Effects of cutting, nitrogen, closing date and water on herbage and seed production in Ruzi grass (*Brachiaria ruziziensis* Germain and Everard)

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ABSTRACT

The successful production of Ruzi grass (*Brachiaria ruziziensis*) for both herbage and seed production requires a knowledge of vegetative and reproductive development and their reaction to management. Several management aspects were investigated in the present study, i.e. defoliation, closing date, nitrogen fertilizer application and water stress effects during reproductive development. In addition, an attempt was made to describe more fully phenotypic variation in a Ruzi grass population, an aspect which may provide information useful for a future plant breeding programme in this species.

Phenotypic variation in Ruzi grass was investigated under plastic house conditions where minimum and maximum temperatures were set at 20 C and 30 C respectively. The seed used was from a commercial seedlot obtained from Thailand. Single plant measurements were made during the vegetative stage (herbage production and tiller development, growth form, plant height, canopy width, leaf width, leaf hairiness, ligule colour, and stem colour) and during the reproductive stage (date of first flower initiation, tiller numbers at harvest, and development of inflorescences).

Erect and semi-erect plants had significantly higher herbage production than prostrate plants but failed to show significant differences in tiller numbers. Seed yield was unaffected by plant growth form. Other parameters such as ligule colour, stem colour, leaf width and hairiness also showed considerable variation from plant to plant. However there was little evidence they were linked to any particular plant growth form.

Management practices for herbage and seed production, particularly in terms of defoliation, time of closing and nitrogen fertilizer application were studied in miniature swards in a plastic house at 20 C and 30 C (night and day temperature). These swards were established in wooden bins each with 49 seedlings at a 15 cm square spacing.

In a complete randomised block design, the treatments comprised a combination of cutting frequencies viz. at 20, 35, 50 and 65 cm height and cutting intensities *viz.* 4 and 12 cm

stubble height, with 3 replications. This experiment was designed to determine the most appropriate defoliation management practice for Ruzi grass "pasture", and to provide a reasoned justification for the defoliation strategy adopted in subsequent studies.

Differences in cutting intensity between 4 cm (hard) and 12 cm (lax) had no significant effect on total plant dry matter, but under lax cutting plants produced significantly greater leaf dry matter and a higher leaf:stem ratio. Despite this, herbage quality was not significantly different mainly due to the longer cutting interval under hard cutting conditions resulting in plants producing bigger leaves and a significantly higher LAI compared with lax cutting. Although plants in the longer cutting frequency treatment had a significantly higher LAI than with more frequent cutting, the greater proportion of stem had a major effect in lowering herbage quality.

The overall assessment of the data from the defoliation treatments concluded that the most appropriate defoliation management for a Ruzi sward was 12-35 cm i.e. cutting when the canopy reached a height of 35 cm down to 12 cm. This was the defoliation strategy subsequently employed in studies on the management of Ruzi swards for herbage and seed production.

The effects of nitrogen and "closing date" (cessation of cutting) on herbage and seed production of Ruzi grass, were examined under three nitrogen levels viz. 50, 150 and 250 kg N/ha and three closing dates viz. early (24th March 1997), medium (7th April 1997) and late (21st April 1997) with 3 replications in a complete randomised block design. The experiment was conducted in "miniature swards" as previously described.

Herbage dry matter production prior to closing increased progressively with increasing levels of nitrogen supply. This nitrogen effect continued to produce significantly higher herbage production (250 kg N/ha) even after seed harvest, but there were no significant differences between 50 and 150 kg N/ha. Different closing dates did not cause similar effects to nitrogen application, simply because plant growth rate declined with the approach of the reproductive stage. This was particularly evident in medium and late closing treatments.

However, as expected, the earlier the closing date the higher the amount of herbage dry matter yield obtained after seed harvest. This was mainly contributed by both new vegetative and old reproductive tillers.

Nitrogen application up to 150 kg/ha increased seed yield mainly by increasing total and harvested ripe inflorescence density, total floret numbers, and seed numbers. However nitrogen had no effect on percentage seed set or seed weight. Early and medium closing dates produced significantly greater seed yields than the late closing date mainly through an effect on total and harvested ripe inflorescence density, seed numbers, seed weight. Closing date had no effect on percentage seed set, but early closing resulted in greater inflorescence size (floret numbers/inflorescence). The interaction of nitrogen level and closing date suggested that higher nitrogen supply (150 kg N/ha) and early closing increased the percentage of pure germinating seed, suggesting that this is the most appropriate management for enhancing seed quality and yield.

The final experiment in this study was established to determine the effects of different levels of water stress applied at different stages of reproductive development on seed yield, yield components and seed quality in Ruzi grass. Individual plants were grown in 10 litre pots filled with potting mixture. Three levels of water stress were imposed (control (nil), mild and severe) at three different reproductive development stages (floral initiation, ear emergence and full flowering).

The response of plants to different levels of water application were clearly shown in terms of physiological and morphological changes particularly when these applications were continued throughout the entire reproductive development stage. Although the higher the amount of water applied the greater the dry matter produced, in terms of reproductive development, there was relatively little difference between non stressed and mild stressed plants. Under severe stress, however, although plants developed inflorescences, they were unable to exsert to full ear emergence. Generally, the stage of plant development and level of water stress applied had a bearing on plant dry matter, seed yield and seed yield components.

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CHAPTER 1

INTRODUCTION and OBJECTIVES

1.1 INTRODUCTION

Ruzi grass (*Brachiaria ruziziensis* Germain and Everard) is currently the most popular and widely-sown grass species used in Thailand for pasture improvement. Its acceptance and expansion by farmers is the consequence of the spectacular development of the Thai dairy industry over the past 35 years, as local dairy farmers moved from the previous, typical one or two cow farmer at the village level, along with rice and often vegetable production, to the present day where a large and steadily increasing number of dairy farmers are solely milk producers. Herds of 40 to 50 dairy cows are now quite common with one farm in the northeast of Thailand milking over 2000 cows. In other words, in the relatively short time span of 35 years there has been a real "explosion" in dairy farming in Thailand which is now an important and viable component of the national economy (Watkin, 1992).

The Thai dairy industry, however, is still in its infancy and much remains to be done. Probably the biggest challenge is the urgent need to control and even reduce on-farm costs of production. As in all dairying countries, input costs on the dairy farm, be they for feed, fuel, fertilizer, animal health or labour are continuing to rise year by year while milk returns to the farmer are showing relatively small and slow increases. This means that the farmer's profit margin is being progressively "squeezed", forcing them to question, to examine and hopefully to reduce their on-farm costs to maintain an economic enterprise.

Currently the biggest cost to the farmer is that of meal concentrate which represents about 60% of the on-farm variable costs of production (O.A.E., 1990). Fortunately, as shown by research conducted at the Dairy Farming Promotion Organisation of Thailand station at Muaklek, Saraburi (Lekchom *et al.*, 1989) this cost can be significantly reduced by greater use of improved pasture and hence less dependence on expensive meal concentrate - and still achieve highly economic milk production.

The recognition by Thai dairy farmers of the value of improved pasture for milk production has led to a significant increase in demand for grass seed, especially that of Ruzi grass. Ruzi grass is unquestionably the favoured grass species presumably because of its relative ease of establishment and high feeding value under proper management for forage production and also its better seed retention for seed harvesting (Manidool, 1992; Phaikaew *et al.*, 1993).

The first recorded introduction of Ruzi grass into Thailand was in 1968. Seed was imported from Australia and sown at the then recently established Thai-Danish Dairy Farm at Muaklek, Saraburi. Following its successful establishment and encouraging forage production, and the recognition that seed production locally was possible, the Department of Livestock Development (Ministry of Agriculture and Cooperatives) initiated a forage seed production programme in 1975 (Manidool, 1992) to overcome the rising constraint of inadequate seed availability. Further introductions were subsequently made in 1980 from the Ivory Coast by the Ministry to facilitate the national seed production programme. Since then, grass seed production in Thailand (predominantly of Ruzi grass) was increased from 80 tonnes in 1984 to over 1000 tonnes in 1994 (Phaikaew, 1994).

In spite of the clear preference and high demand for Ruzi grass, little attention has been given to improving its performance through a plant selection and breeding programme - as it is a cross-pollinating species - or to determining the correct pasture management for optimum quantity/quality production or to improving the current low seed production yield per hectare through better fertilizer practice, optimum "closing date" and improved soil moisture management. In other words, there is an urgent need and justification, because of its current importance to the Thai pastoral industry, to give greater attention to this species to achieve worthwhile improvements in its performance in terms of both herbage and seed yields, and hence to contribute to the more economic production of both milk and meat in Thailand.

Like many tropical grasses, Ruzi grass is a relatively "wild and undomesticated" species with generally low seed yield and poor seed quality. These, according to Boonman (1971a, 1980), are a direct reflection of many factors. These include prolonged head emergence within plants, prolonged anthesis and stigma exsertion within single heads, the decreasing head size and flowering duration in progressively later emerging heads, low seed setting ability, low number of head producing tillers, large variation in time of initial head emergence between plants within a cultivar, and other indirect limiting factors including seed shattering, spikelet diseases, bird damage and ease of lodging.

The following objectives considered to be important for the improved performance and productivity of Ruzi grass, were therefore investigated.

1.2 OBJECTIVES

(i) To evaluate phenotypic variation within a population taken from a commercial seed line obtained from Thailand, and to provide agronomic information which may assist the following studies and provide possible assistance to future plant breeding efforts to improve Ruzi grass for better forage and seed production.

(ii) To gain an understanding of how best to manage Ruzi grass pasture by determining the effects of different defoliation intensities and frequencies of cutting on herbage production in terms of dry matter yield and quality, and to examine the effects of such defoliation on seed production.

(iii) To determine the effects of levels of nitrogen fertilizer and different "closing dates" (cessation of cutting) on herbage and seed production of Ruzi grass.

(vi) To determine the effects of different levels of water stress applied at different stages of reproductive development on seed yield, yield components and seed quality of Ruzi grass.

CHAPTER 2

LITERATURE REVIEW

2.1 INTRODUCTION

Plant productivity during plant growth and reproductive development can be potentially improved by providing optimum conditions and manipulating the balance between vegetative and reproductive growth where necessary. For grass seed crops, the primary aim of management is initially to produce a high density of young shoots of similar age. This will provide synchronised, high yielding fertile tillers by promoting inflorescence development and concentrating the duration of inflorescence emergence, and will finally facilitate harvesting (Loch, 1980; Humphreys and Riveros, 1986). This is usually achieved by defoliation (through cutting or grazing) or burning the old residues and applying nitrogen fertilizer at the start of each cropping cycle. Any delay in applying nitrogen fertilizer will generally cause a reduction of final seed yield by reducing the number of harvestable inflorescences (Boonman, 1972c).

Obviously, the optimum management requirements of pasture for herbage production and for seed yield are different. However, it is possible for farmers to maximize returns from their land through multiple use of their crops for both seed and forage (Humphreys and Riveros, 1986). Essentially, the management of plant growth during the vegetative phase will become the principle factor which determines whether the seed production response is favourable or unfavourable. Apart from defoliation and the fertilizer practices, matching the time of closing (final pasture utilization) to match expected growing conditions will be a crucial factor, particularly to avoid the risk of moisture stress which can affect flowering synchronisation whenever the delay of closing pasture occurred and reduce individual yield components in rain-fed crops. In this regard, irrigation may improve reliability of seed production and also allow the production of higher seed yields.

In general, this review covers the overall objectives of this study, with emphasis on the management of tropical grass for herbage and seed production. However, information on other plant crops are also included when information on tropical grasses is not available.

2.2 GENERAL DESCRIPTION OF THE SPECIES

Brachiaria ruziziensis (Germain and Everard) is synonymous with *Brachiaria eminii* (Mez) (Skerman and Riveros, 1990) and was renamed *Brachiaria decumbens* var. *ruziziensis* comb. nov. by Ndabaneze (1989). However, *Brachiaria ruziziensis* is still the most widely used botanical name (Miles *et al.*, 1996).

The species is known under various common names depending on the countries in which it is grown. These include: Kennedy Ruzi grass (Australia) - Kennedy is now regarded as the Australian cultivar name (D.Loch, personal communication 1999) , Congo Signal grass (Africa), prostrate Signal grass (Kenya), and Ruzi grass (Thailand). The names "Ruzi grass" and *Brachiaria ruziziensis* are used in this study.

Ruzi grass originated from the Lake Edward and Lake Kivu districts of Rwanda, Burundi and the Ruzizi plains in Zaire, but it is now widely distributed throughout the tropics (Skerman and Riveros, 1990). It is regarded as a pioneer species of cleared rain forests in Africa, providing an important grazing species in the wetter tropics (Skerman and Riveros, 1990).

Descriptions of the morphological features of Ruzi grass have been made by Bogdan (1977), Whiteman (1980) and Skerman and Riveros (1990). It is a spreading perennial with short rhizomes, similar in habit to Para grass (*Brachiaria mutica* (Fork.) Stapf). Five stages of morphological changes in the apex, and the visible changes occurring during reproductive development of Ruzi grass have been reported by Wongsuwan *et al.* (1997). The inflorescence consists of dense and spike-like racemes. The spikelets are all sessile and close together, the rachis of the racemes winged, broad and over 3 mm wide. The lower glume is under half the length of the spikelet which is hairy (Harker and Napper, 1960). Ruzi grass has softer leaves than *Brachiaria brizantha* (Schum) Stapf and Hubbard (Deinum and Dirven, 1976).

Many characteristics of Ruzi grass are similar to *B. decumbens* (Humphreys and Riveros, 1986). However, one of the obvious differences between the two species is the mode of reproduction. *B. decumbens* is a tetraploid and an obligate apomictic (Humphreys and Riveros, 1986) while *B. ruziziensis* is a diploid with 18 chromosomes and cross-fertilization occurs at very high frequency under conditions of natural open pollination (Ferguson and Crowder, 1974). Seed-set averages 21% and 0.4% for open pollination and self-pollination respectively, suggesting the operation of a self-incompatibility mechanism. Similarly, CIAT (1972) reports that *B. ruziziensis* clones when cross-pollinated, average 30% of spikelets with a caryopsis, but only 0.5% when selfed. By contrast, Skerman and Riveros (1990) and Bogdan (1959, 1965), state that Ruzi grass appears to be apomictic. However, according to Valle *et al.* (1993) Ruzi grass when used as a mother plant behaved as a sexual diploid in a breeding programme of apomictic *Brachiaria* at the National Centre for Research in Beef Cattle in Brazil, and also in a hybrid population derived from a cross between apomictic *Brachiaria brizantha* and sexual *B. ruziziensis* (Pessino *et al.*, 1998).

Being a tropical species, the main season of growth of Ruzi grass is during the rainy season in the so-called summer or warmer period of the year, with an optimum temperature of 33°C day and 28°C night (Deinum and Dirven, 1972). Plant growth is stimulated by increasing temperature which leads to lower protein content and lower digestibility of organic matter in leaves and stems. Temperature also has a direct negative effect on stem digestibility, apart from its effect on stem development (Deinum and Dirven, 1976). Lower temperatures, as found by Ludlow (1976), adversely affect the growth rate of this species.

Dirven *et al.* (1979) found that first head emergence occurred later in a 12 ½ hour treatment than in two shorter photoperiods (9 and 10¼ hours). Moreover, they found that the shorter the daylength the greater the number of heading tillers produced, and accordingly they concluded that *B. ruziziensis* was a quantitative short-day plant.

Rattray (1973) reported that Ruzi grows successfully at an altitude range of 1000-2000 m above sea level in Kenya and up to 1200 m in Panama. It is most productive under an average annual rainfall of about 1000 mm and can endure hot dry spells (Skerman and Riveros, 1990), and hence is described as drought resistant. It will not, however, withstand flooding or frost.

To achieve high dry matter production Ruzi grass requires a soil of relatively high fertility and good drainage, but performs well on a wide range of soil types (Skerman and

Riveros, 1990). It will tolerate acid soils and also responds well to nitrogen, either from fertilizer or legumes, but has a higher requirement than Guinea grass (Mellor *et al.*, 1973b). On the Adamawa plateau of the Cameroons, Pamo and Pieper (1989) showed that nitrogen fertilization in combination with phosphorus and potassium increased the productivity of Ruzi grass and recommended that a fertilizer rate of between 60-90 kg nitrogen/ha be applied after each cutting, with a single application of 100 kg triple superphosphate and potassium sulphate/ha at the beginning of each rainy season. This response was obtained under a 30 day cutting frequency. In field trials in Ribeirao Preto, Sao Paulo, Brazil, Andrade *et al.* (1996) reported nitrogen increased dry matter and crude protein yields of *B. ruziziensis* by 319% and 598%, respectively, and also significantly increased forage concentrations of S, Zn and Cu, while effects of potassium were not significant.

Dry matter production of Ruzi grass can vary considerably, depending on rainfall, fertility conditions and management. In Tanzania, dry matter yields of 21159 kg/ha have been recorded (Naveh and Anderson, 1967), and at South Johnstone, North Queensland, Grof and Harding (1970) recorded dry matter yields of 19500 kg/ha under a six week cutting intervals and following an input of 220 kgN/ha/year. In Sri Lanka dry matter yields of 16807, 22031 and 25585 kg/ha/year were obtained with nitrogen applications of 112, 224 and 336 kgN/ha respectively (Appadurai, 1975).

Association with legumes such as *Centrosema pubescens* (Mellor *et al.*, 1973a), *Stylosanthes humilis* (Falvey, 1976), *Stylosanthes guianensis* (Pamo and Yonkeu, 1994), *Centrosema pubescens* and *Macroptilium atropurpureum* (Nitis *et al.*, 1976) have all proved successful. In contrast, Wongsuwan and Watkin (1992b) demonstrated clearly the difficulty of keeping Hamata (*Stylosanthes hamata*) in a mixed Ruzi/Hamata pasture. However, Ruzi is grouped into the least shade-tolerant species along with *Setaria sphacelata* cv. Kazungula, and *Digitaria eriantha* cv. Transvala. These compare with *Panicum maximum* cv. Common, *Panicum maximum* cv. Tanganyika, *Digitaria setivalva* and *Brachiaria decumbens* which are regarded as more shade-tolerant grasses (Wong *et al.*, 1985).

Ruzi grass is very palatable and suitable not only as a green forage for dairy cattle (Sanchez and Soto, 1998) but also as hay (Rensburg, 1969) and silage (Risopoulos, 1966).

For seed production, yields of 125 kg/ha in Queensland and 200 kg/ha in Zaire were achieved when harvesting was a single machine operation (Risopoulos, 1966). Davidson (1966) reported that seed yields were often lower if harvested by a tractor-mounted buffel type seed harvester compared with hand harvesting. Like other tropical grasses, Ruzi exhibits a prolonged flowering period with uneven ripening of seed on individual inflorescences and quick shedding of seed when ripe (Boonman, 1971a; Hare and Waranyuwat, 1980; Phaikaew and Pholsen, 1993).

Seed dormancy is generally high in freshly harvested seed, because of an impermeable seed coat (Davidson, 1966; McLean and Grof, 1968), for removing the hull or cutting at the base of the spikelet stimulates germination (Renard and Capelle, 1976). Davidson (1966) found that only 20% of fresh seed germinated and after 12 months in storage germination was increased to 40%. Seed dormancy can be broken by treating the seed with concentrated sulphuric acid for 15 minutes (Banard, 1969) which can increase germination from 17 to 40% (McLean and Grof, 1968), or by mechanical scarification (Jones, 1973a).

For pasture establishment, Bogdan (1964) recommended that the seed be sown at a depth of 2 cm and in rows 60 cm apart, but it can be broadcast over the land after scarification of the soil with a disc harrow or brushcutter, without burning the native pastures (Risopoulos, 1966). In Thailand, the direct introduction of Ruzi grass into native pastures and old deteriorated pastures by direct-drilling has demonstrated satisfactory plant establishment and achieved high levels of herbage production in the first few weeks and months (Sukpituksakul *et al.*, 1992). However, a well prepared seed bed is highly recommended for best results (Skerman and Riveros, 1990; Suksombat *et al.*, 1992; Wongsuwan and Watkin, 1992a).

2.3 RUZI GRASS SEED PRODUCTION IN THAILAND

According to Manidool (1992) and Phaikaew *et al.* (1993), Ruzi grass is the major grass species grown for improved pasture development in Thailand due to its easy establishment, good seed production and acceptance as good quality forage.

The main location of Ruzi grass seed production in Thailand is the north-east region, 14-19 N, 100-300 m above sea level (Hare, 1993). The wet season begins in late June but about 80% of the rain falls from August through to early October, giving an average annual rainfall of 1200 mm. Climatic conditions in this region are a so-called tropical savannah climate, which is considered suitable for seed production due to the characteristic sharp division between the wet and dry seasons which facilitates seed harvesting and processing operations. A sandy soil type is typical in this area. These soils have a low pH (4.6-5.8) and low content of most plant nutrients, especially N, P and S.

In the past, Ruzi grass seed was only produced on government stations, with large scale production areas of 70-280 ha/station. Seed harvesting methods generally include cutting the seed heads, sweating, threshing and then drying. In 1986, however, a small farmer Ruzi seed production programme was started in order to overcome the inadequate supply of pasture seed due to the dramatic increase in numbers of dairy farmers and hence demand for seed in Thailand. According to Hare (1993) and Phaikaew (1994) over 1000 tonnes of Ruzi seed was produced commercially in 1994 with the major portion (60%) coming from over 2700 small farmers.

The small farmers involved in this programme normally plant approximately 0.32 ha and receive training in pasture establishment, management, harvesting and seed cleaning. The seed produced is then purchased by the government at a guaranteed price of US$2/kg. Normally, small farmers produce higher seed yields than government stations (300-500 kg/ha vs. 150-250 kg/ha, respectively). This is because of the more intensive collecting methods are normally practised in small scale seed production. The harvesting procedure usually involves tying groups of adjacent seedheads when the crop ripens into "living sheaves" which are then shaken to allow seed to fall into a broad shallow receptacle. Processing is repeated at 3-5 day intervals on about four occasions over two weeks. The seed is then dried for 2-3 days in the shade followed by 1 day in the sun. Generally, farmers will earn about US$200-320 from this programme.

2.4 EFFECT OF DEFOLIATION MANAGEMENT

"Defoliation" is used to describe the removal of plant shoots by grazing or cutting; and is considered in terms of : frequency - how often plant shoots are removed; intensity - how much plant material remains after defoliation, or how much is removed; and timing - the stage of plant development and the climatic conditions at the time of defoliation (Humphreys, 1987). The literature shows that defoliation interacts with other factors (Wallace, 1981; Ruess and McNaughton, 1984; Ruess, 1984, 1988; McNaughton and Chapin, 1985; Mihaliak and Lincoln, 1989).

Forage production of either C_3 or C_4 grasses depends on cutting regime and is negatively related to cutting frequency (Omaliko, 1980; Ludlow and Charles-Edwards, 1980). The response to cutting regimes differs among forage grasses due to different plant characteristics like tillering potential, meristematic activity in stem basal parts, level and location of carbohydrate reserves and canopy structure.

2.4.1 INFLUENCE OF CUTTING FREQUENCY AND INTENSITY ON HERBAGE PRODUCTION

The growth and tissue regeneration of forage plants following defoliation (cutting or grazing) are of primary importance in pasture management. The intensity and frequency of defoliation can dramatically affect the growth and nutritive value of C_4 grasses such as Ruzi grass (Evers and Holt, 1972; Middleton, 1982). Generally, frequency of defoliation is more important than intensity of defoliation, with the short intervals between defoliations reducing dry matter yield primarily by reduction in leaf area index and light interception (Morgan and Brown, 1983). Moreover, the digestibility, crude protein concentration and proportion of green leaf blade drops correspondingly (Oyenuga, 1959, 1960; Haggar, 1970; Saleem, 1972; Omaliko, 1980). On the other hand, increased dry matter yields as a result of extended cutting intervals are consequences of additional tiller and leaf formation, leaf elongation and stem development (Michelin *et al*., 1968; Akinola *et al.*, 1971; Dovrat *et al.,* 1971). An almost universal finding is that harvested herbage production increases with increasing interval between defoliations (e.g. Paterson (1933) and Wilsie *et al*. (1940) for *Pennisetum purpureum*; Louw (1938) for *Cenchrus ciliaris*, *Chloris gayana* and *Panicum maximum*; Lovvorn (1944) for *Paspalum dilatatum*; Beaty *et al.* (1963) for *Paspalum notatum*; Burton *et al.* (1963, 1969) and Chheda and Akinola (1971) for *Cynodon* spp.; Bryan and Sharpe (1965) for *Digitaria* *decumbens*; Appadurai and Goonewardena (1974) for *Brachiaria ruziziensis;* Whitney (1974) and Kemp (1976) for *Pennisetum clandestinum;* Piot and Rippstein (1976) for *Brachiaria brizantha*; Garcia and Rodriguez (1980) for *Cenchrus ciliaris* L. cv. Gayndah).

The effects of cutting intensity on dry matter yields may be different depending on the species studied, the plant structure and the types of pastures involved (pure or mixed). In some instances, for example, cutting intensity has no effect on yield (Riveros and Wilson, 1970; Olsen, 1973; Murphy *et al.*, 1977), whereas it does in others (Whitney, 1970; Ethredge *et al.*, 1973; Ferraris and Norman, 1973; Jones, 1973b, 1974; Murphy *et al.*, 1977; Ludlow and Charles-Edwards, 1980). Generally, plants which branch freely at ground level (for example, *Cynodon dactylon*: Clapp *et al.,* 1965) yield best at low cutting heights, while erect grasses (for example, *Panicum antidotale*: Wright, 1962) are favoured by higher defoliation.

In a study of *Eragrostis curvula*, cutting heights below 10 cm reduced dry matter production as a result of excessive leaf removal, severe depletion of carbohydrate reserves and a reduction in tiller numbers (Steinke, 1975). Similarly, Tavakoli (1993) noted that the reason that hard defoliation reduced herbage production was due to a decrease in both tiller population density and tiller weight and consequently decreased pasture growth by reductions in LAI, longevity of individual leaves, photosynthetic efficiency, and a shortage of carbohydrate reserves.

More nutritious herbage is obtained with reduced cutting intervals so that an optimum harvest scheme must be chosen to obtain a balance between quality and increased herbage production. Davidson (1966) noted that under grazing, Ruzi grass formed a dense mat and withstood grazing well.

2.4.2 THE EFFECTS OF DEFOLIATION ON SWARD DYNAMICS

Jameson and Huss (1959) found an increase in the number of tillers with clipped compared with unclipped plants of little bluestem (*Andropogon scoparius* Michx.), as similarly reported by Cook and Stoddart (1953) in a study on *Agropyron cristatum.* In contrast, frequent clipping of western wheat grass (*Agropyron smithii*) reduced plant vigour as indicated by a decrease in plant height and basal area (Holscher, 1945). Beaty and Powell (1976) reported that multiple harvests in a season reduced forage production, clonal survival, tillers per clone and tiller height in switchgrass (*Panicum virgatum* L.). Height of regrowth was also reduced by frequent clipping (Dradu and Nabusiu-Napulu, 1977).

Differences in tiller density with differences in management are most likely due to changes in the amount and quality of light penetrating to tiller bases under contrasting defoliation patterns and consequent effects on tiller initiation and appearance (Mitchell, 1953; Mitchell and Coles, 1955; Langer, 1963; Bean, 1964), though direct effects of defoliation on tiller removal may also be involved (Hunt, 1989). Moreover, by changing light quality inside the canopy, the LAI can modify some morphogenetic variable such as leaf elongation rate and tillering rate and, consequently, can change some structural characteristics of the sward, such as tiller density and tiller size (Deregibus *et al.,* 1983; Deregibus *et al.,* 1985; Barthram *et al.*, 1992; Chapman and Lemaire, 1993). Humphreys (1997) notes that tiller populations exhibit considerable homeostasis in their dynamics, and tiller recruitment may balance tiller mortality to give considerable stability in tiller density (Briske and Silvertown, 1993).

2.4.3 THE EFFECTS OF DEFOLIATION ON PHYSIOLOGICAL RESPONSES OF PLANTS

2.4.3.1 Residual leaf area, light interception and photosynthesis

The leaf area of the plant is obviously reduced by defoliation which can cause a reduction in regrowth, depending on the number of leaves and the stage of leaf development at removal (Tainton, 1981). Certainly, maintaining leaf area after defoliation is very important for herbage production, as illustrated by the classical work of Brougham (1956), in which he clearly showed that regrowth increased as the residual LAI increased.

The immediate effects of defoliation depend mainly on defoliation intensity and are best related to a direct measure of the degree of reduction in whole-plant photosynthesis or daily carbon gain (Richards, 1993). The reduction in photosynthesis is often not proportional to leaf-area loss due to changes in canopy microclimate after defoliation, particularly when mature, previously shaded foliage predominates on defoliated plants (Ludlow and Charles-Edwards, 1980; Gold and Caldwell, 1989). This is due to the unequal photosynthetic contribution of leaves of various ages of leaves remaining after defoliation (Ludlow and Charles-Edwards, 1980; Parsons *et al.*, 1983; Gold and Caldwell, 1989). Therefore, canopy measurements of photosynthesis relate better to regrowth capacity than single-leaf measurements or determinations of residual leaf area alone (Richards, 1993).

2.4.3.2 Meristematic tissue

Grass plants are morphologically adapted to survive repeated defoliation before the flowering stage is reached, because leaf formation continues during and after each defoliation from the meristem which is positioned at, or below, the soil surface beyond the reach of animals and machines (Hyder, 1973; Langer, 1979). Although some meristems are removed by defoliation, they may readily be replaced by the appearance of new tillers. Additionally, the meristematic region of individual leaves is located at the base of the leaf, so new leaf material can continue to grow even if older parts of the same leaf are removed by defoliation. Loss of meristematic tissues usually has a much greater effect than the proportional loss of biomass, leaf area or plant resource (e.g. carbon, nitrogen) (Branson, 1953; Booysen *et al.*, 1963; Hyder, 1972; Richards and Caldwell, 1985; Briske, 1986, 1991; Bilbrough and Richards, 1993).

2.4.4 PROCESSES LEADING TO RECOVERY FROM DEFOLIATION

The regrowth of the plant following defoliation can be divided into two phases (Richards, 1993) viz.: firstly, a major shift in allocation of carbon and nutrients to new leaves is required; and secondly, the compensatory processes coupled with preferential shoot growth allocation are continued and take a longer time for full development compared with the first phase.

The efficiency of plant recovery after defoliation is a distinguishing characteristic and can vary due to plant species and genotype (Davidson and Milthorpe, 1966; Caldwell *et al.*, 1981; Volence and Nelson, 1984; Richards and Caldwell, 1985; Volence, 1988; Frankhauser and Volence, 1989; Hodgkinson *et al.*, 1989; Paige, 1992; Mott *et al.*, 1992). The most important part which contributes to rapid refoliation is the presence of active shoot meristem regions remaining on the plant after defoliation which allows leaf expansion to result solely from expansion of already formed cells, rather than requiring new cell production (Briske, 1986, 1991; Richards, 1986; Culvenor *et al.*, 1989). However, at times when most meristems are removed (such as after internode elongation and apical meristem elevation) plants recover very poorly, while they may be quite tolerant of defoliation

shoot meristems remain after defoliation at any time in the season (Hodgkinson *et al.*, 1989; Mott *et al.*, 1992).

In grass species the most important location of the initial source of carbohydrate reserves is in the stem bases or stubble, and high levels can contribute to more rapid regrowth (Davidson and Milthorpe, 1966; Caldwell *et al.,* 1981; Richards and Caldwell, 1985; Danckwerts and Gordon, 1987; Busso *et al.*, 1990). Moreover, it has been demonstrated that frequently defoliated plants will be more productive if additional available carbohydrates are invested in rebuilding photosynthetic area, or if such plants exhibit higher photosynthetic rates following defoliation (Briske, 1996). On the other hand, in a study of *Lolium perenne* and *Festuca rubra* Thornton and Millard (1997) found that increasing the frequency of defoliation had little effect on the uptake of nitrogen by roots which was subsequently supplied to new leaves, but depleted their capacity for nitrogen remobilization, resulting in a reduction in the rate of growth of new leaves.

Recovery from defoliation depends not only on the inherent capacity of the plant and the characteristics of the defoliation, but also on the plant's abiotic and biotic environment (Richards, 1993).

2.4.5 THE EFFECTS OF DEFOLIATION ON PASTURE SEED PRODUCTION

Humphreys and Riveros (1986) noted that defoliation by cutting or grazing had adverse or favourable effects on seed production, according to the influence on the density of inflorescences; assimilate supply to the inflorescence; time of flowering and control of competing species. Similarly, Crowder and Chheda (1982) stated that the influence of defoliation can be considerable, leading to either an increase or a decrease, or no effect in altering seed yield of pasture grasses and legumes, depending on the species, time and extent of the defoliation and length of the growing season.

Although much research on the effects of defoliation on plant growth and reproduction has been reported over many decades, they are still not well understood and it is not possible to predict plant responses with confidence, unless repeated local experience is available (Humphreys and Riveros, 1986). In general, the main objective of defoliation management is to produce a crop of shoots of similar age; at a density suitable for the environment and ready to flower under the weather conditions most opportune for the development of a good seed crop.

2.4.5.1 Reproductive apices

Defoliation which removes reproductive apices is considered inimical to seed production (Tainton and Booysen, 1963). This view is based on the contribution to seed yield which the larger first-formed inflorescences produce, and the smaller seed-yield potential of inflorescences formed late in the growing season from inferior hierarchical positions in the sward (Haggar (1966) for *A. gayanus*; Chadhokar and Humphreys (1973a) for *Paspalum plicatulum*; Bahnisch (1975) for *Setaria anceps* cv. Kazungula). In *Chloris gayana* cv. Callide, Loch (1983) showed that heavy defoliation at the onset of reproductive growth restricted the crop throughout its subsequent development. Inflorescence emergence is slower and takes place over a longer period, lowering final inflorescence numbers compared with a lenient cleaning cut. In contrast, however, continual removal of young inflorescences as they were exserted increased the rate of inflorescence appearance in *Panicum maximum* var. *trichoglume* cv. Petrie (Humphreys, 1966b), and increased vegetative tillering in *Setaria sphacelata* var. *sericea* cv. Narok when defoliation was applied at a stage which removed tiller apices (Bahnisch, 1975).

2.4.5.2 Tillering and tiller development

Defoliation is one of the most important pasture management methods to stimulate the production of a high density of young tillers of the same age which will potentially provide better synchrony of flowering and subsequently facilitate seed harvesting, especially for grasses (Humphreys and Riveros, 1986). Patterns of tillering and tiller development in tropical grass have been reported by Boonman (1971b) and Loch (1985). They found that maximum basal tillering occurred during early vegetative growth and tiller density, which varied for different grasses, generally began to decline before inflorescences emerged, so that substantial numbers of tillers died without completing reproductive development.

The importance of the contribution of early-formed tillers for seed yield has been reported (Haggar, 1966; Bahnisch and Humphreys, 1977b) and explained in terms of their advantage in size and preferential position in the crop for light and nutrients (Humphreys and Riveros, 1986). However, Loch (1983) considered early-formed tillers are important simply because there is a considerable delay before significant tillering activity is renewed. Removal of early tillers by cutting or grazing significantly reduces inflorescence density and therefore seed yield in grasses such as *Andropogon gayanus*, *Chloris gayana* and *Pennisetum polystachion* (Foster, 1956; Haggar, 1966; Mishra and Chatterjee, 1968). Mishra and Chatterjee (1968) found that although cutting stimulated tillering in *Pennisetum polystachion* and *Andropogon gayanus*, tiller fertility was negatively related to cutting frequency.

During the reproductive phase, aerial tillers can be produced on maturing basal culms if adequate soil moisture and nitrogen are available, but they contribute little to a single destructive seed harvest despite their more rapid development (Loch, 1985). In fact, this phenomenon has been found in many tropical grasses (Boonman, 1971b, Dirven *et al* ., 1979), and is referred to as "culm branching" (in *Brachiaria brizantha*, *Brachiaria decumbens*, *Brachiaria ruziziensis*, *Chloris gayana*, *Panicum coloratum* and *Setaria sphacelata* var. *sericea)*.

High tiller densities do not necessarily mean increased inflorescence densities, as shown by Bahnisch and Humphreys (1977b). In *Setaria sphacelata* var. *sericea* cv. Narok tiller fertility was 44% for a low density seedling crop compared with 9% in a second year crop with a higher density of 1100 tillers/m^2. Accordingly, intensive management of some tropical grasses aims to maximize inflorescence density which can be mediated through either tiller density or tiller fertility , or both, and the management practices can be varied due to species. Loch (1983) suggested that increased early tillering (e.g. through closer rows) in some grasses such as *Chloris gayana* cv. Callide, *Paspalum plicatulum* cv. Bryan, and *Setaria porphyrantha* cv. Inverell could lead to better synchronized crops of inflorescences through improved survival of the earliest and most advanced basal tillers. However, reduced early tillering may be an advantage with some other grasses, especially "leafy" cultivars such as *Setaria sphacelata* var. *sericea* cv. Narok and *Bothriochloa insculpta* cv. Hatch where support for weaker, and ultimately sterile, tillers appears to be greater.

2.4.5.3 Closing date

Final cleaning cuts of pasture for seed production are a critical time to match expected favourable climatic conditions whether they can minimise the risk of moisture supply with grasses not affected by daylength or must be appropriately timed to correspond to these inflexible flowering behaviour restricts inflorescence production particular the short-day grasses growing near the equator (Hill and Loch, 1993).

A defoliation management study in Brazil of the short-day grass *Andropogon gayanus* showed that removal of some vegetative material produced in the first half of the growing season was needed, since previously uncut crops were 2.6m high at harvest and produced a lower seed yield than crops cut on 20 January. Swards cut later than this (20 February and 20 March) were able to flower but gave smaller inflorescences and greatly reduced seed yields (Andrade and Thomas, 1981). Irvine (1983) also reported that later cutting dates reduced both the yield and quality of seed harvested.

An incorrect time of closing, especially if earlier than the optimum, will encourage plants to grow taller, produce more dry matter and be more prone to lodging (Loch, 1983, 1991).

2.4.5.4 Assimilate supply

Humphreys and Riveros (1986) noted that assimilate supply to the developing inflorescences is reduced by decreased leaf area consequent upon severe defoliation, resulting in reduced floret differentiation, poorer seed set and decreased seed size. The magnitude of these effects depends on the closing date (Andrade and Thomas, 1981). Generally, the green surfaces of the inflorescence and its supporting stem contribute significantly to the assimilate demands of the developing seed; the upper leaves and especially the flag leaf export assimilates to the seed but the lower leaves do not contribute directly (Humphreys and Riveros, 1986).

2.5 EFFECT OF NITROGEN FERTILIZER APPLICATION

2.5.1 ON HERBAGE PRODUCTION

2.5.1.1 Dry matter yield

The favourable response of tropical grasses to applied nitrogen fertilizer in terms of increased herbage production and chemical components is well known and documented. Generally, dry matter yield increases almost linearly with successive increments of nitrogen fertilizer (Oyenuga and Hill, 1966; Wollner and Castillo, 1968; Grof and Harding, 1970; Henzell, 1970; Salette, 1970; Hendy, 1972; Vicente-Chandler *et al.,* 1974; Crespo *et al.*, 1975; Jennings *et al.*, 1990; Pamo, 1991; Pamo and Pieper, 1995; Pietrosemoli *et al.*, 1996). In fact, differences in response to applied N in terms of dry matter production can vary due to many factors such as species, stage of growth, amount and time of N applied, soil moisture and climatic conditions (Crowder and Chheda, 1982).

In Ruzi grass, the response to nitrogen has been studied in a number of countries and the dry matter yield results show a marked variation due to the different environment and management practices. For example, at South Johnstone, north Queensland Ruzi yielded 19500 kg DM/ha under a six-week cutting interval from an input of 220 kg N/ha/year (Grof and Harding, 1970). In Sri Lanka yields of 16807, 22031 and 25585 kg DM/ha per year were recorded from nitrogen applications of 112, 224 and 336 kg N/ha (Appadurai, 1975). At Gualaca, Panama, Ruzi produced 11000 kg DM/ha without fertilizer and 27000 kg DM/ha when fertilized with 600 kg N/ha/year in a rain fall area of 3997 mm per year (Skerman and Riveros, 1990). At Wakwa, Cameroon, Pamo (1991) showed that dry matter yield of Ruzi grass increased greatly with increasing nitrogen rate up to 80 kg N/ha in all years.

2.5.1.2 Crude protein in herbage

Many workers have shown that crude protein content of grasses depends on soil fertility and rises sharply with increasing levels of applied nitrogen fertilizer (French, 1957; Michelin and Crowder, 1959; Burton and Jackson, 1962; Whitney and Green, 1969; Chheda and Akinola, 1971; Crespo, 1974; Olsen, 1975; Botrel *et al*., 1990). Vicente-Chandler *et al.* (1974) reported that different grass species (Congo, Pangola, Napier and Giant Cynodon) had a different response to applied nitrogen, in terms of crude protein content, at each level, but tended to be less divergent at the highest levels.

2.5.1.3 Time of nitrogen application

All stages of tropical plant growth require constant nitrogen supply to regulate the plant nitrogen content as demonstrated by Henzell and Oxenham (1964). In many studies (Quinn *et al*., 1961; Rodel, 1969; Henzell, 1970; Whitehead, 1970; Whitney, 1974; Wilkinson and Langdale, 1974; Velasquez *et al.*, 1975; Crowder, 1977) the value of split nitrogen fertilizer application under a cutting regime, where an attempt was made to sustain growth, provided an even distribution of herbage, maintained a fairly constant nitrogen content in the herbage. This response was found to depend on the source of nitrogen, quantity of nitrogen used, number and time of topdressing, frequency of cutting, species characteristics and climatic conditions.

2.5.2 ON SEED PRODUCTION

2.5.2.1 Seed yield and yield components

The available nitrogen content of the soil is widely accepted as being the dominant nutritional determinant of grass seed yield (Foster, 1956; Haggar, 1966; Humphreys and Davidson, 1967; Mishra and Chatterjee, 1968; Cameron and Mullaly, 1969; Grof, 1969; Chadhokar and Humphreys, 1970, 1973a; Hacker and Jones, 1971; Boonman, 1972a, 1972b, 1972c; Stillman and Tapsall, 1976; Bahnisch and Humphreys, 1977a) and the application of nitrogen fertilizer is now an important managerial variable which is almost universally profitable and can be manipulated by farmers to maximize seed yields (Humphreys and Riveros, 1986).

According to Humphreys and Riveros (1986) the response of grass seed crops to high nitrogen fertilizer application arises more from a higher proportion of shoots flowering than from the higher photosynthetic capacity of a well-grown canopy, particularly in tropical grasses.

Generally, inflorescence density appears to be the main component of seed yield through which nitrogen responses are mediated in tropical grasses and positive increases have been reported for *Andropogon gayanus* (Haggar, 1966), *Brachiaria mutica* (Grof, 1969), *Cenchrus ciliaris* (Bilbao *et al.*, 1979), *Panicum maximum* (Febles and Padilla, 1974; Sarroca *et al.*, 1980; Febles *et al.*, 1982), *Paspalum plicatulum* (Chadhokar and Humphreys, 1970, 1973a, 1973b; Cameron and Humphreys, 1976; Humphreys, 1976), *Setaria sphacelata* var. *sericea* (Hacker and Jones, 1971; Boonman, 1972a; Bahnisch, 1975; Humphreys, 1976; Bahnisch and Humphreys, 1977a), *and Chloris gayana* (Loch, 1983). However, such increases in inflorescence density from nitrogen fertilizer applied may reflect increases in tiller fertility (Henzell and Oxenham, 1964; Mishra and Chatterjee, 1968; Boonman, 1972a, 1972b; Bahnisch, 1975; Cameron and Humphreys, 1976; Bahnisch and Humphreys, 1977a; Loch, 1983) and/or in tiller density (Chadhokar and Humphreys, 1970, 1973b; Bahnisch, 1975; Cameron and Humphreys, 1976; Loch, 1983).

The influence of nitrogen fertilizer may increase some seed yield components and decrease others. For example, in a study of seed yield of *Paspalum plicatulum,* Cameron and Humphreys (1976) found that nitrogen application increased raceme number on the individual inflorescence but decreased raceme length and individual seed weight, while seed density per unit raceme length did not vary significantly.

The nature of the response curve in seed yield to nitrogen fertilizer application is usually an initially steep increase in yield, followed by a diminishing rate of response as maximum yield is approached. Further increases in fertilizer rate can cause a reduction in seed yield (Humphreys and Riveros, 1986). However, the most efficient and profitable response can occur at high rates of nitrogen fertilizer when split applications are used with an irrigation system provided (Harlan *et al*., 1966), or it is due to the low soil nitrogen levels under which it is usually grown (Cameron and Mullaly, 1969), although this depends on the initial soil nitrogen status.

