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A STUDY OF THE EFFECTS OF
DEFOLIATION AND WATER STRESS
ON GROWTH AND DEVELOPMENT OF
STYLOSANTHES HAMATA (L.) TAUB. CV VERANO

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ABSTRACT

Verano stylo (Stylosanthes hamata (L.) Taub.) is an important pioneer legume in the tropics and its potential as a pasture legume under grazing appears to be promising in Thailand.

This thesis was carried out in two parts - the first part was conducted in the Controlled Climate Rooms at the Plant Physiology Division, DSIR, Palmerston North, New Zealand. The aim of these studies was to obtain basic information on growth patterns and the response of Verano stylo to cutting at different intensities, frequencies and stages of growth and at two levels of water stress in terms of quantity and quality of herbage produced. The second part was a grazing trial conducted at Muaklek, Thailand, to test the grazing management hypothesis derived from the Controlled Climate Room studies.

The results from the Controlled Climate Room studies showed that the growth and development of intact Verano stylo was slow at the pre-flowering stage and increased rapidly after the onset of flowering. Maximum growth rate of 2.04 grams/plant/day was recorded between 70 and 80 days and maximum dry weight of 105 grams/plant was achieved approximately 108 days after seedling emergence. During this post-flowering stage, plant growth in terms of plant dry weight, branch development, leaf number and leaf area increased rapidly.

Flowering commenced 35 days after seedling emergence and continued throughout the experimental period. Stem was the major plant component, followed by the inflorescence and leaf fractions.

In terms of the response to various cutting regimes, the results showed that the more severe the cutting the more deleterious was the effect on regrowth. Cutting the primary branches had a greater effect on plant regrowth in terms of

plant dry weight, branch number, leaf number and leaf area than defoliating the main stem. Severe cutting of primary branches (i.e. to node 0) plus hard cutting of the main stem (i.e. to node 3) resulted in the death of the plant after two cuts. When defoliation was delayed to the later stage of growth (near maximum growth rate), severe cutting of the primary branches (i.e. to node 0) caused extensive plant death following only a single cut. All growth parameters recorded were markedly reduced when the interval between cutting was decreased. It is suggested that the response of Verano stylo to defoliation is dependent upon the number and especially the size of the primary branches, the number of growing points, the amount of stubble reserves and the residual leaf area immediately after cutting.

The differences in yields were largely due to changes in the stem and to a lesser extent the inflorescence and leaf fractions.

Growth of the plant in terms of plant dry weight, branch number, leaf number and leaf area were reduced to a greater extent under severe than under mild water stress. The differences in plant dry weight between the two levels of stress were largely due to the size of the stem fraction. After rewatering there was a rapid increase in growth by both the previously mild and severe water stressed plants, resulting in a marked increase of all the variables recorded. However, growth of plants previously under severe water stress was less than those previously under mild water stress. The increase in total plant dry weight was due to an increase in all plant components, especially leaf and inflorescence fractions. Severity of cutting had less effect on plant variables than water stress. The effect of cutting was more apparent under mild water stress than under severe water stress in terms of plant dry weight, branch number and leaf area, and continued to show this effect on rewatering with respect to leaf number and leaf area.

Verano stylo herbage quality, as measured by crude protein concentration, was relatively high even in the uncut control plants. Defoliation increased the protein concentration, but within the cutting treatments there was little effect of cutting intensities and frequencies on the crude protein concentrations of all plant components, except the stem fraction which was slightly superior under frequent than infrequent cutting. The protein concentration was higher in the leaf and inflorescence and lower in the stem at all cutting intensities and frequencies.

Severe moisture stress increased the crude protein content in the leaves, stems and inflorescences compared with mild moisture stress and continued to show this effect on rewatering with respect to the leaf and stubble fractions.

Hard cutting in the drought period also increased protein concentrations in the leaves, stems and inflorescences compared with lax cutting and continued to show this effect on rewatering with respect to the stubble and stem fractions.

Although the crude protein concentrations in different plant parts and for different cutting intensities, frequencies and stages of cutting and for different water regimes were relatively small, the amounts per plant were large due to the substantial and significant differences obtained in dry weight between treatments. The increase in crude protein was largely due to the inflorescence fraction, especially under lax cutting. Crude protein yields were also seriously reduced under frequent and hard cutting of the primary branches.

Previously stressed plants at either mild or severe levels greatly increased their crude protein yield after rewatering, and this was largely due to the crude protein yield of the leaf and inflorescence components.

In terms of carbohydrate reserves, the results of this study clearly showed that the concentration of these reserves in the residual top and roots of Verano stylo were low ($< 3\%$ of dry weight), were comprised mainly of sugar and were independent of the stage, intensity and frequency of cutting. However, carbohydrate concentrations were substantially increased by severe and especially mild water stress. Starch was the major component and accumulated in all plant parts especially the stubble, stem and tap root fractions. The effects of cutting during the drought period were only evident in the stubble, inflorescence and tap root fractions - the levels declining with increasing intensity of defoliation, particularly of the starch fraction. However, these carbohydrates, especially the starch fraction in the stubble, stem and tap root, almost totally disappeared during the rapid recovery phase, suggesting it was used for regrowth.

In terms of the amounts of carbohydrates, the results showed that the differences between cutting intensity were largely due to the differences in the residual dry weights especially in the stubble. Generally the more severe the cutting, the lower the amount of carbohydrates in the stubble. However, cutting frequency had no significant effect on carbohydrate accumulation. Severe water stressed plants accumulated only half the reserves of the mild water stressed plants during the drought period. Under both mild and severe water stress, the stem was the major accumulator of these reserves, particularly of the starch fraction. On rewatering, there was a marked increase in the accumulation of sugar akin to the increase in dry matter yields. However, starch yields in the stem and tap root showed a substantial drop during this period.

During the drought period, hard cutting significantly depressed the accumulation of sugar and starch especially under mild water stress. In the roots only the starch fraction was affected. On rewatering, previous hard cutting continued to depress carbohydrate yield but only of the starch fraction of those plants under previous severe water stress.

The results from the field experiment confirmed the importance of residual leaf and branch numbers on plant regrowth in terms of dry matter production, branch development, leaf number and leaf area and their persistence. Under climate room conditions, 6 weekly cutting produced significantly higher yields of all growth components than did 3 weekly cutting. However, under field grazing conditions frequent grazing (every 4 weeks) produced significantly higher yields than infrequent grazing (every 8 weeks). Frequent grazing also maintained a higher density of Verano stylo plants and a lower weed content.

The results are discussed in relation to the possible grazing management of Verano stylo in Thailand.

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CHAPTER 1

INTRODUCTION AND OBJECTIVES

More than 50% of the world's ruminant animal population is in the tropics and subtropics (30°S to 30°N) (Whiteman, 1980). These animals are mostly raised on poor natural grassland (Whiteman, 1980) and less than 5% of these pastures have been improved (Mannetje, 1978). The yields of these natural grasslands are generally low and of poor quality due to rapid maturity producing feed of low protein content and resulting in low animal intake of digestible nutrients (Shaw and Bisset, 1955; Norman, 1962). Even with cultivated grass species, the quality is still relatively low when compared with the temperate species (Minson and McLeod, 1970) and is also highly variable between genera and species (Reid et al, 1973). Hence, productivity is poor compared with that of temperate regions (Whiteman, 1980).

To overcome the nutritional limitations of natural and cultivated tropical grassland, the use of supplementary feeding, of nitrogen in conjunction with other fertilisers and of nodulated legumes, has been proposed by several workers (Jones, 1972; Humphreys, 1978a; Whiteman, 1980; Murray, 1983). Of these alternatives, the first two approaches are rather expensive and in the case of nitrogen fertilisers, are too dependent and variable according to the fluctuating environments (Jones, 1972; Whiteman, 1980). The most feasible and economical approach on a large scale basis is through the use of suitable legumes.

The role of legumes in temperate pastures to increase the productivity through symbiotic nitrogen fixation and increased feed quality, is well known. Much research over the years has centred on an effort to find suitable legumes for the tropics (Mannetje 1978; Whiteman, 1978). Australian scientists have played a major role in this area of research and development with the successful introduction of Townsville stylo (Stylosanthes humilis kunth.) in the early 1900's (Humphreys, 1967) to improve the natural grassland in

the northern part of Australia.

Improvement of these natural grasslands encouraged scientists to collect and introduce new species from many parts of the tropics and subtropics for breeding and selection and subsequently the release, as commercial species, of a number of important legume species such as Siratro (Macroptilium atropurpureum (DC) Urb.), Stylo, Desmodium, etc. (Burt et al, 1971; Edye et al, 1974; Hutton and Beal, 1977; Whiteman, 1978; Imrie et al 1983; Edye and Grof, 1983).

However, the search for species suitable for particular areas is difficult since a wide range of climatic and edaphic conditions in the tropics and subtropics is encountered. These include low rainfall, high variability of precipitation (Skerman, 1977; Whiteman, 1980), low soil fertility and in some areas very low soil pH (Edye and Grof, 1983). A short rainy season and a long dry spell is the common occurrence in the monsoonal countries such as Northern Australia, Thailand, Burma, Laos and India, whereas in parts of Latin America and Indonesia, heavy rainfall occurs throughout the year (Crowder and Chheda, 1982; Edye and Grof, 1983). Species that have a high genetic variation tend to adapt well in the former conditions (Staples, 1981) and are illustrated by the annual pasture legume, Townsville stylo, which has been recognised in the northern part of Australia since 1900 (Humphreys, 1967; Whiteman, 1978).

Townsville stylo has proven successful for many years and in many tropical countries such as Thailand (Humphreys, 1978a, 1984). However, it is a poor competitor in association with the vigorous native grasses (Ritson et al, 1971; Torssell, 1973) and is easily attacked by the fungus disease Anthracnose (Colletotrichum gloeosporioides), resulting in a marked decline in yield and seed production (Robertson, 1978; Humphreys, 1984). However, with the introduction and testing of a large number of lines of Stylosanthes species into Australia in 1965 (Burt et al, 1971, 1974; Edye et al, 1974, 1975a, 1975b, 1976) improved cultivars have been selected and released, such as Stylosanthes hamata (L.) Taub.

cv Verano, S. scabra Vog. cv Seca and cv Fitzroys in 1973 (Edye et al, 1975b, 1976; Edye and Grof, 1983).

