of tillers at the previous harvest and by the interval (days) between harvests, and expressed as a percentage.
- Relative Tiller Death Rate (TDR) was calculated from counts of dead tillers, as described above for TAR.
- The percentage of flowering tillers was calculated as the total cumulative number of tillers which produced a seed head in each cohort at harvests H5 (May/1999) and H6 (July/1999) and H15 (May/2000) and last harvest H16 (August/2000), divided by the total number of tillers in the same cohort, and expressed as a percentage.

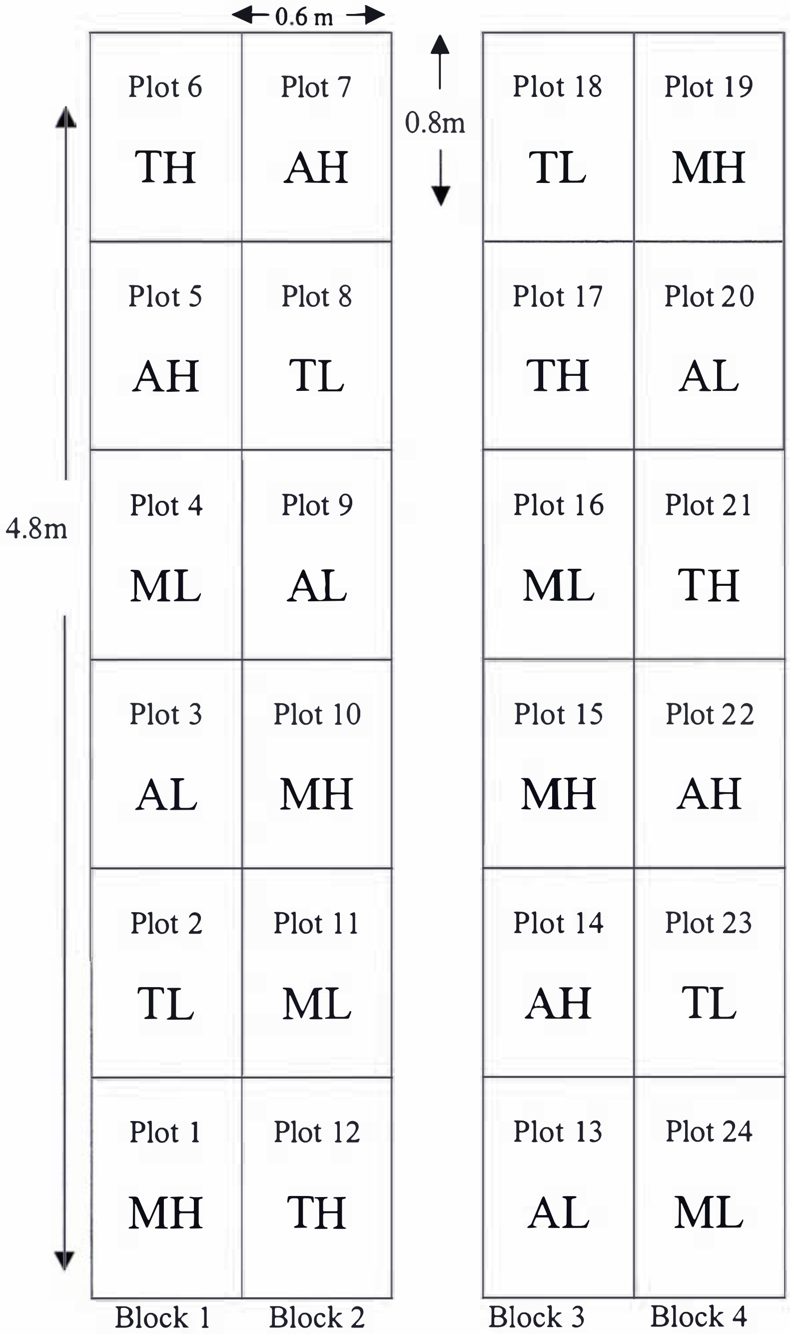
- Tiller life expectancy was calculated as the final number of tillers in each cohort surviving to the last harvest H16 (August/2000) divided by the number of tillers initially present in the same cohort, expressed as a percentage.

The cultivar Aruana exhibited vegetative stem elongation and produced large numbers of small aerial tillers at nodes after two or three months. Due to this very different behaviour compared with the other two cultivars, and the difficulty of counting these small tillers, this cultivar was not included in the tiller dynamics evaluations described above.

3.2.3. Trial design and statistical analysis

The experimental design was a completely randomized block with treatments arranged in a 3x2 factorial (cultivars x cutting height) with four replicates The SAS General Linear Model (GLM) procedure was used for statistical analysis with the Repeated Measures option from the statistical SAS package (SAS® System, 1989) for yield and specific leaf area variables. Due to high variance among treatments, yield and SLA data were log transformed for statistical analysis. Means were compared using Tukey test at 5% significance.

In this study a new approach to statistical analysis of tiller survival information has been used. The points for and against the approach used and the reasons for its adoption are detailed below in the discussion section. For analytical purposes, the survival of each individual tiller cohort (numbers of tillers totaled across replicates for each experimental cultivar x cutting height combination), for each observation period within the experiment was expressed as a probability. The probabilities so obtained were then adjusted by logarithmic proportion to a common 30-day value, and these 30 day survival probabilities analysed by GLM using the statistical package Minitab, to determine how survival probability varied with tiller age, month of observation, cohort (i.e. date of birth), and between the experimental treatments of cultivar and cutting height.



Block 1	Block 2	Block 3	Block 4
Plot 6 TH	Plot 7 AH	Plot 18 TL	Plot 19 MH
Plot 5 AH	Plot 8 TL	Plot 17 TH	Plot 20 AL
Plot 4 ML	Plot 9 AL	Plot 16 ML	Plot 21 TH
Plot 3 AL	Plot 10 MH	Plot 15 MH	Plot 22 AH
Plot 2 TL	Plot 11 ML	Plot 14 AH	Plot 23 TL
Plot 1 MH	Plot 12 TH	Plot 13 AL	Plot 24 ML

Figure 3.1. Diagram of the experimental layout with four blocks of six plots with treatment allocation:
AH / AL: Aruana, High and Low Cut;
MH / ML: Mombaça High and Low Cut;
TH / TL: Tanzânia High and Low Cut;

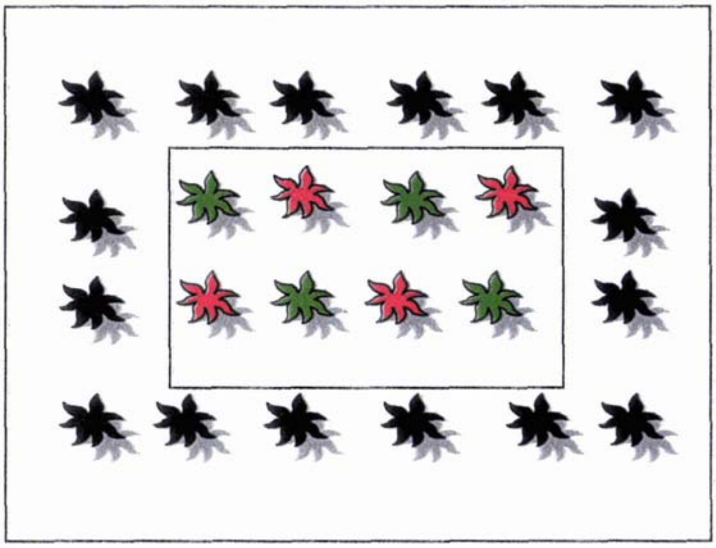


Figure 3.2. Plant layout in individual plots and dimensions.
Total plot: 0.60m x 0.80m.
Central area: 0.24m x 0.40m.
Black plants: border plants.
Red plants: labeled plants used for tiller dynamics measurements.
Red + green: central plants included in herbage accumulation measurements.

a)

b)

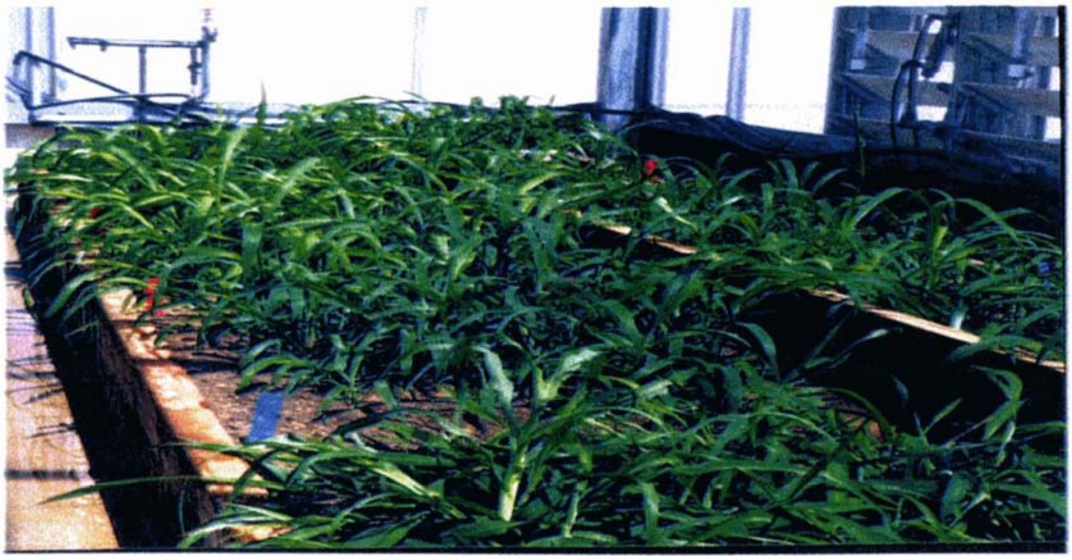


Plate 3.1. Overview of the experimental area (a) soon after transplanting, and (b) four weeks from transplanting.

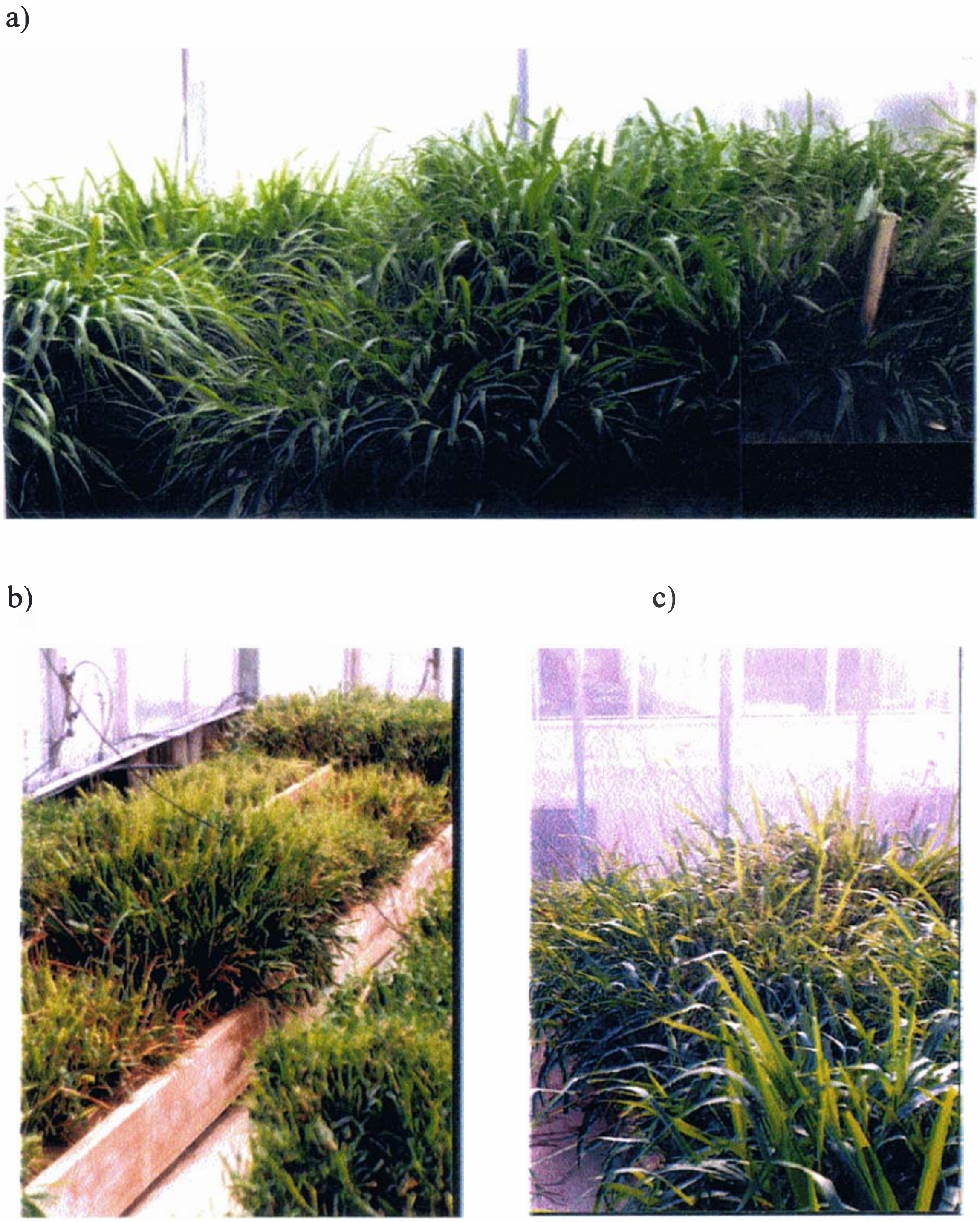


Plate 3.2. Three different aspects during experimental period (a) before harvest in summer; (b) after harvest, and (c) flowering.

3.3. Results

3.3.1. Temperature and light

Maximum and minimum temperatures recorded 1.7 m above ground level are shown in Figure 3.3 as TM-H and tm-H, respectively. Similarly, temperatures measured as sward height are shown as TM-s and tm-s. The variation between maximum and minimum temperature was lower in thermometers located at the sward level than for thermometers 1.7 m above ground. Averaged over all measurements, the maximum temperature was 34.6°C and the minimum, 15.3°C. Light measurements were not made continuously, but do establish the seasonal patterns of variation, even so. On sunny days, PAR inside the glasshouse ranged from approximately 5 MJ/m^2/day in June to approximately 20 MJ/m^2/day in December/January. Fitted curves indicating seasonal variation in temperature and mean daily radiation (MJ/ m^2/day) are also shown in Figure 3.3.

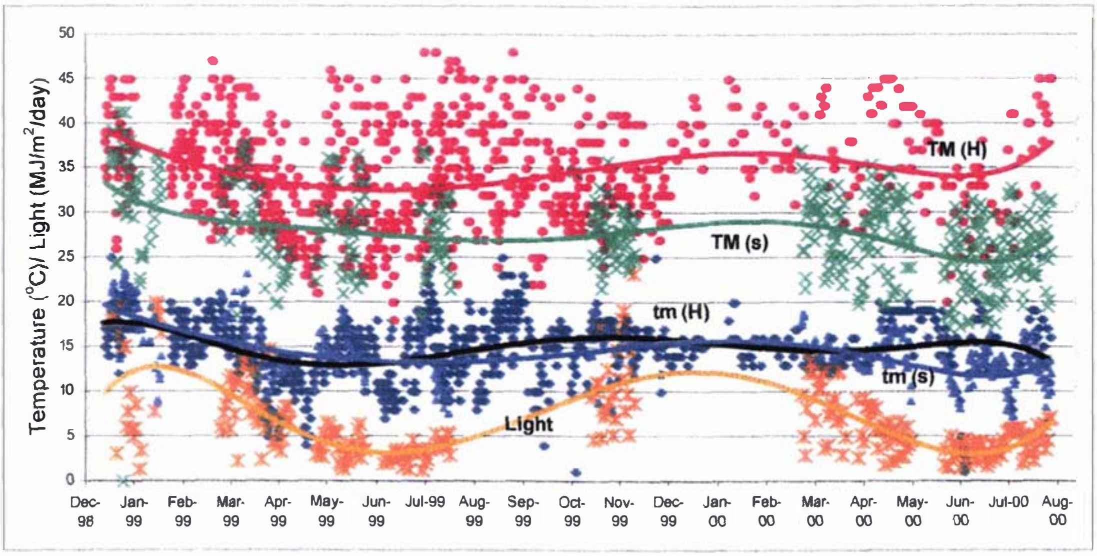


Figure 3.3. Maximum and minimum temperature (° C), and incident light (PAR) inside the glasshouse during the experimental period (January 1999 to August 2000). TM (H) and tm (H) are curves obtained from daily Max and min temperatures measured at 1.7 m from ground level; TM (s) and tm (s) are curves obtained from daily Max and min temperature measured at sward level. The lower curve is incident light (MJ/m^2/day).

3.3.2. Herbage harvested

Total herbage harvested over the entire 18 month experimental period was higher in cv. Mombaça than Tanzânia and Aruana (80200, 60910 and 60610 kg DM/ha s.e. 5669 kg DM/ha, $P < 0.05$) and plants cut to 300mm (HC) produced more than to those cut to 150mm (LC) (76060 and 58420 kg DM/ha s.e. 4628 kg DM/ha, $P < 0.05$). There was no cultivar x cutting height interaction ($P > 0.05$), although there were some trends indicating a possible interaction, especially in the second summer and autumn where cv. Mombaça plants seemed to be less sensitive to LC treatment than cv. Aruana and Tanzânia (Figure 3.4). Figure 3.5 presents seasonal herbage accumulation rates calculated from data in Fig 3.4. Repeated Measures analysis revealed a statistically significant season effect, as well as significant season x cultivar and season x cutting height interactions, but the season x cultivar x cutting height effect was not significant. Averaged over all treatments, summer herbage accumulation was 17870 kg DM/ha or 218 kg DM/ha/day, compared with 3990 kg DM/ha or 36 kg DM /ha/day in winter, 8400 kg DM/ha or 93 kg DM/ha/day in Spring, and 7450 kg DM/ha or 97 kg DM/ha/day in autumn.

Figure 3.6 shows the component yields (leaf, stem and total) in each harvest, comparing treatments HC and LC, for all three cultivars. It is clear that the contribution of stem to herbage harvested was greater in cv. Aruana ($P < 0.05$) than in the other two cultivars in both growing seasons, especially in treatment HC. Conversely, leaf production was greater ($P < 0.05$) in cv. Mombaça in both growing years than in the other two cultivars, especially under treatment LC.

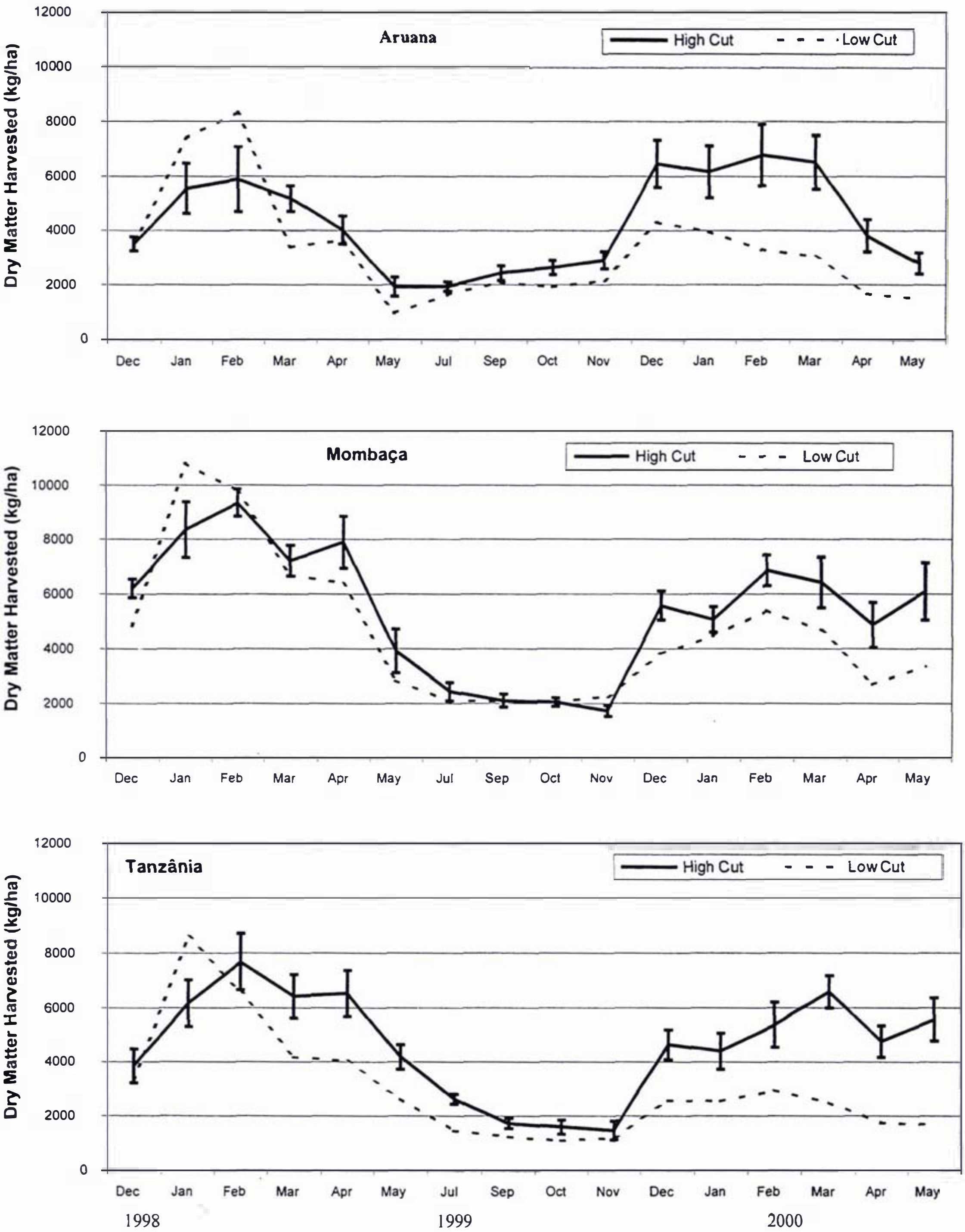


Figure 3.4. Dry matter harvested (kg DM/ha) above cutting height, by harvest, at 150 mm height (Low Cut) and 300 mm height (High Cut) in three *P. maximum* cultivars, Aruana, Mombaça and Tanzânia. (s.e. vertical bars).

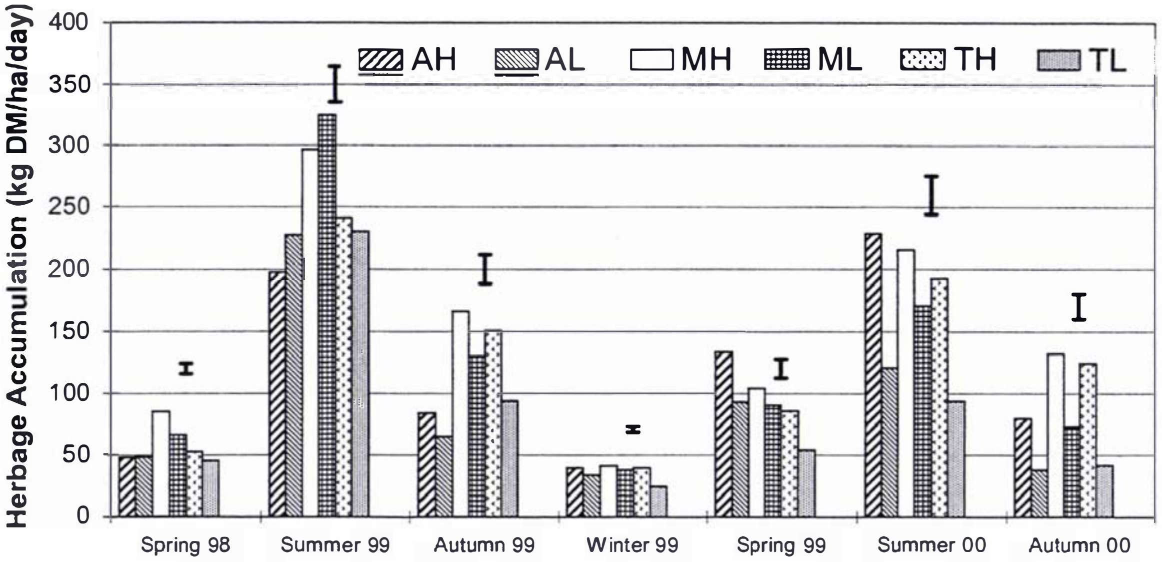


Figure 3.5. Herbage accumulation (kg DM/ha/day), in seven seasons (Spring 98, Summer 99, Autumn 99, Winter 99, Spring 99, Summer 00 and Autumn 00) in three *P. maximum* cultivars, Aruana (A), Mombaça (M) and Tanzânia (T), subjected to two defoliation heights: 150 mm (L) and 300 mm (H). (s.e: bars above the columns).

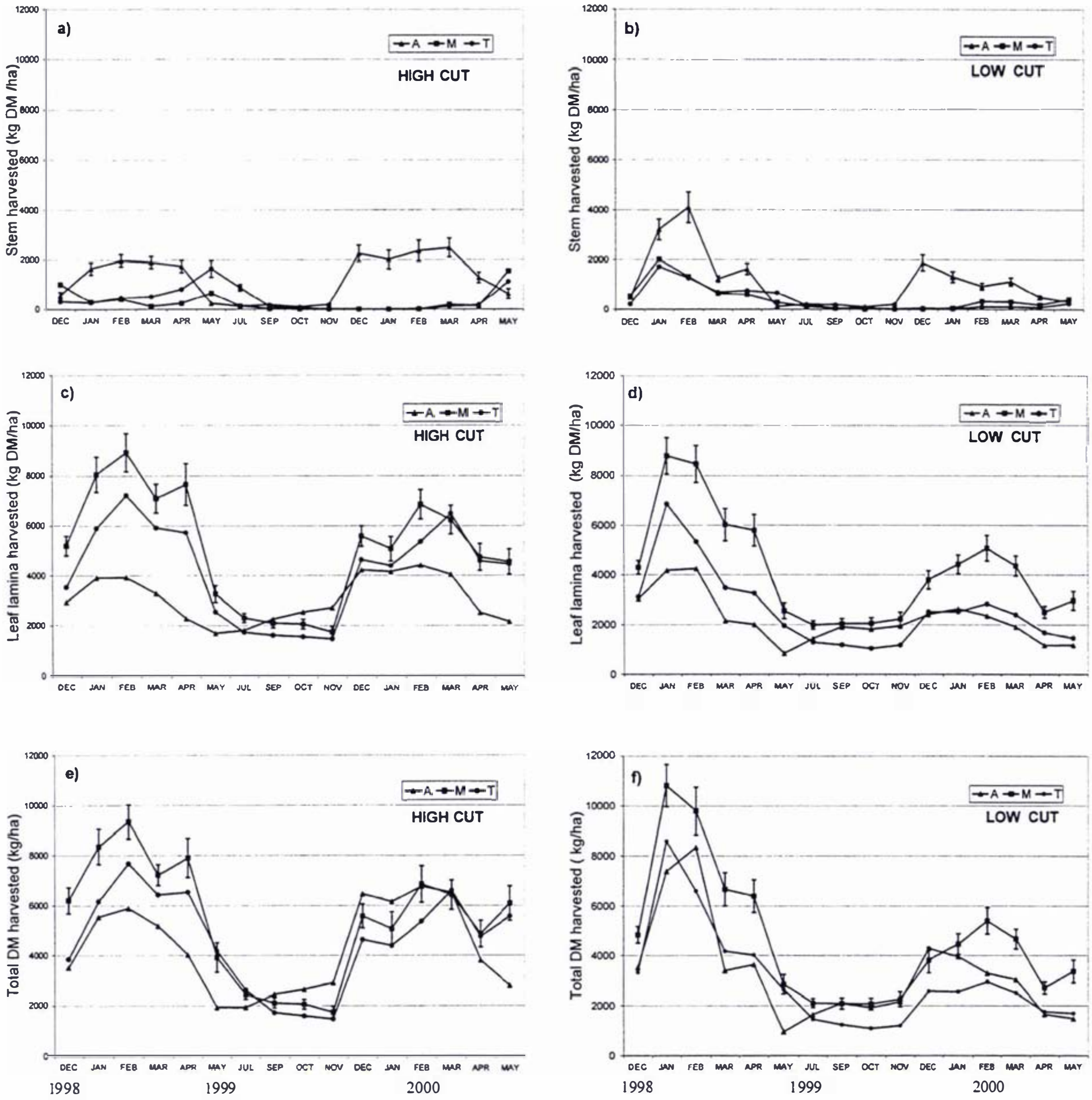


Figure 3.6. Stem (a b), leaf lamina (c, d) and total plant DM yield (kg/ha) (e, f) in Guinea grass cultivars, Aruana (A), Mombaça (M) and Tanzânia (T) under two cutting regimes: High cut (300 mm) (a, c, e), and Low Cut (150 mm), (b, d, f) from December 1998 to May 2000. (s.e. vertical bars).

3.3.3. Specific leaf area

There were significant overall effects ($P < 0.05$) of both cultivar and cutting height on the average specific leaf area (SLA) for the whole experiment, but no interaction effect. Mean values for cultivars Aruana, Tanzânia and Mombaça were 278, 255 and 215 cm^2/g s.e. 2.8 cm^2/g respectively, while overall average SLA for the LC treatment was 259 g/m^2 compared with 240 cm^2/g (s.e. 2.3 cm^2/g) in the HC treatment.

In a Repeated Measures analysis across seasons, there were significant ($P < 0.05$) season and season x cultivar effects but not season x cutting height and season x cutting height x cultivar effects. Considering all cultivars and cutting heights, SLA was higher in autumn and winter with values range from 250 to 272 cm^2/g and lower in spring/summer (range from 232 to 242 cm^2/g) with this season effect more evident in cv. Mombaça than in the other two cultivars (Figure 3.7).

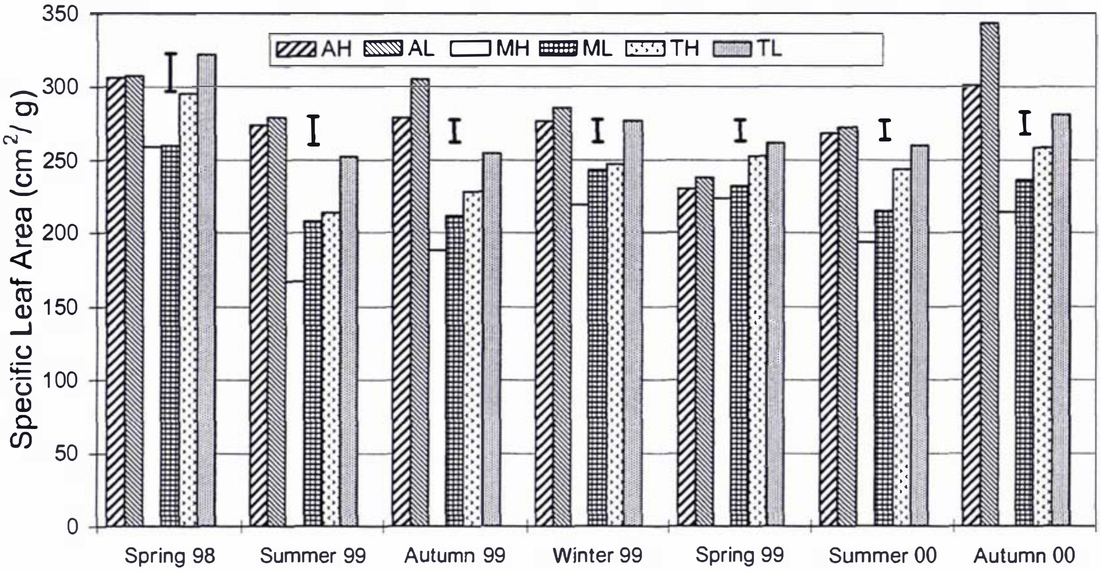


Figure3.7. Average specific leaf area (SLA), in seven seasons (Spring 98, Summer 99, Autumn 99, Winter 99, Spring 99, Summer 00 and Autumn 00) in three *P. maximum* cultivars, Aruana (A), Mombaça (M) and Tanzânia (T), subjected to two defoliation heights 150 mm (L) and 300 mm (H). (Bars above columns are s.e. for each season).

3.3.4. Tiller dynamics

A Repeated Measures analysis of TAR and TDR revealed time (i.e. season), time x cultivar and time x cutting height effects for both variables ($P < 0.05$), but no three-way interaction between time, cultivar, and cutting height effects (Appendices 3.1 and 3.2, and Figures 3.8 and 3.9. The overall mean from H1 to H16 for TAR showed no cultivar, cutting or interaction effect ($P > 0.05$). In the first evaluation in December 1998, before the initial harvest (Hi, see Table 3.1 for harvest dates) cv. Tanzânia had a higher TAR than cv. Mombaça (appendix 3.1) ($P < 0.001$), and also a higher tiller population density, with on average 46% more total tillers in Tanzânia than Mombaça (897 and 615 tillers /m^2 s.e. 301 tillers/m^2, Figures 3.8 and 3.9).

Flowering began in May 1999 (H5) and after this harvest, plants were harvested in July (H6) 60 days later. In winter 1999 (H7 and H8) there was a significantly ($P < 0.05$) higher TAR in cv. Tanzânia compared to Mombaça due to the formation of aerial tillers on decapitated flowering stems in cv. Tanzânia (Fig 3.10), which persisted until spring 1999 (H9). There was a greater TAR ($P < 0.05$) in cv. Tanzânia in the last harvest (H16) than in Mombaça, again related to formation of aerial tillers (Figure 3.10). Aerial tillers were very few in number or absent in cv. Mombaça.

Overall TDR was greater in the low cutting height for both cultivars, averaging 0.28 and 0.37 tillers/100 tillers/day in HC and LC, (s.e. 0.02 $P < 0.05$) respectively, (Appendix 3.2), but by harvest was only significantly different ($P < 0.0.5$) in H2, H3 and H15. TDR was greater in cv. Tanzânia than in Mombaça for both cutting heights after the second harvest in January 1999 (H1) (appendix 3.2) and cutting height effect was evident in February-March 1999 (H2/H3) and autumn 2000 (H15) where LC treatment had greater TDR than HC. This led to a lower tiller number, at the end of the experiment, in LC treatments compared to HC in both cultivars (1297, 3398, 878 and 1717 tillers/m^2 s.e. 494 tillers/m^2) in Mombaça, HC, Tanzânia HC, Mombaça LC, and Tanzânia LC, respectively.

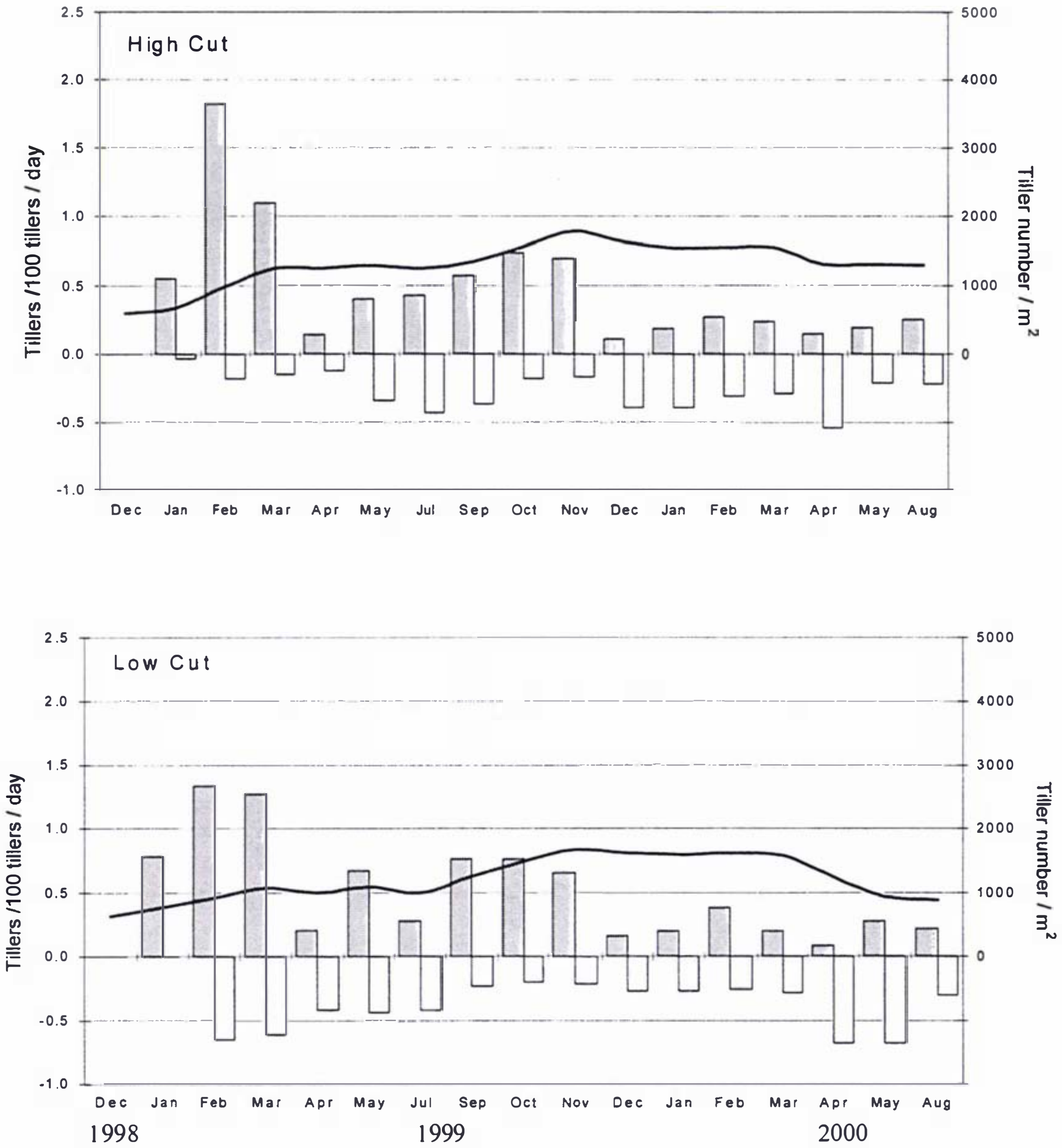


Figure 3.8. Tiller appearance rate (TAR, columns up), tiller death rate (TDR, columns down) and total tiller number (solid line) in Guinea grass, cv. Mombaça, under two defoliation levels: High Cut (300 mm height) and Low Cut (150 mm height) from December 1998 (Hi) to August 2000 (H16).

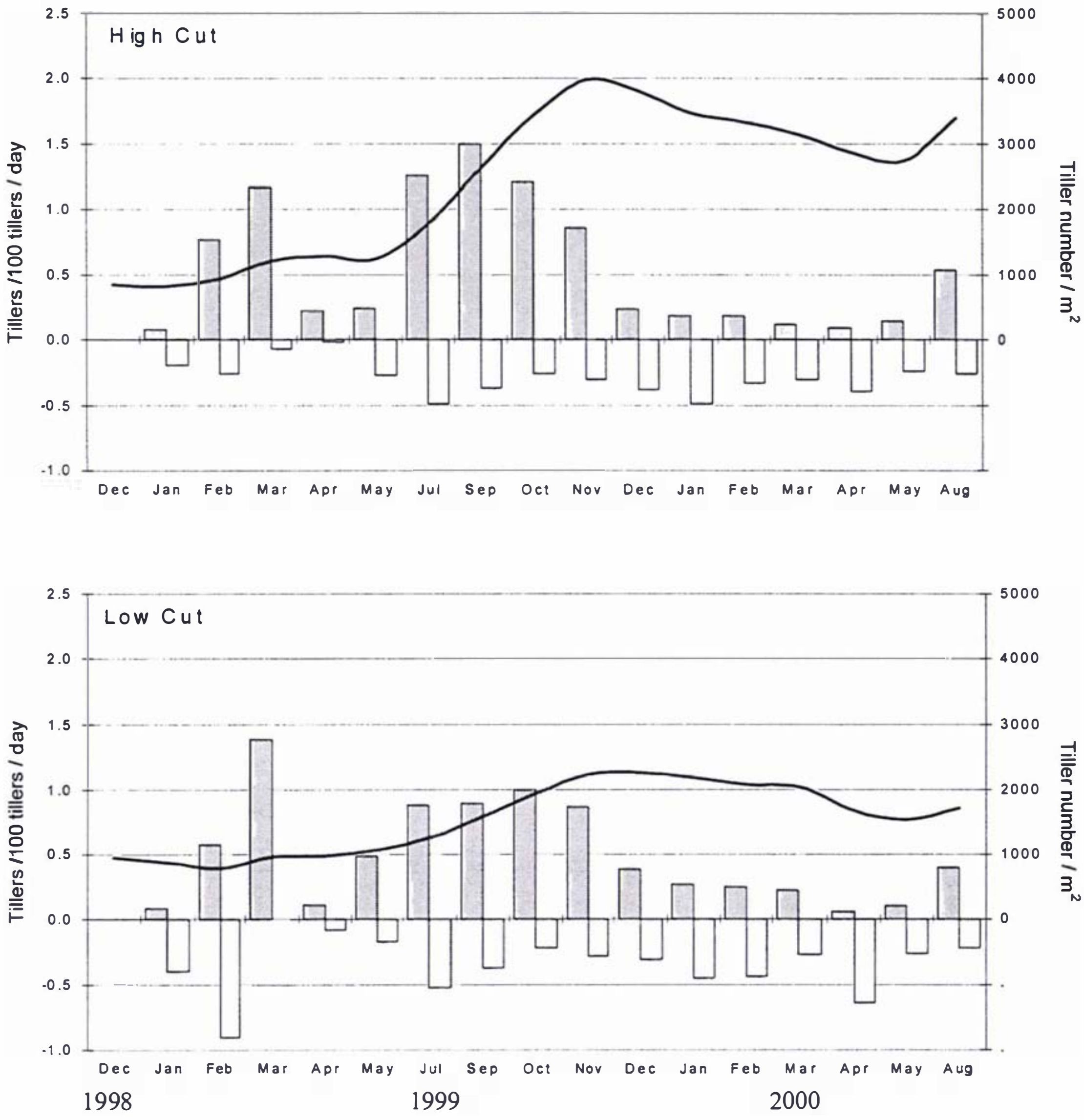


Figure 3.9. Tiller appearance rate (TAR, columns up), tiller death rate (TDR, columns down) and total tiller number (solid line) in Guinea grass, cv. Tanzânia, under two defoliation levels: High Cut (300 mm height) and Low Cut (150 mm height) from December 1998 (Hi) to August 2000 (H16).