2.5.2.2 Species and cultivar

Generally, it is considered that maximum seed yields from established stands of tropical grasses are obtained by applying 100 kg N/ha/crop as reported by many workers viz. with *Chloris gayana* cv. Mbarara (Boonman, 1972a), *Eragrostis curvula* (Ahring, 1970); *Paspalum plicatulum* cv. Rodds' Bay (Chadhokar and Humphreys, 1973b; Cameron and Humphreys, 1976; Humphreys, 1976), and *Setaria sphacelata* var. *sericea* cv. Nandi and Nandi II (Boonman, 1972a; Stillman and Tapsall, 1976).

Despite this generalization, the nitrogen requirement can also vary with different species and cultivars. In the Philippines, Mendoza *et al.* (1975) reported that *Dichanthium aristatum* required only 55 kg N/ha/crop to achieve maximum seed yields, but for *Brachiaria mutica* in north Queensland a rate of 50-100 kg N/ha/crop was required (Grof, 1969). Cameron and Mullaly (1969) also reported a continuing response by *Cenchrus ciliaris* cv. Molopo up to 336 kg N/ha/year. In terms of cultivar differences, Hacker and Jones (1971) reported that maximum seed yield of *Setaria sphacelata* var. sericea (CPI 32930) showed a quadratic response to increasing nitrogen up to 84 kg N/ha, but CPI 33425 continued to respond linearly to 168 kgN/ha.

2.5.2.3 Seed quality

In terms of seed quality, both positive and negative effects of nitrogen have been reported. For example a negative effect was reported for *Setaria sphacelata* var. *sericea* (Boonman, 1972a), for *Chloris gayana* (Boonman, 1972b), and for *Paspalum plicatulum* (Cameron and Humphreys, 1976) i.e. a reduction in seed viability and seed weight, but positive effects have also been reported by Bahnisch (1975) for *Setaria anceps* and Chadhokar and Humphreys (1973b) for *Paspalum plicatulum*, i.e. nitrogen applied at floral initiation increased seed viability and seed weight. However, Javier *et al.* (1975) concluded that seed quality is not usually affected by nitrogen fertilizer or is not consistently related to nitrogen level (Cameron and Mullaly (1969) and Macedo *et al.* (1983) for *Cenchrus ciliaris*; Mejia *et al.* (1978a) for *Panicum maximum*; Grof (1969) for *Brachiaria mutica;* Satjipanon *et al.* (1989) for *Brachiaria ruziziensis*; and Ruiz *et al.* (1996) for *Brachiaria* spp.

2.5.2.4 Crop maturity

The effects of nitrogen fertilizer on flowering and crop maturity have shown varied results. For example, nitrogen hastened floral initiation in *Setaria sphacelata* var. sericea (Bahnisch, 1975; Bahnisch and Humphreys, 1977a, 1977b) and flowering and crop maturity in *Chloris gayana* (Boonman, 1972b), and in *Paspalum plicatulum* (Chadhokar and Humphreys, 1973a, 1973b). On the other hand, Stillman and Tapsall (1976) reported a delay flowering in *Setaria anceps* while Boonman (1972a) found no effect on crop maturity in *Setaria sphacelata* cv. Nandi.

2.6 EFFECT OF WATER STRESS ON SEED PRODUCTION

2.6.1 PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSE

Water deficit stress, which results when the supply of water to the plant is stopped or limited, causes direct changes in the physical environment of the plant. These changes may subsequently affect physiological processes. Lack of water limits global crop productivity more than any other stress factor (Fischer and Turner, 1978; Boyer, 1982). The most unit raceme length did not vary significantly.

The nature of the response curve in seed yield to nitrogen fertilizer application is usually an initially steep increase in yield, followed by a diminishing rate of response as maximum yield is approached. Further increases in fertilizer rate can cause a reduction in seed yield (Humphreys and Riveros, 1986). However, the most efficient and profitable response can occur at high rates of nitrogen fertilizer when split applications are used with an irrigation system provided (Harlan *et al.*, 1966), or it is due to the low soil nitrogen levels under which it is usually grown (Cameron and Mullaly, 1969), although this depends on the initial soil nitrogen status.

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(1994), the caespitose *Hyparrhenia rufa* and *Andropogon gayanus* and the stoloniferous *Brachiaria mutica* and *Echinochloa polystachya* were all subjected to moderate water stress. Net photosynthesis compensation point was reached at the lowest leaf water potential in *A. gayanus* which was considered as the most drought tolerant species.

Leaf extension is particularly sensitive to water stress. In grasses, the zone of leaf extension is limited to the lower region of the leaf enclosed by the leaf sheath of the preceding leaf, with cell division confined more to the basal region (Langer, 1979). Generally, leaf elongation rate declines with decreasing water potential (Boyer, 1968, 1970; Meyer and Boyer, 1972; Ludlow, 1975; Ludlow and Ng, 1976), but the leaf water potential at which leaf elongation ceases varies with the species concerned. For example, Ludlow and Ng's (1976) experiment on leaf elongation of *Panicum maximum* var. *trichoglume* showed that leaf expansion ceased as leaf water potential reached -11 bars which was lower than that for *Zea mays* (-9 bars) and for the average for a number of herbaceous C_3 plants (-9 bars, range -3 to -16) grown under controlled conditions (Ludlow, 1975). Low leaf water potentials may also restrict leaf production through their effects on leaf initiation and the subsequent rate of cell division (Hsiao, 1973; Slatyer, 1973). Leaf area alteration can also be influenced by changes in the time of leaf appearance, in the rate and duration of leaf expansion, and in leaf senescence (Day, 1981). As a consequence, such restriction in leaf area can reduce yield (Hsiao and Acevedo, 1974; Paez *et al.*, 1995).

The total dry matter yield of a stressed crop differs from that of an unstressed crop as a result of the integrated effect of many changes in crop physiology, and can be considered as three processes (Day, 1981). Firstly, light interception; the total green area index was decreased by water stress both by a shortening of the season and by a smaller maximum green area and as a result, a non-irrigated crop may intercept 40% less light than a fully irrigated crop. Secondly, by altering the efficiency of photosynthesis; although measurements did not distinguish any systematic differences in the internal photosynthetic performance of stressed and unstressed leaves in Day's experiment (1981), reduction in net photosynthesis, resulting from closure of stomata, was nevertheless recorded with the tropical grass, *Panicum maximum* var. *trichoglume* (Ludlow and Ng, 1976). Finally, the fraction remaining after respiration; this represents the efficiency of conversion of assimilated carbon into stored dry matter and it is probable that the increased temperature within the stressed crop leads to enhanced respiration rates (McCree, 1970).

Tillering is one of the major growth components involved in pasture herbage production. In general, tiller production and the survival of tillers are inversely related to soil water deficit (Langer, 1979). The variation in total tiller numbers is, according to Luxmoore and Millington (1971), the major morphological parameter associated with variation in total plant dry weight and leaf area.

The differential effects of water deficits on different plant parts will influence not only dry matter production but also the quality of the herbage. With the tropical grass *Panicum maximum* var. *trichoglume*, Wilson and Ng (1975) demonstrated that water stress reduced the herbage quality of specific plant tissue, compared on a physiological basis, with comparable tissue on a well-watered plant. Water stress may accelerate the death of older leaves, thereby rapidly decreasing their digestibility. Younger leaves may be retarded in development and the normal ontogenetical decline in digestibility temporarily halted. However, stress occurring during early vegetative growth may have a beneficial effect on the quality of grass forage, by retarding stem elongation and flowering and maintaining a higher nitrogen content than in well-watered plants which have flowered and matured rapidly. But if flowering stems are well developed when stress occurs, their quality may possibly be markedly reduced through accelerated maturation and through the effects of water stress in lowering cell wall digestibility.

2.6.2. REPRODUCTIVE STAGES AND THEIR SENSITIVITY TO WATER STRESS

Reproductive development holds particular interest because a large part of agricultural production is devoted to the reproductive parts of the plant (Kramer and Boyer, 1995). Accordingly, adequate water availability during the reproductive phase is important for maintaining crop yield. The precise stress sensitivity stages of development have been discussed by Salter and Goode (1967). Generally, early stages of reproduction are more susceptible to losses from limited water than any other stage of development in reproductive crops (Salter and Goode, 1967; Claassen and Shaw, 1970). However, the results may vary among different species.

For determinate crops, grain yield is the product of the two components : grain number and grain size, which are sensitive to drought at early stages of flowering and at grain filling respectively (Fischer and Turner, 1978). Moreover, such crops are generally more uniform genetically and low-tillering, or even produce only one head per culm. Therefore, these crops usually have little ability to overcome the detrimental effects of a desiccated inflorescence by producing secondary inflorescences. In contrast, indeterminate species can produce a new set of flowers and leaves after drought is relieved. For example, during one year of cowpea planting, drought at flowering caused total abscission of flowers and young pods, but when the drought was relieved by irrigation, the plants produced more flowers and leaves and achieved seed yields which were 71% of well irrigated plants (Turk *et al.*, 1980).

In a study on perennial ryegrass (*Lolium perenne* L.) cv. S.23 seed production Hebblethwaite (1977) found that water deficit before stem elongation reduced head numbers, thereby decreasing seed yield. However, a water deficit of less than 100 mm after stem elongation in perennial ryegrass has little effect on floret site utilisation and high seed yields (of over 2000 kg/ha) can be achieved (Rolston *et al.,* 1994). Many workers have shown that the stage of greatest sensitivity to drought, affecting grain yields in wheat, barley and oats, is just before ear emergence (Salter and Goode, 1967; Dubetz and Bole, 1973; Fischer, 1973). In rice plants subjected to water stress during flowering, harvest index can be reduced by as much as 60% due to a reduction in grain set (O'Toole and Moya, 1981; Hsiao, 1982; Garrity and O'Toole, 1994). Moreover, water stress during or just before flowering causes a failure of the panicles to fully exsert (emerge) from the flag leaf sheath, a delay in flowering, reduction in the percentage of spikelets that open at anthesis, and severe desiccation and death of spikelets (O'Toole and Namuco, 1983; Ekanayake *et al.,* 1989). The reasons for non-exsertion of the panicle are not known, but may include inhibition of panicle elongation (Sheoran and Saini, 1996). Lambert (1967) emphasised that moisture stress after anthesis reduces thousand seed weight, probably due to a reduction in photosynthetic area and capacity. By comparison, however, in *Sorghum bicolor* (L.) Moench Ludlow *et al.* (1990) found that water stress prior to anthesis reduced yield more than a post-anthesis stress of the same intensity. Excess water, on the other hand, can increase vegetative tillers (Hebblethwaite, 1980), which have been reported to be a stronger assimilate sink than reproductive tillers and can cause increased abortion and reduced seed yield in *Lolium multiflorum* (Griffith, 1992). However, Warringa and Kreuzer (1996) indicated that there is no major effect of competition on the growth of vegetative tillers after anthesis on seed development.

2.6.3 IRRIGATION PRACTICE AND BENEFITS FOR SEED CROPS

The traditional solution to agriculture water shortage is irrigation (Boyer, 1996). Generally, irrigation can achieve significant benefit to seed production by extending the period of reproductive development and substantially increasing seed yield (Lambert, 1967; Hebblethwaite, 1977; Guy *et al.*, 1990; Rolston *et al.*, 1994). Moreover, it enables additional crops to be grown and harvested for seed which is not possible under non-irrigated conditions (Javier *et al.*, 1975). Sarroca *et al.* (1981) have also shown that irrigation of *Cenchrus ciliaris* cv. Biloela to 80% field capacity gave a seed yield of 842 kg/ha relative to 642 kg/ha in the non-irrigated control.

Although irrigation provides many advantages for seed production, many considerations must be taken into account, such as the appropriate timing of irrigation for plant developmental stages, the type of irrigation, amount of water applied, etc, if a successful outcome is to be achieved. Negative effects of irrigation have been reported by Cameron and Mullaly (1969), who showed that two irrigations of 80 mm of water early in the season decreased seed yield of *Cenchrus ciliaris* cv. Molopo because the irrigation caused excessive leaching of available nitrogen which was applied in a single dressing, thus resulting in reduced seed yield, particularly at the second harvest. Improving the efficiency of water use depends, according to Taylor *et al.* (1983) and Stewart and Nielsen (1990), on three broad categories - increasing the efficiency of water delivery and the timing of water application; increasing the efficiency of water use by the plants; and increasing plant drought tolerance. The first requirement is obviously the most practical and depends largely on engineering and minimally on the crop, but the latter two both depend on a clear understanding of plant biology.

CHAPTER 3

PHENOTYPIC VARIATION IN RUZI GRASS (*Brachiaria ruziziensis*)

3.1 INTRODUCTION

Ruzi grass was introduced into Thailand as seed imported from Australia in 1968 by the Thai-Danish Dairy Farm, for use in the pasture improvement programme. Following successful establishment and trial from this limited import, further introductions were made by the Ministry of Agriculture and Cooperatives in 1980 with seed imported from the Ivory Coast. By this time it was also found that seed could be produced and harvested locally. A Ruzi seed production scheme was initiated by the Department of Livestock Development in 1975 (Manidool, 1992) in order to meet the growing demands of farmers. In 1986, a further Ruzi seed production programme, particularly with smallfarmers, was commenced in order to overcome the constraint of seed availability due to the rapid increase in dairy farming in Thailand. Today Ruzi grass is the most popular and most widely sown pasture species used and represents 80% of the total forage seed production of the country (Hare, 1993; Phaikaew, 1994).

The mode of reproduction of Ruzi grass is still subject to some degree of confusion. For example, Bogdan (1959, 1965) and Skerman and Riveros (1990) report that it is an apomictic species, although the latter authors are not too concerned as they say "it appears to be apomictic" - and hence develops little variation from the "mother" plant. However, Ferguson and Crowder (1974) and a report by CIAT (1972) state that it shows a high frequency of cross fertilisation under conditions of natural open pollination and hence develops considerable genetic variation. Moreover, according to a breeding programme of apomictic *Brachiaria*, sexual *Brachiaria ruziziensis* (Ruzi grass) was used as the mother plant and behaved as a sexual diploid (Valle *et al.*, 1993; Pessino *et al.*, 1998). Certainly, from personal observations there does appear to be considerable variability between plants in Ruzi swards, but whether such variation is purely phenotypic or is the result of genetic expressions of a cross-pollinated population remains uncertain.

The Ruzi grass material used currently in Thailand has not been subjected to any selection or plant breeding programme since its introduction and hence, as a predominantly cross-pollinating species, is likely to be highly variable and retain wild characteristics (Loch, 1991). Relatively few studies on Ruzi grass have been conducted locally and have centred mainly on species comparisons in plot trials and a limited number of seed production studies. For example, Tinnakorn *et al*, (1990) recorded herbage dry weight yields ranging from 3750-18750 kg/ha/yr with the production being reduced 30-50% in the second year of planting. Ruzi grass showed similar herbage production to Para grass, of 18375 kg/ha, when cut every 40-50 days in the rainy season, but less than Guinea, Signal and Napier grass (Tinnakorn, 1988). Boonyawiroj *et al.* (1991) also reported that the response of Ruzi grass to nitrogen fertilizer was very marked in terms of herbage yields, ranging in the first year of the study from 12500, 16875 and 20625 when 0, 125 and 250 kgN/ha respectively was applied. However in the second year, the response was much less and showed no further response beyond an application of 125 kgN/ha. Phaikaew *et al.* (1985) found that similar seed yields of Ruzi grass could be obtained from either cutting for forage 60 days after planting and before leaving for seed production (85 kg/ha pure live seed) or without cutting (82.5 kg/ha pure live seed). However the cutting treatment significantly reduced the "lodging" effect. By comparison pure live seed production of 165 kg/ha was reported in a workshop at DPO by improving the management practices, particularly post harvest processing and drying methods (Brunse and Sukpituksakul, 1992).

Many of the results recorded show wide variation and suggest that there may well be considerable genetic variability within this predominantly cross-pollinating species, quite apart from purely phenotypic variations of the population to possible climatic or edaphic impacts, and hence providing scope for improvement through a comprehensive selection and breeding programme. However, at the present time, the extent of this variability is unknown and accordingly, therefore, the objective of this initial study was to assess the phenotypic variation within a population of commercial seed harvested in Thailand. A wide range of agronomic characters were measured in this experiment as a possible aid to future plant breeders charged with the challenge to improve Ruzi grass for better forage and seed production.

3.2 MATERIALS and METHODS

3.2.1 Environmental Conditions And Establishment Of The Trial Plots

The experiment was carried out from September 1995 to May 1996 in a plastic house at the Plant Growth Unit (PGU), Massey University, Palmerston North, New Zealand. A heating and ventilation system was provided to maintain a temperature of 30/20°C ± 5°C (day/night).

The Ruzi grass seed used in this experiment was obtained from Thailand, having been harvested by hand and processed at the Government Seed Station in the North-east of Thailand. The actual seedlot used in this and associated experiments was purchased from Thailand in June 1995 and had been harvested (October/November 1994) one year before commencing these experiments.

Twenty five seeds were germinated using the top-of-paper technique (ISTA, 1993) on each of 50 sets of germinating seeds i.e. 50x25 seeds, grown in a controlled temperature chamber at 30/20°C (day/night). Three seedlings were then randomly selected from each set of 25 seedlings giving a total of 150 seedlings. From these 150 seedlings 130 were randomly selected and transplanted 2 weeks after the commencement of germination into 5 rows with 50 cm between rows and 50 cm between plants i.e. 5 rows each of 26 plants. The remaining 20 seedlings were kept as "reserve" material should replacements be necessary due to death.

Of the 5 rows of plants only the 3 inner rows were measured with the outer rows acting as guard rows. In other words, the total number of plants measured was 72, from 3 rows each of 24 plants.

The planting medium was a potting mix (ag.lime 3 kg/m^3, dolomite 3 kg/m^3, iron sulphate 0.5 kg/m^3, osmocote (16:3.5:10 + 1.2Mg + fill essential trace elements) 4 kg/m^3, ammonium phosphate 2 kg/m^3 and bark 700 kg/m^3) containing adequate nutrients for the plants over the period of this study (8 months). Water was applied regularly - usually daily - to maintain adequate moisture for growth.

Subsequent cuttings were made every 15 days for data recording. This cutting criteria on tiller length rather than height from ground level was considered more appropriate because of the variation in growth form between plants i.e. their erectness or prostrateness.

As these plants were subsequently allowed to go to seed, each plant was supported with bamboo canes when the height exceeded 50 cm.

3.2.2 Measurements

3.2.2.1 Vegetative stage

(a) Herbage production and tiller development

The plants were cut and total fresh weight per plant recorded every 15 days giving a total of 4 cuts between the commencement on 17 November 1995 and the final cut on 15 January 1996. A subsample of 200 g was then taken and separated into leaf and stem for measuring component dry matter production. Subsamples were dried in an oven at 90 C for 24 hours to determine dry matter percentage. Accordingly, total plant DM, leaf DM and stem DM were obtained and then leaf:stem ratio calculated. Prior to drying, leaf area was also measured using an electronic leaf measurement machine (LI-COR Model 3100). The number of live tillers was counted after each defoliation.

(b) Growth form

Growth form was assessed on 2 occasions immediately prior to defoliation (and also leaf width, leaf hair, ligule colour and stem colour) and divided into 3 types as follows:

1. Erect plant (Plate 3.1a) - The plant shows upright tillers which stand erect and with a tiller angle greater than 70 degrees.
2. Semi-erect plant (Plate 3.1b) - This growth form lies between the erect and prostrate plant types with a tiller angle between approximately 40 and 70 degrees.
3. Prostrate plant (Plate 3.1c) - The plant shows very prostrate growth with an angle of tiller less than 40 degrees.

a

b

c

Plate 3.1 Plant growth form categories (a) erect, (b) semi-erect, and (c) prostrate

(c) Plant height and canopy width

Plant heights were measured before defoliation on two occasions by placing a ruler upright at ground level and determining the point where most of the fully mature leaves were bending over. They were then divided into 3 groups reflecting plant height scorings viz. Group 1. (<35 cm), Group 2. (35-50 cm) and Group 3. (>50 cm).

The measurement of canopy width was also taken on two occasions, by placing a ruler horizontally against the plant and measuring the width across the middle point of the plant.

(d) Leaf width

Leaf width was measured on a fully developed leaf - the third leaf from the newly developing top leaf - and then grouped into 3 sizes as follows:

1. Narrow (<1.8 cm)
2. Medium (1.9-2.2 cm)
3. Wide (>2.3 cm)

(e) Leaf hairiness

Hairiness of the leaf was determined by examining the upper and lower surfaces of the fully developed leaf, and then divided into 2 categories as follows:

1. Few Hairs - The plant had very short hairs or without hairs particularly on the upper leaf surface.

2. Very Hairy - The plant had thick hairs on both the upper and lower leaf surfaces.

(f) Ligule colour

Ligule colour was divided into 3 different groups as follows:

1. White
2. Pale red
3. Red

(g) Stem colour

Stem colour was divided into 4 different groups as follows:

1. Green
2. Pale red
3. Red
4. Very red

3.2.2.2 Reproductive stage

The last cut was made on 15 January 1996, at the same time as the adjacent preliminary defoliation management study (Chapter 4) where reproductive development was observed, and then allowed to "go-to-seed". The following data were recorded :

(a) Date of first flower initiation

This was regarded as the date at which the first spikelet exerted anthers and stigmas (Humphreys and Riveros, 1986). The number of inflorescences was also counted on each plant every day for 4 - 5 weeks to determine the flowering development pattern.

(b) Tiller numbers at harvest

Tillers were counted after the final harvest cut on 16 May 1996 and divided into 3 groups as: vegetative tillers, new reproductive tillers and old reproductive tillers.

(c) Reproductive development of inflorescences

At harvest the reproductive tillers were divided into four types viz. old basal tillers (previously cut), new basal tillers (uncut), old aerial tillers and new aerial tillers. Accordingly, the number of inflorescences were recorded from each particular tiller as:

-inflorescences arising from old basal tillers (OBT)
-inflorescences arising from old aerial tillers (OAT)
-inflorescences arising from new basal tillers (NBT)
-inflorescences arising from new aerial tillers (NAT)

Due to a very small number of inflorescences arising from new aerial tillers, this category has been omitted from the data presentation.

Twenty inflorescences from each of the remaining categories were then selected at random and the number of racemes per inflorescence, the floret numbers per raceme and the total floret numbers per inflorescence determined. Accordingly, the floret numbers from each tiller and the total floret number per plant could be determined.

Unfortunately it was not possible to measure seed yield per plant as the early closing date resulted in most plants growing very tall and touching the roof of the plastic house which adversely affected seed set and seed weight. A further problem associated with this excessively tall plant growth was the extreme shading of the middle row of plants during the inflorescence development stage. As a consequence only plants in the first and third rows were measured.

3.2.3 Statistical Analysis

The data were examined by analysis of variance using the general linear model (GLM) procedure of SAS (SAS, 1989). Analysis of variance for each of the components was also related to plant growth form and comparisons significant at the 0.05 probability level were evaluated.

3.3 RESULTS

3.3.1 Vegetative Stage

3.3.1.1 Herbage production and tiller development

As shown in Table 3.1 presenting the general picture over the 4 cuts involved, there was little change in mean plant dry weight, and leaf dry weight up to the second cut, but thereafter they increased significantly at both the third and fourth cuts. By comparison tiller numbers and leaf area increased dramatically at each cut.

Mean stem dry weight per plant showed relatively little change over time and only increased at the last cut. Because of the relatively similar increases in leaf and stem dry weight the mean leaf :stem ratio showed little change at each cut.

However, when one examines the figures within these means there is considerable variation involved (Table 3.2, Figure 3.1 and Figure 3.2). For example, the variation in total plant dry weight per plant (total 4 cuts) within this population ranged from a minimum of 129 g/plant to a maximum of 391 g/plant.

Leaf dry weight between plants ranged from a minimum of 71 g/plant to a maximum of 211 g/plant while stem dry weight between plants ranged from a minimum of 57 g/plant to a maximum of 180 g/plant. This resulted in relatively small variation in the leaf:stem ratio, indicating that leafiness was not a major variant within the population.

Total leaf area per plant showed high variation between plants, ranging from a minimum of 2.4 m^2/plant to a maximum of 6.4 m^2/plant over 4 cuts.

Mean tiller numbers per plant also varied between plants and ranged from 58 to 148 tillers/plant after 4 cuts.

Table 3.1 Herbage production (plant DW, leaf DW, stem DW), leaf:stem ratio, leaf area and tiller numbers over 4 cuts during vegetative growth

	Cutting no.				LSD	Sig.
	1st 30 Nov.95	2nd 15 Dec.95	3rd 31 Dec.95	4th 15 Jan.96	(5%)	
Plant DW (g/plant)	44.1c	46.4 c	55.9 b	71.5 a	5.29	****
Leaf DW (g/plant)	27.5 b	24.0 c	30.0 b	41.7 a	3.37	****
Stem DW (g/plant)	25.3 b	22.6 b	24.9 b	32.2 a	3.02	****
Leaf / Stem (ratio)	1.2 : 1 ab	1.1 : 1 c	1.2 : 1 ab	1.3 : 1 a	0.08	****
Leaf area (m^2/plant)	0.73 d	0.85 c	1.15 b	1.48 a	0.09	****
Tillers (no./plant)	56 d	78 c	118 b	131 a	7.94	****

means with the same letter in a row are not significantly different at 5% significance level; ****, P<0.0001

Table 3.2 The range, mean and coefficient of variation (% CV) of 72 Ruzi plants after 4 cuts

Characters	72 Ruzi plants		
	Range	Mean	% CV
Plant DM (g/plant)	129.5 - 391.9	228.1	23.2
Leaf DM (g/plant)	71.9 - 211.3	123.2	23.3
Stem DM (g/plant)	57.5 - 180.5	104.9	24.8
Leaf:Stem ratio	0.6 - 2.0	1.31	19.1
Leaf area (m^2/plant)	2.4 - 6.4	4.2	21.9
Tillers (no./plant)	58 - 148	95	20.4

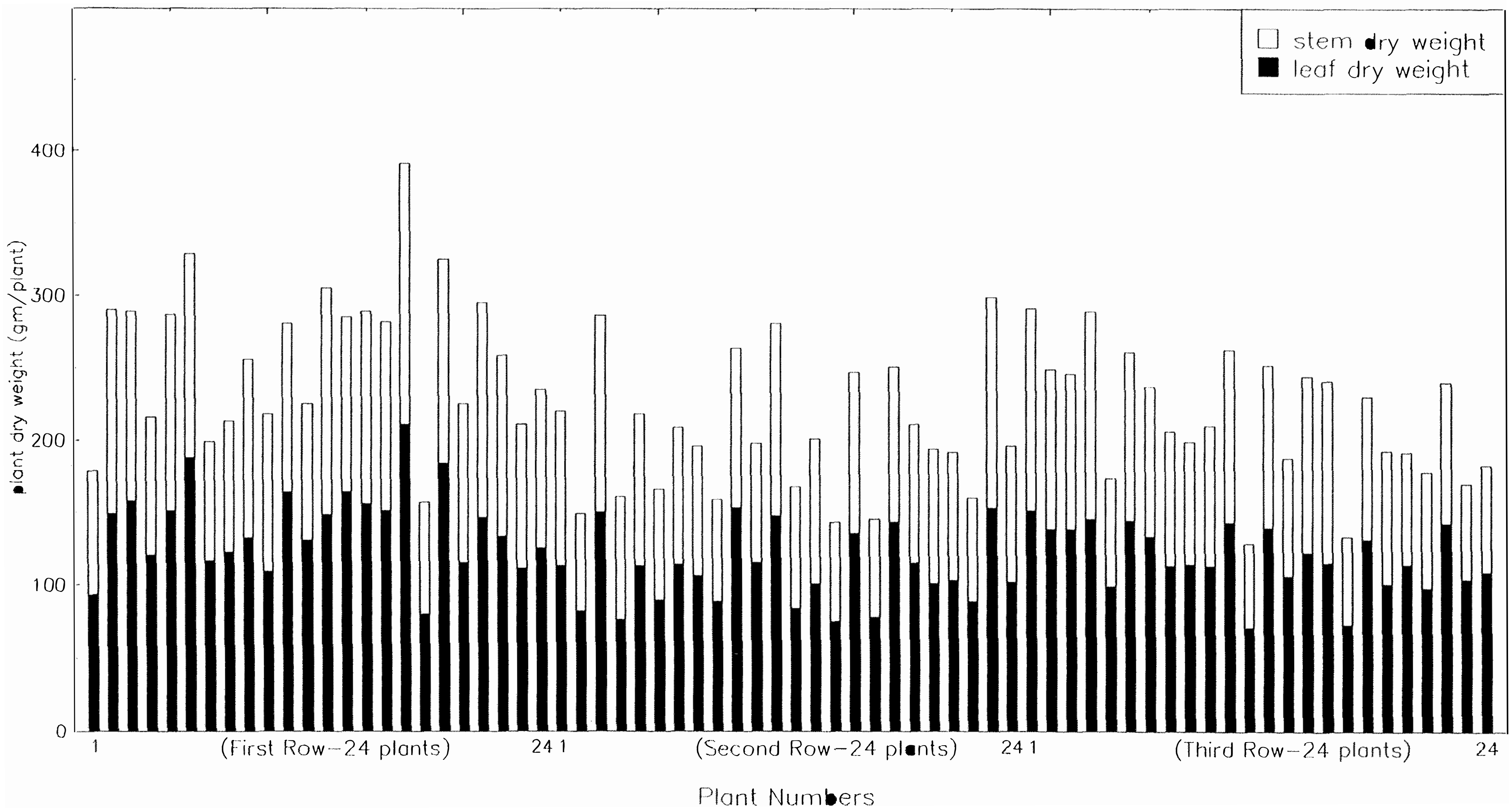


Figure 3.1 A comparison of individual total plant dry weights, including leaf and stem dry weight after four successive cuts

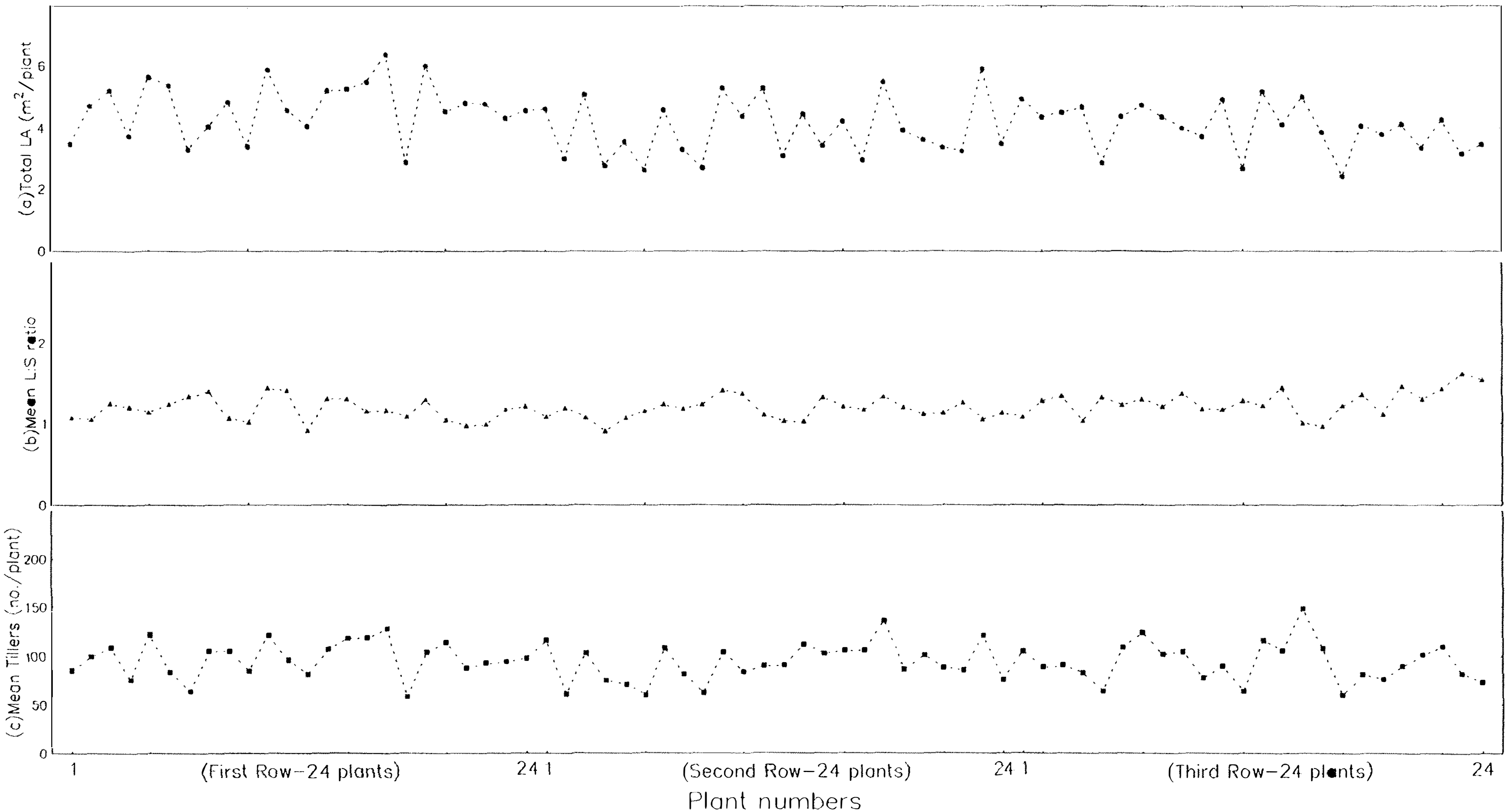


Figure 3.2 A comparison of individual plants development after four successive cuts in terms of (a) Total Leaf Area, (b) Mean Leaf:Stem ratio and (c) Mean Tillers

3.3.1.2 Growth form

As shown in Table 3.3 there was considerable variation in the growth form of the plants in the population studies. While, as one might expect, the greater number were intermediate (semi-erect) in growth form (45%), there was a significant proportion of both erect (33%) and prostrate (22%) plants in the population.

Table 3.3 Number and percentage of plants with different growth form in the population

Growth form	Plants (no.)	Plants (%)
Erect	24	33
Semi-erect	32	45
Prostrate	16	22

Table 3.4 presents the herbage production parameters, totalled over 4 cuts, in relation to growth form of the plant and shows that plant dry weight both leaf and stem, and leaf area increased as the plant grew increasingly more erect. However, growth form had little if any relationship to leaf:stem ratio, or tiller numbers per plant.

Table 3.4 Herbage production parameters in each growth form group

Growth forms	Plant DW (g/plant)	Leaf DW (g/plant)	Stem DW (g/plant)	L/S ratio	Leaf area (m^2/plant)	Tillers (no./plant)
E	249.4	132.7	116.7	1.15	4.5	128.7
SE	229.4	125.7	103.8	1.23	4.2	130.6
P	193.6	104.2	89.4	1.2	3.8	133.1
significance	**	**	**	ns	ns	ns
E vs. SE	ns	ns	ns	ns	ns	ns
E vs. P	*	*	*	ns	*	ns
SE vs. P	*	*	ns	ns	ns	ns

The not significant results are indicated by "ns" and significant by star as *: P<0.05; **: P<0.01; ***: P<0.001; ****: P<0.0001

E = Erect; SE = Semi-erect; P = Prostrate

3.3.1.3 Plant height and canopy width

As one would expect these differences in growth form were reflected in plant height and canopy width - with prostrate plants showing a wider canopy spread (72 cm) and shorter height (42 cm) compared with the erect plants which showing a narrower canopy (59 cm) but were considerately taller (61 cm). The semi-erect plants were generally intermediate in these respects.

Table 3.5 Mean plant height and canopy width (cm) in different plant growth form group

Growth forms	Canopy (cm)	Height (cm)
Erect	59.3	61.1
Semi-erect	68.8	53.8
Prostrate	72	42
significance	****	****
Erect vs. Semi-erect	*	*
Erect vs. Prostrate	*	*
Semi-erect vs. Prostrate	ns	*

*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$; ****: $P<0.0001$; ns, no significance

3.3.1.4 Leaf width, Leaf hair, Ligule colour and Stem colour

The remaining vegetative characteristics measured (leaf width, leaf hair, ligule colour and stem colour) are presented in Table 3.6.

Table 3.6 Leaf width, leaf hair, ligule colour and stem colour characteristics

Leaf width			Leaf hair		Ligule colour			Stem colour			
N	M	W	FH	VH	W	PR	R	G	PR	R	VR
13	47	12	36	36	52	7	13	21	28	5	18
18%	65%	17%	50%	50%	72%	10%	18%	29%	39%	7%	25%

Leaf width : N = Narrow (1.5-1.8cm), M = Medium (1.9-2.2cm), W = Wide (2.3-2.6cm)
Leaf hair : FH = Few hairs, VH = Very hairy
Ligule colour : W = White, PR = Pale red, R = Red
Stem colour : G = Green, PR = Pale red, R = Red, VR = Very red

(a) Leaf width

The majority of plants had leaves of medium width (65%), with the narrow and wider leaves occurring on many fewer, but a similar proportion, of the plant population (18%, 17%). However, when considered in relation to plant growth form (Table 3.7), the predominance of medium width leaves was similarly apparent in all growth forms, but not so for the narrow and wide leaves. In erect plants the percentage of wide leaves was much higher than the percentage of narrow leaves, while in prostrate and semi-erect plants narrow leaves predominated over wide leaves.

Table 3.7 Leaf width and hairiness of plants in each growth form group

Growth Form	Leaf width (%)			Leaf Hairs (%)	
	Narrow	Medium	Wide	Few hairs	Very Hairy
Erect	12.5	62.5	25.0	45.8	54.2
Semi-erect	21.9	65.6	12.5	50.0	50.0
Prostrate	18.8	68.8	12.4	56.3	43.7

(b) Leaf Hairiness

As shown in Table 3.6, the two degrees of hairiness were equally divided amongst the plant population and appeared to be little influenced by the growth form of the plant (Table 3.7).

(c) Ligule Colour

It is interesting to note in Table 3.6 that the majority of plants (72%) displayed white ligules with relatively few showing red (18%) or pale red (10%) ligule coloration. However, in relation to this colour variation between growth forms (Table 3.8), there was a higher proportion of pale red and particularly red ligules apparent in the semi-erect and prostrate plants but relatively few erect plants showed this characteristic.

Table 3.8 Ligule and Stem colour in each plant growth form group

Growth	Ligule colour (%)			Stem colour (%)			
Form	White	Pale red	Red	Green	Pale red	Red	Very red
Erect	83.3	4.2	12.5	12.5	45.8	8.3	33.4
Semi-er.	68.8	12.5	18.7	37.5	37.5	9.4	15.6
Prostrate	62.5	12.5	25.0	37.5	31.3	0	31.2

(d) Stem Colour

As shown in Table 3.6 there was considerable variation in stem colour displayed in the plant population with the majority having a pale red colour (39%) and the least number (7%) having red stems. The remaining two colours identified (green and very red) were quite significant in number and similar in proportion (29%, 25%).

When such stem colour variations were considered in terms of growth form there were relatively small differences from the above trend. However, it is interesting to note that green stemmed plants tended to increase in semi-erect and prostrate plants compared with erect plants, while the proportion of pale red and red stemmed plants was noticeably reduced in prostrate plants (Table 3.8).

3.3.1.5 Relationship between plant parameters and some phenotypic variation recorded during the vegetative growth

Concurrent with the present study on phenotypic variation within plant population, an attempt was made to study the effect of different plant characters on herbage production in order to determine the most powerful plant parameters for assisting plant selections.

It is evident from Table 3.9 that highly significant and positive correlations were found between plant dry weight and the main growth parameters (leaf DM and stem DM) indicating that these parameters are important, as one would expect, in determining herbage yield. It is also interesting and somewhat surprising that growth form was not highly related to plant dry weight - as visually, the erect plants appeared to produce an abundance of forage compared with the prostrate plants.

Table 3.9 Simple correlation coefficients (r^2) between plant parameters and some phenotypic variation recorded during the vegetative growth

	Plant DW	Growth Form	Stem Colour	Ligule Colour	Leaf Width	Hairiness	Mean Tiller no.	Leaf DW	Stem DW	Leaf Area
Plant DW		0.145***	0.002 ns	0.001 ns	0.120**	0.009 ns	0.287****	0.944****	0.931****	0.035 ns
Growth Form			0.021 ns	0.025 ns	0.017 ns	0.005 ns	0.002 ns	0.123**	0.151***	0.006 ns
Stem Colour				0.249****	0.000 ns	0.021 ns	0.009 ns	0.001 ns	0.004 ns	0.000 ns
Ligule Colour					0.051 ns	0.002 ns	0.003 ns	0.001 ns	0.000 ns	0.001 ns
Leaf Width						0.027 ns	0.046 ns	0.133**	0.092**	0.000 ns
Hairiness							0.008 ns	0.018 ns	0.002 ns	0.000 ns
Mean Tiller no.								0.274****	0.265****	0.016 ns
Leaf DW									0.767****	0.023 ns
Stem DW										0.044 ns

Non significant results are indicated by "ns" and significant by star as *: P<0.05; **: P<0.01; ***: P<0.001; ****: P<0.0001

3.3.2 Reproductive Stage

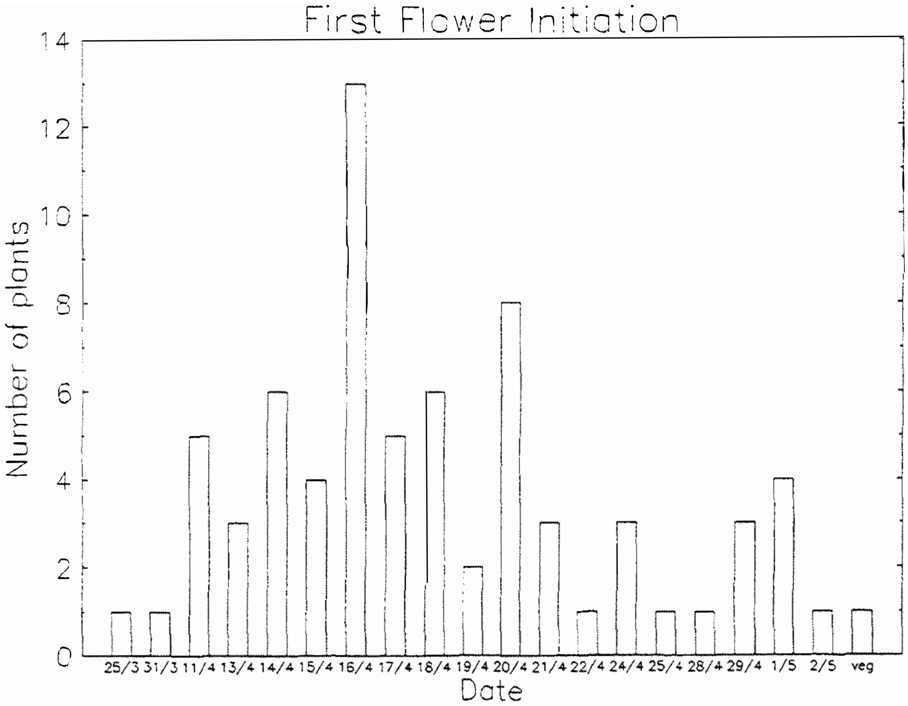
3.3.2.1 Date of first flower initiation

As shown in Figure 3.3 the first plant showing flower initiation occurred on 25th March. This was followed by an increasing rate in the number of plants flowering, reaching a peak 22 days later on 16th April. The rate then declined over the following 16 days with the last plant showing first flower on 2nd May. Only 1 plant failed to initiate a flower. From the results, it can be clearly seen from Table 3.10 that most plants produced their first flower in the first 3-4 weeks and showed little variation as expressed by their low coefficients of variation (Table 3.13). Accordingly, plants in different growth forms also showed similar number of days for first flowering (Table 3.14).

Table 3.10 Number of plants and percentage showing first flower initiation

Plants	Number of weeks after 1st flower initiation (25 March, 1996)					
	1	2	3	4	5	6
Number	2	0	14	41	6	8
%	2	0	20	58	9	11

Although the time of first flower initiation in the total plant population was spread over a period of 32 days, the actual spread of inflorescence appearance in this population was concentrated into a period of only 14 days after first flower initiation as shown in Figure 3.4. This pattern was also apparent in plants of different growth forms (Figure 3.5).