These three perennial cultivars appear to be more productive than the annual Townsville stylo because of their ability to produce herbage more quickly following the opening of the rainy season. This applies in particular to S. hamata cv Verano (Gillard et al, 1980). They are also able to respond to unseasonal rains. With their longer growing season and greater height and yield, these perennial legumes maintain a higher content in the pasture and a greater botanical stability (Gillard et al, 1980). In addition, S. hamata is more resistant to Anthracnose (Humphreys, 1978b; Whiteman, 1978; Vinijsanond and Topark-Ngarm, 1978). This pattern of development is ideal for regions with a highly variable climate such as Australia and Thailand, and it appears to be adapted to a wider range of soil types, and establishes better under lower rainfall than Townsville stylo (Burt et al 1974; Edye et al, 1975a, 1976; Gillard et al, 1980). The better adaptability of S. hamata to low soil fertility and rainfall conditions, has led to a rapid and growing interest in S. hamata as a tropical pasture legume particularly throughout the dry tropics (Humphreys, 1978a; Lenne and Sonoda, 1979; Whiteman, 1980).

Over the past decade, there has been considerable research on the behaviour of S. hamata cv Verano under varying cultural and managerial conditions (Gillard et al, 1980; Gardener, 1981). These studies have revealed that in spite of its promise it still has similar problems of variable establishment and persistence in a mixed, grazed sward (Gillard et al, 1980; Gardener, 1981) as does Townsville stylo, reflecting the common dependence of dry matter production on seedling regeneration from seed reserves in the soil (Gardener, 1981). In a long term study over 9 years at Landsdown, Australia, Gardener (1981) found that the majority of S. hamata plants died in their seedling years and only 0.03% survived to the end of the third year. In most years, S. hamata had to re-establish almost entirely from seed. Therefore, low legume yields were expected when seed-

lings of S. hamata competed poorly with the annual grasses.

A high rate of shoot replacement is necessary for the maintenance of growth under repeated defoliation and the numerous axillary buds close to the crown of a plant will enhance its ability to regrow under these conditions. This has been noted in S. guianensis (Aubl.) Sw. (Grof et al, 1970), Desmodium intortum C.P.I. 23189 (Imrie, 1971) and Psoralea eriantha (Gutteridge and Whiteman, 1975). Most of the research carried out on S. hamata has emphasized the effects of grazing or cutting on seed production (Wilaipon and Humphreys, 1976, 1981; Wilaipon et al, 1979 and Waikakul, 1983). Little information is available on the factors which affect the regrowth of this legume. It seems that the criteria to utilize this legume must be defined in order to achieve maximum persistence and/or production. Therefore, an understanding of the morphological and physiological development of this legume is needed to develop better cutting or grazing practices. With this in mind, a series of experiments was designed to determine the effects of defoliation on S. hamata cv Verano.

The objectives of this work were:-

1. To study the growth pattern of S. hamata under controlled conditions.
2. To define the morphological and physiological characteristics of S. hamata in terms of leaf, stem, inflorescence and branch growth in response to different defoliation regimes.
3. To study the effect of defoliation and water stress on growth characteristics of S. hamata.
4. To study the effects of grazing management on S. hamata production and survival.

CHAPTER 2

LITERATURE REVIEW

2.1 STYLOSANTHES HAMATA CV VERANO

2.1.1 Origin, Taxonomy, Distribution and Ecology

The genus was established in 1788 by O. Swartz (Mohlenbrock, 1958) and most of the detailed systematic work on the genus was done in the 18th and 19th centuries. In recent years, Mohlenbrock (1958) has described 30 species of Stylosanthes including Stylosanthes hamata (L.) Taub. while Burt et al (1971) and Edye et al (1973, 1974) have described a number of morphological and agronomic characters based on numerical classification. The most recent review of this genus is that of Mannetje (1984).

Stylosanthes species occur typically on savannahs and similar areas in Central America, South America, Southern Africa, Southeast Asia, India and in the east of the United States (Mohlenbrock, 1958). The distribution of species including hamata was closely related to the climate in which the species originated. Burt and Reid (1976) have divided Stylosanthes into six climatic types within nine phyto-geographic regions of the tropical parts of Central and South America. Stylosanthes belongs to the tribe Aeschynomeneae and comprises 25 species (Mannetje, 1984). Of these, five were considered by Whiteman (1980) to be of agricultural importance, namely the annual: S. humilis and the perennials: S. guianensis (syn. S. gracilis), S. hamata, S. scabra and S. subsericea.

The popularity of the genus as a tropical forage legume has increased markedly in the past 20 years, partly due to its remarkable hardiness and the adaptability of some of its species to various climatic and soil conditions (Burt et al, 1983; Edye and Grof, 1983). Australia was the first country to recognise the value of Stylosanthes species for improving tropical grassland particularly S. humilis (Humphreys, 1967). Because of the limitations of the natural pastures in

northern Australia, most pasture improvement has been based on introduced pasture species. Among these, a large number of Stylosanthes species were introduced from tropical America. Burt et al (1971) and Edye et al (1974) described and discussed a great number of these introduced Stylosanthes species by using agronomical and morphological characteristics (M-A group). As a result, Stylosanthes hamata cv Verano (Verano stylo) emerged as an outstanding accession and the most promising for a wide range of dry environments among the groups studied (Burt et al, 1971; Edye et al 1975b, 1976). Thus, it was recognised as a valuable forage legume in 1973 (Mackay, 1975) and commercial seed production began in 1974 (McKeague et al, 1978). This cultivar (Verano) has been tested throughout a number of countries in the tropics and subtropics including Thailand (Humphreys, 1978a), Malaysia (Humphreys, 1984) and USA (Lenne and Sonoda, 1979).

During the last decade, the ecology of Verano stylo in pasture systems has been reported by several workers (e.g. Torssell et al, 1976; Gillard et al, 1980; Gardener, 1981). The results of these studies indicated that the main factors affecting the balance of species in the mixed pasture are:

- i) the grazing pressure
- ii) the soil fertility and fertilizer application
- iii) the nitrogen supply from the legume
- iv) the other species in the pasture
- v) the time of opening rain.

Gardener (1981) studied population dynamics and stability of Verano stylo in grazed pastures. He found that the majority of plants died in the seedling year, and in most years Verano stylo had to re-establish almost entirely from seed. Therefore, a large carry over of seed from season to season was essential to maintain the soil seed reserve for the long term persistence of Verano stylo in the pasture system. In addition to these findings, he developed a conceptual model of the plant ecological processes in the grazed pasture. Basic processes in the system, such as: the amount of seed in the diet, the intake of feed, the percentage of intact seed passing through the digestive tract, the amount and rate of hard-seed breakdown and the survival of seedlings, were

considered. He also showed that stocking rate had little effect on seed input. A seed reserve, sufficient to supply the 30 - 100 seedlings/m², was needed each year for the maximum production of the legume. This gave Verano stylo the potential to colonize any site in the community left vacant by previous deaths. Whether this potential is realized depends on the timing and relative growth of the other species competing for the site. Gardener (1981) concluded that germination, establishment, growth, competition and seed production were important for seedling survival as previously reported in Stylosanthes humilis (Torssell, 1973, 1976; Torssell and Mckeen, 1976). Drought avoidance mechanisms such as faster rate of root growth, rapid seed germination and radicle elongation, are important factors for survival during the germination/establishment phase. However, heavy grazing after seed germination favoured the survival of Verano stylo. Gillard et al, (1980) also reported that the stability of a pasture mixture with Verano stylo is greatly limited initially by increasing pressure from the companion grasses following increased soil fertility. Torssell et al (1976) studied the competition and dynamics of the populations of three mixtures in legume-based pastures. Mixtures studied were S. humilis and Digitaria ciliaris; S. hamata and D. ciliaris; S. hamata and Urochloa mosambicensis. They reported that S. hamata yielded more than the other species and its competition with D. ciliaris was stronger than that of S. humilis. The changes in species composition were studied using the conceptual model of Torssell (1973). They reported that the legume proportion was always higher in the mixture S. hamata and D. ciliaris than in any of the other mixtures studied.

2.1.2 Morphological and Growth Habit

Burt et al (1971) classified Verano stylo as a herbaceous semi-erect or prostrate non-determinate plant with profuse branching and slender stems and small leaves. The average number of primary branches up to 5 cm on the main axis is 5.8 - 6.2. Verano stylo is a sympodial branching type and flowering occurs at an early stage of growth (Cameron and Mannetje, 1977). However, growth is continued

by branches developed from axillary buds arising below the floral apex. These branches soon cease growth as a result of conversion of the vegetative apex to the reproductive state. The axillary bud below the floral apex again produces a new branch and develops in a similar manner. As a result, canopy growth of Verano stylo is of a non-determinate, branching habit with a number of primary branches which are limited and vary according to the environment (Cameron and Mannetje, 1977). The plant may grow up to one metre in height in good conditions, but more typically 0.60 metre (Clements, 1980). Many growing buds have been reported close to the ground and a crown may develop under grazing or cutting conditions (Humphreys, 1978b; Burt et al 1983). The stems have short white hairs down one side (Edye et al, 1974). Leaves are trifoliate, leaflets lanceolate, acute glabrous with 4 - 6 pairs of veins and length-breadth ratio of 4.5 - 5.3, rachis 4 - 5 mm long and the bidentate stipules adnate to the base of the petiole with hairs on the sheath and teeth. The inflorescence is an oblong spike with 8 - 14 flowers on a long stem. The loment has two articulations which are usually both fertile. The upper one is usually hairy and has a moderately thick, coiled beak which is from more than half to equal length to that of the pod (Edye et al, 1974).

Verano stylo has a tap root system, with rapid root development at the seedling stage (Gardener, 1978). Roots of Verano stylo can penetrate into the soil up to 75 - 80 cm. These roots are very fine at such depth, and at a depth of 50 - 60 cm roots begin to divide progressively into small roots of approximately the same size (Gutteridge, 1982).

2.1.3 Fertilizer, Nodulation and Yield

Verano stylo is adapted to a wide range of soil types but prefers sand and sandy loam (Humphreys, 1978b, 1980a; Hare, 1985). It exhibits superior adaptation to acid and infertile soils compared with other tropical legumes (Bogdan, 1977; Humphreys, 1980a; Edye and Grof, 1983). Andrew and Norris (1961) attributed that feature of adaptation to the high ability of Stylosanthes species to extract calcium from

soil. Furthermore, Verano stylo exhibited greater tolerance to high aluminium concentration than other Stylosanthes species (S. guianensis cv Cook, S. humilis cv Paterson, S. scabra cv Fitzroy and S. viscosa (Carvalho et al, 1981). Wilaipon et al (1978) reported that Verano stylo and Siratro were more salt-tolerant than Pueraria phaseoloides and Calopogonium mucunoides. Carvalho et al (1980) also reported a remarkably efficient symbiotic association with Rhizobium at their highest aluminium concentration.