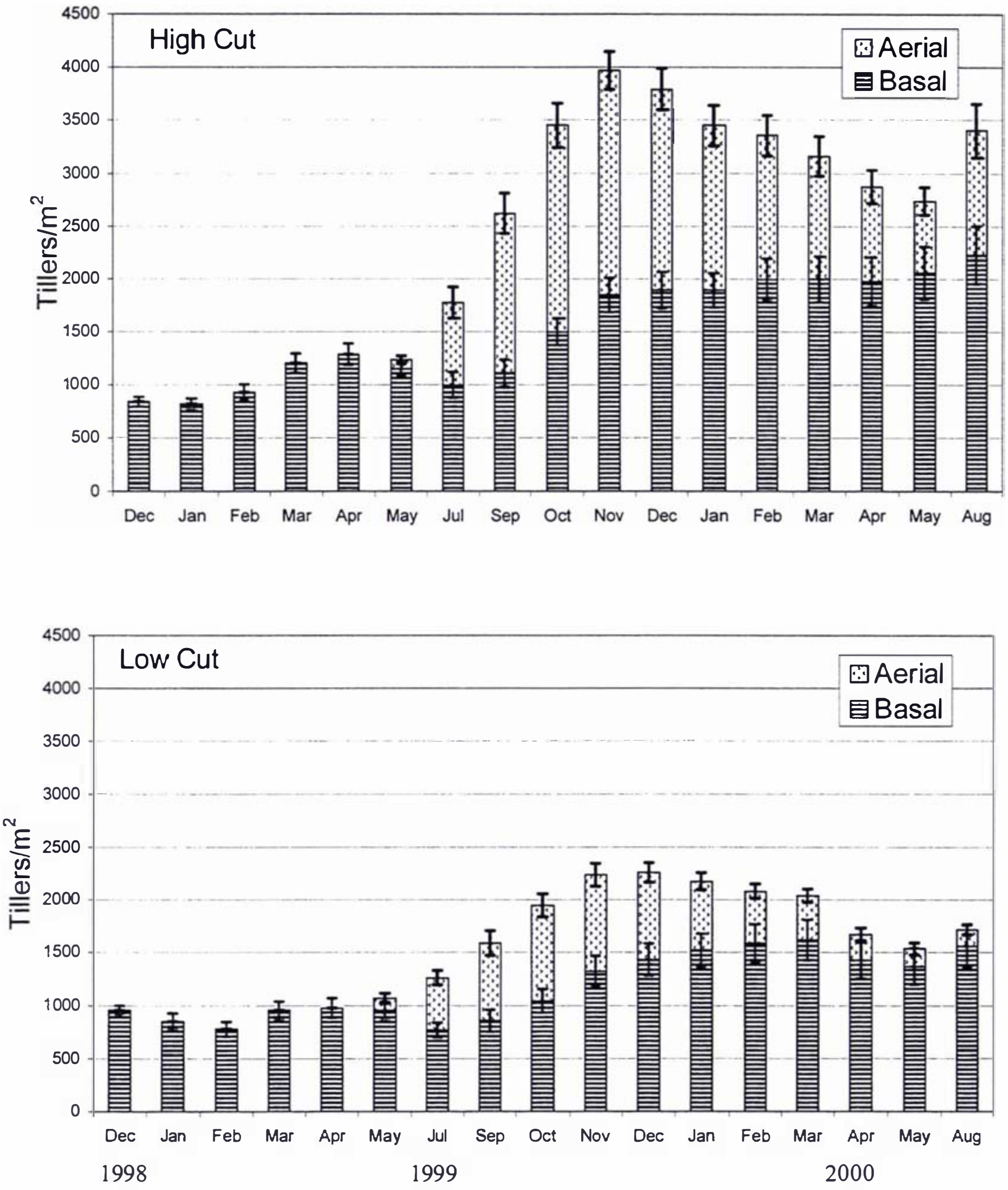


Figure 3.10. Total tiller number and distribution between basal and aerial tillers in Guinea grass cv. Tanzânia under two defoliation heights: High Cut (300 mm) and Low Cut (150 mm) from December 1998 (Hi) to August 2000 (H16). (Bars above column are s.e. for each month and each tiller category).

Table 3.2 shows seasonal change in total tiller population density, while Figures 3.11 and 3.12 indicate the contributions of the various age cohorts to the total density. There was a general increase in tiller number in both cv. Tanzânia and cv. Mombaça and in both cutting height treatments over the first year of the experiment, with a peak in tiller number in mid spring 1999 (H9) in all treatments, followed by a decrease in summer. It is clear cv. Tanzânia maintained, in general, a higher tiller population than cv. Mombaça and lenient defoliation, HC, also sustained more tillers than LC in both cultivars. Averaged from all harvests (Table 3.2) there was a interaction cultivar x cutting height effect ($P < 0.05$) where Tanzânia HC had more tillers than Tanzânia LC and Mombaça treatments HC and LC.

Table 3.2. Tiller number in two Guinea grass cultivars, Mombaça (M) and Tanzânia (T), under two defoliation heights, 150 mm (L) and 300 mm (H) over 17 harvests from December 1998 to August 2000.

	Treatments							
	MH	Ml	TH	TL		significance		
		(tiller number / m^2)			se.	cv.	cut	cv.*cut
Hi	597	633	840	955	58	***	ns	ns
H1	680	773	820	872	93	ns	ns	ns
H2	986	913	929	783	67	ns	*	ns
H3	1261	1069	1204	960	126	ns	*	ns
H4	1261	991	1287	975	216	ns	*	ns
H5	1297	1084	1245	1069	160	ns	ns	ns
H6	1255	996	1769	1261	291	ns	ns	ns
H7	1344	1250	2620	1587	278	**	*	*
H8	1567	1484	3455	1945	286	***	***	***
H9	1790	1670	3974	2231	296	***	***	***
H10	1629	1613	3813	2262	321	***	***	***
H11	1541	1593	3470	2174	316	**	*	*
H12	1546	1619	3336	2075	392	***	*	*
H13	1546	1572	3159	2039	390	**	ns	ns
H14	1312	1240	2874	1670	412	***	*	ns
H15	1302	934	2744	1536	411	***	*	ns
H16	1297	878	3398	1717	494	***	*	ns
Mean	**1306**	**1195**	**2408**	**1538**	**151**	***	**	*

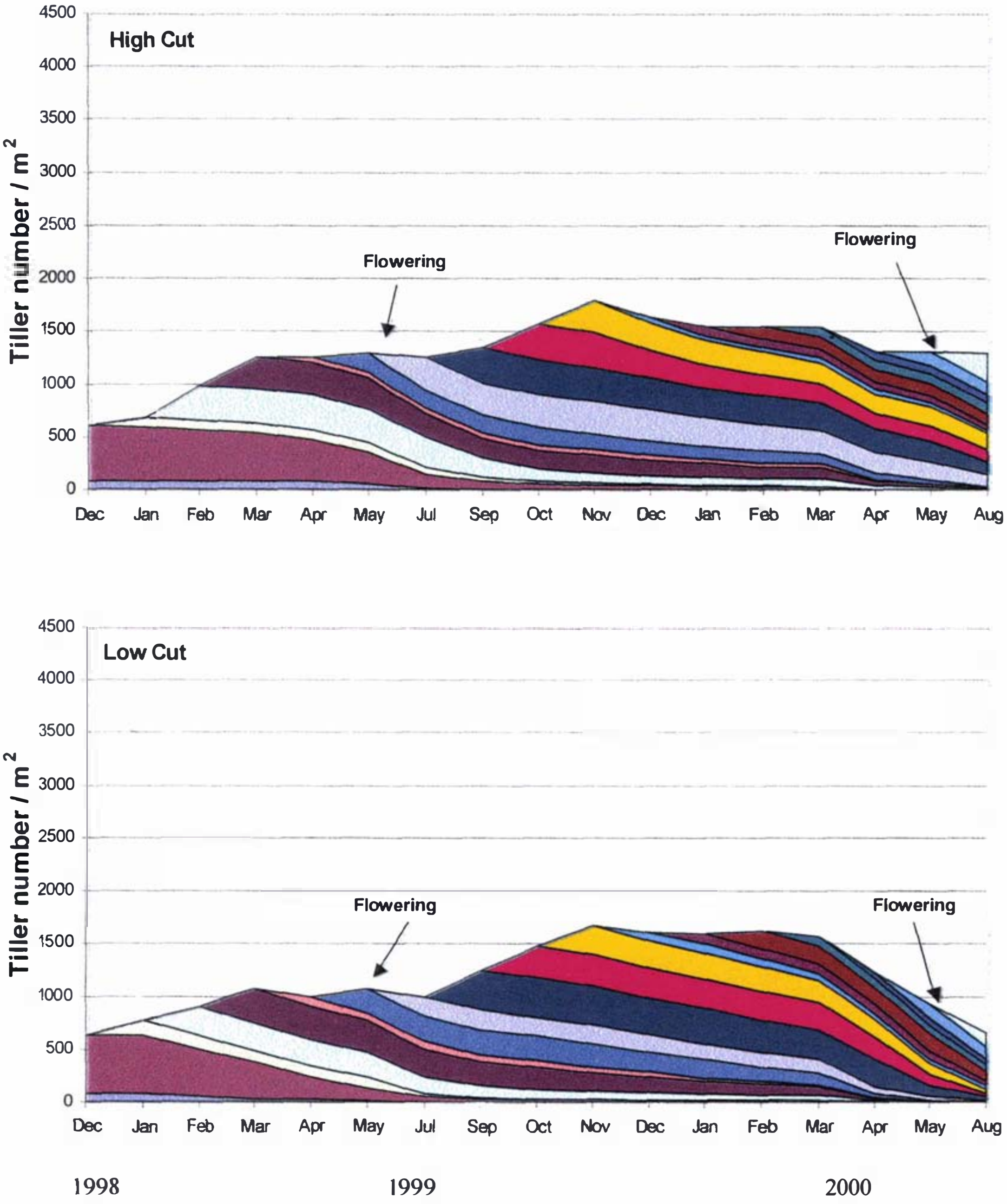


Figure 3.11. Appearance and survival of cohorts of marked tillers in Guinea grass cv. Mombaça, under two defoliation heights: High Cut (300 mm) and Low Cut (150 mm) from December 1998 to August 2000.

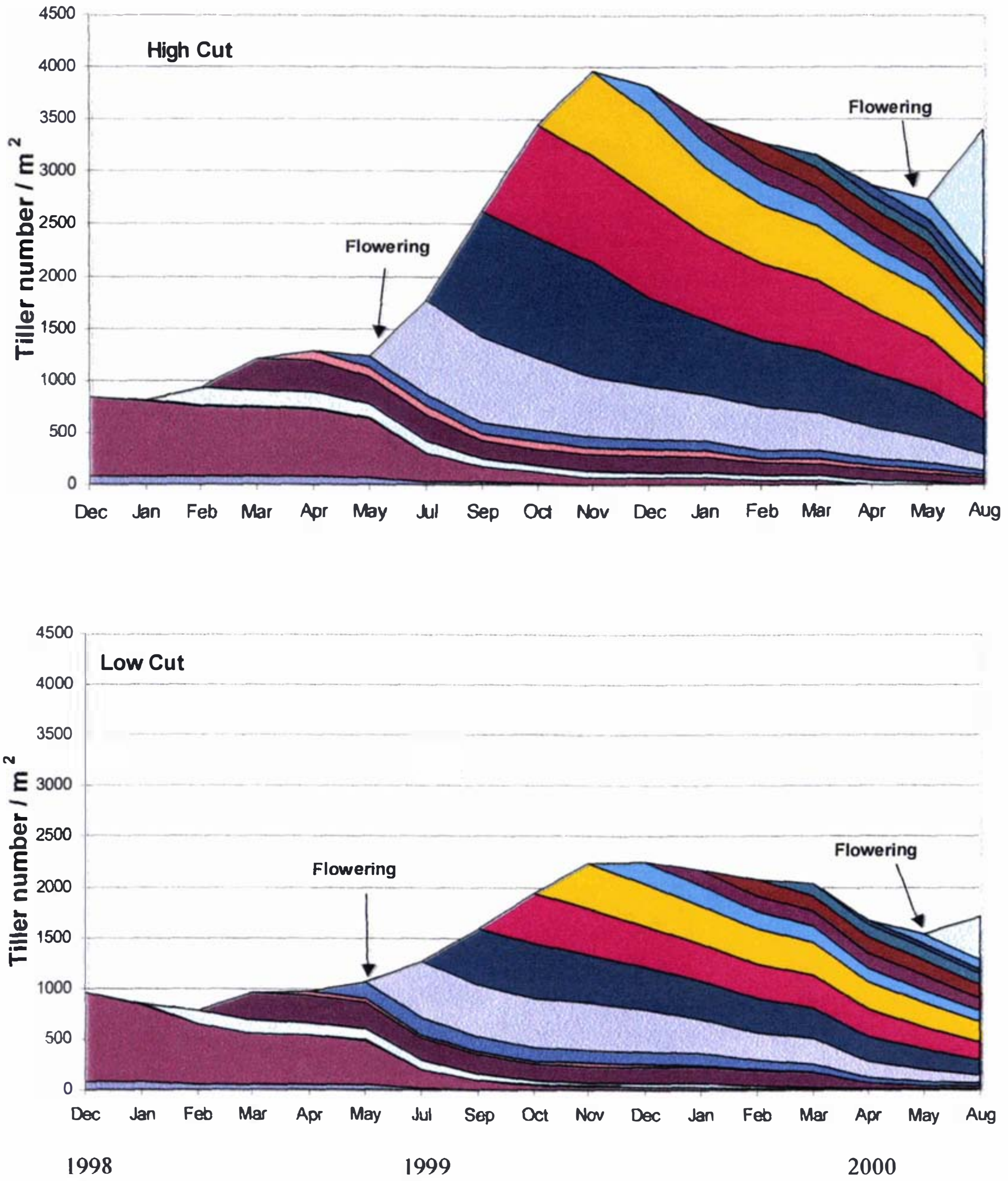


Figure 3.12. Appearance and survival of cohorts of marked tillers in Guinea grass cv. Tanzânia under two defoliation heights: High Cut (300 mm) and Low Cut (150 mm) from December 1998 to August 2000.

Figures 3.11 and 3.12 are essentially survival diagrams built up from counts of the number of tillers remaining in each cohort at successive measurement dates. The slopes of the lines indicate TDR for each cohort in measurement period, but are visually misleading because TDR within a cohort tends to decrease as the number of remaining tillers declines. To correct for this effect, and to assist interpretation of Figures 3.11 and 3.12 by allowing assessment of survival probability (i.e. relative TDR), tiller survival diagrams (Figures 3.13 and 3.14) were devised, showing change over time in the natural logarithm of the number of tillers remaining in each cohort. The two main points revealed by this analysis are a high survival probability for young tillers, with little initial decline in tiller number in most cohorts during the first three measurements (a flat line indicates survival probability of 1.0 over the observation period), and secondly the high tiller losses from most cohorts in both Autumn seasons, particularly in the LC treatment.

Two methods were used to quantitatively test the data in Figures 3.13 and 3.14. First, a general linear model (GLM) was constructed to compute sums of squares for all the survival observations in the four diagrams in Figures 3.11 and 3.12 (486 observations), and to partition from the total sums of squares effects representing cutting height, cultivar, the cutting height by cultivar interaction month of birth (i.e. cohort), month of observation (i.e. season), age of the cohort (i.e. less than or greater than 3 months old). This was primarily to assess the comparative size of these different effects on tiller survival, not their statistical significance (see discussion below). Based on size of the sums of the squares, the model accounted for about half of the variation in survival probability, with the largest effect being season and the next largest tiller age (Table 3.3).

Secondly, to further explore the basis for the possible cultivar and cutting height effects in Table 3.3, the number of tillers remaining in each cohort was expressed as a percentage of the number initially tagged in that cohort (Table 3.4). This analysis indicated that tillers of Tanzânia tended to have a greater longevity than tillers of Mombaça in the current experiment, that tillers in High cut plots had a greater longevity than those in low cut plots, and that basal tillers of Tanzânia tended to have greater longevity than aerial tillers.

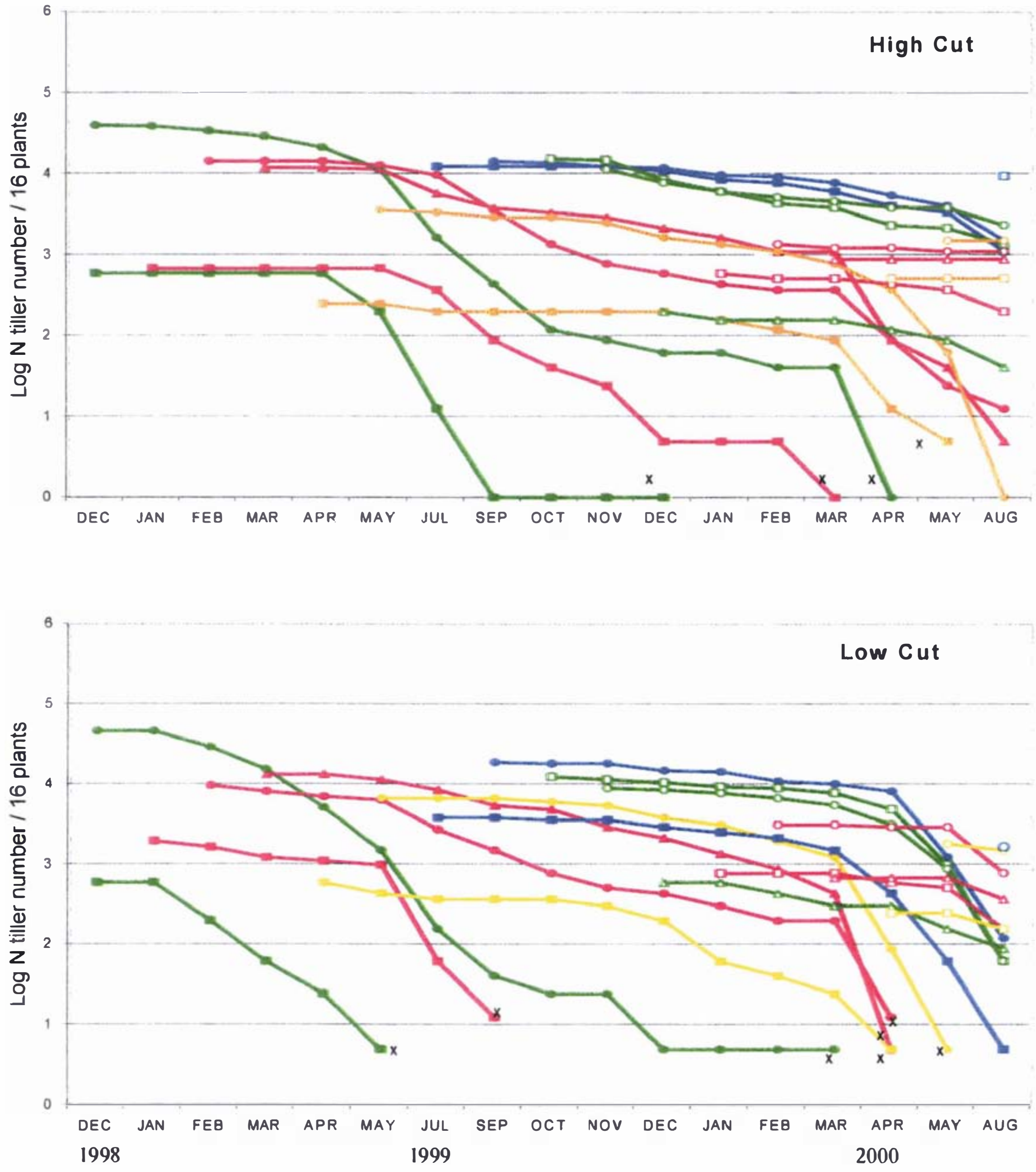


Figure 3.13. Diagram of tiller decay in Guinea grass cultivar Mombaça under two defoliation heights: High Cut (300 mm) and Low Cut (150 mm) from December 1998 to August 2000. Letter (x) means no tiller alive at specific cohort. Colour of the cohort lines are related to season of appearance: green=spring, red=summer, orange=autumn and blue=winter.

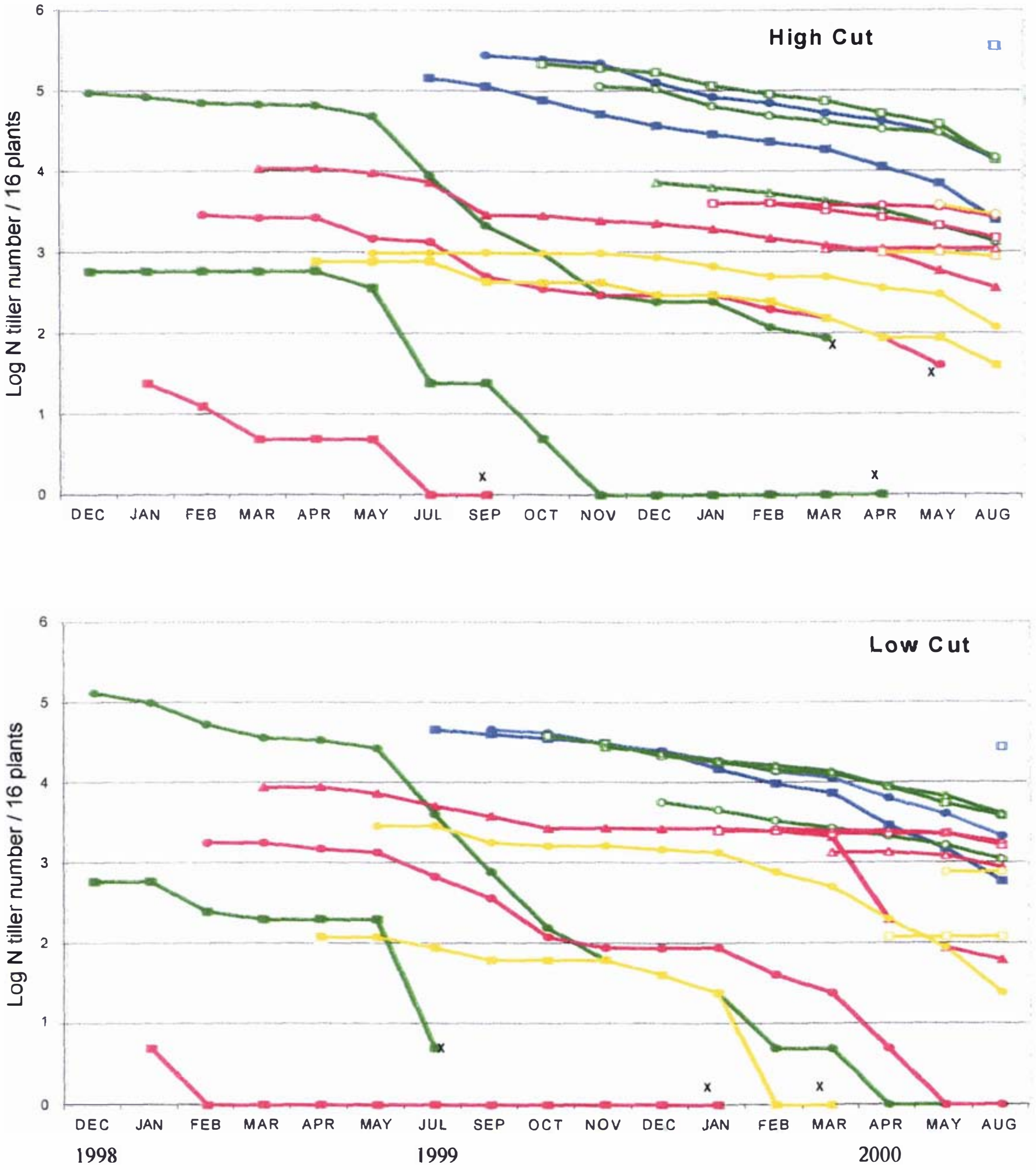


Figure 3.14. Diagram of tiller decay in Guinea grass cultivar Tanzânia under two defoliation heights: High Cut (300 mm) and Low Cut (150 mm) from December 1998 to August 2000. Letter (x) means no tiller alive at specific cohort. Colour of the cohort lines are related to season of appearance: green=spring, red=summer, orange=autumn and blue=winter.

Table 3.3. Analysis of variance for probability of tiller survival with six selected main sources of variation: cutting height (high and low), cultivar (Mombaça and Tanzânia), cohort (considering all cohorts tagged throughout the experimental period December 1998 to August 2000), age (older or younger than 3 months), month (consider the moth when the death occurred).

Source	DF	SS	MS	F
Cutting height	1	0.25797	0.25797	8.47
Cultivar	1	0.12765	0.12765	4.19
Cutting x cultivar	1	0.03411	0.03411	1.12
Cohort	16	1.77955	0.11122	3.65
Age	1	2.21611	2.21611	72.73
Month	9	7.25344	0.80594	26.45
Error	456	13.89514	0.03047	
Total	485	26.68302		

Table 3.4. Percentage of survival from each cohort at the end of experimental period (December 1998 to August 2000) in two Guinea grass cultivars, Mombaça and Tanzânia, under two defoliation levels High Cut (HC= 300 mm) and Low Cut (LC= 150 mm).

	Mombaça HC	Mombaça LC	Tanzania HC		Tanzania LC	
Tiller type	Basal	Basal	Basal	Aerial	Basal	Aerial
Tiller Cohort						
			% of survival			
Main	0.0	0.0	0.0	NP	0.0	NP
Hi	0.0	0.0	0.0	NP	0.9	NP
H1	0.0	0.0	0.0	NP	0.0	NP
H2	4.7	0.0	0.0	NP	6.2	NP
H3	3.4	0.0	22.2	NP	12.1	NP
H4	0.0	0.0	27.3	33.3	0.0	0.0
H5	2.8	0.0	66.7	14.3	28.6	4.6
H6	35.0	5.6	54.2	7.1	38.1	5.4
H7	37.5	11.1	54.2	13.3	54.8	1.7
H8	34.8	10.0	55.	8.4	58.3	5.0
H9	50.0	11.5	56.0	26.5	57.5	0.0
H10	50.0	43.7	76.5	15.4	61.1	21.1
H11	62.5	50.0	73.7	25.0	84.2	NP
H12	91.3	54.5	90.5	50.0	84.2	NP
H13	100.0	76.5	100.0	NP	78.6	60.0
H14	100.0	81.8	91.7	100.0	100.0	100.0
H15	100.0	92.3	85.7	100.0	100.0	100.0

NP: no produced

The number of tillers flowering in each cohort was counted before H5 and H6 (Autumn 1999) and before H15 and H16 (Autumn 2000). In the first year (Table 3.5.a) there were only six and seven generations tagged, and in the second year (Table 3.5.b) there were more generations available to flower. In general there was a higher percentage of flowering tillers in the first year than in the second year in both cultivars and in both cutting heights. The data suggest that cultivar Tanzânia had a higher percentage of flowering tillers (8%) than Mombaça (3%) and more tillers flowered in the High Cut treatment (9.4%) than in the Low Cut treatment (1.6%). In fact, in the second year very few tillers flowered in the Low Cut treatment.

Table 3.5. Total basal tiller number (16 plants) and percentage of flowering tillers for each cohort in two Guinea grass cultivars, Mombaça and Tanzânia, under two defoliation heights: High (300 mm) and Low (150 mm) from December 1998 (Hi) to August 2000 (H16).

a) Cumulative total from counts at successive harvests, May to July (1999);
b) Cumulative total from counts at successive harvests, May to August (2000).

a)		Mombaça High		Mombaça Low		Tanzânia High		Tanzânia Low	
Tagging month	Harvest	Total	%	Total	%	Total	%	Total	%
Dec 98	Hi	16	0.0	16	0.0	16	18.8	16	0.0
Dec98	Hi	99	7.1	106	1.9	146	29.5	168	6.5
Jan 99	H1	17	11.8	27	14.8	4	50.0	4	0.0
Feb 99	H2	64	20.3	54	1.9	32	43.8	26	7.7
Mar 99	H3	59	0.0	62	0.0	57	19.3	52	0.0
Apr 99	H4	11	0.0	16	0.0	18	5.6	8	0.0
May 99	H5	35	0.0	46	0.0	9	0.0	11	0.0
Jul 99	H6	60	0.0	36	0.0	39	0.0	33	0.0

b)		Mombaça High		Mombaça Low		Tanzânia High		Tanzânia Low	
Tagging month	Harvest	Total	%	Total	%	Total	%	Total	%
Jul 99	H6	60	0.0	36	0.0	39	15.4	33	0.0
Sep 99	H7	64	0.0	72	0.0	76	1.3	49	0.0
Oct 99	H8	66	3.0	60	0.0	95	1.1	57	0.0
Nov 99	H9	58	12.1	52	0.0	80	13.8	64	1.6
Dec 99	H10	10	10.0	16	0.0	27	3.7	29	0.0
Jan 00	H11	16	0.0	18	0.0	30	6.7	30	0.0
Feb 00	H12	23	0.0	33	0.0	34	2.	31	0.0
Mar 00	H13	19	10.5	17	0.0	21	0.0	22	0.0
Apr 00	H14	15	0.0	11	0.0	19	0.0	7	0.0
May 00	H15	24	0.0	26	0.0	33	0.0	17	0.0
Aug 00	H16	53	0.0	25	0.0	105	0.0	69	0.0

3.4. Discussion

3.4.1. Herbage accumulation and seasonal distribution

The cultivar Mombaça produced more forage DM than Tanzânia and Aruana in the whole experimental period, in agreement with a number of other results (Jank & Costa, 1990; Savidan et al., 1990; Cecato et al., 1996; Machado et al., 1997). There are exceptions to this result, however. Dias Filho et al. (1995) in a trial evaluating *Panicum maximum* cultivars in the Amazon region found that cv. Tanzânia was better adapted and yielded more than cv. Mombaça. Also Brâncio et al. (2000) found a lower yield and availability in cv. Mombaça when compared with cv. Tanzânia and Massai, and attributed this result to problems in recovery after grazing during a one year experiment.

Seasonal variation in pasture productivity has long been recognized in most regions of the world. This is due primarily to the variation in solar energy input and associated to changes in temperature, and also to regional variation in rainfall (Cooper & Taiton, 1968), but variation in the seasonal distribution of herbage production also varies with different species and cultivars (Pedreira, 1973; Behaeghe, 1974). According to Corsi & Santos (1995), one characteristic of *P. maximum* cultivars is the strong seasonal distribution in DM yield, as shown in Figures 3.5 and 3.6. Jank (1994) evaluating 401 *P. maximum* introductions, during two years in Campo Grande, Brazil, also found that relativity between spring/summer and winter herbage production was similar to that shown in Figures 3.5 and 3.6. The decrease in yield in the second summer and autumn compared to the first year in all cultivars (Figure 3.4) was more evident in treatment LC than in HC. A similar drop in production over time was also reported by Ghisi et al. (1989) evaluating six *P. maximum* cultivars, among them Aruana and Colonião, during two growing seasons. They observed a significant decline in total dry matter production in the second year, in all cultivars and over three N levels. These authors suggested that this could be due to less favourable climatic conditions in the second year or to the effect of the regular cuts at 250 mm height. Pedreira (1973) also describes a large drop (60 to 75%) from the first to the fifth year in total dry matter/year in an experiment with three tropical grasses, *Melinis minutiflora*, *P. maximum* cv. Colonião and *Hyparrhenia rufa*. Researchers agree the most likely reason for this pattern of response is the decline in nutrients in the soil (mainly N, P and K) since *P. maximum* is considered a grass with high nutrient demands (Monteiro, 1995; Vieira & Kichel, 1995) and application rates from 100 to 300 kg N, 30 to 100 kg P and 30 to 60 kg K per / ha per / year are described in literature (Monteiro, 1995). In the present trial, 50 kg / N and 30 kg /K/ha were applied after each harvest throughout the experimental period, and a complete liquid formula fertilizer (see Materials and Methods) was applied in the second year to avoid lack of nutrients mainly, P, S and micronutrients. This suggests that other factors besides lack of nutrients may have been involved in the productivity decline in the second year.

Considering the fact that tropical grasses have elongated internodes, even during vegetative growth, it is important to consider the proportion of stem as a component of the yield because animals normally reject this fraction, when grazing. Minson (1981) also suggests that it may be more valuable to quote separate yields for leaf and stem fractions.

In the HC treatment cv. Aruana yielded more than Mombaça and Tanzânia in the second growing season, (from October to March)(Figure 3.6 e). However the major component of yield in Aruana was the stem fraction, in contrast to the other two cultivars where this fraction was quite insignificant. In treatment LC Mombaça had a higher total yield in the second growing season, though Aruana still produced more stem than the other two cultivars (Figure 3.6 f).

The proportion of stem reflects both the genetic characteristics and growth habit of the plant. The latter can be affected by management strategies such as defoliation height and frequency: more lenient grazing and higher frequency of defoliation may increase the stem component in the grazed forage because it allows animals be more selective, preferably eating leaves rather than stem. Normally in tropical grasses older plants increase their stem component due to internode elongation in the growing season, so the frequency of defoliation is important. The defoliation interval should not be so long as to allow the stem fraction to elongate and be expressed as the main component of the yield. This is a very common observation in the literature on tropical grasses (Pedreira, 1973; Gomide et al., 1979; Andrade, 1987; Humphreys, 1991). In the first growing season there was a higher stem fraction in LC than in HC treatment in all cultivars (Figures 3.6 a, b). In the second growing season there was a change in pattern, probably due the adaptation or plasticity of the plants subjected to lower cutting height. Cv. Aruana produced a lower stem fraction in LC than in HC, and in cv. Tanzânia and in Mombaça this fraction was very reduced at both defoliation levels, increasing again only during the flowering period.

Another trait that differentiates Aruana from Mombaça and Tanzânia is that this cultivar exhibits internode elongations very early in the growing season (Carvalho D.D. et al., 1999), and its flexible stems produce numerous aerial tillers and roots. In field conditions these stems, through animal treading, can touch the soil and through the formation of roots establish a new plant, producing a dense sward that can quickly cover the ground surface (Cecato, 1993). This cultivar has been classified as stoloniferous (IZ, 1989) but according to Matthew et al. (2000) the structures formed by internode elongation of grass stems are not true stolons, and are better categorised in terms of the typical extent of internode elongation and their orientation with respect to the soil surface. In this trial, probably because of the absence of animal treading and because of a high density of aerial tillers, which also displayed internode elongation cv. Aruana formed a dense sward, at around 50 to 100 mm high in treatment LC and around 150 to 200 mm high in HC. The internode elongation in cv. Aruana also explains the high proportion of stem in this cultivar. This behaviour did not occur with the other two cultivars. Mombaça produced very few aerial tillers and at the same time did not exhibit internode elongation, (except that elongated internodes were evident in May, after the start of the flowering period). Cultivar Tanzânia produced numerous aerial tillers during the winter/spring season, most from internodes of decapitated flowering stems but they were small and with a very low stem / leaf ratio.

Gomide et al. (1979) working during three growing seasons with Guinea grass cv. Colonião, evaluating cutting heights (150 and 250 mm) observed that an increase in the height of the apical meristem can be determined by factors such fertilization, growth order, extension of clipping intervals, cutting height and age. These authors stated that for a given height of cutting, more meristems were eliminated, the older the plant at the time of clipping. However, successive low clippings, taken at the same plant age, did not necessarily result in higher elimination of apical meristems since such management tended to lower the height of the stem apices. This illustrates the concept of grazing avoidance (Briske, 1991) which accounts for the relative ability of plants to survive and grow in grazed systems. This plasticity, or change in morphology according to severity of defoliation stress seems to be more evident in cv. Mombaça and Tanzânia than in Aruana.

3.4.2. Specific leaf area

SLA is of interest in the context of these results as an indicator of morphological differences between cultivars and in response to defoliation intensity. In this experiment there was no destructive harvest (at soil level) and only data for biomass (leaves and sheath/stem fractions) above cutting height were available. In these circumstances, it was possible to measure only SLA as an indication of morphological response, since other parameters describing plant morphology require measurements of total plant biomass also (e.g. leaf area ratio, LAR and/or leaf weight ratio, LWR) (Hunt, 1990). SLA is widely used as an indication of response by plants to their environment, and is known to be sensitive to change in light regime (Lambers & Poorter, 1992).

Ludlow & Wilson (1971) evaluating *P. maximum* var. trichoglume cv. Green Panic leaves under effects of attenuated daylight through shade cloth (30 and 11% of the daylight) found that shaded leaves contained fewer, smaller and less densely packed cells and were thinner than unshaded (100% daylight) leaves. In the current experiment, it was found that winter leaves had higher SLA than summer leaves formed in higher light intensities (Figure 3.7) This trait was more evident in cv. Mombaça than in the other two cultivars with smaller leaves and with less necessity to have strong structure to maintain erect leaves. Lambers & Poorter (1992) describe some possible inherent traits that affect SLA plasticity in terms of chemical composition, anatomical differences such as smaller cell sizes, changes in the layer of palisade parenchyma or more support tissue.

Wilson (1976a) evaluating variation of characteristics in leaves at different levels of insertion in *P. maximum* var. trichoglume found a high negative correlation (-0.98) between leaf length and SLA, indicating that longer leaves had lower SLA. Mombaça is known to have longer and larger leaves than Tanzânia and Aruana (Jank, 1995), so it could be expected to have more structural tissue in its leaves. This then is a probable explanation for the significantly lower SLA (heavier leaves) observed in cv. Mombaça than the other two cultivars (Figure 3.7). Leaf length and width were not systematically measured in this experiment, but treatment LC produced, in general, smaller resulting in a higher average SLA than in HC, with more structural tissue to support long leaves. In this context, higher SLA probably indicates increased nutritive value of forage.

Significant negative correlations (ranging from 0.37 to 0.77, $P < 0.05$) were found between SLA and yield in this experiment for all three cultivars under both defoliation heights. This suggests that higher herbage accumulation in summer was partly responsible for the low SLA observed in summer, and the higher SLA in winter, and that these effects were not because of light effects alone.

These results contrast with Humphreys (1966) working with Guinea grass cv. Green Panic where SLA increased with increasing yield. However, in this case the author measured yield at only one harvest date but with different levels of nitrogen. Increased nitrogen level increased yield but at the same time increased SLA.

3.4.3. Tiller dynamics

There is a vast literature on Guinea grass describing data relating tillering and tiller population density under managements involving contrasts in frequency and intensity of defoliation, period of the year, nitrogen levels, etc (Pedreira, 1975a; Mecelis, 1979; Corsi, 1984; Andrade, 1987; Costa et al. 1992; Barbosa et al. 1997; Santos, 1997; Herling et al. 1998; Zimmer et al., 1999) but no data were found describing the dynamic processes of tillering (tiller appearance and death) in this grass species.

3.4.3.1. Seasonal effects on TAR and TDR

Cultivars showed broadly similar patterns of TAR, with highest tiller appearance during the establishment phase and in winter/spring 1999 (Appendix 3.1, Figures 3.8 and 3.9). Notably, in late winter and early spring of 1999 (H7, H8, H9), there was an increase in TAR in both cultivars and at both defoliation levels, leading to an increase in tiller population with a peak at H9. TDR varied from month to month, but not according to any discernible seasonal pattern (Appendix 3.2, Figures 3.8 and 3.9). Analysis of sources of variation in survival probability, closely related to TDR, showed the seasonal variation to be the largest single component, accounting for more than half the variation explained by the model (Table 3.3).

Pedreira (1975a) evaluating tillering in undefoliated plants of Guinea grass cv. Colonião, from November to July, observed two periods with low tillering rates: the end of summer/early autumn and late autumn/early winter. This author suggests possible causes could be the high growth rate in individual tillers during summer causing shading at the base of the plant, or apical dominance from the elongated tillers. In winter the low tillering rate would be due to the response of the plant after flowering. These results contrast with results from this experiment in the first year of evaluation where there was an increase in tillering in both periods mentioned by Pedreira (1975a) as periods of low tillering.

The reason for the high tillering in winter in New Zealand, compared with Brazil, is unclear. Winter is a period of lower rainfall in the central region of Brazil, and this may explain the low tillering in winter in the experiment of Pedreira (1975a). Conversely, low temperatures and associated reduction in leaf elongation may increase carbohydrate available for tillering.

In the present experiment, the occurrence of high TAR in the establishment phase seems intuitively logical, and high TAR at establishment would presumably occur regardless of season. Considering that light plays an important role in tiller initiation and survival of small tillers (Ludlow, 1978; Casal et al., 1990), we might expect high tiller death in autumn, as observed by Bahmani (1999) with perennial ryegrass. Some indications of high TDR in autumn are seen in Low cut swards, but not in High cut swards (Figures 3.8 and 3.9).

3.4.3.2. Cultivar differences

In the establishment period (Hi, Spring 1998) cv. Tanzânia had a TAR 46% higher than Mombaça (Appendix 3.1). This observation is in agreement with Gomide C.A.M. (1997) who also observed a higher tiller number per plant in cv. Tanzânia than Mombaça at 22 days from sowing in potted seedlings. In the two following harvests, however, cultivar Mombaça presented a higher TAR compared with Tanzânia (Appendix 3.1, Figure 3.9), resulting in similar tiller populations in both cultivars by the middle of the first Autumn (H5). TAR of Mombaça again exceeded that of Tanzânia in spring 1999 (Table 3.2) and formation of daughter tillers in Tanzânia (Figure 3.10) would have been partly responsible for this result.

Both of the quantitative survival analyses indicated a tendency for reduced survival of tillers in Mombaça compared with Tanzânia (Tables 3.3 and 3.4), but this was not statistically tested.

3.4.3.3. Defoliation regime

More intense grazing or cutting in grasses affects plant form and normally results in an increase in tiller number and decrease in tiller size, including leaves (Parsons, 1988; Matthew et al., 2000), although a number of researchers have reported reduction in tiller density under very intense defoliation (Bircham & Hodgson, 1983; Matthew et al., 1996; Hernandez-Garay et al., 1999). In this experiment tiller number was not significantly lower ($P > 0.05$) in the HC than in the LC treatment in cv. Mombaça, while in cv. Tanzânia, tiller number was greater in the HC treatment than in the LC treatment ($P < 0.05$). The survival analyses (Tables 3.3 and 3.4) also suggested the LC treatment adversely affected tiller survival, as well as reducing herbage production (Figure 3.5). Taken together, these results suggest the 150 mm defoliation regime was close to or beyond the tolerance limit of these cultivars, for sustainable dry matter yield. but cv Mombaça being more tolerant to LC than cultivars Tanzânia and Aruana (Figures 3.4 and 3.6 f)

3.4.3.4. Flowering

Jank & Savidan (1986) evaluating 156 *P. maximum* introductions, reported that 46% of their plant lines began flowering in May, and classified these as late flowering, while others flowered all year without any defined flowering period. In the current experiment, the flowering period started in the middle of autumn (H5 in 1999 and H15 in 2000), but after this harvest some plants were still flowering in winter (H6 in 1999 and H16 in 2000).

Following internode elongation in cultivar Tanzânia during flowering in autumn 1999, the initiation of aerial buds gave rise to a high population of aerial tillers, reaching in some periods more than 50% of the total tillers (Figure 3.10). The aerial tillers were fewer in number in the LC treatment, and never more than 50% of the total population. It is not clear if this was because of diminished carbohydrate status of LC plants, or reduced numbers of bud sites through lower cutting height.

The small number of tagged plants in this trial, together with a high variability in individual plants precluded a reliable statistical analysis of flowering behaviour. However, since there is no published information about tiller cohort flowering it was decided to present a descriptive data on trends in flowering behaviour in cv. Mombaça and Tanzânia across defoliation treatments (Table 3.5). Both cultivars flowered in the same period of the year (autumn) in both years. It seems that tillers produced at the end of spring (November) to middle of summer (December and January) showed a higher chance of flowering in autumn than tillers appearing in other periods of the year. Similar results were observed by Pedreira (1975b) with Guinea grass cv. Colonião. There was a higher flowering percentage in the first then in the second year as observed by Pedreira (1975b). This author recorded 76.5% of flowering tillers in the first year and 67.7% in the second. In the establishment period of any sward there is a high tillering rate and these tillers are strong and live longer (Nabinger & Medeiros, 1995). In this study, a higher percentage of tillers flowered in cv. Tanzânia than cv. Mombaça at both cutting heights. This arose from both a higher proportion of flowering tillers in each cohort, but also a wider age range of tillers flowering. This information needs to be corroborated in field conditions, although some observations (Da Silva, personal communication) indicate that cv. Tanzânia does produce more flowering tillers than cv. Mombaça in field conditions, also.

It is well known that when the flowering period starts, there is simultaneously stem elongation, decrease in leaf production and leaf /stem ratio, and quality of the pasture decreases (Davies, 1988; Pearson & Ison, 1997). One objective of the farmer is to delay this process through management. This would require elimination or reduction of numbers in specific generations of flowering tillers through grazing, and consequently would prolong the growing season. It seems that one difficulty of cv. Tanzânia under lax defoliation is that this cultivar presents a high percentage of tillers that flower, in contrast to Mombaça with more specific flowering behaviour. Plants in the LC treatments did not flower but also showed a decline in herbage accumulation.

3.4.3.5. Quantitative analysis of survival probability

In previous studies, tiller survival diagrams such as those in Figure 3.11 and 3.12 have received little statistical analysis (Bahmani, 1999). The fitting of exponential decay curves (Korte, 1986) is one approach previously used but this method evaluates only variation in survival probability associated with membership of a particular age cohort. The analysis in Table 3.3 is a first step towards quantification of a range of other factors that clearly also affect tiller survival. Survival probabilities used in that analysis are not biased by the reducing number of survivors in a cohort as the cohort ages. However, it is recognized more sophisticated statistical analysis, beyond the scope of this study, is needed to deal with repeated measures effects and confounding arising from imbalance of numbers of observations, for different terms in the model.

3.4.3.6. Tiller population density as a determinant of herbage production

Increase in sward productivity is defined by two yield components tiller number and weight, and the inverse relationship between tiller weight and tiller number has been established for long time (Langer 1963; Bircham & Hodgson, 1983). However, either tiller number or tiller weight may be more important in determining productivity, depending on circumstances (Nelson & Zarrough, 1981).