Plant number at each flowering date:–
25/3 (1) : (1–4) – (Row1 – Plant No.4)
31/3 (1) : (1–20)
11/4 (5) : (1–6, 14); (3–6, 10, 23)
13/4 (3) : (1–1, 5); (3–9)
14/4 (6) : (1–2, 10, 13); (2–24); (3–11, 13)
15/4 (4) : (3–1, 15, 20, 22)
16/4 (13) : (1–3, 16, 17, 22); (2–2, 7, 13); (3–3, 4, 8, 16, 17,
17/4 (5) : (1–7, 11); (2–22); (3–5, 14)
18/4 (6) : (1–12, 21, 23); (2–14); (3–12, 19)
19/4 (2) : (1–9, 15)
20/4 (8) : (1–8, 18, 19, 24); (2–1, 4, 23); (3–24)
21/4 (3) : (3–2, 7, 21)
22/4 (1) : (2–3)
24/4 (3) : (2–5, 10, 15)
25/4 (1) : (2–12)
28/4 (1) : (2–8)
29/4 (3) : (2–9, 16, 18)
1/5 (4) : (2–6, 11, 17, 20)
2/5 (1) : (2–19)
veg. (1) : (2–21) – Vegetative stage

Figure 3.3 Date of first flower initiation in the Ruzi plant population

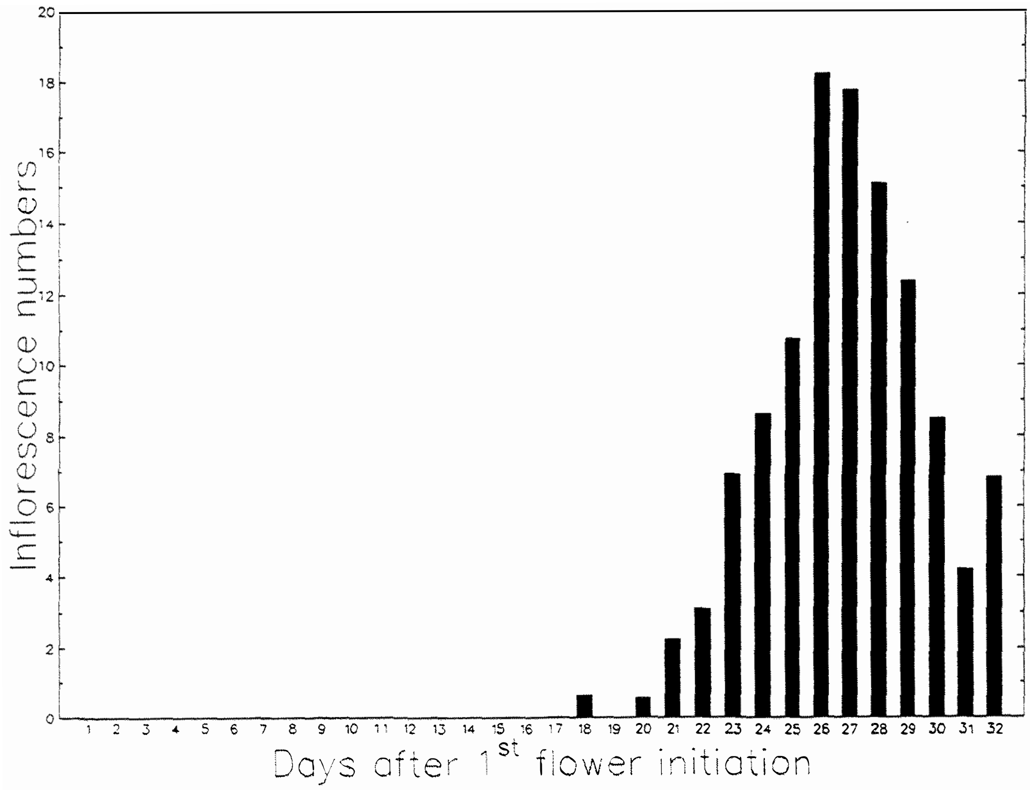


Figure 3.4 The pattern of inflorescence development per plant per dcy based on first flower initiction

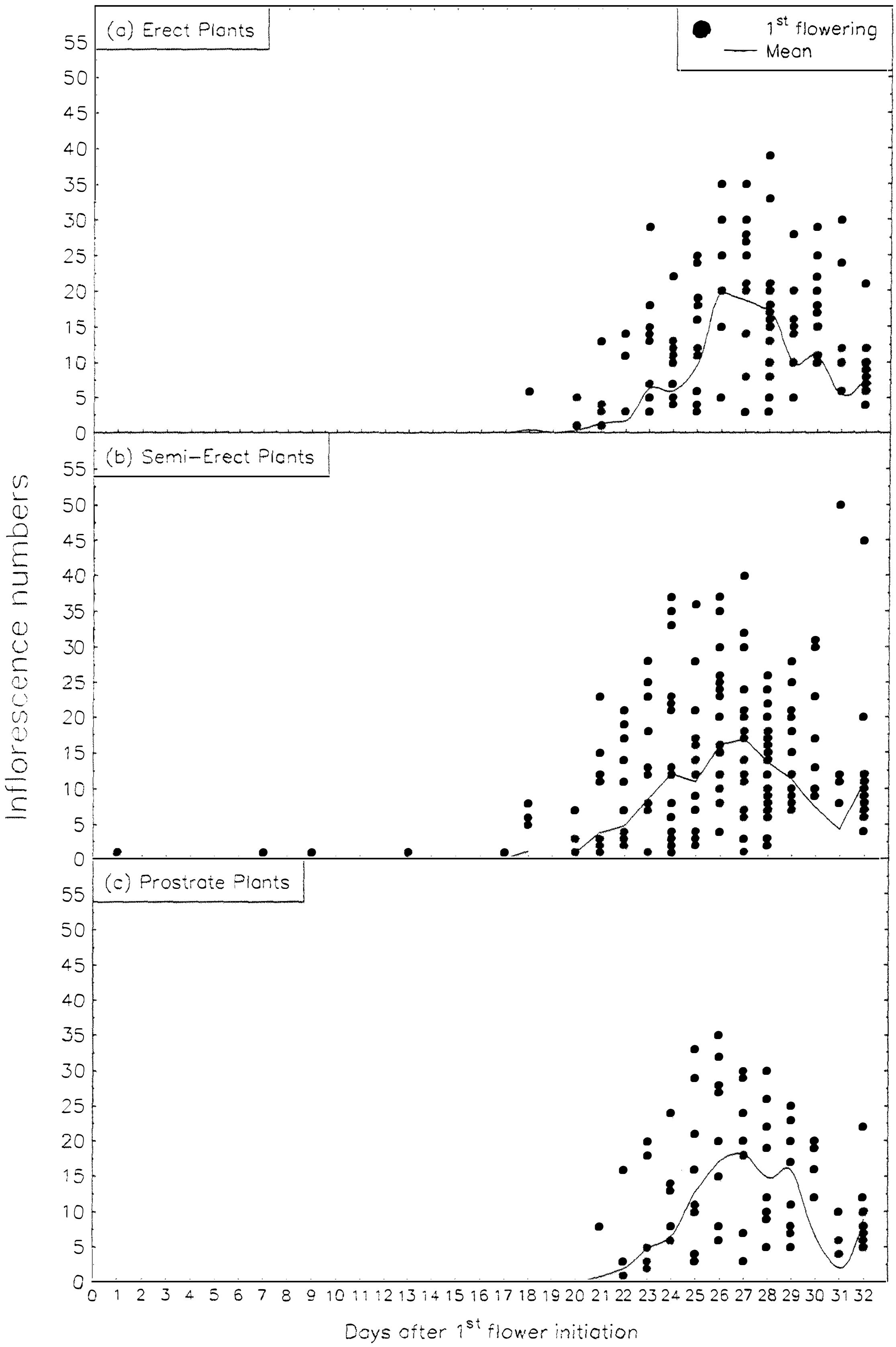


Figure 3.5 A comparison of inflorescence development per plant per day from different plant growth forms and means of each growth form

3.3.2.2 Tiller numbers at harvest

The middle row plants showed a drastic decrease in tiller numbers per plant due to the shading effect from "closing" for seed production too early (Figure 3.6). Accordingly, therefore, these plants have been omitted for data analyses. Table 3.11 presents the mean number of old and new basal reproductive tillers and vegetative tillers per plant recorded at the final harvest cut and show that of the total number recorded (179 tillers) virtually developed to the reproductive stage (90%). Of these reproductive tillers, 66% were old basal tillers and 34% were new basal tillers.

Table 3.11 Reproductive (old, new and total) and vegetative tillers and percentage at harvest

	Reproductive tillers			Vegetative tillers	Repro. tiller /plt (%)	Veg. tiller/plt (%)
	Old basal	New basal	Total			
Tillers (no./plant)	107.0 ± 24.0	56.2 ± 30.7	163.2 ± 27.3	15.8 ±12.3	91.1	8.9

3.3.2.3 Inflorescence Development

In terms of the number of inflorescences per plant arising from the different reproductive tillers (i.e. from old basal tillers, new basal tillers and old aerial tillers), the data (Table 3.12) shows that the dominant contributor was old aerial tillers with a range of 76-510 inflorescences per plant (Figure 3.7b), followed by old basal tillers ranging from 51 to 160 inflorescences/plant (Figure 3.7a) and with the lowest contribution coming from new basal tillers showing a minimum of 12 and a maximum of 154 inflorescences/plant (Figure 3.7c). However the biggest inflorescences were usually produced by old basal tillers (Figure 3.8) as reflected in their high floret numbers (129 florets/ inflorescence) and high raceme number per inflorescence (6 raceme/inflorescence) compared with the inflorescences produced by old aerial and new basal tillers, which were similar in this regard. Nevertheless, the old aerial tillers proved to be the major contributor to floret numbers per plant due to the greater number of inflorescences produced per plant (Table 3.12 and Figure 3.10).

In all the reproductive characters recorded there was a marked variation within the plant population studied and particularly by the dominant type of tillers contributing to that particular character (Figures 3.7, 3.8, 3.9, 3.10). As a result, wide variation in the various characters measured was apparent (inflorescence numbers at 32 days, total inflorescence numbers and total floret numbers), as shown by their high coefficients of variation (Table 3.13).

Table 3.12 Mean inflorescence numbers and components

Emerged from	Inflorescence Development				
	Inflorescence no./plant	Raceme no./inflo.	Floret no./raceme	Floret no./inflo.	Floret no./plant
Old basal tillers	107.0 ± 24.0	6.3 ± 1.5	20.8 ± 5.4	129.3 ± 39.0	13991± 5667
Old aerial tillers	248.3 ± 116.2	4.1 ± 0.9	16.3 ± 3.7	66.3 ± 19.1	16232 ± 8718
New basal tillers	56.2 ± 30.7	4.2 ± 0.9	16.2 ± 3.6	68.1 ± 22.3	4160 ± 3176

Table 3.13 The range, mean and coefficient of variation (% CV) of 48 Ruzi plants

Characters	48 Ruzi plants		
	Range	Mean	% CV
1st Flower (days)	70 - 97	91	5.28
Inflorescences (32 days-no./plant)	51 - 205	120	32.18
Total Inflorescences (no./plant)	191 - 652	411	30.2
Total Florets (no./plant)	10561 - 73885	34384	36.9

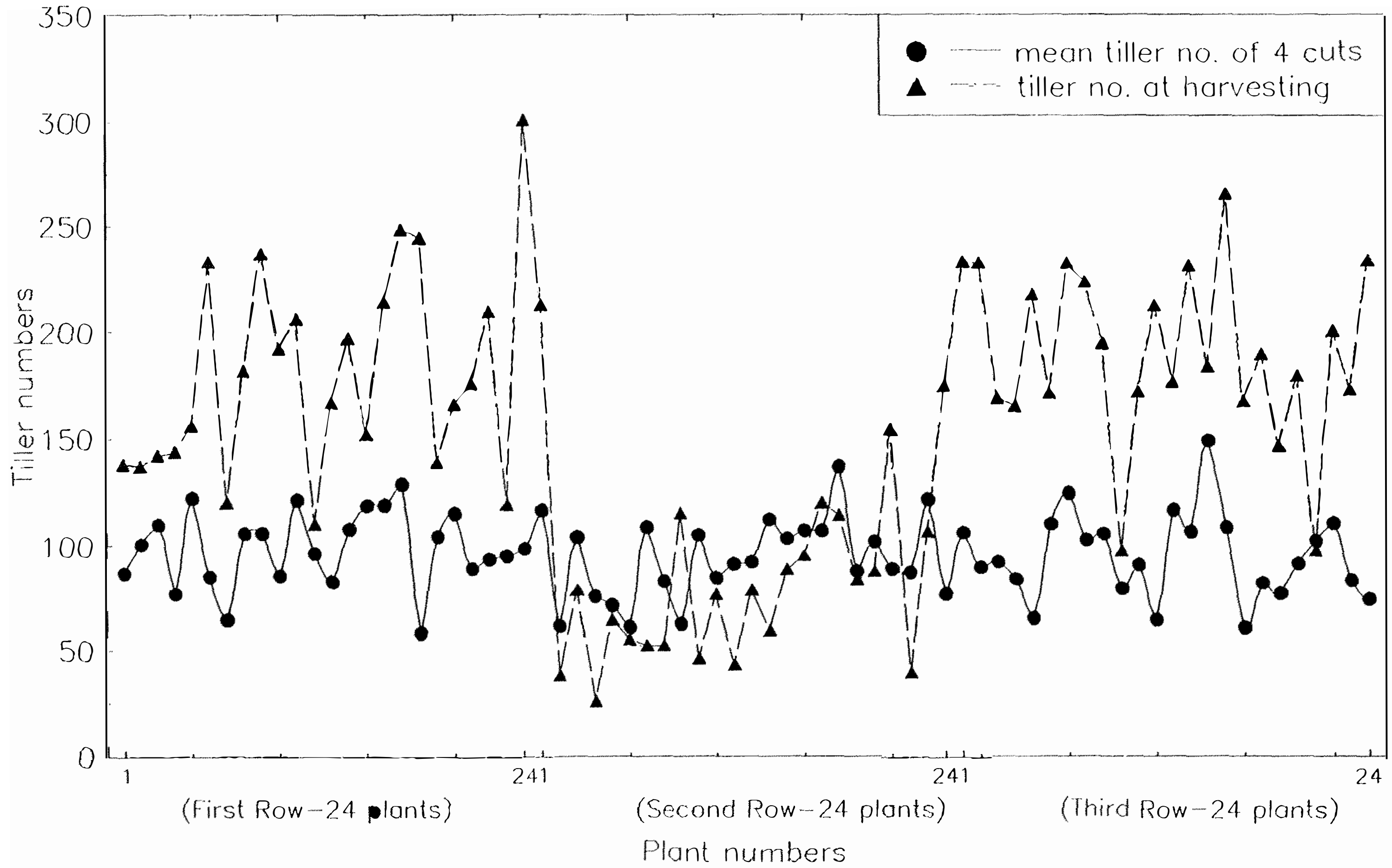


Figure 3.6 A comparison of tiller numbers at harvest and mean tiller numbers produced over the vegetative stage

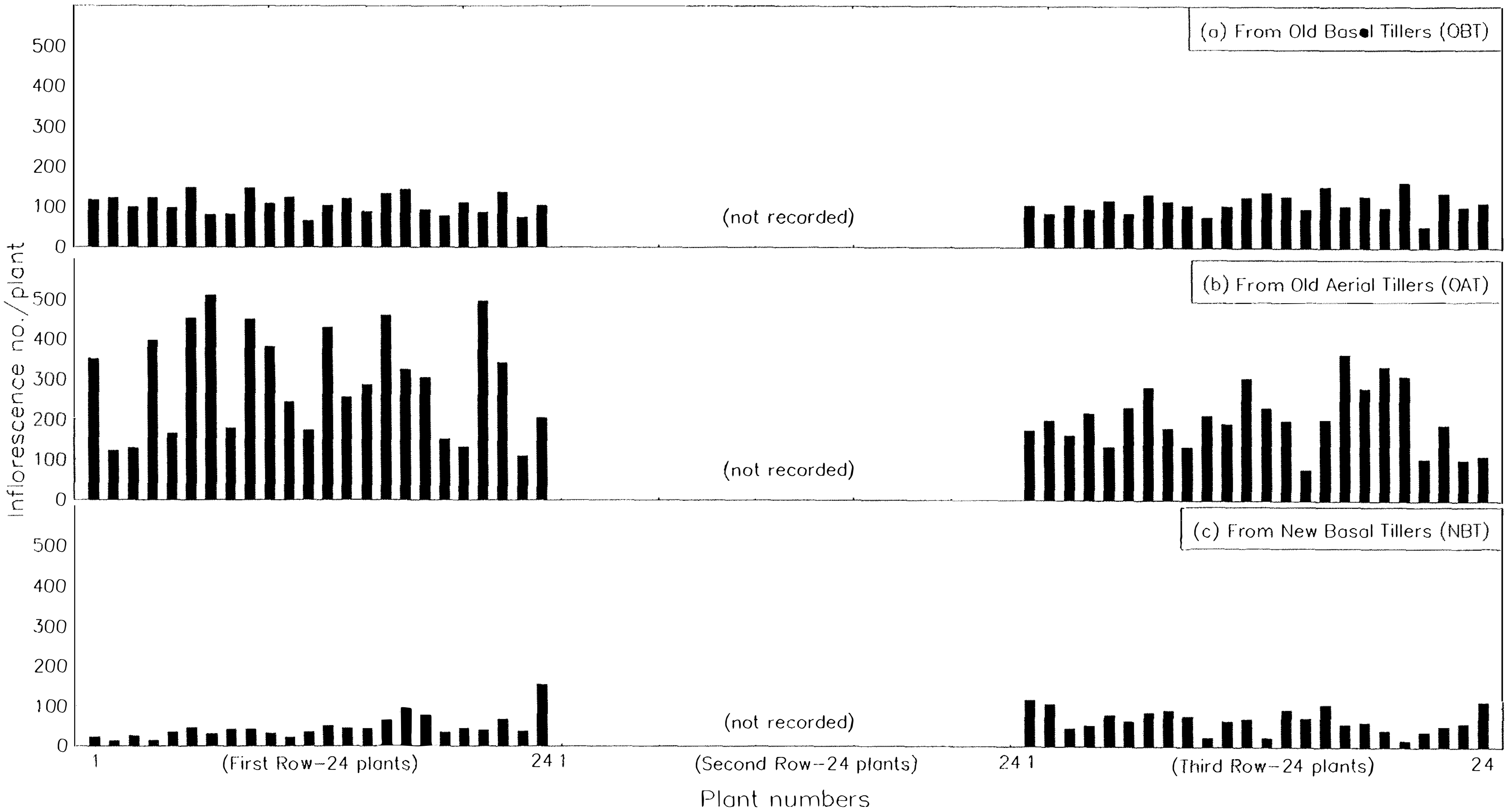


Figure 3.7 A comparison of mean inflorescence numbers per plant from different reproductive tillers

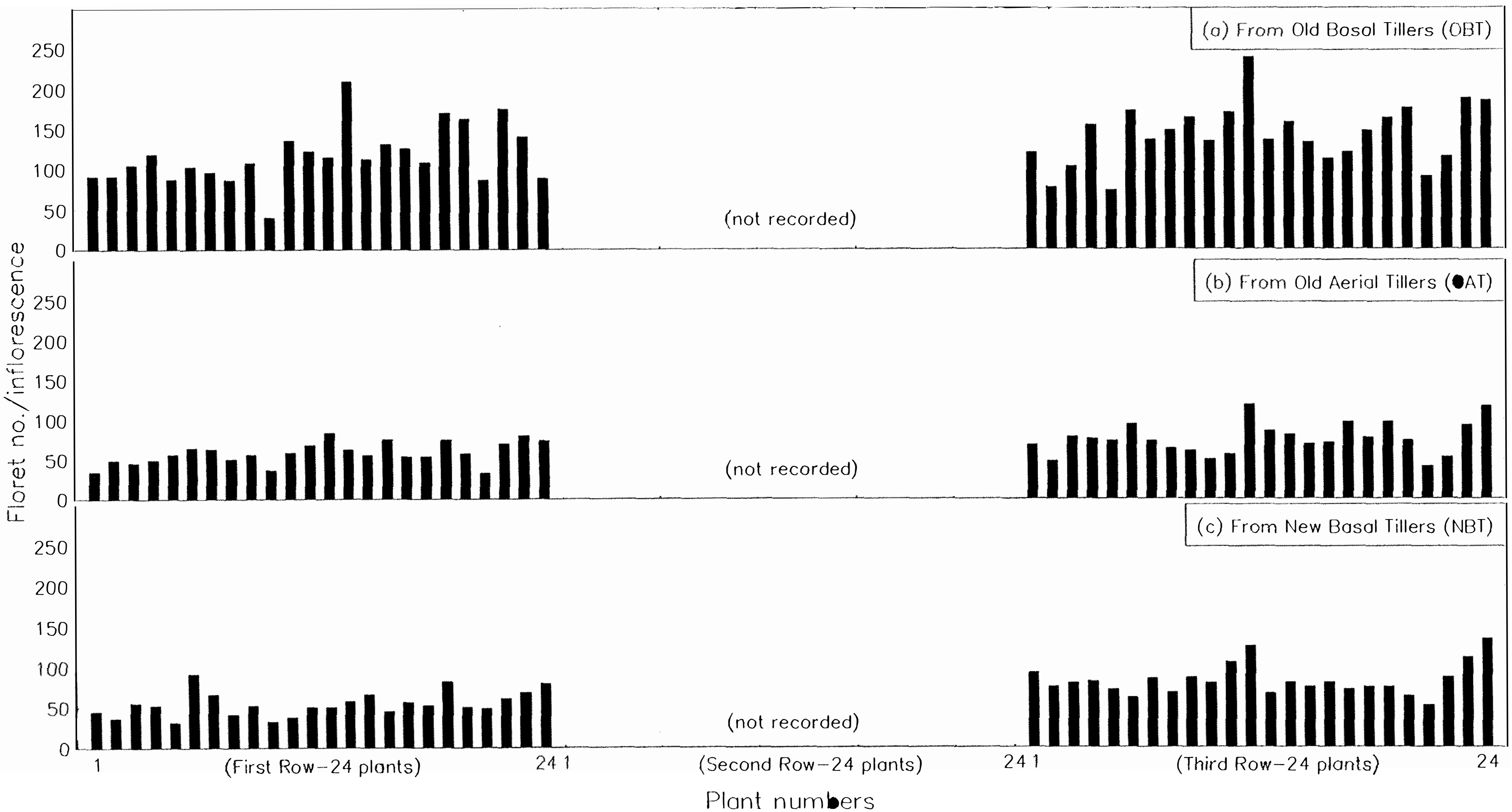


Figure 3.8 A comparison of mean floret numbers per inflorescence per plant from different reproductive tillers

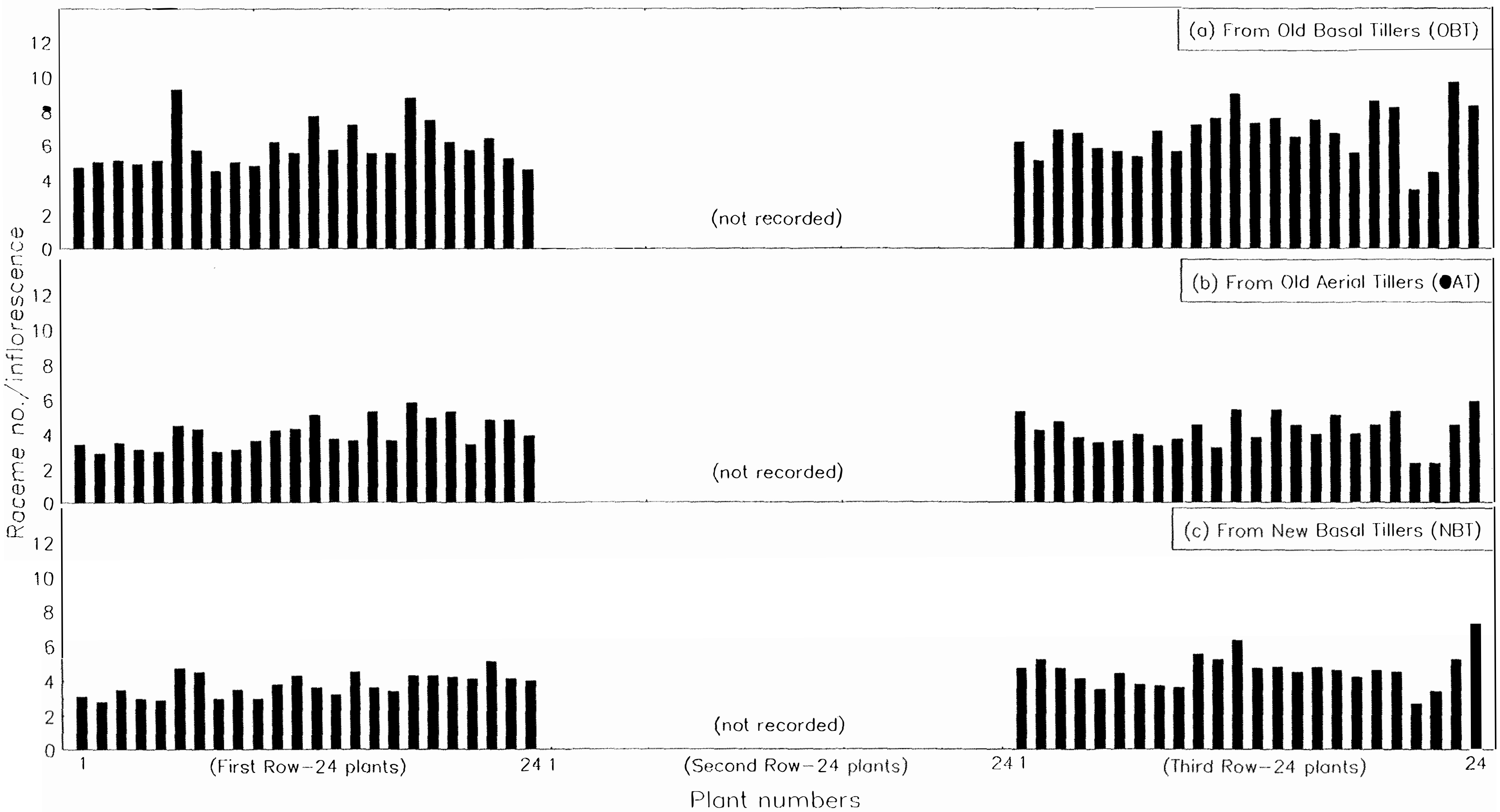


Figure 3.9 A comparison of mean raceme numbers per inflorescence per plant from different reproductive tillers

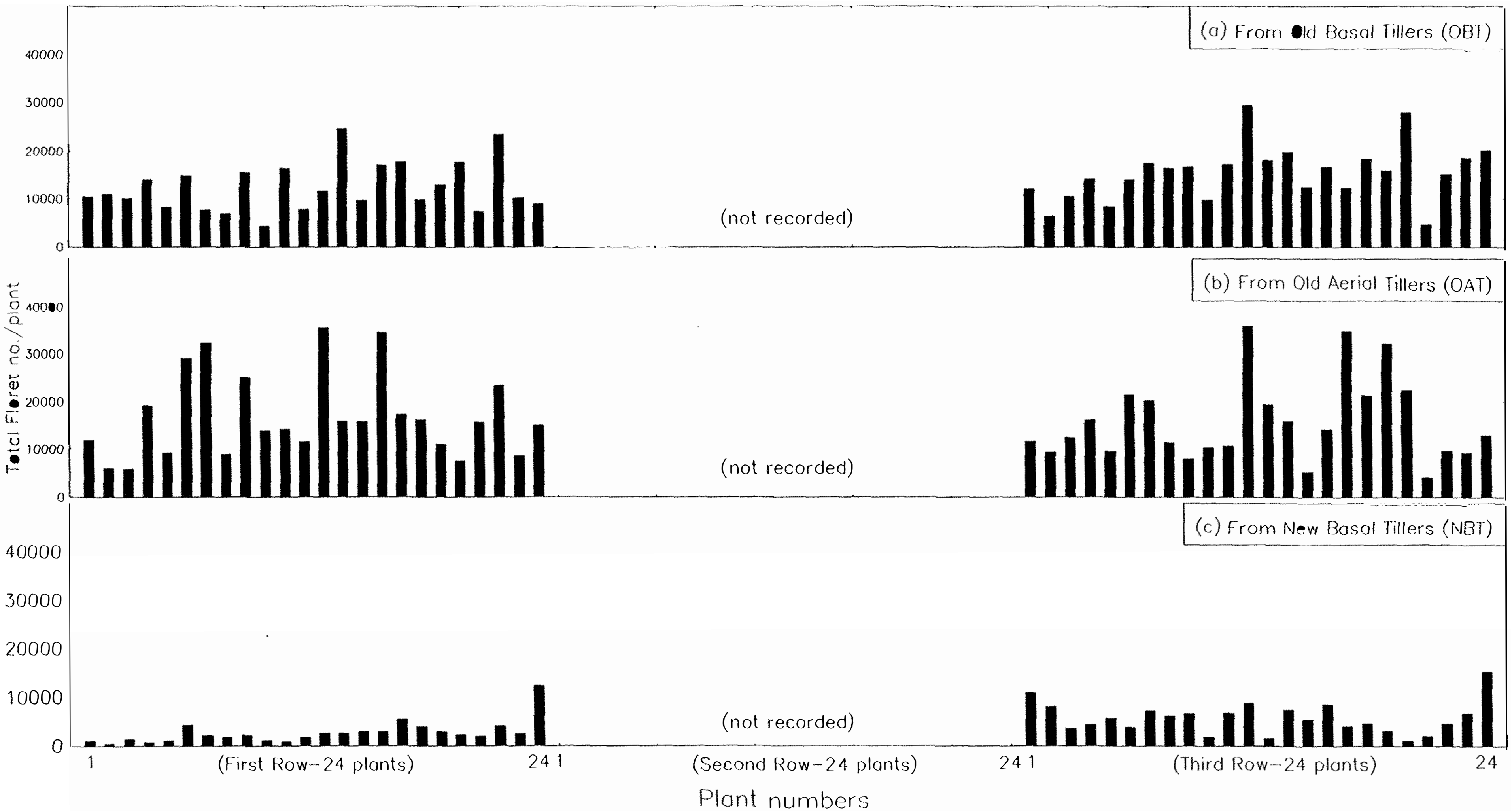


Figure 3.10 A comparison of mean floret numbers per plant from different reproductive tillers

3.3.2.4 Inflorescence Development and Growth Form

Table 3.14 presents the inflorescence numbers and the components per plant produced from different tiller development (old basal tillers, old aerial tillers and new basal tillers), and compared between the different growth forms. Data showed that growth form of the plant had no significant effect on the relative contribution of the different tiller origins to total inflorescence numbers nor to total floret number per plant.

Similarly, growth form had little effect on raceme number per inflorescence and floret number per raceme on the tillers of different origins, but did show some interesting differences in floret number per raceme and per inflorescence, particularly between erect and prostrate plants.

3.3.2.5 Relationship between plant parameters and some phenotypic variation recorded during the vegetative and reproductive growth

As shown in Table 3.15 all of the parameters determination (48 plants) for herbage yields during the vegetative stage, and also for seed yields during reproductive stage, were not or only slightly correlated with their phenotypic variation.

Table 3.14 Inflorescence development in each plant growth form group

Growth Form	1st Flower (days)	Inflorescence no. per plant				Raceme no. per inflorescence			Floret no. per raceme			Floret no. per inflorescence			Floret no. per plant			
		OBT	OAT	NBT	Total	OBT	OAT	NBT	OBT	OAT	NBT	OBT	OAT	NBT	OBT	OAT	NBT	Total
E	92	108	268	54	430	5.9	3.8	3.8	18.3	15.6	15.1	105.7	58.6	58.6	11419	14961	3532	29911
SE	90	108	254	54	416	6.4	4.4	4.2	22.3	15.6	16.3	141	66.9	67.8	15509	16881	3825	36216
P	93	103	204	65	371	6.8	4.2	4.8	21.8	18.7	17.9	144.7	77.9	84.9	15178	17032	5931	38140
sig.	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	**	*	*	ns	ns	ns	ns
EvsSE	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	ns	*	ns	ns	ns
EvsP	ns	ns	ns	ns	ns	ns	ns	*	ns	*	*	*	*	*	ns	ns	ns	ns
SEvsP	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns

The not significant results are indicated by "ns" and significant by star as *: P<0.05; **: P<0.01; ***: P<0.001; ****: P<0.0001

E = Erect; SE = Semi-erect; P = Prostrate

OBT-inflorescences arising from old basal tillers; OAT-inflorescences arising from old aerial tillers; NBT-inflorescences arising from new basal tillers

Table 3.15 Simple correlation coefficients (r^2) between plant parameters and some phenotypic variation recorded during vegetative and reproductive growth

	Plant DW	Growth Form	Stem Colour	Ligule Colour	Leaf Width	Hairiness	Mean Tiller no.	Leaf DW	Stem DW	Leaf Area	First Flowering	Inflo. no. (30 days)	Total Inflo. no.	Total Floret no.
Plant DW		0.175**	0.000 ns	0.051 ns	0.205**	0.012 ns	0.300****	0.933****	0.926****	0.041 ns	0.000 ns	0.015 ns	0.019 ns	0.011 ns
Growth Form			0.101*	0.032 ns	0.043 ns	0.000 ns	0.011 ns	0.140**	0.188**	0.013 ns	0.004 ns	0.000 ns	0.028 ns	0.065 ns
Stem Colour				0.192**	0.000 ns	0.036 ns	0.003 ns	0.001 ns	0.000 ns	0.047 ns	0.001 ns	0.000 ns	0.012 ns	0.007 ns
Ligule Colour					0.115*	0.005 ns	0.084*	0.044 ns	0.050 ns	0.002 ns	0.002 ns	0.003 ns	0.002 ns	0.015 ns
Leaf Width						0.061 ns	0.079 ns	0.247***	0.139**	0.000 ns	0.002 ns	0.084*	0.000 ns	0.069 ns
Hairiness							0.012 ns	0.029 ns	0.001 ns	0.001 ns	0.003 ns	0.000 ns	0.090*	0.026 ns
Mean Til. no.								0.290****	0.268***	0.054 ns	0.000 ns	0.030 ns	0.056 ns	0.059 ns
Leaf DW									0.738****	0.017 ns	0.000 ns	0.024 ns	0.008 ns	0.007 ns
Stem DW										0.069 ns	0.001 ns	0.006 ns	0.031 ns	0.015 ns
Leaf Area											0.018 ns	0.004 ns	0.007 ns	0.002 ns
First Flower.												0.032 ns	0.000 ns	0.000 ns
Inf. no.(32ds)													0.090*	0.116*
Total inf.														0.400****

The not significant results are indicated by "ns" and significant by star as *: P<0.05; **: P<0.01; ***: P<0.001; ****: P<0.0001

3.4 DISCUSSION

The main objective of this initial study was simply to have a closer look at phenotypic variation within Ruzi grass since little in-depth knowledge of this species is available.

The results obtained clearly show a wealth of variation in many plant characters, both vegetative and reproductive, and suggest that there may well be considerable scope for genetic improvement in this predominantly cross-pollinated species, through a comprehensive selection and breeding programme in the future towards more desirable and productive cultivars.

Of particular interest and possible importance was the significant variation in growth form recorded (Plate 3.1, Table 3.3), with a considerable proportion of plants expressing the full range of erect to prostrate growth habit. As stated by several workers, plant growth form can significantly influence important physiological processes in plants as well as impinging on the efficiency of prehensility by the grazing animal. For example, Rhodes (1973) considered tiller angle as one of the major factors determining canopy structure in terms of presentation of the photosynthetic material to incoming light, while Stobbs (1973) regarded sward bulk density, (that is the dry-matter yield of the sward divided by its average height), as the major factor determining the size of bite taken by the grazing animal. Van Wijk (1980) also found that erect-growing plants of *Setaria sphacelata* (Nandi I) were the most productive in terms of dry-matter yield and had the highest competitive ability in mono and mixed culture. Furthermore, tillers from erect-growing plants had a higher digestibility than those from prostrate plants. In other words a predominantly erect growing sward of Ruzi grass is likely to produce greater forage yield than a predominance prostrate-growing sward - as supported by the greater predominance of erect-growing plants in this study compared with prostrate plants - and is also likely to improve the ease of prehensility and potential intake of more digestible forage by the grazing animal. Clearly the variation recorded in the present population of Ruzi plants presents a potential for significant improvement in productivity and prehensilability through selection towards predominantly erect or semi-erect plants. While recognising the potential importance of selection of those plants, one must not overlook the other important agronomic characters, such as resistance to severe defoliation and for animal trampling and pugging damage, that much be considered in a successful selection programme.

Although, in grass breeding, dry matter yield is a major objective which is directly influenced by plant tolerance to biotic and abiotic factors affecting the persistence of the sward (Van Wijk, 1980), there are several other factors involved in breeding objectives. Humphreys (1987) noted that plant selection by scientists and farmers has given rise to distinct varieties suited to particular district and farm situations. For example, *Panicum maximum* is used as an illustration of the diversity recognised : West African forms (such as cv. Hamil, cv. Coloniao) are very tall, bulky varieties; cv. Makueni and cv. Riversdale are medium height forms, and better adapted to drier condition particularly cv. Riversdale; cv. Gatton is a lower growing, leafy form used in the sub-tropics. Similarly, with Ruzi grass, such differences in cultivar development may need to be taken into account when one considers the environmental range over which it is being used and in which it is expected to perform with credit.

Tiller density is another factor that can impinge on pasture productivity (Volence and Nelson, 1983; Humphreys, 1997). Individual tiller numbers per plants recorded in this study showed considerable variation - about 3 fold - and hence provide scope for change (Table 3.2, Figure 3.2c). However mean variation in tiller numbers between different growth forms was negligible indicating that tiller density would not be adversely affected whatever the growth form desired (Table 3.4). Such a factor might also be important in the production of increased tiller numbers - and more particularly fertile tiller numbers - as a major determinant of seed yield (Boonman, 1971b; Loch, 1985). However, as pointed out by Humphreys and Riveros (1986) it is the proportion of tillers which survive and continue through to inflorescence and seed production which really determines seed yield and not merely total vegetative tiller numbers.

As far as the more peripheral measurements made are concerned (Table 3.6), i.e. ligule colour, stem colour, leaf width and hairiness, although these are of unknown importance, they also showed considerable variation from plant to plant. However there was little evidence that they were linked significantly to any particular plant growth form (Table 3.9).

In terms of the reproductive characters measured, there was once again wide variation displayed (Figures 3.3, 3.4, and 3.5, Table 3.12). Of particular value and importance is the potential shown to restrict the spread of inflorescence development and concertina the peak of seed production into a more convenient and productive time frame through an effective selection and breeding programme. Similarly the considerable variation recorded in total floret numbers per plant (Table 3.12) and in raceme numbers per inflorescence (Table 3.12), particularly of the most important basal tillers in terms of seed production (Loch, 1983) suggests they may well provide scope for significantly improving seed yield also.

Considering plant improvement for herbage and seed production, there are some positive and negative correlations between these dual purposes in terms of pasture utilization. For example, Burton and DeVane (1953) reported a negative response in dry matter yield when selecting for seed yield in tall fescue. However, Schaaf *et al.* (1962) found no significant relationship between forage and seed yield in Crested wheatgrass, while Lewis (1966), Knowles *et al.* (1970) and Hacker and Bray (1981) emphasised that selection for improved seed yield had no adverse effects on forage yield in meadow fescue, smooth bromegrass and *Setaria sphacelata*, respectively. Van Wijk *et al.* (1993) noted that breeding for high seed yield has been regarded as incompatible with herbage quality and with persistence, but gave no explanation. The relationship between plant size and seed yield found in this study was under spaced-plant conditions, which does not necessarily mean that the same relationships exist in a closed-crop canopy for large-scale seed production (Van Wijk, 1980). This may be a worthwhile further step in plant selection of Ruzi grass. The spaced-plant population method used in this study has advantages and disadvantages. Generally, observed differences between spaced-plants and sward performance may be caused by differences in genotype x environment interaction. For example, under spaced-plant conditions, more light is intercepted, while more nitrogen and minerals are available underground than under closed-canopy conditions. Accordingly, Van Wijk (1980) noted that the major disadvantage of the evaluation of a spaced-plant population is the absence of competitive stress. For example, wide spacing exaggerates the plants ability to survive long periods of drought and may also give too optimistic an impression about seed-yielding ability. Spaced-plant populations, however, are a convenient means of scoring for characteristics such as time of head emergence, growth habit and resistance to pests and diseases. Although the presence or absence of competition influences the morphological composition of the plant (Ribiero, 1970), initially observed differences between spaced-plants for digestibility can not always be reproduced under sward conditions (Breese and Davies, 1970; Kamstra *et al.*, 1973; Van Wijk, 1980). In general it has been found that the prediction of sward yield based on the performance of widely spaced plants is unreliable (Ribiero, 1970). However, Van Wijk (1980) suggests that selection at wide spacings might be applied at the initial stages of a breeding programme when differences between plants can still be easily distinguished. In addition, when the population has been narrowed after this first screening, a second, more laborious testing of the selected plants under more competitive stress in monoculture or mixed culture, can then be carried out.

3.5 CONCLUSION

The phenotypic variation in this plant population was determined by measuring the performance of single, spaced plants. The major proportion of the plant population was semi-erect (45%) with medium leaf width (65%), medium leaf hairiness (50%), white ligule colour (72%), and with a pale red stem colour (39%).

These obvious plant growth form characteristics may enhance plant selection, particularly in the production of erect and semi-erect plants in order to improve herbage yield. However, more work needs to be conducted to obtain more information on the timing and management of the plant to improve seed production.

Although the variation in this plant population occurs as above mentioned, this will not have or have a very small effect in the overall seedlot use for further study. It is simply because almost 80% of plant population are erect and semi-erect plants which have no significant differences in herbage production and particularly seed yield (as recorded in terms of inflorescences and floret numbers in this study) shows no significant differences among these plant growth forms.

CHAPTER 4

THE EFFECTS OF DEFOLIATION ON HERBAGE AND SEED PRODUCTION IN RUZI GRASS

4.1 INTRODUCTION

Forage plants differ considerably in terms of their ability to recover from defoliation which is strongly influenced by management practices, particularly the frequency, intensity and timing of cutting. Responses of forage plants to defoliation can be explained by two guiding principles (Bazzaz *et al.*, 1987). The first, and the most axiomatic, is that defoliation disturbs the carbohydrate supply for plant growth by removing photosynthetic tissue. The second, more subtle factor, is that plant growth processes generally operate to maintain plants in a dynamic equilibrium with their environment so that optimum use is made of all resources for growth and reproduction. The relationship between herbage production and the frequency and intensity of defoliation has received widespread attention with regard to dry matter yield, botanical composition and quality of tropical pasture plants (Oyenuga, 1959, 1960; Haggar, 1970; Saleem, 1972; Ferraris and Norman, 1976; Omaliko, 1980; Hsu *et al.*, 1989; Tenreiro, 1993). Generally, it has been found that the more infrequent the cutting, the higher the DM yield, the higher to proportion of stem and the higher the crude fibre concentration. Digestibility, crude protein concentration and proportion of green leaf blade drop correspondingly. Moreover, many workers recorded no effect of cutting height on yield (Riveros and Wilson, 1970; Olsen, 1973; Murphy *et al.*, 1977), whereas it did in others (Ethredge *et al.*, 1973; Ferraris and Norman, 1973; Jones, 1974; Ludlow and Charles-Edwards, 1980). Their results may well have reflected the actual amount of leaf area remaining after cutting.

According to Volence and Nelson (1983), herbage production in the sward is divided into two components viz. the number of tillers per unit area and the yield per individual tiller. Obviously this is also influenced by tiller dynamics i.e. the balance between the production of new tillers and death of established tillers. Recovery from defoliation can be determined by many aspects such as shoot apex survival (Sheard and Winch, 1966), leaf area (Ward and Blaser, 1961), non-structural carbohydrate content (Ward and Blaser, 1961; Brown and Blaser, 1968) and tiller potential (Paulsen and Smith, 1969). However, it also depends, not only on the inherent capacity of the plant and the characteristics of the defoliation, but also on the plant's abiotic environment e.g. light, water, nutrients (Cox and McEvoy, 1983; McNaughton *et al.*, 1983; Bryant, 1987; Caldwell *et al.*, 1987; Busso *et al.*, 1989, 1990; Maschinski and Whitham, 1989; Ourry *et al.*, 1990; Mott *et al.*, 1992) - and biotic environment e.g. plants with undefoliated or more herbivore-tolerant neighbours (Mueggler, 1972; Crawley, 1983; Caldwell and Richards, 1986; Cottam, 1986; Bryant, 1987). Thus, responses of plants to defoliation can vary, ranging from short-term physiological acclimatization (Richards, 1993) to longer-term morphological adaptation (Chapman and Lemaire, 1993). However, the responses of pasture to management can be varied in different seasons. Many workers have suggested that defoliation practices must be adjustable to the season and climatic conditions of the year (Brougham, 1970; Tainton, 1974; Sheath and Bircham, 1983). Tainton (1974) reported that lax infrequent grazing increased herbage production by 20% in a dry summer season, while those pastures which were alternately lax and hard grazed outyielded by 63% those which were hard grazed in the vegetative growth period in autumn. In contrast, there is much less seasonal variation in recovery potential of grazing-tolerant tropical grasses (e.g. *Cenchrus ciliaris, Heteropogon contortus* and *Panicum maximum*) with asynchronous tiller development, and with a recovery potential which is generally high due to the active shoot meristems remaining after defoliation at any time of the year (Hodgkinson *et al.*, 1989; Mott *et al.,* 1992).