Similar to other species in the genus Stylosanthes, Verano stylo has a very low phosphorus requirement for growth compared with Siratro and Centrosema, and has a high ability to extract nutrients from soils compared with these legumes (Robinson, 1983). Jehne (1984) suggested that the presence of endotrophic mycorrhiza found on the roots of Verano stylo could account for its apparent low requirement for soil phosphorus. He also noted that mycorrhiza may aid the tolerance of the species to environmental and soil stress. Although some reports show the adaptation of this species to low phosphorus fertilizer, other reports have also shown strong responses to phosphorus fertilizer (Topark-Ngarm et al, 1979; Hall, 1979; Shelton et al, 1979).

Verano stylo nodulates freely and can be effectively nodulated with a broad spectrum of cowpea inoculant (Bogdan, 1977). Nodulation begins within 8 days after germination (Date et al, 1980).

Verano stylo grows well under an annual rainfall between 500 and 1270 mm and with a pronounced dry season (Burt et al 1974; Edye et al, 1975b; Gillard et al, 1980; Gilbert and Shaw, 1980). It has been reported to be drought tolerant (Burt and Miller, 1975) but has no tolerance to water-logging (Humphreys, 1980b). Verano stylo flowers early and vegetative growth continues while conditions are favourable (Cameron and Mannelje, 1977; Edye and Grof, 1983). The potential yields, therefore, are closely associated with the length of growing season as demonstrated by Edye et al (1977). They showed that the growth of one accession of S.

hamata and 25 accessions of S. guianensis were highly seasonal, and that the yield differences among accessions were greatest at the beginning and end of the growing season. Plants capable of producing feed under highly variable climates could diminish the problem of forage availability which is considered to be a major limiting factor in animal production. Topark-Ngarm and Akkasaang (1978) reported yields of 4.3 to 5.8 ton/ha/year under 4 and 6 week cutting in Thailand. Edye et al (1975b) reported from the dry tropics of Australia that in a three-year trial, S. hamata CPI 38842 (cv Verano) was superior in dry matter yield to the other accessions at a number of different sites. Bishop et al (1980) also demonstrated its outstanding performance in terms of dry matter yield, persistence and seedling regeneration under the high rainfall conditions of the Central Queensland wet coast. A mixture of Guinea grass (Panicum maximum) and Verano stylo was also shown to produce the total yield of 8.5 ton/ha in Thailand (Wilaipon and Humphreys, 1983). In this trial, Verano stylo yield and density in the second year was superior to that of Siratro under grazing conditions.

2.2 Effect of Defoliation on Tropical Legume

Defoliation is defined as the process of partial removal of the above-ground parts of plants by grazing animals or cutting machines (Hodgson, 1979). Defoliation by hand or machine cutting often involves more complete and sudden removal of plant tissues than occurs under grazing (Humphreys, 1978b, 1981). However, grazing by animals is characterised by a spatial heterogeneity of removal in both the vertical and horizontal dimension. Grazing also involves animal treading, selecting and the return of nutrients to pasture as dung and urine (Watkin and Clements, 1978). Defoliation has often been considered in terms of frequency, intensity and timing (Harris, 1978; Humphreys, 1978b).

The effects of defoliation on pastures have been reviewed by many workers (e.g. Jameson, 1963; Humphreys, 1966a; Harris, 1978; Watkin and Clements, 1978). These

authors pointed out that defoliation either by grazing animals or by cutting can influence morphology, regrowth ability, dry matter yield, root systems and herbage quality of the plant. Thus, the effects of defoliation on tropical legumes will be discussed in relation to the effects on these parameters.

2.2.1 Morphology and Growth Habit

Grazing or cutting modifies the growth form of many tropical legume species, and through phenotypic adaptation high rates of herbage production or persistence may still occur under these conditions. Hare (1986) observed that when Townsville stylo was grazed heavily from the start of the wet season, it developed a prostrate habit with many fine branches growing close to the ground. In areas reserved for seed production which were uncut throughout the wet season, it grew tall and erect with only a few branches close to the ground. Jones, R.M. (1973a) found that after three years of continuous grazing of Siratro (Macroptilium atropurpureum), the size of crown of Siratro was greatly affected. At the lightest stocking rate, most crowns were large (>1.0 cm diameter) with appreciable rhizome development, whereas at the heaviest stocking rate there was negligible rhizome development and most crowns were small (< 0.5 cm in diameter).

Jones (1974) also showed that in Siratro repeated defoliation to remove all leaves will result in reduced stolon development, reduced vigour and even death of plants. This effect could be even greater when the legume is growing in competition with grass. He found a close correlation between dry matter yield and stolon development.

The death of plants weakened by excessive defoliation has also been reported, particularly under late cutting with species such as Townsville stylo (Fisher, 1973), Crotalaria juncea (Kessler and Shelton, 1980) and Psoralea eriantha (Gutteridge and Whiteman, 1975). Treading by grazing animals may also affect growth and survival of plants (Watkin and Clements, 1978).

2.2.2 Regrowth Following Cutting

According to Humphreys (1981), successful pasture plants must be able to tolerate defoliation by cutting or grazing, by making adequate regrowth after defoliation and by surviving long enough to reproduce. Initially, regrowth is determined by the number of growing points (Mannetje et al, 1980). The rate of regrowth is determined by the leaf area remaining on the plant, the energy reserves and the water and nutrient uptake by roots (Ward and Blaser, 1961; Humphreys, 1966a, 1966b; Humphreys and Robinson, 1966; Grof et al, 1970; Jones, 1974; Yamada, 1975; Harris, 1978; Ludlow and Charles-Edwards, 1980; Mannetje et al, 1980; Hodgkinson and Williams, 1983).

2.2.2.1 Location and number of growing points

The location and number of growing points are determined by the plant habit and growth form of the species, the stage of plant development and the previous pasture management.

Tropical legumes are more variable in growth habit and location of growing points than grasses (Hodgkinson and Williams, 1983). The growing points of stoloniferous, prostrate legumes such as Lotononis, Townsville stylo, Desmodium trifolium and D. heterocarpon are located close to the ground and are well-protected by small leaves (Whiteman, 1969; Mannetje et al, 1980; Humphreys, 1981). This is in contrast to climbing or trailing or to an erect growing legume such as Siratro (Whiteman, 1969; Jones, 1974) and Desmodium (Jones, 1973) with the growing points located along the trailing stem or higher above the ground such as in one accession of Psoralea eriantha (Gutteridge and Whiteman, 1975). As such, close defoliation of these latter legumes removes the major proportion of the young active buds, leading to a reduced rate of regrowth and ability to compete with companion grasses. For example, Grof et al (1970) found poor survival and regrowth owing to poor basal branching and deficiency of basal bud sites in an erect genotype of Stylosanthes guianensis. A similar effect was found in an erect line of Psoralea eriantha (Gutteridge and Whiteman, 1975), Desmodium and Siratro (Whiteman, 1969; Jones, 1967,

1973, 1974).

Imrie (1971) subjected five lines of D. intortum to defoliation 10 or 30 cm from the crown, at 4-week intervals. The severe 10 cm treatment substantially reduced yield in four lines, but not in CPI 23189. The superior performance of this legume under severe cutting was due to defoliation stimulating growth from the axillary bud close to the crown of the plant. The other line initiated growth only from one or two buds immediately below the point of stem cutting. These findings illustrated the importance of growing points on regrowth.

During the vegetative stage, it is unlikely in most common tropical legumes for the growing point to be damaged by grazing or cutting. The position of the growing point above the cutting height late in the growing season, or with long cutting intervals, was reported to be the main factor contributing to low yield and mortality of Townsville stylo (Robertson et al, 1976). In some legumes, leaf senescence plus twining habit caused most of the growing points to be removed (Whiteman, 1969; Jones, 1967, 1973, 1974; Gutteridge and Whiteman, 1975).

2.2.2.2. Leaf area remaining

Under conditions of adequate water and nutrient supply, pasture growth depends on leaf area and light interception (Watson, 1952; Donald and Black, 1958; Brown and Blaser, 1968). Brougham (1960) found that productivity was also closely related to the amount of chlorophyll in leaf and non-leaf components. Although stem, petiole, leaf sheath and inflorescence intercepted light and participated to varying degrees in photosynthesis, the major contribution came from the leaf and hence lead Brougham (1960) to determine and use leaf area as a measure of productivity (leaf area being commonly expressed as leaf area index (LAI), i.e. the ratio of leaf area to ground area (Watson, 1947)).

The significance of leaf area in pasture growth has been reviewed by several workers (e.g. Donald and Black, 1958;

Brown and Blaser, 1968). In a young stand or in defoliated pasture, the quantity of light available is greater than can be intercepted and utilised by the plants and hence much of it is "lost" to the ground. As the plant grows and new leaves are produced, more and more of the incident light is intercepted by the leaf canopy until interception is complete. Competition for light then develops among the plants and among the leaves on the plant. As the density of the leaf canopy increases, older leaves receive insufficient light and may become parasitic on the plant - although some authors (Vickery, 1981) question this parasitic state. Finally, lower leaves begin to die and, in time, the rate of death of older leaves is equal to the rate of appearance of new leaves. A maximum or ceiling herbage growth rate has now been reached. Leaf area index at this point was classified as the optimum or critical leaf area index (Brougham, 1958). The critical and optimum LAI value varies among species because of the difference in their growth habit (Black, 1957; Brougham, 1958; Humphreys, 1966b). As LAI increases above the optimum, leaf loss and shedding cause the growth rate to drop (Donald and Black, 1958).

The relationship between LAI and pasture growth rate explains the general response of pasture to defoliation. Reduction in growth rate under low LAI is explained on the basis of inadequate light interception, while that occurring under a high LAI value is a result of accelerated senescence and increased respiratory load of leaves near or below their light compensation point (Donald and Black, 1958). In terms of pasture practice, Harris (1978) suggested that:

- 1) defoliation frequency should be such that the regrowth interval is extended until pasture growth rate begins to decline from its maximum

- 2) intensity of defoliation should be to the level that leaves the amount of biomass at which maximum growth rate is first attained.

However, there are many factors affecting the application of the LAI concept to defoliation practice. This is because the critical LAI value appears to vary with the environment (Brougham, 1958; Davidson and Donald, 1958; Black, 1963),

with the angle of sun elevation (Brougham, 1958) with light intensity (Stern and Donald, 1962; Black, 1963) and with the quality of the residual leaves (Humphreys, 1978b).