With the possible exception of the establishment period, the relationship between tiller population density and yield was weak in this experiment and can be visualise graphically in Appendix 3.3 where results from herbage harvested of Mombaça and Tanzânia (Figure 3.4) was put together with tiller number from Table 3.4. On a seasonal basis, tiller densities were highest at a time of lower productivity (winter/ spring 1999), and the more productive cultivar, Mombaça, tended to have a lower tiller population density. Thus, it appears that in most situations higher productivity is associated with larger tiller size. This principle has been established for the temperate grass species perennial ryegrass where cv. Ellet swards has larger and fewer tillers and higher average yields than cv. Grassland Ruanui (Bahmani, 1999). In the second growing season (1999/20000, H11 to H14) tiller population density was higher than the previous year, yet the productivity declined. This suggests there would be value in quantifying the relative contribution of seasonal production of the different tiller age class of tillers as suggested by Tallowin (1981). Such information might also be valuable to find out how rapidly new tillers develop to a point of contributing to productivity, and whether or not older tillers become inactive. This issue will be further evaluated in Chapter 5.

3.4.3.7. Perennation strategy

The age-cohort survival diagrams (Figure 3.11 and 3.12) allow visual evaluation of whether or not there is a particular perennation strategy underlying the seasonal and cultivar effects discussed above. The one consistent feature would appear to be the loss of older tillers in autumn, presumably through flowering, and the appearance of younger replacement tillers. However, the percentage of tillers flowering (Table 3.5) and the associated turnover of the tiller population are much less than that which occurred in *Phleum pratense* (Jewiss, 1966) and similar to that observed for another tropical grass, *Digitaria decumbens*, by Sbrissia et al. (1999). The role the aerial tillers play in cv. Tanzânia is not clear since it seems that persistence is more related to basal tillers than aerial tillers. One possibility is that aerial tillers provide a mechanism for temporary increase in LAI when environmental conditions are appropriate, with less investment in stem tissue.

3.5 Conclusions

The experiment has demonstrated that there are differences in herbage production, and sward structure (as indicated by measurements such as SLA, tiller mean weight, and tiller population density), with cv. Mombaça yielding 32.3 and 31.7% more DM/ha than Tanzânia and Aruana, respectively.

- The HC treatment produced 30.2% more herbage than the LC treatment with increased tiller death in the LC treatment and some indications that cv. Mombaça tolerated LC more than cv. Tanzânia.
- There were also seasonal effects on TAR and TDR associated flowering, with more tillers flowering in cv. Tanzânia than cv. Mombaça.
- These observations at the sward level provide the basis for more detailed studies at the tiller level, to better understand the mechanisms and detail of the various responses observed.

CHAPTER 4: Leaf and tiller morphogenesis in three Guinea grass cultivars growing under two different environmental conditions.

4. 1. Introduction

Sward productivity and perenniality depend on the continuous development of leaves and tillers (Gomide, J.A., 1997) and factors affecting these processes have been studied for many years in temperate grasses (Ryle, 1964; Silsbury, 1970; Langer, 1979). In tropical grasses more attention has been paid to other aspects of regrowth such as survival of the apical meristem (Gomide et al., 1979; Favoretto et al., 1987; Herling, 1998; Coelho et al., 2000) levels of reserves (Botrel & Gomide, 1981; Herling et al., 1995) and number of growing points or buds after harvest (Belyuchenko, 1977).

Morphogenesis, defined as the dynamic process of generation and growth of plant parts, is expressed normally as the rate of appearance, expansion and senescence of plant organs. It can be considered that plants have a genetically programmed morphogenesis in which the rate of development is temperature dependent (Gillet et al. 1984, quoted in Lemaire & Agnusdei, 2000). In forage grasses, according to Bahmani et al. (2000) the morphogenetic leaf variables such as leaf appearance rate (LAR), leaf elongation rate (LER), leaf elongation duration (LED), final leaf length (FLL), and tiller appearance rate (TAR) are all interdependent (Figure 2.1). Leaf appearance rate plays a central role and controls both number of tiller buds produced and LED. A decrease in LAR leads to a decrease in tiller buds, since there is one bud in the axil of each leaf, but an increase in LED, resulting in longer leaves. However, tiller development depends on tiller bud activity. Davies (1974) first estimated the ratio of tillers produced: leaf production (site filling ratio) with a theoretical maximum of 0.69 (Neuteboom & Lantinga, 1989). More recently concepts of site usage (Skinner & Nelson, 1992) and nodal probability (Matthew et al., 1998) have been developed, defined effectively as the proportion of tiller buds that eventually form new tillers with a theoretical maximum value of 1.0

The results of the experiment described in Chapter 3 provided evidence of differences in aspects of tiller dynamics and sensitivity to defoliation in Guinea grass cultivars, but the management procedures adopted made it difficult to draw categorical conclusions about some of these contrasts. The two short-term experiments described in this Chapter provide more detailed information about leaf and tiller morphogenesis of the same three Guinea grass cultivars under defoliated or undefoliated treatments. This information is necessary to improve management practices and helps a better understanding and interpretation of experimental results with these grasses.

4.2. Materials and Methods

Experiment 1 (E1)

This experiment was carried out in a growth cabinet at the Institute of Natural Resources, Massey University, from April to August (16 weeks). Conditions were controlled with an ambient temperature range from 28-30°C, humidity around 80%, 24h photoperiod and average light intensity of 350 μmoles photons/m^2/s (5MJ/m^2/day).

Seeds of three Guinea grass cultivars (Aruana, Mombaça and Tanzânia) were sown in two-litre pots filled with sand and fertilised (6g/pot) with a slow release fertiliser (15% N, 4.8% P, 10.8% K, 1.2% Mg, 3.0% S, 0.4%Ca plus trace elements, B, Cu, Fe, Mn, Mo and Zn). Seven days after germination seedlings were thinned to four of similar size per pot. The first harvest was made after 28 days, followed by three further harvests at 21 day intervals. There were three defoliation levels: low cut, (50mm height, LC), high cut, (200mm height, HC) and no defoliation (continuous growth, CG). Plants were watered daily with tap water and 200 ml of a commercial nutrient solution (similar to that described in Chapter 3) was applied weekly to each pot after the first harvest.

Experiment 2 (E2)

This experiment was conducted in a glasshouse, located at the Plant Growth Unit, Massey University from mid September to mid December (12 weeks) in natural daylight (approx. 5 to 12 MJ/m^2/day) with diurnal temperature fluctuation from 15 to 25°C.

Seeds from the same cultivars as in Experiment 1 were germinated in a tray at 25°C, and after two weeks, four seedlings of similar size were transplanted to each of fifteen two-litre pots (five for each cultivar) filled with the same growth medium as in E1. All plants were allowed to grow undefoliated and were watered daily with tap water. Each week, 200 ml of the nutrient solution as used in E1 was applied to each pot.

4.2.1. Measurements

4.2.1.1. Herbage harvested and dry matter partitioning

Experiment 1

After each of the four harvests all herbage collected was separated into three fractions: leaf lamina, stem (leaf sheath, pseudostem and true stem) and senescent material and oven dried for 48 h at 60°C. Yield per tiller was calculated by dividing total dry matter harvested (above cutting height) by the total number of tillers present in each pot, counted before harvesting.

At the end of the experiment the labeled plants were destructively harvested and all tillers present were classified into one of the following eight categories: large (height > 200mm) main tiller, large primary tillers, large secondary and tertiary tillers, small (height < 200 mm) primary tillers, small secondary and tertiary tillers, aerial tillers from the main tiller, aerial tillers from primary tillers and aerial tillers from secondary and tertiary tillers. Each tiller category was separated into fractions leaf, pseudostem, true stem, and senescent material. These were oven dried for 48 h at 60°C and dry matter for each category was calculated.

Experiment 2

At the end of the experiment each plant was destructively harvested and tiller fractions (leaf lamina, pseudostem, stem and senescent material) were separated oven dried for 48h at 60°C, and weighed. Tillers were classified as: main tiller, primary tiller from each leaf insertion from the main tiller (tiller 1 from leaf one, tiller 2 from leaf two, and so on) and secondary tillers from the primary tillers.

4.2.1.2. Leaf and tiller turnover

Twice weekly, in both experiments, the number of leaves present on the main tiller (including the elongating leaf) and the number of tillers per plant was counted and the leaf length (mm) of all leaves on the main tiller was measured. From these data, it was possible to estimate:

LAR (leaf appearance rate) as the number of leaves which appeared per day on the main tiller, and expressed as leaves/ main tiller/day;

LER (leaf elongation rate) as the cumulative leaf length per tiller per day, expressed as mm leaf/day/main tiller;

FLL (final leaf length) expressed in mm/leaf lamina for each leaf on the main tiller;

LLS (leaf life span) as the period of time (days) between the date the tip leaf first appeared until it became fully senescent;

SF (Site filling) as the slope of the regression line of $\log_n$ tiller number per plant on cumulative leaf number on the main tiller;

In E1, only one plant per pot was randomly selected to make leaf measurements and tiller counts for site filling estimates. When calculating herbage harvested and its relationship to tiller number all plants in the pot were considered.

In E2 besides measurements on main tillers, LAR and LER were measured on one selected primary tiller (located at leaf 4 on the main shoot for all cultivars), following the same procedure. In this experiment, two plants per pot were selected to make leaf and tiller measurements in an attempt to decrease variance. Site usage was estimated through counting the number of tillers formed at each leaf position on the main tiller.

LAR and LER were compared over two periods: P1 (from week 2 (E1) or week 3 (E2) to week 7: "establishment") and P2 (from week 8 to week 12: "mature" plants) since these variables change throughout time. SF was estimated only in the second period since initial plots showed varying degrees of non-linearity in the first period, and this issue was not explored further.

4.3. Results

4.3.1. Leaf development and dynamics

Leaf Appearance Rate (LAR)

LAR was estimated over two periods in both experiments. In E1 (Table 4.1) the cutting height effect was analysed only for cv. Mombaça and Tanzânia, but not for cv. Aruana because the main tiller stopped producing new leaves due to elimination of the growing point in treatments HC and LC following early internode elongation in this cultivar. In E2, (Table 4.2) the analysis of variance for LAR was carried out separately for P1 and P2. Measurements were made on main tillers in both periods, but for one primary tiller only on each main tiller in P1 because successive tillers represent different physiological stages during the development of the plant.

In the establishment period, (P1) in E1 there was a cultivar effect ($P < 0.01$) but no cutting height or cultivar x cutting height interaction, although there was a tendency for lower leaf appearance rate in uncut plants than in cut plants in both cultivars. Conversely, in P2 there was a cutting height effect ($P < 0.05$) but no cultivar effect; the cultivar x cutting height interaction approached significance ($P = 0.07$). LAR was higher in P1 in E1 than the same period in E2 in uncut plants for all cultivars. In contrast, there was a tendency for a higher LAR in P2 in E2 than in E1 in uncut plants.

In E2, average LAR for all cultivars was 8% lower on primary tillers than on main shoots when compared over P1. There was a significant cultivar effect for both main tiller and primary tillers in P1 and for main tiller in P2. Uncut plants of cv. Aruana showed 7 to 29% higher LAR than cv. Mombaça and Tanzânia in both periods in E1 and higher LAR than cv. Mombaça in both periods of E2 ($P < 0.001$) but in E2 results for Aruana and Tanzânia were similar. Primary tillers from cv. Tanzânia showed a higher LAR than these from the other two cultivars.

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In E2, averaged LAR for all cultivars was 8% lower on primary tillers than on main shoots when compared over P1. There was a significant cultivar effect for both main tiller and primary tillers in P1 and for main tiller in P2. Uncut plants of cv. Aruana showed 7 to 29% higher LAR than cv. Mombaça and Tanzânia in both periods in E1 and higher LAR than cv. Mombaça in both periods of E2 ($P < 0.001$) but in E2 results for Aruana and Tanzânia were similar. Primary tillers from cv. Tanzânia showed a higher LAR than these from the other two cultivars.

Table 4.1. Leaf appearance rate, LAR, (number of leaves/tiller/day), on main tiller, in two periods: P1 (from week 2 to week 7, establishment) and P2 (from week 8 to week 12, mature plants) in three Guinea grass cultivars, Aruana (A), Mombaça (M) and Tanzânia (T) under three defoliation regimes, uncut (CG), cut at 200 mm high (HC) and cut at 50mm high (LC), in experiment E1.

P1	A	M	T	Average	P2	A	M	T	Average
CG	0.268	0.217	0.250	0.233	CG	0.129	0.100	0.114	0.107
HC	-	0.247	0.253	0.250	HC	-	0.107	0.150	0.128
LC	-	0.238	0.256	0.247	LC	-	0.171	0.157	0.164
cv. Average		0.234	0.253				0.126	0.140	
s.e. (Aruana)	0.010					0.007			
s.e. cv	0.004 **					0.008 ns			
s.e. cut ht.	0.005 ns					0.010 **			

ns (P > 0.05) ** (P < 0.01)

Table 4.2. Leaf appearance rate, LAR, (number of leaves/tiller/day), in two periods: P1 (from week 3 to week 7, establishment), on main and primary tiller, and P2 (from week 8 to week 12, mature plants) on main tiller of three Guinea grass cultivars, Aruana, Mombaça and Tanzânia, under continuous growing, in experiment E2.

	Aruana	Mombaça	Tanzânia	s.e.
P1- Main Tiller	0.191 a	0.166 b	0.200 a	0.003 ***
P1 Primary Tiller	0.164 b	0.157 b	0.188 a	0.003 ***
P2 Main Tiller	0.149 a	0.120 b	0.137 a	0.004 ***

Means followed by same letter on the rows are not statistically different (P > 0.05)

Leaf Elongation Rate (LER)

LER was measured at tiller level, i.e. all leaves elongating on the main tiller per day, and not for each leaf specifically. In E1, from week 8 to week 12, there was usually only one leaf elongating per tiller for cv. Aruana and Mombaça, but 1.2 leaves per tiller for cv. Tanzânia (P < 0.05). In E2 numbers of elongating leaves were 1.2, 1.0 and 1.1 for Aruana, Mombaça and Tanzânia, P < 0.05). LER estimates for individual leaves excluded the interval within which a leaf first appeared, and that in which elongation ceased. LER was also evaluated in two distinct periods, P1 and P2, as for LAR. In both periods in E1 there was a significant cutting height effect on LER ($P < 0.05$) but no cultivar effect, and no cultivar x cutting height interaction (Table 4.3), though cv. Mombaça showed a trend to have the highest LER in both periods. Cv. Aruana could only be evaluated in treatment CG because of removal of main tiller apical meristems when defoliating this cv. Flowering in cv. Aruana in the second period may be the cause for lower LER compared to the other two cultivars. In E2, there was no cultivar effect in P1 for main shoot or primary tillers (Table 4.4); in P2, cv. Aruana showed higher LER than the other two cultivars, but differed statistically ($P < 0.05$) only from Tanzânia. Also in E2, primary tillers averaged 30% greater LER than main tillers in P1. Comparing uncut plants in both experiments, LER was almost two times greater in E1 than in E2 in P1 for all cultivars. Comparing mature plants in P2, LER was 30% lower in E2 than E1 in Mombaça and Tanzânia plants, but somewhat greater (9%) in cv. Aruana.

Table 4.3. Leaf elongation rate, LER, (mm leaf/tiller/day), on main tillers, in two periods: P1 (from week 2 to week 7, establishment) and P2 (from week 8 to week 12, mature plants) in three Guinea grass cultivars, Aruana (A), Mombaça (M) and Tanzânia (T), under three defoliation regimes: uncut (CG), cut at 200 mm high (HC) and cut at 50 mm high (LC), in experiment E1.

P1	A	M	T	Average	P2	A	M	T	Average
CG	73.0	73.5	71.8	72.6	CG	57.5	84.0	75.7	79.8
HC	-	69.1	58.4	63.7	HC	-	73.1	77.8	75.4
LC	-	66.8	63.1	64.9	LC	-	71.3	57.9	64.2
cv. average		69.8	64.4				76.1	70.4	
s.e. (Aruana)	2.0				2.1				
s.e. cv	1.9 ns				3.1 ns				
s.e. cut ht.	2.3 *				3.7 *				

ns ($P > 0.05$) (*) ($P < 0. 05$)

Table 4.4. Leaf elongation rate, LER, (mm leaf/tiller/day), in two periods: P1 (from week 3 to week 7, establishment), on main and primary tillers, and P2 (from week 8 to week 12, mature plants) on main tillers only of three Guinea grass cultivars, Aruana, Mombaça and Tanzânia, under continuous growth, in experiment E2.

	Aruana	Mombaça	Tanzânia	s.e
P1- Main Tiller	34.6	32.8	33.3	1.4 ns
P1 Primary Tiller	45.1	43.4	41.8	1.5 ns
P2 Main Tiller	62.9	58.4	51.0	2.1**

ns ($P > 0.05$) ** ($P < 0.01$)

Leaf Life Span (LLS)

LLS, in days (Figure 4.1) was evaluated until leaf number 12 (L12) in all cultivars in E1, and to L6 in cv. Mombaça and L8 in cv. Aruana and Tanzânia in E2, for two reasons. In E1, the experimental period was longer (16 weeks) than in E2 (12 weeks) and also average LAR and senescence were lower in E2 than in E1. In E1, LLS was not more than 20 days up to L7 in all cultivars. From L8 on there was a trend to increase LLS with leaf number in all cultivars but the effect was most evident in cv. Mombaça. On average, LLS was 22, 21 and 18 days (s.e. 2.1 days, $P < 0.05$) for Mombaça, Tanzânia and Aruana, respectively. In E2, there was the same trend: Mombaça showed a higher LLS at almost all leaf positions with values 45, 40 and 39 days (s.e. 1.1 days, $P < 0.05$) for Mombaça, Tanzânia and Aruana, respectively. LLS was substantially greater in E2 than in E1.

Final Lamina Length (FLL)

Leaf lamina lengths for all fully elongated leaves in sequence of insertion on the main tiller are shown in Figure 4 2. for uncut plants. In E1 there were minor differences in leaf length among the three cultivars until L7, but from L8 up to L15 Mombaça showed longer leaves than Tanzânia and Aruana in all levels of insertion and the average leaf length was 437, 322 and 265 mm (s.e. 50.7 mm $P < 0.05$) for Mombaça, Tanzânia and Aruana, respectively. In E2, cv. Mombaça showed significantly ($P < 0.05$) longer leaves than the other two cultivars for most insertion levels up to L12.

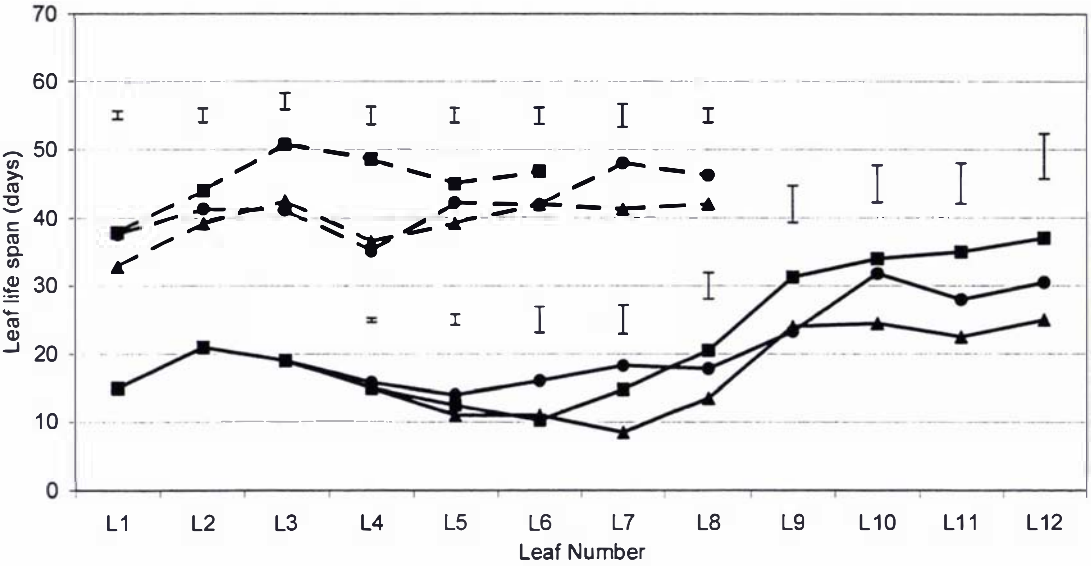


Figure 4.1. Leaf life span, LLS, (days) in sequential leaves in three Guinea grass cultivars Aruana (▲), Mombaça (■) and Tanzânia (●) in experiments **E1 (solid lines)** and **E2 (dashed lines)**. Bars above lines are s.e. for each leaf number in E1 and E2.

Averaged from L1 to L12, Mombaça had longer leaves followed by Tanzânia and Aruana (332, 243 and 222 s.e. 38.6mm $P < 0.05$). On average, FLL in cv. Mombaça and Tanzânia was 12% lower in E2 than in E1, while in cv. Aruana FLL was about 8% greater in E2 than in E1.

The effect of cutting treatments on FLL in E1 was evaluated in Mombaça and Tanzânia only because all measurements were made on main tillers and in cv. Aruana the main tiller stopped producing leaves due to elimination of the growing point in treatments HC and LC following early internode elongation in this cultivar. Since the interval between harvests was 21 days not all leaves were fully elongated at harvest, and comparisons are based in data from L10 to L15 for cv. Mombaça and L11, L12, L4 and L15 for Tanzânia. Averaged over all leaf positions, there was a significant effect of cutting height on FLL (CG > HC > LC, 694, 501 and 407mm, respectively, s.e. 49.4 mm $P < 0.05$) and cv. Mombaça seemed to be more sensitive to defoliation than Tanzânia. The average FLL for the CG treatment was 48% and 91% greater than for HC and LC (775, 522 and 405 mm) in cv. Mombaça, and in cv. Tanzânia the proportions were 22 and 40 % (575, 469 and 409 mm).

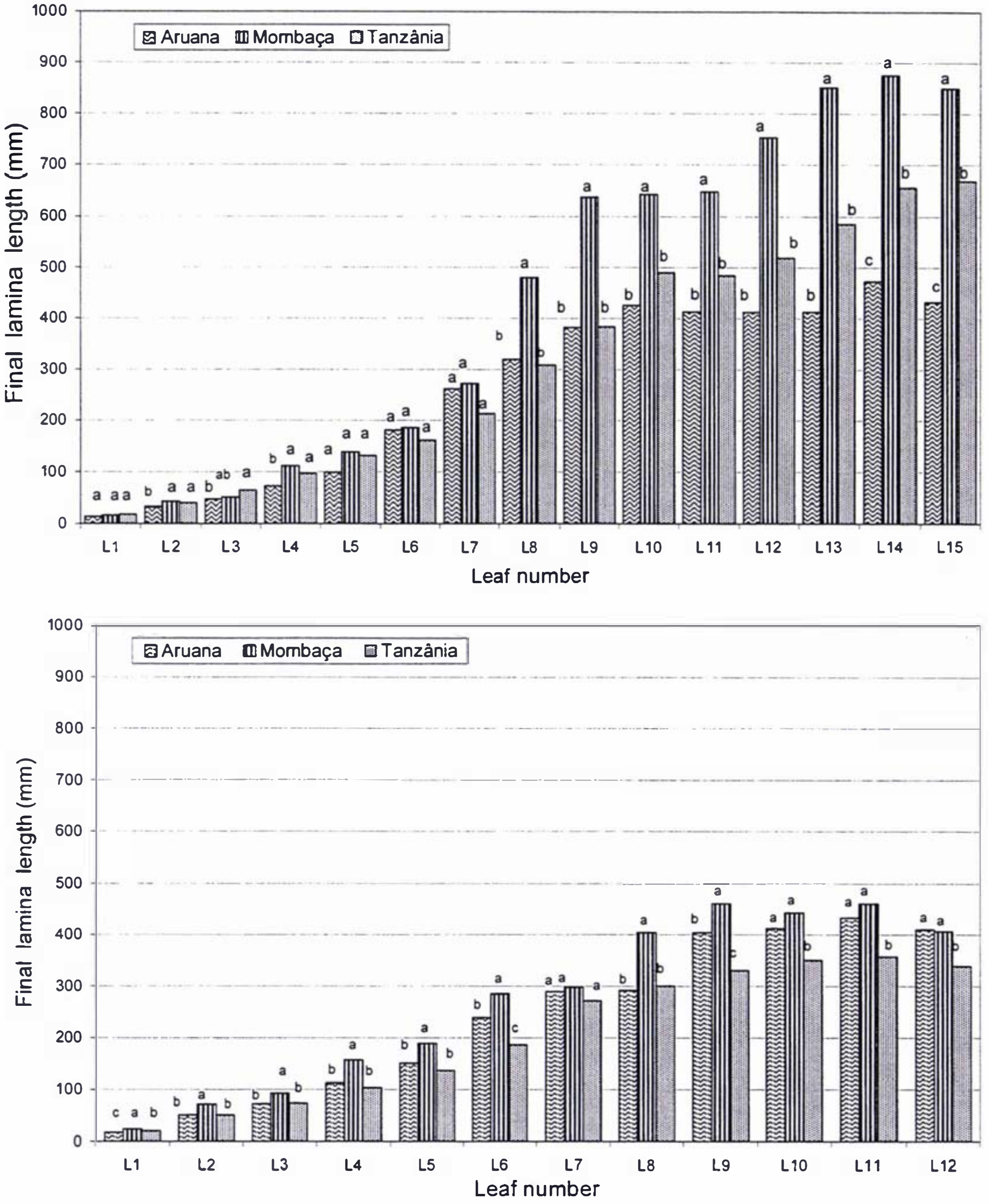


Figure 4.2. Final lamina length, FLL, (mm) in Aruana, Mombaça and Tanzânia, Guinea grass cultivars in Experiment **E1 (top)** and Experiment **E2 (bottom).** Columns within leaf number with the same subscript are not significantly different ($P > 0.05$).

Number of live leaves (NLL)

The numbers of green leaves per main tiller (NLL) in E1 and E2 are shown in Figure 4.3. There were no significant cultivar differences overall in either experiment, but NLL was consistently higher in E2 than in E1 (6.0, 5.8 and 6.3, s.e. 0.38) and 4.3, 3.9 and 4.2, s.e 0.24) for Aruana, Mombaça and Tanzânia, respectively. The trend to increase NLL in cv. Aruana after week 9 in E1 was probably due to its precocious development behaviour where, at week 12, all plants were flowering and smaller leaves (flag leaf included) were produced, resulting in more leaves on main tiller.

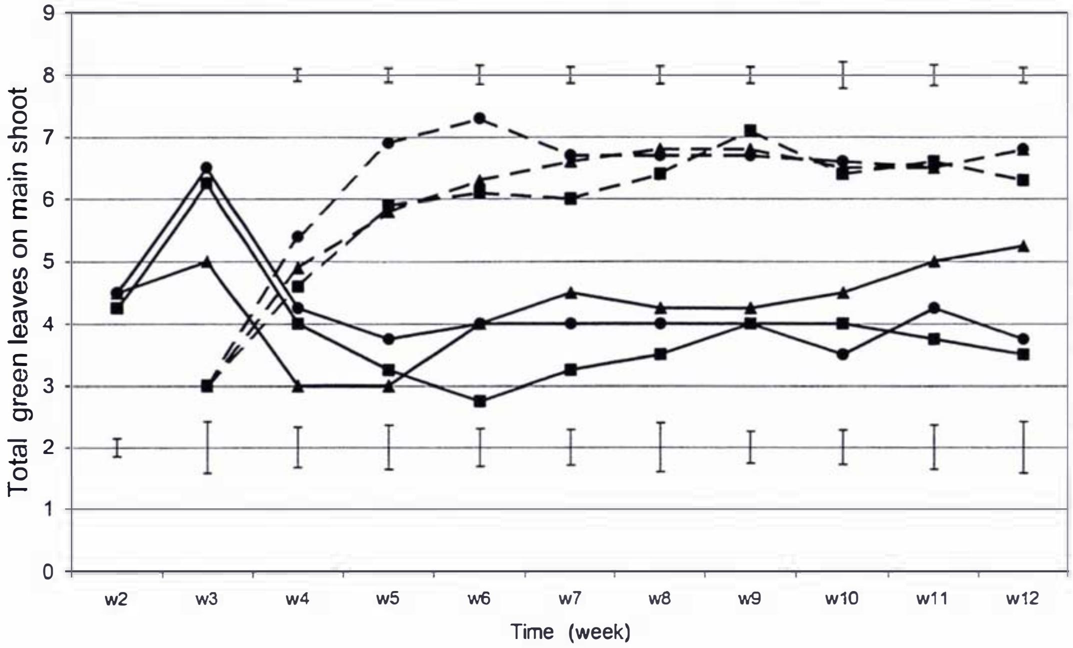


Figure 4.3. Number of live leaves, NLL, on the main shoots in three Guinea grass cultivars, Aruana (▲), Mombaça (■) and Tanzânia (●) in **E1 (solid lines)** and **E2 (dashed lines)** experiments. Bars below the lines in El and above lines in E2 are s.e. for each week.

4.3.2. Tillering activity

Site Filling (SF) and Site Usage (SU)

Average SF estimated from week 8 to week 12 is shown in Figure 4.4 for cv. Aruana, Mombaça and Tanzânia in E1 and E2. Comparing the slopes of the regression lines, in E1 cv. Tanzânia showed lower SF ($P < 0.05$) than cv. Aruana and Mombaça, but in E2 there was no difference in SF among cultivars. Values were lower in E1 than E2 for all cultivars.

Site usage (the probability of tiller development at each bud site on the main shoot), and calculated only for primary tiller on the main shoot (Table 4.5 a) was higher in Aruana plants than in Mombaça and Tanzânia plants only for late leaf positions (L9 and L10). Conversely, in the first leaves, site usage was higher in cv. Mombaça than in cv. Aruana, though the differences were not statistically different.

The total number of secondary tillers (Table 4.5 b) produced per primary tiller was proportionally higher for Aruana than for Mombaça plants from L3 up to L6, but the difference was significant only at L5 ($P < 0.001$) and marginal at L6 ($P = 0.06$). In cumulative terms these differences resulted in 37 and 31% more tillers per plant in cv. Aruana than Mombaça and Tanzânia, respectively, at the end of experiment E2 (12 weeks).

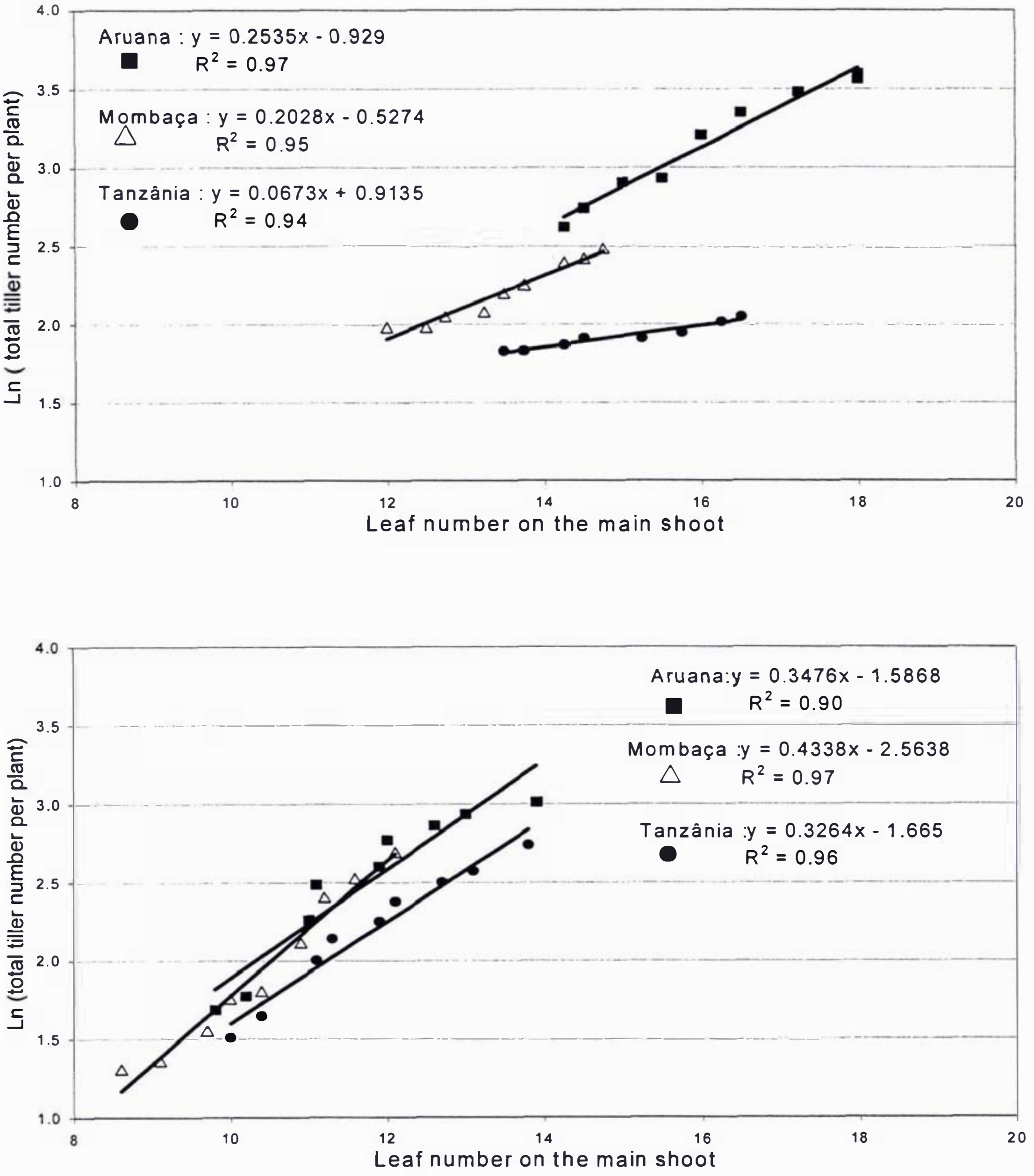


Figure 4.4. Site filling, SF, (slope of the regression line of log $_n$ tiller number on cumulative leaf number on main tiller) in Guinea grass cultivars, Aruana, Mombaça and Tanzânia in **Experiment 1 (top)** and **Experiment 2 (bottom)** from week 8 to week 12 in both experiments.

Table 4.5. (a) Site usage, SU, (probability of a tiller bud developing at each leaf number) on main shoots, and (b) number of secondary tillers produced by primary tiller in three Guinea grass cultivars Aruana, Mombaça and Tanzânia grown without defoliation, in E2. P and S are primary and secondary tillers at each leaf position (L1, L2, L3, L4...).

(a)		L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14
Aruana	P	0.0	0.3	0.9	1.0	1.0	1.0	1.0	1.0	1.0	0.8	0.0	0.0	0.0	0.0
Mombaça	P	0.0	0.7	1.0	1.0	1.0	1.0	1.0	0.4	0.0	0.0	0.0	0.0		
Tanzânia	P	0.1	0.4	0.4	1.0	1.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.0	0.0
χ^2test		-	ns	ns	-	-	-	-	ns	**	***	-	-	-	-
(b)		L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13	L14
Aruana	S	0.0	1.2	3.8	3.2	2.6	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mombaça	S	0.0	1.4	1.4	2.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
Tanzânia	S	0.0	1.0	1.0	2.7	0.7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
χ^2test		-	ns	ns	ns	**	0.06	-	-	-	-	-	-	-	-

(ns) $P > 0.05$, (**) $P < 0.001$. (***) $P < 0.001$

Figure 4.5 shows the number of tillers per pot evaluated before each harvest in E1 for all treatments. Repeated Measures analysis revealed significant ($P < 0.001$) harvest, harvest x cultivar, harvest x cutting height and also harvest x cultivar x cutting height effects. Final tiller number at the final measurement was always lower in the LC treatments compared to HC treatment, although this difference was not statistically significant in cv. Tanzânia. As before, early flowering affected the pattern for Aruana. In this case the elongated internodes produced numerous aerial tillers mainly in treatment HC. There was virtually no stem elongation in cv. Mombaça and Tanzânia up to the end of the experiment.

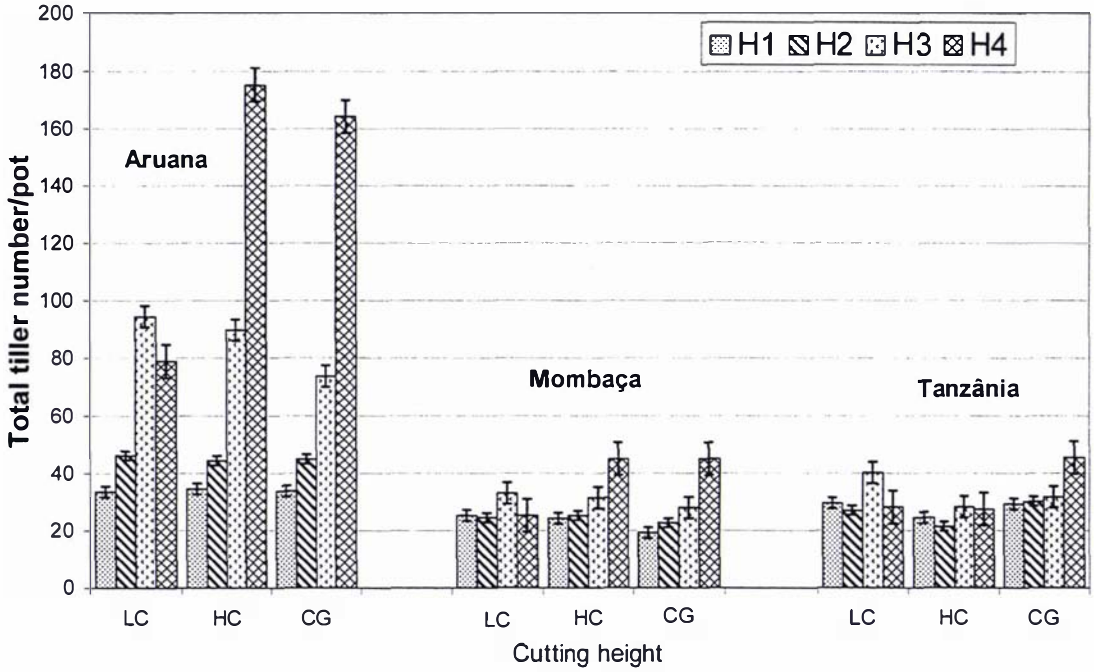


Figure 4.5. Total tiller number/pot (four plants) in four sequential harvests (H1, H2, H3 and H4) in three Guinea grass cultivars, Aruana, Mombaça and Tanzânia, under three cutting heights: 50 mm (LC), 200 mm (HC) and uncut (CG) in experiment E1. (Bars above columns are s.e. for each harvest).

4.3.3.Plant structure

The effects of cutting regimes on the frequency distribution of tiller hierarchy and size (see material and methods) is shown in Figure 4.6 for the three Guinea grass cultivars at the end of E1. Severity of defoliation affected tiller number and distribution within categories differently in the three cultivars. In cv. Aruana, aerial tillers played an important role, at least numerically. In plants under treatments CG or HC, about 53% of the tillers in the plant were aerial, while the category LO (secondary or tertiary tillers larger than 200 mm high) accounted for about 27% of the total. On the other hand, in treatment LC aerial tillers were only 17% of total tillers and the LO category accounted for 70% of tillers. In cv. Mombaça and cv. Tanzânia aerial tillers represented less than 10% of the total in treatment CG and were practically absent in treatments HC and LC. There was a trend (more evident in cv. Mombaça) for the proportion of large primary tillers to decrease with increasing severity of defoliation (CG > HC > LC) while the proportion of large secondary and tertiary tillers increased in the same sequence. This indicates tiller size adjustment (plasticity) in the population according to defoliation severity. An analysis of variance carried out on final total tiller number per plant revealed no cultivar x cutting height interaction but significant cultivar (Aruana > Mombaça = Tanzânia; 51, 21 and 17 s.e 3.3, $P < 0.001$) and cutting height (CG > HC > LC; 36, 28 and 24 .s.e. 3.3, $P < 0.05$) effects.

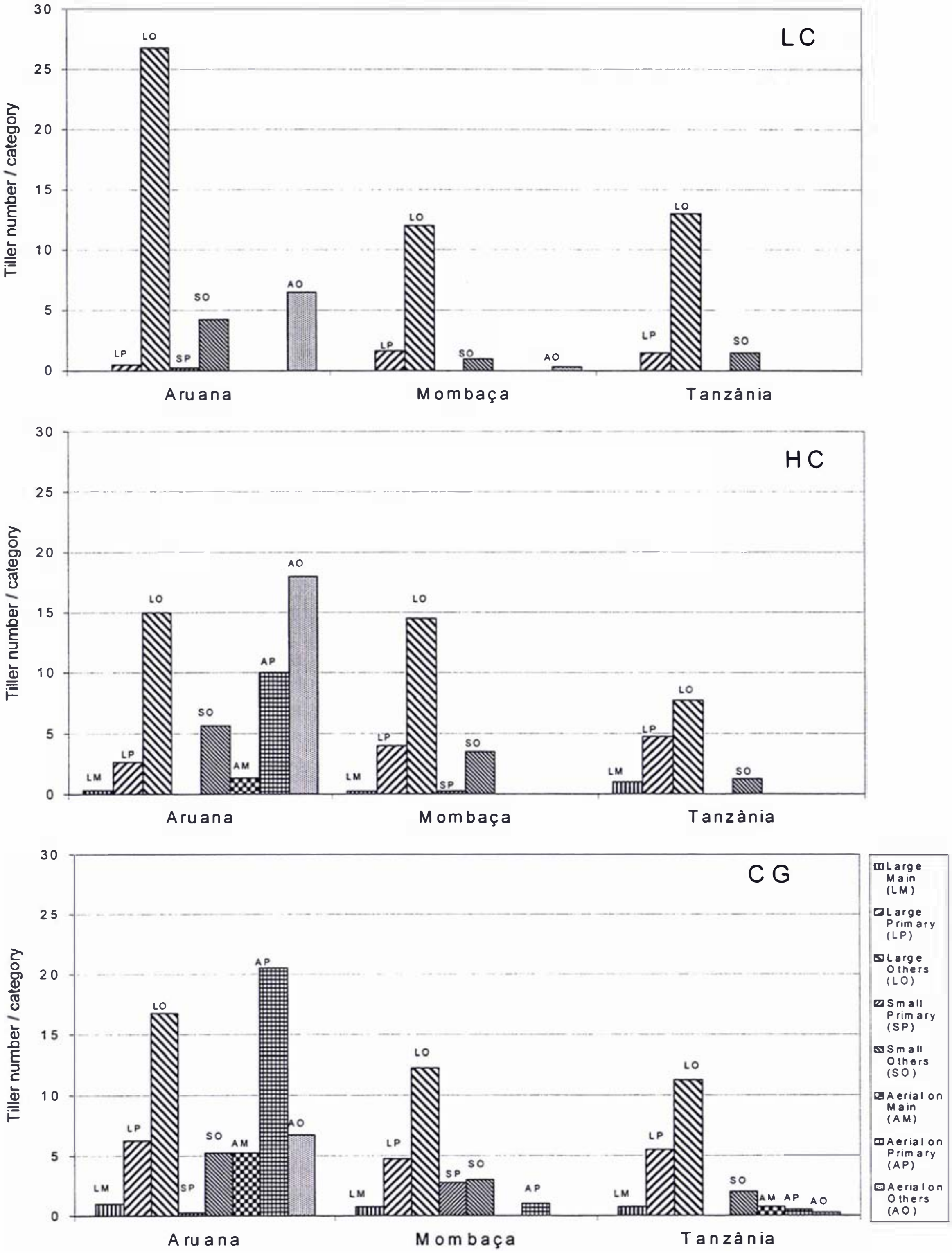


Figure 4.6. Total tiller number/plant at the end of Experiment 1 classified into eight categories in Guinea grass cultivars, Aruana, Mombaça and Tanzânia subjected to three defoliation heights: cut at 50 mm (LC), cut at 200 mm (HC), and uncut (CG).

4.3.4. Herbage production and herbage harvested

Figure 4.7 shows total and component dry matter harvested per pot at each harvest in E1. Repeated Measures analysis revealed significant effects ($P < 0.001$) of harvest, cutting height x harvest and harvest x cultivar ($P < 0.05$). Low cutting reduced herbage harvested in all cultivars. In cv. Aruana this occurred at the third harvest and in cv. Mombaça and Tanzânia at the last harvest. There was more leaf on high cut than low cut plants and a trend to increase the proportion of stem with time. There was a cultivar effect on total herbage harvested over four cuts (62, 68 and 50 g/pot s.e. 8.9 g/pot $P < 0.05$) for Aruana, Mombaça and Tanzânia, respectively and a cutting height effect (64 and 56 g/pot, s.e. 5.2 $P < 0.05$) for treatments HC and LC, but no interaction effect.