The present work was undertaken to gain some understanding of how best to manage a Ruzi grass sward by determining the effects of different defoliation intensities and frequencies of cutting on herbage production in terms of dry matter yield and quality. This preliminary study was regarded as an essential pre-requisite to the subsequent sward management studies, as no information is available in the literature on the appropriate defoliation strategy for Ruzi grass, Because of the comprehensive range of defoliation treatments provided in this experiment, the opportunity was also taken to examine the effects of such defoliation on seed production.

4.2 MATERIALS and METHODS

4.2.1 Site and Study Period

The experiment was conducted under controlled temperature conditions of 25±5 C in a plastic house at the Plant Growth Unit, Massey University, Palmerston North, N.Z.(Latitude 40 S, Longitude 170 E). The study period extended over 9 months, from 26th August, 1995 to 18th May, 1996 (see Table 1 for management programme) i.e. from the beginning of the local spring season to the end of autumn. During this period the natural photoperiod increased from 10 hours in August to a peak level of 15 hours around the middle of December, 1995 and then declined to 9.5 hours by the end of the study in May, 1996.

4.2.2 Design and Treatments

Miniature swards were established in 24 wooden bins (each 1.0 m x 1.0 m x 0.70 m) with 49 transplanted seedlings in 15 cm rows and 15 cm apart in the row (Figure 4.1, Plate 4.1). Seed obtained from Thailand was germinated using the top-of-paper method (ISTA 1993) in a controlled cabinet which provided a temperature of 30/20 C ± 5 C (day/night) 70%RH and 12 hours of light. After 14 days 49 germinated seedlings were then transplanted into each bin containing a uniform potting mixture (ag.lime 3kg, dolomite 3kg, iron sulphate 0.5g, osmocote (16:3.5:10 + 1.2Mg + fill essential trace elements) 4kg/m^3, ammonium phosphate 2kg, and bark 700kg).

Any weak or dead seedlings were replaced by new seedlings within 10 days after initial transplanting. In order to achieve a uniform sward plants in all bins were cut to a common height of 8 cm above soil level at 35 days from after transplanting. The different defoliation treatments were then commenced and the various plant parameters measured throughout the subsequent 9 months of the experiment.

Table 4.1 The management programme in this study

Date	Treatment	Activities
Plant preparation		
12/8/95	-	seed germination in cabinet
26/8/95	all	transplanting of seedlings
27/8-5/9/95	as required	replacement of weak or dead seedlings
1/10/95	all	cutting to 8 cm above soil level
Defoliation treatments - date of 1st treatment cut		
5/10/95	20cm height	topping to intensity requirement (4 or 12 cm height)
11/10/95	35cm height	as above
14/10/95	50cm height	as above
19/10/95	65cm height	as above
Subsequent cutting and intervals presented in Table 4.2		
Fertilizer applications		
6/11/95	all	compound fertilizer (27-6.5-10), 15g/m^2
4/12/95	all	as above
23/1/96	all	as above
Seed production		
21/4-12/5/96	all	sampling of inflorescences for seed set
15/5-18/5/96	all	seed harvesting

In the taller treatments, of 50cm and 65cm pasture heights, it was necessary to support the plants with a surrounding framework of bamboo and string (Plate 4.1d). The plants were watered to field capacity by hand every 3-4 days a week. Applications of N-P-K fertilizer were also applied to ensure adequate nutrition for growth (Table 4.1).

Figure 4.1 Plant layout per bin (BP -border plant; P -recorded plant)

BP	BP	BP	BP	BP	BP	BP
BP	P	P	P	P	P	BP
BP	P	P	P	P	P	BP
BP	P	P	P	P	P	BP
BP	P	P	P	P	P	BP
BP	P	P	P	P	P	BP
BP	BP	BP	BP	BP	BP	BP

Each bin contained 49 plants. This allowed 25 non border plants (P) to be used for data collection.

A complete randomised block design was used in the experiment. The treatments comprised a combination of cutting frequencies (F) - plant height at harvest (20, 35, 50 and 65cm) was determined as the average height of plants from ground to the second or third fully mature leaf of an 'average' plant; and cutting intensities (I) - residual stubble height or length (4 and 12 cm) was determined by using the length of each stem from the basal emerging tillers (Plate 4.1c,b); with 3 replications. The layout of the experiment is shown as total 24 boxes in Figure 4.2.

Figure 4.2 The layout of treatments in the defoliation study

Replicate 1	Replicate 2	Replicate 3
4 -50	12 - 65	4 - 50
12 -50	4 - 50	12 -20
12 - 35	4 - 35	4 - 35
4 - 20	4 -65	12 - 65
12 - 20	12 -35	4 - 20
12 - 65	12 - 20	12 - 50
4 - 65	12 - 50	12 - 35
4 - 35	4 - 20 *	4 - 65

* example: 4-20 means plants were cut to 4 cm whenever they reached 20 cm in height

4.2.3 Measurements

4.2.3.1 Herbage Production

When the appropriate plant height was reached in each treatment, all border plants (BP) were cut and the cut herbage discarded. Only the inner plants (P- 25 plants/bin) were harvested for measurement (Plate 4.1a). At each defoliation, the herbage was weighed for total fresh weight. In terms of DM production, due to the differences between treatments in the total length of the defoliation period the total DM then corrected to average 94 days of cutting. Moreover, the comparison of different sward productions and also leaf and stem components were considered in terms of growth rate per day.

Sub-samples (minimum 50% of total fresh weight if there was less than 200 g, usually used 200 g fresh weight) were then divided into leaf and stem; and taken for dry matter determination in a forced-air draught electronic oven at 105 C for 24 hours. As a consequent, leaf, stem and total plant dry matter (leaf+stem), and also leaf:stem ratio were calculated (Appendix 4.1). Leaf area (from leaf sample before taken for dry matter determination) was also determined using an electronic leaf measurement machine (LI-COR Model 3100) and LAI calculated as total leaf area from 25 harvested plants per 5625 cm^2 (Appendix 4.1).

Dried herbage of the whole plants were then ground through a 1mm screen in a high-speed laboratory mill and crude protein determined by the Kjeldahl method.

The total number of live tillers was counted in each bin after each cutting. Because of the large variation in cutting frequencies between treatments (e.g. 13 cuts for the 12-20cm vs. 3 cuts for 4-65cm) it was decided to divide the tiller data into early, medium and late tillers representing their development in October/November, November/December, and January.

The last defoliation, representing the closing date for seed development, was made when the first visible sign of the onset of reproductive growth (double-ridge stage) was evident by dissecting 5 older tillers in each treatment immediately prior to cutting.

When the height of plants exceeded 50 cm, each bin was supported with bamboo canes or sticks and surrounded with string for protecting plant lodging. However, as these plants were subsequently allowed to go to seed, every bin was managed in this regard (Plate 4.1d).

4.2.3.2 Seed Production

The decision for seed harvesting was based on the colour change of fertile floret from green to light brown and substantially the average seed set was approximately 50% of total basal inflorescence numbers. Then, fifty complete inflorescences were taken from each bin to investigate raceme number per inflorescence, floret number per raceme, percent seed set and seed weight. Every plant in each bin of the same treatment was then cut to ground level and ready for harvest inflorescences counted. This allowed potential seed yield to be calculated from the percent seed set, seed weight and inflorescence number at harvest.

4.2.4 Statistical Analysis

The data were examined by analysis of variance using the general linear model (GLM) procedure of SAS (SAS, 1989). Analyses of variance for each of the components of cutting intensity and frequency were based on plot means of 8 treatments with 3 replications per treatment.

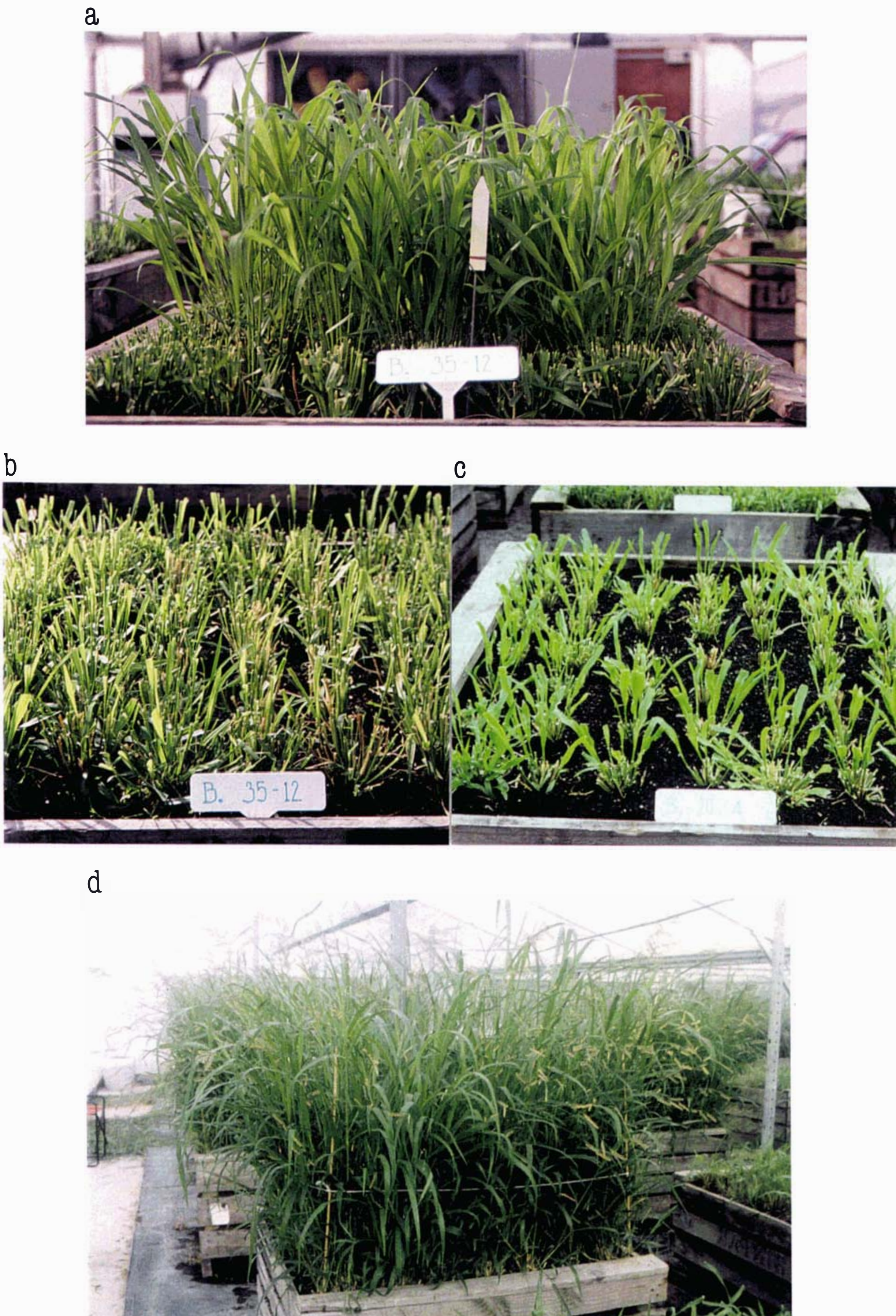


Plate 4.1 Miniature 'swards' showing effect of removal of guard rows before cutting (a); plants after cutting to 12 cm (b) or 4 cm (c). Plate (d) shows the method of plant support to prevent lodging

4.3 RESULTS

4.3.1 Number of cuts, Cutting interval and Total herbage production

The number of cuts, cutting intervals and total herbage production are presented in Table 4.2. Over the 6 month period of the experiment (from initial defoliation treatment to closing date for seed production) this represented 13 cuts in the most frequent, lax defoliation treatment (12-20cm) but only 3 cuts in the least frequent, hard defoliation treatment (4-65cm). Defoliating herbage at different mean sward heights obviously resulted in marked differences in defoliation frequencies, ranging in cutting intervals of 13 days to 29 days between cutting at hard defoliation intensity (4cm) and from 8 days to 23 days at lax defoliation (12cm) intensity. The effects of cutting intensities and frequencies on numbers of cuts and cutting intervals are presented in Figure 4.3.

Table 4.2 Number of cuts, cutting interval and total herbage production in different defoliation treatments

Defoliationtr eatments	Number of cuts	Cutting interval (days)	DMproduction (kg/ha) (during vegetative stage)	
			Total	Corrected to avg. 94 days of cutting
4-20cm	8	12.5 ±2.2	8222 ± 82	7731
4-35cm	5	19.4 ±3.9	10611 ± 520	10284
4-50cm	4	23.7 ± 0.9	9484 ± 471	9385
4-65cm	3	29.0 ± 4.5	12990 ± 518	14034
12-20cm	13	7.6 ± 1.1	10608 ± 80	10388
12-35cm	7	13.2 ± 2.4	13126 ± 222	13268
12-50cm	5	19.2 ± 6.3	12026 ± 592	11776
12-65cm	4	22.5 ± 3.0	11148 ± 604	11644

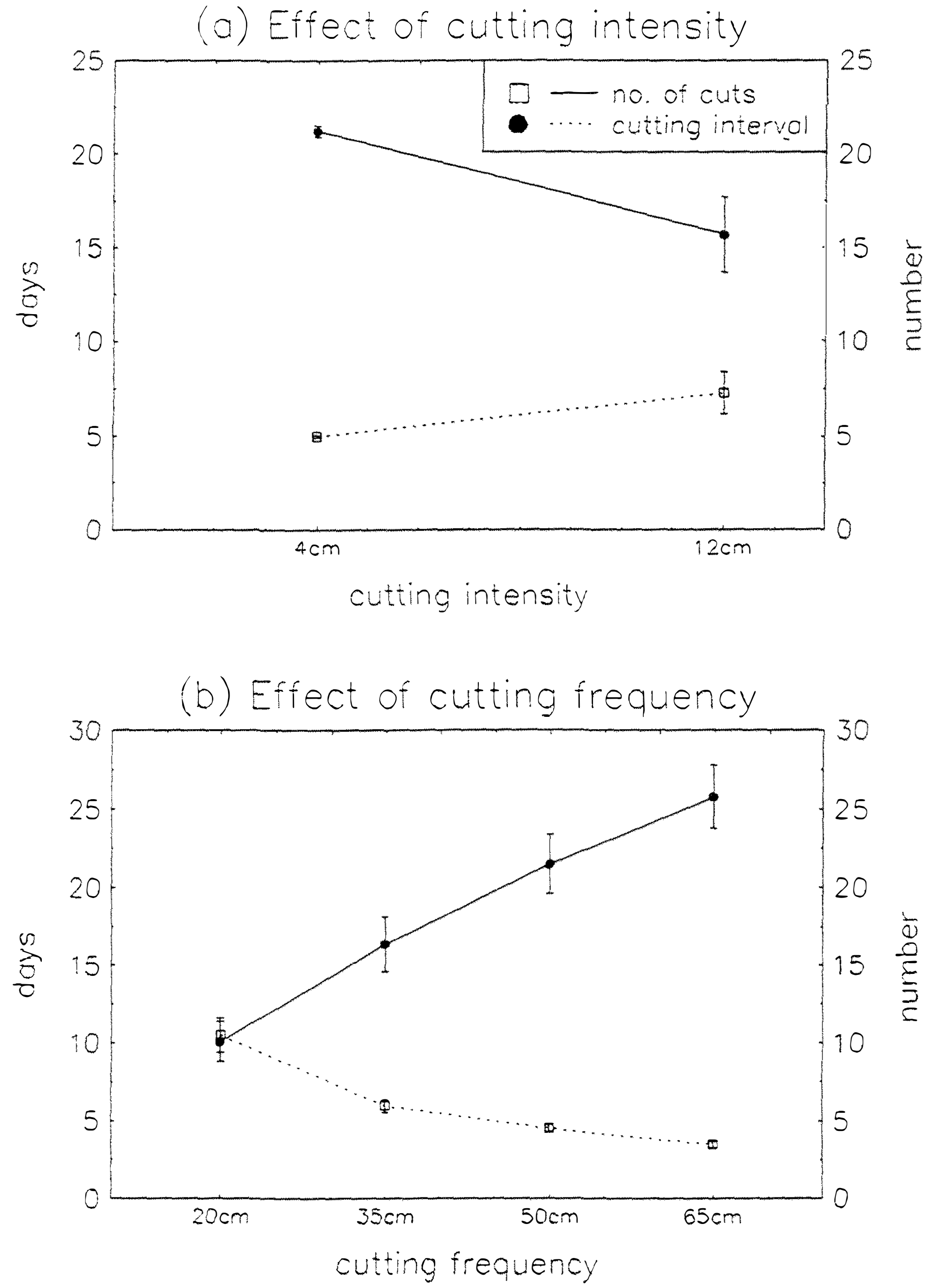


Figure 4.3 Effect of cutting intensity (a) and frequency (b) on numbers of cuts and cutting interval (days). Vertical bars show standard error of the mean.

In terms of DM production, Table 4.2 shows that the 4-65 cm and 12-35 cm treatments were clearly more productive than the remaining treatments, with the intensive, frequently defoliated treatment, of 4-20 cm, being clearly the least productive.

4.3.2 Growth and Growth components

4.3.2.1 Growth rate of sward (total plant)

The growth rate of sward DM in the different defoliation intensity and frequency treatments presented in Table 4.3 shows that the main effect of defoliation intensities, down to 4 cm or 12 cm, was not significantly different ($P<0.05$). By contrast significant differences in defoliation frequencies were detected ($P<0.001$). The data also show that DM yield generally increased as defoliation frequency decreased but only under hard defoliation. Under lax defoliation, however, there was a significant increase in yield of forage cut at 35 cm and above compared with a 20 cm sward cutting height but further increases in sward height above 35 cm (i.e. further reduction in defoliation frequency) failed to show any further increase in DM yield. However, the significant interaction of cutting frequency and intensity indicates that this effect was more pronounced under hard defoliation than under lax defoliation.

Table 4.3 Mean growth rate of sward (kgDM/ha/day)

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	78.2	108.0	98.6	142.4	106.8 a
12 cm	100.8	125.4	125.0	122.2	118.4 a
Mean[2]	89.5 c	116.7 ab	111.8 b	132.3 a	
		I	F	I x F	
Significance		ns	***	*	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P\leq 0.05$)

4.3.2.2 Growth rate of leaf

The growth rates of leaf DM in the different treatments are shown in Table 4.4. Under lax defoliation mean leaf growth rate was significantly greater than under hard defoliation ($P<0.01$). In terms of cutting frequency, the data tended to suggest that cutting at 35 cm height encouraged leaf growth but little difference occurred between the other cutting frequency treatments. However, the significant ($P<0.05$) interaction (IxF) indicated that under lax cutting leaf growth rate tended to increase as defoliation frequency increased of particular 35-12 treatment but not under hard defoliation.

Table 4.4 Mean growth rate of leaf DM (kg/ha/day)

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean
	20 cm	35 cm	50 cm	65 cm	
4 cm	52.66	64.24	53.05	68.15	59.53 b
12 cm	72.25	80.68	66.96	62.43	70.58 a
Mean	62.46 b	72.46 a	60.00 b	65.29 ab	
		I	F	I x F	
Significance		**	ns	*	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P\leq 0.05$)

4.3.2.3 Growth rate of stem

The growth rate of stem DM showed a consistent increase as defoliation frequency decreased under both hard and lax defoliation intensities (Table 4.5). By comparison there was no significant effect of cutting intensities. However, the significant interaction of cutting frequency and intensity indicates that this effect was more pronounced under hard defoliation than under lax defoliation, by comparing between the lowest height at cutting (20 cm) to the highest (65 cm) treatment.

Table 4.5 Mean growth rate of stem DM (kg/ha/day)

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	27.8	44.68	45.27	74.74	48.12 a
12 cm	36.57	47.17	58.69	62.41	51.21 a
Mean[2]	32.19 c	45.93 b	51.98 b	68.57 a	
		I	F	I x F	
Significance		ns	****	*	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

4.3.2.4 Leaf : Stem ratio

When these two parameters are combined, to determine the leaf/stem ratio, there was a marked decline in the proportion of leaf in the sward as defoliation frequency decreased (Table 4.6) or conversely the greater the defoliation frequency the higher the proportion of leaf relative to stem. Lax defoliation also encouraged higher leaf DM yield and thus shows significantly higher ratio of leaf relative to stem compared with hard defoliation ($p<0.0001$), particularly under the most frequent defoliation (20 cm).

Table 4.6 Mean DM leaf: stem ratio

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	2.13 : 1	1.49 : 1	1.19 : 1	0.91 : 1	1.43 : 1 b
12 cm	3.01 : 1	1.89 : 1	1.19 : 1	1.02 : 1	1.78 : 1 a
Mean[2]	2.57 : 1 a	1.69 : 1 b	1.19 :1 c	0.97 :1 d	
		I	F	I x F	
Significance		****	****	****	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

4.3.2.5 Leaf area index (LAI)

In terms of LAI there was a significant increase as defoliation frequency decreased and as defoliation intensity decreased (Table 4.7) and, although not statistically significant, this effect tended to be greater extent under hard defoliation than under lax defoliation. It is interesting to note that the relatively high LAI recorded in the 4-65cm treatment was considerably higher than in the 12-65cm treatment presumably due to the greater leaf size when the cutting interval was prolonged (Table 4.2).

Table 4.7 Mean leaf area index

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	2.66	3.95	5.08	7.06	4.69 a
12 cm	2.14	4.02	4.45	5.73	4.09 b
Mean[2]	2.40 d	3.99 c	4.76 b	6.40 a	
		I	F	I x F	
Significance		*	****	ns	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

4.3.3 Tiller Development

Tiller numbers at each defoliation in the different treatments are illustrated in Figure 4.4. The number of live tillers in all treatments showed a general increase over much of the experimental period and then declined at the final cut, except for treatment 4-20 cm which tended to increase again after decreasing but only marginally. The 12-65 cm treatment appeared likely to be the best management to produce highest tiller numbers. However, the differences in tiller development became less at seed harvest as shown in Figure 4.5.

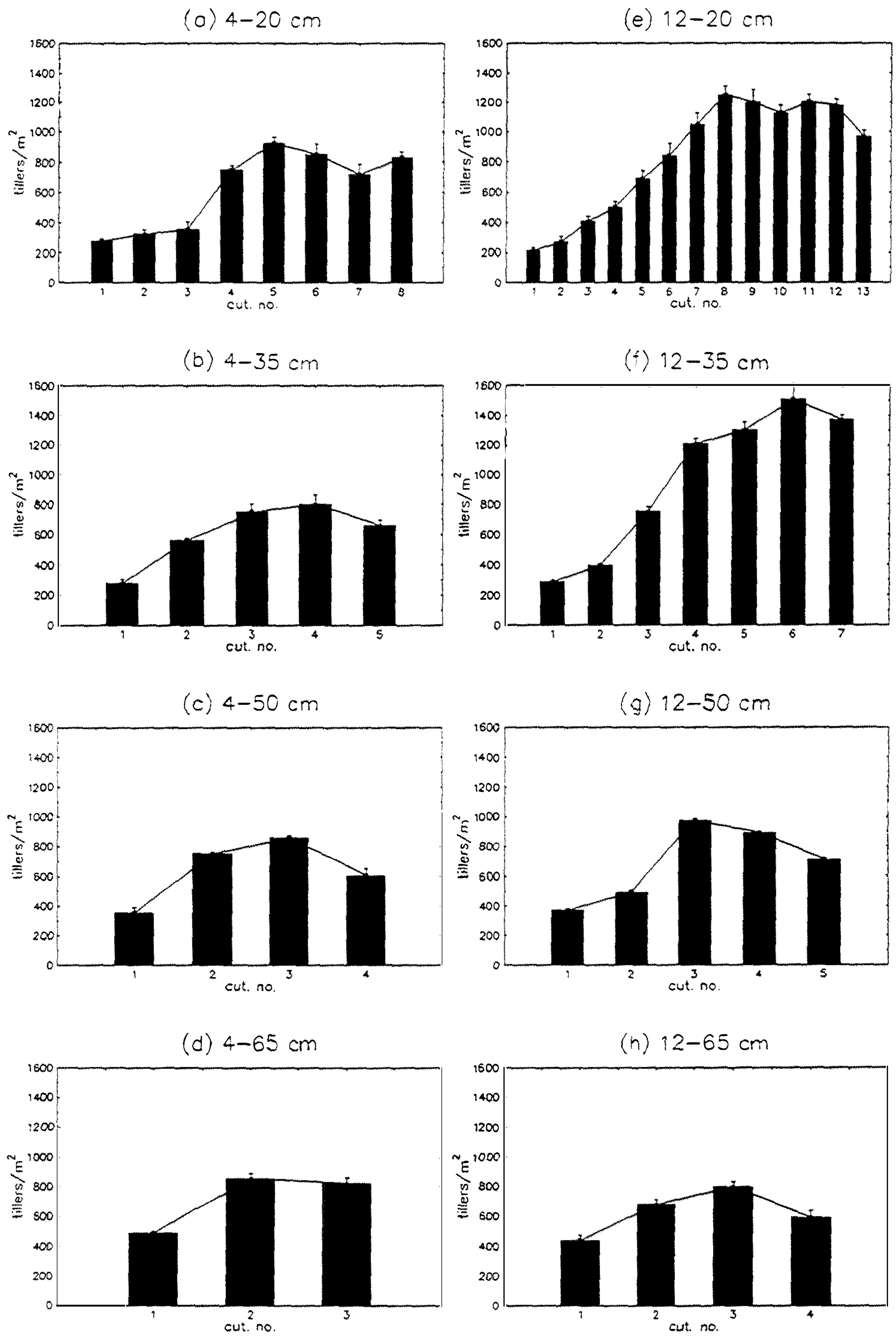


Figure 4.4 Tiller development at each of the cutting intensities and frequencies used in the defoliation study. Vertical bars show standard error of the mean.

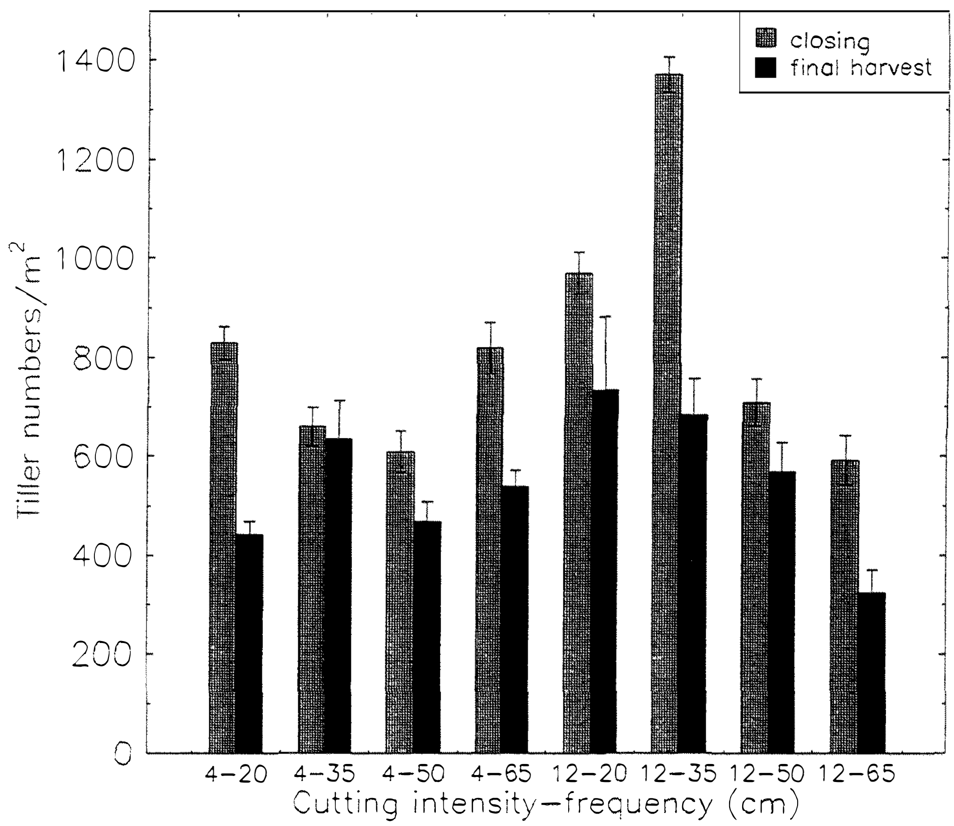


Figure 4.5 A comparison of tiller number development at the date of closing and final tiller number at seed harvest. Vertical bars show standard error of the mean.

To compare tiller development over the same period of time from each treatment, they were divided into 3 groups i.e. early, medium and late tillers (Table 4.8). Early tiller development, over the first 2 months, showed a significant response to decreasing defoliation frequency but not to defoliation intensity. However, during the middle stage of the experiment the main effect of cutting intensity showed that tiller number per m^2 was significant higher under lax cutting than under hard cutting. Also the significant interaction recorded showed that in the least frequent cutting treatment under lax defoliation decreased tiller numbers significantly more than more frequent cutting. At the late stage of the experiment decreasing defoliation frequency under lax cutting showed a surprising increase in tiller numbers (from 12-20 to 12-35) then steadily declined with less frequent defoliation. However, under hard defoliation, there was little change in tiller numbers with changing cutting frequency except for a noticeable drop in the 4-50 cm treatments when compared with the 4-65 cm treatment.

Table 4.8 Early, medium and late tiller development of each treatment during herbage production

Defoliation treatments	early tillers no. per m^2	medium tillers no. per m^2	late tillers no. per m^2
4-20	319	839	800
4-35	491	751	730
4-50	355	805	609
4-65	493	853	820
12-20	347	1007	1121
12-35	343	1088	1440
12-50	431	978	801
12-65	441	738	592
LSD P<0.05	129	208	207
C.V.(%)	18.36	13.53	13.68
Intensity (I)	ns	*	***
Frequency (F)	*	ns	***
I x F	ns	*	***

ns : no significant difference; * : P<0.05; *** : P<0.001

4.3.4 Crude protein

As expected crude protein percentage declined markedly as defoliation frequency decreased and showed no significant difference whether defoliated lax or hard (Table 4.9). These results largely reflect the declining leafiness of the sward as defoliation frequency decreased, as shown by their leaf/stem ratios.

Table 4.9 Mean crude protein percentage

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	19.7	14.92	13.95	14.01	15.65 a
12 cm	19.25	17.9	14.57	13.47	16.30 a
Mean[2]	19.47 a	16.41 b	14.26 c	13.74 c	
		I	F	I x F	
Significance		ns	****	ns	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

4.3.5 Seed production

As an adjunct to this defoliation management study, it was decided to continue the experiment through into the reproductive phase and gain some additional information of such management practices on potential seed yield. Unfortunately, it was found that the closing date, which commenced in January when some border plants showed reproductive signs, was in fact too early for seed production, as the majority of plants showed floral initiation in April. Therefore, the continued vegetative growth lead to considerable lodging. As shown in Table 4.10, although there was no significant effect of defoliation intensity on seed yield the results did show a significant reduction in seed yield under less frequent defoliation, particularly under lax cutting. Moreover, seed yield tended to have a high relationship to tiller numbers at seed harvest as shown in Figure 4.6. However, it must be remembered however that these were calculated and not actual seed yields - this aspect will be studied in greater detail in a later experiment.

Table 4.10 Mean calculated seed yield (kg/ha)

Cutting intensity (Residual stubble height)	Cutting frequency (Plant height at harvest)				Mean[1]
	20 cm	35 cm	50 cm	65 cm	
4 cm	275	355	169	204	261 a
12 cm	356	421	201	112	273 a
Mean[2]	315 ab	388 a	185 b	178 b	
		I	F	I x F	
Significance		ns	*	ns	

[1] and [2] means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

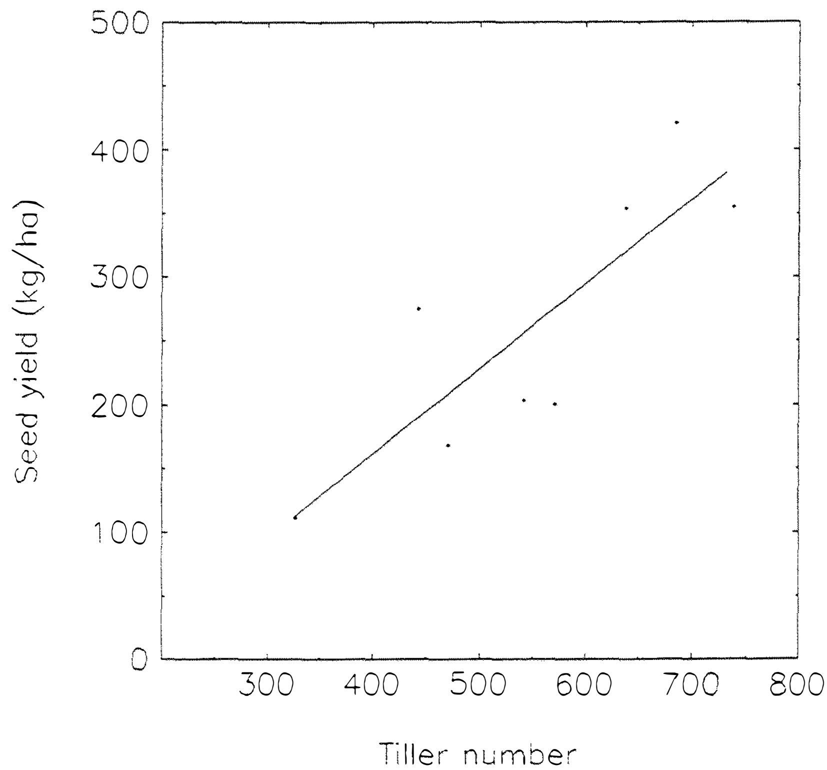


Figure 4.6 Relationship between seed yield and tiller number at seed harvest.
$Y = -104.767 + 0.666015*x$, $r^2 = 70.64\%$

4.4 DISCUSSION

In this study, the defoliation frequency of the sward was based on plant height where most workers base it on time e.g. cut every week or every month (Ludlow and Charles-Edwards, 1980; Omaliko, 1980; Butt *et al*., 1993; Pamo, 1991; Ruggieri *et al.*, 1995; Caraballo *et al*., 1997). Although, a cutting interval based on time provides an accurate statistical comparison between treatments, it does not take account of the variation in plant physiological stage that can occur between cutting intervals due to the different regrowth of plants responding to environmental changes. Accordingly, therefore, the methodology used in this study, of plant height was an endeavour to provide a similar physiological stage of growth when harvested at each cutting. Therefore, cutting intervals varied somewhat within as well as between the different cutting heights (Table 4.2).

Generally, many studies have shown that the more infrequent the cutting, the higher the DM yield obtained (Ludlow and Charles-Edwards, 1980; Tainton, 1984; Alcantara, 1986; Hsu *et al*., 1989). In the present study significant differences in the growth rate on yield of the sward due to different defoliation were also detected, showing an increase as defoliation frequency decreased but only under hard defoliation intensity (Table 4.3). Under lax defoliation, there were no significant increase beyond the 35 cm cutting height (Table 4.3). Other studies have shown increased dry matter yield with extended cutting intervals, a response which is considered to be a consequence of additional tiller and leaf formation, leaf elongation and stem development (Michelin *et al.*, 1968; Akinola *et al*., 1971). However, according to Nourrissat (1965) and Haggar (1970) the period of maximum herbage production varies with different grass species. It was noticeable in this study that the ability of plants to recover from defoliation under lax (12cm) but frequent cutting (at 20 and 35 cm plant height) was much greater compared with 50 and 65 cm height, probably because increased frequency of cutting (Table 4.2) encouraged relatively higher new tiller emergence (Table 4.8). Similarly, Tainton (1984) and Hsu *et al.* (1989) also indicated that tiller numbers increased under more frequent cutting management. In fact, differences in tiller density between managements are most likely to arise from changes in the amount and quality of light penetrating to tiller bases under contrasting defoliation patterns and the consequent effects on tiller initiation and appearance (Mitchell, 1953; Mitchell and Coles, 1955; Langer, 1963; Bean, 1964; Deregibus *et al.*, 1985; Barthram *et al.*, 1992; Chapman and Lemaire, 1993). This may have been the case under lax cutting in this study (Table 4.8).

As defoliation frequency and/or severity increases, tiller density should also increase and tiller size should reduce, according to Davies (1988). Although tiller size was not measured in this study, tiller numbers (Table 4.8) did show an increase as defoliation frequency increased and showed the same results under lax cutting but not under hard cutting. Tiller numbers however are not a precise indicator on which to predict herbage production as found by Boonman (1971b), although they must surely contribute to herbage yield particularly under certain circumstances. In this study the increase in tiller numbers recorded (Table 4.8) probably assisted an increase in herbage yield (Table 4.3) but only under lax defoliation and only as defoliation frequency decreased, by cutting at 35 cm height.

Unfortunately, measurement of the amount of residual leaf remaining after cutting was not carried out in this study, but from observation it was apparent that frequent defoliation had a higher amount of residual leaf remaining after lax cutting. Certainly maintaining leaf area after defoliation is very important for herbage production as regrowth increased as the residual LAI increased (Brougham, 1956 ; Langer, 1959). Moreover, Grant *et al.* (1981) found that leaf extension rate was positively related to the amount of green leaf remaining after defoliation. However, the reduction in photosynthesis is often not proportional to leaf-area loss due to changes in canopy microclimate after defoliation, particularly when mature, previously shaded foliage predominates on defoliated plants (Ludlow and Charles-Edwards, 1980; Gold and Caldwell, 1989), and due to the unequal photosynthetic contribution of leaves of various age, if young leaves remain after defoliation (Ludlow and Charles-Edwards, 1980; Parsons *et al.*, 1983; Gold and Caldwell, 1989). Davies (1974) suggested that removal of older laminae had less effect than removal of young laminae, and pointed to the re-allocation of plant growth resources to regrowing leaf material as the mechanism whereby plants were able to compensate for leaf removal (Richards, 1993). The capacity for rapid recovery is considered a distinguishing characteristic of defoliation-tolerant plants and genotypes (Davidson and Milthorpe, 1966; Caldwell *et al.*, 1981; Volence and Nelson, 1984; Richards and Caldwell, 1985; Volence, 1988; Fankhauser and Volence, 1989; Hodgkinson *et al.*, 1989; Mott *et al.*, 1992; Paige, 1992).

There was no significant effect of defoliation intensity, down to 4 cm or 12 cm, on DM yield in this study (Table 4.2), although higher cutting intensity (12 cm) tended to produce significantly higher growth rate DM except at 65 cm cutting frequency. In Sri Lanka, Appadurai and Goonewardene (1973) also found that the yields of Ruzi grass dry matter did not vary significantly with monthly cutting down to 2.5 cm or 7.6 cm. Similar results had also been reported from other tropical grass studies (Olsen, 1973; Murphy *et al.,* 1977). However other workers (Riveros and Wilson, 1970; Ethredge *et al.,* 1973; Ferraris and Norman, 1973; Jones, 1974; Steinke, 1975) have reported beneficial effects from lax cutting. For example Riveros and Wilson (1970) found that cutting pure stands of *Setaria sphacelata* down to 15 cm produced greater DM yield than cutting down to 7.5 cm. They stated that this was because more residual leaf area remained after cutting to 15 cm compared with little or no leaf remaining after cutting to 7.5 cm. A similar difference in residual leaf area after cutting to 12 cm and 4 cm was also observed in this study and may well have contributed to the generally better production from the lax cutting (12 cm) treatments.

Brown and Blaser (1968) considered that residual LAI appears to be a useful tool for understanding forage growth and regrowth and for developing better varieties and management practices. However, problems of using this LAI concept have been discussed by various authors (Humphreys, 1966a, 1966b; Vickery *et al.*, 1971; Ferraris and Norman, 1976; Ludlow and Charles-Edwards, 1980). Such problems and limitations have arisen mainly from work on temperate pasture species and Ludlow and Charles-Edwards (1980) consider that these limitations are minor (from their work in Setaria/Desmodium swards) and that residual LAI is a major determinant of pasture regrowth. On the other hand, others workers claim that the most important characteristic that contributes to rapid recovery, is the presence of active shoot meristem regions remaining on the plant after defoliation which allows leaf expansion to occur from elongation of already formed cells, rather than requiring new cell production (Richards, 1984; Briske, 1986, 1991; Culvenor *et al.*, 1989; Hodgkinson *et al.*, 1989; Mott *et al.,* 1992). If that is the case then the lack of any difference in DM regrowth between cutting intensities (that is cutting to 4 cm or 12 cm) in this study suggests that the shoot meristem in Ruzi grass is sited below 4 cm in the sward and thereby little if any active meristem remains safely for adequate regrowth after defoliation.

Ruzi grass can also be regarded as a grazing-tolerant tropical grasses i.e. a so-called caespitose species which is largely a function of active meristem availability at the time of defoliation as occurs in other grasses such as *Cenchrus ciliaris*, *Heteropogon contortus* and *Panicum maximum* (Hodgkinson *et al.*, 1989; Mott *et al.*, 1992). However, care must be taken to consider the effect of long term management as noted by Crowder and Chheda (1982). Cutting near ground level increases total and seasonal forage production over a short period as compared to more elevated cutting height, but plants are adversely affected in the same way as too frequent harvesting. In addition, over time, plants become weakened, stands thin out, weeds invade and spots of bare ground between plants lead to soil erosion. For example, the data of Burns *et al.*, (1998) from 'Carostan' flaccidgrass (*Pennisetum flaccidum* Griseb.) study provided evidence in this aspect that continuous of hard defoliation of 38-8 cm (38 cm -plant height at harvest, 8 cm -stubble height after defoliation) over 3 years caused a sustantially decrease dry matter yield when compared with lax defoliation of 38-15 cm, although no significant differences were shown in the first year.

The results obtained in this study also showed that the effects of a long interval between cuts increased growth rate mainly by producing a higher proportion of stem (Table 4.5) rather than leaf (Table 4.4). In other words, frequent cutting encouraged a higher proportion of leaf than infrequent cutting as shown by the leaf:stem ratios (Table 4.6). Humphreys (1987) noted that this is partly because defoliation stimulates branching and leaf differentiation, and partly because the sward is maintained in a more juvenile condition.

Although cutting intensity had no significant effect on the growth rate of the sward (Table 4.3), the data did show that lax cutting significantly increased the growth rate of leaf more than hard cutting (Table 4.4) especially when cutting frequency applied at 20-50 cm height - as supported by the leaf:stem ratios recorded (Table 4.6).

The quality of herbage was determined by crude protein percentage in the present study and ranged from 13 to 19%. Results clearly show that the more infrequent the cutting, the lower the crude protein concentration (Table 4.9) reflecting the declining leafiness of the sward (Table 4.6). Similar results have been reported in other studies (Oyenuga, 1959, 1960; Haggar, 1970; Saleem, 1972; Kamel *et al.*, 1984; Hsu *et al.,* 1989; Jeangros and Scehovic, 1996). Generally, increasing cutting frequency reduced forage contents of cellulose, lignin and other cell-wall components but increased contents of crude protein, soluble sugars and minerals, leading to higher organic matter digestibility and nutritive value (Ruggieri *et al.*, 1995; Jeangros and Scehovic, 1996). However, there was no significant differences in herbage quality between cutting intensities (Table 4.9), which is in agreement with other workers (Huokuna, 1964; McFeely, 1978), although it disagrees with work by Reid (1959) and Binnie (1974). The present results again reflect the similar degree of leafiness produced at all defoliation frequencies (Table 4.6) irrespective of whether the sward was cut hard or lax.

In general, maximum tillering occurs during the vegetative growth phase and then begins to decline before inflorescences emerged (Boonman, 1971b; Bahnisch and Humphreys, 1977b; Loch, 1985). In this study tiller numbers also increased steadily during the vegetative phase and then levelled off or declined as the reproductive phase began (Table 4.8). This cycle of development was more apparent as tiller numbers reached higher levels under lax cutting than under hard cutting. This contrasts with findings by Riveros and Wilson (1970) who reported that hard cutting to 7.5 cm stimulated more tiller development than lax cutting at 15 cm in *Setaria* grass. However they did say that tillers under low cutting tended to be weak and many died. It is possible that under lax cutting in this experiment where the sward was physically supported by frames, the young, new tillers received a better light environment than there would be in a relatively tall and lodged sward and hence were encouraged to survive and grow.