The significance of LAI on subsequent regrowth has been demonstrated in both tropical and temperate pasture species. With a tropical legume, Jones (1974) found that the regrowth yield of Siratro was linearly related to residual LAI on the stubble at the start of growth up to 70 days. This is in contrast to lucerne which showed the beneficial effect of residual leaf area for only a short period of regrowth (Leach, 1967). Ludlow and Charles-Edwards (1980) reported that residual leaf area index is a major determinant of *Setaria/Desmodium* sward regrowth. Grof et al (1970) reported that poor regrowth of *S.guianensis* was associated with low leaf number and area remaining at low cutting frequency. Because of low leaf areas in the lower part of the plant, cutting at the late stage or late in the growing season resulted in poor regrowth (Fisher, 1973; Kessler and Shelton, 1980).

2.2.2.3 Reserves

The significance of energy reserves including carbohydrates, protein and other labile plant fractions for regrowth, have been reviewed by several researchers (e.g. May, 1960; Humphreys, 1966a; McIlroy, 1967; Smith, 1973; Yamada, 1975; Harris, 1978). These authors concluded that such energy reserves are utilized as a substrate for respiration and for new shoot and root growth when photosynthesis is insufficient to meet the demand. The main reserve organs are the basal stem (crown), stolon or rhizome and tap root (Yamada, 1975; Harris, 1978). Subsequent regrowth is dependent on leaf area and photosynthesis, and the rate of nutrient uptake by the roots. The main energy reserves involved are non-structural carbohydrates, namely glucose, fructosan, dextrin and starch (McIlroy, 1967).

The accumulation of these reserves appears to be characteristic of the species and is influenced by climatic conditions and cutting management. These aspects are

discussed in Section 2.2.4. Immediately following intense cutting or grazing, root growth may cease for several days (Troughton, 1957). Substrates for the respiration process are drawn from carbohydrate reserves including nitrogenous compounds (Davidson and Milthorpe, 1966), and to provide energy for initiation of new root and shoot growth. Respiration requirements and structural compounds of this new growth are supported by export of reserves from root and stubble until photosynthesis is sufficient to meet the demand for respiration and growth requirements of the plant (Davidson and Milthorpe, 1966). Recent work has shown that the reduction in carbohydrate of both root and stubble following defoliation was largely accounted for, by respiration, particularly of roots. The direct contribution of reserves to new growth tissue was small and transitory (Davidson and Milthorpe, 1966). For example, in Dactylis glomerata which was severely defoliated, the carbohydrate reserves contributed only 50 mg compared with 700 mg from photosynthesis during the eight days following defoliation. Regrowth rate of this grass depended on carbohydrate reserves for only the first 2 - 4 days. Ueno and Smith (1970) also reported that in alfalfa only one third of the initial total non-structural carbohydrate in roots was utilized during the period from cutting to the time of greatest reduction of total non-structural carbohydrate (1 - 3 weeks after cutting). These demonstrated that not all reserves were utilized for regrowth. However, the length of time to become independent is greater after more severe cutting.

While numerous experiments have been carried out with temperate pasture species, limited information is available for tropical pasture species, particularly legumes. Adegbola (1966) reported a positive correlation between the actual carbohydrate content of the stolons and rhizomes of giant star grass and the regrowth potential. Dovrat and Cohen (1970) working with Rhodes grass (Chloris gayana kunth.) found that the amount of shoot weight produced was positively correlated with the percentage of total soluble carbohydrate in the root.

The accumulation of carbohydrates in tropical legumes is discussed in Section 2.2.4. but the role of reserves in recovery of tropical legumes after defoliation is not considered significant. This was illustrated by Jones (1974) with Siratro. He found a positive relationship between regrowth and leaf area rather than with the carbohydrate level. The poor persistence of this legume was due to the low number of active growing points close to the crown. No further information is available for other tropical legumes. Thus, the role of carbohydrate in tropical legumes demands more attention.

2.2.2.4 Water and Nutrient Uptake.

The rate of regrowth of pasture species is also markedly dependent on water movement to and within the plant and from the plant to the surrounding atmosphere. Restriction of water movement will influence nutrient uptake and distribution within the plant.

Defoliation can influence nutrient and water uptake through the cessation or reduction of root growth. Reduced root growth prevents the extension of root into regions not already depleted of soil moisture (Jacques and Edmond, 1952; Oswalt et al, 1959; Davidson, 1978). This is important particularly in dry soil as demonstrated by Jantti and Kramer (1957). Lack of water may prevent the resumption of growth by many buds which would quickly resume growth in plants supplied with adequate water.

Defoliation can also influence nutrient and water uptake through the reduction in water absorption by reducing transpiration (Jantti and Kramer, 1956). Restriction of water movement leads to limitation of the flow of photosynthate or reserves from top to root for respiratory substrate (Hatrack and Bowling, 1973). This will also limit active ion uptake (Milthorpe and Davidson, 1966).

In summary it appears that carbohydrate reserves, residual leaf area of the stubble, the availability of growing points and the extent of water and mineral uptake by

roots, all influence the rate of regrowth of pasture after cutting or grazing. The relative importance of these parameters on regrowth will vary between species, with environments and with grazing or cutting management.

Although the quantity of carbohydrate reserves required may be small, it can be highly important under severe cutting when leaf area is severely limited and when the ability of the root to take up water and nutrients is restricted. Effects of defoliation on these parameters may be modified by plant morphology and genetic make-up and defoliation management.

2.2.3 Dry Matter Yield

The effects of defoliation on total dry matter production of tropical legumes can be interpreted as an effect derived from the influence of defoliation on the components of that yield. Among these are the rate of branch or stolon and leaf development.

Jones (1974) reported that total stolon production (number/plant) of Siratro increased with increasing leaf number remaining after cutting (23.2 - 67.3 / plant). This indicates that under severe and frequent cutting which leads to low numbers of leaves remaining, a low dry matter yield results. This was also demonstrated by Whiteman (1969). Gutteridge and Whiteman (1975) reported that in Psoralea eriantha mean shoot number was markedly reduced with three week cutting intervals. Hence, low dry matter was obtained in this treatment. Loch and Humphreys (1970) reported that cutting at floral initiation increased the rate of branching, which lead to an increase in dry matter yield of Townsville stylo. The increase in branch number when cut at an early stage may explain the increased accumulated yield of Townsville stylo in Fisher's (1973) experiment.

The number of expanding leaves and the rate of leaf appearance has been reported to increase at all stages of cutting, particularly early cutting (Loch and Humphreys, 1970). Although there was no report directly on rate of leaf

appearance, a high rate of net assimilation may be reflected in the high rate of leaf appearance following cutting, as shown in Townsville stylo (Fisher, 1973). As a result, leaf dry weight was not sensitive to cutting when compared with stem dry weight. The latter fraction increased substantially following long cutting intervals (Mufandaedza, 1976).

Delayed flowering due to cutting has been frequently reported (Loch and Humphreys, 1970; Kessler and Shelton, 1980; Humphreys, 1981) and intense and frequent cutting can lead to low flowering fractions, in contrast to long cutting intervals (Mufandaedza, 1976).

2.2.4 Underground Plant Organs

There is little information on the effect of defoliation on underground plant organs of tropical legumes. Agronomic experiments seldom include root data and grazing experiments seldom include a measure of roots (Davidson, 1978).

In terms of the information available, various studies have shown that root growth is retarded by partial defoliation. The lower the height of cutting, or the more frequent the defoliation, the greater will be the retardation of root growth such as in Crotalaria juncia (Kessler and Shelton, 1980) and Centrosema pubescens (Bowen, 1959). Root system reduction in Centrosema pubescens is usually evident both in weight and length and defoliation also reduces the number of roots initiated (Bowen, 1959). Thus, the defoliated plant will produce a shallow and sparse root system.

Kessler and Shelton (1980) have shown that a single cutting of Crotalaria juncea above node 4 or 10 at 6, 8 or 10 weeks after planting, significantly reduced root growth. In the severely defoliated treatment, root weight was reduced in the immediate post-defoliation period, followed by recovery except after late defoliation at node 4, when plants died. Late defoliation was more damaging than early defoliation, and the differences in root weight between node 4 and node 10 treatments increased with time. Crider (1955) has also shown that removal in a single cutting of 40% or more of the top

growth of several species, stopped root elongation. The larger the percentage removed, the longer the period of root growth stoppage. Mufandaedza (1976) reported that the dry matter yield of the roots of Stylosanthes guianensis decreased under more frequent cutting at 4 cm cutting height, but not at 10 cm cutting height.

Defoliation also reduces the growth of rhizomes and the number of rhizomes initiated in Siratro under grazing conditions (Jones, R.M., 1973a).

Losses of root and root nodules have been reported in many tropical legumes. Bowen (1959) reported that cutting to simulate heavy grazing resulted in a loss of two thirds of the Centrosema pubescens roots by weight, and inactivation and sloughing of a major proportion of the nodules. Whiteman (1970) and Whiteman and Lulham (1970) have shown that the population of nodules of Siratro, Greenleaf desmodium and Silverleaf desmodium, decreased following defoliation. In Desmodium, the reduction in nodule population was greater with more severe defoliation and greater when young active leaves were removed, than when older, less active leaves were removed. This indicates that a heavy defoliation or grazing can lead to poor nitrogen fixation. Loss of roots and nodules after severe defoliation has also been reported in temperate legumes (Butler et al, 1959).

These effects of defoliation on the root system may be modified by the growth habit of the species. Shaw (1961), Robertson et al (1976) and Fisher (1973) reported that Townsville stylo developed a prostrate habit when it had been grazed. This also occurred with Verano stylo (Wilaipon and Humphreys, 1976) and Lotononis bainesii (Whiteman 1969). These legumes develop a substantial amount of the residual leaf close to the crown. Thus, the effect of defoliation on root growth should be less than in the climbing legumes such as Siratro, Desmodium and Glycine (Jones, 1967, 1973, 1974 and Whiteman, 1969). A similar reaction has also been reported in some grass species. For example, Weinmann and Goldsmith (1948) demonstrated that the root growth of bermuda

grass was not restricted by repeated cutting due to its dense prostrate growth habit preventing severe defoliation. It seems likely, therefore, that a prostrate legume will have better regrowth than a twining type under heavy grazing.