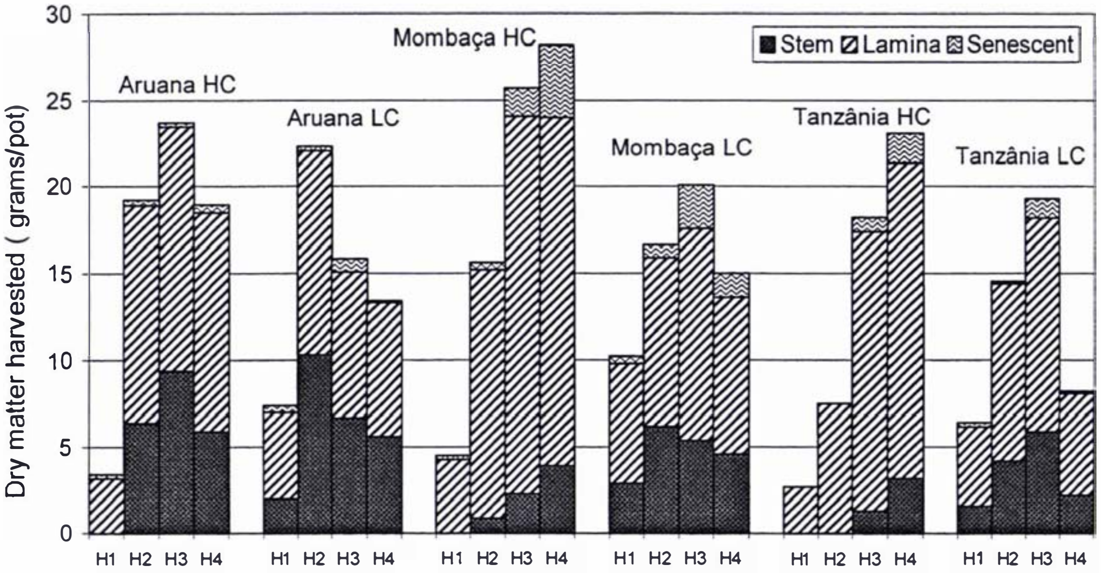


Figure 4.7. Stem (true stem and pseudo stem), leaf lamina and senescent components in total dry matter harvested (grams/pot) in four sequential harvests (H1, H2, H3 and H4) in Guinea grass cultivars, Aruana, Mombaça and Tanzânia under two defoliation heights: 200 mm (HC) and 50 mm (LC) in experiment E1.

At the end of experiment E1, undefoliated plants of cv. Aruana, most of the dry weight (Figure 4.8) was accounted for by the LP category (large primary tillers) followed by large secondary and tertiary tillers (LO) and large main tiller (LM). All aerial categories accounted for 25% of the total dry weight. Due to death of main tiller and some primary tillers in treatment HC, aerial tillers were responsible for 43% of the total dry weight of the plant while in treatment LC 5 % of the total dry weight was accounted for by the LO category (large secondary and others). In cv. Mombaça and cv. Tanzânia (Figure 4.8) also, total dry weight were distributed among large tiller categories, the emphasis moving toward the LO categories with increasing defoliation severity. There was also a cutting height effect on the final plant dry weight (CG > HC = LC; 24.8, 10.5 and 7.5 g s.e. 2.61 $P < 0.001$) but no cultivar or cultivar x cutting height effect.

At the end of E2, dry matter partitioning was evaluated from tillers categorised as main, primaries from each leaf insertion and total secondary tillers from the same leaf levels (Figure 4.9). As in E1, cv. Aruana plants had more tillers than the other two cultivars at the end of the experiment (21, 15 and 16 tillers/plant, s.e. 2.2 tillers/plant $P < 0.01$, for Aruana, Mombaça and Tanzânia respectively). Due to its early internode elongation true stem was already present on cv. Aruana main tillers and old primaries (from L2 to L5), but was absent in the other two cultivars. Although cv. Aruana produced more primary and secondary tillers than cultivars Mombaça and Tanzânia, as discussed previously, the pattern of dry weight distribution was similar among cultivars. Primary tillers originating from low insertion leaves were smaller than the later primary tillers. Differences between cultivars in dry weight of secondary tillers can be accounted for by different tiller numbers, as shown in Table 4.5.

In E2, there was no significant difference between cultivars in total plant dry weight (10.8, 9.8 and 8.6g/plant, s.e. 0.82g/plant for cultivars Aruana. Mombaça and Tanzânia, respectively), in the dry weight of any component (lamina, sheath-stem and senescent material) and in the proportion they contributed to total dry weight. Considering that cv. Aruana produced more tillers than cv. Mombaça this leads to the conclusion that cv. Mombaça had, on average, heavier tillers than cv. Aruana.

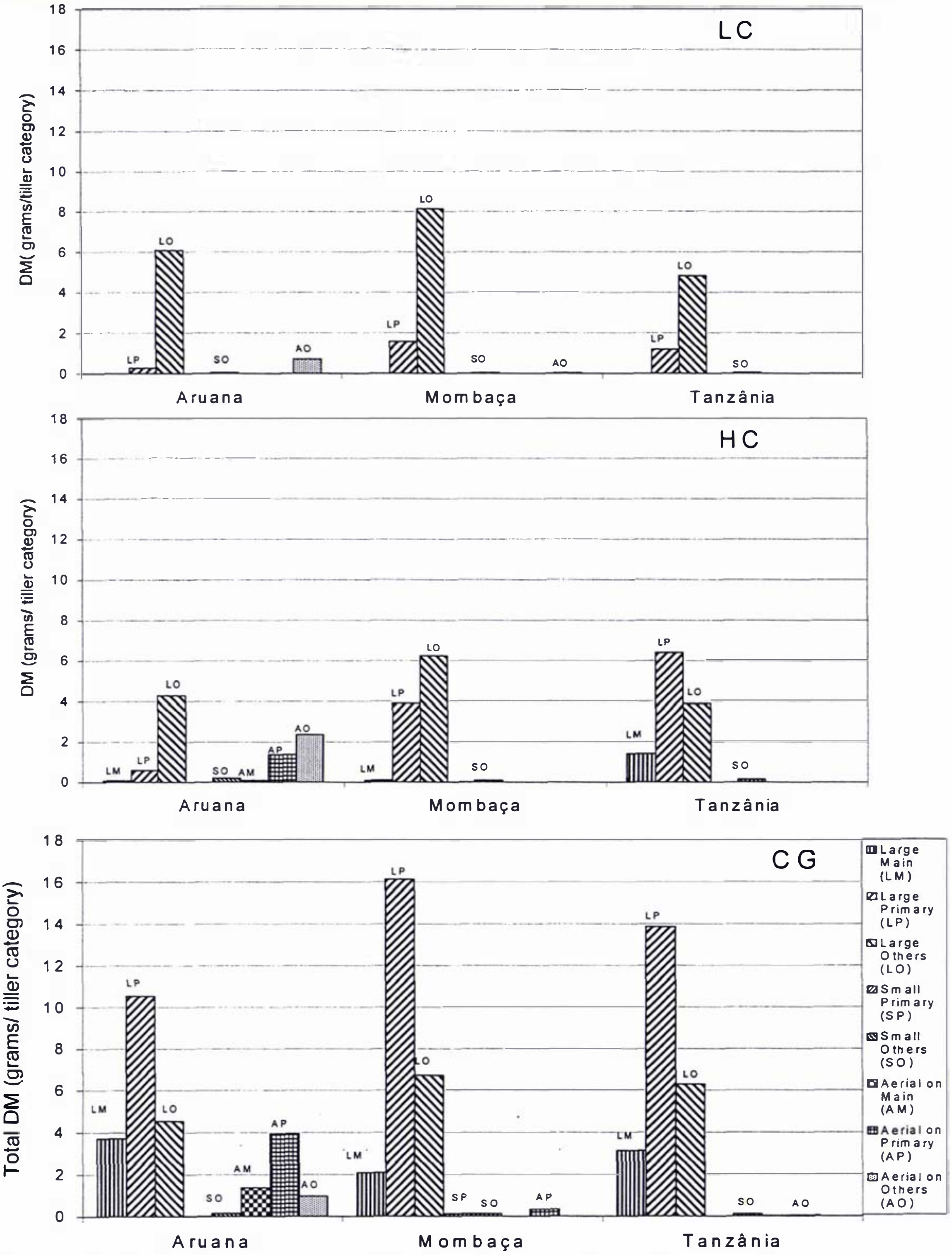


Figure 4.8. Total dry matter (grams/plant) at the end of experiment E1 distributed within tillers classified into eight categories in Guinea grass cultivars, Aruana, Mombaça and Tanzânia subjected to three defoliation heights: cut at 50 mm (LC), cut at 200 mm (HC), and uncut (CG).

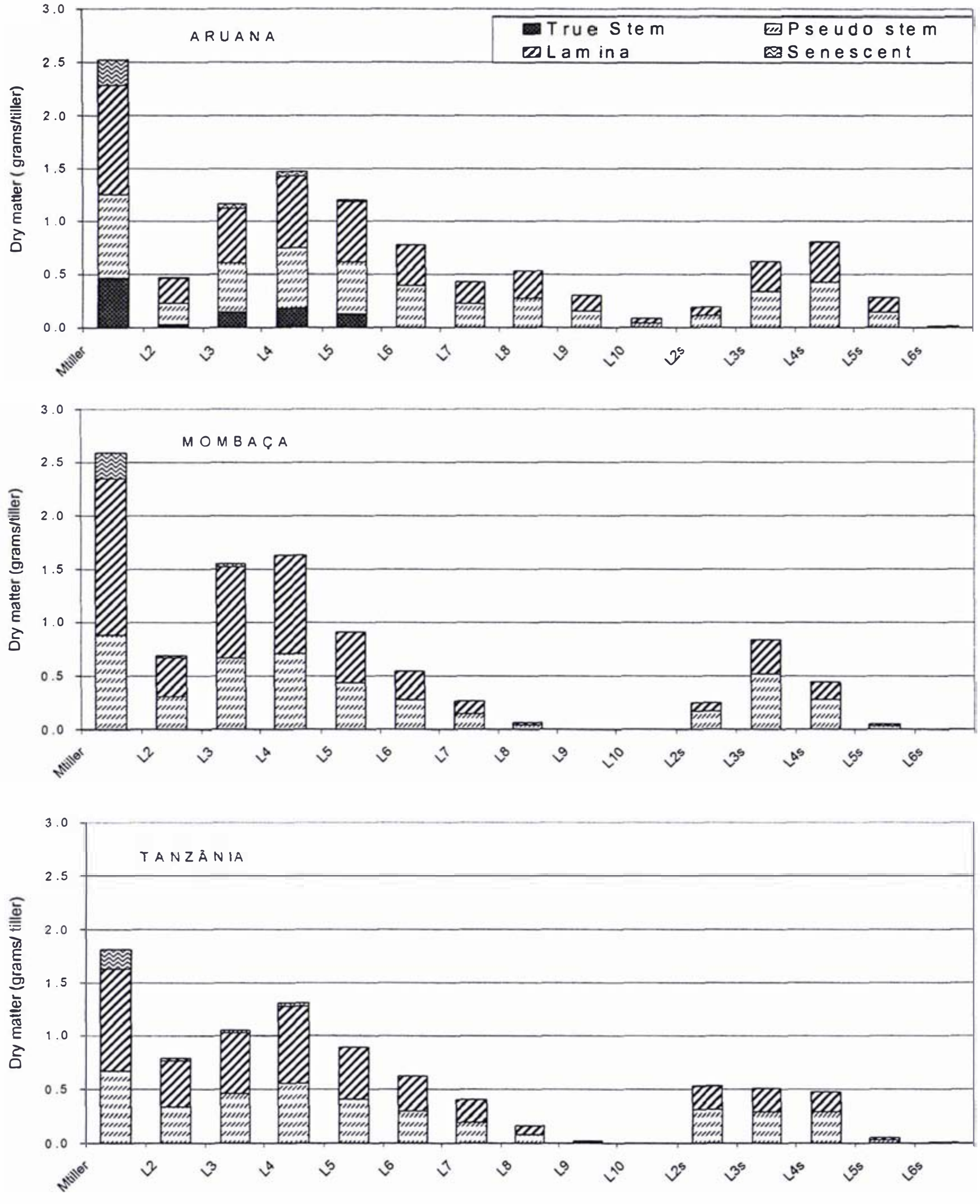


Figure 4.9. Dry matter partitioning (g/DM/plant) into true stem, pseudo stem, leaf lamina and senescent fractions in plants of Guinea grass cultivars, Aruana, Mombaça and Tanzânia in experiment E2. Columns refer to each tiller hierarchy within the plant: Mtiller = main shoot; L2 = primary tiller from leaf two on main shoot, L3 = primary tiller from leaf three on main shoot; L2s = total secondary tillers from L2; L3s = secondary tillers from L3.

4.3.5. Herbage accumulation and senescence

Patterns of cumulative change in leaf extension, senescence and net accumulation (mm/tiller) are shown in Figure 4.10 over periods of 12 weeks in E1 and E2. In E1 total leaf length extension on the main stem was higher in cv. Mombaça and Tanzânia than in cv. Aruana (6110, 5760 and 4970 mm s.e. 253 mm, $P < 0.05$), but there was no statistical difference in leaf senescence or net leaf length accumulation among the cultivars. In E2, on the contrary, cv. Aruana showed greater leaf length extension but, statistically, differed only from Tanzânia (3520, 3280 and 3070 mm, s.e. 82 mm, $P < 0.05$ for Aruana, Mombaça and Tanzânia, respectively). There was no cultivar difference in leaf senescence but net leaf accumulation was lower in cv. Tanzânia than in cv. Aruana and Mombaça (2130, 2600 and 2550 mm s.e. 100 mm, $P < 0.01$). Leaf extension and senescence were, on average, 41% and 72% respectively higher in E1 than in E2. In E1 the net leaf accumulation appeared to stabilise about week 5 in cv. Aruana and later (weeks 8-10) for the other two cultivars. In E2 leaf senescence started later and net accumulation was still increasing at the end of the experiment.

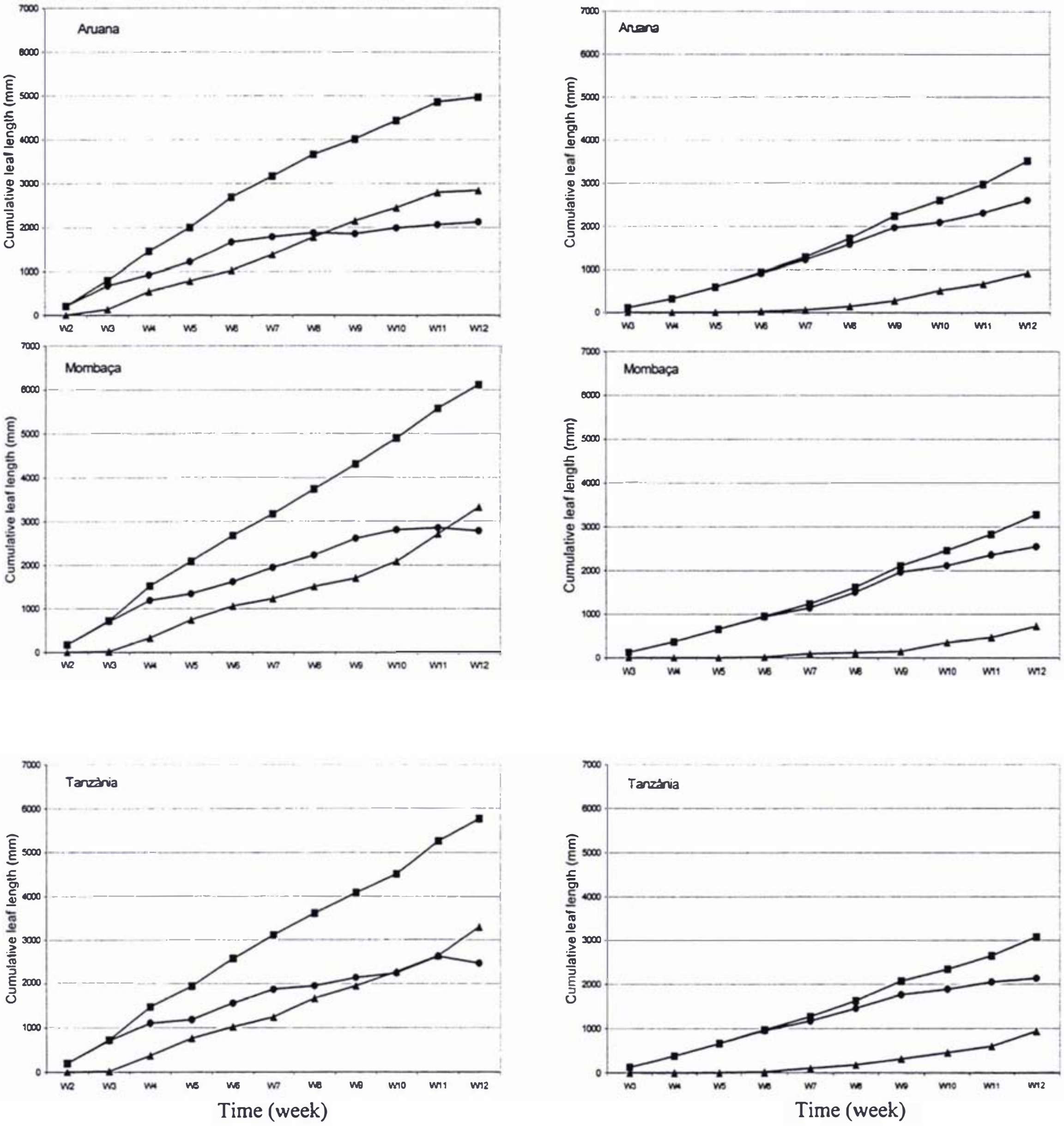


Figure 4.10. Total leaf length extension (■), senescence (▲) and net leaf accumulation (●) in three Guinea grass cultivars, Aruana, Mombaça and Tanzânia in experiments **E1 (left)** and **E2 (right)**.

4.4. Discussion

The two experiments reported in this Chapter were originally planned to test procedures for growing and managing a tall tropical grass under growth cabinet (E1) and glasshouse (E2) conditions. They provide detailed information on aspects of the dynamics of leaf and tiller development on individual plants which complement the results reported in Chapter 3, and they also provide preliminary information on plant responses to contrasts in ambient temperature and light environment in the two studies. These latter effects are considered first, followed by a more detailed evaluation of the effects of defoliation management and genotype on plant behaviour.

4.4.1. Environmental effects

Plants in E1 had a greater LAR (Tables 4.1 and 4.2), generally greater LER (Tables 4.3 and 4.4), greater lamina length (Figure 4.2), lower leaf life span (Figure 4.1) and fewer live leaves per tiller (Figure 4.3) than those in E2. Tiller number in cv. Aruana and the dynamics of leaf development and senescence in all cultivars were substantially greater in E1 than in E2 (Figure 4.10). These effects are generally consistent with the greater ambient temperatures in E1 than E2 (Lemaire & Agnusdei, 2000). However use of thermal time (Σ growing degree days, (GDD) above a defined basal temperature (T_b) is a more appropriate way to compare development under different environmental conditions. The higher LAR in P1 than in P2 in both experiments may be due to the small size of the first leaves (Figure 4.1) resulting in more leaves produced in the establishment phase. The lower LAR in primary tillers when compared to main tillers suggests dominance of the oldest tiller in relation to the younger one during this period supporting similar results obtained by Gomide, C.A.M. (1997).

Thermal times were estimated from values for mean ambient temperature in the two studies (29°C and 20° C for E1 and E2 respectively) and an assumed basal temperature of 10°C for C4 plants (Cross & Zuber, 1972). On that basis, GDD in E1 were almost double those in E2. Estimates for undefoliated plants (means of three cultivars over two periods in each case) showed that values of LAR (leaves/tiller/day) were 20% higher in E1 than E2 (Tables 4.1 and 4.2), and values of LER (mm/tiller/day) were 59% greater (Tables 4.3 and

4.4). In contrast, equivalent values for LAR and LER per GDD were 23% and 17% lower for E1 than E2.

It is difficult to be categorical in explaining the reasons for the generally better performance per GDD of plants in E2. Light intensity was probably greater in E2 (glasshouse conditions in the spring – see Figure 3.3) than in E1, which would be expected to offset the advantage in E1 of continuous illumination. Leaves of this tall growing species were notably more crowded in the limited growth cabinet space (E1) than in the glasshouse (E2), probably resulting in lower levels of illumination within the canopy and reduced R/FR ratio at the base of the plants in E1. This may well explain the higher SF values in E2 than E1 (Casal et al., 1986; Bos & Neuteboom, 1998; Gautier et al., 1999). Also, lower temperatures may cause an increase in tillering activity (Kobayashi et al., 1977) due to changes in carbohydrate accumulation and partitioning, as described for temperate species (Pollock & Jones, 1979). One possible explanation of the greater values of LAR and LER per GDD in E2 than in E1 may be that in the period week 8 to week 12, plants were elongating leaves of a higher level of insertion in E1 (L12 to L19) than in E2 (L8 to L13). Leaves of a lower level of insertion are known to be shorter and have higher values of LAR and LER than later leaves (Wilson, 1976a; Pinto et al., 1994).

Lemaire & Agnusdei (2000) presented LLS values of several species measured at different seasons in a natural grassland community in the pampas region of Argentina. Some C3 species (*Hordeum stenosachys* and *Chaetrotopis elongata*) showed a greater LLS in spring than in winter, while *Stipa neeriana* LLS did not differ seasonally. Vine (1983) found that LLS in perennial ryegrass was 50-60 days in summer and 120-140 days in autumn and winter, indicating a seasonal variation probably related to temperature and light.

Santos et al., (1999) working with cv. Mombaça and Tanzânia in field conditions observed increased NLL in the flowering period in autumn. Also Gomide C.A.M. (1997) related an increase in NLL in *P. maximum* cv. Vencedor to earlier flowering in this cultivar compared to three others. In E2 conditions the plants developed more slowly, and produced fewer and smaller leaves than in E1, but with a longer life span (Figure 4.1). That is, senescence started later (Figure 4.10) resulting in more green leaves per tiller.

4.4.2. Leaf dynamics and tillering behaviour

Leaf appearance rate (LAR) plays a central role in determining plant behaviour because of its direct influence on each of the three sward structural characteristics (leaves per tiller, tiller density and leaf size) Also LAR, LED, LER, FLL and tiller appearance rate, TAR are all interdependent (Chapman & Lemaire, 1993; see Figure 2.1)

Estimates of LER shown in Tables 4.3 and 4.4 refer only to measurement intervals where individual leaves were observed to be actively elongating, and exclude information from intervals in which leaves either appeared or ceased elongation, because of the uncertainty of attributing a specific start or finish day within the interval of 3 or 4 days (see material and methods). This is a potentially important constraint where leaves were only elongating for periods of 4-10 days (Tables 4.1 and 4.2). To check the values shown in Tables 4.3 and 4.4, LER was also estimated by dividing final leaf length (FLL) by leaf appearance interval (the reciprocal of LAR, Tables 4.1 and 4.2). LAR is itself susceptible to end-point error of estimation, but in this case it is reasonable to expect that errors would be self-canceling over a population of tillers and leaves.

Table 4.6 compares values of LER from Table 4.3 and 4.4 with the values from the alternative procedure outlined above, taking as a basis for comparison the values for undefoliated plants of each cultivar in P2 of each experiment. Discrepancies between measurements using procedure 1 (based on LER per tiller) and procedures 2 and 3 (based on LER per leaf) are explained by the observed cultivar differences in the number of elongating leaves per tiller (see Table 4.6). Procedures 2 and 3 give similar results in qualitative terms. Surprisingly, the estimate based on the full elongation period of a leaf (procedure 3) gives higher estimates than that derived only for recording intervals in which LER could be calculated directly (procedure 2), which might have been expected to over-estimate average LER for a leaf. However, procedural differences seem unlikely to have affected cultivar comparisons of LER.

Table 4.6: Comparison of estimates of LER (mm/day) derived from undefoliated plants in E1 and E2 using three alternative calculation procedures.

	Experiment 1 period P2			Experiment 2 period P2		
	Aruana	Mombaça	Tanzânia	Aruana	Mombaça	Tanzânia
Procedure						
1	57	84	76	63	58	51
2	47	63	55	50	58	46
3	67	85	69	49	54	45
Elongating leaves per tiller	1.0	1.0	1.2	1.2	1.0	1.1

Procedure 1: LER per tiller, estimated from records for recording intervals with active elongation (from Tables 4.3 and 4.4)

2: LER per leaf, estimated as in 1 above

3:LER per leaf, estimated as FLL (mm) divided by LED (days) for all fully extended leaves

In general, plant behaviour was affected more by environmental conditions (including defoliation) than genotype (cultivar) effects, even taking into account differences in developmental stages between E1 and E2. However, there were significant cultivar effects on most parameters. Plant age trends in LAR (Tables 4.1 and 4.2) accord with the observation of Gomide, C.A.M. (1997) evaluating four Guinea grass cultivars, which also found higher LAR in the establishment stage. In the same experiment this author also observed a lower LAR for primary tillers compared to main tillers.

LER is genetically controlled in many cool season grasses but there is reasonable plasticity due to effects of shade, temperature, N supply and water stress (Nelson, 2000). There is information on LER in tropical grasses (Gomide, J.A., 1997) but comparisons between studies are difficult due to differences in management (Santos, 1997), type of tiller (Carvalho & Damasceno, 1996), nitrogen status (Gomide et al., 1998), period of the year (Beretta et al., 1999) and species (Oliveira et al., 1998). There was a higher LER in all cultivars in E1 than in E2 (Tables 4.3 and 4.4) and contrasts were greater in cv. Mombaça than cv. Aruana. This is consistent with the observation that cv. Aruana has a smaller seasonal variation in DM productivity than other Guinea grass cultivars (Ghisi et al., 1989).

It is known that final leaf length is related to the length of the sheath from the previous leaf (Skinner & Nelson, 1995), and Wilson & Laidlaw (1985) observed that reducing sheath length by cutting reduced subsequent blade length. This effect probably occurred in experiment E1, where severe defoliation (LC) resulted in some sheath being defoliated, and as a result leaves were smaller and with greater LAR than in the other treatments. It was not possible to evaluate final length from all leaves because the short interval (21 days) between harvests meant that some leaves were not fully elongated at defoliation. Defoliation reduced FLL to 27% (HC) and 40% (LC) of that of undefoliated plants, with cv. Mombaça apparently more sensitive to defoliation than cv. Tanzânia, due possibly to its longer leaves (Figure 4.2).

Final leaf length increased with level of insertion in both experiments and in all cultivars (Figure 4.2), in agreement with the observations of Wilson (1976a) for *P.maximum* cv. Green panic where FLL increased progressively up to L10 before decreasing. Skinner & Nelson (1995), describe final blade length as a function of the associated sheath length in successive leaves of vegetative canopies, until reaching a constant length and then decreasing as the internodes move upward, causing a shortening of the whorl. In reproductive shoots the longest leaf is located in the mid canopy and the short flag leaf blade has a relative long sheath. Aruana produced its longest leaf at level L14 in E1, with subsequent decline until flag leaf number 19 in E1 (data not shown). In E1 all main tillers died in cv. Mombaça and the latest fully elongated leaf was L15, so it was not possible to know if this cultivar had already reached its maximum leaf length at this stage. Cv. Tanzânia had its longest leaf at L 17, but L18 was not completely elongated at the end of the experiment in E1 (data not shown). Cv. Mombaça and Tanzânia produced longer leaves in E1 than in E2 mainly from L8 on, but cv. Aruana showed less variation in FLL than the other cultivars (Figure 4.1).

It is well known that the number of leaves formed on the tiller axis determines the potential tiller appearance rate, there being one tiller bud in each leaf axil (Matthew et al., 2000). In contrast to leaf appearance and growth, which appear to be continuous processes, tillering is regulated independently in an on/off manner at each site (Nelson, 2000). Long leaves have been associated with low LAR and long LED resulting in low tiller number per plant (Lemaire & Chapman, 1996). This relationship was also confirmed in E1 and E2, where cv. Aruana had shorter leaves, higher LAR and lower LED than cv. Mombaça, resulting in more tillers/plant in Aruana (Figure 4.5 and Table 4.5). Cv. Tanzânia presented, in general, intermediate values. Differences in behaviour were more pronounced between experiments than between cultivar and cutting height effects within experiments, suggesting that, although *P. maximum* is able to grow fast at high temperatures, such responses leave the plant physiologically stressed due to excess of carbon demand over supply. This is an effect of high temperature also seen in temperate grasses (Chatterton et al., 1989)

The theoretical maximum value of site filling is 0.693 (Neuteboom & Lantinga, 1989) but values ranging from 0.300 to 0.546 are found in the literature for perennial ryegrass (Davies & Thomas, 1983; Hume, 1991). Estimate for E1 were lower than this (Figure 4.4) with that for cv. Tanzânia being particularly low, but estimates for E2 fell within the range quoted. No other evidence was found of SF values for Guinea grass cultivars and the present data require confirmation. Site filling was affected more by environmental conditions than cultivar differences, as observed in Figure 4.4. SF values approaching maximum are frequently observed in the establishment phase for perennial ryegrass (Neuteboom et al., 1988; Van Loo, 1992). However in established swards, each tiller has to replace only one in its lifetime to maintain the population. In this thesis attention is focused principally on the behaviour of established plants, and results from the early establishment phase (Carvalho D. D. et al., 1999) were therefore ignored in estimating the regression fits shown in Figure 4.4.

Tillering behaviour is known to be influenced by repeated disturbances, leading to bias in estimates of tiller production (Matthew, 1992). This effect was assessed by comparing total tiller numbers per plant at the end of E2 between the two plants per pot which were regularly measured and the two which were not measured (though not necessarily undisturbed). Averaged across cultivars, the total number of tillers was substantially greater on regularly measured plants than the unmeasured plants (17 vs. 11

tillers/plant s.e. 0.8, $P < 0.001$), emphasising the need for care in interpreting the results of field measurements on labeled plants and tillers, particularly where these involve long-run observations.

4.4.3. Leaf turnover and herbage production

Leaf life span (LLS) can be used to characterise the ability of species/cultivars to accumulate green leaf tissue (Lemaire & Chapman, 1996). Gomide & Gomide (2000) calculated LLS by counting the number of leaves per tiller and their elongation rate, resulting in estimates of 18 days during the establishment and 34 days in the regrowth among four Guinea grass cultivars.

The morphogenetic leaf trait, LLS, associated with leaf appearance rate (LAR) will define NLL which according to Gomide J.A. (1997), can be a useful indicator for timing of defoliation in rotational grazing systems with the aim to maximise efficiency in utilisation and to prevent losses by senescence. NLL is reasonably constant for each species or cultivar under constant environmental and management conditions (Gomide, J.A., 1997).

In El there was a decline in NLL from five to six leaves per tiller stabilising around four green leaves per main tiller by week 6 in all cultivars (Figure 4.3). Gomide, C.A.M. (1997) also found six leaves on average on the main stem when evaluating four *P. maximum* cultivars in the second week of the experiment. After that, a decline in number of leaves occurred which stabilised at approximately three to four leaves on the main stem in the sixth week. In E2, NLL increased from three leaves in the beginning of the measurement period and stabilised between six and seven leaves for all cultivars also by week 6 (Figure 4.3). Cv. Aruana plants were flowering by week 12 in E1, but there was no indication of flowering in E2. However it is important to keep in mind the limitations of these results, which relate to one type of tiller in uncut plants.

Harvestable production is the part of primary production that can be harvested before senescence. This depends on the LLS and also on the pattern of leaf accumulation and senescence. In E1 net cumulative leaf length stabilized at a lower level in cv. Aruana than in cv. Mombaça and Tanzânia (Figure 4.10). In E2 leaf turnover was substantially slower, and there was no indication of a plateau in net leaf accumulation in any cultivar by week 12.

4.4.4. Plant structure

Two alternative approaches were used to investigate suitable methodology for evaluating dry matter partitioning and yield components. In E1 tillers were categorised by size and position on the plant, and tiller number (Figure 4.6) and dry weight (Figure 4.8) were evaluated. The proportions of these tiller categories and their contribution to total weight of the plant were then assessed in a descriptive way. In E2, where plants were growing uncut, tillers were categorised at leaf level and also components (leaf, pseudo stem, true stem and senescent material) were compared (Figure 4.9). The approach used in E1, based in tiller size, is easier to use and can be applied in field studies in mature swards. The method in E2 based on tiller sequence is more suitable for comparative studies at more detailed level under controlled conditions. It is important to evaluate growth potential and strategies of plants in response to environmental stress, and the way they distribute photoassimilates. This approach could be useful for modelling systems where more detailed and precise data on plant behaviour are needed. It is not useful in field conditions and established swards where primary and secondary tillers have already lost their identity.

Increase in the proportion of stem is one of the concerns when working with tropical grasses where internode elongation with time is common. This occurred mainly in the present experiment with cv. Aruana under both cutting heights (Figure 4.7). The same observation was made in Chapter 3, where cv. Mombaça and to a less extent cv. Tanzânia showed more plasticity than cv. Aruana in respect to cutting height, though the defoliation heights were 150 and 300 mm in that experiment compared with 50 and 200 mm in E1.

It seems that over time defoliation at 50mm is a drastic treatment for Guinea grass cultivars, at least at the frequency of defoliation used here (three weeks) due to the large tillers size, and the resulting depression in tillering and productivity. Cv. Mombaça was more tolerant of frequent defoliation than the other two cultivars (Figure 4.5 and 4.7). Depletion of carbohydrates could be a possible explanation of depressed performance although Gomide & Zago (1980) found a stabilisation of carbohydrate content after 21 days of regrowth in *P. maximum* cv. Colonião at 150 mm cutting height. No other examples of defoliation treatment were found comparable to the 50 mm cutting height every three weeks as in E1.

4.5. Conclusions

The contrasts between experiments E1 and E2 made it difficult to draw unequivocal conclusions about the influence of light and temperature in Guinea grass, but served to indicate that plant development could be satisfactorily maintained over a range of climatic conditions.

The results illustrate the plasticity of response in leaf and tiller dynamics by Guinea grass to quite extreme defoliation management for this tall growing tropical species. The results taken together with the results in Chapter 3, indicate the limits that are likely to be detrimental for swards in the field. Of the three cultivars involved, Aruana was shown to have both a much earlier onset of flowering and a much greater development of ephemeral aerial tillers than Mombaça and Tanzânia these traits caused difficulties in comparing between cultivars. In the rest of this thesis attention will be concentrated primarily on cv. Mombaça and Tanzânia.

Cutting heights caused a great change in tiller distribution within plants of these three cultivars and a high variability in tiller size and weight. This illustrates one of the greatest difficulties in methodology in field conditions with tropical plants, i.e., selection of tiller types as representative of the population to provide estimates of the parameters involved with productivity. This aspect will be explored in more detailed in the next chapter.

CHAPTER 5: Effect of cutting height on dry matter harvested, tiller dynamics, and contribution of individual tiller cohorts to dry matter yield in Guinea grass cultivars.

5. 1. Introduction

It is known that pasture is a dynamic system with birth and death of tillers occurring simultaneously through the year. A pasture is considered a stable community of tillers when tiller death is balanced by birth of new tillers. However this equilibrium is affected by environmental factors and also by the management practices. Tiller life span varies greatly among grasses and tillers can survive for more than one year or some times not more than one month.

For many years, the effects of intensity and/or frequency of defoliation on dry matter yield of tropical pasture grasses have been studied (Mecelis, 1979; Drudi & Favoretto 1987; Favoretto et al., 1987; Cecato et al., 1994; Correa et al. 1998), but few general principals have emerged. Neither cutting height nor frequency has a consistent effect on yield (Ludlow & Charles-Edwards, 1980). There has been little attempt to quantify the changes that occur in the structure of the sward, more specifically in the tiller, the basic component. One of the difficulties in studying tropical bunch grasses is the great variability in tiller size and age (stage of maturity) and it is not known how much difference in defoliation level interferes with the morphogenetic traits of different tiller age groups. In temperate grass, *Lolium perenne*, for instances, the number of green leaves per tiller has been used as a criterion to define defoliation time (Fulkerson & Slack, 1995). In tropical Guinea grass this approach seems inapplicable since leaf size and leaf life span increase with the level of insertion (Wilson, 1976a, Figures 4.1 and 4.3 in Chapter 4). Moreover the variation in development stage between individual tillers within a tiller population in the pasture may create difficulties in determining which generation or generations of tillers have greatest impact on production (Santos, 1997).

The previous experiment (Chapter 4) provided preliminary information on these parameters in three Guinea grass cultivars. Results indicate some genetic variation in tillering behavior and define the effect of defoliation to different cutting heights on the distribution of tiller size. This chapter describes an experiment designed to measure the contribution of different tiller cohorts to harvested dry matter and to quantify the effect of defoliation intensities in the components of production.

5.2. Materials and Methods

5.2.1. Plant material and experimental management

The experiment was carried out in a glass house located at the Plant Growth Unit, Massey University, Palmerston North (40°16'S, 175°17'E) from August 1999 to April 2000 and comprised two Guinea grass cultivars, Mombaça and Tanzânia, subjected to three defoliation levels: 100 mm (M100, T100), 200 mm (M200, T200) and 400 mm above the soil surface (M400 and T400)

Seeds were germinated in a tray at 25°C and after two weeks, four similar size seedlings were transplanted to each of 150 five-litre pots filled with a mixture of sand and soil (1:1) and fertilized (15 g/pot) with a controlled release fertiliser (15% N, 4.8% P, 10.8% K, 1.2% Mg, 3.0% S, 0.4% Ca plus trace elements, B, Cu, Fe, Mn, Mo and Zn).

One week later seedlings were thinned to one plant per pot with similar size and pots were allocated to treatments and placed on five trolleys (experimental replicates). The trolleys were rotated weekly (Figure 5.1a) to ensure variation in light level within the glasshouse did not bias results. On each of the five trolleys (blocks) pots were distributed into three rows (cutting treatments) and harvest and cultivars were randomly distributed as shown in Figure 5.1b. In an attempt to simulate shade from neighboring plants in field swards, screens of 50% shade cloth were placed between each row of pots so that tops of screens were just below cutting height of the treatment in question (Figure 5.2). The 400 mm cutting height treatment was always allocated to the central row since the influence of others treatment (heights) would affect it less than any other positions. Plants were watered daily with tap water and 200 ml of a 0.25% solution prepared with a commercial soluble fertilizer (20% N, 8.7 % P, 16.6 % K plus S, Mg, B, Cu, Fe, Mn, Mo and Zn) was applied three times a week in each pot.

All plants were initially harvested (Hi) at 200 mm height after 8 weeks from sowing. Four weeks later, another harvest (H0) was performed, when treatments (different cutting heights) were imposed. Following H0, plants were harvested at approximately monthly intervals up to the end of the experiment designated H1, H2, H3, H4 and H5. At each of these harvests a group of 30 pots (five replicates of six treatments) were destructively harvested and measurements were performed on each plant. Further details are presented in Table 5.1.

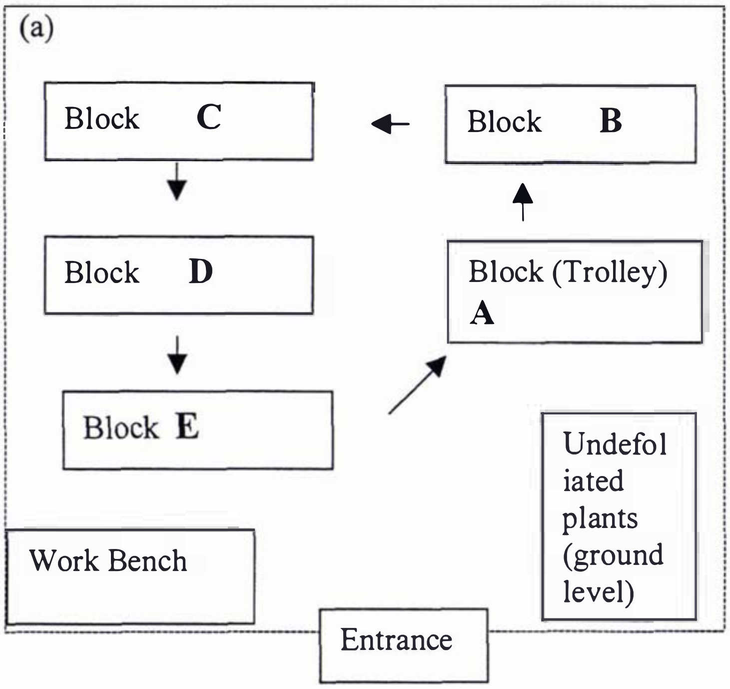
A group of ten potted plants (five of each cultivar) with no cutting treatment were placed on the ground near the trolleys and used to informally assess effect of cutting on variables such as tiller appearance and death rate in undefoliated plants. They were also used to provide estimates of flowering behaviour.

5.2.2. Measurements

Ambient temperature was monitored using a thermometer placed in the center of the glasshouse, at 1.7 m above ground level.

5.2.2.1. Herbage accumulation

At Hi and H0 all pots (150) were harvested and green herbage above the cutting height was separated into leaf and stem (pseudostem plus true stem) fractions and oven dried at 60°C for dry matter calculation. From H1 on, all plants were subjected to this same procedure apart from the 30 allocated for destructive harvest. At the final harvest (H5) there were only 30 pots remaining. All senescent material was collected from the plants at each tiller tagging date (see next section and Table 5.1) and put into paper bags, oven dried and weighed to calculate the total senescent material accumulated to the end of the experiment.



(b)

M 100 H1	M 100 H5	M 100 H4	M 100 H2	M 100 H3	T 100 H3	T 100 H2	T 100 H5	T 100 H4	T 100 H1
M 400 H3	M 400 H2	M 400 H1	M 400 H4	M 400 H5	T 400 H1	T 400 H5	T 400 H4	T 400 H2	T 400 H3
T 200 H2	T 200 H3	T 200 H5	T 200 H4	T 200 H1	M 200 H5	M 200 H1	M 200 H4	M 200 H3	M 200 H2

Figure 5.1. (a) Position of undefoliated plants and the five trolleys (replicates) within the glasshouse. Arrows indicate rotation of trolleys the movement of moving trolleys; (b) Initial arrangement of 30 potted plants on each trolley (2 cultivars x 3 cutting heights x 5 harvests). Treatments (cultivars and harvests) allocation in one of the blocks (trolley). Each trolley had a different (random) distribution for harvest dates within each row.

M 100/T 100 : Mombaça and Tanzânia cut at 100 mm height;
M 200 / T 200 : Mombaça and Tanzânia cut at 200 mm height;
M 400 / T 400 : Mombaça and Tanzânia cut at 400 mm height;
Harvests: H1, H2, H3, H4, H5

Table 5.1. Schedule of activities during the experimental period.

Date	Activity	Tiller tags placed		Week
24/08/99	Sowing on trays			
31/08/99	Germination			W1
07/09/99	Transplanting to pots			W2
14/09/99	Thinning to one per pot			W3
21/09/99	Labelled main + primary	green & white	G1	W4
28/09/99	Label	blue		W5
05/10/99	Label	orange		W6
12/10/99	Label	violet		W7
19/10/99	Cut at 200mm label **HARVEST Hi**	pink		W8
26/10/99	Label	yellow	G2	W9 (1)
				W10 (2)
09/11/99	Label	green		W11 (3)
16/11/99	Cut with treatments (100, 200 and 400mm high) **HARVEST H0**			W12 (4)
23/11/99	Label	red	G3	W13 (1)
30/11/99				W14 (2)
07/12/99	Label	white dot		W15 (3)
14/12/99	**HARVEST H1**			W16 (4)
21/12/99	Label	grey	G4	W17 (1)
28/12/99				W18 (2)
03/01/00	Label	brown		W19 (3)
10/01/00	**HARVEST H2**			W20 (4)
17/01/00	Label	orange dot	G5	W21 (1)
				W22 (2)
31/01/00	Label	green dot		W23 (3)
07/02/00	**HARVEST H3**			W24 (4)
15/02/00	Label	grey dot	G6	W25 (1)
				W26 (2)
29/02/00	Label	silver dot		W27 (3)
07/03/00	HARVEST H4			W28 (4)
14/03/00	Label	dot orange	G7	W29 (1)
				W30 (2)
28/03/00	Label	blue dot		W31 (3)
11/04/00	**HARVEST H5**			W32 (5)

Plate 5.1- Overview of the experimental area with five blocks (a); detailed view of one block before harvest (b) and overview of two blocks after harvest (c).