In terms of cutting frequency, Tainton (1981) found that tiller numbers of ryegrass increased under more frequent cutting management. In this respect, Ruzi grass performed similarly but only under lax cutting whereas under hard cutting tiller numbers showed no difference between frequent (20 cm) and infrequent cutting (65 cm) (Table 4.8). The range in tiller density of Ruzi grass in this study was from 600-1400 tillers per m^2 which is reasonably similar to the mean figure of 1280 tillers per m^2 recorded by Boonman (1971b) in his second year.

It is evident from Table 4.10 that cutting intensity had no effect on seed yield but frequent cutting tended to increase seed yield. However, these results were confounded by an inappropriate closing date - as the decision to cease defoliation and allow seeds to develop was based unfortunately on the reaction of the border plants which showed reproductive development in January while the majority of plants did not show floral initiation until April. Hence the majority of the plants in the sward continued vegetative growth to a considerable height before becoming reproductive. Nonetheless, the higher tiller numbers during herbage production clearly showed a continued response by encouraging more tiller development during the reproductive stage particularly under lax cutting (Figure 4.5). Moreover, there was a clear and positive relationship between tiller numbers at seed harvesting and seed yield (Figure 4.6), particularly under lax cutting, and in this case linear in function. These aspects relating to seed yield are dealt with in greater detail in the next Chapter.

4.5 CONCLUSION and RECOMMENDATION

As stated at the outset of this study, the main purpose of this experiment was to determine the most appropriate defoliation management practice for Ruzi grass "pasture", and thereby provide a reasoned justification for the defoliation strategy to be adopted in subsequent studies.

Table 4.11 presents data obtained from the different defoliated swards for those characters considered to be important in a Ruzi sward capable of relatively high production and quality i.e. the best management for best overall performance. Data are also presented using a simple ranking order (Rank.) for each character in the different defoliation treatments. Ranking value was obtained by allocating a number from highest (1) to lowest (8) for each treatment.

In terms of sward productivity, lax defoliation generally resulted in higher growth rate than hard defoliation. The obvious exception was the hard defoliation treatment under the longest cutting interval of 65 cm. This also resulted in the highest LAI but unfortunately showed poor quality.

In contrast, the hard defoliation treatment when cut most frequently gave the lowest growth rate but, as one could expect, a high leaf/stem ratio producing a sward of the highest quality in terms of crude protein. Although tiller numbers were medium the short time interval between cuttings prevented these tillers from expressing a high growth rate and also appeared to restrict tiller density.

The most frequent but lax cut sward also showed relatively inferior growth with very high leaf/stem ratio and quality. Again tiller development was restricted, resulting in very low LAI. However, tiller density was relatively high, suggesting that the lax defoliation ensured minimum damage to new tillers compared with the adverse affect under hard defoliation. The intermediate defoliation frequency treatment cut at 50 cm ranked relatively poorly in all characters measured, especially under hard defoliation.

The other intermediate defoliation frequency treatment cut at 35 cm reacted relatively poorly when cut hard, with only average leaf/stem ratio, LAI development, tiller density, daily growth rate and crude protein level. However when subjected to lax defoliation this intermediate cutting frequency produced a very encouraging overall performance, particularly in terms of leaf/stem ratio, tiller density, daily growth rate and crude protein. In addition, when taking reproductive plant performances in terms of tiller numbers and seed yield into consideration this treatment also showed high potential in this regard.

Therefore, in terms of an overall assessment of the data from the various defoliation treatments it was decided, with reasonable justification that the most appropriate defoliation management for the Ruzi sward was 12-35 cm i.e. cutting whenever the canopy reached a height of 35 cm down to 12 cm. This cutting regime was therefore chosen as the most appropriate defoliation strategy in subsequent studies on the management of Ruzi swards for seed production.

Table 4.11 Ranking of different parameters (1 = highest; 8 = lowest) in each cutting treatment

Trts.	Growth Table 4.3	Rank.	LAI Table 4.7	Rank.	L:S ratio Table 4.6	Rank.	CP Table 4.9	Rank.	Tillers (veg.) Fig. 4.5	Rank.	Tillers (harvest) Fig. 4.5	Rank.	Seed yield Table 4.10	Rank.	Total relative ranking	Rank.
4-20	78.2	8	2.66	7	2.13	2	19.7	1	830	3	443	7	275	4	32	5
4-35	108.1	5	3.95	6	1.49	4	14.9	4	660	6	636	3	355	3	31	4
4-50	98.6	7	5.08	3	1.19	5	13.9	7	609	7	469	6	169	7	42	7
4-65	142.4	1	7.06	1	0.91	7	14	6	820	4	540	5	204	5	29	3
12-20	100.8	6	2.14	8	3.01	1	19.2	2	970	2	736	1	356	2	22	2
12-35	125.4	2	4.02	5	1.89	3	17.9	3	1370	1	684	2	421	1	17	1
12-50	125.1	3	4.45	4	1.19	5	14.5	5	710	5	569	4	201	6	32	5
12-65	122.3	4	5.73	2	1.02	6	13.4	8	592	8	325	8	112	8	44	8

CHAPTER 5

Effects of different nitrogen application levels and closing dates during a decreasing photoperiod on seed production of Ruzi grass

5.1 INTRODUCTION

Many experienced and successful pasture seed producers utilize their pastures for the dual role of seed and herbage production (Padilla and Febles, 1980; Loch, 1983, 1985; Mecelis and Oliveira, 1984). They are capable, through good defoliation management, of providing an abundance of green herbage for livestock during much of the growing season as well as achieving high seed production through timely "closing" of the pasture at the beginning of the reproductive phase. As reported by Loch (1985), appropriate defoliation management can not only increase herbage yield and quality but also encourage a high density of fertile tillers of similar age which achieves better synchronised seed maturation to facilitate seed harvest. Humphreys and Riveros (1986) however noted that grazing or cutting can have both adverse and favourable effects on flowering and seed formation due to their influence on (1) the density of inflorescences, (2) the assimilate supply to the inflorescence, (3) the time of flowering and (4) the control of competing species.

The increasing use of fertilizer and of soil amendments to overcome constraints to pasture growth occasioned by mineral deficiencies is a significant feature of intensive pasture systems in the tropics (Humphreys, 1991). Although there are many nutrients which may play specific roles in pasture also used for grass seed production (e.g. boron in *Setaria sphacelata* (de Bruyn, 1966a); calcium in *Setaria sphacelata* (de Bruyn, 1966b); phosphorus in *Cenchrus ciliaris* (Ayerza, 1980)), this chapter confines its attention to the most important nutrient - nitrogen, where other nutrients are non-limiting, and also moisture (Foster, 1956; Haggar, 1966; Humphreys and Davidson, 1967; Mishra and Chatterjee, 1968; Cameron and Mullaly, 1969; Grof, 1969; Chadhokar and Humphreys, 1970, 1973a, 1973b; Hacker and Jones, 1971; Boonman, 1972a, 1972b, 1972c; Stillman and Tapsall, 1976; Bahnisch and Humphreys, 1977a, 1977b; Febles *et al.*, 1982; Diulgheroff *et al.*, 1991; Hacker, 1994; Ramirez and Hacker, 1994, 1996;

Ezenwa *et al.*, 1996).

Nitrogen availability is the primary mineral constraint to plant and animal production from grassland (Humphreys, 1997) and accepted as the major limiting factor to production in most tropical regions (Date, 1973). Moreover, it becomes one of the major cost items in specialist grass seed production (Loch and Hannah, 1977). However, negative effects of nitrogen fertilizer application for grass seed production can occur, such as excessive (i.e. toxic) levels (Chadhokar and Humphreys, 1973b), where there are imbalances of other nutrients (Kowithayakorn *et al.*, 1979; Ayerza, 1980), and under environmental stresses through creating lodging problems (Boonman, 1972a, 1972b; Cameron and Humphreys, 1976; Bahnisch and Humphreys, 1977a).

The role of nitrogen fertilizer in increasing tropical grass seed yield may function in several ways viz. by increasing the photosynthetic capacity of a well grown canopy and by stimulating a higher proportion of flowering shoots (Humphreys and Riveros, 1986). In *Setaria sphacelata* var. *sericea* cv. Narok for example, Banisch and Humphreys (1977b) found that fertility of the main stem was positively related to additional nitrogen supply and high nitrogen increased tiller fertility and accelerated flowering. However, the response to added nitrogen by increasing inflorescence density can vary in different grass species by increasing either tiller density or tiller fertility (Loch, 1985). For example, nitrogen increased tiller fertility for *Bothriochloa insculpta* cv. Hatch and *Setaria sphacelata* cv. Narok, but increased tiller density for *Paspalum plicatulum* cv. Bryan and *Setaria porphyrantha* cv. Inverell. *Chloris gayana* cv. Callide and *Panicum coloratum* cv. Bambatsi, were classified as intermediate in this regard.

Generally, the supply of nitrogen will stimulate some yield components but will also reduce others, especially when competition is induced. For example, Cameron and Humphreys (1976) found that the application of nitrogen to *Paspalum plicatulum* increased tiller density, tiller fertility, and raceme number on the individual inflorescence, but decreased percent tiller survival, raceme length, and individual seed weight, while seed density per unit raceme length did not vary significantly. However, many workers have concluded that inflorescence density is the main component of seed yield in tropical grasses (Febles and Padilla, 1974; Javier *et al.* ,1975; Mejia *et al.,* 1978b; Loch, 1980, 1983).

Various forms of nitrogen fertilizer have been applied to warm climate grasses. Perez, *et al.* (1984) for example, found that urea was less efficient than other nitrogenous fertilizers and Kitamura (1986) who worked with tropical grass in Japan showed that ammonium sulphate gave the best result followed by CDU (calcium diammonium urea) > ammonium chloride = ammonium nitrate > urea > calcium cyanide in descending order. However, Humphreys and Riveros (1986) considered that source of nitrogen fertilizer did not seem to be a major consideration in predicting response levels.

Some producers recommend split applications of nitrogen to the seed crop but evidence to support this practice is not conclusive. In general, nitrogen application early in the life of the crop, after the cleaning cut, to generate sufficient sites for future inflorescence development has been confirmed by many workers (Boonman, 1971a, 1972c; Stillman and Tapsall, 1976; Bahnisch and Humphreys, 1977a; Bilbao *et al.*, 1979; Febles *et al.*, 1982; Humphreys and Riveros, 1986). Importantly, Chadhokar and Humphreys (1973a, 1973b) indicated that adequate nitrogen from sowing to floral initiation promoted tillering and adequate nitrogen from floral initiation to seed head emergence encouraged better survival of tillers resulting in increased seed yield. By comparison, additional nitrogen fertilizer from head emergence to seed harvest seldom had any beneficial influence on seed production.

In terms of seed quality, the application of nitrogen fertilizer has shown both positive effects (Chadhokar and Humphreys, 1973b; Bahnisch, 1975; Cameron and Humphreys, 1976; Jin *et al.*, 1996) and negative or no effects (Cameron and Mullaly, 1969; Grof, 1969; Boonman, 1972a, 1972b; Javier *et al.*, 1975; Cameron and Humphreys, 1976; Mejia *et al.*, 1978a; Macedo *et al.*, 1983; Carmo *et al.,* 1988.; Cruz *et al,* 1989). Humphreys and Riveros (1986) suggested that the growing condition of the grass seed crop will modify the effect of nitrogen on seed quality and careful attention to correct harvest time and seed grading will tend to offset any negative effects of nitrogen fertilizer.

The decision as to the time of closing pasture is considered to be another important factor as it relates not only to the duration of herbage production, but can have a significant effect on seed production, particularly as Ruzi grass is affected by daylength (Dirven *et al.*, 1979), and closing too late will remove or damage reproductive tillers.

Despite numerous reports documenting nitrogen fertilizer response in warm climate grasses, work with *Brachiaria ruziziensis* has been very limited for both herbage and seed production. In addition, as mentioned above "closing date" (cessation of cutting) is another important management decision. Accordingly, therefore, this experiment was conducted to determine the effects of three levels of nitrogen fertilizer and three different "closing dates" on herbage production and also on seed production of Ruzi grass (*Brachiaria ruziziensis*).

5.2 MATERIALS and METHODS

5.2.1 Plant Preparation and Study Period

The preparation of planting materials and growing conditions for this experiment were the same as that reported in Chapter 4. This experiment was carried out from December 1996 to June 1997, when the plants were approximately one year old. During the first year after planting (December 1995) all plants were maintained under a defoliation intensity and frequency of 12-35 cm (plants were cut to 12 cm whenever they reached 35 cm in height), and this same cutting regime was carried on in this experiment.

In December 1995, the growing medium had provided nitrogen sources incorporated as Osmocote (16% Nitrogen). This product is expected to provide nutrients for no more than 9 months, and so it is assumed that after 12 months (December 1996) when this experiment began very little nitrogen would still be available. However, this was not measured.

5.2.2 Design and Treatments

A complete randomised block design was used in this experiment. The treatments were:

(a) three nitrogen levels: 50, 150 and 250 kg N/ha

Nitrogen was applied at rates of 50, 150 and 250 kg N/ha in the form of urea (46%N). Those rates were divided into 3 applications viz at the commencement of the experiment on 22nd December 1996, after the 2nd defoliation on 7th February 1997 and after defoliation at the time of the early closing date treatment on 24th March 1997.

Phosphorus and potassium fertilizer (Mono potassium phosphate 0-51-33) was also applied once, at the commencement of the experiment at rate of 100 kg/ha and 65 kg/ha respectively.

(b) three closing dates:

Early closing date (E) (24th March 1997) - Two weeks prior to the Medium closing date.

Medium closing date (M) (7th April 1997) - This was considered the most suitable time for the final defoliation as determined from the seedhead development study in the first year (Chapter 3 and 4). A two week difference (duration of plant regrowth after cutting for the 12-35 cm regime) was used to determine the early and late closing dates.

Late closing date (L) (21st April 1997) - Two weeks after the Medium closing date.

(c) Each treatment was replicated three times

The experiment therefore comprised 27 bins of miniature swards in 3 blocks (rows) of 9 random treatments.

5.2.3 Measurements

5.2.3.1 Herbage production

All swards were harvested whenever the average height was 35 cm. They were cut down to 12 cm, the herbage removal and its dry weight recorded. This process continued until the closing date treatment required. The management details are shown in Table 5.1.

Table 5.1 The number of cuts and cutting interval for the different closing treatments

Cutting for herbage production	Treatments		
	Early closing	Medium closing	Late closing
Number of cuts	4	5	6
Duration of cutting (days)	12/1/97 - 24/3/97 (71)	12/1/97 - 7/4/97 (85)	12/1/97 - 21/4/97 (99)

Data collection was only for total plant cut dry matter during the vegetative stage. After the final seed harvest plants were cut to determine dry matter production (Appendix 4.1) which was also partitioned into leaf dry matter, stem dry matter and tiller dry matter from each type of tiller (see 5.2.3.4 also). Leaf : stem ratio and leaf area (from leaf samples before dry matter was determined) were also determined using an electronic leaf measurement machine (LI-COR Model 3100). LAI was calculated as total leaf area from 25 harvested plants per 5625 cm^2 (Appendix 4.1).

5.2.3.2 Seed production

After closing, plants were supported with bamboo canes or sticks and each bin was surrounded with string to prevent plant lodging.

As the objective was to measure maximum seed production per treatment, it was necessary to harvest individual inflorescences daily until the maturation of the latest seedhead in the late closing treatment. Seed harvesting then ceased. Hence seed harvesting occurred over a period of 2-3 weeks and not on a specific date (Table 5.2). The decision as to when to harvest an inflorescence was based on the changing of floret colour from green to light brown.

Table 5.2 Range of harvest dates in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Early closing		Medium closing		Late closing	
	Harvest dates	Duration (days)	Harvest dates	Duration (days)	Harvest dates	Duration (days)
50	15/5-31/5	16	18/5-2/6	15	1/6-15/6	14
150	14/5-3/6	20	14/5-4/6	21	25/5-8/6	14
250	14/5-2/6	19	14/5-4/6	21	25/5-10/6	16

All harvested ripe inflorescences from each plant were counted and then divided into different groups according to raceme number per inflorescence (e.g. group 1 (1 raceme), group 2 (2 racemes)..etc. Subsequently a total of 20 inflorescences per bin was taken on a proportional basis to represent each group of raceme numbers per inflorescence. These inflorescences were then dissected and divided into two categories : (1) seed number (fertile floret) - where the floret contained a caryopsis (Ferguson and Crowder, 1974) at the firm or "hard" stage (Humphreys and Riveros, 1986); (2) sterile floret - a floret which did not contain a caryopsis. Accordingly, the total number of seeds and florets from harvested inflorescences were obtained and thus the percentage seed set calculated. Seeds were cleaned by using a blower (Micro Blower Type 35) at 70 m/sec for 2 minutes. Thousand seed dry weight (TSDW) was then determined using the air-oven method, with samples (200 seeds per replication) being dried at 103°C for 17 hours (ISTA, 1993). Then, the actual seed yield (dry weight basis) was calculated as the ratio of seed dry weight and seed fresh weight divided by the total of seed fresh weight.

Any immature inflorescences were also counted before plants were cut for the final dry matter determination. Accordingly, the total number of inflorescences produced (harvested and immature inflorescences) and the percentage of harvested and also unharvested immature inflorescences from each treatment were calculated.

5.2.3.3 Seed quality

Germination tests (ISTA, 1993) on cleaned seed samples were conducted 6 months after seed harvest, the samples having been stored at 5°C during this time. Fifty seeds per replicate (three replicates per treatment) were used and tested on germination paper (top of paper method) soaked in 0.2 % KNO_3. Blotters were placed in a germination cabinet at 30°C/25°C day and night temperature respectively, 70% RH and 12 hour light/day. Germination was evaluated at 7 days for the first count and 21 days for the final count. Tests were examined and the following categories recorded; germinated seeds (normal and abnormal seedlings), and ungerminated seeds (fresh ungerminated seeds and dead seeds). The percentage of pure germinating seeds (% PGS) from each plant was then calculated and PGS yield was determined as follows :

%PGS = (germinated seed numbers/total seed germination test numbers) x 100

PGS yield = Seed yield x % PGS

5.2.3.4 Tiller development

Live tiller numbers per m^2 were counted at three occasions viz. after the first cut for herbage production, after herbage cutting at the early closing date, and at the final cut after seed harvest. At the final cut, all harvested tillers were divided into 2 main categories, *viz.* vegetative and reproductive tillers, and then further subdivided into old (had been cut) and new (had not been cut) tillers within each main category. Consequently, there were 4 groups of tillers representing new vegetative tillers (NVT), old vegetative tillers (OVT), new reproductive tillers (NRT) and old reproductive tillers (ORT).

5.2.3.5 Crop index and Harvest index

The crop index and harvest index was determined in this experiment as follows:

- Crop index : the ratio of total seed yield to total herbage dry matter yield (as a percentage)
- Harvest index : the ratio of total seed yield to herbage dry matter yield at the final cutting after seed harvest (as a percentage)

5.2.4 Statistical Analysis

The data were analysed using a SAS programme (SAS, 1989). ANOVA was used to evaluate the two main treatment effects and interactions of the parameters measured.

5.3 RESULTS

5.3.1 Herbage Production

5.3.1.1 Until closing

The herbage dry matter production totals from the first cut to the respective closing dates are presented in Table 5.3, as are the treatment means. As expected, increasing the nitrogen applied significantly ($P<0.0001$) increased herbage dry matter yield; there was a positive and virtually linear response to added nitrogen.

The late closing date treatment, which was closed 4 weeks later than the early closing treatment and 2 weeks later than the medium closing treatment, recorded the highest mean herbage yield and the early closing date treatment the lowest mean herbage yield with the medium closing date treatment being intermediate in this respect. However, these means did not differ significantly at $P \leq 0.05$, and there was no interaction between closing date and nitrogen for herbage yield (Table 5.3).

Table 5.3 Total herbage dry matter production from first cut to closing in different nitrogen and closing date treatments (kg/ha)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	9095	8929	10620	9548 c
150	10781	12242	14523	12518 b
250	14782	15651	14645	15026 a
Mean[2]	11553 a	12274 a	13266 a	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	ns	****	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

5.3.1.2 After seed harvest

Herbage dry matter production from closing to the completion of the seed harvest is presented in Table 5.4. The early closing treatment, which had approximately 14 days more growth than the medium closing treatment and approximately 28 days more growth than the late closing treatment before the final cut, produced significantly more herbage than the medium and late closing treatments, while the medium closing treatment produced significantly more dry matter than the late closing treatment.

Table 5.4 Mean herbage dry matter production from closing date to final harvest in different nitrogen and closing date treatments (kg/ha)

Nitrogen (kg/ha)	Closing date			Mean[1]
	Early	Medium	Late	
50	5544	2978	2444	3655 b
150	5302	3487	2483	3757 b
250	7822	3864	2575	4767 a
Mean[2]	6236 a	3443 b	2501 c	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

The extended period of growth allowed by the early closing treatment encouraged more new vegetative tiller growth, but particularly allowed greater production from new and old reproductive tillers from Table 5.5 but not old vegetative tillers compared with the medium and late closing treatments. The latter treatments showed no significant differences with the exception of dry matter production by old reproductive tillers (Table 5.5).

There were no significant differences in herbage production under low (50 kg/ha) and medium (150 kg/ha) nitrogen applications (Table 5.4). However, the application of 250 kg/ha nitrogen increased herbage production significantly except at late closing. This was mostly a result of a significant increase in new reproductive tiller dry weight.

The dry matter yields recorded from new tillers, however, showed that there was significant interaction between nitrogen levels and closing dates (Table 5.5 and Appendix 5.1).

When the season's total herbage dry matter lie from first cut to closing (Table 5.3) and closing to seed harvest (Table 5.4), were combined and analysed for the response to nitrogen and closing date effects, increasing the nitrogen application significantly increased herbage production (Figure 5.1a). However, the closing treatments did not differ significantly (Figure 5.1b) due to a compensatory effect between the number of cuts before closing and the duration from closing to seed harvest. For example, the early closing treatment had potentially less herbage production than the late closing treatment, but the earlier treatment had more time to produce herbage before the final cut after seed harvest.

Table 5.5 Relationship between nitrogen application and closing date on tiller dry matter (kg/ha) originating from old and new vegetative and reproductive tillers

Treatment effects	Tiller dry matter			
	Vegetative stage		Reproductive stage	
	New	Old	New	Old
N (kg/ha) -N				
50	546.6 a	1006.8 a	375.2 b	1728.0 a
150	378.8 a	462.4 b	777.2 ab	2140.4 a
250	522.4 a	773.2 ab	1231.6 a	2240.0 a
significance	ns	ns	*	ns
Closing date -C				
Early	842.4 a	602.4 a	1986.8 a	2806.0 a
Medium	309.6 b	596.0 a	380 b	2157.2 b
Late	294.4 b	1044.0 a	17.2 b	1145.6 c
significance	**	ns	****	****
NxC	ns	ns	*	ns

Means in each column which are followed by the same letter do not differ significantly at the 5% level

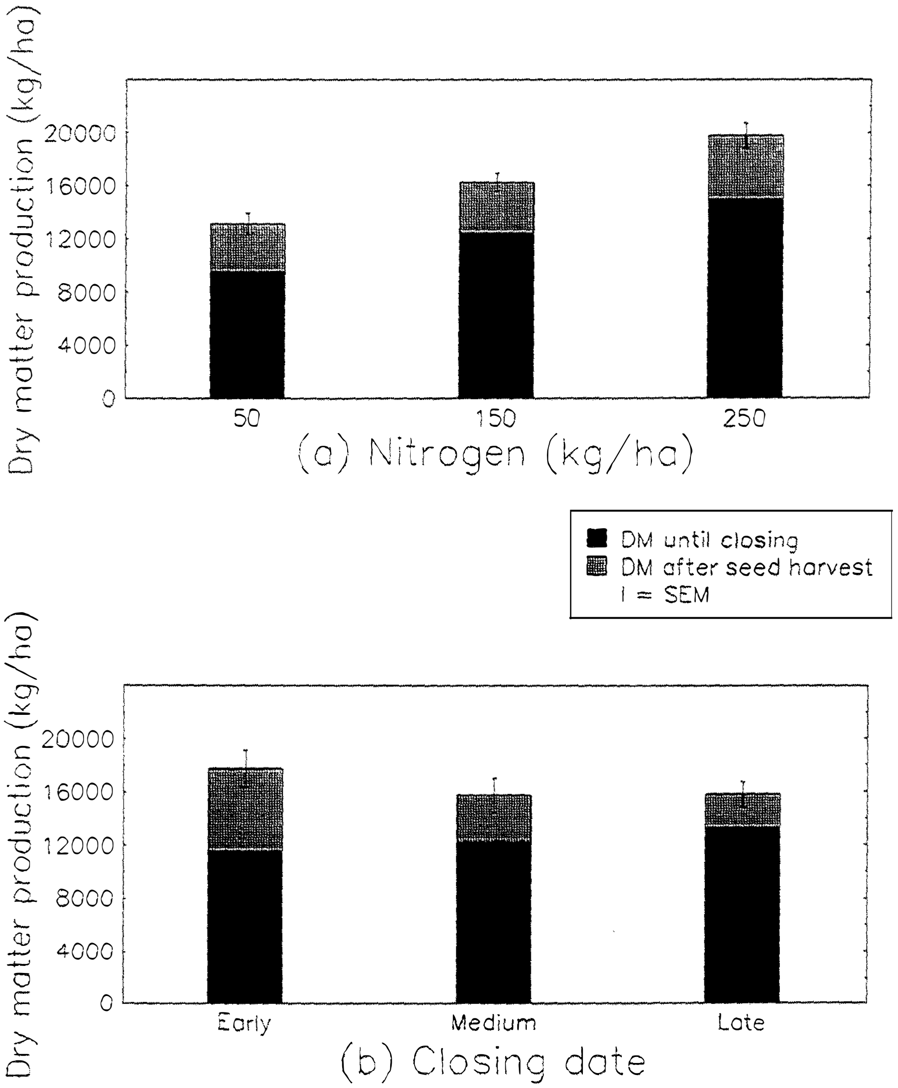


Figure 5.1 Effect of nitrogen fertilizer and closing date on total dry matter (DM) production from the first cut to closing (DM until closing) and after seed harvest (DM after seed harvest). Vertical bars indicate the standard error (SEM) of the mean (total dry matter).

At the final cut after seed harvest, the early and medium closing treatments had produced a higher proportion of stem compared to leaf than the late closing treatment, as reflected in the leaf:stem ratio (Table 5.6). This was due to the extended period of growth, from closing date to harvest, in these treatments compared with the shorter time involved in the late closing treatment. Added nitrogen, on the other hand, failed to influence leaf:stem ratio (Table 5.6).

Table 5.6 Mean leaf:stem ratio after seed harvest in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date			Mean[1]
	Early	Medium	Late	
50	1:2.6	1:2.2	1:1.3	1:2.0 a
150	1:3.4	1:2.5	1:1.9	1:2.6 a
250	1:3.1	1:2.3	1:1.1	1:2.2 a
Mean[2]	1:3.0 a	1:2.3 a	1:1.4 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	**	ns	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

The leaf area index of the herbage at the completion of harvest was highest in the early closing treatment but did not differ between the medium and late closing treatments (Table 5.7). Added nitrogen only increased LAI at the highest application rate of 250 kg/ha.

Table 5.7 Mean LAI after seed harvest in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date			Mean[1]
	Early	Medium	Late	
50	1.64	0.53	1.08	1.08 b
150	1.29	1.33	0.97	1.19 b
250	3.02	1.67	1.21	1.96 a
Mean[2]	1.98 a	1.18 b	1.08 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	*	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

5.3.2 Seed yield and yield components

5.3.2.1 Actual seed yield

Early and medium closing produced very significantly ($P<0.0001$) greater seed yields than the late closing date treatment (Table 5.8). The small difference between early and medium closing treatments was not significant. The application of 150 kg/ha nitrogen significantly ($P<0.05$) increased seed yield over the 50 kg/ha treatment, but there was no further response to 250 kg/ha.

Table 5.8 Mean total seed yield obtained from different nitrogen and closing date treatments (kg/ha)

Nitrogen (kg/ha)	Closing date			Mean[1]
	Early	Medium	Late	
50	144.0	168.4	29.6	114.0 b
150	310.8	279.2	57.6	216.0 a
250	316.0	264.0	57.6	212.4 a
Mean[2]	256.8 a	237.2 a	48.0 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P\leq0.05$

5.3.2.2 Seed yield components

(a) Inflorescence development

The total inflorescence number per m^2 was influenced by closing date (Table 5.9). Although there was no significant difference in inflorescence numbers between the early and medium closing date treatments, both these treatments produced significantly greater numbers of inflorescences than the late closing treatment ($P<0.001$).

The application of 150 and 250 kg/ha nitrogen also significantly increased the total numbers of inflorescences produced ($P<0.01$).

Table 5.9 Total inflorescence numbers from different nitrogen and closing date treatments (m^2)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	320	336	128	261 b
150	472	473	301	415 a
250	668	386	326	460 a
Mean[2]	486 a	398 a	252 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	***	**	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

The harvested ripe inflorescence numbers (in the bag) are presented in Table 5.10 and show the same response to closing dates and nitrogen application as presented in Table 5.9.

Harvested ripe inflorescence numbers were significantly and positively correlated with seed yields (Figure 5.2).

Table 5.10 Mean harvested ripe inflorescence numbers from different nitrogen and closing date treatments (m^2)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	197	228	102	176 b
150	342	337	128	269 a
250	358	288	120	255 a
Mean[2]	299 a	284 a	116 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	**	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

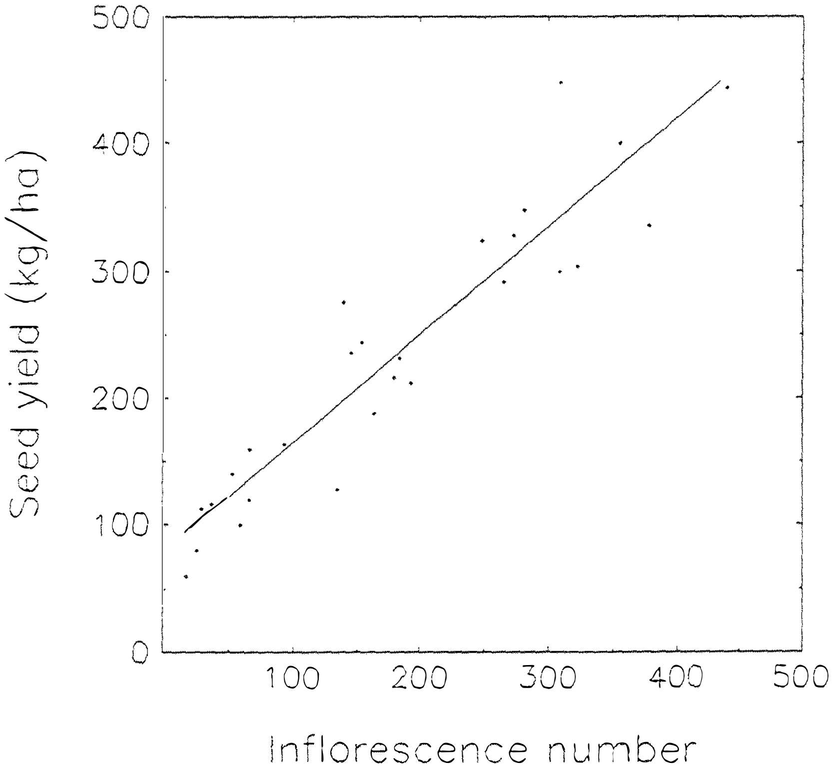


Figure 5.2 The relationship between seed yield and ripe inflorescence number at seed harvest. $y = 79.9523+0.850125*x$, $r^2 = 87.16\%$

Unharvested immature inflorescence numbers did not differ among closing date treatments (Table 5.11). However, nitrogen at the highest rate significantly increased the number of unharvested immature inflorescences over the lowest rate of nitrogen application, but there was no significant difference compared with the medium rate of nitrogen application.

Table 5.11 Mean unharvested immature inflorescence numbers from different nitrogen and closing date treatments (m^2)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	123	108	25	85 b
150	129	136	173	146 ab
250	309	98	203	203 a
Mean[2]	187 a	114 a	133 a	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	ns	*	ns	

[1] and [2] means sharing the same letter are not significantly different at P 0.05

Of the total inflorescences produced, however, very different percentages among treatments were actually harvested as ripe seed over the extended harvesting period. Hence very different percentages of inflorescences also remained as immature seed on the plant at final harvest in the different treatments. The percentage of harvested inflorescences declined as nitrogen rate increased (Figure 5.3), and conversely there were more immature inflorescences at the highest nitrogen rate for closing date, the medium closing had the greatest percentage of harvested inflorescences and the late closing the least (Figure 5.3).

It is interesting to note the number of old and new tillers which actually contributed to the total number of inflorescences produced, as shown in Table 5.12. As one would expect, old tillers made a major contribution to total inflorescence numbers at all closing dates. The early closing also allowed more time for new tillers to develop inflorescences compared with the other closing date (Table 5.12). The application of 150 kg/ha nitrogen also increased the inflorescence number from both old and new tillers, but these did not further increase when 250 kgN/ha was applied. The significant interaction between nitrogen and closing date also showed (Table 5.12 and Appendix 5.2).

Table 5.12 Comparison of mean inflorescence numbers produced by old and new tillers in different nitrogen and closing date treatments

Treatment effects	Inflorescence no. (no./m²)	
	Old tillers	New tillers
Nitrogen (kg/ha) -N		
50	232 b	29 b
150	339 a	76 a
250	339 a	120 a
sig.	*	**
Closing date - C		
Early	313 ab	173 a
Medium	350 a	48 b
Late	248 b	3 b
sig.	ns	****
NxC	ns	**

Means in each column which are followed by the same letter do not differ significantly at the 5% level

(b) Thousand seed dry weight (TSDW)

In terms of TSDW, late closing adversely affected this component significantly ($P<0.001$) while the early and medium closing treatments did not differ (Table 5.13). Application of nitrogen had no effect on TSDW.

Table 5.13 Mean TSDW at harvest from different nitrogen and closing date treatments (g)

Nitrogen (kg/ha)	Closing date: Early	Medium	Late	Mean[1]
50	6.0	6.3	5.6	6.0 a
150	6.1	6.0	5.5	5.9 a
250	6.2	6.1	5.4	5.9 a
Mean[2]	6.1 a	6.2 a	5.5 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	***	ns	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

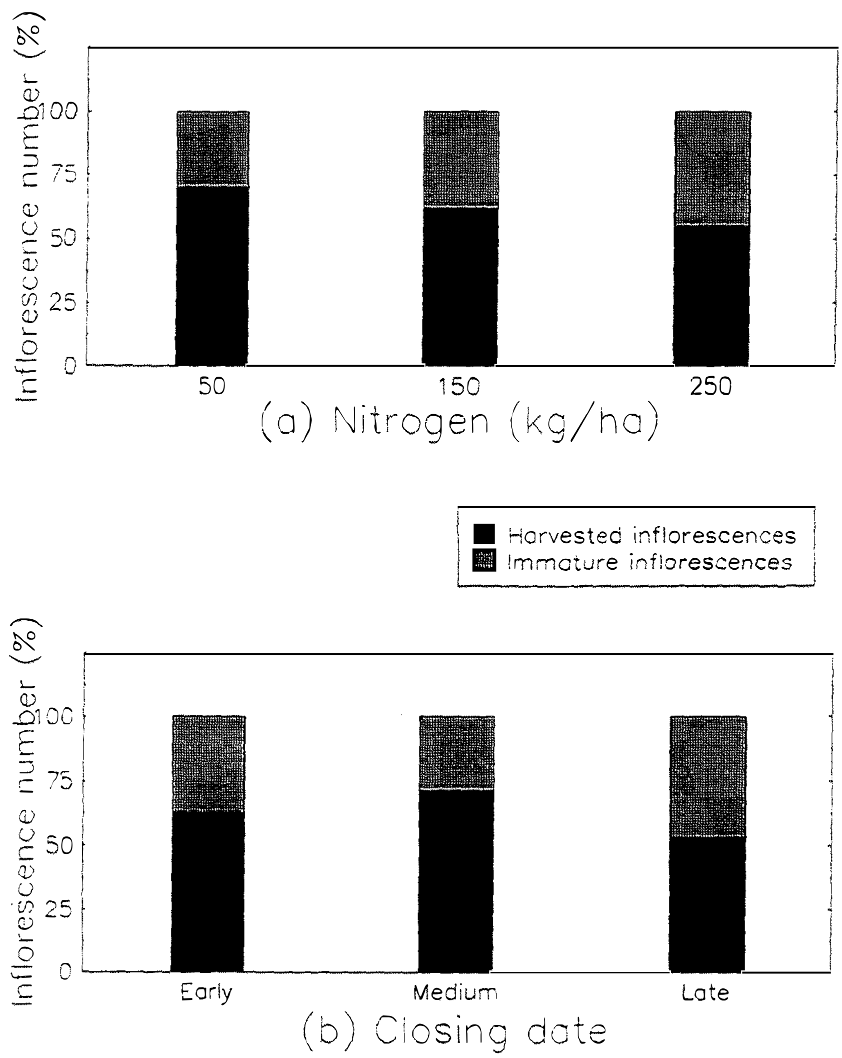


Figure 5.3 Effect of nitrogen fertilizer and closing date on percentage of harvested and immature inflorescences

(c) Floret numbers from harvested ripe inflorescences

Floret number per m^2 was dependent on closing date, being highest for the early closing and progressively decreasing as the closing date was delayed (Table 5.14). Application of 150 and 250 kg/nitrogen also significantly increased floret numbers.

The size of harvested ripe inflorescences (floret no./inflorescence) tended to increase with increasing nitrogen and decrease as closing was delayed (Figure 5.4).

Table 5.14 Mean total floret numbers at harvest from different nitrogen and closing date treatments (no./m^2)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	6533	6005	2850	5129 b
150	12973	11684	3560	9406 a
250	15638	9994	4031	9888 a
Mean[2]	11715 a	9228 b	3480 c	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	***	ns	

[1] and [2] means sharing the same letter are not significantly different at $P<0.05$

(d) Seed number

The total numbers of seeds harvested per m^2 is shown in Table 5.15. The number of seeds per unit area over the extended harvest period was significantly influenced by closing date ($P<0.01$), as late closing reduced seed number significantly compared with early and medium closing.

Application of 150 and 250 kg/ha nitrogen significantly increased seed number.

Table 5.15 Mean total number of seeds harvested from different nitrogen and closing date treatments (no./m^2)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	3696	3437	1570	2901 b
150	8029	7055	2249	5776 a
250	9288	5920	2585	5931 a
Mean[2]	7004 a	5471 a	2135 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	**	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

(e) Percentage seed set

Although the differences in the total number of seed between treatments were significant for late closing and low nitrogen (Table 5.15), there was no significant effect of closing date or nitrogen on the percentage seed set (Table 5.16).

Table 5.16 Mean percentage seed set from different nitrogen and closing date treatments (%)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	57.2	57.2	55.1	56.5 b
150	61.6	60.3	62.3	61.4 ab
250	59.2	58.8	63.7	60.6 ab
Mean[2]	59.3 a	58.8 a	60.4 a	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	ns	ns	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

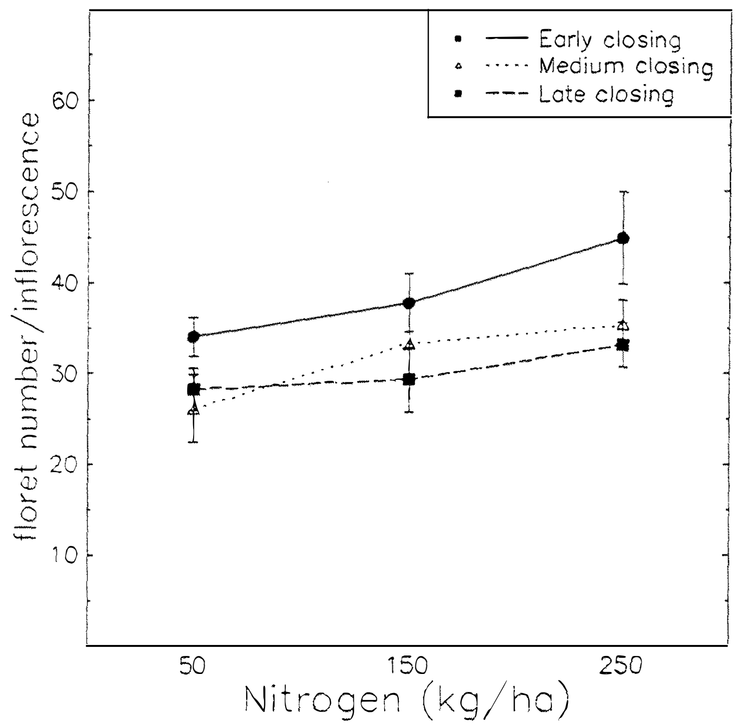


Figure 5.4 Effect of nitrogen fertilizer and closing date on floret number per inflorescence (harvested ripe inflorescence). Vertical bars indicate the standard error of the mean.

(f) Seed quality

The application of nitrogen and the different closing date treatments had no effect on the means for percentage pure germinating seed (Table 5.17). However, the significant interaction between nitrogen levels and closing dates indicated that the application of added nitrogen improved seed quality at early closing but depressed quality at late closing, particularly under high nitrogen levels (150 and 250 kg/ha).

Pure germinating seed yields were dependent on closing date, being highest in the early closing treatment and progressively decreasing as the closing date was delayed (Table 5.18). There was a significant increase in pure germinating seed yield between the nitrogen levels of 50 and 150 kg/ha, but further increasing the nitrogen applied to 250 kg/ha had no further significant increase.

Table 5.17 Mean percentage pure germinating seed from different nitrogen and closing date treatments (%)

Nitrogen (kg/ha)	Closing date			Mean[1]
	Early	Medium	Late	
50	20.0	31.7	36.7	29.4 a
150	38.3	28.3	16.7	27.8 a
250	51.7	41.7	18.3	37.2 a
Mean[2]	36.7 a	33.9 ab	23.9 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	ns	ns	*	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

The significant interaction effects for yield of PGS had a similar tendency to that which occurred in %PGS, where the combination of high nitrogen and early closing increasing the PGS yield (Table 5.18). Again, this mainly happened at the 150 to 250 kg N/ha applications. At the lowest nitrogen application rate, PGS yield was best at the medium closing. When nitrogen efficiency (kg seed/kg nitrogen applied) was calculated the most efficient response

(>1.0) came from the medium closing at the lowest nitrogen application rate (Figure 5.5). This was followed by the 150 kgN/ha rate for the early closing.

Table 5.18 Mean yield of Pure Germinating Seed from different nitrogen and closing date treatments (kg/ha)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	29.4	53.4	10.9	31.2 b
150	122.0	76.4	9.3	69.2 a
250	162.0	101.0	11.0	91.3 a
Mean[2]	104.4 a	77.0 b	10.4 c	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	***	**	

[1] and [2] means sharing the same letter are not significantly different at P≤0.05

5.3.3 Tiller development

Tiller numbers increased from the first cut to the early closing date but declined from then on (Table 5.19). Nitrogen application had no effect on tiller numbers at the first cut but 250 kgN/ha increased tillers numbers at the early closing and final harvest cut.

At the final harvest cut closing dates significantly influenced tiller numbers per m^2, being highest in the early closing treatment, lowest in the late closing treatment and intermediate in the medium closing treatment. However, the significant interaction recorded between nitrogen and closing date (Appendix 5.3) showed that added nitrogen resulted in a higher tiller numbers when applied at early closing but not at late closing.

The addition of 150 and 250 kgN/ha significantly increased total reproductive tiller number (Table 5.20). This was largely a reflection of the increase in both old and new reproductive tillers. However, only new reproductive tiller number increased significantly as additional nitrogen was applied. Total vegetative tiller numbers on the other hand did not increase as nitrogen was increased.

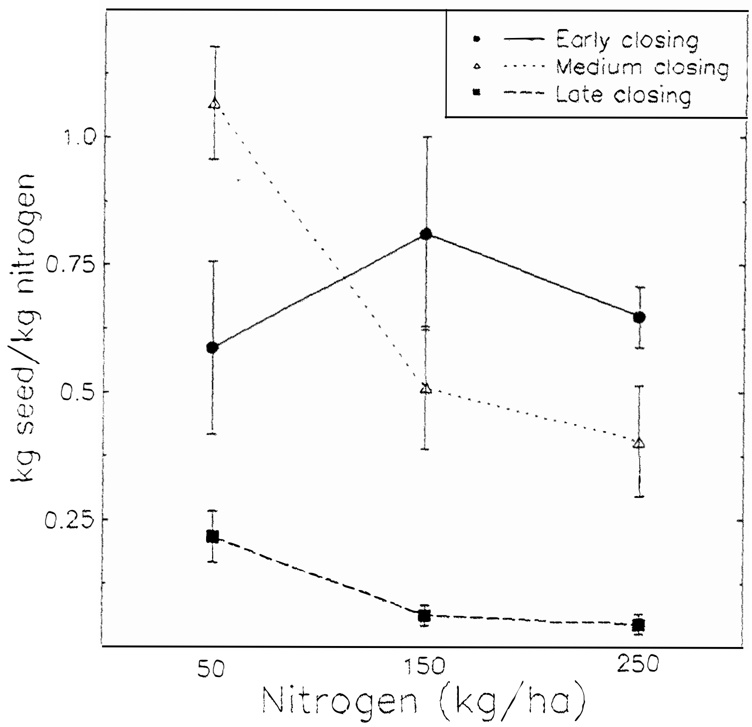


Figure 5.5 Effect of nitrogen fertilizer and closing date on nitrogen efficiency (kg pure germinating seed per kg nitrogen applied). Vertical bars indicate the standard error of the mean.