The significance of carbohydrate reserves in legume regrowth has been well recognised in temperate species (Harris, 1978) and in some tropical grasses (Humphreys, 1966b; Humphreys and Robinson, 1966). By comparison, few studies have centred on tropical legumes.

Hunter et al (1970) reported that at the vegetative stage, Glycine wightii (leaf), Greenleaf desmodium (leaf) and Silverleaf desmodium (stem) contained negligible quantities of starch, while the more mature plants (at flowering) contained 1 - 2% starch in dry matter. Noble and Lowe (1974) reported a high alcohol-soluble carbohydrate content in autumn for Desmodium intortum and Glycine wightii.

There is little information available on the effect of defoliation on the carbohydrate content in the root of tropical legumes. Jones (1974) found that increasing intervals between cutting did not increase root size and concentration of soluble carbohydrates. This was unlike the response obtained with lucerne, where increasing the interval between cutting increased the size of the root system and greatly increased the available carbohydrates (Graber et al, 1927). Mufandaeđa (1976) also reported that cutting intensity and frequency had no significant effect on total non-structural carbohydrates in the roots and stubble of S. guianensis. It seems that the effect of defoliation on the level of the available carbohydrates in tropical legumes warrants more attention.

2.2.5 Herbage Quality

Nutritive value of herbage may be expressed in terms of chemical composition and digestibility. Protein content is a common and measurable parameter of the nutritive value of the plant. Decrease in the percentage of crude protein in forage plants with advancing maturity is well documented

(Milford, 1967; Milford and Minson, 1966; Fisher, 1969, 1970). Frequent cutting generally results in a higher percentage of protein in forages. Mufandaedza (1976) reported that nitrogen concentration of several strains of S. guianensis increased with more frequent cutting. Similar results were reported for S. humilis (Robertson et al, 1976; Hendy, 1971; Ive, 1974), Pigeon pea (Akinola and Whiteman, 1975) Crotalaria juncea (Kessler and Shelton, 1980) and Desmodium (Jones, 1967). Under grazing and cutting conditions, Whiteman (1969) reported similar levels between the two types of defoliation and both were higher than in the control plants.

For phosphorus concentration, Wilaipon et al (1981) reported that cutting Verano stylo every three weeks produced higher phosphorus in the apex compared with uncut plants. However, Robertson et al (1976) and Fisher (1973) reported that in Townsville stylo phosphorus concentration in the apex was unaffected by cutting interval.

Dry matter digestibility is generally higher under frequent cutting, with long cutting intervals markedly reducing dry matter digestibility because of the high stem fraction (Mufandaedza, 1976).

2.3 EFFECT OF DEFOLIATION ON STYLOSANTHES HAMATA CV VERANO

2.3.1 Morphology and growth habit

Verano stylo acts as an annual if it is left ungrazed or uncut for too long. The plant will grow tall and erect and may drop its leaves and die (McKeague et al, 1978). At Landsdown, Australia, Gardener (1981) observed that flowering and vegetative growth occurred together in the wet season. He then recorded heavy flowering and seed set in April/May and subsequent death of all above-ground parts and many plants despite the presence of adequate soil water. Little new growth arose from the crown of the surviving plants in response to winter rains. Plants occasionally survived through the dry season, only to die immediately after the

opening rains. No explanations have been offered by these workers. However, plant death may be due to the absence of new growing points or buds when plants are allowed to reach such an advanced stage of maturity. This is supported by Wilaipon and Humphreys (1981) who found that rejuvenation of the plant by grazing late in the wet season increased the number of perennating plants. Gillard et al (1980) also reported a rapid regrowth of a stand of Verano stylo when heavily grazed at the onset of rains (early stage); it made more growth than a stand re-established from reserves of seed in the soil. They suggested that the rapid regrowth ability of this species seems to be one of the main advantages compared with the annual Stylosanthes humilis.

Wilaipon and Humphreys (1976) also observed that the number of branches of Verano stylo increased following a single heavy grazing at the early stage of growth, resulting in increased seed production. Many workers have pointed out that early grazing encourages the plants to become prostrate or creeping as well as checking the companion grasses and improving light penetration.

2.3.2 Dry matter yield

Dry matter yield of tropical legumes cut at the early and late stage appears to be correlated positively with the number of buds or growing points left, and persistence is also related to the severity of defoliation. However, few experiments have recorded the number of growing points at different growth stages.

Wilaipon and Humphreys (1976) found that a single grazing or mowing at an early stage (first flower) produced superior dry matter yield to intermittent grazing at later stages. Dry matter yield was also reduced by grazing at the late stage due to the increase in voluntary grasses. This indicates that differences in the timing of defoliation appeared to alter the competitive balance between the legume and the grass, with grass dominance being accentuated by late defoliation (Wilaipon and Humphreys, 1976).

As with many other tropical legumes, as previously reviewed, frequent cutting or grazing generally leads to an overall reduction in dry matter yield. Topark-Ngarm and Akkasaeng (1978) reported that under a four-week cutting frequency, Verano stylo yields were significantly lower than a six week cutting frequency. The yield reduction was more pronounced in the establishment year than in the second year.

2.3.3 Underground plant organs

There are no data available for the effect of defoliation on the root size, root nodule and the energy reserves in the roots of Verano stylo. However, in general, similar effects may apply to Verano stylo as those which have been discussed in the previous section.

2.3.4 Herbage quality

Both nitrogen and phosphorus concentration have been reported to increase under frequent cutting (Wilaipon et al, 1981).

The above review clearly shows that the response of Verano stylo to defoliation in terms of growth, yield and chemical composition warrant more attention.

2.4 EFFECT OF WATER STRESS ON TROPICAL LEGUMES

The previous section has considered the effect of defoliation on plant growth and yield of tropical legumes. This section considers the effect of water stress on plant growth and development of tropical forage legume species, where data are available. Where data are not available, other tropical species are used to illustrate the point.

2.4.1 Germination, Establishment and Survival

According to Pearen and Koeghan (1982), the development of pasture seedlings may be divided into three distinct phases:

- 1) Germination
- 2) Establishment
- 3) Growth.

The success or failure of seedling establishment will in large measure depend on the extent to which favourable conditions for promotion of these phases can be met. Germination requirements include a permeable seed coat, and provision of adequate air and moisture (Humphreys, 1978b). Winkworth (1969) showed that seeds of Townsville stylo (Stylosanthes humilis) required a moist soil above -0.1 MPa (-1 bar) for field germination to occur. Similar results have also been reported for Stylosanthes hamata, S. scabra and S. viscosa (Mott et al 1976). It has been shown that at an osmotic stress of - 9 bars (- 0.9 MPa), the germination of S. guianensis, S. scabra and S. viscosa declined rapidly but there was much less effect on S. hamata, S. humilis and S. subsericea (McIvor, 1976), indicating a difference in the rate of water uptake by seeds of different species.

Under hot arid climates where the soil dries out rapidly after rainfall, the presence of vegetative cover or a layer of litter that reduces the evaporative load on the seedling is advantageous (Murtagh, 1963; Miller and Perry, 1968; Keya et al, 1972).

Once the germination process is underway, the rate of seedling root development and seedling vigour are often very important in conditions of rapid soil drying. These are related to seed size (Tudsri and Whiteman, 1977b; Gardener, 1978) and differ between species (Gardener, 1978). For example, S. hamata and S. humilis exhibit rapid rates of germination and root elongation compared with S. scabra, S. viscosa and S. frutica (McIvor, 1976; Mott et al, 1976; Gardener, 1978). This allows the former to survive under rapid soil drying conditions.

In most pasture regimes of the world, a period of soil moisture stress, either short term or long term (drought) is common during the growing season (Whiteman, 1980). Thus, during the establishment and growth phases, plants may experience water stress. In order to adapt and survive, plants have to develop both morphological and physiological mechanisms to enable them to withstand and adapt to such water stress. This aspect has been recently reviewed by Mannetje et al (1980); Ludlow (1980a) and Fisher and Ludlow (1984). These authors suggested that the adaptation of these plants could take three forms: escape from drought, avoidance of low leaf water potential, and tolerance of low leaf water potential.

The first morphological adaptation is a reduction in transpiration by the presence of a cuticle capable of protecting the plant against excess moisture loss (Whiteman, 1980).

Another drought-avoidance and survival mechanism is the ability to shed leaves at relatively high leaf water potentials. For example, Siratro leaves are shed at leaf water potentials of -1 MPa but some plants retain small, thick, turgid leaves near the apex. If stress continues, whole branches die until only the crown remains, most of which is under the soil surface (Peake et al, 1975; Fisher, 1983). This phenomenon has also been observed in Townsville stylo (Stylosanthes humilis), which appears to be an avoider of drought by dropping its leaves early and surviving via seed (Fisher, 1969; Gillard and Fisher, 1978).

Many tropical legume species also avoid water stress by a reduction in the exposed leaf area during drought. For example L. leucocephala folds its leaves during drought (National Academy of Science, 1977). In Townsville stylo, leaves are orientated parallel towards the sun (parahelionasty) (Begg and Torrsell, 1974; Fisher and Campbell, 1977). This phenomenon has also been observed in Siratro, which also forms smaller leaves when water-stressed than when water is well-supplied (Fisher, 1983; Jantakool, 1983).

Reduction in the size of new leaves caused a reduction in leaf temperature and water loss (Fisher and Ludlow, 1982; Fisher, 1983).

Several plants have also adapted to drought survival by developing deep and extensive root systems to fully exploit the available soil moisture, such as Siratro (Macroptilium atropurpureum) (Peake et al, 1975; Mannetje et al, 1980; Sheriff and Ludlow, 1984). A rapid development of a deep tap root was also reported in Townsville stylo (Torssell et al, 1968) which also showed rapid root development as a seedling growing under limited soil moisture conditions, viz 50 - 60 cm of root growth being recorded after only 38 mm of rain.

An annual pasture species avoids the drought period by growing and setting seed over the wet season, and by passing through the dry season as seed, e.g. Townsville stylo. Seeds are also protected by embryo dormancy and impermeable seed coat (Mott et al, 1981). These seeds are able to survive water potentials in equilibrium with air of 20 to 50% relative humidity, which is equivalent to water potentials of approximately - 95 to - 220 MPa (Gaff, 1980). Thus, the seeds will not germinate after light out-of-season rain (Mott et al, 1981).