5.2.2.2.Tiller population dynamics

On week four after sowing, the main tiller on each plant was labeled with a colored wire ring (green) and all others (primary tillers) with a second colour (white). From this first labeling up to the initial harvest (Hi) tillers were labeled weekly, giving six cohorts, which were later classified as group 1 (G1). On weeks one and three after each subsequent harvest, new tillers were counted and labeled with a different colour. In all over the five harvests, 17 age cohorts of tillers were labeled in this way, but these were later reclassified into seven age groups (G1, G2, .. G7) to avoid excessive detail in data analysis (see Table5.1). Tillers were considered dead when completely dried and senescent, and in this case the ring was discarded.

Estimates of Relative Tiller Appearance Rate (TAR) and Relative Tiller Death Rate (TDR) were made, as described in Chapter 3, to assess tiller dynamics. Although measurements were made on all pots destructively harvested at each of the five harvests, TAR and TDR data presented are limited to plants of H5, which were present throughout the experiment. The percentage of flowering tillers on undefoliated plants was calculated at the end of the experiment.

5.2.2.3. Destructive harvests and dry matter partitioning

At each destructive harvest all tillers present were separated from the roots and the fresh weight of each tiller was obtained. For analytical purposes, tillers were classified into five weight categories: very light, VL, (weight up to 5 g), light, L (weight from 5.1 to 10 g), intermediate, IN (between 10.1 to 15 g); heavy, H (between 15.1 to 20 g) and very heavy, VH (more than 20 g). Also, tiller height was measured from the base of the tiller (ground level) to the ligule of the last fully elongated leaf and classified as small, SM (less than 100 mm high), intermediate, IN (between 101mm and 200 mm) and large, LA (longer than 200mm).

Tillers of each cohort were then placed together on a table, and cut at the specified cutting height for tillers of that treatment, measured from the base of the tiller. The herbage above cutting height was then separated into leaf and harvestable stem, and the herbage below cutting height also sorted into leaf and stem components. This material was oven dried for 48 h at 60 °C for further estimate of the total dry weight of the plant and its components.

5.2.2.4.Tissue turnover and photosynthesis on leaves of aging tillers.

After harvest four (H4) the tiller age groups G1 - G6 present at that time were again reclassified, this time into three groups, old, mature and young, defined as follows: Old: any tiller from groups G1, G2 and G3, i.e. more than three months old Mature: any tiller from G4 or G5, i.e. more than one and less than three months old), and Young: G6 i.e. less than one month old. Measurements described below were performed in randomly selected tillers within each age group per plant.

Leaf elongation rate was measured in two ways: LER_a the cumulative leaf length measured above cutting height per tiller per day and expressed as mm leaf/tiller/day; LER_t the cumulative leaf length in all elongating leaves per tiller per day measured from the ligule of the previous leaf and also expressed as mm leaf/tiller/day

Leaf appearance rate, LAR, as the number of leaves appeared per day on the selected tiller, and expressed as leaves/ tiller/day.

Specific leaf area of harvested leaves from each tiller age group, SLA (cm^2/g), as the ratio between leaf area above cutting height (measured with a LICOR LI-3000 area meter), and mass (dry weight) of those leaves.

Photosynthesis rate, PR, was measured on the youngest fully elongated leaf of three selected tillers of each plant, one per tiller age category (old, mature and young). The equipment used was a LI-6200 portable photosynthesis meter (LI-COR, Lincoln, Nebraska). The length and width of the portion of the leaf enclosed inside the chamber was measured in order to convert the photosynthesis rates calculated to a leaf area basis (μmol CO_2/m^2leaf/s).

5.2.2.5. Root Measurements

A piece of PVC pipe (350mm x 25mm) was placed vertically in the centre of each pot before filling the pots with the soil-sand mixture (Plate 5.2). Within 1-2 days after H0, the 30 pots allocated to H1 had this pipe removed and the hole filled with sand, creating a volume of new soil at the center of the pot, with no roots present. It was intended that coring within this volume of soil at harvest one month later would give a measure of rate of new root production, suitable for assessing the extent to which defoliation treatments affected root growth. This procedure was repeated at H1 and for successive harvests.

At each destructive harvest the roots grown inside the sand-filled holes described above were collected with a soil corer of marginally smaller diameter than the original PVC pipe. These samples were washed and dry weight evaluated. Samples were then ashed and weight of ash residue subtracted to provide estimates of root organic matter weight. The remaining root mass in each pot after extraction of this core sample was also recovered by washing. However, because of the much larger samples a more vigorous washing procedure was used. Total root dry weight and ash-free dry weight were calculated for these samples as before.

5.2.3. Trial design and statistical analysis

The experiment was analysed as a 2 x 3 factorial design (2 cultivars and 3 defoliation levels) with five replicates. The SAS® system (1989) General Linear Model (GLM) procedure was used for statistical analysis. For some variables such as dry matter harvested (Table5.3), tiller number (Table 5.5), TAR (Table 5.6) and TDR (Table5.7) the Repeated Measures option was used to consider data for all five harvests together and test for differences in timing of cultivar responses (i.e. a cultivar x time interaction). When necessary data were log transformed to reduce variance. An analysis including tiller age effects the model used was as split-plot with cutting the main effect and age split into cutting height. The undefoliated plants were not placed in the same conditions as defoliated plants (see materials and methods) therefore they were not considered in statistical analyses and data in the tables and figures are presented only for comparison with cutting treatments.

Although the majority of measurements were performed at all harvests, the results and analyses presented will focus mainly on the two last harvests (H4 and H5) because data from these better reflect the cumulative or equilibrium response of plants when the respective defoliation regimes were sustained over time.

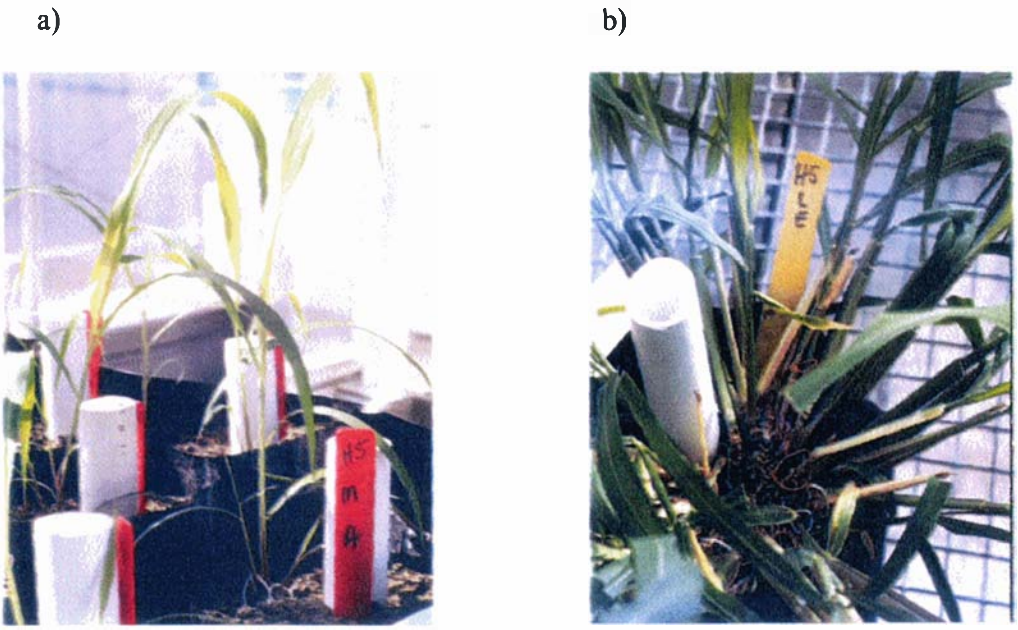


Plate 5.2. Procedure for introducing a volume of new soil into each pot four weeks before harvest for assessment of root growth (Section 5.2.2.5). View of pipe position inside the pot in the establishment period (a) and when plants were well established (b).

5.3. Results

5.3.1. Temperature

Figure 5.2 shows the range of variation in daily temperature during the experimental period. The overall means for maximum and minimum temperatures, respectively, are 34.6 °C and 16.2 °C.

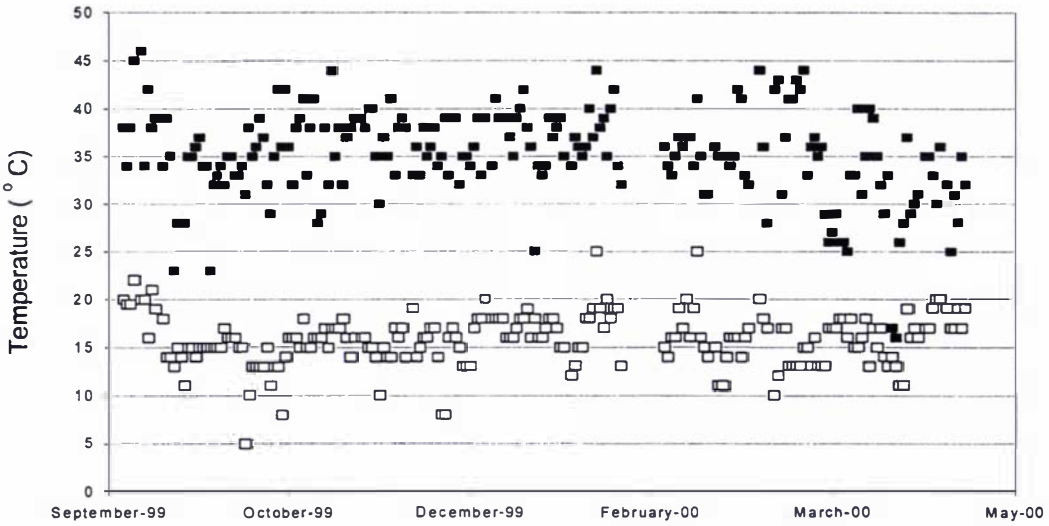


Figure 5.2. Daily maximum (■) and minimum (□) temperature range (°C) inside the glasshouse during the experimental period (September 1999 to April 2000).

5.3.2. Herbage harvested and tiller dynamics

The cumulative herbage harvested (green leaves, pseudostem and true stem) above cutting height over the whole experiment and cumulative senescent material (leaves and tillers) is shown in Table 5.2. There was a cultivar x cutting height interaction effect ($P < 0.05$) reflecting higher sensitivity to defoliation for cv Mombaça than cv Tanzânia. There was no cultivar effect (cultivar means for Mombaça and Tanzânia were, respectively, 79 and 83 g DM/plant, s.e: 2.0 g, $P > 0.05$) but there was a cutting height effect in that cutting at 100 mm height produced more herbage than cutting at 400 mm height (Table 5.2), although this effect was more noticeable in early harvests and diminished at H4 and H5 (Table 5.3). The cumulative production of senescent material (leaf and stem) was not statistically different ($P > 0.05$) between cultivars and there was also no significant interaction between cultivar and cutting height, (Table 5.2), but there was a cutting height effect (24, 31 and 39 g/plant, s.e. 1.6, $P < 0.001$ for 100, 200 and 400 mm height, respectively).

Table 5.3 shows, for each of the six treatments, the dry matter harvested at each of the seven harvests (Hi to H5) from the 30 pots allocated to H5, and present throughout the experiment. The Repeated Measures analysis revealed significant effects for harvest and the interactions harvest x cultivar and harvest x cutting height ($P < 0.001$), but no harvest x cultivar x cutting height effects ($P > 0.05$). Cv. Mombaça accumulated more dry matter than cv. Tanzânia through almost all harvests, but this effect was only statistically significant at Hi and H0. Cutting at 100 mm height resulted in greater DM harvested ($P < 0.05$) than cutting at 200 and 400mm in almost all harvests. The cultivar x harvest interaction arises from better performance for cv. Mombaça at Hi and H0 and better performance for cv. Tanzânia at H5 reflecting a higher pseudostem/ stem fraction in cv. Tanzânia than in cv. Mombaça mainly in the last harvest when internode elongation had already been initiated. Another analysis was performed with data from all destructive harvests (H1, H2, H3, H4 and H5) to evaluate total dry matter harvested. In this case harvest was considered an independent factor in a 2x3x5 factorial design. The results were similar. Cutting at 100 and 200mm height accumulated more dry matter than at 400mm height. Harvest H3 and H5 were the most productive, followed by harvest H4, H2 and H1 (20.3, 19.2, 16.7 14.6 and 11.9 g DM/plant s.e. 0.06 $P < 0.001$), respectively. In this analysis there was no significant interaction effect (cultivar x cut, cultivar x harvest or harvest x cut, $P > 0.05$) as in the Repeated Measures analyses.

Table 5.2. Cumulative total dry matter harvested (green leaves, stem/ pseudostem) above cutting height and senescent material collected from two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm over the experimental period (seven harvests).

	DM harvested			Senescent material		
	Cutting height			Cutting height		
Cultivar	100 mm	200 mm (g/plant)	400 mm	100 mm	200 mm (g/plant)	400 mm
Mombaça	99.8	82.3	54.6	23.1	29.2	36.4
Tanzânia	93.4	87.4	67.7	24.2	32.9	40.6
s.e. cultivar.	ns			ns		
s.e. cut ht.	2.50 ***			1.63 ***		
s.e. cv. x cut ht.	3.51 *			ns		

(*) P < 0.05; (**) P < 0.01; (***) P < 0.001, (ns) P > 0.05

Table 5.3. Total dry matter harvested (green leaves, pseudo stem and true stem) above cutting height (g/plant) and percentage of stem, by harvest (Hi, H0, H1, H2 H3 H4, H5) in two Guinea grass cultivars, Mombaça and Tanzânia, at three defoliation heights, 100, 200 and 400 mm.

Cultivar	cut		Harvest						
	(mm)		Hi	H0	H1	H2	H3	H4	H5
Mombaça	100	DM (g/plant)	3.2	12.5	14.6	16.3	17.7	16.0	19.6
		Stem (%)	0.0	12.0	12.0	11.0	7.9	8.6	13.7
	200	DM (g/plant)	2.6	6.2	11.8	14.8	15.4	13.1	18.3
		Stem (%)	0.0	0.0	1.7	2.7	1.2	1.5	4.4
	400	DM (g/plant)	2.5	1.4	6.7	9.1	10.2	11.0	13.6
		Stem (%)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tanzânia	100	DM (g/plant)	1.5	8.2	12.1	15.7	18.2	15.9	21.7
		Stem (%)	0.0	10.1	14.3	14.9	12.7	12.0	16.5
	200	DM (g/plant)	2.0	4.5	10.6	13.8	18.1	16.6	21.7
		Stem (%)	0.0	0.0	1.4	3.1	1.6	3.6	15.8
	400	DM (g/plant)	1.6	1.4	9.1	10.7	10.9	13.8	20.2
		Stem (%)	0.0	0.0	0.0	0.0	0.0	0.3	5.9
s.e. cv.			0.20 *	0.45 **	ns	ns	ns	0.64 *	0.75 **
s.e. cut ht.			ns	0.55 ***	0.79 ***	0.47 ***	0.73 ***	0.79 *	0.92 *
cv. x cut ht.			ns	ns	ns	ns	ns	ns	ns

(*) P < 0.05; (**) P < 0.01; (***) P < 0.001, (ns) P > 0.05

Figures 5.3 and 5.4 show the dry weight of leaves harvested above cutting height on each treatment, within tiller cohorts, for all five destructive harvests. The values at each point in each graph represent the contribution of all tillers in each cohort and the statistical analysis for this data is shown in Table 5.4. DM harvested was marginally greater in cv. Tanzânia than cv. Mombaça, averaged over five destructive harvests (15.9 and 15.0 g DM/plant/harvest s.e. 0.32 P = 0.052) and plants cut to 100 and 200 mm yielded more than these cut to 400 mm (16.1, 17.3 and 13.0 g DM/plant/harvest, respectively, s.e.: 0.40 , P < 0.001) (Table 5.4). At H3 and H5 significantly more leaf dry matter per plant was harvested than at H4 and H2 and H1 (19.1, 18.1, 15.8, 13.9 and 11.3 g DM/plant s.e.0.51, P < 0.001) respectively, but the interactions harvest x cutting height, harvest x cultivar and harvesting x cutting height x cultivar were all non-significant

Table 5.4. Dry weight of leaves (g/plant) harvested above cutting height in five destructive harvests (H1, H2, H3, H4 and H5) of two *P. maximum* cultivars, Mombaça and Tanzânia, subjected to three defoliation heights, 100, 200 and 400 mm.

Cut ht.	Cultivar	Harvest				
(mm)		H 1	H 2	H 3	H 4	H 5
			Leaf DW (g/pot)			
	Mombaça	11.0	15.5	20.1	17.2	16.9
100	Tanzânia	12.0	15.3	18.4	16.4	18.1
200	Mombaça	12.8	14.9	22.2	18.3	17.5
	Tanzânia	13.5	15.8	21.8	18.0	18.3
400	Mombaça	8.1	11.3	15.3	10.5	13.6
	Tanzânia	10.5	10.9	16.6	14.2	19.0
	s.e. cultivar 0.51 *					
	s.e. cut ht. 0.40 ***					
	s.e. cv x cut ht. 0.72 *					

(*) $P < 0.05$; (**) $P < 0.01$); (***) $P < 0.001$, (ns) $P > 0.05$

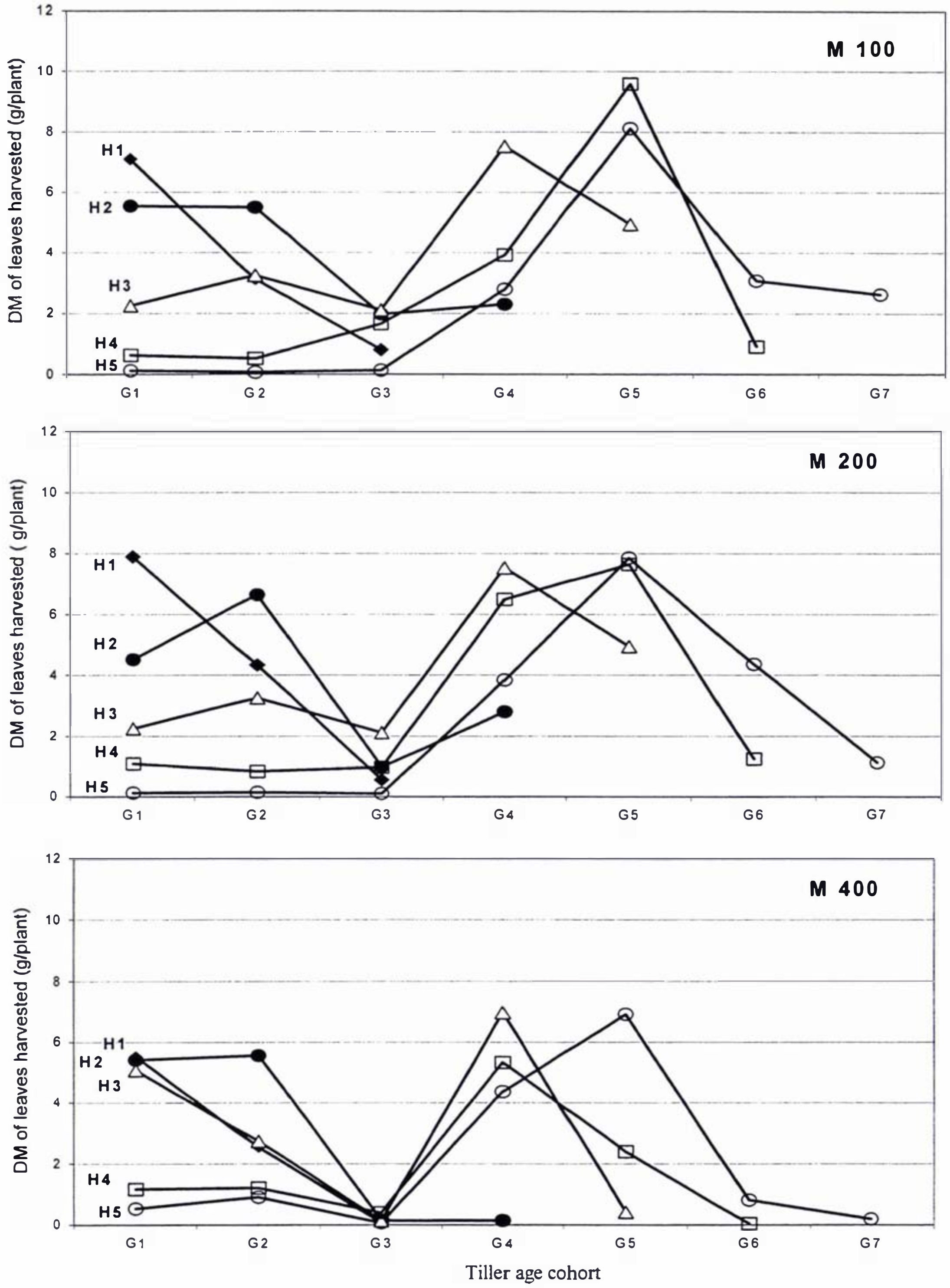


Figure 5.3. Dry weight of leaves harvested above cutting height per pot, by harvest: H1 (◆), H2 (●), H3 (△), H4 (□) and H5 (○), for each age group of tillers (G1, G2, G3, G4, G5, G6 and G7) in *P. maximum,* cv. Mombaça, subjected to three defoliation heights, 100, 200 and 400 mm.

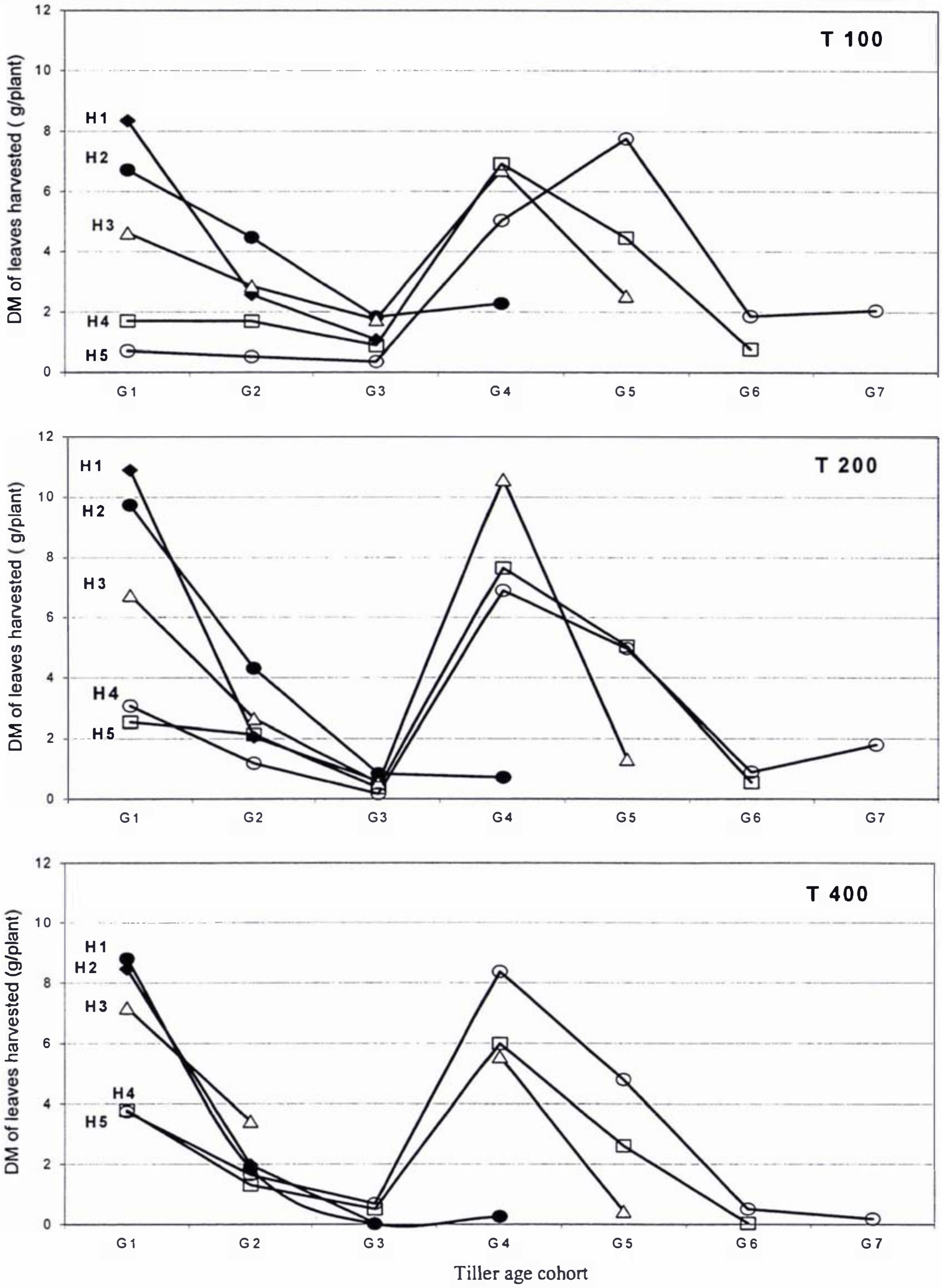


Figure 5.4. Dry weight of leaves harvested above cutting height per pot, by harvest: H1 (◆), H2 (●), H3 (△), H4 (□) and H5 (O), for each age group of tillers (G1, G2, G3, G4, G5, G6 and G7) in *P.maximum,* cv. Tanzânia, subjected to three defoliation heights, 100, 200 and 400 mm.

Tiller number per plant at each harvest for each treatment is shown in Table 5.5. Repeated Measures analyses revealed harvest and cutting height x harvest date interaction effects ($P < 0.001$) but no cultivar x harvest and cultivar x cutting height x harvest effects ($P > 0.05$). Cultivar Tanzânia had a higher tiller number averaged over the whole experiment, but the difference was not statistically significant at H3 and H4. Defoliation intensity also affected tiller number where plants cut at 100 mm had more tillers than these cut at 400mm ($P < 0.05$) from H2 until the end of the experiment. The interaction between cutting height x harvest date appears to arise from two events. Between harvests 2 and 3, tiller numbers per plant increased more sharply in plants cut at 100 mm than in the other treatments, while between harvests 4 and 5 plants cut at 100 mm showed a small decrease in tiller number while tiller numbers increased in plants cut at 200 and 400 mm height.

Table 5.5. Tiller number/plant by harvest (Hi, H0, H1, H2 H3 H4 and H5) in two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm and undefoliated plants grown separately.

Cultivar	Cut	Harvest						
		Hi	H0	H1	H2	H3	H4	H5
	(mm)			Tiller number /plant				
Mombaça	100	10.4	19.4	22.6	31.2	46.6	48.2	46.8
	200	11.0	16.8	17.8	24.0	36.0	40.6	40.6
	400	10.0	17.0	17.6	22.2	32.4	34.0	35.0
Tanzânia	100	15.0	20.6	22.2	33.8	50.4	53.2	53.0
	200	14.0	19.6	20.6	30.4	36.6	38.6	45.0
	400	13.8	22.4	23.0	29.4	36.4	40.4	44.8
s.e. cv.		0.72 ***	0.79 *	0.87 *	1.41 *	ns	ns	1.50 **
s.e. cut		ns	ns	ns	2.43 *	2.05 ***	2.62 ***	2.61 **
cv. x cut		ns	ns	ns	ns	ns	ns	ns
Mombaça	undef.	13.4	23.2	26.6	44.6	61.2	68.6	74.8
Tanzânia	undef	12.0	26.4	35.4	58.0	84.6	91.8	101.4
T-test		ns	ns	*	ns	***	***	***
s.e. cv.		1.0	1.0	2.2	3.9	4.2	4.2	5.0

(*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$; (ns) $P > 0.05$

Similar results were found when analyses where carried out on destructive harvests, considering harvest as an independent factor. Cv. Tanzânia had a higher average tiller number than cv. Mombaça ($P < 0.001$) and plants cut at 100 mm produced more tillers than these cut at 200 and 400 mm height ($P < 0.001$). At the end of the experimental period a T-test showed significantly ($P < 0.05$) higher tiller number in cv. Tanzânia compared to cv. Mombaça (101.4 and 74.8 tillers/plant) in undefoliated plants.

Tiller appearance rate (TAR) and tiller death rate (TDR) are presented in Tables 5.6 and 5.7 for both cultivars and defoliation intensities. The Repeated Measures analyses for TAR showed a significant harvest date effect and a significant harvest date x cultivar interaction ($P < 0.001$) but the interactions between harvest date and cutting height and between harvest date, cultivar, and cutting height were non-significant ($P > 0.05$).

Table 5.6. Tiller appearance rate, TAR, (tillers/100 tillers/day) by harvest (Hi, H0, H1, H2 H3 H4, and H5) in two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200, 400 mm and undefoliated.

Cultivar	Cut ht.	Harvest						
		Hi	H0	H1	H2	H3	H4	H5
	(mm)			TAR (tillers/100 tillers/day)				
Mombaça	100	18.61	4.40	0.64	1.58	2.06	0.43	0.43
	200	19.60	2.53	0.20	1.41	2.22	0.68	0.24
	400	17.86	3.47	0.22	1.19	2.01	0.33	0.25
Tanzânia	100	26.79	1.51	0.29	2.50	1.86	0.30	0.39
	200	25.00	1.81	0.20	2.13	1.33	0.28	0.75
	400	24.61	2.58	0.30	1.80	1.03	0.39	0.39
s.e. cv.		1.29 **	ns	ns	0.21*	ns	ns	0.07*
s.e. cut ht.		ns	ns	ns	ns	ns	ns	ns
cv. x cut ht.		ns	ns	ns	ns	ns	ns	ns
Mombaça	undef.	23.91	2.64	0.51	2.46	1.48	0.47	0.34
Tanzânia	undef.	21.43	4.91	1.29	2.37	1.78	0.35	0.42
T-test		ns	ns	ns	ns	ns	ns	ns
s.e. cv.		1.75	0.63	0.30	0.41	0.30	0.05	0.09

(*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$, (ns) $P > 0.05$

Considering individual harvests, cv. Tanzânia had a higher TAR than cv. Mombaça in Hi, H2 and H5, while cv. Mombaça produced more tillers in all other harvests but these differences were not statistically significant (Table 5.6). Undefoliated plants of cv. Mombaça initially had higher TAR than defoliated treatments, while in cv. Tanzânia undefoliated plants had lower TAR at Hi but higher values from H0 to H2, compared to defoliated treatments.

The Repeated measures analysis showed that TDR differed significantly between harvest dates, and the harvest date x cultivar and harvest date x cutting height ($P < 0.001$), interactions were also significant, but the interaction effect of cultivar x cutting height x harvest date was not significant. Tiller death was first observed at H1 with no difference between cultivars, but at H2 TDR was higher in cv. Tanzânia than in cv. Mombaça ($P < 0.05$). From H3 onwards, cv. Mombaça had a higher TDR than cv. Tanzânia, but the difference was only significant ($P < 0.05$) at H4. These effects explain the harvest date by cultivar interaction in the Repeat Measures analysis. The cutting height effect was only statistically significant at H5 when plants cut to 100 mm had higher TDR than the cut at 200 and 400 mm. ($P < 0.05$), and this effect explains the harvest date by cutting height interaction of the Repeat Measures analysis. Tiller death in undefoliated plants started later than defoliated plants.

Tiller cohort diagrams, using the same presentation format as in Chapter 3 (Figures 5.5 and 5.6) show the number of tillers (total of all 5 replicates) appearing in each week of the experiment. The diagrams allow comparison of the number of tillers present, variation in tiller appearance for each generation and the contribution of individual generations to TDR. From these diagrams, the higher tiller death rate in the 100 mm cutting height treatment and in Mombaça plants towards the end of the experiment, as mentioned above, are evident, and are seen to mainly involve older tillers. The high tiller death in plants of Tanzânia at H2 is shown to arise from loss of younger tillers.

Table 5.7. Tiller death rate, TDR, (tillers/100 tillers/day) by harvest (Hi, H0, H1, H2 H3 H4 and H5) in two *P. maximum* cultivars, Mombaça and Tanzânia under three defoliation heights 100, 200, 400 mm and undefoliated.

Cultivar	Cut ht.	Harvest						
		Hi	H0	H1	H2	H3	H4	H5
	(mm)			TDR (tillers/100 tillers/day)				
Mombaça	100	0	0	0.04	0.19	0.18	0.29	0.46
	200	0	0	0.00	0.08	0.35	0.21	0.22
	400	0	0	0.03	0.25	0.24	0.14	0.12
Tanzânia	100	0	0	0.04	0.50	0.08	0.09	0.36
	200	0	0	0.03	0.52	0.20	0.07	0.15
	400	0	0	0.13	0.66	0.13	0.00	0.05
s.e. cv.		ns	ns	ns	0.07 ***	ns	0.04 *	ns
s.e. cut ht.		ns	ns	ns	ns	ns	ns	0.08 *
cv. x cut ht.		ns	ns	ns	ns	ns	ns	ns
Mombaça	undef.	0	0	0.00	0.00	0.01	0.05	0.32
Tanzânia	undef.	0	0	0.00	0.00	0.00	0.28	0.11
T-test		-	-	-	-	ns	ns	ns
s.e. cv.		-	-	-	-	0.007	0.124	0.076

(*) $P < 0.05$; (**) $P < 0.01$); (***)$P < 0.001$), ns ($P > 0.05$)

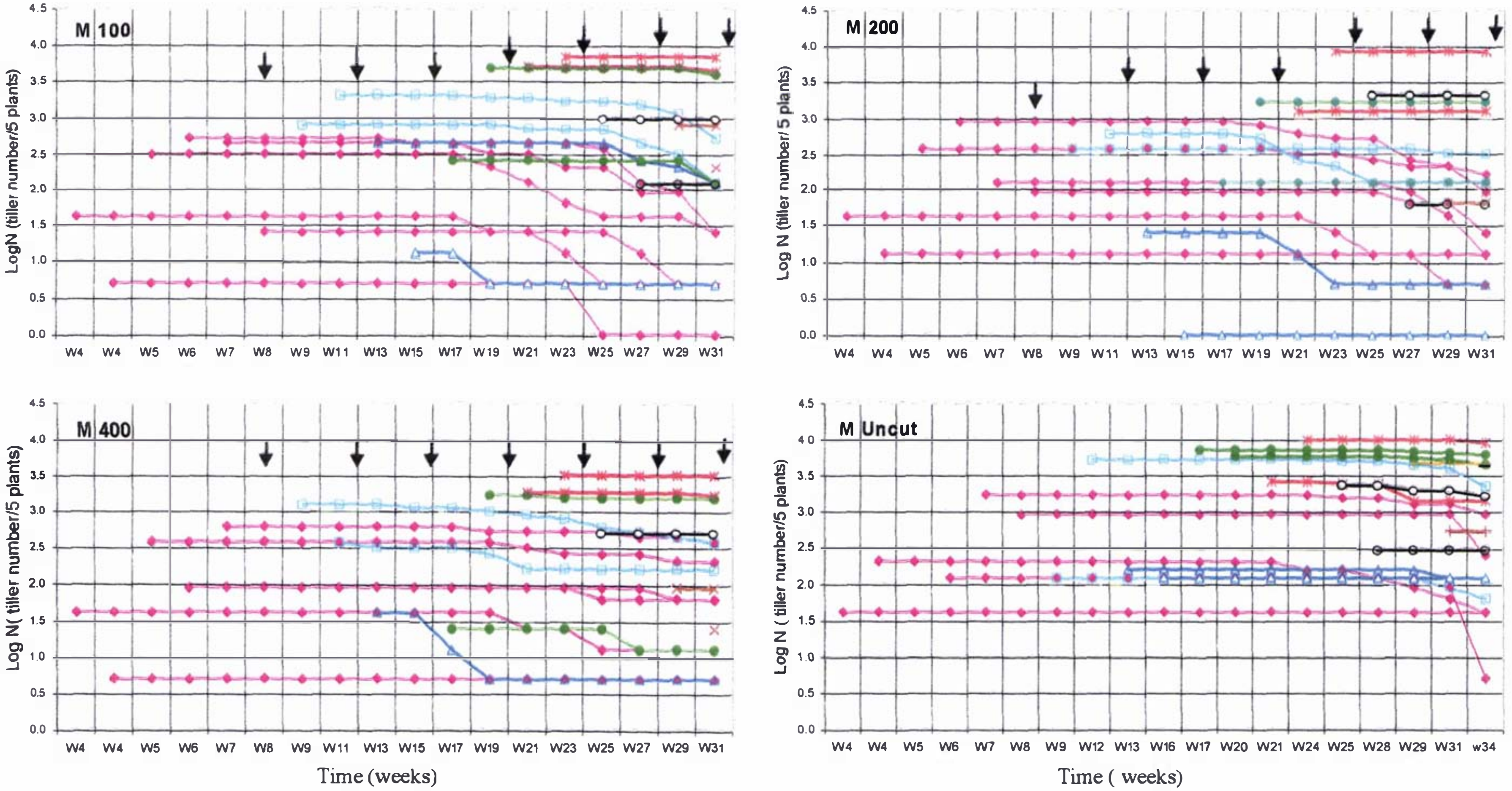


Figure 5.5. Diagrams of appearance and death in cohorts of tillers in *P.maximum* cv. Mombaça, subjected to three defoliation heights, 100, 200, 400 mm and uncut, from September 1999 to April 2000. Arrows indicate all sequential harvests (H1 to H5). Line colors represent each age cohort (G1 = ◆), (G2 = □), (G3 = △), (G4 = ●), (G5 = ✱), (G6 = O) and (G7 = ×)

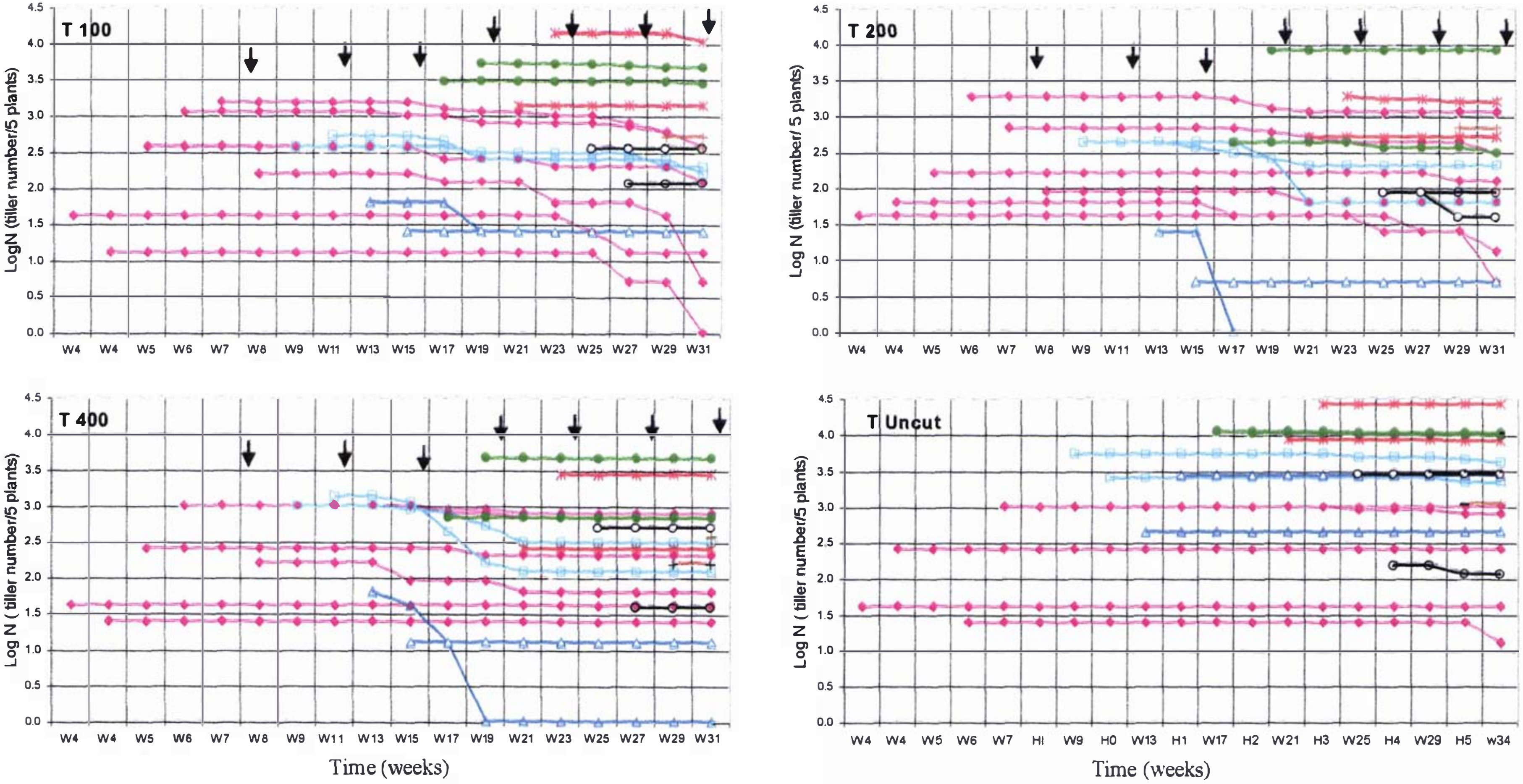


Figure 5.6. Diagrams of appearance and death in cohorts of tillers in *P.maximum* cv. Tanzânia, subjected to three defoliation heights, 100, 200, 400 mm and uncut, from September 1999 to April 2000. Arrows indicate harvests (Hi to H5). Line colors represent each age cohort (Gl = ◆), (G2 = □), (G3 = △), (G4 = ●), (G5 = *), (G6 = O) and (G7 = ×)

5.3.3. Leaf appearance rate, leaf elongation rate, specific leaf area and photosynthesis in aging tillers

Leaf appearance rate, LAR, in old, mature and young tillers for both cultivars and cutting height is shown in Table 5.8. The statistical analysis revealed no cultivar effect (0.076 and 0.070 leaves/tiller/day, s.e.: 0.007, $P > 0.05$, for cvs. Tanzânia and Mombaça) but the main effect of cutting height was statistically significant (0.083, 0.075 and 0.056 leaves/tiller/day for 100, 200 and 400 mm, respectively, s.e. 0.006, $P < 0.01$), as was the age effect (0.045, 0.076 and 0.098 leaves/tiller/day for old, mature and young tillers, respectively, s.e. 0.006, $P < 0.001$). There was a significant interaction between cultivar and tiller age ($P < 0.05$,Table 5.8) due to very low LAR in old tillers in cv. Mombaça when compared to cv. Tanzânia. The cutting height x tiller age interaction was not significant ($P > 0.05$).

Table 5.8. Leaf appearance rate, LAR, (leaves/tiller/day) on leaves of three different tiller age categories (old, mature, and young) of two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm.

Cut ht.		Tiller age	
(mm)	Old	Mature	Young
100	0.045	0.090	0.130
200	0.045	0.080	0.100
400	0.045	0.060	0.065
Cultivar			
Mombaça	0.026	0.080	0.103
Tanzânia	0.063	0.073	0.093
s.e. cv.	ns		
s.e. cut ht.	0.006 **		
s.e. age	0.006 ***		
s.e cv. x age	0.008 *		
s.e cut ht. x age	ns		

(*) $P < 0.05$; (**) $P < 0.01$); (***)$P < 0.001$), ns ($P > 0.05$)

Table 5.9 shows leaf elongation rate, LER on tillers designated old, mature and young for the six treatments. LER was measured either (LER_a) above cutting height or (LER_t) from the ligule of the next older leaf for all elongating leaves in the tiller. The analysis of LER_a showed significant effects for cultivar ($P < 0.01$), cutting height ($P < 0.01$), age ($P < 0.001$) and also the cultivar x cutting height interaction ($P < 0.05$) and the cutting height x tiller age interaction ($P < 0.001$). The analysis of LER_t yielded only significant effects for tiller age ($P < 0.001$) and the cultivar x tiller age interaction ($P < 0.05$).

Table 5.9. Leaf elongation rate, LER, (mm leaf/tiller/day), of tillers of three different ages (old, mature, and young) of two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm. Data for (LER_a) were measured above cutting height. Data for (LER_t) were measured from the ligule of the previous fully elongated leaf on the stem.