The early and medium closing treatments produced a significantly higher total reproductive tiller number than the late treatment (Table 5.20). The contribution to these results arose from new and old reproductive tillers, but only new reproductive tillers clearly showed a significant response to closing date, in that the earlier the closing date the more new reproductive tillers were produced.

An interaction between nitrogen application and closing date only occurred for new reproductive tiller numbers (Table 5.20 and Appendix 5.4), indicating that early closing and high nitrogen application stimulated new reproductive tiller production.

Table 5.19 Tiller numbers from different nitrogen and closing date treatments at the time of the first cut, at the early closing date and at the final cut

Treatments	Tiller numbers/m^2		
	1st cut	Early closing date	Final cut
Nitrogen (kg/ha)-N			
50	829 a	952 b	519 b
150	864 a	1075 b	564 b
250	803 a	1263 a	702 a
sig.	ns	**	***
Closing date -C			
Early	808 a	1054 b	688 a
Medium	798 a	1247 a	594 b
Late	890 a	988 b	503 c
sig.	ns	**	***
NxC	ns	ns	*

Means in each column which are followed by the same letter do not differ significantly at the 5% level

Table 5.20 Tiller partitioning between old and new vegetative and reproductive tillers at the final cut

Treatment effects	Tiller numbers/m^2					
	Vegetative tillers			Reproductive tillers		
	Total	New	Old	Total	New	Old
N (kg/ha) -N						
50	235 a	65 a	170 a	289 b	27 c	262 b
150	143 a	74 a	69 b	420 a	63 b	357 a
250	228 a	94 a	134 ab	472 a	121 a	353 ab
significance	ns	ns	*	**	****	ns
Closing date -C						
Early	196 a	93 a	103 a	491 a	159 a	332 ab
Medium	170 a	66 a	104 a	424 a	48 b	376 a
Late	239 a	73 a	166 a	268 b	3 c	265 b
significance	ns	ns	ns	***	****	ns
NxC	ns	ns	ns	ns	****	ns

Means in each column which are followed by the same letter do not differ significantly at the 5% level

5.3.4 Crop index and Harvest index

Similar patterns of response for crop index (Table 5.21) and the harvest index (Table 5.22) to nitrogen fertilizer application and closing treatments were obtained. Both indices were significantly increased by 150 kgN/ha but not beyond, and the early and medium closing treatment did not differ but were significantly greater than the late closing treatment.

Table 5.21 Crop index in different nitrogen and closing date treatments (%)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	1.00	1.46	0.24	0.89 b
150	1.96	1.72	0.33	1.34 a
250	1.42	1.36	0.34	1.04 ab
Mean[2]	1.45 a	1.51 a	0.30 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

Table 5.22 Harvest index in different nitrogen and closing date treatments (%)

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	2.67	5.86	1.39	3.31 b
150	6.11	7.69	2.39	5.40 a
250	4.18	6.95	2.89	4.47 ab
Mean[2]	4.32 a	6.83 a	2.02 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	*	ns	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

5.4 DISCUSSION

Many workers (Haggar, 1966; Boonman, 1971b; Bahnisch and Humphreys, 1977b; Loch, 1985; Humphreys and Riveros, 1986; Hill and Loch, 1993; Ramirez and Hacker, 1996) have stated that the tiller is the basic unit of development in the grass and high forage and seed yield require adequate tiller density.

The pattern of tiller development in this experiment (Table 5.19) was similar to that reported by others working with tropical grass (Haggar, 1966; Boonman, 1971b; Bahnisch and Humphreys, 1977b; Loch, 1985) i.e. a steady increase in number from the early vegetative stage to a peak at or near the onset of reproductive development and then a decline during the seeding stage. During this period, up to the early closing date and onset of reproductive development, application of additional nitrogen fertiliser produced a significant response in tiller numbers per unit area which no doubt contributed significantly to the linear response to nitrogen in terms of herbage production (Table 5.3).

However, there is not a great deal of information specifically in Ruzi grass with regard to tiller density and seed yield, nor on the relationship between these two components. Skerman and Riveros (1990) state an average figure of 125 kg of seed/ha obtained from Ruzi grass grown in Queensland, while Brunse and Sukpituksakul (1992) in Thailand recorded field-harvested seed yield ranging, in a linear feature, from 229 kg/ha (or 82 kg/ha of pure live seed) from a fertile tiller population of 154 seedheads/m^2 to 349 kg/ha (or 174 kg/ha of pure live seed) from a fertile tiller population of 247 seedheads/m^2.

In the current experiment with a daily seed harvest over a 2-3 week period, it was not possible to compare the results obtained with those from the normal practice of a single harvest mentioned above. Obviously, seed yield in this study would have been less than the data recorded if seed harvest had been used because of the need to compromise between some loss due to seed shedding from the early formed inflorescences, and maximising seed recovery from the remaining mature inflorescences. In fact, an optimum time for seed harvesting and also seed processing after seed harvest are critical factors in determining seed yield and seed quality, but these were not directly applicable in this study.

It is clear that there was a very strong and positive relationship between seed yield and inflorescence number (Figure 5.2). Similarly, Humphreys and Riveros (1986) noted that nitrogen fertilizer had a pronounced effect on seed yield mainly through increasing inflorescence density as has been reported in other tropical and subtropical grasses. Hence it is extremely important to encourage vegetative tiller production well prior to closing for seed production, particularly as it is the older reproductive tillers that contribute most to seed yield - as is well known for many temperate grasses and legumes (Hill, 1971; Marshall, 1985; Evans *et al.*, 1986; Bullitta *et al.*, 1989).

Encouraging tiller production is not only important for seed production but also for herbage production, as shown in the defoliation study reported in Chapter 4. Hence by adopting appropriate defoliation practices which encourage tillering, farmers are able to obtain more herbage production for livestock and subsequently higher seed production. The results also show that at the final harvest cut - following the extended period of daily seed harvesting - there was still a significant population of immature inflorescences yet to develop, representing 30-50% of the total fertile tiller population (particularly in the late closing treatment receiving higher levels of fertilizer nitrogen) which made no contribution to seed yield (Figure 5.3). Obviously this highlights the need for a concerted selection/breeding programme to try and synchronise seed production into a narrower time frame and thereby reduce the present restriction to higher seed yields due to the very extended reproductive period. Apart from the behaviour of the plant itself, this response may also be due to the environmental effects involved, such as photoperiod. Decreasing photoperiod may prolong flowering period because Ruzi grass is a quantitative short day plant (Dirven *et al.*, 1979). In addition, as water was not limited in this experiment the new tillers continued emerging and became reproductive.

The significance of nitrogen fertilizer in stimulating tillering prior to closing is also important and clearly seen in the results where a significant response to 250 kg N/ha was recorded at the early closing of the final cut after seed harvest (Table 5.19). This no doubt accounted significantly to the sizeable linear herbage response recorded, particularly in the closing treatment (Table 5.3) - although it is recognised that there is no accurate prediction for the herbage yield relationship with tillering as reported by Ivory and Whiteman (1978).

However in terms of seed yield the application of up to 150 kg N/ha was sufficient to meet the requirements for seed production as there was no further response to 250 kg N/ha (Table 5.8). This is explained in terms of the identical stimulus in the number of old tillers to these two upper levels of nitrogen (Table 5.12) - as it is recognised in many grass species, both temperate and tropical, that it is the early formed or older tillers that make the major contribution to seed yield (Haggar, 1966 in *Andropogon gayanus*; Hill, 1971 in *Lolium perenne* L.; Bahnisch and Humphreys, 1977b in *Setaria anceps* cv. Narok). As Humphreys and Riveros (1986) explained, these early-formed tillers have an advantage in size and preferential position in the crop for light and nutrients. In contrast the significant increase recorded in new reproductive tiller production even at 250 kg N/ha did not serve to contribute to seed yield as shown in terms of unharvested inflorescences (Table 5.11).

In some tropical grasses, (e.g. *Chloris gayana* (Loch, 1983)) if there is a considerable delay before tillering activity is renewed during the reproductive phase, then aerial tillers can develop on basal tillers but these generally contribute little to mature seed crops. Ruzi grass also behaves similarly in this regard, particularly if there is a long duration from closing to seed harvest, but it did not occur in this study even for the early closing treatment. Plants produced more new tillers rather than aerial tillers. This result is probably due to the cutting at or near the reproductive stage. This removal of plant material so that more light can penetrate to the base of plant encouraged more new tillers.

As noted by Humphreys and Riveros (1986), the nature of the response curve to additional rates of nitrogen fertiliser applied is a steep increase in yield followed by a diminishing rate of response as maximum yield is approached and further addition of nitrogen may cause a reduction in seed yield. This was also indicated in the current experiment where plants were very responsive to nitrogen supply up to 150 kg N/ha but showed no further response to 250 kg N/ha (Table 5.8). The possibility of a reduction in seed yield if even further nitrogen had been applied could not be confirmed.

In terms of efficiency of nitrogen use i.e. the kg of seed produced per kg of N applied, the lowest application rate proved the most efficient and the highest least efficient (2.28, 1.44, 0.85 kg seed per kg N at the 50, 150 and 250 kg N/ha respectively), and this also occurred for each closing. Similar seed yield responses to nitrogen fertiliser were also recorded by Cameron and Humphreys (1976) working with *Paspalum plicatulum,* although other workers (Harlan *et al.*, 1966; Carmeron and Mullaly, 1969; Mendoza *et al.*, 1975; Gomez *et al.,* 1978; Sarroca *et al.*, 1980) reported greater efficiencies of nitrogen use at higher rather than lower rates of nitrogen fertilizer application. However a comparison of these results with those from other trials is not valid, because in no case was the amount of nitrogen available to the plant from the soil before any nitrogen applications measured.

Humphreys and Riveros (1986) also pointed out that the increase in grass seed yield in response to nitrogen fertilizer may be due to nitrogen producing a leafier, dense sward with higher photosynthetic capacity, capable of supporting a higher density of tillers and also lead to an increase in the proportion of fertile tillers. This increase in the proportion of fertile tillers from added nitrogen has also been reported by several workers (Henzell and Oxenham, 1964; Cameron and Humphreys, 1976; Bahnisch and Humphreys, 1977a; Mecelis and Oliveira, 1984; Ramirez and Hacker, 1996) although Loch (1983) found that this effect also varied considerably between grass species. In contrast Wong and Wilson (1980) working with *Panicum maximum* var. *trichoglume* and Ramirez and Hacker, (1996) working with *Digitaria eriantha* cv. Premier reported a depression in fertile tiller numbers due to shading from excessive forage dry matter produced by high nitrogen application.

The significance of closing date in affecting harvested seed yield is also clearly shown in the results with the early and medium closing dates being similar and vastly superior to late closing (Table 5.8). Although the respective treatments were managed identically prior to closing there was a significant decline in tiller numbers in the late closing treatment but only new reproductive tillers were affected (Table 5.20). The major contribution of old reproductive tillers has already been noted, but the late closing produced significantly lower harvested inflorescence numbers when compared with earlier closing treatments (Table 5.10). This resulted in the major drop in seed yield due, no doubt, to the defoliation and weakening of old developing tillers at the late closing defoliation - as the common problem in practice of seed shedding was avoided in this study. Again it is also interesting to note that although the early closing treatment allowed more time for significantly more new reproductive tillers to develop (Table 5.20), particularly at the highest nitrogen level up to the final cut, this gave no boost to seed production when compared with the medium closing treatment which produced fewer new reproductive tillers but yielded the same quantity of seed (Table 5.8).

When one examines the treatment effects on seed components they show that floret numbers at harvest were progressively and significantly higher the earlier the closing date (Table 5.14 and Figure 5.4). This is likely due to the larger inflorescence size produced, as there were 39, 32 and 30 florets/inflorescence from early, medium and late closing respectively. This advantage of early closing may exist because of a longer duration of vegetative growth (Table 5.4) which because reproductive tillers were initiated earlier, they provide a longer time for floret initiation, hence more florets. Other workers have found that early-emerged tillers had larger inflorescences than late-emerged tillers (Chadhokar and Humphreys, 1973a; Hill and Watkin, 1975; Ramirez and Hackar, 1996). In terms of actual numbers of seeds fertilised and harvested in the three closing date treatments the early and medium closing treatment were clearly superior to late closing in this respect (Table 5.15).

The same type of response was also apparent from additional nitrogen application i.e. floret number was progressively and significantly higher in the higher fertilizer level, but the numbers of seed harvested, although showing the some trend, were not significantly increased beyond the 150 kg N/ha level (Table 5.15). Both higher rates of application were clearly superior to the lowest nitrogen treatment.

In other words, early closing of the sward for seed production plus high nitrogen application encouraged the greatest development of florets. The medium closing date also encouraged a similarly high production of fertilised seeds, at least up to 150 kg N/ha applied, as percentage seed set was virtually the same across all treatments (Table 5.16). Late closing on the other hand severely depressed both floret numbers and fertilised seed numbers particularly when lacking adequate nitrogen. The negative effect that late closing had on seed yield of Ruzi grass was mostly associated with decrease in harvested inflorescences. This cutting removed reproductive apices which would normally produce the largest inflorescences and would have accounted for the major part of the harvest. In addition the residual basal tillers and new tillers were often deeply shaded and rudimentary, and so for both these reasons seed yield potential was reduced. However, such phenomenon may be an advantage in other grass species. Bahnisch (1975) found that in *Setaria sphacelata* var. *sericea* cv. Narok, cutting increased tillering and seed yield. Application of higher nitrogen (150 and 250 kg/ha) had progressively increased inflorescence numbers during the late closing (Table 5.9), but almost 60% were immature inflorescences (Figure 5.3a). As mentioned earlier, these inflorescences were later formed and required a longer period to be ready for harvest.

Boonman (1972a) found that in *Setaria sphacelata* cv. Nandi II the relative reduction in seed set of an early closing treatment which had received a high level of nitrogen, when compared with its high potential in floret numbers may have been due to an increase in head length leading to prolonged flowering and therefore reduced seed set. But this did not occur in Ruzi grass as the percentage seed set was not affected by nitrogen or closing date (Table 5.16). In practice a negative effect of high nitrogen on seed set can also be a consequence of crop lodging as reported by Hebblethwaite *et al.* (1978) in *Lolium perenne*, Ramirez and Hacker (1994) in *Digitaria erianthua* cv. Premier although this does not always occur (e.g. Cameron and Mullaly (1969) in *Cenchrus ciliaris*, Ramirez and Hacker (1996) in *Digitaria erianthua* cv. Premier). These different responses are likely to occur due to the stage of plant growth when the lodging begins. If it occurs at or before anthesis, it has potentially caused an unfavourable environment for pollination and seed development, which may result in low seed set, but if it occurs at a later stage in seed development, it has less effect. Moreover, environmental factors may cause more damage to plants. For example, continuous rain during flowering reduces cross-pollination and thus seed set (Dennis, 1984). However, in this study such effects, particularly crop lodging, did not occur as the swards were physically supported by frames.

The relatively high percentage of seed set achieved (55-63%) is considered very favourable when one reads the comments of Ferguson and Crowder (1974) who regarded a 30%

seed set as high frequency at cross-fertilisation for Ruzi grass. The advantage in this aspect may arise from the daily inflorescence harvest and also under the controlled environment which reduced pollen loss from wind.

In terms of thousand seed weight (Table 5.13), only seed from the late closing treatment was significantly lighter. Late-emerged inflorescences from this late closing developed in less favourable conditions for pollination, and seed development occurred on plants which mainly were smaller when compared with earlier closing plants and probably had a reduced assimilate supply to the inflorescence. Humphreys and Riveros (1986) noted that the green surfaces of the inflorescence and its supporting stem contribute significantly to the assimilate demands of the developing seeds. Then the adverse effects of late grazing or cutting may occur as having been caused by decreased photosynthetic rate. Added nitrogen failed to have any effect on this component as agreeing with reports for other tropical grasses (Hacker and Jones, 1971; Boonman, 1972a; Bahnisch and Humphreys, 1977a; Ramirez and Hacker, 1996), but in disagreement for the others (Chadhokar and Humphreys, 1973b; Cameron and Humphreys, 1976).

The summary data reflected in the crop (Table 5.21) and harvest indices (Table 5.22) again clearly show that the seed producers must close their Ruzi pasture for seed production earlier (early or medium closing) rather than later and must apply relatively high levels of nitrogen fertiliser, at least up to 150 kg N/ha, if they are to achieve high seed yields.

However, in spite of all these recorded effects on seed yield and its components, the ultimate measure of success must surely be in the yield of pure germinating seed (Table 5.18). Obviously the buyer, normally the farmers who are keen to develop pasture for animal production, are only interested in viable seed in order to achieve their desired end. In this regard it is rather disappointing, although interesting to note, the relatively poor seed quality recorded in many of the treatments. The results showed that both nitrogen application and closing had not significantly affected percentage germination of Ruzi grass (Table 5.17). In agreement with these results, percentage germination of *Digitaria eriantha* cv. Premier (Ramirez and Hacker,

1994) seed did not differ among nitrogen application treatments. In contrast, Chadhokar (1971), Chadhokar and Humphreys (1973b), and Carmo *et al.* (1988) reported a germination increase for *Paspalum plicatulum*, *Paspalum plicatulum* and *Brachiaria decumbens* respectively. Cameron and Humphreys (1976), on the other hand, reported a reduction in germination of *Paspalum plicatulum* seed. Like the earlier the closing date, the higher the percentage of pure germinating seed occurred, but it failed to show significant differences between treatments (Table 5.17). The variable germination percentage, ranging from 18-52% in this study, indicates that other factors e.g. dormancy, uneven seed maturity, and/or non-viable seed, are likely associated with these treatments (nitrogen and closing). Nonetheless, there was a significant interaction affect between nitrogen and closing treatment, these suggested that the earlier closing with at least 150 kg/ha nitrogen application would expect high percentage seed germination, but under low nitrogen (50 kg/ha) the later closing preferred.

As nitrogen application did not directly affect seed germination (Table 5.17), pure germinating seed yield, therefore, showed a similar trend with the same seed yield when application of nitrogen was 150 or 250 kg/ha, both being significantly higher than the lowest application (Table 5.18). However, seed germination played an important role for the different closing treatments, even though there was a similar response when compared with nitrogen effect. Pure germinating seed yields were progressively increased as earlier the closing concerned (Table 5.18). This result is different when compared with seed yield response (Table 5.8) as being no significant differences either early or medium closing occurred. The interaction between nitrogen and closing may likely to be the case (Tables 5.17, 5.18) as resulted in this regard.

This ultimate measure of superiority in the current study i.e. the yield of pure germinating seed (Table 5.18) clearly shows that the farmers must ensure an early closing of their seed crop and application of high levels of nitrogen fertiliser, in this case 250 kg N/ha, if they are to achieve real success. However, in terms of economic point of view regarding the relationship between PGS production and nitrogen levels applied at early closing (Figure 5.5), the results indicate that the medium nitrogen level (150 kg/ha) provided the most effective PGS kg seed production per kg N applied (0.588, 0.813, and 0.648 from 50, 150, and 250 kg N/ha, respectively). In fact, the medium closing with the lowest nitrogen application (Figure 5.5) was the most efficient for pure germinating seed yield overall (1.068) but production per hectare was very low. Accordingly, therefore, the price of seed and also nitrogen fertilizer in the market are the major parameters to be considered when deciding which options should be the best to maximise profit. In addition, the herbage yield after the seed harvest should also be taken into account.

As mentioned earlier, this experiment with its daily seed harvesting method, preventing plant lodging and planting under controlled environment produced results which may not be directly transferable to a field situation. Under field conditions, it is still highly necessary to have more information, particularly regarding when and how to harvest, and further information on seed processing after harvest, as these are important factors for enhancing the improvement of seed production.

5.5 CONCLUSION

Herbage dry matter production prior to closing increased progressively as increasing levels of nitrogen were applied. This nitrogen effect was carried on through reproductive growth so that the 250 kg N/ha treatment still had significantly more dry matter after seed harvest, but there was no significant difference between the 50 and 150 kg N/ha rates. In contrast, closing date did not significantly affect dry matter production, because plant growth declined when plants were approaching the reproductive stage, especially for the medium and late closing treatments. However, as expected, the earlier the closing the more herbage dry matter was obtained after seed harvest, the major contributory being new and old reproductive tillers. Tiller numbers increased up to the early closing and then declined after seed harvest. The response to nitrogen and closing date of tillers after seed harvest were parallel to herbage dry matter production.

Nitrogen application increased seed yield up to 150 kg/ha mainly through increasing total and harvested ripe inflorescence density, floret numbers, and seed numbers; but it had no effect on seed weight and percentage seed set. Early and medium closing produced significantly greater seed yields than the late closing mainly through the effects on total and harvested ripe inflorescence density, seed numbers, and seed weight. Moreover, the earlier the closing the bigger the inflorescence size (floret number/inflorescence) obtained.

The interaction between nitrogen and closing (Table 5.17) tended to show that the higher nitrogen applied at early closing, the greater percentage of pure germinating seed. Consequently, a higher pure germinating seed yield (Table 5.18) was associated with the application of 150 kg N/ha at the early closing date, and this was the most efficient high quality seed yield response.

CHAPTER 6

EFFECTS OF WATER STRESS ON SEED PRODUCTION IN RUZI GRASS

6.1 INTRODUCTION

The major environmental factors which influence plant growth and development include solar radiation (or net radiation), air temperature, air water vapour content, wind speed, soil temperature and soil water availability (Barfield and Norman, 1983). In this regard water deficits probably limit global crop productivity more than any other stress factor (Fischer and Turner, 1978; Boyer, 1982), although the reproductive failure under water stress is not directly due to lack of moisture but because of inadequate essential nutrients supplied or an inhibitory substance produced by the plant (Boyer, 1992). However, the extent to which it damages the plant depends not only on the nature and extent of the deficit, but also on the developmental stage of the plant at when it occurs.

Many cash crops such as grain, fruit, nut, and vegetable are more susceptible to losses from limited water during reproductive development than at any other stage (Salter and Goode, 1967; Claassen and Shaw, 1970). Day (1981) also noted that the physiological responses observed, and their relative importance for crop productivity, varied with species, soil type, nutrients and climate.

Many workers have pointed out that grain yield of wheat, barley, and oats was most sensitive to drought during and just before ear emergence (Salter and Goode, 1967; Dubetz and Bole, 1973; Fischer, 1973). In Day *et al.*'s (1978) study on spring barley, the number of grains per ear was related to the water deficit in the first six weeks of growth when the ear was developing; the number of ears to the deficit in the next period, up to anthesis, when tiller numbers were declining; and grain mass to the deficit in the grain filling period. For rice and maize grain yields, two distinct peaks of sensitivity have been reviewed by Saini and Lalonde (1998). The first peak occurs during meiosis which is similar in wheat, barley and oats, but is more conspicuous in rice (Namuco and O'Toole, 1986) than in maize (Moss and Downey, 1971).

However, both rice and maize show a second peak of extreme sensitivity to water deficit at anthesis and during the initial stages of grain development (Hsiao, 1982; O'Toole and Namuco, 1983; Ekanayake *et al.*, 1990).

In other grasses, Hebblethwaite (1977) reported in ryegrass studies that a water deficit before stem elongation causes a decrease in seed yield of ryegrass by reducing seedhead numbers, but after this stage a water deficit of less than 100 mm had little effect on floret site utilisation, and seed yields of over 2000 kg/ha can be obtained (Rolston *et al.*, 1994). Lambert (1967) found in timothy (*Phleum pratense*) studies that thousand seed weight could be decreased if moisture stress was applied after anthesis, probably due to a reduction in photosynthetic area and capacity. Many of these effects of water stress in plant characteristics have been well presented in the excellent review by Turner (1997). Unfortunately, little detailed research on these aspects in tropical grasses has been published, although some more general studies have shown that timely irrigation can possibly support the realization of seed yield potential and benefit to the seed industry (in *Cynodon dactylon* by Ahring *et al.* (1974); in *Cenchus ciliaris* cv. Biloela by Sarroca *et al.* (1981)). However, in Ruzi grass (*Brachiaria ruziziensis*), no detailed publications could be found relating to the direct effects of water deficit stress on seed production although Skerman and Riveros (1990) did emphasize the general need for reasonably high rainfall (1000 mm or more) in plant development of this species and noted that it had "good drought tolerance".

Therefore, the objective of this study was decided to investigate this aspect in some details with Ruzi grass, to determine the effects of different levels of water deficit stress applied at different stages of reproductive development on seed yield, yield components and seed quality in Ruzi grass, particularly in view of the fact that, in Thailand - which is of particular interest to the author - seed development occurs towards the end of the rainy season when changeable rainfall patterns could well lead to short-term periods of water deficit stress over one or more of these reproductive stages.

5.4 DISCUSSION

Many workers (Haggar, 1966; Boonman, 1971b; Bahnisch and Humphreys, 1977b; Loch, 1985; Humphreys and Riveros, 1986; Hill and Loch, 1993; Ramirez and Hacker, 1996) have stated that the tiller is the basic unit of development in the grass and high forage and seed yield require adequate tiller density.

The pattern of tiller development in this experiment (Table 5.19) was similar to that reported by others working with tropical grass (Haggar, 1966; Boonman, 1971b; Bahnisch and Humphreys, 1977b; Loch, 1985) i.e. a steady increase in number from the early vegetative stage to a peak at or near the onset of reproductive development and then a decline during the seeding stage. During this period, up to the early closing date and onset of reproductive development, application of additional nitrogen fertiliser produced a significant response in tiller numbers per unit area which no doubt contributed significantly to the linear response to nitrogen in terms of herbage production (Table 5.3).

However, there is not a great deal of information specifically in Ruzi grass with regard to tiller density and seed yield, nor on the relationship between these two components. Skerman and Riveros (1990) state an average figure of 125 kg of seed/ha obtained from Ruzi grass grown in Queensland, while Brunse and Sukpituksakul (1992) in Thailand recorded field-harvested seed yield ranging, in a linear feature, from 229 kg/ha (or 82 kg/ha of pure live seed) from a fertile tiller population of 154 seedheads/m^2 to 349 kg/ha (or 174 kg/ha of pure live seed) from a fertile tiller population of 247 seedheads/m^2.

In the current experiment with a daily seed harvest over a 2-3 week period, it was not possible to compare the results obtained with those from the normal practice of a single harvest mentioned above. Obviously, seed yield in this study would have been less than the data recorded if seed harvest had been used because of the need to compromise between some loss due to seed shedding from the early formed inflorescences, and maximising seed recovery from the remain mature inflorescences. In fact, an optimum time for seed harvesting and also seed processing after seed harvest are critical factors in determining seed yield and seed quality, but these were not directly applicable in this study.

It is clear that there was a very strong and positive relationship between seed yield and inflorescence number (Figure 5.2). Similarly, Humphreys and Riveros (1986) noted that nitrogen fertilizer had a pronounced effect on seed yield mainly through increasing inflorescence density as has been reported in other tropical and subtropical grasses. Hence it is extremely important to encourage vegetative tiller production well prior to closing for seed production, particularly as it is the older reproductive tillers that contribute most to seed yield - as is well known for many temperate grasses and legumes (Hill, 1971; Marshall, 1985; Evans *et al.*, 1986; Bullitta *et al.*, 1989).

Encouraging tiller production is not only important for seed production but also for herbage production, as shown in the defoliation study reported in Chapter 4. Hence by adopting appropriate defoliation practices which encourage tillering, farmers are able to obtain both herbage production for livestock and subsequently seed production. The results also show that at the final harvest cut - following the extended period of daily seed harvesting - there was still a significant population of immature inflorescences yet to develop, representing 30-50% of the total fertile tiller population (particularly in the late closing treatment receiving higher levels of fertilizer nitrogen) which made no contribution to seed yield (Figure 5.3). Obviously this highlights the need for a concerted selection/breeding programme to try and synchronise seed production into a narrower time frame and thereby reduce the present restriction to higher seed yields due to the very extended reproductive period. Apart from the behaviour of the plant itself, this response may also be due to the environmental effects involved, such as photoperiod. Decreasing photoperiod may prolong flowering period because Ruzi grass is a quantitative short day plant (Dirven *et al.*, 1979). In addition, as water was not limited in this experiment the new tillers continued emerging and became reproductive.

The significance of nitrogen fertilizer in stimulating tillering prior to closing is also important and clearly seen in the results where a significant response to 250 kg N/ha was recorded at the early closing of the final cut after seed harvest (Table 5.19). This no doubt accounted significantly to the sizeable linear herbage response recorded, particularly in the closing treatment (Table 5.3) - although it is recognised that there is no accurate prediction for the herbage yield relationship with tillering as reported by Ivory and Whiteman (1978).

However in terms of seed yield the application of up to 150 kg N/ha was sufficient to meet the requirements for seed production as there was no further response to 250 kg N/ha (Table 5.8). This is explained in terms of the identical stimulus in the number of old tillers to these two upper levels of nitrogen (Table 5.12) - as it is recognised in many grass species, both temperate and tropical, that it is the early formed or older tillers that make the major contribution to seed yield (Haggar, 1966 in *Andropogon gayanus*; Hill, 1971 in *Lolium perenne* L.; Bahnisch and Humphreys, 1977b in *Setaria anceps* cv. Narok). As Humphreys and Riveros (1986) explained, these early-formed tillers have an advantage in size and preferential position in the crop for light and nutrients. In contrast the significant increase recorded in new reproductive tiller production even at 250 kg N/ha did not serve to contribute to seed yield as shown in terms of unharvested inflorescences (Table 5.11).

In some tropical grasses, (e.g. *Chloris gayana* (Loch, 1983)) if there is a considerable delay before tillering activity is renewed during the reproductive phase, then aerial tillers can develop on basal tillers but these generally contribute little to mature seed crops. Ruzi grass also behaves similarly in this regard, particularly if there is a long duration from closing to seed harvest, but it did not occur in this study even for the early closing treatment. Plants produced more new tillers rather than aerial tillers. This result is probably due to the cutting at or near the reproductive stage. This removal plant material so that more light can penetrate to the base of plant and encourage more new tillers.

As noted by Humphreys and Riveros (1986), the nature of the response curve to additional rates of nitrogen fertiliser applied is a steep increase in yield followed by a diminishing rate of response as maximum yield is approached and further addition of nitrogen may cause a reduction in seed yield. This was also indicated in the current experiment where plants were very responsive to nitrogen supply up to 150 kg N/ha but showed no further response to 250 kg N/ha (Table 5.8). The possibility to a reduction in seed yield if even further nitrogen had been applied could not be confirmed.

In terms of efficiency of nitrogen use i.e. the kg of seed produced per kg of N applied, the lowest application rate proved the most efficient and the highest least efficient (2.28, 1.44, 0.85 kg seed per kg N at the 50, 150 and 250 kg N/ha respectively), and this also occurred for each closing. Similar seed yield responses to nitrogen fertiliser were also recorded by Cameron and Humphreys (1976) working with *Paspalum plicatulum,* although other workers (Harlan *et al*., 1966; Carmeron and Mullaly, 1969; Mendoza *et al.*, 1975; Gomez *et al.,* 1978; Sarroca *et al*., 1980) reported greater efficiencies of nitrogen use at higher rather than lower rates of nitrogen fertilizer application. However a comparison of these results with those from other trials is not valid, because in no cases was the amount of nitrogen available to the plant from the soil before any nitrogen applications provided.

Humphreys and Riveros (1986) also pointed out that the increase in grass seed yield in response to nitrogen fertilizer may be due to nitrogen producing a leafier, dense sward with higher photosynthetic capacity, capable of supporting a higher density of tillers and also lead to an increase in the proportion of fertile tillers. This increase in the proportion of fertile tillers from added nitrogen has also been reported by several workers (Henzell and Oxenham, 1964; Cameron and Humphreys, 1976; Bahnisch and Humphreys, 1977a; Mecelis and Oliveira, 1984; Ramirez and Hacker, 1996) although Loch (1983) found that this effect also varied considerably between grass species. In contrast Wong and Wilson (1980) working with *Panicum maximum* var. *trichoglume* and Ramirez and Hacker, (1996) working with *Digitaria eriantha* cv. Premier reported a depression in fertile tiller numbers due to shading from excessive forage dry matter produced by high nitrogen application.

The significance of closing date in affecting harvested seed yield is also clearly shown in the results with the early and medium closing dates being similar and vastly superior to late closing (Table 5.8). Although the respective treatments were managed identically prior to closing there was a significant decline in tiller numbers in the late closing treatment but only new reproductive tillers were affected (Table 5.20). The major contribution of old reproductive tillers has already been noted, but the late closing produced significantly lower harvested inflorescence numbers when compared with earlier closing treatments (Table 5.10). This resulted in the major drop in seed yield due, no doubt, to the defoliation and weakening of old developing tillers at the late closing defoliation - as the common problem in practice of seed shedding was avoided in this study. Again it is also interesting to note that although the early closing treatment allowed more time for significantly more new reproductive tillers to develop (Table 5.20), particularly at the highest nitrogen level up to the final cut, this gave no boost to seed production when compared with the medium closing treatment which produced fewer new reproductive tillers but yielded the same quantity of seed (Table 5.8).

When one examines the treatment effects on seed components they show that floret numbers at harvest were progressively and significantly higher the earlier the closing date (Table 5.14 and Figure 5.4). This is likely due to the larger inflorescence size produced, as there were 39, 32 and 30 florets/inflorescence from early, medium and late closing respectively. This advantage of early closing may exist because of a longer duration of vegetative growth (Table 5.4) which because reproductive tiller were initiated earlier, provide a longer time for floret initiation, hence more florets. Other workers have found that early-emerged tillers had larger inflorescences than late-emerged tillers (Chadhokar and Humphreys, 1973a; Hill and Watkin, 1975; Ramirez and Hackar, 1996). In terms of the actual numbers of seeds fertilised and harvested in the three closing date treatments the early and medium closing treatment were clearly superior to late closing in this respect (Table 5.15).

The same type of response was also apparent from additional nitrogen application i.e. floret number was progressively and significantly higher in the higher fertilizer level, but the numbers of seed harvested, although showing the some trend, were not significantly increased beyond the 150 kg N/ha level (Table 5.15). Both higher rates of application were clearly superior to the lowest nitrogen treatment.

In other words, early closing of the sward for seed production plus high nitrogen application encouraged the greatest development of florets. The medium closing date also encouraged a similarly high production of fertilised seeds, at least up to 150 kg N/ha applied, as percentage seed set was virtually the same across all treatments (Table 5.16). Late closing on the other hand severely depressed both floret numbers and fertilised seed numbers particularly when lacking adequate nitrogen. The negative effect that late closing had on seed yield of Ruzi grass was mostly associated with decrease in harvested inflorescences. This cutting removed reproductive apices which would normally produce the largest inflorescences and would have accounted for the major part of the harvest. In addition the residual basal tillers and new tillers were often deeply shaded and rudimentary, and so for both these reasons seed yield potential were reduced. However, such phenomenon may be an advantage in other grass species. Bahnisch (1975) found that in *Setaria sphacelata* var. *sericea* cv. Narok, cutting increased tillering and seed yield. Application of higher nitrogen (150 and 250 kg/ha) had progressively increased inflorescence numbers during the late closing (Table 5.9), but almost 60% were immature inflorescences (Figure 5.3a). As mentioned earlier, these inflorescences were later formed and required a longer period to be ready for harvest.

Boonman (1972a) found that in *Setaria sphacelata* cv. Nandi II the relative reduction in seed set of an early closing treatment which had received a high level of nitrogen, when compared with its high potential in floret numbers may have been due to an increase in head length leading to prolonged flowering and therefore reduced seed set. But this did not occur in Ruzi grass as the percentage seed set was not affected by nitrogen or closing date (Table 5.16). In practice a negative effect of high nitrogen on seed set can also be a consequence of crop lodging as reported by Hebblethwaite *et al.* (1978) in *Lolium perenne*, Ramirez and Hacker (1994) in *Digitaria erianthua* cv. Premier although this does not always occur (e.g. Cameron and Mullaly (1969) in *Cenchrus ciliaris*, Ramirez and Hacker (1996) in *Digitaria erianthua* cv. Premier). These different responses are likely to occur due to the stage of plant growth when the lodging begins. If it occurs at or before anthesis, it has potentially caused an unfavourable circumstance for pollination and seed development, which may result in low seed set, but if it occurs at a later stage in seed development, it has less effect. Moreover, environmental factors may cause more damage to plants. For example, continuous rain during flowering reduces cross-pollination and thus seed set (Dennis, 1984). However, in this study such effects, particularly crop lodging, did not occur as the swards were physically supported by frames.

The relatively high percentage of seed set achieved (55-63%) is considered very favourable when one reads the comments of Ferguson and Crowder (1974) who regarded a

30% seed set as high frequency at cross-fertilisation for Ruzi grass. The advantage in this aspect may arise from the daily inflorescence harvest and also under the controlled environment which reduced pollen loss from wind.

In terms of thousand seed weight (Table 5.13), only seed from the late closing treatment was significantly lighter. Late-emerged inflorescences from this late closing developed in less favourable conditions for pollination and seed development occurred on plants which mainly were smaller when compared with earlier closing plants and probably had a reduced assimilate supply to the inflorescence. Humphreys and Riveros (1986) noted that the green surfaces of the inflorescence and its supporting stem contribute significantly to the assimilate demands of the developing seeds. Then the adverse effects of late grazing or cutting may occur as having been caused by decreased photosynthetic rate. Added nitrogen failed to have any effect on this component as in agreement with report for other tropical grasses (Hacker and Jones, 1971; Boonman, 1972a; Bahnisch and Humphreys, 1977a; Ramirez and Hacker, 1996), but in disagreement for the others (Chadhokar and Humphreys, 1973b; Cameron and Humphreys, 1976).

The summary data reflected in the crop (Table 5.21) and harvest indices (Table 5.22) again clearly shows that the seed producers must close their Ruzi pasture for seed production earlier (early or medium closing) rather than later and must apply relatively high levels of nitrogen fertiliser, at least up to 150 kg N/ha, if they are to achieve high seed yields.

However, in spite of all these recorded effects on seed yield and its components, the ultimate measure of success must surely be in the yield of pure germinating seed (Table 5.18). Obviously the buyer, normally the farmers who are keen to develop pasture for animal production, are only interested in viable seed in order to achieve their desired end. In this regard it is rather disappointing, although interesting to note, the relatively poor seed quality recorded in many of the treatments. The results showed that both nitrogen application and closing had not significantly affected percentage germination of Ruzi grass (Table 5.17). In agreement with these results, percentage germination of *Digitaria eriantha* cv. Premier (Ramirez and Hacker, 1994) seed did not differ among nitrogen application treatments. In contrast, Chadhokar (1971), Chadhokar and Humphreys (1973b), and Carmo *et al.* (1988) reported a germination increase for *Paspalum plicatulum*, *Paspalum plicatulum* and *Brachiaria decumbens* respectively. Cameron and Humphreys (1976), on the other hand, reported a reduction in germination of *Paspalum plicatulum* seed. Likely the earlier the closing date, the higher the percentage of pure germinating seed occurred, but it failed to show significant differences between treatments (Table 5.17). The variable germination percentage, ranging from 18-52% in this study, indicates that other factors e.g. dormancy, uneven seed maturity, and/or non-viable seed, are likely associated with these treatments (nitrogen and closing). Nonetheless, there was a significant interaction effect between nitrogen and closing treatment, these suggested that the earlier closing with at least 150 kg/ha nitrogen application would expect high percentage seed germination, but under low nitrogen (50 kg/ha) the later closing preferred.

As nitrogen application did not directly affect seed germination (Table 5.17), pure germinating seed yield, therefore, showed a similar trend with the same seed yield when application of nitrogen was 150 or 250 kg/ha, both being significantly higher than the lowest application (Table 5.18). However, seed germination played an important role for the different closing treatments, even though there was a similar response when compared with nitrogen effect. Pure germinating seed yields were progressively increased as earlier the closing concerned (Table 5.18). This result is different when compared with seed yield response (Table 5.8) as being no significant differences either early or medium closing occurred. The interaction between nitrogen and closing may likely to be the case (Tables 5.17, 5.18) as resulted in this regard.

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5.5 CONCLUSION

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6.1 INTRODUCTION

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Therefore, the objective of this study was decided to investigate this aspect in some details with Ruzi grass, to determine the effects of different levels of water deficit stress applied at different stages of reproductive development on seed yield, yield components and seed quality in Ruzi grass, particularly in view of the fact that, in Thailand - which is of particular interest to the author - seed development occurs towards the end of the rainy season when changeable rainfall patterns could well lead to short-term periods of water deficit stress over one or more of these reproductive stages.

6.2 MATERIALS and METHODS

6.2.1 Plants and Experimental site

The experiment was conducted under controlled temperature conditions of 30±5°C during the day (12 h) and of 20±5C° during the night (12 h) in a plastic house at the Plant Growth Unit, Massey University, Palmerston North, N.Z.(Latitude 40°S, Longitude 170°E).

Ten litre pots were used for planting and filled with a potting mixture containing 100% CAN Fines (Cambium bark added nitrogen stabilizer) and a compound fertilizer of 0.5 mg Iron sulphate, 0.5 kg PG mix., and 3 kg osmocote (16:3.5:10 + 1.2Mg + fill essential trace elements) per m^2 providing adequate nutrients for 9 months.

Ruzi grass was established by sowing 5 seeds per pot, on 1 January, 1997. Two weeks after the seedlings germinated, they were randomly thinned to 1 seedling per pot. Water was applied daily to maintain moisture supply at or near field capacity.

All plants were defoliated whenever they reached a height of 35 cm by cutting down to 12 cm above soil level. Before commencing the water deficit stress aspect of the experiment the plants were defoliated on 3 occasions (3 February, 26 February and 15 March, 1997).

The water deficit stress study began on 6 April, 1997. This was the date when the transition from the vegetative to the reproductive stage was first determined by the first visible sign of "double ridge" formation in dissected main stem apices.

6.2.2 Design and Treatments

There were 3 levels of water stress imposed on the plants *viz* no stress (W), mild stress (D_1) and severe stress (D_2). These stress levels are defined as follows :-

- Control or No stress (W) - soil moisture at or near field capacity by applying water to the plant in the pot and allowing it to drain through the soil profile until the excess water drains from the base of the pot into the tray beneath. Additional water was then added to fill the tray. Subsequent daily water applications were 400-800 ml/pot/day depending on the varying environmental conditions i.e. maximum amount of water applied under the hot day but less applied in the cloudy or rainy day. Under these conditions of moisture supply leaf extension rate (LER) and relative leaf water content (RWC) were expected to average 6 cm/day (4-8 cm/day) and 75-90% respectively.

- Mild stress level (D_1) - water applied at approximately half the field capacity level (200-400 ml/pot/day), which was intended to achieve approximately half the LER and RWC compared with W level i.e. average 3 cm/day and 60-70% respectively.

- Severe stress level (D_2) - water applied at approximately half the mild stress level (100-150 ml/pot/day, which was intended to achieve a LER of less than 1 cm/day and 35-50%. RWC.

Because of the small amount of water required, particularly at the severe stress level water was therefore injected by syringe under the soil surface in order to minimise evaporation loss and encourage effective uptake by the plant.

Leaf extension rate and relative leaf water content was used to determine and check whether the required levels of water stress were achieved. Plants received water application and also leaf measurement twice daily, once in the morning at 6 a.m. and the other in the evening at 6 p.m.. Generally, mild stress plants obtained half amount of water applied under no stress plants, but severe plants received less than half when compared with mild stress plants. The compensation of leaf extension could be achieved during the night growth particularly during the hot day by increased water supply in the evening. However, only RWC was used when the flag leaf appeared.

Each level of water stress was imposed on plants at 3 different stages of plant reproductive development, defined as follows :-

-floral initiation stage (FI) - the transition from vegetative to reproductive stage and described as the "double ridge" stage.

-ear emergence (EE) - the first sign of inflorescence exserted from the flag leaf.

-full flowering (FF) - when all the florets within the inflorescence showed the exsertion of anthers and stigma.

The experimental design therefore comprised 3 levels of water stress commencing at 3 reproductive development stages, with 3 block replicates except that the two levels of mild and severe (D_1 & D_2) were not combined within the developmental stages. This gave a total of 15 treatments listed as follows (Table 6.1).