Closure of the stomata during drought is an important physiological mechanism to reduce water loss and maintain a high level of water potential. This has been well demonstrated in Siratro (Macroptilium atropurpureum). In this legume, stomata close at high leaf water potentials (- 1.2 to 1.5 MPa) and respond to falling atmospheric humidity independent of water potential (Ludlow and Ibaraki, 1979). This contrasts with Desmodium uncinatum cv Silverleaf, which lacks stomatal control mechanisms that respond to humidity (Sheriff and Kaye, 1977) and to leaf water potential (Ludlow and Ibaraki, 1979).

Many differences in the leaf water potential for stomatal closure can be accounted for by differences in the osmotic potential or osmotic adjustment of the plant (Turner,

1974; Begg and Turner, 1976; Ludlow, 1980a). Osmotic adjustment is the main mechanism of stomatal adjustment which allows stomata to remain partially open at progressively lower water potentials as water stress increases. Siratro has small osmotic and stomatal adjustments and therefore the survival of this legume depends mainly on avoidance mechanisms (Ludlow, 1980a, 1980b; Fisher and Ludlow, 1984). Stylosanthes species, however, exhibit both osmotic and stomatal adjustment (Ludlow 1980a; Fisher and Ludlow, 1984) but the variation in osmotic adjustment between them is small (0.8 - 1.1 MPa). Fisher and Ludlow (1984) suggested that osmotic adjustment may not be an important characteristic influencing growth and survival in different moisture environments in these species. However, the differences in sensitivity to desiccation among Stylosanthes species are considerable, and appear to be correlated well with the moisture availability in the areas to which they are adapted (Fisher and Ludlow, 1984). This suggests that the high tolerance to drought of these species may be due to the insensitivity to desiccation - desiccation sensitivity being the leaf water potential at which the last visible leaf dies (Fisher and Ludlow, 1984).

2.4.2 Morphological Effects

Cell enlargement depends on turgor (Hsiao, 1973). As a consequence, restriction in water supply is likely to affect leaf expansion. Ludlow and Ng (1976) showed an 80% reduction in leaf elongation rate of Panicum maximum var. trichoglume, when the leaf water potential fell from - 4 to - 7 bars (- 0.4 to - 0.7 MPa), and elongation ceased at - 1 MPa. With tropical legumes, Williams and Gardener (1984) demonstrated that leaves of the annual tropical legume, S. humilis, will lose all turgor and die at the leaf water potential of - 1.3 MPa. Death of S. hamata does not take place until - 3.0 MPa, whilst S. scabra leaves are able to reduce their leaf water potential to less than - 4.0 MPa and survive through the drought with living tissue.

Low leaf potentials also influence leaf production through their effects on leaf initiation in meristems and

subsequent rate of cell division (Hsiao, 1973; Slatyer, 1973). The rate of leaf initiation may become slower or even cease as stress continues. The desiccation sensitivity of Stylosanthes species varies between - 6 and - 12 MPa (Fisher and Ludlow, 1984), which is in contrast to Siratro (- 2.3 MPa) (Wilson et al, 1980).

Although low leaf water potential has a large effect on the rate of production of new leaves, it also causes a reduction in the existing leaves. For example, Fisher (1983) found that Siratro lost old leaves from the base to the top as the water stress continued, as did Townsville stylo (Fisher, 1969; Fisher and Campbell, 1977).

One of the most important consequences of the sensitivity of cell enlargement to a small water deficit is a marked reduction in leaf area. Leaf area may be reduced through an increase in rate of leaf senescence, which has been discussed earlier. A reduction in leaf area will reduce crop growth rate particularly during the early stages of growth when there is incomplete light interception.

2.4.3 Physiological Effects

As available soil moisture declines, an internal water deficit develops in the plant, leading to loss of turgor, until the plant reaches a state of wilting when sufficient moisture can no longer be extracted from the soil to maintain turgor. As plant turgor declines, progressive stomatal closure causes reduction in the rate of CO₂ uptake (Begg and Turner, 1976). As a consequence, restriction in water supply is likely to affect the rate of the photosynthetic process. This aspect was reviewed by Hsiao (1973), Begg and Turner (1976), and Turner and Begg (1978). Mostly these reviews concentrate on crops and temperate pasture species. Therefore, emphasis in this review will be placed on stomatal behaviour and photosynthesis.

Since stomata have an important role in regulating the pathway for gaseous exchange between the plant and atmosphere (Turner and Begg, 1978), the behaviour of stomata in response

to environmental influences is of considerable physiological importance. In terms of tropical pasture species, Ludlow (1980a, 1980 b) and Wilson *et al*, (1980) have been notably active in this field of research. Stomatal opening depends on turgor (Hsiao, 1973), and the main mechanism of turgor maintenance is osmotic adjustment (Ludlow, 1980a, 1980b). As such, many of the differences in leaf water potential for stomatal closure can be accounted for by differences in the osmotic adjustment (Turner and Begg, 1978; Ludlow, 1980a, 1980b; Fisher and Ludlow, 1984). These have been discussed in Section 2.4.1.

Reduction in net photosynthesis, resulting from closure of stomata, was demonstrated by Ludlow and Ng (1976) with the tropical grass, Panicum maximum var. trichoglume. They showed that stomatal closure causing net photosynthesis to cease occurs at leaf water potentials of - 12 bars (- 1.2 MPa) in controlled environments. However, in the field where water deficits usually build up more slowly, and roots exploit a greater depth for moisture, photosynthesis will cease at - 1.9 MPa (Ludlow and Ng, 1976). For tropical legumes, no such data could be found related to photosynthesis.

2.4.4 Dry Matter Yield

Shortage of soil moisture, resulting from variation in rainfall, is closely correlated with differences in herbage yield from year to year according to McCown *et al* (1974). They demonstrated that cumulative yields of native spear grass plus S. humilis, or buffel grass (Cenchrus ciliaris) plus S. humilis varied widely over 5 years, but yield was closely related to evapo-transpiration. They used a simple water analysis to predict the effect of soil water storage on pasture yield at Townsville, Australia.

Williams and Gardener (1984) using rainfall, evaporation and temperature in a weekly balanced analysis, calculated a multiplicative growth index for each of the intervals over which stem elongation was measured on Verano stylo. They found that extension growth was substantially reduced when the growth index fell below 0.5. They concluded that for

conditions in which water and temperature are the only factors limiting dry matter yield of Verano stylo, it is possible to estimate dry matter yield at a given site from rainfall, evaporation and temperature.

The effects of water stress on total yield can be interpreted as an effect derived from the influence of water stress on the components of that yield. Among these are the rate of branch and leaf development.

Evidence suggests that both rate and number of branches decrease with increasing stress. Waikakul (1983) reported that the number of branches and rate of branching in Verano stylo when under stress were directly related to the water supply. At the end of this experiment, the plant that had been stressed at the vegetative phase produced only 35% of the control. Similar results have been reported in Siratro (Peak et al, 1975 and Juntakool, 1983). The effects of water stress were not only to decrease the branch number but also to reduce stem elongation of these branches. For example, Williams and Gardener (1984) reported that when the relative leaf water content at 15.00 hr fell below approximately 75%, the stem elongation rate of Verano stylo was small - usually less than 2 mm/day. As a result, total dry matter yield was reduced through a reduction in stem elongation.

Water stress can influence total yield through the reduction in leaf area by restricting the rate of leaf expansion and by accelerated senescence of older leaves (Fisher, 1969, 1983; Fisher and Campbell, 1977; Carvalho, 1978; Waikakul, 1983; Juntakool, 1983). Reduction in leaf area leads to reduced photosynthesis and yield (Hsiao, 1973).

Leaf number and leaf size were also reduced by water deficit. Fisher (1983) reported that in Siratro the new leaves that were produced during stress were small in size and fewer in number (Juntakool, 1983). As a result of reduction in leaf number and leaf size, leaf dry weight was also reduced (Fisher, 1969; Carvalho, 1978).

The stage in plant growth at which the stress occurs is another important effect of water stress on plant performance. Fisher and Campbell (1977) reported that the yield of Townsville stylo was low if stress occurred at the vegetative stage, whereas water stress during and after flowering had little effect on herbage yield. This response seemed to be related to the fact that growth rate decreases with maturation. They noted that water stress during vegetative growth hastened flowering by two weeks. Pod dry matter yields were also reduced when water stress was applied late in the flowering period. Similar results were also reported in Verano stylo and Siratro (Waikakul, 1983 and Juntakool, 1983). Carvalho (1978) also reported a delay in flowering of about 8 days in the water stressed S. hamata plants when compared with the control. Yields were also reduced in both S. guianensis and S. hamata.

2.4.5. Herbage Quality

It must be emphasized that water stress influences not only dry matter yield but also forage quality. Pasture quality generally refers to the nutritive value and influences forage consumption. The former is characterized by chemical composition, digestibility and the nature of the digested product whereas the latter is the rate of forage intake by animals. Chemical composition is associated with only the plant and its environments while the latter two are associated with both plant and animal. The effect of water stress, therefore, will be discussed in terms of chemical composition and digestibility.

Wilson and Ng (1975) demonstrated that lignin content in green leaves of Panicum maximum var. trichoglume did not differ between stressed and non-stressed plants at any plant age. With tropical legumes, Carvalho (1978) showed that Stylosanthes hamata cv Verano and S. guianensis exposed to a cycle of water stress always had low cell wall percentages in both stem and leaves. This contrasted with Macroptilium atropurpureum cv Siratro in which the small, stress adapted leaves were higher in lignin and cellulose content. But hemicellulose was markedly lower than that in non-stressed

plants (Wilson, 1983).

The accumulation of some soluble carbohydrates such as inositol in stressed leaves of Vigna species and Siratro, was reported by Ford (1982) and Ford and Wilson (1981). However, glucose and sucrose did not accumulate in stressed leaves of Siratro whereas sucrose increased substantially in tropical grasses (green panic, buffel and spear grass) (Ford and Wilson, 1981).

Water stress decreases the phosphorus concentration in many tropical pasture and grain legumes. Fisher (1980) showed that phosphorus concentration in the plant top (above ground) of Stylosanthes humilis was significantly reduced by water stress (0.08 vs 0.23% phosphorus). This effect was most marked when the stress occurred at an early stage of growth. Similar results have been reported for Seca and S. viscosa CPI 34904 (Probert, 1984) and the tropical grain legumes (Glycine max cv Buchanan and Durack, Lablab atropurpureus cv Highworth, Cajanus cajan cv Royes, Vigna unguiculata cv Red Caloona, V. mungo cv Regur and V. radiata cv Berken (Wilson and Muchow, 1983). Water stress had only small effects on nitrogen concentration. In fact, an increasing nitrogen concentration in the plant top was frequently reported under water stress (Carvalho, 1978; Fisher, 1980; Wilson and Muchow, 1983) In grass species, the increase in nitrogen concentration arose largely from the delayed development of the stem fraction under stress (Gate, 1968; Wilson and Ng, 1975).