Cut ht.	Cultivar	Tiller age			Cut ht.	Cultivar	Tiller age		
		Old	Mature	Young			Old	Mature	Young
(mm)		LER_a (mm leaf/tiller/day)			(mm)		LER_t (mm leaf/tiller/day)		
100	Mombaça	4.9	27.6	39.9	100	Mombaça	4.3	24.9	34.3
	Tanzânia	12.4	25.0	34.8		Tanzânia	18.6	26.3	34.1
200	Mombaça	5.3	23.4	31.0	200	Mombaça	7.0	27.3	38.1
	Tanzânia	16.9	29.0	42.0		Tanzânia	16.2	30.6	35.4
400	Mombaça	9.1	25.6	19.4	400	Mombaça	10.3	31.1	34.9
	Tanzânia	15.4	26.5	22.2		Tanzânia	13.6	21.7	31.7
	s.e. cv.	1.1 *				s.e. cv..	ns		
	s.e. cut ht	1.3 *				s.e. cut ht	ns		
	s.e. age	1.1 ***				s.e. age	1.4 ***		
	s.e. cv. x cut ht.	1.9 *				s.e. cv. x cut ht.	ns		
	s.e. cv. x age	ns				s.e. cv. x age	2.0 *		
	s.e. cut ht. x age	1.9 ***				s.e. cut ht. x age	ns		

(*) $P < 0.05$; (**) $P < 0.01$; (***)$P < 0.001$), ns ($P > 0.05$)

Specific leaf area, SLA, is shown in Table 5.10. Missing values in cv. Mombaça measurements required a separate analyses of variance for each cultivar. Both analyses demonstrate significant cutting height and age effects but the interaction between these effects was only significant for cv. Tanzânia. Old tillers showed higher SLA than mature tillers in cv. Mombaça contrasting to cv. Tanzânia where the higher SLA was found in young tillers. Both cultivars had a higher SLA when cut at 100 than at 400 mm.

Table 5.10. Specific leaf area, SLA, (cm^2/g leaf), for leaves of three different tiller age categories (old, mature, and young) of two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm.

Treatment	Tiller age			Treatment	Tiller age		
	Mombaça				Tanzânia		
Cut ht (mm).	Old	Mature	Young	Cut ht	Old	Mature	Young
100	302.0	236.0	265.7	100	291.3	253.3	278.3
200	270.6	219.2	235.5	200	240.9	227.7	302.1
400	225.9	188.4	219.8	400	201.2	210.0	275.3
s.e cut ht.	8.9*			s.e. cut ht	7.6 **		
s.e. age	7.4***			s.e. age	4.7 ***		
s.e. cut ht. x age	ns			s.e. cut ht x age	8.2 ***		

(*) $P < 0.05$; (**) $P < 0.01$); (***)$P < 0.001$), ns ($P > 0.05$)

Photosynthetic activity was measured as the CO_2 absorbed per unit area of green leaf per unit time (μmol CO_2/m^2 leaf/s) on the youngest fully elongated leaf of old, mature and young tillers in both cultivars and at all cutting heights, and results are shown in Table 5.11. The statistical analysis revealed a tiller age effect (12.2, 15.8 and 15.8 μmol $CO_2/m^2/s$, s.e: 0.70, $P < 0.001$ for old, mature and young tillers, respectively) but no cultivar or cutting height effect ($P > 0.05$). There was also a cultivar x tiller age interaction ($P < 0.01$) was due to less efficiency in CO_2 uptake from leaves of old tillers in cv. Mombaça when compared to similar leaves from old tillers in cv. Tanzânia.

Table 5.11. Photosynthesis rate, PR, (μmol CO_2/m^2 leaf/s) for three tiller age categories (old, mature, and young) of two *P. maximum* cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm.

Cultivar	Tiller age		
	Old	Mature	Young
Mombaça	10.0	16.5	15.9
Tanzânia	15.0	15.2	15.8
s.e. cv.	ns		
s.e. cut ht.	ns		
s.e. tiller age	0.58 ***		
s.e. cv. x age	0.83 **		
s.e. cut ht. x age	ns		

(*) $P < 0.05$; (**) $P < 0.01$); (***)$P < 0.001$), ns ($P > 0.05$)

5.3.4. Descriptive morphology of cultivars Mombaça and Tanzânia

Figure 5.7 categorises tiller population of the undefoliated plants and the proportions of vegetative, flowering and dead tillers within the tiller cohorts. A T test showed significant effects of cultivar on total tiller number (101.4 and 74.8 tillers/plant $P < 0.05$), number of flowering tillers (31.0 and 13.8 $P < 0.05$) and number of dead tillers (6.0 and 16.8 $P < 0.05$) in cvs Tanzânia and Mombaça.

By the end of the experiment it was noted that a proportion of tillers remained alive, but with no discernible leaf elongation. Therefore, at the end of the experiment, H5, the proportion of live tillers still in the process of elongating at least one leaf was measured (Figure 5.8). The occurrence of tillers with no elongating leaf was greatest among old tiller groups (G1, G2 and G3), while the youngest groups (G6 and G7) had almost all tillers with at least one leaf in the process of elongation. Occurrence of tillers without elongating leaves was also more evident in cv. Mombaça, and in the 100 mm cutting height.

The length of the youngest fully elongated leaf was measured in all tillers in the last harvest and results are plotted in Figure 5.9. On average cv. Mombaça plants produced longer leaves than cv. Tanzânia (342 and 296 mm/leaf, respectively, s.e. 3.5, $P < 0.001$) in all cutting heights, but in general, older tillers (G1, G2) produced shorter leaves than mature tillers (G4, G5) in the same treatment for both cultivars (Figure 5.9).

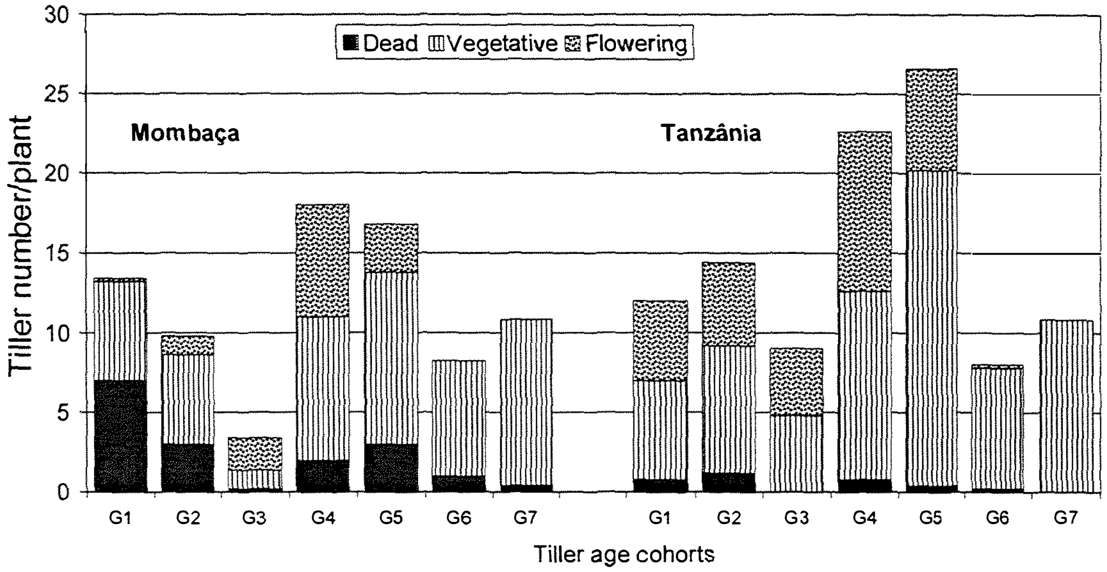


Figure 5.7. Total tiller number/plant for undefoliated plants grown separately, classified according to tiller age (G1, G2, G3, G4, G5, G6, G7) and reproductive status (dead, vegetative and flowering categories), in two Guinea grass cultivars, Mombaça and Tanzânia, at the end of the experimental period (April 2000).

Figures 5.10 and 5.11 summarize data collected from pots at H4 where tillers were classified according to tiller height and tiller fresh weight within age categories. Although no statistical analysis was carried out, differences in distribution of tiller size and tiller weight groups among cultivars are evident. At 100 mm cutting height cv. Mombaça showed similar proportions of small and intermediate tillers while cv. Tanzânia had almost three times more intermediate sized tillers than small-sized tillers (Figure 5.10). For both cultivars less than 1% of the tiller population was in the large tiller category in this treatment. At 200 mm cutting height both cultivars had about 12% of small tillers but only 4% of the tiller population was categorized as large in cv. Mombaça, while Tanzânia had 32% in this category. On the other hand, when cut at 400 mm both cultivars had a similar proportion of large tillers (approximately 60%) and small proportion (less than 5%) of small tillers.

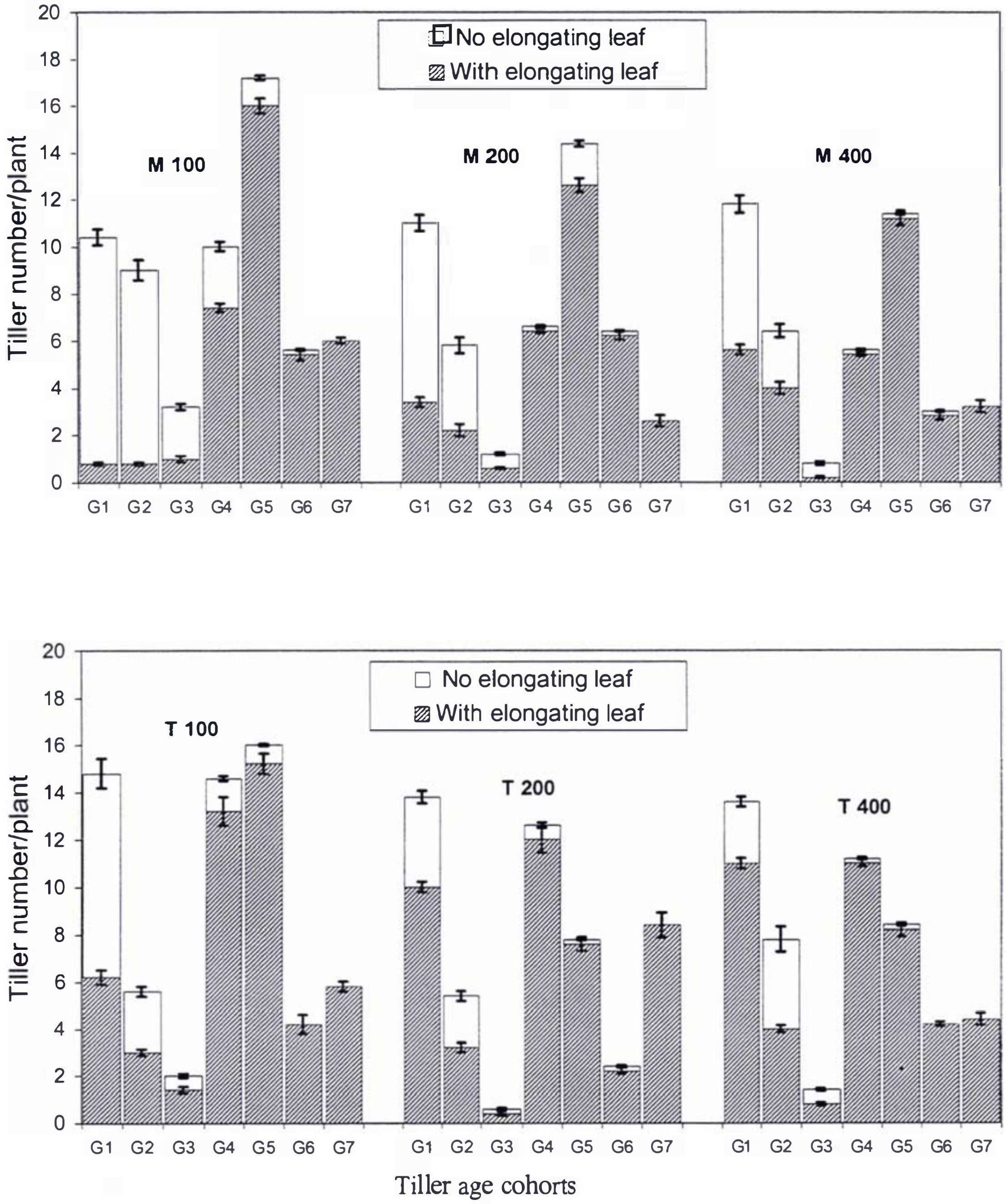


Figure 5.8. Proportion of live tillers at the last harvest (H5) with and without elongating leaves in two *P. maximum* cultivars, Mombaça (M) and Tanzânia (T), subjected to three defoliation heights, 100, 200 and 400 mm. Tillers are classified into age groups (G1, G2, G3, G4, G5, G6 and G7). Bars are s.e.

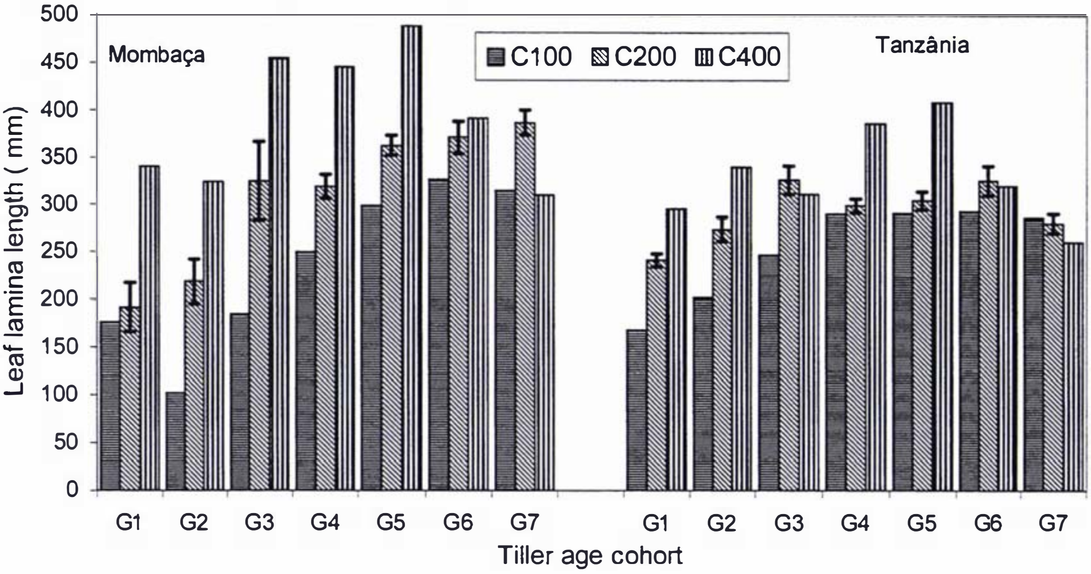


Figure 5.9. Average lamina length (mm) for the last fully elongated leaf in two *P. maximum* cultivars, Mombaça and Tanzânia, under three cutting heights 100, 200 and 400 mm. Tillers are classified into age groups (G1, G2, G3, G4, G5, G6 and G7). Bars are the s.e. for each age group of each cultivar.

In general cv. Mombaça tillers were heavier than Tanzânia tillers, and this can be seen from the larger number of heavier tillers in cv. Mombaça when tiller size profiles of a particular age group and cutting height are compared (Figure 5.11). At 100 mm both cultivars had all tillers distributed into three categories, but cv. Mombaça had 70 % and 6% in very light and intermediate categories, whereas cv. Tanzânia had 78% and 0.8 % in the same categories. At 200 mm both cultivars presented similar distribution in categories very light, light and intermediate, but cv. Mombaça had 6% and 1%, respectively, of its tillers classified into heavy and very heavy categories, while cv. Tanzânia had only 2% in the heavy category and no tillers in the very heavy category. When cut at 400 mm, cv. Mombaça had 8% and 30% of tillers in the extreme categories (very light and very heavy) in contrast with cv. Tanzânia which had 19% of very light tillers and only 8% of its tillers classified as very heavy.

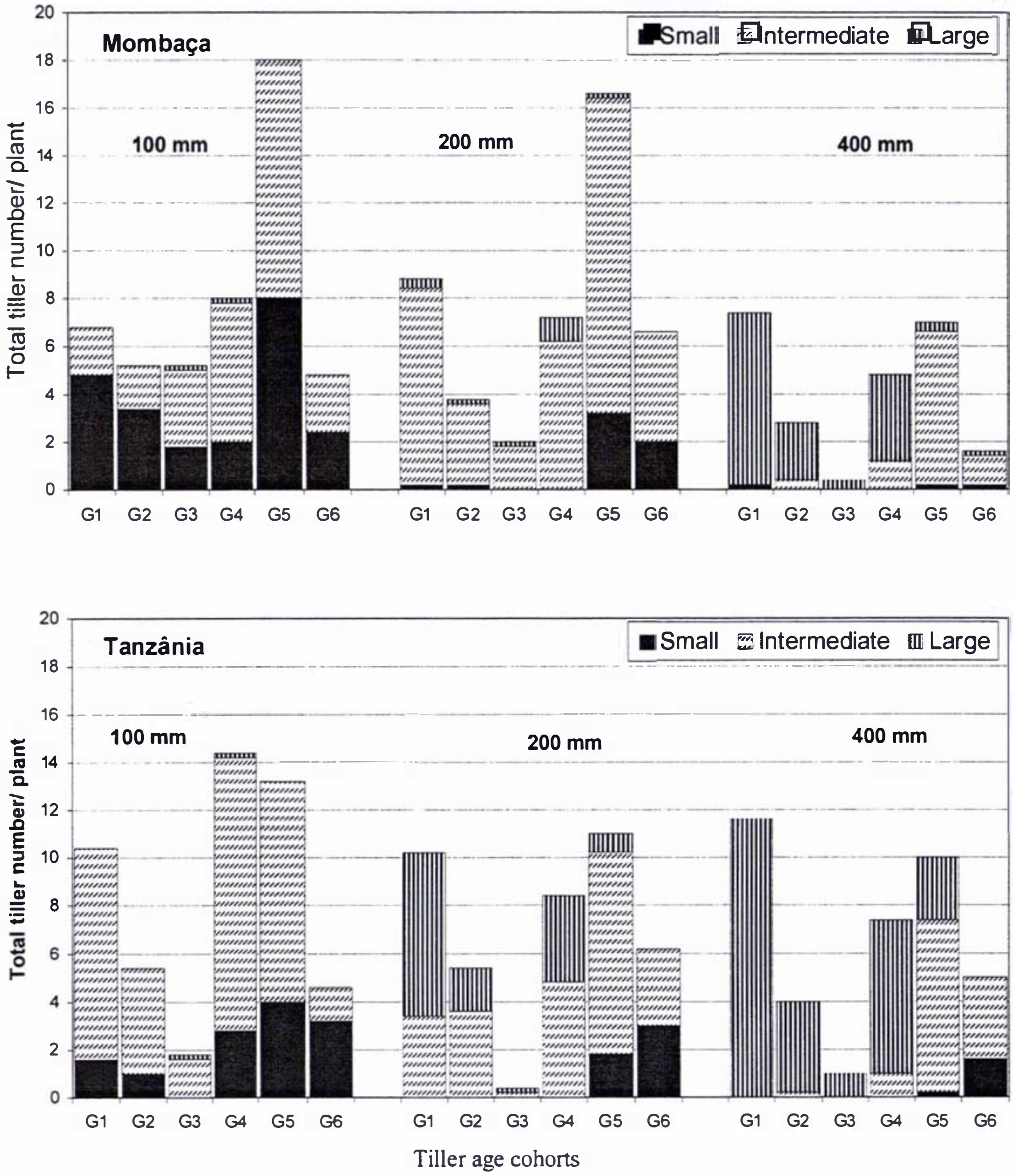


Figure 5.10. Total tiller number/plant distributed into age groups (G1, G2, G3, G4, G5, G6 and G7) and classified into height categories: small (<100 mm height), intermediate (100 to 200mm) and large (>200 mm height) in two *P. maximum* cultivars, Mombaça and Tanzânia, subject to three defoliation heights, 100, 200 and 400 mm.

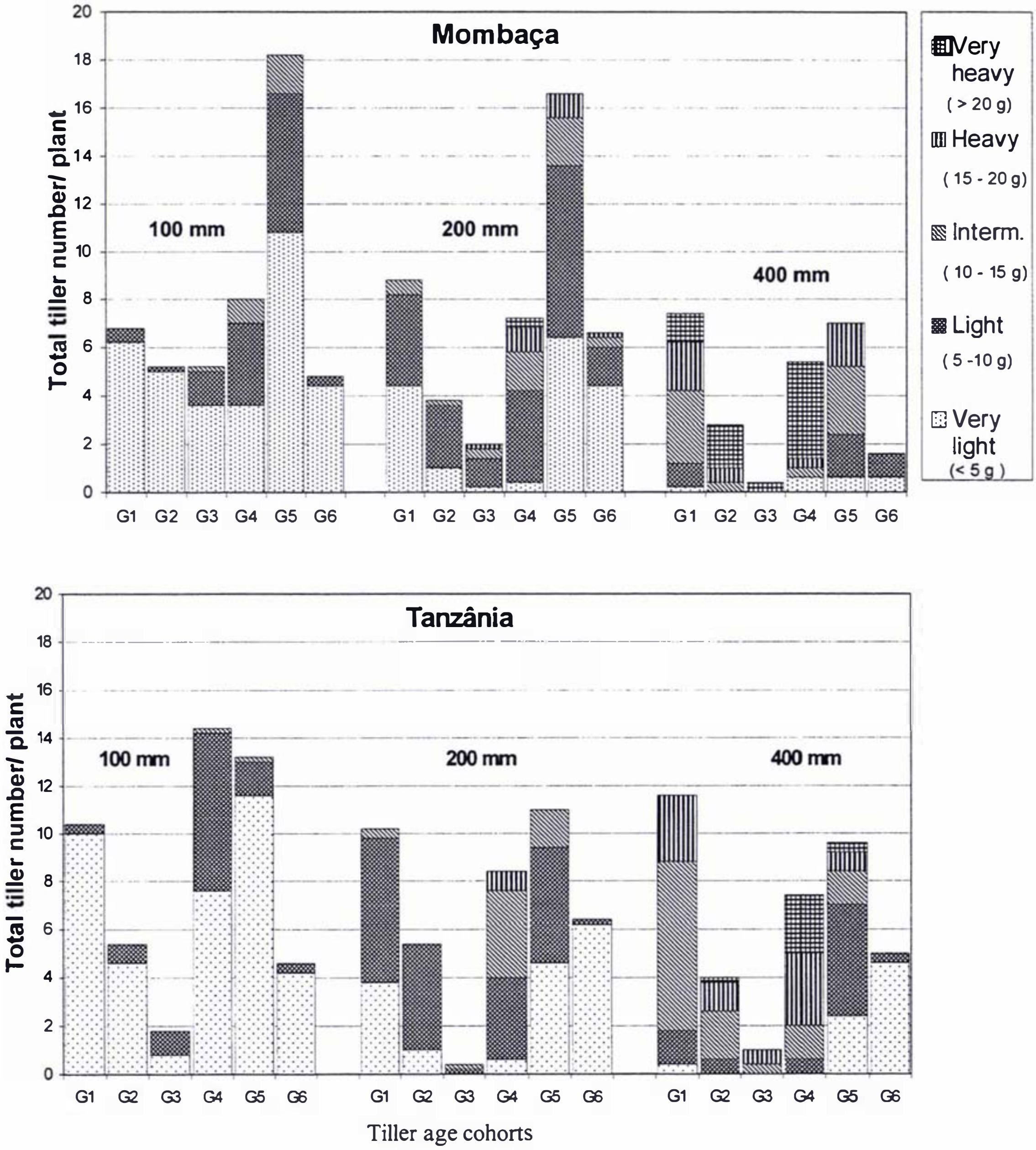


Figure 5.11. Total tiller number/plant sorted by age groups (G1, G2, G3, G4, G5, G6 and G7) and classified according to fresh weight as very light (0.1 to 5.0 g), light (5.1 to 10.0 g), intermediate (10.1 to 15.0 g), heavy (15.1 to 20.0 g) and very heavy (>20.0 g) in two *P. maximum* cultivars, Mombaça and Tanzânia, subjected to three defoliation heights, 100, 200 and 400 mm.

5.3.5. Root Mass

Total root mass (g OM/pot) at each harvest is shown in Table 5.12. On average, cv. Mombaça produced more root mass than cv. Tanzânia (18.6 and 17.1g/pot s.e: 0.44, $P < 0.05$) and plants cut at 400mm height produced more root mass than those cut at 200 or 100 mm (21.9, 16.4 and 15.2, s.e. 0.53, $P < 0.001$). There was a harvest effect, with root mass increasing at successive harvests (10.7, 13.7, 20.1, 20.2, and 24.6 g OM/pot for H1, H2, H3, H4 and H5, respectively, s.e 0.53, $P < 0.001$). There was a significant effect for the harvest x cutting height interaction ($P < 0.001$) due likely to a high increment in root mass in the last harvest (H5) in both cultivars at the 400 mm cutting height, but not at the 100 mm and 200 mm cutting heights. There was no interaction between cultivar and harvest date, cultivar and cutting height or cultivar, cutting height and harvest date.

Table 5.13 shows the root mass accumulated between harvests within the sand-filled cores. The results showed a pattern similar to that observed for total root mass, where cv. Mombaça produced more root mass than cv. Tanzânia (125 and 108 mg OM/core, respectively, s.e. 4.6, $P < 0.05$), plants cut at 400mm produced more than those cut at 200 and 100 mm height (148, 101 and 99 mg OM/core, s.e. 5.6 $P < 0.001$). In H5 there was more root mass produced than in the other harvests (65, 72, 117, 124 and 202 mg OM/core for H1, H2, H3, H4 and H5 respectively, s.e. 7.0, $P < 0.001$). There was an interaction between harvest and cutting height ($P < 0.01$) likely explained by the increasing difference in root production in the last harvest (H5) at 400 mm treatment compared to the other two cutting heights. The interactions cultivar x cutting height, cultivar x harvest date and cultivar x harvest date x cutting height were not statistically significant ($P > 0.05$).

Table 5.12. Root mass accumulated (g OM/pot) at successive destructive harvests (H1, H2, H3, H4 and H5) for two *P. maximum* cultivars, Mombaça and Tanzânia, subjected to three defoliation heights, 100, 200 and 400 mm.

Cut ht.	Cultivar	Harvest				
(mm)		H1	H2	H3	H4	H5
			Organic Matter (g/pot)			
	Mombaça	11.9	13.4	18.2	18.8	19.2
100	Tanzânia	8.9	11.2	16.3	15.8	18.6
200	Mombaça	10.4	12.1	20.0	20.6	22.5
	Tanzânia	10.3	12.2	17.5	16.9	21.8
400	Mombaça	13.2	17.4	24.7	23.8	33.0
	Tanzânia	9.9	15.9	24.4	24.5	32.1

s.e. cv. 0.44*

s.e hv 0.69 ***

s.e. cut ht 0.53 ***

s.e. cv x hv 0.98 ns

s.e. cv x cut ht. 0.76 ns

s.e. hv x cut ht 1.19***

s.e. cv x cut ht x hv 1.69ns

(*) $P < 0.05$; (**) $P < 0.01$); (***) $P < 0.001$ ns ($P > 0.05$)

Table 5.13. New root production in core holes (mg OM/core/pot) between destructive harvests (H1, H2, H3, H4 and H5) for two *P. maximum* cultivars, Mombaça and Tanzânia, subjected to three defoliation heights, 100, 200 and 400 mm.

Cut	Cultivar	Harvest				
(mm)		H 1	H 2	H 3	H 4	H 5
			Organic Matter (mg/core/pot)			
	Mombaça	55.5	49.6	130.6	131.5	142.9
100	Tanzânia	55.2	59.5	86.3	104.7	178.2
200	Mombaça	65.4	72.5	119.9	115.4	198.8
	Tanzânia	55.1	60.9	104.7	88.8	142.0
400	Mombaça	88.2	102.3	139.7	167.8	288.6
	Tanzânia	71.5	89.7	178.2	137.1	262.0

s.e. cv. 4.60 *

s.e hv 7.27 ***

s.e. cut ht. 5.63 ***

s.e. cv. x hv 10.28 ns

s.e. cv x cut ht. 7.96 ns

s.e. hv x cut ht. 12.60 **

s.e. cv x cut ht x hv 17.81ns

(*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$, ns ($P > 0.05$)

5.4. Discussion

5.4.1. Herbage mass harvested and tiller dynamics

Results in the literature show cv. Mombaça generally having higher DM yield than cv. Tanzânia, but not always (Dias Filho et al., 1995). In the present study where plants were harvested to different cutting heights there was no cultivar effect on total DM harvested (Table 5.2) but dry matter harvested tended to be greater from cv. Mombaça in the first two harvests and was significantly greater from cv. Tanzânia in the last two (H4 and H5), (Table 5.3).

The cutting height effect was evident for total dry matter harvested (leaves and stem/pseudostem, Table 5.3) and for leaves alone (Table 5.4). Total green herbage DM harvested increased with increasing defoliation severity in both cultivars (Table5.2). However, results from Chapter 3 (Figures 3.5 and 3.6) indicate that these grasses cannot maintain productivity in the long term when defoliated at 150 mm or lower.

There was an increase in DM harvested in the last harvest (H5) for all treatments (Table 5.3), and this was associated, partially with an increase in stem material. The proportion of pseudo stem/true stem fraction increased to about 15% in cv. Tanzânia at 100 and 200 mm cutting heights in H5 (Table 5.3) resulting in similar DM harvested in all treatments. In contrast cv. Mombaça had a low proportion of stem material (4.4%) at 200 mm cutting and complete absence of this fraction at 400 mm cutting height resulting in less dry matter harvest at this treatment compared to cv. Tanzânia. Similar results were found by Brâncio et al. (2000) evaluating cv. Tanzânia and Mombaça under grazing. These authors found a similar proportion of stem fraction in the spring and summer period before grazing, but this proportion increased to about 25% in both cultivars in autumn, the period of faster internode elongation due to flowering.

There is some inconsistency in the results from Tables 5.3 and 5.4 where at some harvests leaf DM harvested above cutting height (Table 5.4) appears to be greater than the DM of leaf plus stem harvested at the same height (Table 5.3) This discrepancy probably reflects minor variation in actual defoliation height for plants harvested 'in situ'

(Table 5.3) and those cut after destructive harvest (Table 5.4). Also, the two data sets represent different populations of plants (see Materials and methods), thereby introducing sampling error.

More lenient cuts, as expected, resulted in more senescent material (Table 5.2), in agreement with the classical curve of growth, net production and senescence in perennial ryegrass/white clover swards (Bircham & Hodgson, 1983). In these circumstances care is necessary to manage the plant since low cuts are deleterious leading to a drop in yield and possible degradation of the sward, while under more lenient defoliation senescent material losses are higher. There is little information about senescence in field conditions with tropical grasses (Rodrigues & Reis, 1995) and this kind of measurement should be evaluated under grazing systems since animals have a strong influence on losses as well. In this context Quadros et al. (2001), evaluating forage losses in well fertilized pastures of Tanzânia and Mombaça grazed rotationally each 28 days with a post grazing residual about 30-40 cm height, concluded that cv. Tanzânia showed a higher percentage of forage losses in the plant due to senescence than cv. Mombaça, while cv. Mombaça had higher losses caused by animal grazing, probably because of the more open architecture of the leaves.

Productivity is related to number and size of tillers present at a given time in one population (Nelson & Zarrough, 1981) and dynamic changes in population density have been discussed earlier (Chapter 3 and 4). However, though there is a great variability within the sward in tiller cohort populations at different stages of development (Rodrigues & Reis, 1995), little is known about contribution of individual cohorts to herbage production. In this study destructive harvests over time and evaluation of the dry weight of leaves for each tiller cohort provided information on the changes over time in tiller age cohorts (Figures 5.3 and 5.4). In both cultivars Mombaça and Tanzânia the early tiller cohorts (G1, G2 and G3) contributed progressively less to yield over time (Figures 5.3 and 5.4). The contribution of the youngest cohorts at each harvest was limited because the tillers were too small to reach the defoliation height, particularly at 400 mm. Tillers from G3 (tagged between harvest H0 and H1 in November /December) were few in number (Figure 5.8) and made a correspondingly small contribution to yield in all treatments and at all harvests. The reason for this is not clear, but may relate to the sequence of ontogenetic development. Pedreira (1975a) also observed a decline in tillering activity after a high initial tillering rate in the initial growth phase of Guinea grass cv. Colonião. A feature common to both cultivars in Figure 5.3 and 5.4 is the progressive decline in contribution to yield with time of the oldest cohort groups G1, G2 and G3, in all cutting heights. Also, as expected, the contribution to yield for younger cohorts, G6 and G7, at 400 mm height (at harvest H4 and H5, respectively) was very low because those tillers were below defoliation height. On the other hand at 100 mm, more tillers, including the young ones, could contribute to yield since most of them had at least reached the 100 mm height. This is likely to be one of the reasons why low cuts produced more herbage harvested than high treatment with more tillers contributing to yield as discussed previously.

The most important difference between cultivars is the tendency for tillers to live longer in cv. Tanzânia than in cv. Mombaça. This can be seen from the higher contribution to yield of older tillers (G1, G2, and G3) in cv. Tanzânia than in cv. Mombaça at later harvests (H4 and H5) (Figures 5.3 and 5.4) and from the fact that for later harvests the strongest contribution to yield came from G4 in cv. Tanzânia but from G5 in cv. Mombaça. This fact suggests there is a group of tillers contributing more to DM harvest than others and this group changes with time. However the observation the contribution of old tillers is restricted, is more evident under the more severe defoliation treatment. Santos et al. (2001) working with swards of cv. Tanzânia under three grazing intensities (1000, 2000 and 4000 kg DM/ha post grazing residual) concluded that there was no particular age cohort contributing to yield when evaluation was carried out in June (end of autumn). Differences in the two sets of results may be due to the late autumn harvest sampling in the study of Santos et al. (2001), in contrast to the early autumn harvest and cutting height sampling resulting in substantially higher stem proportions of the former case.

Tiller appearance rate was higher at the beginning of the experiment, as expected and described in other experiments with other grasses (Pedreira, 1975a) and also for these two cultivars (Chapter 3). Also, cv. Tanzânia had higher TAR in the first harvest (Hi) than cv. Mombaça which is in agreement with the results illustrated in Chapter 3, and also in the literature (Gomide, C.A.M., 1997).

Tiller population per plant increased progressively with time, and with increasing severity of defoliation, though it was substantially greater for undefoliated plants than for the defoliated plants (Table 5.5). Defoliation effects on TAR and TDR within harvest period were generally not significant but cumulative effects over time were significant (Tables 5.5, 5.6, 5.7)

The effects of cutting height on tiller number per pot or per area reported in the literature for temperate and tropical grasses vary within and between grass species. Close cutting may increase (Hernández - Garay et al., 1999; Carvalho C.A. et al., 1999), decrease (Auda et al., 1966; Carvalho D. D. et al., 1999) or have no effect (Barbosa et al., 1996) on tillering. The main factor used to explain the effects of defoliation is the depletion in carbohydrate content for plant recovery (Brown & Blaser, 1965; Gomide & Zago, 1980) although other behavioral traits such as size/density compensation for instance, also play an important role in defining tillering activity (Matthew et al., 2000).

There was an increase in tiller number over time in all treatments in both cultivars (Table 5.5). Tiller number was consistently higher in cv. Tanzânia than cv. Mombaça in agreement with results from Chapters 3 and 4 and other experiments with these two cultivars (Santos, 1997; Gomide, C.A.M., 1997; Barbosa, et al.1996). This advantage may be related to the greater LAR in cv. Tanzânia (Table 4.1), although differences in TAR and TDR between cultivars were small and inconsistent. However this non-significant TAR will add over time to a highly significant ($P < 0.01$) total tiller number in cv. Tanzânia than cv. Mombaça (Table 5.5) at the end of the experiment.

The greater tiller number in undefoliated plants than in defoliated plants substantiates the findings of Kaneko et al. (1990) who observed the same results in seven lines of *P. maximum*. This observation that undefoliated plants produced more tillers than defoliated plants, contradicts the assumption about apical dominance in tropical grasses (Murphy & Briske, 1992).

In the classical experiment carried out by Pedreira (1975a) where tillering was measured in undefoliated potted plants of *P. maximum* cv. Colonião, the author measured just the number of tillers that appeared in the first year from sowing in September (spring) to July (winter). The results were quite similar to these in the present trial with an intense initial tillering rate decreasing over time, but some increase in TAR near the flowering period (autumn). Unfortunately tiller death was not evaluated by Pedreira (1975a). In the current study, tiller death started later in undefoliated plants than in defoliated plants. Kaneko et al. (1990) evaluating contrasting tillering lines of *P. maximum* also found a later onset of death and lower death rate in undefoliated plants when compared to defoliated ones but in contrast to the current results, it was observed that lines with high tillering abilities had higher tiller death compared to low tillering lines.

The diagrams presented in Figure 5.5 and 5.6 allow visualisation of the number of tillers appearing in each cohort, their persistence, and their contribution to tiller death. They illustrate the high persistency of young tillers and the great losses of old than young tillers at time of stress (harvests). This behaviour contrasts with that reported for temperate grasses. Temperate grasses under environmental stress, recently formed tillers tend to die first when the whole plant is stressed (Langer, 1963, Ong, 1978).

Although tiller death occurred mainly in older generations (G1 and G2) there were some unexpected observations such as the increase in tiller death in H2 in cv. Tanzânia (Table5.6) that also encompassed the new generation G3 at that time. There was no obvious explanation for this occurrence.

This kind of diagram also allows visualization of the numbers of tillers in each cohort and the identification of cohorts with small numbers of tillers. In cv. Mombaça cut at 400mm, for ex. two cohorts (on week 15 and week 27) were not produced (Figure 5.5).

Figure 5.8 highlights cutting height and cultivar effects on tiller number per plant, distinguishing between those with and those without elongating leaves. Older tiller cohorts (G1, G2 and G3) were less efficient in leaf production than young cohorts, the effect decreasing with decrease in defoliation severity. This effect appears to have an influence on herbage production (Figures 5.3 and 5.4). Figure 5.9 confirms observations reported in Chapter 4 when more drastic defoliation reduced final leaf length (see page 67).

LER in this experiment was measured in two different ways (Table 5.9): LERa above cutting height and LER_t the whole profile, monitoring all leaves elongating on the tiller in each case. Estimates of LER by the two methods were similar for both cultivars and all tillers ages except for young tillers in 400 mm treatment, where the estimate of LER above cutting height clearly underestimate actual LER.

5.4.2. Evidence for tiller aging

In developing improved grazing systems the level of herbage utilization in pastures is important, and more efficient grazing systems attempt to avoid losses by senescence (Hodgson, 1990). Causes of tiller and/or leaf death on grazed pastures have been attributed to physiological or physical process (Ong, 1978; Ong et al, 1978; Vine, 1983; Woodward, 1998). The cause of tiller death most often discussed in tropical bunch grasses is the elimination of the growing point after stem elongation that occurs during vegetative growth, contrasting with most of the temperate grasses where elongation only occurs in the flowering period. But few studies with tropical grasses have considered death by causes other than decapitation itself (Rodrigues & Reis, 1995).

Studies have been reported on the morphological and physiological differences in leaves according to the position or insertion level on the stem (Brown et al., 1966; Wilson & Cooper, 1969; Wilson, 1976 a, b). It is important to define leaf age in such studies. The old leaf can be considered the first emerged on a tiller and the youngest the last emerged. But under defoliation, when tillers are compared from different dates of appearance an "old" tiller may be elongating for example its 12th leaf and the youngest its 7th, even though both leaves may be the last fully elongated on the tiller at that specific time. So according to the management imposed an "old" tiller is likely to have been subjected to more defoliation events than a young tiller and this fact can affect morphology and physiology of the leaf rather than position on the stem. In this experiment the insertion level was not quantified but, using data from a previous experiment (Chapter 4), it could be estimated that old tillers (between H4 and H5) were elongating their 12th or higher leaf, the mature tillers between 7th and 9th leaf and the youngest the 4th to 6th leaf.

In the present study it was observed that tillers died even with their growing point intact, indicating a progressive loss of vigour, which was more evident in cv. Mombaça (Figure 5.7). This effect was also reported in Chapter 4 with undefoliated plants of Mombaça. Detailed measurements were performed to quantify this effect and define the effect of defoliation intensity on it. LAR declined with tiller age, and LAR in old tillers averaged 46% of young tillers, and cv. Mombaça was more severely affected than cv.

Tanzânia (Table 5.8). The effects of the physiological characteristics in cultivar performance and on management deserve further studies.

LER also declined very substantially with increasing tiller age, so that LER in old tillers averaged 34 % of that in young tillers (Table 5.9). This contrast was reflected in tiller age differences in final leaf length (Figure 5.9). Similar results in LER were observed in minisward experiment (Chapter 3) though overall values were lower in that experiment because measurements were made in winter (LER 4.9 vs. 12.9 mm leaves/tiller/day s.e. 0.79, $P < 0.001$ for "old" and "young" tillers respectively). In addition the number of non-elongating leaves as a proportion of total leaves increased progressively and substantially with increasing tiller age in all treatments in the current experiment (Figure 5.7)

In Chapter 3 it was found that cv. Mombaça had heavier leaves with lower SLA than cv. Tanzânia. In this experiment cv. Mombaça again had on average lower SLA on leaves from mature and young tillers, but not from old tillers compared to cv. Tanzânia (Table 5.10). This suggests that leaves from older tillers in cv. Mombaça had not only differences in morphogenetic variables like LER and LAR but anatomical differences also, since SLA is related to tissue characteristics like the amount and position of mesophyll cells. Wilson & Cooper (1969) evaluating *Lolium* genotypes found that lower (older) leaves had greater photosynthetic activity than the upper (younger) leaves, and these effects were closely associated to differences in mesophyll cell size. Wilson (1976b) also found variation in leaf anatomy in leaves at different insertion level in *P. maximum* var. trichoglume. This author states that leaf blades of higher insertion had a greater proportion of schlerenchyma and vascular tissue and smaller average size of mesophyll. Although anatomical studies were not performed in the current experiment this shows that changes in anatomy can affect physiological responses in leaves. This is one possible explanation for the low photosynthesis rate in leaves from old tillers in cv. Mombaça compared to mature and young tillers (Table 5.11).

The accumulated evidence points to a progressive and serious decline in vigour with increasing tiller age, which appears to be a consistent pattern of behaviour in Guinea grass.

5.4.3. Descriptive morphology

Comparative information on the population characteristics from undefoliated plants is shown in Figure 5.7 to highlight some morphological and physiological differences between these two cultivars at tiller level and distribution in the plant. The higher total tiller number at the end of the experiment in cv. Tanzânia plants (Table 5.5) is again observed, one of the reasons for this being the higher tiller death in cv. Mombaça, mainly in old tiller groups. Cv. Tanzânia had a higher proportion of flowering tillers than cv. Mombaça (Figure 5.7). This effect reflects the higher flowering in cv. Tanzânia in G4 and G5 tillers, together with the greater retention of G1 and G2 tillers in flowering conditions. This trait, which was also observed in Chapter 3, and is considered a problem to be faced for pasture management, since animals avoid grazing flowering tillers (Watkin & Clements, 1978).

There was a very low proportion of aerial tillers on undefoliated plants in cv. Tanzânia This observation suggests that appearance of aerial tillers is stimulated by decapitation of the flowering seed head as in ryegrass (Matthew, 1992). Conversely, basal tillers were produced throughout the study, indicating that other factors play an important role in tillering than he traditional and accepted assumption of apical meristem dominance (Murphy & Briske, 1992). The increased tillering on severely defoliated plants reflects the combined effects of decapitation of the growing points, the influence of light reaching the base of the plant and also the increase in LAR leading to an increase in tiller buds.

Variability in the size and weight of individual tillers reflects the effects of external (biotic and abiotic) and internal (age, development stage, genotype) factors (Laterra et al., 1997). Knowledge of this diversity is a key issue to understanding and predicting effects of management on plant population and sward persistence. The results summarized in Figures 5.10 and 5.11 illustrate variability both between and within cohorts in tiller number per plant and tiller size and weight, and demonstrate a substantial degree of plasticity in plant responses to defoliation management. The relative proportions of large tillers increased and small tillers decreased respectively as defoliation height increased from 100 to 400 mm. This effect was apparent for both cultivars, and for height (Figure 5.10) and fresh weight (Figure 5.11) measurements. There was some indication of a greater degree of plasticity of tiller size distribution in cv. Mombaça than in cv. Tanzânia. Tiller number per plant was greater in cv. Tanzânia at the end of the experiment (Table 5.5) and there was some indication of a greater proportion of tall tillers in cv. Tanzânia (Figure 5.10) reflecting the initiation of internode extension. These factors combined may explain the greater harvested yield in cv. Tanzânia at the end of the experiment (Table 5.3).