Each plant was allotted at random to a particular treatment combination i.e. selected stress level, selected stage of reproductive development and selected duration of stress. This allowed the combination of treatments shown in Table 6.1. These ranged from a full water treatment continued throughout reproductive development i.e. WWW to the most extreme treatment, severe stress throughout reproductive development $D_2D_2D_2$.

The decision to omit the D_1 and D_2 combinations across the different developmental stages was made for several reasons. Firstly, because of the difficulty in making effective and meaningful change in water stress within relatively short periods between developmental stages (e.g. only 6-7 days from ear emergence to first flowering). Secondly, a particular interest in the effect of specific and constant stress levels at different developmental stages. Thirdly, the need to keep the total number of pots to an acceptable level to allow full attention to the possible difficult task of maintaining stress levels as precisely as possible. However, some departure from this decision was granted by including the more simple treatment of returning to field capacity (W) following the completion of allotted periods of stress and examining the effects of these changes e.g. D_1D_1W, D_2D_2W, D_2WW.

Table 6.1 Water stress treatments used in this study

Treatments	Reproductive stage at which stress treatment was initiated			Treatment combination code
	Floral initiation to Ear emergence	Ear emergence to Full flowering	Full flowering to Seed harvest	
1	W	W	W	WWW
2	D_1	D_1	D_1	$D_1D_1D_1$
3	D_2	D_2	D_2	$D_2D_2D_2$
4	D_1	W	W	D_1WW
5	W	D_1	W	WD_1W
6	W	W	D_1	WWD_1
7	D_2	W	W	D_2WW
8	W	D_2	W	WD_2W
9	W	W	D_2	WWD_2
10	D_1	D_1	W	D_1D_1W
11	W	D_1	D_1	WD_1D_1
12	D_1	W	D_1	D_1WD_1
13	D_2	D_2	W	D_2D_2W
14	W	D_2	D_2	WD_2D_2
15	D_2	W	D_2	D_2WD_2

Experimental layout of water stress study

A14	A11	A2	A7	A8	A3
A13	A4	A1	A15	A6	A9
P	A12	A5	P	A10	P
B3	B7	B10	B11	B8	B14
B15	B4	B6	B12	B1	B2
P	B5	B9	P	B13	P
C2	C8	C4	C6	C3	C14
C11	C13	C9	C7	C5	C1
P	C10	C12	P	C15	P

The experimental layout comprising 3 replications (A, B, and C) of 15 treatments (1-15) is presented above. In addition, 3 "dummy" plants (P) were placed in each replicate to minimise the influence of environmental variation among the plants (Plate 6.1a). All plants were supported with bamboo canes or metal sticks and tied with rope to prevent lodging effects as they grew taller (Plate 6.1c).

6.2.3 Measurements

6.2.3.1 Leaf extension rate (LER)

Leaf extension rate was determined by measuring the change in the length of the youngest leaf emerging from the preceding leaf sheath and unfolded only at the tip (Plate 6.1b). The measurement was made with a ruler placed against the base of the plant using the soil surface as a reference point, and recorded twice daily in the morning and afternoon, 7 a.m. and 5 p.m. respectively. The measurement of LER was continued on that leaf for a period of 4-5 days and then ceased and was replaced with the emergence the next new leaf and so on until the emergence of the flag leaf when LER measurements stopped.

(a)

(c)

(b)

Plate 6.1 General view of plants used in the water deficit study (a); initiated leaf used for leaf extension measurement (b); and the plant support system used to prevent lodging (c)

6.2.3.2 Relative leaf water content (RWC)

For RWC measurement, samples were taken from the fully developed youngest leaf from each replicate. The leaves (2-3 fully developed leaves from the upper part of tiller) were sampled using a hole punch (0.5 cm diameter) and ensuring that only the leaf laminae was obtained without the mid rib. The punched samples (approx. 0.5 g per replication) were then weighed to determine fresh weight and floated in distilled water for 2 hours to reach a fully turgid state. After the turgid weight had been recorded, the samples were then dried in the oven at 90 C for 24 hours to determine the dry weight. RWC was then calculated as follows (Barrs and Weatherley, 1962):-

%RWC = {(FW-DW)/(turgid wt.-DW)}x 100

6.2.3.3 Reproductive development

Due to the variation of reproductive development among plant population, a number of plants was required to ensure the effect of water stress occurred within the certain treatments. The date of onset of the FI stage was determined when 5 plants showed the double ridge stage on the same day. These dissections were made from a group of reserve plants kept especially for this determination. The transition date from the FI to EE stage and also EE to FF stage was determined when at least 2 of the 3 replicates showed the required developmental stage i.e. first exsertion of inflorescence for EE and all florets of 3 inflorescences per plant showing exsertion of anthers and stigmas for FF.

6.2.3.4 Seed harvesting and data collection

Seedheads were harvested when more than half of the inflorescences on a plant were considered ripe by showing change in colour of the florets from green to light brown. This colour change was found by experience to occur 2-3 days before seed shedding began. Seedheads were cut by hand and kept in a paper bag. Seed harvest was made only once. The whole plant was then cut to ground level, the non-ripened inflorescences remaining on the plant counted, and the plant dry weight determined.

All harvested ripe inflorescences from each plant were counted and then divided into different groups according to raceme number per inflorescence (e.g. group 1 (1 raceme), group 2 (2 racemes)..etc. Subsequently a total of 20 inflorescences per plant was taken on a proportional basis to represent each group of raceme numbers per inflorescence. These inflorescences were then dissected and divided into two categories : (1) seed number (fertile floret) - where the floret contained a caryopsis (Ferguson and Crowder, 1974) at the firm or "hard" stage (Humphreys and Riveros, 1986); (2) sterile floret - a floret which did not contained a caryopsis. Accordingly, the total number of seeds and florets from harvested inflorescence were obtained and thus the percentage seed set calculated. Seeds were cleaned by using blower machine (Micro Blower Type 35) 70 m/sec for 2 minutes. Thousand seed dry weight (TSDW) was then determined using the air-oven method, with samples (200 seeds per replication) being dried at 103°C for 17 hours (ISTA, 1993).

As a result of water stress some plants developed deformed inflorescences, which were recorded at harvest. However, inflorescences showing missing florets or undeveloped florets on the raceme were still recorded as "normal" as long as the raceme and the floret numbers could be identified.

Unfortunately seeds of some treatments were consumed by mice before measuring total seed fresh weight. Hence it was necessary to ignore the actual weighed seed yield samples and use derived seed yield per plant from the data available on the total number of seeds and seed dry weight (Calculated seed yield = total seed numbers x seed dry weight).

Total inflorescence numbers (including harvested, unripened and deformed inflorescences) were classified into 4 types depending on the tiller type and inflorescence position as follows:-

-inflorescences on old basal tillers (OBT) = those produced on basal tillers which had been cut previously during the vegetative stage

-inflorescences on old aerial tillers (OAT) = those produced on an aerial tiller borne on an old basal tiller

-inflorescence numbers on new basal tillers (NBT) = those produced on basal tillers which had never been cut

-inflorescence numbers on new aerial tillers (NAT) = those produced on an aerial tiller borne on a new basal tiller

6.2.3.5 Percentage of Pure Germinating Seed (% PGS) and PGS yield

Germination tests (ISTA, 1993) on cleaned seed samples were conducted 8 months after seed harvest, the samples having been stored at 5 C during this time. Fifty seeds per replicate (three replicates per treatment) were used and test on germination paper (Top of Paper method) soaked in 0.2 % KNO_3. Blotters were placed in a germination cabinet at 30 C/25 C day and night temperature respectively, 70% RH and 12 hour light/day. Germination was evaluated at 7 days for the first count and 21 days for the final count. Tests were examined and the following categories recorded; germinated seeds (normal and abnormal seedlings), and ungerminated seeds (fresh ungerminated seeds and dead seeds). Percentage of PGS from each plant was then calculated and further PGS yield was determined as follows:

%PGS = (germinated seed numbers/total seed germination test numbers) x 100

PGS yield = Cal. seed yield x % PGS

6.2.3.6 Plant dry weight and dry weight partitioning

Plant fresh weight and dry weight measurements were made after seed harvest - when plants were cut to ground level. Sub samples of approximately 200 g fresh weight were taken and dissected into leaf, stem and dead material, then dried at 80 C for 24 hours and the dry weight of each component recorded. As the amount of dead material recorded was negligible these data were omitted in the result presentation.

Before a leaf sample was taken for drying, this sample was determined for leaf area by using an electronic leaf measurement machine (LI-COR Model 3100).

6.2.3.7 Tiller development

Tiller numbers were counted after plant harvest and divided into 3 categories viz.:-

-vegetative tillers (VT) = those developed from axillary or adventitious buds at the base of a stem, and which did not produce an inflorescence

-old reproductive tillers (OMT) = those developed from tillers which had been previously defoliated, and had produced an inflorescence

-new reproductive tillers (NMT) = those developed from tillers which had not been previously defoliated, and had produced an inflorescence

6.2.3.8 Harvest Index (HI)

Harvest index was calculated from the ratio of calculated seed yield to total herbage dry matter yield at harvest, expressed as a percentage.

6.3 RESULTS

6.3.1 Leaf extension rate (LER) and Relative leaf water content RWC (%)

As shown in Figure 6.1, it was encouraging to see that the intention to establish 3 different levels of water deficit stress within the experiment was successfully achieved and maintained.

Changes in LER (Figure 6.1a) quickly reflected the differing levels of water stress, within a matter of 2-4 days, and were maintained throughout the 16 day period up to the exsertion of the flag leaf when LER measurements were discontinued and replaced by RWC determinations. These results show the levels of LER originally proposed i.e. W 4-8; D_1 3; D_2 1 cm/day were relatively well maintained (Figure 6.1a). However, it is also interesting that it took about 4-6 days for leaf extension rate under full water (11 cm/day) to drop to the 1 cm/day LER used as the benchmark of the D_2 treatment. A similar situation arose with leaf RWC with W >80%, D_1 60-70%, D_2 35-50% (Figure 6.1b).

6.3.2 Reproductive development

As shown in Table 6.2 the application of mild water stress (D_1) throughout the reproductive stage did not significantly extend the total number of days from the commencement of the water stress applied to the completion of seed harvest or final cut (FI-SH) compared with the no stress treatment (W). This period was only extended significantly when water stress was severe (D_2) throughout the reproductive stages. The only exception was when severe stress was applied at the late full flowering stage (WWD_2) which showed a similar result to the mild stress treatments. Generally, the plants could be divided into three groups due to a duration from FI-SH and a potential to produce seed as: a short duration FI-SH (41-48 days) with seed production (WWW, $D_1D_1D_1$, D_1WW, WD_1W, WWD_1, WWD_2, D_1D_1W, WD_1D_1, D_1WD_1, a long duration FI-SH (69-76 days) with seed production (D_2WW, WD_2W, D_2WD_2), and a long duration FI-SH (70-74 days) without seed production ($D_2D_2D_2$, D_2D_2W, WD_2D_2).

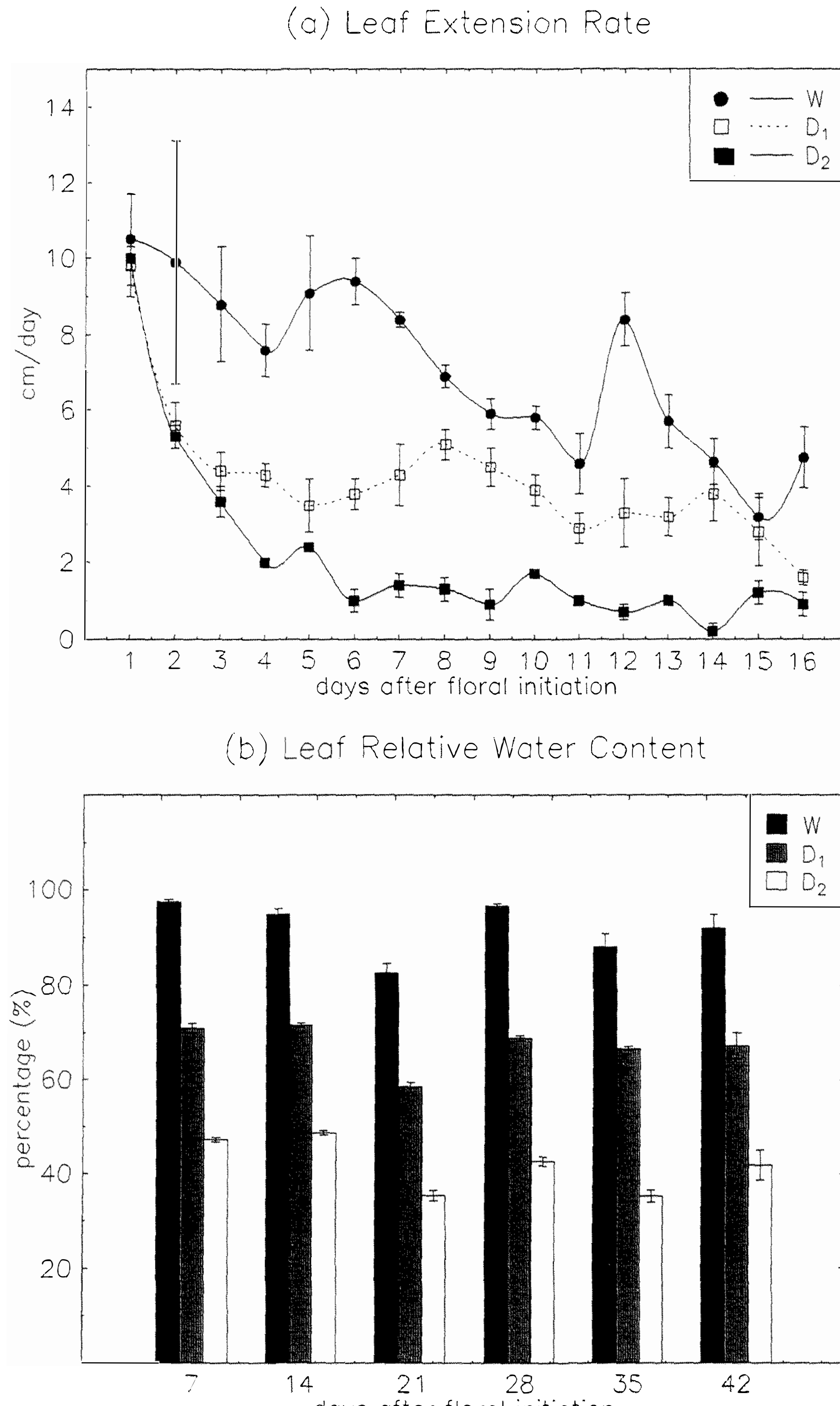

Figure 6.1 The effect of water stress on (a) Leaf Extension rate and (b) Leaf Relative Water Content. Vertical bars show standard error of the mean

When each reproductive development stage was examined in detail it is interesting to note that the period from FI-EE ranged from 13-21 days under no stress (W) a slightly longer period of 21-24 days under mild stress (D_1), but a very extended period of 43-50 days under severe stress (D_2). The EE to FF period ranged over 10-16 days and 10-13 days respectively for plants under no stress and mild stress but it took ∝ (no completion) to 38 days to complete this stage under severe stress. For the last period, from FF-SH the plants required ∝ - 27 days, 9-15 days and ∝ - 19 days under W, D_1 and D_2 respectively, to reach seed harvest.

Table 6.2 The number of days from the commencement of water stress (FI) to the completion of seed harvest (SH) or final cut, and for the transition periods FI-EE, EE-FF, and FF-SH

Treatment	Transition Periods (days)			
	FI-EE	EE-FF	FF-SH	FI-SH
WWW	W : 17	W : 13	W : 11	41 b
$D_1D_1D_1$	D_1 : 22	D_1 : 12	D_1 : 10	44 b
$D_2D_2D_2$	D_2 : 47	D_2 : ∝	D_2 : ∝	74 a
D_1WW	D_1 : 21	W : 10	W : 10	41 b
WD_1W	W : 19	D_1 : 13	W : 10	42 b
WWD_1	W : 19	W : 11	D_1 : 13	43 b
D_2WW	D_2 : 43	W : 13	W : 16	72 a
WD_2W	W : 15	D_2 : 27	W : 27	69 a
WWD_2	W : 18	W : 13	D_2 : 17	48 b
D_1D_1W	D_1 : 24	D_1 : 10	W : 8	42 b
WD_1D_1	W : 21	D_1 : 11	D_1 : 15	48 b
D_1WD_1	D_1 : 22	W : 13	D_1 : 9	44 b
D_2D_2W	D_2 : 50	D_2 : ∝	W : ∝	74 a
WD_2D_2	W : 13	D_2 : 38	D_2 : 19	70 a
D_2WD_2	D_2 : 43	W : 16	D_2 : 17	76 a
LSD < 0.05	20.9			
significance	***			

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

6.3.3 Seed yield and yield components

6.3.3.1 Seed production at harvest

(a) Calculated seed yield (g/plant)

Application of water stress generally caused a significant reduction in seed yield the extent of which depended on the level of stress and the reproductive stage at which it was applied (Table 6.3). In the extreme case a prolonged and severe stress (D_2) over 2 or 3 stages of reproductive development resulted in total failure of the plants to produce seed, except in the D_2WD_2 treatment which produced a small but insignificant quantity of seed.

The mild stress treatment, applied at the earliest reproductive stage, from floral initiation to ear emergence (D_1WW), had no detrimental effect on seed yield, compared with the no stress treatment (WWW). However, if applied at either ear emergence (WD_1W) or full flowering (WWD_1) only, it resulted in a significant reduction in seed yield. The extension of this mild stress over 2 stages also reduced seed yield particularly if it occurred over the EE-FF period (WD_1D_1). In contrast, if temporary relief from mild stress was given during the ear emergence to full flower stage (D_1WD_1) a significant increase in seed yield was achieved compared with the WD_1D_1 treatment, and in fact was not significantly different from the yield obtained from the no stress treatment (WWW). Even when plants were subjected to mild stress throughout the entire reproductive period ($D_1D_1D_1$) seed yield did not show any difference from that recorded from plants subjected to only 2 stages of mild stress.

Table 6.3 Effect of water stress on seed yield (g/plant)

Trt.	seed yield	Trt.	seed yield	Trt.	seed yield
WWW	19.5 a	$D_1D_1D_1$	11.3 bcd	$D_2D_2D_2$	0 f
D_1WW	19.4 a	WD_1W	10.2 bcd	WWD_1	13.0 bc
D_2WW	7.0 de	WD_2W	15.6 ab	WWD_2	14.4 ab
D_1D_1W	11.8 bcd	WD_1D_1	7.7 cde	D_1WD_1	14.8 ab
D_2D_2W	0 f	WD_2D_2	0 f	D_2WD_2	4.2 ef
LSD ≤ 0.05	5.7				
c.v. (%)	34.3				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

(b) Harvested ripe inflorescence numbers

As shown in Table 6.4 harvested ripe inflorescence number was depressed significantly when water stress was severe over 2 and 3 developmental stages. However, it is interesting that, as in Table 6.2 where temporary relief of severe water stress was given during the EE-FF period (D_2WD_2), plants showed some recovery which enabled some inflorescences to be harvested, resulting in no significant difference in the number of ripe inflorescences produced compared with the fully watered plants.

A further result of interest is that the application of a single severe stress at only the early stage of FI-EE also seemed to reduce inflorescence numbers significantly, while severe stress applied at only the mid-stage of EE-FF resulted in a significant stimulus to inflorescence numbers. In fact, this treatment (WD_2W) produced the highest number recorded (106). This is reflected in Table 6.3 on seed yields when D_2WW treatment is compared with WD_2W. In contrast the application of severe stress over the final stage only (FF-SH), as shown in treatment WWD_2 appeared to have no great effect on inflorescence number compared with the control treatment (WWW).

These results clearly suggest that severe stress at floral initiation only is highly detrimental to inflorescence number. However, this is not the case if severe stress occurs at full flower, and may even stimulate the development of inflorescences when applied at ear emergence only, even though but they require a longer period to develop (Table 6.2).

The effect of mild stress on inflorescence number was of relatively minor importance, although mild stress over the EE-FF stage was more detrimental to harvested inflorescence number than at the full flower stage.

Table 6.4 Effect of water stress on harvested ripe inflorescences per plant and percentage of total inflorescences harvested

Treatment	Harvested ripe inflorescences per plant	% harvested ripe inflorescence
WWW	56 cd	42.4
$D_1D_1D_1$	46 cd	38.8
$D_2D_2D_2$	0 e	0
D_1WW	60 bc	47.6
WD_1W	52 cd	27.1
WWD_1	77 b	39.3
D_2WW	38 d	20.0
WD_2W	106 a	32.9
WWD_2	56 cd	53.8
D_1D_1W	40 d	34.5
WD_1D_1	39 d	28.1
D_1WD_1	48 cd	40.0
D_2D_2W	0 e	0
WD_2D_2	0 e	0
D_2WD_2	39 d	31.7
LSD < 0.05	19	
c.v. (%)	16.5	
significance	****	

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

(c) Total inflorescence numbers produced per plant

Table 6.5 shows total inflorescence number produced per plant. The results show that, as with harvested inflorescence numbers (Table 6.4), mild stress generally caused no significant depression of total inflorescence number compared with adequate water (WWW). In fact, there was evidence of a stimulus to total inflorescence number when mild stress was applied at ear emergence (WD_1W) or full flowering (WWD_1) only. Even when mild stress was extended over 2 and 3 developmental stages the total number of inflorescences recorded was not significantly different than those recorded in the control treatment (WWW).

Similarly, even when severe stress was applied at only one developmental stage there was no adverse effect on total inflorescence numbers compared with the fully-watered treatment (WWW) and even showed a marked increase in this regard when applied at the EE-FF stage (WD_2W), as also shown in Table 6.4.

Severe stress applied at 2 and 3 developmental stages, however, had a dramatic depressing effect on total inflorescence numbers, except when plants received temporary relief from stress during EE-FF (D_2WD_2).

Table 6.5 Effect of water stress on total inflorescence numbers produced per plant

Trt.	no./plant	Trt.	no./plant	Trt.	no./plant
WWW	132 bcd	$D_1D_1D_1$	125 cd	$D_2D_2D_2$	9 f
D_1WW	126 cd	WD_1W	192 b	WWD_1	196 b
D_2WW	189 bc	WD_2W	322 a	WWD_2	104 cd
D_1D_1W	116 d	WD_1D_1	139 bcd	D_1WD_1	119 d
D_2D_2W	27 f	WD_2D_2	45 ef	D_2WD_2	123 d
LSD $\leq$ 0.05	65				
c.v. (%)	29.5				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

(d) The percentage of harvested ripe inflorescences and partitioning of total inflorescence numbers

The percentage of ripe inflorescences harvested is presented in Table 6.4. Apart from the extreme treatments recording zero harvested inflorescences the variation in ripe harvested inflorescences ranged from 20 to 54 % between treatments. Although a delay in seed harvesting date can achieve a higher percentage of mature inflorescences this invariably leads to a lower seed yield due to excessive seed shedding which is prevalent in many tropical grasses, and particular so in Ruzi grass.

Although it was difficult to see any obvious pattern in the proportion of ripe inflorescences harvested between treatments, there was the tendency for a lower head harvest if severe stress occurred during the earlier development stages rather than during the later stage following full flowering.

The total number of inflorescences produced were derived from different types of tillers and are presented in Table 6.6. The main crop of inflorescences originated from old basal tillers (OBT) but there was no significant difference in the contribution of this type of tiller between treatments. The only obvious trend was a noticeable reduction in OBT inflorescences arising from plants severely stressed for lengthy periods over 2 and 3 developmental stages, particularly when this included the developmental stage EE-FF. The remaining treatments showed only minor differences.

In terms of inflorescences borne on old aerial tillers (OAT), again numbers were markedly reduced in those treatments subjected to severe stress for lengthy periods, while the remaining treatments showed minor differences. However the exception to this generalisation was the interesting stimulus to inflorescence number from OAT when plants were subjected to severe stress during the individual earlier stages, (particularly EE-FF) compared with severe stress during the late stage (66 : 88 : 14 for D_2WW : WD_2W : WWD_2 respectively).

Again inflorescence numbers arising from new basal tillers (NBT) were markedly reduced in those treatments subjected to severe stress for 2 or more developmental stages. However if severe stress only occurred at one developmental stage there was no significant detrimental effect on inflorescence numbers arising from NBT.

The number of inflorescences arising from new aerial tillers (NAT) were also reduced by severe water stress for lengthy periods, otherwise there was little effect from lesser water stress throughout the reproductive period. The only exception to this was the sizeable stimulus to inflorescences from NAT when plants were subjected to severe stress during the EE-FF stage (WD_2W).

Table 6.6 Effect of water stress on total inflorescence numbers partitioned into inflorescences borne on old basal tillers (OBT), old aerial tillers (OAT), new basal tillers (NBT) and new aerial tillers (NAT)

Treatments	Inf.no./plant from OBT	Inf.no./plant from OAT	Inf.no./plant from NBT	Inf.no./plant from NAT
WWW	45	35 bcde	34 abcde	18 bc
$D_1D_1D_1$	43	46 bcd	23 defg	13 bc
$D_2D_2D_2$	5	0 f	4 gh	0 c
D_1WW	48	22 def	36 abcde	20 bc
WD_1W	57	60 abc	28 cdef	47 bc
WWD_1	49	41 bcde	55 a	52 b
D_2WW	56	66 ab	33 bcde	34 bc
WD_2W	45	88 a	51 ab	139 a
WWD_2	42	14 def	41 abcd	6 bc
D_1D_1W	33	27 cdef	28 cdef	28 bc
WD_1D_1	38	21 def	48 abc	33 bc
D_1WD_1	49	31 cdef	25 defg	15 bc
D_2D_2W	26	0 f	1 h	0 c
WD_2D_2	16	12 ef	11 fgh	6 bc
D_2WD_2	60	36 bcde	18 efgh	10 bc
LSD ≤ 0.05	33	33	21	51
c.v. (%)	49.0	59.9	43.6	108
significance	ns	***	***	**

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

It is again interesting to note (Table 6.6) the reaction of plants subjected to stress (particularly severe stress during the EE-FF (WD_2W)) resulting in a considerable increase in the number of inflorescences from aerial tillers both old (OAT) and new (NAT). This may be explained by the advantage of an extended time frame between FI to SH when compared with the no stress treatment (Table 6.2).

(e) Harvested seed numbers

As shown in Table 6.7, the highest number of seeds harvested per plant was obtained from the non-stress plants (WWW). Mild stress only reduced harvested seed number significantly when it was applied during the EE-FF stage of development and when imposed over longer periods including the FI-FF stage. In fact, when water stress was temporarily relieved during the EE-FF period (D_1WD_1) there was a noticeable improvement in seed numbers - which was also apparent under severe stress.

Severe water stress, when applied at only one developmental stage, was generally no more damaging to total seed numbers than mild stress, except when applied at floral initiation (D_2WW). When this occurred, seed number was severely reduced compared with mild stress. However when this single stage of severe stress occurred at ear emergence or full flower, then harvested seed numbers were similar to those produced by the full water treatment (WWW).

Severe water stress extended over 2 developmental stages caused a significant depression in seed numbers, particularly if it occurred during the floral initiation and ear emergence stages. Again, the temporary relief of stress during EE-FF, appeared to reduce the depressing effect of extended water stress. However, there was no doubt that severe stress throughout the entire period ($D_2D_2D_2$) was devastating to seed number - yielding no seeds.

Table 6.7 Effect of water stress on harvested seed numbers per plant

Trt.	no./plant	Trt.	no./plant	Trt.	no./plant
WWW	3713 a	$D_1D_1D_1$	2413 bcde	$D_2D_2D_2$	0 g
D_1WW	3480 ab	WD_1W	2183 cdef	WWD_1	2653 abcd
D_2WW	1300 ef	WD_2W	2844 abc	WWD_2	2862 abc
D_1D_1W	2517 bcd	WD_1D_1	1636 def	D_1WD_1	2740 abcd
D_2D_2W	0 g	WD_2D_2	0 g	D_2WD_2	1012 fg
LSD ≤ 0.05	1184				
c.v. (%)	36.2				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

(f) Thousand Seed Dry Weight (TSDW)

Water stress applied at either mild or severe levels and at any stage of seed development had only minor effects on TSDW (Table 6.8) except in treatments $D_2D_2D_2$, D_2D_2W, and WD_2D_2 where no seed was produced. However when applied at a mild level over the floral initiation and ear emergence periods, there was a significant reduction in TSDW. Again, removing water stress temporarily during the ear emergence period (EE-FF) alleviated the detrimental effect on TSDW at the mild stress level, and also lessened the detrimental effect even at the severe level of water stress.

Table 6.8 Effect of water on thousand seed dry weight

Trt.	g. per 1000 seeds	Trt.	g. per 1000 seeds	Trt.	g. per 1000 seeds
WWW	5.32 abc	$D_1D_1D_1$	4.76 bcd	$D_2D_2D_2$	0 e
D_1WW	5.61 a	WD_1W	5.03 abcd	WWD_1	5.46 abc
D_2WW	5.47 ab	WD_2W	5.49 ab	WWD_2	5.06 abcd
D_1D_1W	4.69 cd	WD_1D_1	4.74 bcd	D_1WD_1	5.42 abc
D_2D_2W	0 e	WD_2D_2	0 e	D_2WD_2	4.33 d
LSD ≤ 0.05	0.76				
c.v. (%)	11.2				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

(g) Floret numbers at seed harvest

The harvested floret numbers are shown in Table 6.9. Water stress applied at a mild level and at all single stages of seed development had little effect on floret numbers at harvest except when applied at ear emergence (WD_1W) which significantly reduced floret number compared with the control treatment (WWW). However, under severe water stress floret numbers were only significantly reduced when stress occurred at the early floral initiation stage (D_2WW). When severe stress was applied over 2 or more stages then floret numbers were dramatically reduced, except when stress was temporarily relieved during the EE-FF stage (D_2WD_2), although even in this treatment, floret numbers were still significantly less than in the control treatment (WWW), and also D_1WW, WWD_1 and WWD_2 Treatments.

Table 6.9 Effect of water stress on harvested floret numbers

Trt.	no./plant	Trt.	no./plant	Trt.	no./plant
WWW	6967 a	$D_1D_1D_1$	4618 abcd	$D_2D_2D_2$	0 f
D_1WW	6438 abc	WD_1W	4132 cd	WWD_1	6161 abc
D_2WW	1690 ef	WD_2W	4426 bcd	WWD_2	6515 ab
D_1D_1W	4287 bcd	WD_1D_1	3549 de	D_1WD_1	4092 cd
D_2D_2W	0 f	WD_2D_2	0 f	D_2WD_2	2374 de
LSD $\leq$ 0.05	2373				
c.v. (%)	38.5				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

(h) Percentage seed set

Water stress appeared to have relatively small effect on percentage seed set in most treatments (Table 6.10). However the subjection of plants to severe stress during the period from full flowering to seed harvest (WWD_2) and even extended mild stress over the ear emergence and full flowering stages (WD_1D_1) caused a potential reduction in the mean percentage of seed set.

Again extended severe stress over 2 or more developmental stages reduced seed set very significantly, except in the D_2WD_2 treatment where there was temporary relief to stress during the EE-FF stage. In this treatment there was significant evidence of recovery in percentage seed set.

Table 6.10 Effect of water stress on seed set per plant (%)

Trt.	seedset	Trt.	seedset	Trt.	seedset
WWW	52.7 bc	$D_1D_1D_1$	52.0 bc	$D_2D_2D_2$	0 d
D_1WW	58.8 abc	WD_1W	50.8 bc	WWD_1	50.8 bc
D_2WW	75.2 a	WD_2W	67.2 ab	WWD_2	43.5 c
D_1D_1W	58.7 abc	WD_1D_1	45.9 c	D_1WD_1	68.4 ab
D_2D_2W	0 d	WD_2D_2	0 d	D_2WD_2	42.6 c
LSD ≤ 0.05	17.9				
c.v. (%)	24.1				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

(i) Deformed inflorescence numbers

During this study some treatments resulted in the exsertion of inflorescences which were deformed (Plate 6.2a,b,c). This deformity of harvested inflorescences are presented in Table 6.11. Only the severe stress level caused deformed inflorescences and only when applied at the floral initiation (D_2WW) and the ear emergence stages (WD_2W) and when the severely stressed plants were given temporary relief during the ear emergence stage (D_2WD_2), which apparently adversely affected normal development of the inflorescence (Plate 6.2d,e).

6.3.3.2 Percentage of pure germinating seed (%PGS) and PGS yield

Water stress appeared to have little effect on percentage of pure germinating seed in those treatments that produced seed (Table 6.12). There were no significant differences in this aspect when mild stress was applied at any single developmental stage or even for the entire

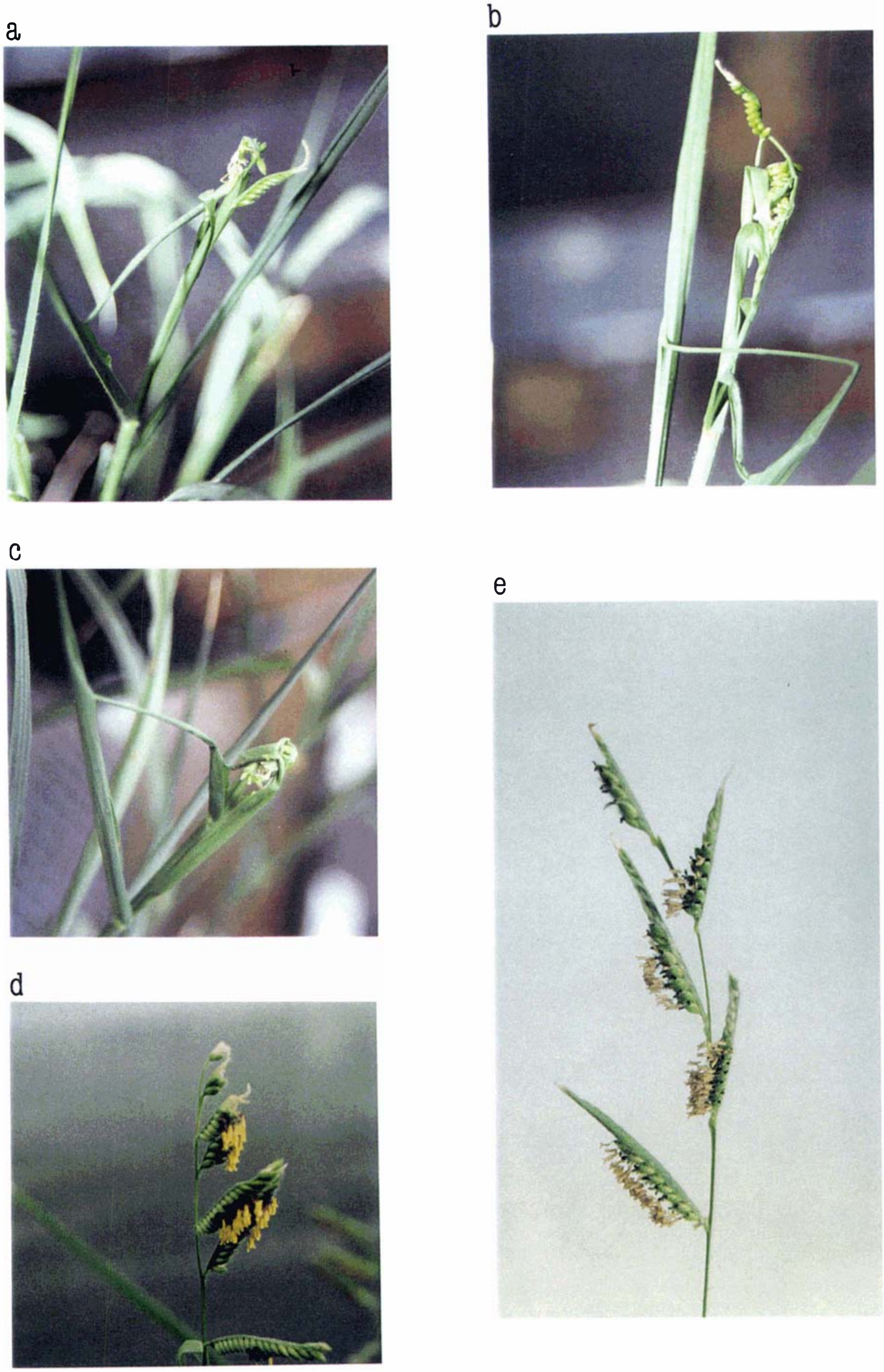

Plate 6.2 Examples of deformed (non) fully exserted inflorescences in severe water stress treatment (a, b, c); rewatering recovery of inflorescences (d, e)

period compared with the control treatment (WWW). Similarly, the application of severe stress at any single stage showed no adverse effect on percentage of pure germinating seed compared with the WWW treatment. However the application of severe stress over 2 or 3 developmental stages which included the FI-EE and EE-FF stage resulted in the total failure of the plant to produce seed.

Table 6.11 Effect of water stress on the number of deformed inflorescences per plant

Trt.	no./plant	Trt.	no./plant	Trt.	no./plant
WWW	0 c	$D_1D_1D_1$	0 c	$D_2D_2D_2$	0 c
D_1WW	0 c	WD_1W	0 c	WWD_1	0 c
D_2WW	35 ab	WD_2W	42 a	WWD_2	0 c
D_1D_1W	0 c	WD_1D_1	0 c	D_1WD_1	0 c
D_2D_2W	0 c	WD_2D_2	0 c	D_2WD_2	30 b
LSD $\leq$ 0.05	10				
c.v. (%)	84.0				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P\leq 0.05$)

The effects of water stress on the yield of pure germinating seed (PGS) showed a similar pattern to that recorded for %PGS, except that an extended mild stress occurring over 2 developmental stages, and when such stages included the EE-FF stage, showed a significant reduction compared with the control treatment (WWW). In contrast, the D_2WD_2 treatment - with its temporary removal of water stress during the EE-FF stage - again showed a notable recovery and achieved a high %PGS which was not significantly different from the control treatment. However, despite this, PGS yield was only a little more than one third that of the control (WWW) treatment. The importance of adequate water supply during the most sensitive period from ear emergence to full flowering is also reinforced by the adverse effect recorded in the WD_1W treatment when mild stress was only applied during this period.

All the other extended severe stress treatments failed to produce any seed.

Table 6.12 Effect of water stress on pure germinating seed (%PGS) and PGS yield (g/plant)

Treatment	PGS (%)	PGS yield (g/plant)
WWW	35.0 abcd	6.8 ab
$D_1D_1D_1$	37.3 abcd	4.4 abcd
$D_2D_2D_2$	0 e	0 e
D_1WW	31.7 abcd	6.5 abc
WD_1W	26.7 cd	2.7 cde
WWD_1	26.7 cd	3.4 bcde
D_2WW	55.0 a	4.0 bcd
WD_2W	48.3 abc	8.1 a
WWD_2	45.0 abc	6.3 abc
D_1D_1W	18.3 de	1.9 de
WD_1D_1	15.0 de	1.1 de
D_1WD_1	30.0 bcd	4.2 bcd
D_2D_2W	0 e	0 e
WD_2D_2	0 e	0 e
D_2WD_2	53.3 ab	2.4 de
LSD < 0.05	24.7	3.7
c.v. (%)	48.3	64.4
significance	***	***

means with the same letter in a column are not significantly different compared by LSD ($P \leq 0.05$)

6.3.4 Plant dry weight and dry weight partitioning

6.3.4.1 Total plant dry weight

Any level of water stress applied at any seed developmental stage caused a significant reduction in plant growth when compared with the no stress treatment (Table 6.13). In fact, when one compares the no stress treatment with what might be called the extreme treatments

($D_1D_1D_1$ and $D_2D_2D_2$), then, there is a significant and linear reduction in plant dry weight as the level of stress is increased (Plate 6.3).

The degree of reduction was not significantly different however among the plants under mild stress at a single stage, but at the severe stress level the reduction was most evident when plants received this stress at the floral initiation stage (D_2WW). When water stress was applied over 2 developmental stages, severe stress caused a significant reduction in plant dry weight compared with mild stress especially when stress occurred over the FI-FF stage as in the D_2D_2W treatment.

As might be expected, when stress was applied at all 3 stages then the severe level was more damaging than the mild stress level. From the results presented it is clear that applying water stress at the floral initiation stage is more damaging to plant growth than during the ear emergence or full flowering stage, particularly if the stress is severe.

Generally, the response of plant total dry matter to water stress showed a similar pattern when compared between mild and severe stress. Dry matter tended to increase when water stress occurred from early stage to late stage. Moreover, the earlier the water was applied (especially at floral initiation) the higher the dry matter obtained.

Table 6.13 Effect of water stress on total plant dry weight (g/plant)

Trt.	dry weight	Trt.	dry weight	Trt.	dry weight
WWW	228.7 a	$D_1D_1D_1$	135.6 def	$D_2D_2D_2$	60.5 h
D_1WW	143.5 cdef	WD_1W	169.3 bcd	WWD_1	174.8 bc
D_2WW	111.8 fg	WD_2W	163.7 bcd	WWD_2	184.4 b
D_1D_1W	122.2 ef	WD_1D_1	153.2 bcde	D_1WD_1	122.0 ef
D_2D_2W	66.8 h	WD_2D_2	109.0 fg	D_2WD_2	81.7 gh
LSD ≤ 0.05	37.2				
c.v. (%)	16.5				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

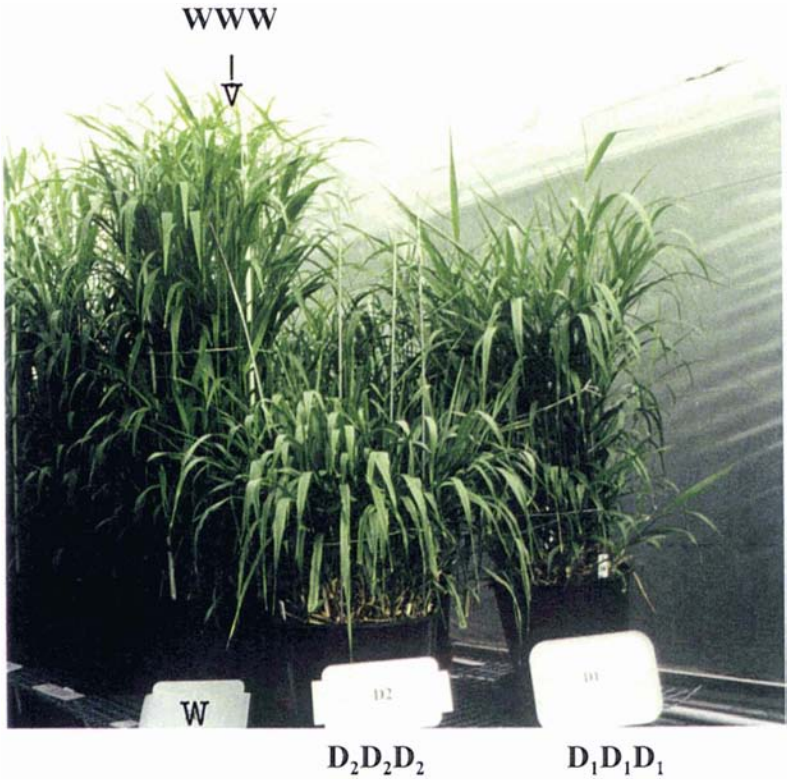

Plate 6.3 Examples of differences in dry matter production according to the level of water supply. Full water throughout (WWW); mild stress ($D_1D_1D_1$) and severe stress ($D_2D_2D_2$)

6.3.4.2 Leaf dry weight

As shown in Table 6.14 both levels of water stress when applied at any reproductive developmental stage tended to reduce leaf growth. Where only mild stress was applied at a single stage, that applied during FF-SH was most depressing (WWD_1) but less at the FI-EE (D_1WW) stage and especially the EE-FF stage (WD_1W). In these two treatments leaf dry weight was in fact not significantly different from fully watered plants (WWW). This effect was even more striking at the severe level of stress and was similar to the degree of leaf dry weight reduction recorded in plants subjected to extended periods of stress (e.g. WWD_2; $D_2D_2D_2$; D_2WD_2). As expected, subjecting the plant to severe stress for two or more developmental stages caused a significant reduction in leaf dry weight.

Table 6.14 Effect of water stress on leaf dry weight (g/plant)

Trt.	dry weight	Trt.	dry weight	Trt.	dry weight
WWW	53.8 a	$D_1D_1D_1$	38.6 bc	$D_2D_2D_2$	23.4 def
D_1WW	41.2 abc	WD_1W	45.9 ab	WWD_1	33.1 cde
D_2WW	38.4 bc	WD_2W	37.7 bc	WWD_2	21.2 ef
D_1D_1W	34.9 bcd	WD_1D_1	30.7 cdef	D_1WD_1	35.1 bcd
D_2D_2W	19.4 f	WD_2D_2	22.6 def	D_2WD_2	22.3 ef
LSD $\leq$ 0.05	12.6				
c.v. (%)	22.7				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

6.3.4.3 Stem dry weight

As shown in Table 6.15 the reaction of stem dry weight to different levels of water stress at different or all developmental stages was similar to the reaction of total plant dry weight (Table 6.13). This is not surprising as total plant dry weight was predominantly stem material.