Water stress frequently increases the dry matter digestibility of tropical pasture species (Wilson and Ng, 1975; Carvalho, 1978; Wilson, 1981; Wilson and Munchow, 1983). In terms of the limited information on tropical legumes, Carvalho (1978) showed that water stress cycles increased in vitro organic matter digestibility in stem and in leaves of S. hamata and S. guianensis. Wilson and Muchow (1983) also reported an increase in dry matter digestibility of leaf, stem and whole tops of several tropical grain legumes. For the whole tops, such increases ranged from 2 to 3.7% units.

2.5 MANAGEMENT OF TROPICAL FORAGE LEGUMES

For some years, tropical pasture legumes have been used to improve production from tropical pasture as well as soil fertility (Skerman, 1977). The success of these legumes has depended on the climatic conditions and agronomic techniques of pasture establishment such as adequate land preparation, correcting any nutrient deficiency, the selection of the right species and proper seed treatment, the appropriate depth and method of sowing and the correct early management of the establishing sward.

A particular problem in many subtropical and tropical pasture regions is that of moisture stress which can be very severe for part of the year. Under such conditions, legume growth can be affected, particularly when grown with grasses. For example, Jones et al (1967) showed that the growth of Siratro (Macroptilium atropurpureum) in a mixture with Paspalum plicatulum was linearly related to the effective rainfall over the growing season ($r = 0.987$). Variation between legumes in this regard has also shown that Townsville stylo, for example, was unable to persist under 800 mm of annual rainfall, whereas Verano stylo, Seca and Fitzroy, performed quite well under these conditions (Burt et al, 1974; Edye et al, 1975b, 1976; Gillard et al, 1980). As a result of many years of evaluation and in some cases considerable breeding, selection and testing, a range of forage legume species and cultivars has been released to the farmer as being highly suitable under particular conditions of improved tropical grassland production. The agronomic practices favourable to these species have been presented by O'Reilly, (1975); Bogdan, (1977); Skerman, (1977); Humphreys, (1980a); Whiteman, (1980).

The techniques of pasture establishment vary from place to place and depend on the area of land to be improved. In a dense forest, clearing the whole area needs to be done before seed preparation. However, in the open grassland or savannah woodland, there are several possibilities available instead of the complete land preparation. The cheapest and possibly

the most economical method is to sow the legume seed into the existing native pasture directly (Jones, 1972; Humphreys, 1978a, 1978b, 1982; Whiteman, 1980; Murray, 1983). However, in most cases the use of selected strategies including burning, spraying with herbicide, heavy grazing or cutting to reduce the competition from the existing grasses or weeds, have been employed successfully throughout the tropics.

In Northern Australia, burning in the early wet season has been recommended for the establishment of Townsville stylo in the spear grass country (Norman, 1965; Miller and Perry, 1968). In Kenya, burning in the dry season and planting in the early wet season have been recommended for oversowing Silverleaf desmodium into Hyparrhenia rufa pasture (Keya et al, 1972). In the highland areas of Thailand, Falvey et al, (1985) successfully introduced Macrotyloma axillare and Greenleaf desmodium into a blady grass pasture after burning late in the dry season. Doughlas (1965) also successfully established Siratro and Stylosanthes guianensis by oversowing after burning blady grass (Imperata cylindrica) but the establishment of Lotononis, Silverleaf desmodium and Glycine was less successful under these conditions.

The success of legume establishment following burning, particularly for Townsville stylo, appears more dependent on the rainfall and soil moisture than on the pre-treatment (Miller, 1967) and in some cases the reduction of grass cover gave poorer establishment due to less favourable surface moisture conditions (Miller and Perry, 1968). In fact, pre-treatment may not be necessary if the competition from the existing grasses or natural grasses is not excessive. Robertson (1978) reported a good establishment of Townsville stylo, Siratro, and Stylosanthes into native bamboo grass and the communal land areas which consisted of Arundinaria pusilla, Dactyloctenium aegyptium and Brachiaria reptans pasture in Northeastern Thailand.

Chemical spraying to reduce competition has been suggested in both tropical and temperate regions (McLeod, 1962; Murtagh, 1963; Evans, 1964; Campbell, 1969; White,

1972a). The advantages claimed for using herbicide are that it ensures rapid filling of the existing pasture and improving soil fertility, reduces weed competition, prevents soil erosion, and spraying can be carried out in areas where normal cultivation cannot be done (e.g. steep areas). In areas where the rainfall is low, the dead material remaining can reduce soil moisture loss and minimise the adverse effects of cold weather on plant growth (Dowling et al, 1971). Keya et al (1972) reported that the density of Silverleaf desmodium was much higher under sprayed plot than burning or cutting prior to sowing. However, in relatively dense vegetation, Tudsri and Whiteman (1977a) found less advantage with chemical spraying than with burning or cutting before oversowing Siratro. This was because much of the Siratro seed oversown on the sprayed plot failed to reach ground level and hence establishment was poor.

Re-establishment of legumes into depleted sward of cultivated tropical grasses has generally been less successful than oversowing of legumes into natural grasses, as previously reviewed. Under favourable conditions of soil moisture and fertility, competition from the already established grasses is a major factor affecting successful establishment. Tudsri and Whiteman (1977a) demonstrated that pretreatments of cutting, burning or spraying with "Paraquat" of a Setaria anceps sward did not sufficiently reduce tiller density to allow oversown Siratro to establish. Light cultivation was also unsuccessful (Middleton, 1973). Only rigorous cultivation of the Setaria stand allowed successful establishment of Siratro (Tudsri and Whiteman, 1977a). However, Lotononis bainesii was successful by merely oversowing into Setaria anceps (Tudsri and Whiteman, 1977b).

With full or complete cultivation, there is generally no problem with establishment and growth. This is probably due to the complete removal of competition and the provision of suitable soil conditions for germination (Tudsri and Whiteman, 1977a; Wilaipon and Pangskul, 1983; Cook, 1984). Furthermore, with tropical legumes that are slow to nodulate (e.g. Glycine wightii), cultivation can increase the rate of

mineralization which can assist the legume to establish at an early stage of growth (Henzell, 1977). The problem with full cultivation is one of cost and topography.

Pastures are usually grown on lower fertility soils which are not well suited to cropping (Williams and Andrew, 1970). Thus, soil fertility problems are found in most tropical pasture situations. The major limiting nutrients for growth on most soil in the tropics and subtropics are nitrogen and phosphorus. In some areas many are also deficient in potassium and sulphur and notably some of the trace elements.

Tropical pasture legumes have the ability to fix nitrogen through nitrogen-fixing bacteria living in the root nodules. This allows them to grow and reproduce in soil which is low in nitrogen (Humphreys, 1978b). Therefore, in general terms, the application of large amounts of nitrogen fertilizer is not common practice with such mixed pastures. The disadvantage of applying nitrogen fertilizer at a high rate is the stimulation of grass growth and subsequent increased competition for light and nutrients, leading to reduction in the legume content. Furthermore, nitrogen fertilizer will inhibit nodulation and reduce the rate of nitrogen fixation (Whiteman, 1980). Small amounts of nitrogen, however, are suggested for some tropical legumes (e.g. Glycine wightii) to assist their establishment (Skerman, 1977).

Phosphorus plays a very important role in tropical forage legume growth. Numerous studies have shown that the application of phosphorus fertilizer at the time of sowing stimulates legume seedling growth (Blunt and Humphreys, 1970; Keya et al, 1971; Olsen and Moe, 1971; Tudsri and Whiteman, 1977b) and results in good legume establishment. In addition, Gate (1974) showed that phosphorus fertilizer enhanced early nodule formation and nitrogen fixation. The nodule dry weight, number and density increased with increasing level of phosphorus up to at least 25 kg phosphorus / hectare.

The beneficial effects of phosphorus on legume establishment and nitrogen fixation, as mentioned above, and the response in terms of dry matter yields, have been reported by many workers (Keya et al, 1971; Olsen and Moe, 1971; Tudsri and Whiteman, 1977b). There are differences in phosphorus responses between and within legume species. Stylosanthes humilis and Lotononis bainesii were the least responsive when compared with other legumes (Andrew and Robins, 1969). The ability of S. humilis to absorb greater quantities of phosphorus from a soil with low available phosphorus was shown by Andrew (1966). White (1972b) suggested that the better growth of S. humilis in a phosphorus deficient situation may be related to the translocation of phosphorus from older to younger tissues. This results in better growth of this legume under poor soil fertility, as reported by Robinson (1983) and Robertson et al (1976). Jones, R.K. (1974) described differences in phosphorus requirement of a range of Stylosanthes species. In general, the basal level of phosphorus application varies from place to place. In Queensland, Australia, a basal dressing of 250 - 500 kg/ha of single Mo superphosphate plus 125 kg/ha superphosphate for maintenance is recommended (Jones and Jones, 1971). In Thailand, a basal dressing of 200 - 250 kg/ha of superphosphate is recommended (Tudsri, 1980).

In terms of potassium, Andrew and Pieter (1970) showed that Silverleaf desmodium (Desmodium uncinatum), Perennial stylo (Stylosanthes guianensis) and Townsville stylo (Stylosanthes humilis) were sensitive to potassium deficiency. Hall (1971) also demonstrated that the dry matter yield of Silverleaf desmodium was significantly depressed when allowed to compete with Setaria in the nil potassium treatment. By contrast, either the addition of potassium fertilizer or the separation of the roots of the two species, resulted in good legume growth comparable to that of the companion setaria (Setaria anceps). This indicated that the grass species was stronger in competition for available potassium than the legume. Thus, the botanical competition of the mixed pasture can vary under high and low potassium supply. Jones (1965a)

reported that the dry matter yield of Siratro was only 13% of total dry matter yield in a mixed sward under no potassium fertilizer. This is in contrast to the plot that received potassium fertilizer at a rate of 190 kg/ha, which produced a Siratro dry matter yield of 29% of total dry matter yield. Hall (1971) pointed out that potassium was the key fertilizer for the establishment of Siratro when mixed with green panic grass on poor soil. In this experiment, the application of potassium alone increased Siratro yield substantially. Accordingly the use of potassium fertilizers is now generally recommended - according to Jones and Jones (1971) it should be 662 - 250 kg/ha KCl annually, while Teitzel (1975) considers that 50 - 200 kg/ha KCl annually is adequate in high rainfall areas.