The classification in fresh weight of the tillers in Figure 5.11, on the other hand, shows cv. Mombaça with a trend to have heavier tillers than cv. Tanzânia. On these diagrams the range of tillers weight within the same category was more evident in more lenient harvests when the size range and weight increased

Position within the plant is another cause of variation in tiller size and weight. Xia (1991) in prairie grass swards under two managements, hard and lax grazing, compared the effect of tiller position (center or peripheral on the plant) and observed higher rates of herbage growth, senescence and net production per tiller located in a peripheral position than for central tillers, though the differences were not statistically significant. In the present study it was observed, but not quantified, that tillers had morphological differences according the age of the parental tiller and their position on the plant. For example, new tillers (G6 for ex) when originating from old tillers (G1 or G2) were smaller and less vigorous compared to tillers originating from mature generations (G4) (data not shown). The analyses shown in Figures 5.10 and 5.11 provide alternative ways of describing the great variation in size and growth potential within the tiller population, but further work is necessary to rationalise that information so that it can be used to determine criteria for accurate and predictable sward management (Laterra et al., 1997).

5.4.4. Root mass

Root and shoot development represent a series of harmonious events on the tiller axis and the reduction in root growth after defoliation is well established (Humphreys, 1991; Richards, 1993). It is well known that more severe defoliation affects root production (Paula et al., 1969; Evans, 1973; Deinum, 1985; Matthew, 1992) and the present results suggest that in the long term cuts at 100 or 200mm are deleterious for Guinea grass.

Root mass was marginally but significantly greater in cv. Mombaça than in cv. Tanzânia (Table 5.12) in accord to its greater shoot mass production (Table 5.3).

The core technique seemed to be reliable and treatment differences in root accumulation (Table 5.13) were consistent with differences in root mass (Table 5.12). However there was no consistent correlation between root production between harvests (cores) and the respective shoot mass above cutting height in any treatment.

5.5. Conclusions

The results suggest that there is a tiller cohort population responsible for yield (mature tillers) with ages between 2-3 month, and this population changes over time. So to maintain productivity it is important to manage these grasses in such a way to allow a permanent turnover of tillers. Both cultivars exhibited symptoms of tiller aging after few months, and this behaviour seems to be more evident on cv. Mombaça where the aging process was more accentuated.

The data also suggests that the concept of defoliation to avoid decapitation of apical meristem may be misdirected, since old tillers will be less efficient with time and contribute less to dry matter harvested. Conversely, young tillers were shown to be more efficient in yield components LAR, LER, FLL and photosynthetic rate.

The present results indicate an unexpected plasticity of Guinea grass in maintaining production under severe defoliation pressure, though this plasticity was tested over relatively short period of time (nine months) compared with the study described in Chapter 3 (18 months).

Tiller populations in the two cultivars categorized by age and size (as measured by height or fresh weight) showed that cv. Tanzânia has larger numbers per plant of smaller, longer lived tillers compared to cv. Mombaça. The significance of these differences in terms of competitive growth strategy is unclear.

CHAPTER 6: Distribution of current photosynthate in two Guinea grass (*Panicum maximum* Jacq.) cultivars.

6.1. Introduction

Carbon translocation within the plant provides basic physiological information to help understand plant development and growth (Williams, 1964; Clifford et al., 1973; Colvill & Marshal, 1981), and the growth strategies of different species or cultivars with respect to interaction between tillers of different hierarchical positions. Information on the extent to which assimilates move between tillers in Guinea grass (P. *maximum*) is potentially relevant for development of grazing management strategies. The results shown in Chapters 3, 4 and 5 indicate that cv. Tanzânia produces more tillers than cv. Mombaça (see also Gomide, C.A.M.1997; Santos 1997; Carvalho D.D. et al., 1999) and tends to maintain older tillers for longer (Chapter 5). This behaviour may arise from intrinsic difference between these two cultivars in the pattern of photoassimilate distribution within the plant.

This chapter reports an experiment designed to test this hypothesis, more specifically:

a) to compare for two Guinea grass cultivars, Mombaça and Tanzânia, the pattern of photoassimilate translocation within the plant, when different tillers at different positions were labeled with radiocarbon;

b) to verify if in *P. maximum* plants, as found by Clifford et al. (1973) for ryegrass, there is a reciprocal transfer of photoassimilates between main and daughter tillers and quantify the rate at which this occurs

c) to verify whether the ability of cv. Tanzânia plants to support old tillers longer can be explained by observed differences in translocation of photoassimilates.

6.2. Materials and Methods

6.2.1. Plant material and experimental management

The experiment was carried out in a glass house, located at the Plant Growth Unit, Massey University, Palmerston North (40°16'S, 175°17'E) from May- July 2000 and included two Guinea grass cultivars, Mombaça and Tanzânia.

Seeds of each cultivar were germinated in a tray at 25°C and after two weeks, two similar size seedlings were transplanted to each of 24 one-litre pots (twelve for each cultivar) filled with a mixture of sand and soil (1:1) and fertilized (3 g/pot) with a controlled release fertiliser (15% N, 4.8% P, 10.8% K, 1.2% Mg, 3.0% S, 0.4%Ca plus trace elements, B, Cu, Fe, Mn, Mo and Zn). One week later seedlings were thinned to one per pot of similar size. Plants were watered daily with tap water and 100 ml of a 0.25% solution (w/v) prepared with a commercial soluble fertilizer (20%N, 8.7 %P, 16.6 %K plus S, Mg, B, Cu, Fe, Mn, Mo and Zn) was applied two times a week to each pot.

Plants were allowed to grow uncut for approximately eight weeks from sowing and then randomly selected for application of the treatments. The treatments comprised three categories of tiller to be labeled with ^{14}C, (one category per plant) on individual plants of each cultivar: main tiller (TM), one young primary tiller, (TY: the first or second most recently developed primary tiller on the main stem, with at least three fully emerged leaves) and one old primary tiller, (TO: the fourth or fifth tiller on the main stem with at least two daughter tillers). These treatments were replicated four times, making a total of 12 plants for each cultivar.

Radiocarbon labeling was spread over two days for logistic reasons, one cultivar per day. The whole tiller to be labeled was enclosed in a plastic bag (Figure 6.1) which was closed around the base of the stem. A silicone jointing compound was applied to the culm at the point where the plastic bag was to be closed, to ensure an-air tight seal. Release of $^{14}CO_2$ was achieved by injecting, with a hypodermic syringe, acetic acid to $NaH^{14}CO_3$ solution placed in a pocket in the plastic bag. The needle holes were sealed with petroleum jelly and bags were left in place until geiger counter readings showed that radioactivity had transferred from solution to the tiller being labeled. To complete the uptake of all ^{14}C by plants usually takes 3 to 4 hours but after this period it was observed the transfer was incomplete and it was decided to leave plants with bags overnight, to be removed in the next morning after 20 hours. Plants were then destructively harvested, dissected and individual tillers with attached roots laid out in hierarchical order and dried in newspaper sheets for 24 h. For each plant the main tiller, one young primary tiller and one old primary tiller with daughter tillers, one of these being the radiocarbon-labeled tiller, were selected for autoradiography. The remaining tillers for each plant/treatment were labeled and placed in paper bags and dried in an oven for 48h at 60°C for later scintillation counting. Tillers selected for autoradiography were placed against X-ray films in a dark room, and wrapped in aluminium foil to exclude light. After two months exposure the X-ray films were processed and visually evaluated.

Table 6.1. Schedule of activities during the experimental period.

Date	Activity
07/05/00	Sowing on trays
14/05/00	Transplanting to pots
03/07/00	Tagging tillers
05/07/00	Expose Mombaça plants to $^{14}CO_2$
06/07/00	Destructive harvest and prepare to dry Mombaça plants
06/07/00	Expose Tanzânia plants to $^{14}CO_2$
07/07/00	Destructive harvest and prepare to dry Tanzânia plants
07/07/00	Place Mombaça selected tillers in contact with X-ray films
08/07/00	Place Tanzânia selected tillers in contact with X-ray films
29/09/00	Processing X-ray films and visual analysis
30/05/01	Scintillation counting

Roots and shoots were separated into the following categories within each plant for autoradiography and scintillation counting: (bold type indicates the labeled tiller):

a) Treatment (TM) where the main tiller was labeled:

G1 (Main) main tiller;

G2 (P-Y): the two youngest primary tillers (T1 and T2)

G3 (P-I): the two intermediate primary tillers (T3 and T4)

G4 (P-O): all other older primary tillers, T5, T6, T7 (if present);

G5 (Sec-All): all secondary tillers;

Note: No young primary tillers (P-Y) had secondary tillers

b) Treatment (TY) where the young tiller was labeled

G1: main tiller

G2L (P-Y-L) youngest primary tiller labeled -Tiller 1 or Tiller 2

G2 (P-Y): the other youngest primary tiller non-labeled

G3 (P-I) the two intermediate primary tillers (T3 and T4)

G4 (P-O): all other old primary tillers (T5, T6...);

G5 (Sec) all secondary tillers. Since younger tillers did not have secondary tillers, separation of secondary tillers of labeled and non-labeled tillers was not an issue.

c) Treatment (TO) where an old tiller was labeled:

Gl (Main): main tiller

G2: (P-Y): the two youngest primary tillers (T1 and T2)

G3 (P-I): the two intermediate primary tillers (T3 and T4)

G4L (P-O-L) one old primary tiller labeled (Tiller 5)

G4- (P-O) all other old primary tillers (T6, T7...);

G5 (Sec-Ot) all secondary tillers from non-labeled tillers

G6 (Sec-O-L) all secondary tillers from the labeled tiller (normally two tillers).

Plate 6.1. Overview of the plant during ^{14}C application.

6.2.2. Measurements

Ambient temperature was recorded daily using a maximum-minimum thermometer placed in the center of the glasshouse at 1.7 m above the ground level.

6.2.2.1. Tiller number and shoot - root dry weight

Before separating tillers into groups as described in the previous section, all primary and secondary tillers per plant were counted for further comparison among cultivars. Each group of tillers was put in a separate paper bag and oven dried for 48 h at 60°C. Before grinding for scintillation counting, tillers were separated into shoot (leaves plus stem/pseudostem) and root fractions and dry weight recorded to determine total plant dry weight and contribution of each group of tillers to the total dry weight.

6.2.2.2. Scintillation counting

All samples were ground in a kitchen coffee grinder and a 90 mg sub sample was combusted in a Harvey OX 400 oxidiser. ^{14}CO2 was trapped in scintillation vials using the method described by Jeffay & Alvarez (1961), and scintillation counting (disintegrations per minute, dpm) was performed on a Wallac 1409 liquid scintillation counter. Two calibration discs (CF 101, Amersham product) were used to adjust the quench correction at the scintillation counter.

6.2.3. Trial design and statistical analysis

For analytical purposes, each of the three 'treatments' (TM, TY, TO) was treated as a separate experiment, with two cultivars and four replicates. The SEM for percentage of ^{14}C recovered from each tiller category is shown and T-tests are used to test for cultivar differences in distribution of ^{14}C (expressed as a % of the total in the whole plant) to the different categories of tillers.

6.3. Results

Over the experimental period, daily minimum temperature averaged 17.8°C, and daily maximum temperature averaged 32.0° C.

6.3.1. Tiller number and dry weight

On average, total tiller number per plant was 22% higher in cv. Tanzânia than cv. Mombaça. (Table 6.2) and secondary tillers accounted for this difference rather than primary tillers

Table 6.2. Number of primary, secondary and total tillers per plant in two Guinea grass cultivars, Mombaça and Tanzânia.

Cultivar	Tiller type		
	Primary	Secondary	Total
	Tiller number/plant		
Mombaça	5.9	5.9	12.8
Tanzânia	6.6	8.1	15.7
s.e.	0.24	0.45	0.57
Significance	P = 0.06	**	**

T-test: ** (P < 0.01)

The dry weight of shoot and root components was higher in cv. Mombaça than cv. Tanzânia: respectively, 14.1 vs. 10.9 g/plant, s.e. 0.81(P < 0.05) and 3.2 and 2.7 g/plant s.e. 0.17 (P = 0.08) and the average tiller dry weight was 58% heavier in Mombaça. There was no statistical difference in root/shoot ratio between the cultivars. The dry weights of shoot and root fractions for each tiller group for both cultivars are shown in Table 6.3. For tiller groups in all treatments, cv. Mombaça shoot and root fractions were generally heavier than the corresponding tiller group of cv. Tanzânia but not all differences were statistically significant.

Table 6. 3. Shoot and root fractions dry weight (mg) for all tiller groups for each treatment, TM (main tiller labeled, **G1**), TY (young primary tiller labeled, **G2L**) and TO (old primary tiller labeled, **G4L)** in two Guinea grass cultivars, Mombaça and Tanzânia. (s.e within brackets). Bold type indicates labeled tiller.

Cultivar	Fraction	**Treatment**	**TM**	Tiller Group			Total Plant
		G1	G2	G3	G4	G5	Shoot+ Root
Mombaça	Shoot	**2270 (151.6)**	1810 (220.7)	3370 (405.1)	3190 (1328.0)	3030 (224.1)	17,030 (1735.1)
	Root	**1400** (90.5)	110 (58.4)	620 (87.8)	950 (225.0)	290 (69.7)	
Tanzânia	Shoot	**1540** (109.2)	1190 (75.2)	2880 (295.4)	4980 (1394.4)	1630 (323.5)	15,090 (1439.1)
	Root	**790** (66.1)	48 (20.1)	470 (106.9)	1360 (363.0)	190 (39.3)	
Significance	Shoot	**	*	ns	ns	*	ns
	Root	**	*ns	ns	ns	ns	

Cultivar	Fraction	**Treatment**	**TY**	Tiller Group				Total Plant
		G1	**G2L**	G2	G3	G4	G5	Shoot+ Root
Mombaça	Shoot	2160 (187.5)	**190** (43.5)	890 (291.1)	2550 (696.7)	4590 (583.8)	4250 (234.3)	17,500 (961.6)
	Root	1220 (56.8)	**0.9**	6	240 (109.1)	1090 (11.9)	300 (57.8)	
Tanzânia	Shoot	1630 (287.6)	**350** (79.2)	560 (64.9)	2150 (199.1)	3490 (488.8)	2480 (852.4)	13,560 (1413.7)
	Root	710 (53.9)	**22** (17.4)	39 (13.1)	450 (87.2)	1310 (208.4)	370 (196.9)	
Significance	Shoot	ns	ns	ns	ns	ns	ns	P=0.08
	Root	*	ns	ns	ns	ns	ns	

Cultivar	Fraction	**Treatment**	**TO**	Tiller Group					Total Plant
		G1	G2	G3	**G4L**	G4	G5	G6	Shoot+ Root
Mombaça	Shoot	2300 (133.3)	2340 (364.4)	1220 (125.0)	**1860** (368.7)	2610 (131.9)	2110 (163.9)	1630 (864.0)	17,290 (2076.6)
	Root	950 (29.6)	250 (65.1)	270 (49.3)	**460** (170.7)	940 (82.2)	140 (22.2)	230 (185.5)	
Tanzânia	Shoot	1520 (146.7)	760 (112.1)	1490 (224.8)	**1220** (262.1)	2010 (506.4)	1330 (145.6)	1070 (392.2)	11,760 (1694.8)
	Root	878 (73.8)	12 (5.6)	220 (42.6)	**430** (125.4)	640 (162.4)	97 (32.3)	90 (37.4)	
Significance	Shoot	*	**	ns	ns	ns	*	ns	P=0.09
	Root	ns	*	ns	ns	ns	ns	ns	

T test ns; non significant (P > 0.05) * (P < 0.05) ** (P < 0.01)

6.3.2 Autoradiography

Figures 6.1, 6.2 and 6.3 show radiocarbon distribution in plants in the three treatments, (TM, TY and TO) for cv. Mombaça and Tanzânia. In each radiograph tillers are shown in a sequential order (main, young primary, old primary and its daughter tillers). The results suggest a greater photoassimilate translocation to non-labeled tillers (D) in cv. Tanzânia than Mombaça and also high levels of radiocarbon in root tips on non-labeled tillers in both cultivars in treatment TM (Figure 6.1), and in cv. Mombaça in Figures 6.2 and 6.3.

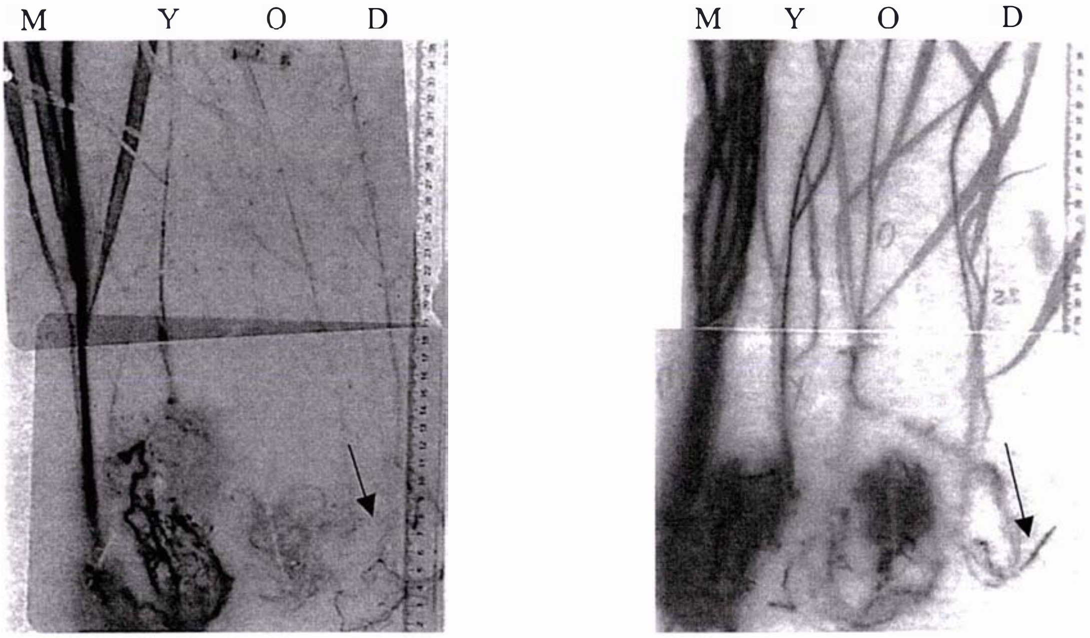


Figure 6.1. **Treatment TM** in Mombaça (left) and Tanzânia (right). Main tiller, M (at left) labeled. Young primary (Y) and old primary (O) tillers from the same plant visible at the centre and centre right, respectively. Old primary daughter (D) tillers are visible at far right. Arrows indicate high level of radiocarbon tracer present in root tips of non-labeled tillers.

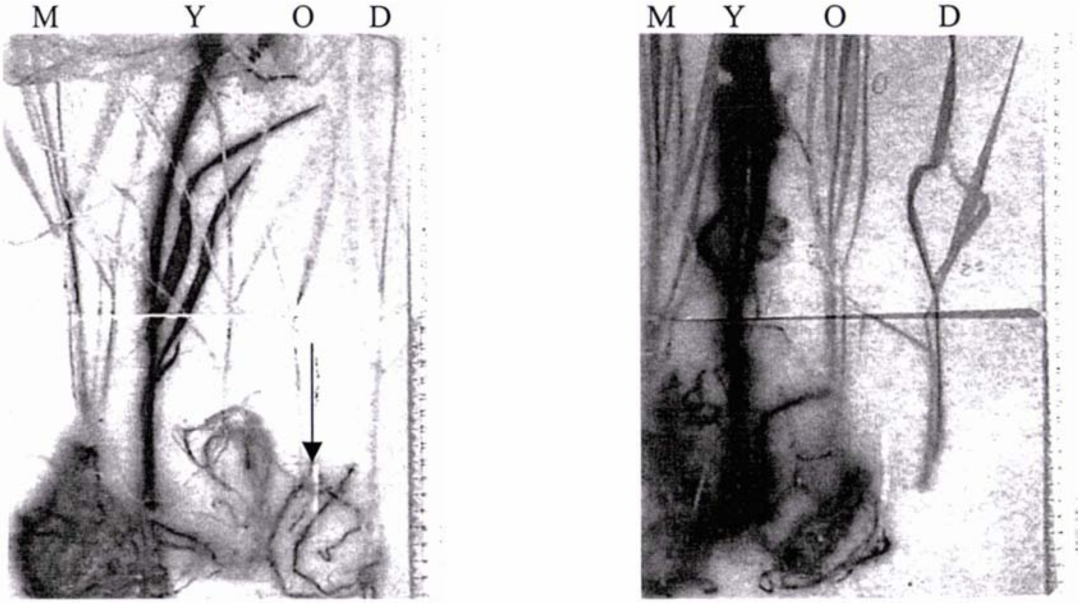


Figure 6. 2. **Treatment TY** in Mombaça (left) and Tanzânia (right). Main tiller, M (at left). Young primary (Y) labeled and old primary (O) tillers from the same plant visible at the centre and centre right, respectively. Old primary daughter (D) tillers are visible at far right. Arrow indicates high level of radiocarbon tracer present in root tips of non-labeled tillers.

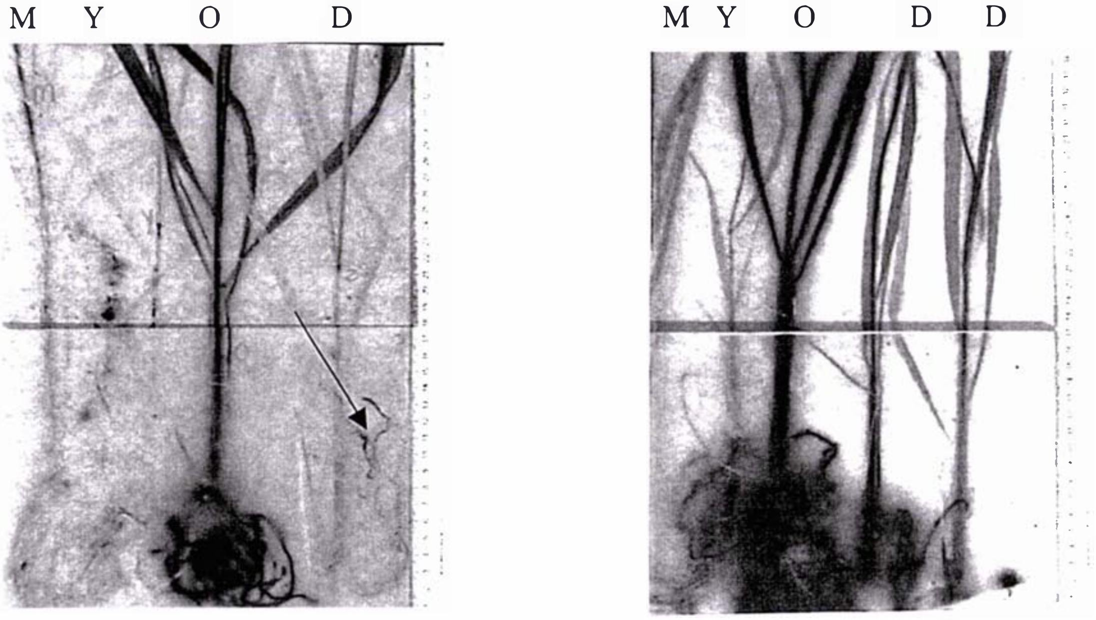


Figure 6.3. **Treatment TO** in Mombaça (left) and Tanzânia (right). Main tiller, M (at left). Young primary tiller (Y) and old primary (O) tiller labeled from the same plant visible at the centre and centre right, respectively. Old primary daughter (D) tillers are visible at far right. Arrow indicates high level of radiocarbon tracer present in root tips of non-labeled tillers.

6.3.3. Distribution of radiocarbon

The average radiocarbon recovered from Tanzânia and Mombaça plants were 533 and 428 kBq/plant, s.e. 71.9 P = 0.31, respectively, but there was trend to plants in TM treatment recovering more than plants in TY and TO treatments, (607, 434 and 387 kBq/plant, respectively, s.e. 68.3, P = 0.07). In general the percentage of exported carbon from a labeled tiller was low, but in both cultivars young primary tillers (TY) tended to export more than main (TM) and old tillers (TO) (20.5, 14.3 and 12.6%, respectively, s.e. 3.1, P =0.19).

Shoots from old labeled tillers (TO) retained more radiocarbon in cv. Mombaça than cv. Tanzânia (Table 6.4). Consequently there was significantly more radiocarbon recovered in shoot and root of non-labeled tillers in cv. Tanzânia. However, both cultivars had, in general, a similar percentage of recovered radiocarbon in unlabeled tillers in both shoot and root fractions in plants where main (TM) and young primary tillers (TY) were labeled. The percentage of recovered radiocarbon was higher in shoot than root fractions in all treatments on labeled and non-labeled tillers for both cultivars (Table 6.4).

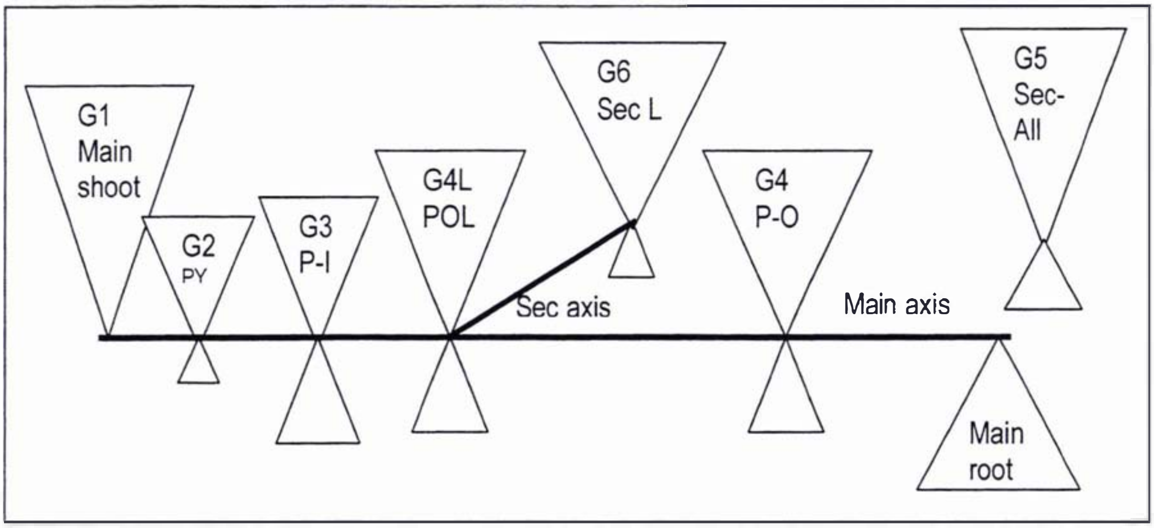
Table 6.4. Percentage of radiocarbon recovered in shoot and root fractions of labeled and non-labeled tillers in plants subjected to different treatments TM (main tiller labeled), TY (young primary tiller labeled) and TO (old primary tiller labeled) in two Guinea grass cultivars Mombaça and Tanzânia. (s.e. within brackets).

Treatment	Cultivar	Label		Non label	
		Shoot	Root	Shoot	Root
		% radiocarbon recovered of the total uptake			
TM	Mombaça	70.6 (9.0)	15.8 (5.9)	10.4 (3.8)	3.2 (0.8)
	Tanzânia	73.7 (3.9)	11.9 (2.1)	10.3 (2.3)	4.1 (1.2)
TY	Mombaça	78.4 (5.4)	0.04 (0.03)	11.5 (1.7)	10.0 (3.8)
	Tanzânia	78.1 (3.8)	2.5 (1.4)	9.8 (2.2)	9.6(2.9)
TO	Mombaça	84.9 (3.5)*	5.9 (2.1)	7.3 (1.3)*	1.9 (0.2) *
	Tanzânia	70.7 (2.2)	12.3 (2.3)	12.4 (2.2)	4.6 (0.6)

(*) T-test ($P < 0.05$)

In Figure 6.4 the spatial orientation on the tiller axis of the different tiller groups is described diagrammatically, with the area of triangles scaled in proportion to the dry weight of shoot and root fractions for each tiller category. In reality, axis length between the shoot and root is very short (about 10 mm long) but on the diagram the axis is expanded for clarity and extended horizontally to allow illustration of root and shoot fractions of each tiller category and to show all tiller connections. The shoot and root triangles in the top right of each figure represent secondary tillers that originated from different old and intermediate tillers, and therefore cannot be linked to a specific tiller group. When the treatment has secondary tillers from labeled old tillers a second axis is represented indicating the connection. The definition of young, intermediate and old tiller groups is related to the sequential period of appearance of these tillers on the main axis.

Figure 6.4. General format for presentation of results for scintillation counting of radiocarbon distribution. Note that G6 was presented only in treatment TO, illustrated here. For definition of groups (G1 to G6) (Materials and methods) P = primary tiller, Sec = secondary tiller, L = labeled with radiocarbon.



The diagrams in Figures 6.5 to 6.7 and Appendix 6.1 show for each treatment (TM, TY and TO) and for both cultivars the proportion of radiocarbon distributed within each tiller group subdivided into shoot and root fractions. Bold triangles represent the labeled tiller of the plant in question. Where ^{14}C was applied to the main shoot (TM) distribution to roots of the main tiller was about 22 and 15% of the total recovered from the main shoot in cv. Mombaça and Tanzânia respectively (Figure 6.5). Conversely, in treatment TO (Figure 6.7) plants of cv. Mombaça allocated less radiocarbon to roots of labeled tillers and to secondary tillers on labeled tillers than did plants of cv. Tanzânia. An interesting feature of the TY treatment is the comparatively high allocation to the root system of the main tiller in both cultivars.

The overall average specific activity for all labeled tillers was 367 kBq/mg and for unlabeled tillers was 11 kBq/mg, although this difference was not always statistically significant when comparing cultivars in different treatments (Table 6.5). The differences were more evident on treatment TO than in the other treatments where cv. Tanzânia daughter tillers had much greater specific activity in shoot and root fractions, compared with cv. Mombaça. The specific activity in treatment TY labeled tillers (Table 6.5) was greater than in the labeled tillers in treatments TM and TO for both cultivars because of the lower dry weight of these tillers (Table 6.3).

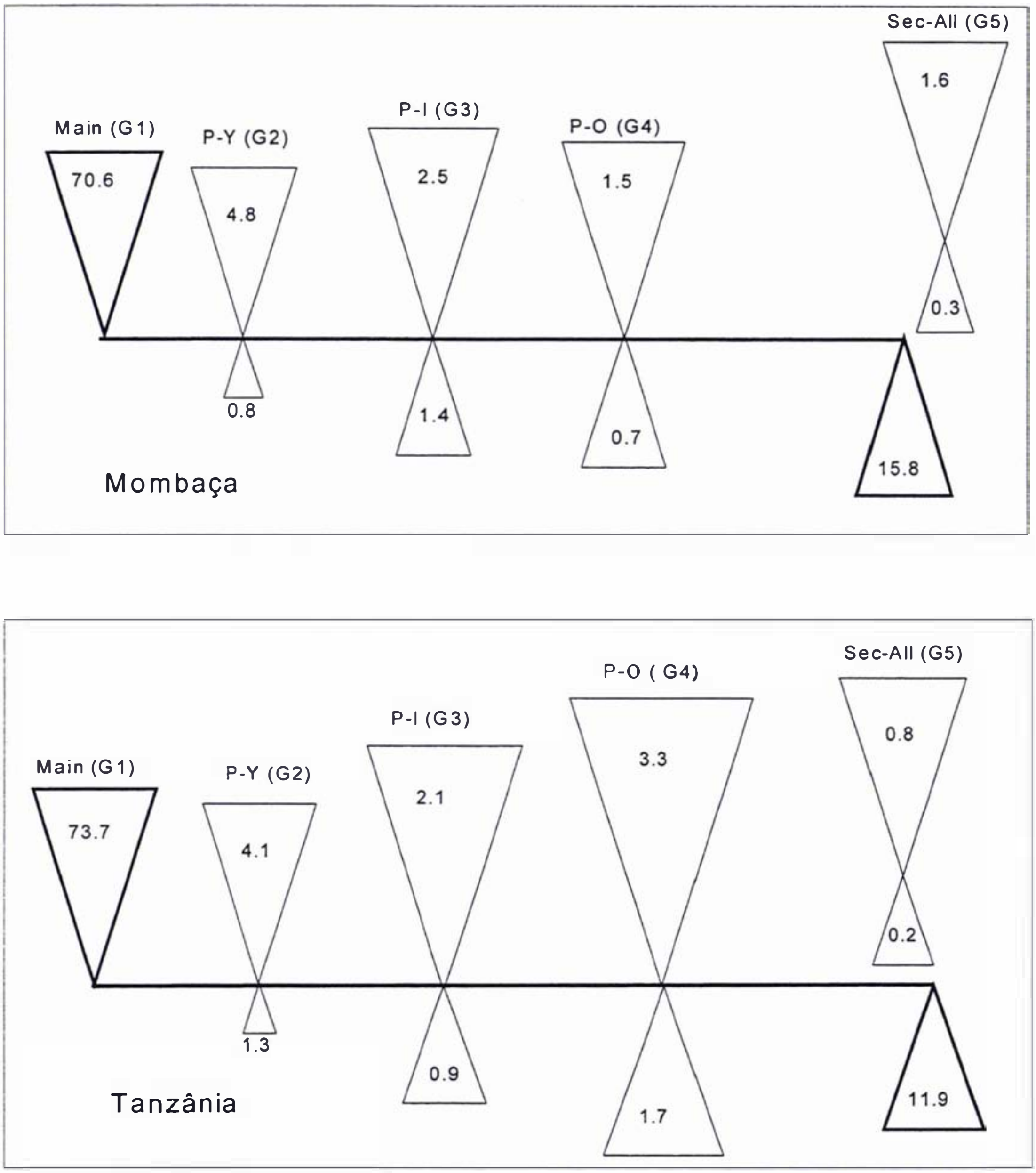


Figure 6.5. Distribution of photoassimilate in plants subjected to $^{14}CO_2$ application to the main stem (TM) in two Guinea grass cultivars, Mombaça and Tanzânia. Numbers inside the triangles represent the percentage of the total radiocarbon recovered in each tiller group in shoot and root fractions. Letters above triangles indicate tiller group as Main or G1, P-Y (primary young tillers) or G2, P-I (primary- intermediate tillers) or G3, P-O (primary old tillers) or G4 and Sec all (all secondary tillers in the plant) or G5

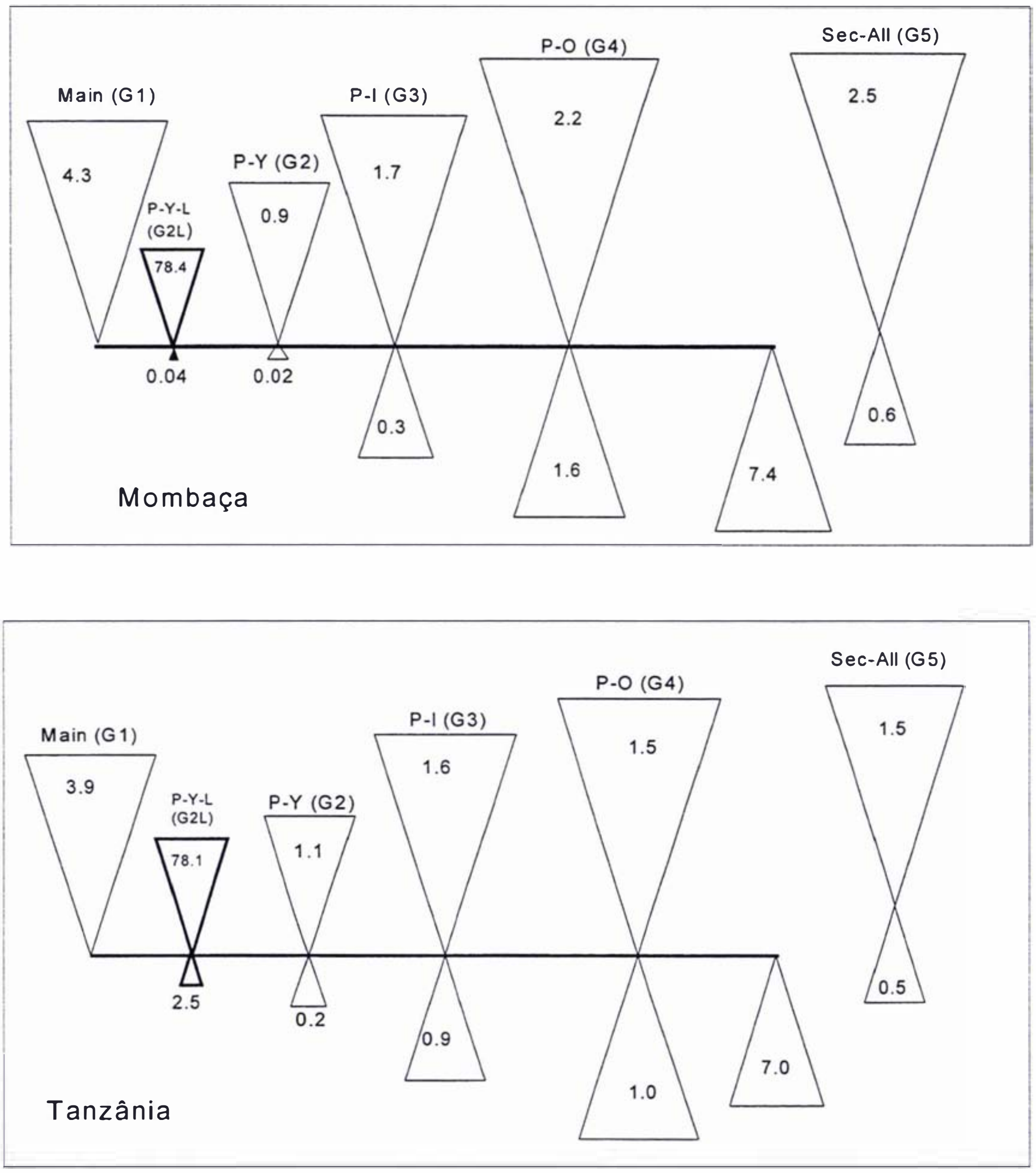


Figure 6.6. Distribution of photoassimilate in plants subjected to $^{14}CO_2$ application to a young primary tiller (TY) in two Guinea grass cultivars, Mombaça and Tanzânia. Numbers inside the triangles represent the percentage of the total radiocarbon recovered in each tiller group in shoot and root fractions. Letters above triangles indicate tiller group as Main or G1, P-Y-L (primary young labeled tiller) or G2, P-Y (primary young labeled tiller) or G3, P-I (primary-intermediate tillers) or G4, P-O (primary old tillers) or G5 and S-All (all secondary tillers) or G6.

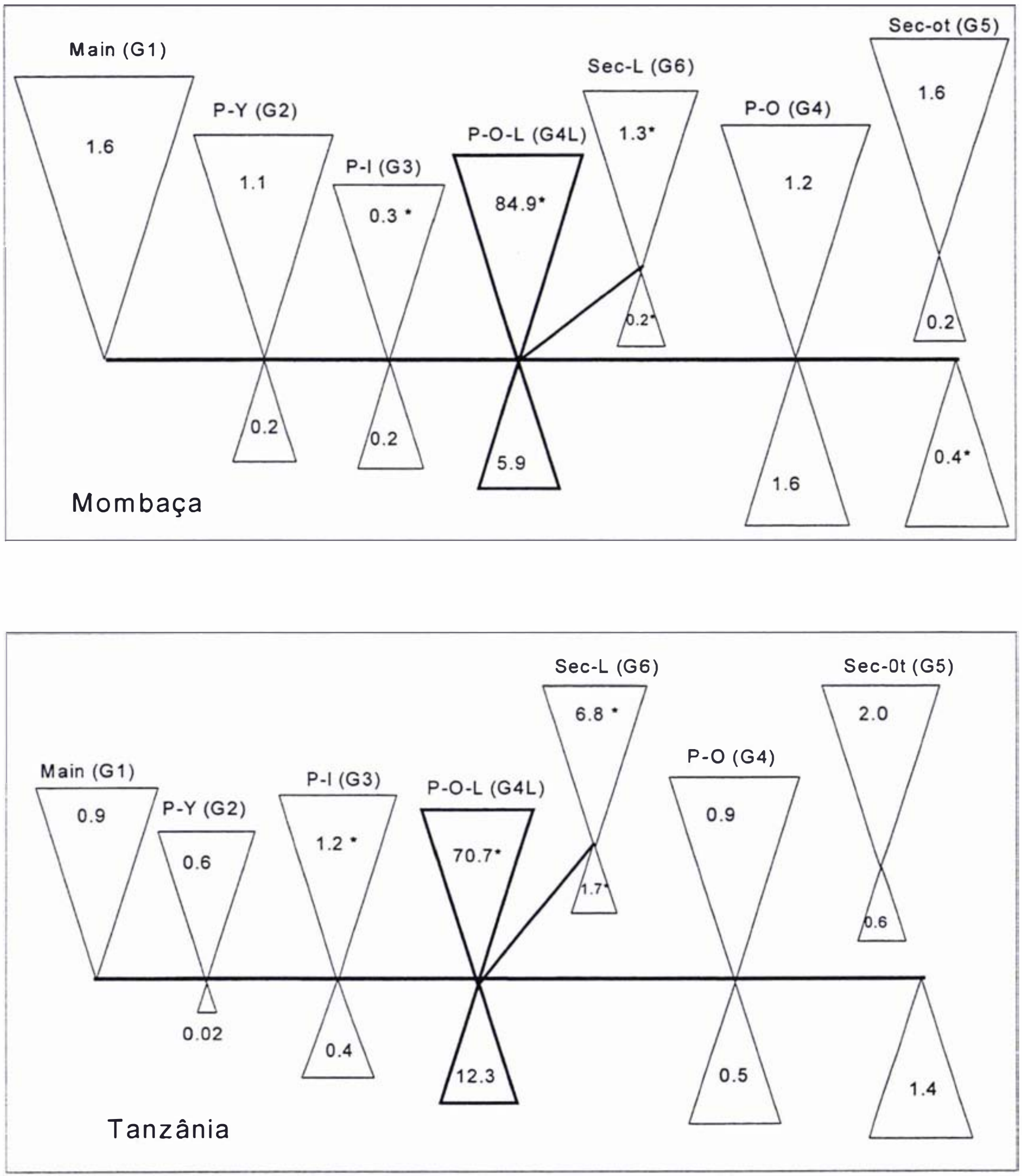


Figure 6.7. Distribution of photoassimilate in plants subjected to $^{14}CO_2$ application to an old primary tiller (TO) for two Guinea grass cultivars, Mombaça and Tanzânia. Numbers inside the triangles represent the percentage of the total radiocarbon recovered in each tiller group in shoot and root fractions. Letters above triangles indicate tiller group as Main or G1, P-Y (primary young tillers) or G2, P-I (primary- intermediate tillers) or G3, P-O-L (primary old labeled) or G4L, P-O (primary old tillers) or G4, Sec-L (secondary tillers from the old labeled tiller) or G5 and Sec-Ot (all other secondary tillers) or G6. (*) T-test ($P < 0.05$)

Table 6. 5. Specific activity (kBq/mg) of shoot and root fraction from all tiller groups categories (Gl, G2, G3, G4, G5 , G6) according to treatment TM. TY and TO in two Guinea grass cultivars, Mombaça and Tanzânia. (s.e within brackets). Bold type indicates labeled tiller.