The fact that WWW and WWD_2 both produced plants with similar stem dry weight again stresses the greater sensitive of plants to water stress in the FI-FF stages of development.

Table 6.15 Effect of water stress on stem dry weight (g/plant)

Trt.	dry weight	Trt.	dry weight	Trt.	dry weight
WWW	174.9 a	$D_1D_1D_1$	97.0 de	$D_2D_2D_2$	37.11 h
D_1WW	102.2 de	WD_1W	123.4 cd	WWD_1	141.7 bc
D_2WW	73.4 def	WD_2W	126.0 cd	WWD_2	163.2 ab
D_1D_1W	87.3 ef	WD_1D_1	122.5 cd	D_1WD_1	86.9 ef
D_2D_2W	47.3 gh	WD_2D_2	86.4 ef	D_2WD_2	59.6 fgh
LSD ≤ 0.05	29.5				
c.v. (%)	17.3				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

6.3.4.4 Leaf area

Application of water stress generally reduced leaf area of the plant compared with no stress, particularly when it occurred over the full flowering to seed harvest period and was generally more damaging when severe (Table 6.16). However, when plants were subjected to mild (WD_1W) or severe (WD_2W) stress at the ear emergence to full flowering stage only, they were able to recover from the temporary water shortage and achieve a marked increase in leaf area by seed harvest which was not significantly different from the control plants (WWW).

When water stress was extended over two or more developmental stages at either mild or severe stress levels, there was a significant reduction in leaf area, particularly under severe stress. This reduction in leaf area to extended periods of stress, imposed at specific developmental stages showed no significant difference i.e. damage occurred at all stresses of plant development in response to water stress.

Table 6.16 Effect of water stress on leaf area (cm^2/plant)

Trt.	leaf area	Trt.	leaf area	Trt.	leaf area
WWW	14238 a	$D_1D_1D_1$	7727 cd	$D_2D_2D_2$	3569 ef
D_1WW	10383 bc	WD_1W	12556 ab	WWD_1	6961 cde
D_2WW	9079 bc	WD_2W	11502 ab	WWD_2	3871 ef
D_1D_1W	9302 bc	WD_1D_1	7689 cd	D_1WD_1	9085 bc
D_2D_2W	2177 f	WD_2D_2	3899 ef	D_2WD_2	4353 def
LSD ≤ 0.05	3655				
c.v. (%)	28.2				
significance	* **				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

6.3.4.5 Leaf : Stem ratio

There were few treatments that showed a significant response to water stress in terms of L/S ratio (Table 6.17). The only effect of note was that water stress applied at the full flowering stage, particularly if severe, caused a marked increase in the proportion of stem (WWD_2).

Table 6.17 Effect of water stress on leaf:stem ratio

Trt.	leaf:stem	Trt.	leaf:stem	Trt.	leaf:stem
WWW	1:3.2 bcd	$D_1D_1D_1$	1:2.7 cde	$D_2D_2D_2$	1:1.6 e
D_1WW	1:2.5 cde	WD_1W	1:2.9 bcde	WWD_1	1:4.3 b
D_2WW	1:1.9 de	WD_2W	1:3.4 bcd	WWD_2	1:8.8 a
D_1D_1W	1:2.6 cde	WD_1D_1	1:4.1 bc	D_1WD_1	1:2.5 cde
D_2D_2W	1:2.5 cde	WD_2D_2	1:4.4 b	D_2WD_2	1:2.7 cde
LSD ≤ 0.05	1:1.6				
c.v. (%)	28.6				
significance	****				

means sharing the same letter are not significantly different compared by LSD (P≤ 0.05)

6.3.5 Tiller development

Generally, water stress applied at both mild and severe levels at any single developmental stage had no significant effect on tiller numbers per plant (Table 6.18). Even when this was extended over two or more developmental stages at the mild stress level there was no significant effect on tiller numbers. However, when severe stress was applied over an extended period covering the ear emergence and full flowering stages (WD_2D_2) and especially the floral initiation and ear emergence stages (D_2D_2W), there was a marked depression in tiller numbers, but not in the D_2WD_2 treatment where temporary relief from stress was provided by water application during the EE-FF stage.

In terms of development of the different categories of tillers (Figure 6.2), the results generally showed that old main (reproductive) tillers (OMT) represented the largest proportion of the total tiller population (apart from these treatments subjected to severe stress over several stages) where vegetative tillers made the major contribution. The exception to this latter reaction was in treatment D_2WD_2 which reflected the importance of providing adequate water during the EE-FF stage and thereby ensured the retention of a high proportion of old tillers in the total population.

New main (reproductive) tillers (NMT) only appeared to be encouraged relative to old reproductive tillers when plants were given adequate water or not subjected to stress during the floral initiation to ear emergence stage (FI-EE).

Table 6.18 Effect of water stress on tiller numbers per plant

Trt.	tiller no.	Trt.	tiller no.	Trt.	tiller no.
WWW	96 abc	$D_1D_1D_1$	70 cdef	$D_2D_2D_2$	35 f
D_1WW	100 abc	WD_1W	103 abc	WWD_1	108 ab
D_2WW	126 a	WD_2W	112 ab	WWD_2	87 bcd
D_1D_1W	79 bcde	WD_1D_1	91 abc	D_1WD_1	88 bc
D_2D_2W	45 ef	WD_2D_2	52 def	D_2WD_2	88 bcd
LSD $\leq$ 0.05	36				
c.v. (%)	25.2				
significance	***				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

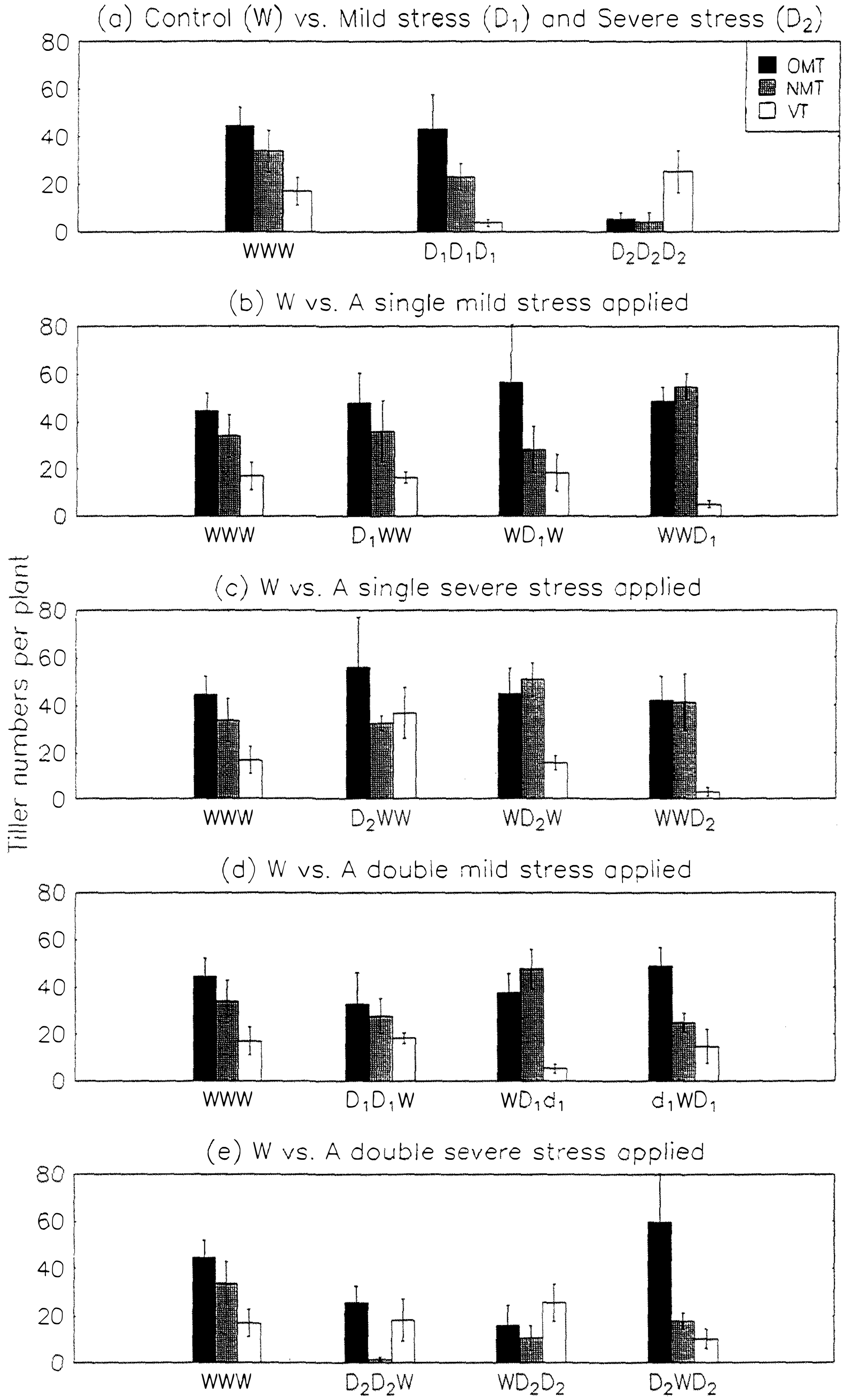

Figure 6.2 Effect of water stress on tiller development viz. old main tillers (OMT), new main tillers (NMT) and vegetative tillers (VT). Vertical bars show standard error of the mean.

6.3.6 Harvest Index (HI)

Harvest indices are presented in Table 6.19. These results show that plants subjected to mild water stress throughout the reproductive developmental stages ($D_1D_1D_1$) had a similar potential to produce seed as the plants which were fully watered (WWW).

In terms of the effect of mild stress at specific developmental stages, the results show the importance, once again, of providing adequate water during the ear emergence to full flowering stage, as reflected in the high indices recorded in the D_1WW and D_1WD_1 treatments.

Severe water stress was very damaging to harvest index when the stress occurred over two to three reproductive developmental stages compared with the fully watered treatment. However, the effect of removing severe stress during the FF-SH stage (WD_2W) was in evidence and served to lessen the degree of damage significantly.

Table 6.19 Effect of water stress on harvest index (HI)

Trt.	HI	Trt.	HI	Trt.	HI
WWW	8.4 cde	$D_1D_1D_1$	8.5 cde	$D_2D_2D_2$	o g
D_1WW	13.6 a	WD_1W	6.0 ef	WWD_1	7.5 cdef
D_2WW	6.5 def	WD_2W	9.5 bcd	WWD_2	7.8 cdef
D_1D_1W	9.8 bc	WD_1D_1	5.1 f	D_1WD_1	12.3 ab
D_2D_2W	0 g	WD_2D_2	0 g	D_2WD_2	5.1 f
LSD ≤ 0.05	3.2				
c.v. (%)	29.1				
significance	****				

means sharing the same letter are not significantly different compared by LSD ($P \leq 0.05$)

6.4 DISCUSSION

In the current study the application of water deficit stress to Ruzi grass through the reproductive stages of development generally caused a marked and increasing reduction in the vegetative components of the plant as the degree of stress increased. This is well illustrated in Tables 6.13, 6.14, 6.15, and 6.16.

This reaction to water stress was also reported by Boyer (1968) and Hsiao (1973) who found that cell expansion and cell division in the leaf were the first processes to be affected as water stress developed. In a study of prairie grass (*Bromus catharticus*), Chu (1979) found that leaf extension rate was extremely sensitive to reduction in leaf water potential especially in the early stages of desiccation, and then it became much less responsive to further reductions in leaf water potential as desiccation developed more severe. Barker *et al.* (1989) also concluded that the dynamic processes in canopy synthesis (leaf extension rate and leaf appearance rate) were most sensitive to water stress. Certainly in the present study, leaf area (Table 6.16) was the component most affected by stress and which suffered the biggest reduction loss when plants were subjected to severe and extended levels of water stress.

The relative importance of stress applied at different individual developmental stages is of particular interest. Plants under mild stress were similarly depressed, statistically, at all stages in terms of plant dry weight. However there did appear to be a greater reduction when stress was only applied at the early stage during floral initiation (FI) rather than when stress was applied at later developmental stages (Table 6.13). This reaction was reinforced in the treatments subjected to severe stress at a single stage which showed clearly and significantly that water stress, particularly if severe, can seriously depress plant growth if it occurs at floral initiation. This trend was again evident in treatments subjected to extend stress over two stages of development, and was due more to changes in stem dry weight than in leaf dry weight (Table 6.17). Leaf area (Table 6.16), on the other hand, was most sensitive to water stress when it was applied during the last stage (full flowering (FF) to seed harvest (SH)) following adequate water during the earlier stages.

Tiller development results (Table 6.18) generally support Langer's (1979) statement that tiller production and survival is inversely related to soil water deficit, and also Chu (1979) who demonstrated in prairie grass that the overall effect of the desiccation treatment was least for tiller numbers and the greatest for shoot dry weights as plant showing 64%, 48%, 32% and 27% of control values for tiller number, leaf number, leaf area and shoot dry weight per plant respectively. In the current study, however, this effect only reached significance if such stress was severe and extended over two or three reproductive stages. In contrast, the significance of even temporary removal of stress during the EE to FF stage was highlighted in the D_2WD_2 treatment, where, in spite of the plants being subjected to a lengthy severe period of stress, they were still able to achieve total tiller numbers equal to the control treatment (WWW). This reflected the provision of adequate water during this EE-FF stage. It is important to remember, however, that tillering is a dynamic process involving formation and death and hence the "spot" counting of tillers is only a "spot census" of an ever-changing population (Boonman, 1971b; Briske and Silvertown, 1993; Humphreys, 1997).

As shown in Figure 6.2 many of the reactions in tiller numbers to water stress were largely an expression of changes in the old tiller population, especially where plants were under severe stress for extended periods and were not given temporary relief of this stress at the EE-FF developmental stage.

New fertile tillers, on the other hand, tended to show an increase in numbers and proportion when subjected to stress, provided the plants received adequate water following floral initiation. As stated by Slatyer (1973) and Fisher and Campbell (1977) rewatering of plants following drought stress can result and often compensatory in remarkable recovery in all growth parameters and even result in relative growth rates which are greater than in fully-watered plants. This is, according to Ludlow and Ng (1977), due to the rapid expansion of cells which had continued to be accumulated during the stress period as cell division is less sensitive to water stress than cell expansion. Similarly, Chu (1979) also reported that in prairie grass a higher recovery growth increases than control rates occurred over several days in terms of leaf extension, tiller number, leaf number and leaf area, but however, the overall effects of these accelerated responses on plant dry weight were minimal due to the duration of the period of water deficit applied. In the present study recovery of stress plants, in terms of tiller numbers, was apparent following rewatering in many treatments and enabled these populations to regain levels similar to non-stressed plants. This recovery, however, only reached "remarkable" levels when plants were rewatered after severe stress during the early floral initiation stage, as shown in the D_2WW and D_2WD_2 treatments (Table 6.18).

Water stress applied at both levels and at all reproductive stages caused a reduction in seed yield which reached significance in many treatments (Table 6.3). Even under mild stress, seed yield was seriously reduced if it occurred during the ear emergence to full flowering stage (WD_1W) or during full flowering to seed harvest (WWD_1), but was totally unaffected if it occurred from floral initiation to ear emergence (D_1WW), as also found by Scott (1973) in his work with perennial ryegrass. This effect happened despite a marked increase in the total number of inflorescences recorded (Table 6.5) in the two former treatments (WD_1W and WWD_1), (largely aerial tillers (Table 6.6)), to result in a final population which was even higher than in the fully watered control treatment. Total seed numbers per plant (Table 6.7) in these depressed treatments were also considerably reduced but seed weight was largely unaffected (Table 6.8). A simple comparison between these treatments serves to emphasise the importance of adequate soil moisture during ear emergence and seed filling and the serious damage to seed yield if even mild stress occurs at these stages. The impact of water stress applied during these later stages of development was much greater on reproductive than on vegetative parameters as plant dry weight and leaf weight in these two treatments were not significantly different (and perhaps higher) from the unaffected treatment D_1WW. Stanhill (1957) also reported this difference in response to water stress between reproductive and vegetative parameters, while Saini and Aspinall (1981) along with Morgan and King, (1984) and Dorion *et al.* (1996) found that the water potential (ψ_w) of the spikes, spikelets, anthers or other floral organs in water stressed wheat plants either does not change or declines much less than that of the leaf. In wheat, relative water content of the spikelets also remains unchanged in water-stressed plants (Morgan, 1980). The plant may also, according to Day (1981), adjust itself to available water supply by reducing its leaf size but maintaining leaf number prior to seedhead emergence, as observed in the mild stressed plants in the present study.

When mild stress was extended over two consecutive developmental stages, which included the ear emergence to full flowering stage, the detrimental effect on seed yield was again evident (Table 6.3). However, when the extended stress was broken by temporary relief during this period (EE-FF) the plant (D_1WD_1) was capable of showing quite remarkable recovery and achieve relatively high seed yield. This depression in seed yield from plants deprived of adequate water particularly during EE-FF, appeared to be due to a number of adversely affected components, both significant and non-significant statistically, showing a lower percentage of harvested inflorescence, reduced floret and seed numbers, lower percentage seed set and lower seed weight.

However, the production of seed from plants subjected to severe stress at a particular developmental stage was quite different. Severe stress at the early stage (D_2WW) depressed seed yield remarkedly compared with the control treatment (WWW) due mainly to low percentage number of harvestable inflorescences, low floret and seed numbers per plant and in spite of high seed set (Table 6.10). When applied at the ear emergence stage (WD_2W) or full flowering stage (WWD_2) the reduction in seed yield as a result of severe water stress was much less and in fact not significantly different from the yield of the control treatment. In the treatment subjected to severe stress during ear emergence to full flowering stage (WD_2W) there was even a striking increase in total and harvested inflorescence numbers emerging mainly from old and particularly new aerial tillers (Table 6.6). This would therefore suggest that aerial tillers may well contribute significantly to seed yield in this treatment and helped to recover some of the otherwise damaging effects of stress at this stage. In contrast, in plants, severely stressed at the late stage (WWD_2), there was no significant increase in aerial tillers as occurred in WD_2W, but plants still managed to produce a relatively high seed yield due to high floret and seed numbers per plant, high percentage seed set and a high percentage of harvested inflorescences. As expected, during this seed-filling stage seed weight showed a small but non-significant reduction. It is also pertinent to record that in those treatments severely stressed over specific developmental stages the time (days) to complete that stage (and even the subsequent stage in the WD_2W treatment) was significantly extended (Table 6.2). This was also accompanied by the appearance of a considerable number of deformed inflorescences (Table 6.11) in these treatments and by the production of relatively high numbers of aerial tillers (D_2WW and WD_2W) (Table 6.6). This latter effect was presumably an attempt by the plant to recover from the severe stress when rewatered.

When severe stress was extended over two or three developmental stages, the results was dramatic and clear cut with virtual total failure of the plant to produce seed, as also found by Scott (1973). The only exception to this was, again, in the treatment given temporary relief from stress during ear emergence to full flowering (D_2WD_2) which enabled some inflorescences to complete their seed production cycle and produce a small quantity of seed (Table 6.3). This seems to reinforce the finding stated previously and highlights the sensitivity of Ruzi grass to stress during ear emergence, as well as the remarkable ability of the plant to show some recovery even from severe and extended conditions of moisture deficit provided such stress is alleviated during the stage from ear emergence to full flowering. All parameters nonetheless, both vegetative and reproductive, reacted adversely and significantly to extended severe stress compared with fully watered plants.

A more detailed examination of the effects of water stress on reproductive parameters shows that there was a poor relationship between seed yield and total inflorescence numbers due, no doubt, to differences in inflorescence size between treatments and to different numbers of florets and seeds per inflorescence. Unfortunately, it was not possible, in this experiment, to segmentally tag emerging inflorescences in the different treatments. However in a previous study on Ruzi grass (Wongsuwan, 1994) it was found that during reproductive development early emerging inflorescences generally arose from the larger basal tillers and contributed most to seed yield. This was followed by generally smaller inflorescences from either new basal or old aerial tillers; and finally from an increased proportion of smaller new aerial tillers emerging at the late development stage. Therefore if seed harvest was late, yields were relatively low, due to the smaller sized inflorescences of the late emerging fertile tillers and the loss of seed by shedding from earlier formed basal tillers. Boonman (1971b), working with *Chloris gayana,* also found that the number of racemes per head and mean raceme length both decreased at progressively later stages of heading. This general reaction under adequate soil moisture conditions can, however, be radically changed by water stress, particularly when severe and depending on the period when it occurs. For example, in this study, non-stressed plants appeared to follow the sequence mentioned above, as did mildly stressed plants to a large extent, but severely stressed plants showed a remarkable "flush" in inflorescences arising from aerial tillers during the early stage (FI-EE) and particularly during the mid stage (EE-FF) as reported earlier. Importantly, however, these inflorescences were much smaller and less productive producing a mean of seven harvestable seeds per inflorescence and nine harvestable seeds per inflorescence respectively in the D_2WW and WD_2W treatments, compared with twenty-eight harvestable seeds per inflorescence in the control treatment. In contrast, those plants exposed to severe stress at the late stage (WWD_2) produced inflorescences equal in size to those from the control treatment and with similar seed weight. In other words, it appears that a major reason for the failure of plants exposed to early severe stress (D_2WW) to recover when followed by adequate water through to seed harvest was due to low numbers of seeds per inflorescence resulting in low seed yield. By comparison those plants exposed to severe stress only during the mid stage (WD_2W) were able to recover subsequently when rewatered due mainly to an upsurge in fertile aerial tillers which, although still low in seed number per inflorescence, were sufficient in numbers to achieve a seed yield similar to the control treatment. The appearance of deformed inflorescences may indicate that early formed inflorescences were damaged in both D_2WW and WD_2W treatments. The other single severe stress treatment (WWD_2) receiving adequate water for an extended period prior to stress, allowed plants to retain the capacity to achieve seed yields comparable with the control plants due presumably to the successful completion of the seed production cycle by a relatively high proportion of large, old, early-formed basal tillers each forming high numbers of harvestable seeds per inflorescence. It is important also that while severe stress applied during the early and middle stress of reproductive development (FI-EE and EE-FF) generally extended the time taken to complete the stage, there was no extension of time when stress was applied during the late stage (FF-SH).

Generally, percentage seed set of plant which can produce seeds is satisfactory in the range of 43-68%, indicating the appropriate harvesting time applying in this study. In fact, this relatively high percentage of seed set achieved is considered very favourable when one reads the comments of Ferguson and Crowder (1974) who regarded a 30% seed set as high frequency at cross-fertilisation for Ruzi grass. The advantage in this aspect of the current experiment may arise from the basis of a single plant study and also under the controlled environment which has less seed shedding.

As mentioned earlier the effects of water stress on seed weight was generally small and non-significant although there was a tendency for reduced seed weight under extended water stress. The only exception was the significant reduction recorded in the treatment subjected to severe stress over two developmental stages (D_2WD_2) - where some seed was able to be harvested and measured. These results agree with Hebblethwaite (1980) who found that moisture stress during seed-filling reduced seed weight significantly.

It might be expected that heavier seeds would show better germination than lighter seeds. This was not clearly apparent since the lightest seeds produced from the most severely stressed treatment (D_2WD_2) showed the highest percentage germination (Table 6.12). However, conclusive evidence cannot be drawn from this data on TSDW as differences recorded were largely non-significant. Perhaps, however, plants were reacting to stress by reducing yield dramatically while still retaining acceptable seed quality.

The overall efficiency of the plant in terms of harvest index (Table 6.19) showed some important differences between treatments. According to Humphreys and Riveros (1986) seed crops such as cereals generally show a high harvest index due to a greater distribution of assimilate to seed rather than to stem, roots and late-formed leaves. In tropical grasses Bahnisch (1975) and Boonman (1972c) have both reported relatively low harvest indices for *Setaria anceps* of less than 1% but Chadhokar and Humphreys (1973a) recorded a figure of 8% for *Paspalum plicatulum*. In this experiment the figure obtained are similar to those of Chadhokar and Humphreys (1973a), but it must be remembered that they are derived from single plants rather than swards. Nonetheless the comparative picture between treatments is relevant and interesting.

The most striking improvement in harvest index, compared with fully watered plants, came from the treatments subjected to mild stress during the early stage of floral initiation followed by no-stress during the next stage of ear emergence - up to 13.6% and 12.3% in the D_1WW and D_1WD_1 treatments respectively. However, when stress was severe and extended there was a significant reduction in the harvest index. It appears, therefore, that the early and temporary stress imposed on the plant followed by rewatering lead to a significant diversion of assimilates into seed production and hence a significant increase in harvest index.

6.5 CONCLUSION

The response of plants to different levels of water application were clearly shown in terms of physiological and morphological changes, particularly when these applications were continued throughout reproductive development (WWW, $D_1D_1D_1$ and $D_2D_2D_2$). As a result, although the higher amount of water applied resulted in greater dry matter production, in terms of reproductive development there was relatively little difference between non stressed and mildly stressed plants. However, under severe stress during two or three developmental stages, plants developed inflorescences which were unable to emerge, or, if they did , were severely deformed. The stage of plant development and level of water stress applied were both important in affecting plant dry matter production, seed yield and seed yield components.

Under mild water stress there was a similar effect in the duration of the reproductive developmental stages of plant (41-47 days) compared with fully watered plants (41 days). However, in mild stressed plants (D_1) the particular stages of ear emergence (WD_1W) and full flowering (WWD_1) were most sensitive to reduction in seed yield, and further decreases occurred if mild stress continued until seed harvest (WD_1D_1). Mild stress also had significant effects on reducing the percentage of harvestable inflorescence as well as inflorescence size when compared with the control treatment. Some reduction in floret numbers, seed numbers and seed setting percentage was also recorded in mildly stressed plants.

Subjecting plants to severe water stress dramatically extended the duration of seed developmental stages (48-76 days). The most sensitive reproductive stage when a single stress was applied during the period from floral initiation to ear emergence (D_2WW) compared with other stages (WD_2W, WWD_2). Moreover, stress at this time led to total failure of reproductive development particularly if it continued from floral initiation through to full flowering (D_2D_2W), or from ear emergence to seed harvest stage (WD_2D_2). However, those plants receiving temporary relief from severe stress by watering during the EE-FF stage (D_2WD_2) did manage to complete the reproductive processes through to seed harvest, - albeit with limited success. It is also apparent that if plants suffer severe stress during the final stage (e.g. WWD_2), from FF-SH, this appears to have relatively little affect on the length of the reproductive process (48 days). Similarly, components of seed yield were affected at mild stress levels, but seed weight was also decreased especially when severe stressing continued from full flowering onwards after temporary stress relief by watering at the ear emergence stage (D_2WD_2).

Water stress sensitivity at different stages of reproductive development influenced seed yield differently. Under mild water stress, the earlier in the reproductive developmental stage the stress was applied the faster the plants developed and the less the danger to inflorescence components, compared with the situation where water stress occurred during later stages after inflorescences had emerged. Conversely however, under severe stress situations occurring during the earlier stages of reproductive development, from floral initiation to ear emergence, this had a severe effect in damaging inflorescence numbers and quality, particularly as deformed inflorescences. Moreover, basal tillers were stunted and were capable of only limited regrowth after re-watering.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1 INTRODUCTION

Pasture improvement with improved pasture species is becoming more widely accepted for dairy farming in Thailand. As a result, labour-intensive specialist systems of seed production have been developed to fulfill the increasing high demand for seed. Presently, production is mainly focused on seed production only. So, an opportunity exists to maximise the net return from seed fields by imposing management practices which improve pasture utilisation as herbage for animal feeding during the vegetative stage. This suggests that Thai dairy farmers, particularly newly established groups, may utilise this dual management system to provide animal feeding and seed production as a source of additional income. Pasture management practices for herbage production and seed production are likely to be different but are not well understood in terms of the effects of defoliation on plant growth and reproduction (Humphreys and Riveros, 1986). This philosophy provided the focus for the present study on Ruzi grass; this species was chosen because of its widespread use for improved pasture production in Thailand.

7.2 PHENOTYPIC VARIATION OF PLANT POPULATION

7.2.1 Comparison of plant population

The results obtained from the spaced plant evaluation of Ruzi grass in this study showed that plants grown from a commercial seedlot from Thailand displayed significant differences within the same plant population. These findings generally support similar results by Valle *et al.* (1993) who studied the morphological characterisation of *Brachiaria* germplasm and showed phenotypic variation could be divided into 8 clusters. When Ruzi grass was considered in a similar way in the present study plants could be divided into 2 groups: firstly, a group having intermediate characteristics for all descriptors (medium height, short inflorescences, few and short racemes; and secondly, a group which included the tallest plants with larger inflorescences and numerous racemes. However, apart from these two different growth forms, the results did not entirely conform to these definition groups proposed by Valle *et al.* (1993) in *Brachiaria* spp. This was particularly true characteristics where no significant differences occurred within the population and none of the plant parameters were well correlated (Table 3.15). The results, however, have indicated that prostrate plants produced the lowest plant dry matter, but there were no significant differences between erect and semi-erect plants in these terms (Table 3.4). Somewhat surprisingly, all plant growth forms had similar seed yield potential in terms of both inflorescence and floret numbers/plant (Table 3.14). However, strong evidence of variation in old basal tiller numbers between plants in the population at final cutting may be the key factor (Table 3.11).

Other characters recorded (stem colour, ligule colour, leaf hairiness, leaf width) showed similar proportions between groups, but were not correlated with main agronomic features especially dry matter yield and seed yield components as shown in Table 3.15.

7.2.2 Plant performance under spaced plant and miniature sward conditions

Although plant performance under spaced-plant and miniature sward conditions was not initially involved in the study objectives, it is interesting that significant differences occurred in this regard. In particular, greater plant growth rates occurred in single plants than in a sward (i.e. 4.0 gDM/plant/day (adjusted from Table 3.1) compared with only 0.2-0.4 g/plant/day (adjusted from Table 4.3 and Table 5.3) respectively). This comparison might be considered spurious. However the results were obtained during a similar cutting duration (approx. 2 weeks) during which time all other factors such as nutrients and stand age were similar. A significantly higher seed yield was also obtained in single plants than in swards. This was thought to have occurred as a result of greater tiller numbers per plant in single plants and consequently higher herbage and seed production. Similar results were reported by Ribiero (1970) in a study on perennial ryegrass (*Lolium perenne* L.) who suggested that the prediction of sward yield based on the performance of widely spaced plants was unreliable. However, it is possible, particularly during the initial stages of a breeding programme that sufficient seed is not readily available to be able to carry out experiments under sward conditions. As a result the breeder may have to resort to the use of individually spaced plants for initial plant evaluation (Van Wijk, 1980).

7.2.3 Plant selection and recommendations

In order to improve herbage production of Ruzi grass, this study suggests that the selection should be focused on high dry matter yield and high tiller numbers from erect or semi-erect plants. These two performance parameters may also useful for improved pasture utilization, since Stobbs (1973) has suggested they may both be major factors affecting bite size taken by cows during grazing.

Seed production improvement from spaced-plants was smaller than herbage production improvement. As mentioned earlier, there were no significant differences in potential seed yield among growth form plants (Table 3.14) and also no correlation between the plant parameters recorded (Table 3.15). However, attempts to select single plants for higher seed yield will generally involve plants breeding a higher number of inflorescences and fertile tillers which may lead to increased seed yield. This certainly occurs under sward conditions (Figures 4.6, 5.2).

7.3 MANAGEMENT PRACTICES FOR HERBAGE AND SEED PRODUCTION

7.3.1 Effect of defoliation

Understanding the capacity of plants to regrow after defoliation is clearly a central theme of grassland research, and grassland scientists have continued to seek ways of manipulating genotypes to improve their capacity for regrowth, or of manipulating management to minimise the adverse impact of defoliation on growth (Parsons, 1983).

In Chapter 4, the results of plant DM daily growth rates of Ruzi grass showed no significant differences under 4 cm and 12 cm cutting intensities (Table 4.3), indicating the suitability of Ruzi grass sward utilisation in both grazing and cut and carry systems. Despite this, there was a definite advantage of higher cutting (12 cm) due to improved leafiness (Table 4.4) a higher leaf:stem ratio (Table 4.6), and most importantly higher tiller numbers (Table 4.8). In terms of cutting frequency, however, the results clearly showed that the less frequent cutting resulted in higher plant dry matter yield (Table 4.3), despite the tendency to decrease both herbage quality (Table 4.9) and also tiller numbers. This was particularly the case under lax cutting (Table 4.8). Accordingly, the 'most appropriate' recommendation for cutting frequency and intensity of Ruzi grass pasture management was 35 and 12 cm, respectively. This cutting regime was therefore adopted for further experiments in this study.

The pattern of tillering and tiller development have been documented in well-fertilised seed crops covering eight tropical grass species by Boonman (1971b) and Loch (1985). Both showed that maximum tillering occurred during early vegetative growth and then declined before inflorescences emerged due to some tillers dying without completing reproductive development. In the current study of Ruzi grass, tiller development in both spaced-plant (Table 3.1) and miniature swards (Table 4.8) showed a substantial increase over time after the appropriate cutting management had been applied. In fact, both frequency and intensity of defoliation management had a profound influence on tiller development. This was particularly apparent when different cutting treatments were compared as shown in Table 4.8. Only 2 treatments (12-20 and 12-35 cm) successfully and consistently increased tiller numbers. However, after the seed harvest (at final cutting) only plants in miniature swards had lowered tiller numbers (Figure 4.5 and Table 5.19). The continued increase of tillers in spaced-plants may simply reflect the longer period from closing to seed production and the extra space available for growth.

This work suggests that for dual purpose use of Ruzi pasture for herbage and seed production management emphasis should focus on how to encourage high tiller numbers during the vegetative stage and how to maintain a high proportion of survival of reproductive tillers.

7.3.2 Effect of closing pasture (the last defoliation for seed production)

Ruzi grass is sensitive to photoperiod, behaving as a quantitative short day plant as defined by Dirven *et al.* (1979). Although it is easy to be mislead by a few border plants producing inflorescences during the declining photoperiod in January (15 to 14 hrs), the majority of plants produced a main crop of inflorescences in late April and May in a decreasing photoperiod from 11 to 10 hrs.

The date of 'closing' of plants (cessation of cutting) had no significant effect on herbage yield (Table 5.3), perhaps due to the slow regrowth of plants because of the pending approach of reproductive growth onset. Despite this, early closing significantly increased dry matter yield (Table 5.4) and affected tiller development at the final cut (Table 5.19). As a result, there were no significant differences in seed yield between early and medium closing treatments but both were significantly higher than that obtained from the late closing treatment (Table 5.8). Tiller dry weight partitioning as showed in Table 5.5 positively affected the size of inflorescences produced in terms of total floret numbers (Table 5.14) as well as also reflecting on seed quality particularly pure germinating seed yield (Table 5.18). These features provide clear evidence to support the advantage of early closing over the medium and late closing treatments. Perhaps this can be explained by the fact that the green surfaces of the inflorescence and its supporting stem contribute significantly to the assimilate demands of the developing seed as noted by Humphreys and Riveros (1986). In addition, the timing of cutting or grazing should be considered in relation to crop development and to likely subsequent environmental conditions, since both can affect ultimate seed yield (Humphreys, 1991).

7.3.3 Nitrogen fertilizer

Nitrogen availability has long been considered as the primary mineral constraint to plant and animal production from grassland since Mulder (1952) identified the need for grassland uptake of 300 kg N/ha to produce a yield of 10 t/ha, and the long term use of nitrogen fertilizer for grass seed crops (Humphreys and Riveros, 1986). However, little information is available on the nitrogen management requirement particularly nitrogen fertilizer application on dual purpose pastures (for herbage and also seed production).

In this study (Chapter 5), nitrogen fertilizer clearly had an influence on herbage, seed and dry matter yields after seed harvesting, as shown in Tables 5.3, 5.8, and 5.4, respectively. In addition, it is interesting to note that applied nitrogen generally encouraged tiller production, particularly during vegetative growth (Table 5.19). It is also possible that the defoliation intensity and frequency treatments applied which adopted from Chapter 4 may have contributed in this regard prior the start of the experiment and had a carry over effect for the nitrogen experiment in the second year of these swards. Once again, reproductive tiller numbers decreased dramatically when compared with vegetative tiller numbers (Table 5.19). Importantly, though, nitrogen fertilizer application increased seed yields (Table 5.8) and also pure germinating seed (PGS) yields (Table 5.18) mainly by stimulating more inflorescence numbers (Table 5.9) and harvested inflorescence numbers (Table 5.10). This effect was significant up to 150 kg N/ha but not beyond. Despite the effect of nitrogen in increasing seed yield, nitrogen had no effect on seed quality, in particular TSDW (Table 5.13) and %PGS (Table 5.17).

7.4 THE EFFECTS OF WATER STRESS ON SUBSEQUENT REPRODUCTIVE DEVELOPMENT AND SEED YIELD

7.4.1 The sensitivity of vegetative growth to plant water stress

The results from this study confirm that Ruzi grass has good drought tolerance (Skerman and Riveros, 1990), and showed that the plant is quite able to survive a prolonged and severe moisture limitation without seriously impairing its ability to recover. This dehydration tolerance is associated with leaf extension (numbers of leaves produced), stem elongation (plant height) and decreasing plant dry weight. A decrease in chlorophyll concentration as observed in the pale green colour of the leaves and wilt and shrinkage of leaves during the stress period, was also noticed. These reactions are physiological and morphological responses when soil water is gradually depleted and a number of plant functions are inhibited (Boyer, 1970; Herrero and Johnson, 1981; Westgate and Boyer, 1985). Obviously, reductions in leaf area may assist the plant to conserve soil water and may be regarded as a means of drought adaptation by the plant (Begg and Turner, 1976; Turner and Begg, 1978; Chu, 1979; Paez *et al.*, 1995).

Basal tiller numbers were the most striking visual evidence of the effect of water deficit associated with "survival" of the plant. As an example in Table 6.18, shows that live tiller numbers in $D_2D_2D_2$ and D_2D_2 W treatments were 35 and 45 respectively compared with 96 in the full water (WWW) treatment. This implies that tiller number are less sensitive to water stress, once they are initiated and are generally able to survive particularly under the severe water stress by remaining "dormant" i.e. cessation of cell elongation. As a result stressed plants were much smaller than those in the control treatment.

Leaf area was very responsive to water deficits but recovered quickly upon rewatering as shown in Table 6.16. For example, plants exposed to the WD_2W treatment had a similar leaf area to fully watered plants. However plants in the WWD_2 treatment were unable to respond in this aspect (Table 6.16). During the recovery period following water application total leaf area was markedly increased by a rapid increase in leaf numbers, particularly before inflorescence exertion. This is one of the most important roles of water in maintaining the turgor which is essential for cell enlargement and growth and for maintaining the form of herbaceous plants (Kramer and Boyer, 1995).

The effect of water deficit on leaf area and leaf number may greatly affect total plant dry matter yield. In other words, any increase in the water supplied to the plant increases plant dry matter yield by encouraging stem elongation and increased leaf and dry weight. This result is clearly shown in terms of leaf:stem ratio (Table 6.17).

7.4.2 The sensitivity of seed yield and yield components to plant water stress

The timing and degree of water stress is important in Ruzi grass seed production. Under mild water stress conditions the result show that the earlier the stress is applied the greater the opportunity for plants to recover without any detrimental effects on seed yields. Conversely, severe stress conditions were not reversible because early formed inflorescences were damaged and deformed (Table 6.11; Plate 6.2a,b,c). Water stress at the flowering stage had similar effects on seed yield in both mild and severe water stressed plants (Table 6.3). However, there was a compensatory growth effect in plants under severe water stress at the stage from floral initiation to ear emergence. These plants were able to recover after rewatering but required a lengthy recovery period (Table 6.2) to initiate and develop ultimately harvestable inflorescences arising from new basal tillers and also from new and old aerial tillers (Table 6.6).

The results of this study show that an extended period of water stress may cause seed yield reduction particularly when it occurs during the early stages of development and that yield loss is more serious under severe water deficit conditions.

As far as the quality of seed produced is concerned, water stress had little or no effect on this aspect in term of seed weight (Table 6.8) or %PGS (Table 6.12). Consequently, PGS yields (Table 6.12) were similar under mild and a single severe stress conditions except when continued water stress occupied two stages.

Fully watered plant obviously received an oversupply of water which was directed into plant dry matter instead of seed production. Basically, plants require sufficient water to maintain tiller survival after the closing cut since tillers present at this time will be the major contributors to seed yield and less dry matter is produced. In addition, too much vegetative production can reduce seed yield by causing lodging especially in the field.

7.5 CONCLUSIONS

The phenotypic variation in plant population of Ruzi grass has been identified in this study. The obviously different plant growth forms (erect, semi-erect and prostrate) may be useful for plant breeders to consider in plant selection. Erect and semi-erect growth form plants showed significantly higher herbage yields than prostrate plants but similar seed yields. Under sward conditions, growth form became less important since competition between plants resulted in smaller plants, with fewer tillers per plant, and lower growth rates.

The dual purpose of pasture utilisation for both herbage and seed production was successfully demonstrated under sward conditions. The defoliation of 12-35 cm selected was considered to be the most appropriate for Ruzi grass as it successfully brought together relatively high dry matter production, high leaf:stem ratio and high herbage quality (protein content) and also potentially produced high seed yield. In particular, the increase in live tiller numbers during the vegetative stage shows how correct defoliation management can work effectively, and enhance seed yields.

Plant dry matter yield was dramatically linearly increased with the addition of nitrogen fertilizer applied up to 250 kg N/ha. However, in terms of seed yield significant increases to nitrogen fertilizer were only found at application rates up to 150 kg N/ha but not beyond.

Closing date had no significant effect on herbage production although growth rate was reduced as plants approached the onset of the reproductive stage. Seed yields were, however, related to closing time, with earlier closing returning the highest seed yield in terms of both quantity and pure germinating seed.

The interaction between nitrogen fertilizer application rate and time of closing on seed yield indicates that if Ruzi crops are closed for seed early and nitrogen supplied at 150 kg N/ha both high yield and quality seed can be produced.

Levels of water stress and stage of reproductive development at which stress applied related to plant dry matter and seed yield. Water stress occurring between floral initiation and ear emergence reduced the number of basal fertile tillers. This in turn had a significant effect on seed yield. After flowering, water stress was less detrimental to seed yield, although the recovery of plants after relief of water stress by rewatering was slower and smaller inflorescences were produced.

Appendix 4.1 Method of calculating herbage production, leaf:stem ratio and leaf area index

Herbage production

Total fresh weight at harvest from 25 plants (TFW) = X (g)

Sample (~ 200g) from X for dry weight = Y (g); and divided into leaf (Y_1) and stem (Y_2)

Total leaf fresh weight (LFW) = $(XY_1)/Y$

Total stem fresh weight (SFW) = $(XY_2)/Y$

The dry weight of leaf (Y_1) = a; and the dry weight of stem (Y_2) = b

Total leaf dry weight (LDW) = (aX)/Y

Total stem dry weight (SDW) = (bX)/Y

Leaf (L) : Stem (S) ratio

L:S = (LDW) : (SDW)

Leaf Area Index (LAI)

Taken leaf (Y_1) to measure leaf area = L cm^2

Total leaf area for 25 plants = (XL)/Y cm^2

The area of 25 plant growing is 5625 cm^2

LAI = (XL)/(5625Y)

Appendix 5.1 Mean tiller dry matter production (kg/ha) of new reproductive tillers in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	911	214	0	375.2 b
150	1902	429	0	777.2 ab
250	3146	497	51.2	1231.6 a
Mean[2]	1986.8 a	380 b	17.2 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	*	*	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

Appendix 5.2 Mean inflorescence numbers (numbers/m^2) produced by new tillers in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	67	24	0	29 b
150	168	61	0	76 a
250	289	60	9	120 a
Mean[2]	173 a	48 b	3 b	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	**	**	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

Appendix 5.3 Mean tiller numbers at final cutting (tiller numbers/m^2) in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	585	538	432	519 b
150	570	648	473	564 b
250	906	596	604	702 a
Mean[2]	688 a	594 b	503 c	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	***	***	*	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

Appendix 5.4 Mean new reproductive tiller numbers (tiller numbers/m^2) in different nitrogen and closing date treatments

Nitrogen (kg/ha)	Closing date Early	Medium	Late	Mean[1]
50	56	24	0	27 c
150	128	61	0	63 b
250	293	60	9	121 a
Mean[2]	159 a	48 b	3 c	
	Closing date(C)	Nitrogen(N)	C x N	
Significance	****	****	****	

[1] and [2] means sharing the same letter are not significantly different at $P \leq 0.05$

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