Cultivar	Fraction			Tiller Group	**Treatment**	**TM**
		G1	G2	G3	G4	G5
Mombaça	Shoot	**171.6** (34.8)	13.6 (7.0)	4.0 (1.0)	2.5 (0.6)	2.7 (0.6)
	Root	**65.5** (33.7)	40.8 (9.9)	40.8 (9.9)	3.7 (1.1)	4.8 (0.6)
Tanzânia	Shoot	**321.9** (65.1)	20.8 (6.8)	4.7 (0.7)	3.3 (0.4)	3.2 (0.4)
	Root	**96.7** (19.4)	118..5 (56.1)	12.4 (2.5)	7.0 (0.6)	6.9 (2.8)
Significance	Shoot	P = 0.09	ns	ns	ns	ns
	Root	ns	ns	ns	ns	ns

Cultivar	Fraction			**Tiller Group**		Treatment	**TY**
		Gl	**G2L**	G2	G3	G4	G5
Mombaça	Shoot	8.2 (4.8)	**1049.6** (98.3)	10.9 (8.1)	2.5 (0.6)	1.6 (0.2)	2.0 (0.2)
	Root	22.3 (9.4)	**125.8** (61.2)	10.6 (3.1)	10.3 (7.2)	5.8 (3.6)	8.0 (0.2)
Tanzânia	Shoot	9.7 (1.9)	**1080.0** (179.1)	6.7 (1.2)	3.3 (0.4)	1.9 (0.3)	2.4 (0.3)
	Root	36.1 (11.0)	**879.9** (178.1)	17.0 (4.5)	8.1 (2.3)	3.9 (1.3)	5.3 (1.5)
Significance	Shoot	ns	ns		ns	ns	ns
	Root	ns	***		ns	ns	ns

Cultivar	Fraction			Tiller Group			Treatment	**TO**
		Gl	G2	G3	**G4L**	G4	G5	G6
Mombaça	Shoot	2.0 (0.9)	1.4 (0.4)	0.9 (0.4)	**166.7** (51.3)	1.5 (0.1)	2.4 (0.9)	6.5 (4.7)
	Root	1.6 (0.5)	2.6 (0.8)	2.7 (1.5)	**42.3** (18.0)	2.1 (0.3)	4.2 (1.7)	2.7 (0.2)
Tanzânia	Shoot	2.5 (0.2)	3.4 (0.4)	3.2 (0.2)	**266.6** (41.0)	2.1 (0.2)	6.2 (1.5)	27.7 (7.8)
	Root	6.1 (0.3)	4.8 (1.6)	6.9 (0.6)	**139.0** (37.5)	3.4 (0.3)	33.4 (10.9)	93.4 (12.5)
Significance	Shoot	ns	*	**	ns	*	*	*
	Root	***	ns	ns	*	*	*	***

T test : ns (P > 0.05) * (P <0.05) *** (P < 0.001)

6.4. Discussion

Patterns of photoassimilate distribution within plants growing under uniform conditions are governed by factors such as distance between source and sink, relative strength of the sinks and the vascular connection architecture of leaves and stems. Age and position of the sources (leaves) or the physiological stage of the plant (vegetative or reproductive) can change the distribution model in the same plant (Lloyd, 1980; Colvill & Marshall, 1981; Chapman et al., 1991; Fetene et al., 1997). In the present study the interest is not only to find how different sources (tiller hierarchical position) can translocate photoassimilates, but also to compare two Guinea grass cultivars with defined morphogenetic differences, since morphological traits arise from physiological processes (Chapman et al., 1991). Previous studies showed that cv. Mombaça produces fewer but larger tillers than cv. Tanzânia (Chapters 4 and 5). Again in this experiment in plants eight weeks old, Tanzânia plants produced 10 and 32% more primary and secondary tillers, respectively, than cv. Mombaça and average tiller weight for Mombaça was 58% more than for Tanzânia (Tables 6.2 and 6.3).

In this experiment the amount of radiocarbon applied to the plants was not quantified and so the overall recovery as a percentage of that initially applied could not be determined. Since the same procedure was applied to all plants (same amount and period of radiocarbon application) differences in distribution would be due to treatment and cultivar effects.

The total amount of radiocarbon recovered was 24% greater in Tanzânia plants than Mombaça plants. It is not clear if this arises from a differential uptake during labeling or a greater loss between labeling and harvests, 24 hours after labeling was complete. Total radiocarbon recovery for plants under treatment TM was 40 and 57% higher than plants in treatments TY and TO, and this can be related to efficiency in ^{14}C uptake of the main tiller compared to primary tillers. This result contrasts with data obtained with Bahiagrass (*Paspalum notatum*) where no statistical difference was found in the amount of ^{14}C recovered in plants on which young, mature or old tillers were labeled (Beaty et al., 1974).

In many studies evaluating translocation radiocarbon is applied to individual leaves to observe effects of position, age and efficiency of the leaf labeled in relation to the rest of the plant (Clifford et al., 1973; Lloyd, 1980; Chapman et al., 1991; Fetene et al., 1997, Ahmad & Marshall, 1997). In the present study however, the main aim was to evaluate translocation from the tiller as a unit, and tillers were grouped according to age/position on the main axis. This system requires care in interpretation. For instance the high specific activity of young tillers in TY (Table 6.5) will be mainly due to the small mass of those tillers, but may also reflect the high proportion of new tissue in this category of tiller compared to old or main tillers where there may have more leaf mass, but at the same time, have less demand on photoassimilate for growth.

There were no great differences between cultivars in radiocarbon export from labeled to non-labeled tillers in treatment TM (Table 6.4), but a gradation in recovery is apparent (Figure 6.5) from position G2 to position G5 on the main stem that can be attributed to distance from the assimilate source, since G2 is the youngest and closest tiller group to the main tiller, G4 the oldest and G5 all the secondary tillers. Distance from the source is one of the factors known to influence radiocarbon recovery from one specific sink (Matthew & Kemball, 1997). There was similar behavior in both cultivars in treatment TY (Figure 6.6) where the recovery was higher in the shoot of the young labeled tiller than in the shoots of treatment TM, but in contrast to treatments TM and TO the percentages of recovered radiocarbon in root and shoot fractions were similar in all unlabeled tillers (Table 6.4). This may be due to the great demand in photoassimilate from roots of the main tiller (Figure 6.6) the nearest sink from the source, young tiller.

The radiocarbon recovered in G2 was about 6.5% of that recovered in G1 in treatment TM for both cultivars (Figure 6.5). By contrast, percentage of total radiocarbon recovered from the main tiller (G1) in treatment TY (Figure 6.6) was 14% of that recovered in G2 (where the young tiller was labeled). This observation was similar to Beaty et al. (1974) working with Bahiagrass, who found that more of the ^{14}C translocated from young tillers went to the main plant than was the case for ^{14}C from mature or old tillers. This suggests that transfer to the main tiller is in part related to distance and strength of the sink. When the reverse situation occurs, for the photoassimilate be transferred to other tillers (G3, G4 or G5) there is a need to pass through the parent tiller first, before reaching the rest of the plant. This results in the retention of more radiocarbon in the main tiller in treatment TY than in treatment TM. It is important to note that in treatment TM, G2 contains the two youngest tillers while in treatment TY the G2 group contains only the young labeled tiller and G3 the other young tiller. In this situation recovery in the other young tiller was very low, and more related to its low mass compared to other tiller groups than to specific activity, which was higher than in the other tillers (Table 6.5). Also Clifford et al. (1973) obtained a similar response when evaluating reciprocal translocation between main and primary tillers in *Lolium multiflorum*. Recovery of radiocarbon by the main shoot was higher when the primary was labeled than when the main tiller was labeled, despite single leaves being labeled, rather than the entire shoot.

In treatment TO, in cv. Mombaça only 9.2% of the total photoassimilate was exported in the rest of the plant, while in cv. Tanzânia this value was about 17%. It seems that in cv. Tanzânia old primary tillers formed an independent "family" (Colvill & Marshall, 1981) and behaved with their daughter tillers in a way similar to the parental main tiller while cv. Mombaça, transferred less assimilate to the rest of the plant. There was a similar proportion (2%) of radiocarbon recovered when considering the flux from main tiller to old tiller in TM and vice versa (TO) in cv. Mombaça, in contrast with cv. Tanzânia where old tillers (G4) received 5% from the main tiller (G1) in TM and translocated 2% to the main tiller in treatment TO. Moreover in cv. Tanzânia it seems that due to the position and sink strength of the daughter tillers with high specific activity (Table 6.5) the old tiller sent less photoassimilate to the parental tiller than to its daughter tillers. This data confirms the visual analysis (Figure 6.2), where concentration of radiocarbon is much more evident in cv. Tanzânia than in cv. Mombaça daughter tillers. These findings do not necessarily explain why cv. Tanzânia retains its older tillers longer than cv. Mombaça plants, but they do indicate the ability of this cultivar to translocate more assimilates of old tillers to the rest of the plant.

The autoradiography visual analysis suggests a higher level of radiocarbon tracer in root tips of cv. Mombaça than cv. Tanzânia (see arrow Figures 6.2 and 6.3). This could not be confirmed by scintillation counting because the sampling systems considered the whole root mass from the tiller group and not just the tips as in Matthew & Kemball (1997). These authors analysed roots in nodal positions and found that root tips had higher specific activity than the root axis because of the meristematic region, and also that there was a gradation in recovered radiocarbon according to the nodal position from the youngest to oldest root on the main tiller axis. Another reason may be the higher total root mass in cv. Mombaça than in cv. Tanzânia roots causing a dilution effect in the specific activity.

Expanding leaves with a carbon requirement for growth act as a strong sink for incorporated radiocarbon (Lloyd, 1980). In the present experiment the proportion of meristematic tissue to the total leaf mass was possibly greater in young tillers (G2) than in main (G1) or old ones (G4, G5) resulting in a high specific activity (Table 6.5). The same reasoning can be applied to root fractions where the mass was very small in young tillers labeled in TY, compared to roots of other tillers labeled.

This study demonstrated the existence of reciprocal translocation within the plant and its fractions from different tiller ages or categories. Since these events occurred simultaneously, this means that there is a dynamic exchange within the plant where the main stem translocates assimilates to its daughter tillers (primary) and even to its secondary tillers, but as a low proportion of total photoassimilate. Old primary tillers also translocate to parental tillers, but in a greater proportion to their own daughter tillers acting as a family. This effect is more evident in cv. Tanzânia, suggesting that the independence is not absolute (Chapman et al., 1991).

Many findings of this study are consistent with the distance from the source being important factor determining translocation observed, in TM, for example. Specific activity and percentage of recovered radiocarbon (Tables 6.4 and 6.5) diminishes basipectally down the tiller axis, with successive tiller groups allocated less assimilates. In TY also the distance and the connections to the parental tiller could play an important role, where, curiously, the root fraction in G1 recovered more photoassimilate than the shoots (Table 6.4) even taking into account the greater shoot mass.

The results are not simple to interpret because of interaction between distance from the source, the strength of the sink itself and the dilution factor caused by different tiller groups having different mass. All these features could influence the final interpretation of the data. An experiment analyzing different fractions of the shoot and roots may clarify these points and explain the differences between these cultivars.

There are still many questions to be answered about the physiological differences between these two cultivars and the effect of defoliation on translocation as in Clifford et al. (1973). In previous experiments a natural aging process was observed as an ontogenetic trait for all tillers in both cultivars, and cv. Mombaça was more sensitive to this particular event than Tanzânia. In the present experiment it seems that Mombaça was more self-restricting in its photoassimilate partitioning within the plant, and the results show possible evidence for this trait. It is worth carrying out more experiments in this area with mature plants to evaluate for instance translocation from senescing tillers to young new tillers, as in the studies by Chafai-Elalaoui & Simmons (1988) and Chafai-Elalaoui et al. (1992), since from other experimental observations cv. Mombaça seemed to have higher tiller turnover than cv. Tanzânia plants (Chapter 5). Earlier death in cv. Mombaça old tillers could be an adaptive trait and be useful in the environment in which this grass had evolved.

6.5. Conclusions

The distribution of radiocarbon observed could be largely explained by variation in sink strength and proximity to the source of assimilates;

- In both cultivars, young labeled tillers retained less radiocarbon (79%) than main (86%) and old (87%) labeled tillers, probably of their small size and comparatively large dose;
- Cv. Tanzânia old primary tillers translocated more photoassimilate to their daughter tillers, and to the rest of the plant, than cv. Mombaça;
- In both cultivars there was a gradation in photoassimilates distribution and specific activity from young to old tillers when the main tiller was labeled;
- Comparatively high specific activities were observed in roots of unlabeled tillers near to labeled tillers;

Chapter 7: Overview and conclusions

7.1. Introduction

The objective of graziers is to maximise meat or milk production without prejudicing pasture perenniality, and the contribution of forage science is to provide understanding of and procedures for enhancing the quantity and nutritive value of forage produced. However, in the planning phases of the work reported in this thesis it was decided to focus attention primarily on the components of herbage production, rather than on production itself, for three reasons. In the first place, review of the literature (Chapter 1 and 2) revealed the shortage of information available on aspects of the morphology and ecophysiology of tropical forage species from which to draw inferences about improvements in their selection and management. Secondly, there was specific interest in providing information of this kind to aid evaluation of cultivars of Guinea grass, a species of major interest in the Brazilian tropics. And thirdly, the need to work in a glasshouse or growth chamber in order to maintain environmental conditions comparable to those experienced in the normal habitat made it difficult to provide adequate areas of sward for estimates of production.

In the planning stage there were some concerns about the use of information from potted plants in greenhouse and growth cabinet conditions to predict field behaviour in tropical conditions. However, levels of production and aspects of plant response to defoliation measured in these studies were similar to equivalent observations under field conditions in Brazil (Pedreira, 1973; Ghisi, et al., 1989; Santos, 1997), giving confidence in the interpretation of results from the current project.

The approach taken was to explore a number of different aspects of plant behaviour with a view to establishing their sensitivity to defoliation management, rather than to concentrate on a single facet of plant behaviour. Thus, the experiments reported have explored aspects of tiller dynamics (Chapters 3 and 5), leaf tissue turnover and morphogenesis (Chapters 4 and 5), and photosynthate translocation (Chapter 6). Details of these studies are summarised in Appendix 7.1. Plans for the programme drew heavily on experience of research on the growth and development of temperate species, which have been studied for many years as a tool for developing pasture management strategies in temperate countries (Cooper, 1951; Mitchell, 1953; 1954; Brougham, 1956). There is a vast literature of component knowledge on temperate forage species (Jones & Lazenby, 1988; Davies, 1993; Lemaire et al., 2000), though the majority of this information is derived from studies on just two grasses (*Lolium perenne* and *Festuca arundinacea)* and one legume (*Trifolium repens)* (Hodgson & Da Silva, 2000).

Defoliation effects can be understood in terms of frequency, intensity or timing. In this thesis attention was concentrated on manipulation of defoliation height, which ranged from 50mm to 400mm in the different experiments, in order to quantify cultivar differences in morphological plasticity in leaf production and tillering behaviour (Chapman & Lemaire, 1993), since there is little information on this subject for C_4 grasses adapted to humid areas (Nelson, 2000).

Three Guinea grass cultivars were used in the studies. Cv Mombaça and cv. Tanzânia are those most commonly used by farmers in the central regions of Brazil; cv. Aruana is more restricted in area but has shown promise in sheep grazing systems (Santos L.E. et al., 2001). As the study progressed it became clear that patterns of behaviour in cv. Aruana were so different from those in the other two cultivars as to make comparative evaluation difficult (Chapter 3). Cv. Mombaça and Tanzânia also differed in aspects of leaf and tiller dynamics as well as in production, but these differences were more relevant to understanding how component information might be used to influence future plant selection and pasture management, and attention was concentrated on these two cultivars in the later studies.

7.2. Herbage production and leaf tissue turnover.

For the most part, herbage production was measured on a per plant basis as a way of determining the combined effects of morphogenetic responses to defoliation. This evidence was augmented by information from undefoliated plants. Area-based measurements of total and seasonal production are available from Chapter 3 on a seasonal and monthly basis (Figures 3.4 and 3.5), and the estimates of 60-80 tonnes DM harvested per ha over a period of 18 months confirms the well-recognised high production potential of tropical species (Cooper, 1970). Cv Mombaça was more productive than cv. Aruana and Tanzânia, particularly in the summer season (Figures 3.5, 3.6), consistent with its better performance in field trials (Jank, 1995; Cecato et al., 1996), though differences between cv. Mombaça and Tanzânia were less clear in Chapter 5.

Cutting height affected production in all cultivars. Initially low level cuts resulted in greater herbage DM harvested than more lax defoliation, but production from the more severely defoliated plants declined with time, the effect being greater in cv. Aruana and Tanzânia (Figures 3.4 and 4.7). Regular defoliation below 200 mm should be avoided in these cultivars, though possible interactions between the effects of severity and frequency of defoliation remain to be investigated under grazing.

In these studies attention was concentrated on the measurement of herbage accumulation above cutting height (herbage harvested). However, collection of all dead leaves between harvests in the experiment reported in Chapter 5 made it possible to construct estimates of tissue turnover (Table 5.2). The results are shown in Figure 7.1 for the full duration of the experiment.

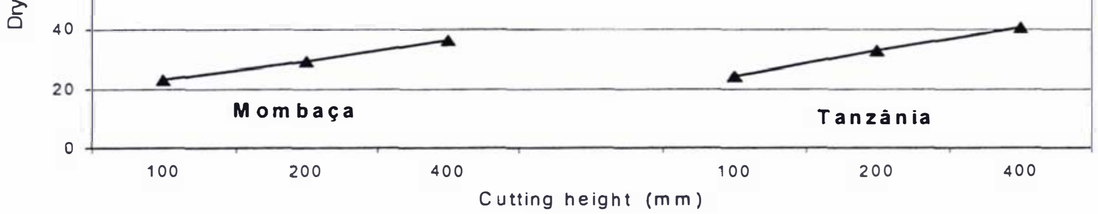


Figure 7.1. Total DM harvested (■), senescence (▲) and net herbage harvested (•) in seven months of the experimental period, in two Guinea grass cultivars, Mombaça and Tanzânia, under three defoliation heights, 100, 200 and 400 mm.

It is clear from Figure 7.1 that, overall, net herbage production declined substantially over the range of cutting height from 100 mm to 400 mm, due in part to a limited reduction in herbage growth and in part to an increase in losses to senescence. These results suggest substantial plasticity in the morphogenetic responses of Guinea grass plants to defoliation cf. Bircham & Hodgson (1983) for similar evidence for *L. perenne* though, as indicated earlier, there was evidence of progressive loss in productive performance on the most severely defoliated treatments.

The roots studies reported in Chapter 5 (Tables 5.12 and 5.13) provide a valuable addition to the limited data available for tropical species and a link to comparable information for temperate species (Matthew, 1992). Pattern of variation in root mass across cultivars and cutting treatments, and over time (Table 5.12) were similar to the corresponding information for herbage mass (Tables 5.2 and 5.3), and were reinforced by the estimates of root production derived from the technique using sand-filled cores (Table 5.13).

7.3. Tiller population dynamics

Compensatory changes in tiller size and population density in response to defoliation management have been described for temperate grasses (Kays & Harper, 1974; Matthew et al., 1995), and more recently for *Cynodon dactylon* (Sbrissia et al., 1999). The underlying mechanism involved remains unclear, but is likely to involve morphogenetic correlation between leaf size and tiller bud growth, and/or light-mediated effects on tiller bud initiation and hence site filling. The same general pattern of tiller size/density compensation was observed in the plants of both cv. Mombaça and Tanzânia in Chapter 5, and is summarized in Figure 7.2.

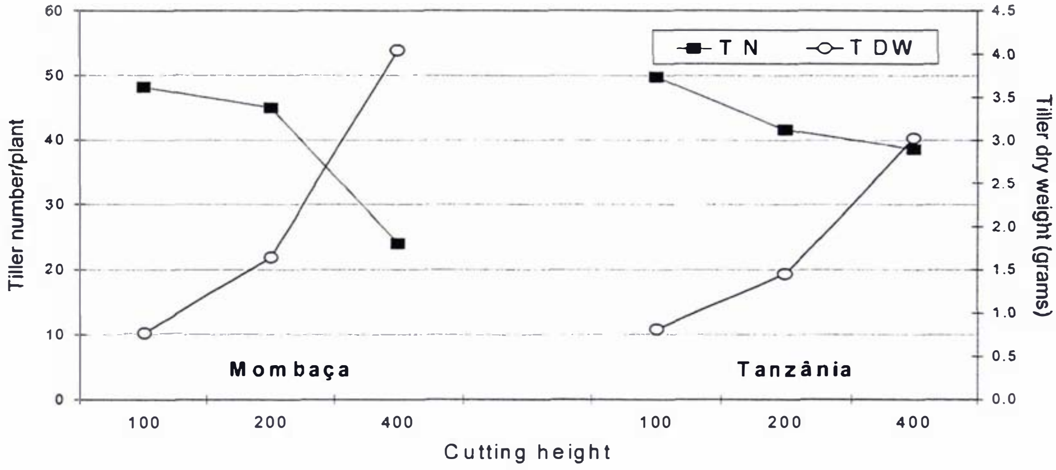


Figure 7.2. Relationship between average tiller number (■) and tiller weight (O) (grams) in potted plants of two Guinea grass cultivars, Mombaça and Tanzânia, under three defoliation heights, 100 mm, 200 mm and 400 mm.

Compensating adjustments in tiller size and density contribute to the productive plasticity shown in Figure 7.1. Traditionally Guinea grass pastures are managed to avoid tiller decapitation with the aim of avoiding limitation to regrowth (Gomide et al., 1979; Gomide & Zago, 1980, Humphreys, 1981), because these plants elongate internodes during vegetative as well as reproductive phases of growth (Humphreys, 1981, 1991), and because animals normally avoid grazing stem (Sollenberger & Burns, 2001). This can result in a progressive increase in the height and mass of post-grazing residues and in herbage wastage. The results summarised in Figures 7.1 and 7.2 indicate the scope for using periods of close defoliation (200-400 mm height) in summer to control stem elongation without prejudice to herbage production. This management will help to maintain the leaf content of pasture (Figure 3.6) and hence the nutritive value for grazing animals (Minson, 1981).

The results shown in Figure 7.2 refer to the period immediately before the appearance of substantial numbers of small aerial tillers in cv. Tanzânia (see Figure 3.10), and the cultivar comparison in Figure 7.2 would clearly have been different if it had included this transient tiller population. The physiological significance of these aerial tillers remains to be clarified, but may relate to the potential for rapid regeneration of leaf area at critical times of year with lower DM costs. Aerial tillers have been noted in the field in both cv. Mombaça and Tanzânia (Barbosa et al., 1996), but not usually in the numbers observed in this study.

Cv. Tanzânia consistently had more rooted tillers per plant than cv. Mombaça, in accord with the results of Cecato et al. (1996) and Santos (1997), resulting from an initially greater tiller appearance rate (TAR). Apart from the periods of aerial tiller appearance there was no difference between cultivars in TAR after this initial phase of plant development (Appendix 3.1). Tiller death rate (TDR) did not differ consistently between cultivars either, except that severe defoliation, particularly in the flowering period, increased TDR primarily in cv. Mombaça (Figure 3.13 and Appendix 3.2). This provides confirmatory evidence of the greater sensitivity of tiller population dynamics in cv. Mombaça than cv. Tanzânia to severe defoliation.

Young tillers in both cv. Mombaça and Tanzânia showed very high survival for at least the first three months of life, irrespective of severity of defoliation, and tiller death appeared to be associated mainly with older tillers in periods of stress like flowering initiation (Figures 3.13, 3.14, 5.5 and 5.6). These findings contrast with the observations of Ong (1978) for temperate species, who noted that death occurs predominantly in young tillers when plants are under stress.

Death of older tillers may be associated with the observed loss of vigour in older tiller generations (defined as those older than four months from appearance) in this study. Loss of vigour is indicated by reduced leaf appearance rate, leaf elongation rate, and photosynthetic activity, and eventually a virtual failure to contribute to herbage production (Figures 5.6 and 5.7). The effect was observed in both defoliated and undefoliated tillers, and was not associated with decapitation. This phenomenon does not appear to be associated simply with the reproductive phase of development. It may confer some survival advantage if it provides for re-mobilisation of assimilates to support the development of younger tillers (Chafai-Elalaoui et al., 1992), but its potential effect on overall plant performance is substantial and deserves further attention.

Incipient tillers showing evidence of truncated development were noted regularly in destructive harvests, but were not counted. The reasons for their presence, and their influence in plant development, remain to be investigated.

The morphogenetic characters leaf appearance rate (LAR), leaf extension rate (LER), final leaf length (FLL), number of live leaves per tiller (NLL) and leaf life span (LLS) are all inter-related (Chapman & Lemaire, 1993; see figure 2.1).

There is still limited understanding at the physiological level of the inter-relationships among these variables (Bahmani, et al., 2000), and a lack of clarity about how to manipulate them to improve plant production. However, behavioural contrasts between cv. Mombaça and Tanzânia provide some indication of potentially important sources of variation. The production advantage of cv. Mombaça over cv. Tanzânia noted above was associated with higher LER and lower LAR, and larger leaves with greater SLA, but no difference between cultivars in NLL and LLS

The studies reported in this thesis demonstrated very substantial individual variability in size and productivity between and within tiller cohorts (Figures 5.3, 5.4, 5.10 and 5.11). This variability may reflect the relatively large size of tillers in Guinea grass, and indeed in other tropical bunch grasses. This appears to be one of the first studies to address the question of variability in tiller size, and there is little information available for comparative purposes. This variability maybe be related to tiller age and position within the family hierarchy, as well as to the timing of development and access to assimilate. Tiller size is also likely to be influenced by the size of the plant and position within the plant as observed by Xia (1991) in prairie grass (*Bromus willdenowii*).

Variability of this magnitude creates problems in sampling for research purposes, and in practical sward management; its causes and consequences deserve further study. Additionally, the observation of substantial differences between tiller cohorts in their contribution to herbage harvested, independent of the aging factor noted above, is of potential practical importance. This effect (Figures 5.3 and 5.4) could not be readily explained. In a recent field study with Guinea grass, Santos P.M. et al., (2001) concluded that tiller cohorts did not differ consistently in total tissue accumulation measured to ground level. However, no other evidence has been found for this or any other grass species and this question, too, requires further investigation.

7.4. Assimilate movement

The results reported in Chapter 6 demonstrate differences between cv. Mombaça and Tanzânia in assimilate distribution within plants, which are consistent with the cultivar differences in sensitivity and defoliation noted above. Translocation from primary tillers to daughter or secondary tillers was significantly greater in cv. Tanzânia than in cv. Mombaça (Table 6.4), indicating that plants of cv. Tanzânia share their assimilates within tiller "families" in a more efficient way than plants of cv. Mombaça. This effect, however, does not appear to be a reflection of the more rapid loss of vigour with age in cv. Mombaça tillers which was noted above, since all the plants in the ^{14}C study were relatively young. A consistent feature of the results was the relatively high specific activity in the roots of unlabelled tillers adjacent to the labeled tiller (Table 6.5), indicative of the high sink value of the roots and their needy access to assimilate from adjacent tillers.

7.5. Conclusions and recommendations

The major conclusions from the project are as follows:

Severe defoliation (below 200mm) should be avoided in managing Guinea grass, but the species shows substantial morphological plasticity and may be grazed more heavily than is the current practice of farmers in Brazil (400-600mm) (Costa et al., 1992). This will provide better control of internode elongation in summer, but control of reproductive stem development in autumn may still be difficult, particularly in cv. Tanzânia. This aspect requires further study.

Cultivars Mombaça and Tanzânia differ in morphological characteristics and response to defoliation. Cv. Mombaça characteristically has fewer, larger tillers than cv. Tanzânia, and has higher potential herbage production, but adjustment in tiller size in response to increasing severity of defoliation is greater in cv. Tanzânia than cv. Mombaça. Differences between these cultivars offer scope for breeding and selection to control leaf morphology and leaf and tiller dynamics to suit the requirements of intensive grazing managements.

The numerous aerial tillers in cv. Tanzânia appear to play an important role in regrowth in some seasons of the year, but do not necessarily contribute materially to herbage production. Further evaluation of this behaviour, and means to control it, is necessary.

The study provided the first clear evidence of the declining vigour of older tiller cohorts, and additionally of contrasts between cohorts of similar age in the contribution to plant performance, together with evidence on the structure of tiller "families" and cultivar differences in the movement of assimilates within families. All of these factors are of potential importance to plant survival and herbage production, and deserve further study.

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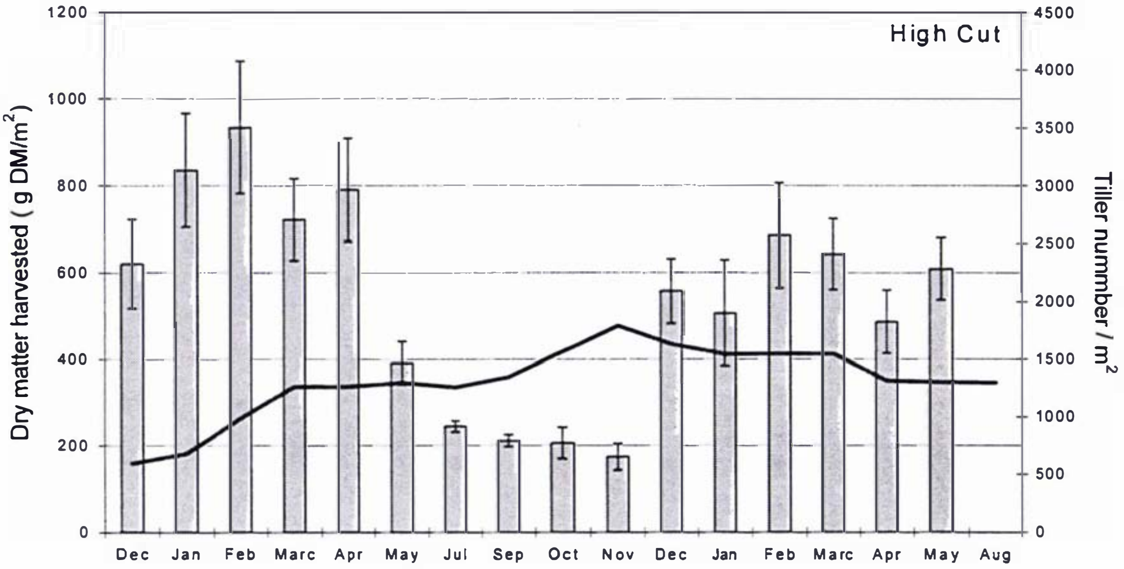
Appendix 3.1. Tiller appearance rate (TAR) in two Guinea grass cultivars, Mombaça (M) and Tanzânia (T) under two defoliation heights, 150 mm (L) and 300 (H) over all harvests from December 1998 to August 2000.

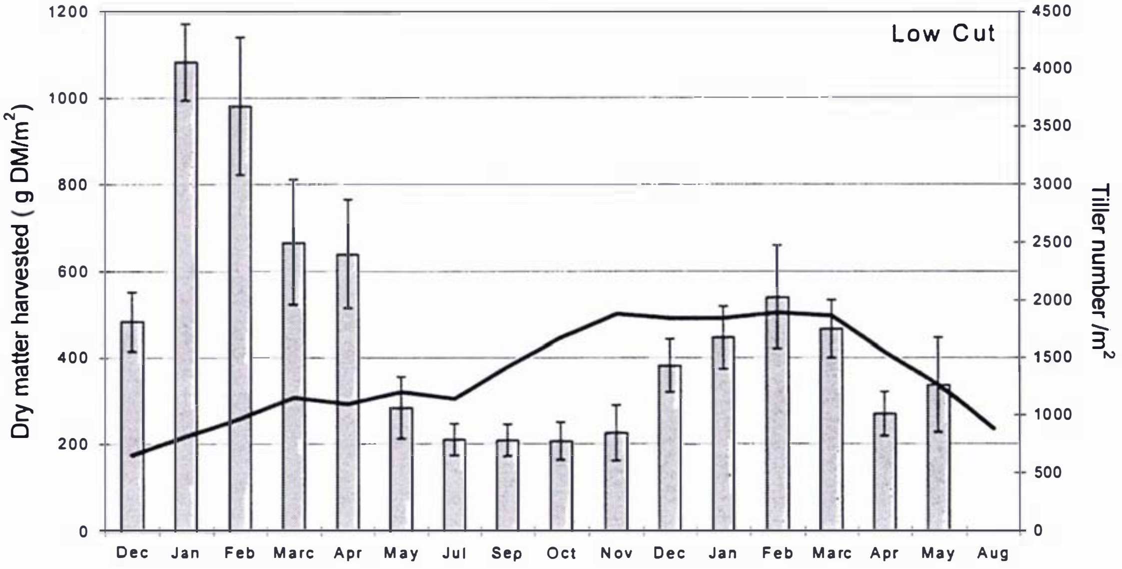
	Treatments							
Harvests	MH	ML	TH	TL	significance			
	TAR (tillers/100 tillers/day)				s.e.	cv	cut	cv*cut
Hi	10.86	11.62	16.01	18.42	1.23	***	ns	ns
H1	0.55	0.78	0.08	0.04	0.24	***	ns	ns
H2	1.82	1.34	0.77	0.60	0.28	***	ns	ns
H3	1.10	1.27	1.17	1.35	0.46	ns	ns	ns
H4	0.14	0.21	0.22	0.12	0.09	ns	ns	ns
H5	0.40	0.67	0.24	0.47	0.19	ns	ns	ns
H6	0.43	0.28	1.26	0.82	0.45	*	ns	ns
H7	0.57	0.76	1.50	0.89	0.28	*	ns	ns
H8	0.74	0.76	1.21	1.00	0.20	*	ns	ns
H9	0.69	0.65	0.86	0.84	0.17	ns	ns	ns
H10	0.11	0.16	0.23	0.37	0.09	*	ns	ns
H11	0.19	0.20	0.18	0.25	0.09	ns	ns	ns
H12	0.27	0.38	0.18	0.26	0.12	ns	ns	ns
H13	0.24	0.20	0.12	0.20	0.07	ns	ns	ns
H14	0.15	0.09	0.09	0.06	0.04	ns	ns	ns
H15	0.20	0.28	0.14	0.11	0.11	ns	ns	ns
H16	0.25	0.22	0.54	0.39	0.13	*	ns	ns
Mean	**0.49**	**0.52**	**0.55**	**0.49**	**0.03**	**ns**	**ns**	**ns**

Appendix 3.2. Tiller death rate (TDR) in two Guinea grass cultivars, Mombaça (M) and Tanzânia (T), under two defoliation heights, 300 (H) and 150 mm (L) over all harvests from December 1998 to August 2000.

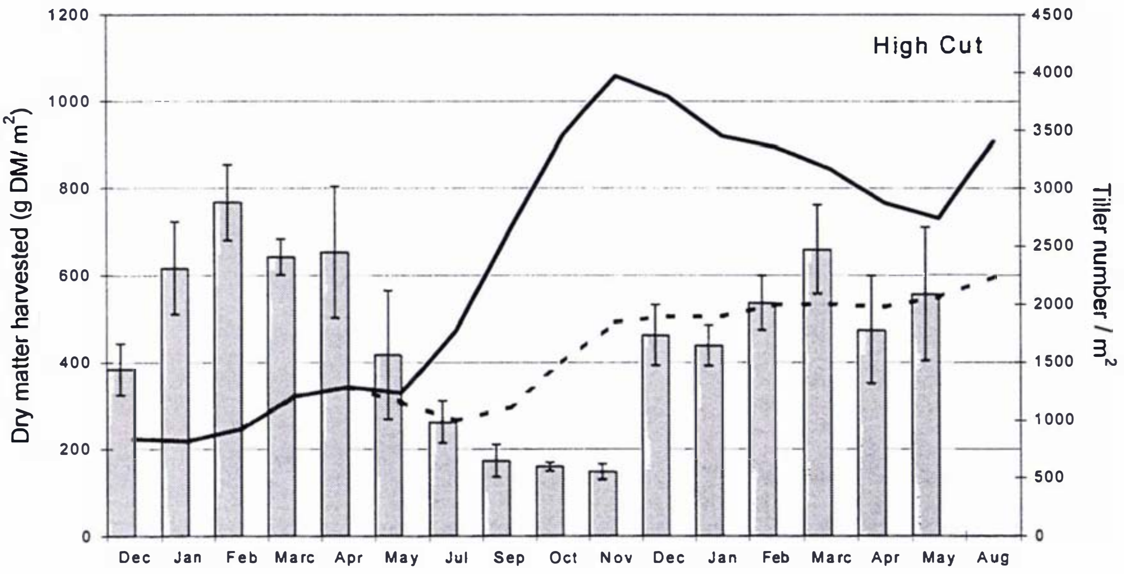
	Treatments							
Harvests	MH	ML	TH	TL		significance		
	TDR (tillers/100 tillers/day)				s.e.	cv	cut	cv*cut
Hi	0.00	0.00	0.00	0.00	0.00	ns	ns	ns
H1	0.03	0.00	0.19	0.39	0.11	***	ns	ns
H2	0.18	0.65	0.26	0.91	0.26	ns	**	ns
H3	0.15	0.61	0.07	0.45	0.23	ns	*	ns
H4	0.12	0.42	0.02	0.08	0.13	*	ns	ns
H5	0.34	0.44	0.27	0.21	0.21	ns	ns	ns
H6	0.43	0.42	0.49	0.53	0.06	*	ns	ns
H7	0.37	0.23	0.37	0.37	0.12	ns	ns	ns
H8	0.18	0.20	0.26	0.25	0.09	ns	ns	ns
H9	0.17	0.21	0.30	0.29	0.09	ns	ns	ns
H10	0.39	0.27	0.38	0.32	0.20	ns	ns	ns
H11	0.39	0.27	0.49	0.39	0.16	ns	ns	ns
H12	0.31	0.26	0.33	0.41	0.13	ns	ns	ns
H13	0.29	0.28	0.30	0.27	0.12	ns	ns	ns
H14	0.54	0.68	0.39	0.60	0.20	ns	ns	ns
H15	0.21	0.68	0.24	0.29	0.13	ns	*	*
H16	0.22	0.30	0.26	0.21	0.10	ns	ns	ns
Mean	**0.27**	**0.37**	**0.29**	**0.37**	**0.024**	ns	*	ns

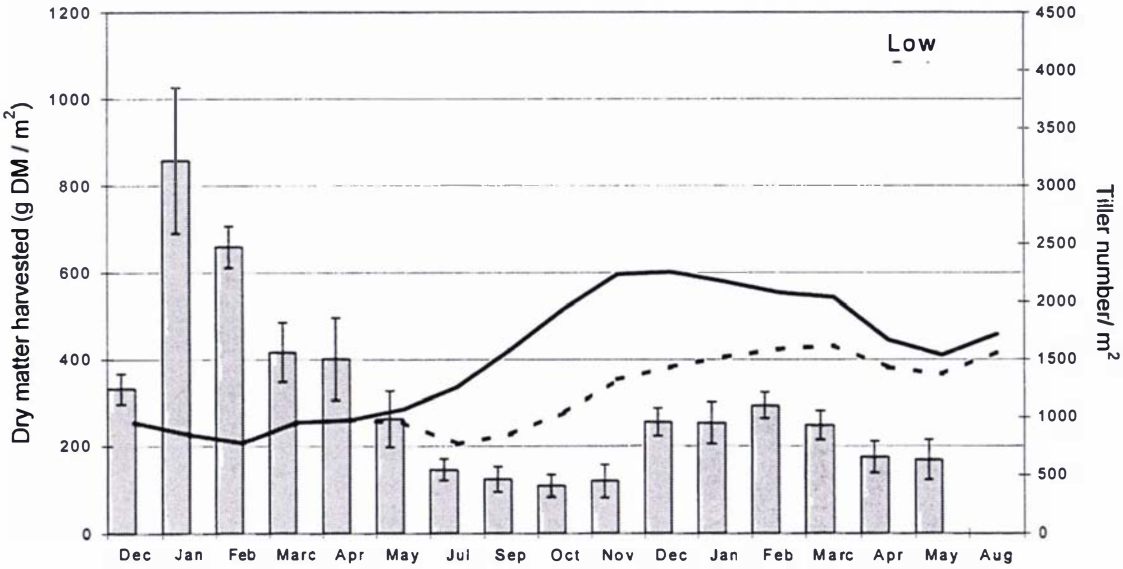
Appendix 3.3. Dry matter harvested above cutting height by harvest in g DM/m^2 (columns) and tiller population density in tillers/m^2 (solid line) in Guinea grass cv. Mombaça under two defoliation heights: Low Cut (150 mm) and High Cut (300 mm) from December 1998 to August 2000.





Appendix 3.4. Dry matter harvested above cutting height by harvest in g DM/m^2 (columns) and tiller population density in tillers/m^2 (solid line= total tillers and doted line= basal tillers) in Guinea grass cv. Tanzânia under two defoliation heights: Low Cut (150 mm) and High Cut (300 mm) from December 1998 to August 2000.





Appendix 6.1. Percentage of the total radiocarbon recovered on shoot and root fractions from tiller categories (G1, G2, G3, G4, G5, G6) according to treatments TM, TY and TO, in two Guinea grass cultivars, Mombaça and Tanzânia. Bold type indicates labeled tiller (s.e. within brackets).

Treatment TM

Cultivar	Fraction	Tiller Group Treatment TM				
		G1•	G2	G3	G4	G5
Mombaça	Shoot	**70.6** (9.0)	4.8 (2.8)	2.5 (0.6)	1.5 (0.6)	1.6 (0.5)
	Root	**15.8** (5.9)	0.8 (0.3)	1.4 (0.6)	0.7 (0.2)	0.3 (0.09)
Tanzânia	Shoot	**73.7** (3.9)	4.1 (1.5)	2.2 (0.4)	3.3 (1.7)	0.8 (0.2)
	Root	**11.9** (2.1)	1.3 (1.1)	0.9 (0.2)	1.7 (0.7)	0.2 (0.09)
Significance	Shoot	ns	ns	ns	ns	ns
	Root	ns	ns	ns	ns	ns

Treatment TY

Cultivar	Fraction	Tiller Group					
		G1	**G2L**	G2	G3	G4	G5
Mombaça	Shoot	4.3 (1.8)	**78.4** (5.5)	0.9 (0.1)	1.7 (0.3)	2.2 (0.4)	2.4 (0.2)
	Root	7.4 (2.6)	**0.04** (0.03)	0.02 (0.01)	0.3 (0.1)	1.6 (0.9)	0.6 (0.3)
Tanzânia	Shoot	3.9 (1.2)	**78.2** (3.6)	1.1 (0.4)	1.7 (0.3)	1.5 (0.5)	1.5 (0.5)
	Root	7.0 (2.9)	**2.5** (1.4)	0.2 (0.1)	0.9 (0.4)	1.0 (0.3)	0.5 (0.2)
Significance	Shoot	ns	ns	ns	ns	ns	ns
	Root	ns	ns	ns	ns	ns	ns

Treatment TO

Cultivar	Fraction	Tiller Group						
		G1	G2	G3	**G4L**	G4	G5	G6
Mombaça	Shoot	1.7 (1.0)	1.1 (0.5)	0.3 (0.1)	**84.9** (3.5)	1.2 (0.1)	1.6 (0.6)	1.3 (0.5)
	Root	0.4 (0.1)	0.2 (0.1)	0.2 (0.1)	**5.9** (2.1)	0.62 (0.1)	0.2 (0.1)	0.2 (0.1)
Tanzânia	Shoot	0.9 (0.07)	0.6 (0.02)	1.2 (0.3)	**70.7** (2.2)	0.9 (0.05)	2.0 (0.5)	6.7 (2.3)
	Root	1.4 (0.3)	0.02 (0.01)	0.4 (0.1)	**12.3** (2.3)	0.5 (0.1)	0.6 (0.2)	1. 8 (0.6)
Significance	Shoot	ns	ns	*	*	ns	ns	*
	Root	*	ns	ns	ns	ns	ns	*

Appendix 7.1. Summary of the five cut/uncut experiments carried out

	Experiment 1 Chapter 4	Experiment 2 Chapter 4	Experiment 3 Chapter 3	Experiment 4 Chapter 5	Experiment 5 Chapter 6
Site	Growth cabinet	Glass house	Glass house	Glass house	Glass house
Period	April to August 1998	September to December/1998	October 1998 to August 2000	September 1999 to April 2000	May to July 2000
Plants/pot	4 plants, one evaluated	4 plants, 2 evaluated	Mini sward 24 plants - 4 evaluated	1 plant	1 plant
Pot volume	2 litres	2 litres	0.6 x 0.8x 0.3 144 litres	5 litres	1 litre
Cultivar	Aruana, Mombaça Tanzânia	Aruana, Mombaça Tanzânia	Aruana, Mombaça Tanzânia	Mombaça Tanzânia	Mombaça Tanzânia
Cutting height	50, 200mm and undefoliated	undefoliated	150 and 300 mm	100, 200 and 400mm undefoliated	undefoliated
Statistical design	RBD, Factorial 3cv. x 3 heights, 4 blocks	CRD 3 cultivars, 5 replicates	RBD, Factorial 3 cv. x 2 heights, 4 blocks	RBD, Factorial 2 cv. x 3 height x 5 harvests, 5 blocks	RBD-Factorial 2cv. x 3 tiller types x 4 replicates
Measurements	Dry mater harvest LAR, LER, site filling, leaf length, Leaves/tiller	Dry mater harvest, LAR, LER, site filling, leaf length, leaves /tiller	TAR, TDR, LER, dry matter harvested, flowering,	LER, leaf length, tiller categories, photosynthesis root mass, TAR, TDR,	Tiller number Root mass Specific activity
Destructive harvest	Yes (at the end)	Yes (at the end)	No	Yes (every harvest)	Yes (at the end)