It should be noted however that the application of KCl at rates of 100 - 200 kg/ha can cause the death of seedlings of Desmodium intortum (Jones, R.M., 1973b). Eyles et al (1973) also reported KCl toxicity with Townsville stylo and Centrosema under higher rates of application and recommended the alternative use of potassium sulphate.

Many of the tropical legumes such as Siratro, Glycine, and Calopogo are readily nodulated by Rhizobium strain CB 756 (cowpea group) which occurs naturally in tropical soils. Therefore, Rhizobium inoculation for these legumes is not required (Humphreys, 1978b, 1980a). However, some genera have specific Rhizobium requirements, which may differ between species and even between cultivars within species. For example, within Stylosanthes guianensis, cultivars such as Schofield, Cook and Endeavour are nodulated by the general cowpea inoculant CB 756. However, the cultivar 'Oxley' was shown to have a specific Rhizobium requirement (Whiteman, 1978; 1980). Lotononis, Leucaena, Centrosema and Kenya white clover also had specific Rhizobium requirements (Humphreys, 1980a). Mannetje (1969) also demonstrated that Stylosanthes contains species and forms within the species, which have specific Rhizobium requirements.

Breaking seed dormancy or overcoming hard-seededness

prior to sowing is recommended for Siratro, Lotononis, Stylosanthes species, Centrosema and Leucaena. The common method is the hot water treatment at 80°C for ten minutes (Skerman, 1977; Whiteman, 1980).

Many tropical pasture legume seeds are small and have limited stored reserves. Therefore, depth of sowing is a critical factor in promoting successful establishment. Seeds that are left uncovered are subject to rapid changes in soil moisture conditions and are readily killed by drought following light showers that promote germination (e.g. Stylosanthes humilis). Seeds that are placed too deep may fail to emerge due to insufficient energy reserves. Also following germination, a crusted soil surface may prevent emergence, especially on fine-textured soils. Therefore, for small seeded legumes such as Lotononis, Stylosanthes and Kenya white clover, only light cover at sowing is recommended. However, with large seeds such as Siratro and Lablab, a depth of 0.5 to 1.5 cm is preferred (Smith, 1967; Stonard, 1969).

Insect pests and diseases are also very important in legume establishment. One of the most noticeable - the fungal disease Anthracnose - was found on Townsville stylo in Australia in 1973 and was subsequently reported in Thailand in 1976 (Humphreys, 1978a). This significantly reduced the potential of this species for improving natural grassland. Rhizoctonia solani was also recorded in Siratro in the high rainfall tropics, making this species less productive. The legume "little leaf virus" caused by mycoplasma, was also found in Lotononis (Bryan, 1969; Hutton, 1970), and along with the Amnemos weevil, also attacks Silverleaf desmodium (Skerman, 1977).

Ants can cause substantial losses of seed through their "food-gathering" habit and often require control by dieldrin spraying. Siratro is also readily attacked by bean fly (Melanagromyza phaseoli) during seedling stages (3 - 4 weeks) (Skerman, 1977), but this can be prevented by seed treatment with dieldrin, aldrin or endrin at 2 - 4 g.a.i./kg of seed

(Jones, 1965b). Leptopius weevil (Leptopius spp.) was found to damage Greenleaf desmodium (Clements et al, 1983) and in the northern part of Queensland, many tropical legumes have been destroyed by caterpillars, Heliothis and Lamprosema species (Skerman, 1977).

It is therefore obvious that this period of establishment is a critical stage in the life of a pasture if one is to achieve a high yielding sward free of weeds and capable of high stocking capacity.

In a mixed sward, after the legume germinates, it soon starts to compete with grasses or weeds for water, nutrients and light. The correct early management at this stage can have a very marked effect on the legume content and on total legume yield and survival. However, tropical legumes appear to respond in different ways to the same management treatments. For instance, in the case of Townsville stylo, heavy grazing or cutting at an early stage of growth can enhance legume survival and encourage branching. This is attributed to the reduction in competition from grasses allowing more light to the legume (Shaw, 1961; Norman and Phillips, 1970; Fisher, 1973; Torssell et al, 1976; Torssell and McKeon, 1976; Skerman, 1977). Grazing or cutting at a late stage of growth or late in the growing season, can be disadvantageous in terms of legume yield and survival. However, in the case of twining legumes, such as Siratro, competition for light is less intense owing to its twining habit (Whiteman 1969). Therefore, grazing should be carried out at an advanced stage of growth or following twining and allowing the legume to set seed (Skerman, 1977). Siratro prefers light grazing, as frequent and hard grazing can lead to rapid reduction in yield (Jones, 1967; Whiteman, 1969). Similar responses were found in Desmodium intortum (Jones, 1973) and Glycine wightii (Whiteman, 1969).

2.6 MANAGEMENT FOR STYLOSANTHES HAMATA CV VERANO (VERANO STYLO)

Although Verano stylo has been released for commercial use for the last decade, detailed information on the behaviour of the plant under varying cultural and managerial conditions is lacking. However, its resemblance to Townsville stylo has caused several workers to believe that the same type of general management can be applied to both (McKeague et al, 1978; Humphreys, 1980a).

Unlike most of the tropical legumes, Verano stylo is better suited to areas of erratic rainfall because it can flower at any time and vegetative growth continues after the onset of flowering (Cameron and Mannetje, 1977; Gillard et al, 1980). It also persists in areas receiving an annual rainfall as low as 600 mm and usually produces more forage yield than Townsville stylo under such conditions (Burt et al, 1974; Edye et al, 1975b; Gillard et al, 1980).

Verano stylo can be sown in exactly the same way as Townsville stylo or other tropical legumes that have been previously reviewed. It is well adapted to a wide range of soil types and climatic conditions and shows a greater resistance to anthracnose disease than Townsville stylo (Vinijtsanond and Topark-Ngarm, 1978). Use of this legume to improve natural and cultivated grasses is commonly employed in many parts of the tropics, such as Thailand (Humphreys, 1978a; Gutteridge, 1982) and Malaysia (Whiteman, 1978).

Seed-bed preparation may not be essential if the existing grasses or weeds are short (Robertson, 1978; Humphreys, 1982, 1984; McKeague and Holmes, 1979). However, cultivation of the land prior to sowing generally results in better germination, establishment and dry matter yield (Wilaipon, 1980; Wilaipon and Pongskul, 1983).

Verano stylo can nodulate freely with native soil Rhizobium. Work in Thailand indicates that Verano stylo can produce high yields on contrasting soil types (Korat and Nam-Pong Series). Nitrogen fixation also appears to be

efficient, as no difference was recorded in terms of both dry matter and nitrogen yields in the presence or absence of added nitrogen fertilizer in the field, conducted by Ruaysoongnern (1978).

Although Verano stylo is easily established, poor seed germination can be a problem reducing effective establishment (Gardener, 1975). Unless Verano stylo seed is treated to reduce hard-seededness, only about 10% field germination can be expected in the establishment year (Mott et al, 1981). Therefore, seed treated with hot water at 80°C for 5 - 10 minutes is recommended (Whiteman, 1980; Crowder and Chheda, 1982). However, to cope more effectively with large quantities of seed, Mott (1979) developed a rotating drum in which to treat such seed for 15 - 20 seconds at 155°C. The result showed that such a heat treatment increased Verano stylo germination 10-fold compared with the control at Katherine, Australia. Legume yields from the resulting pasture were 16 times those of the control (Mott, 1979).

In common with the other tropical legumes previously reviewed, planting date had a marked effect on the establishment of Verano stylo, with early sowing being strongly recommended in Thailand (Wilaipon and Pongskul, 1983; Humphreys, 1984). In Australia, it is recommended that Verano stylo be sown just before the wet season, into burnt or short grass. Aircraft or ground equipment can be used, but markers are needed for accurate aircraft sowing into standing timber (McKeague et al, 1978).

Basal fertilizers are also recommended prior to sowing. The addition of phosphorus fertilizer increased dry matter yields and percentage Verano stylo in a number of experiments (Hall, 1979). Hall (1979) also reported that the basal superphosphate of 300 kg/ha on a deep sandy yellow earth increased the dry matter yield of Verano stylo from 1 ton to 2.5 ton/ha. However, in Thailand, the response of Verano stylo to phosphorus and sulphur fertilizers has been variable, and in some cases non-existent (Gutteridge, 1978; Wilaipon and Pongskul, 1983). These authors suggested that

the native levels of soil phosphorus and sulphur were often adequate for Verano stylo growth. Nitrogen fertilizer however was not recommended in a mixed pasture, but in a pure stand of Verano stylo, Brolman and Sonoda (1981) reported a better dry matter yield when nitrogen, at the equivalent of 180 kg N/ha, was added.

Verano stylo is not only sown with natural and cultivated tropical grasses but also with upland crops. These include rice, cassava and kenaf. Work at Khon Kaen University, Thailand, has shown that Verano stylo can be established in stands of cassava and kenaf without seriously affecting the yield of the companion crop. However, the time of sowing is important. Wilaipon et al (1981) found that when Verano stylo and cassava were planted at the same time, there was a significant reduction in cassava yield compared with the cassava alone treatment (7.6 vs 26.8 ton/ha). But when Verano stylo was sown six weeks after the cassava, there was a very small and insignificant reduction in cassava yields (24.5 vs 26.8 ton/ha). Pongskul et al (1982) found that kenaf yields when planted alone were 12.1 ton/ha. When sown in combination with Verano stylo, yields were reduced to 8.9 ton/ha. However, Verano stylo yields were reduced five-fold by delaying the sowing in the kenaf. Although there were no beneficial effects from sowing Verano stylo in these crops in terms of yields, it provided a substantial amount of additional forage for livestock. This forage can be utilized before harvesting kenaf or cassava.

Newly sown Verano stylo needs early grazing to check grass growth and to encourage the legume to branch. It is desirable to encourage the plant to act as a perennial and judicious grazing may be influential. If Verano stylo grows and flowers unchecked for too long, it may drop its leaves and die. Regrowth from seed is usually reliable but weeds are more likely to invade when the legume is allowed to act as an annual. However, the long term persistence of the legume in heavily grazed situations is nevertheless dependent on the appropriate form of grazing management to ensure adequate seeding and seedling regeneration in subsequent

seasons (Wilaipon and Pongskul, 1983). In communal land areas where the Verano stylo was lightly stocked in the wet season and only moderately stocked during the dry season, the legume content at the end of the second wet season increased from 34% in 1978 to 56% in 1979. This is in contrast to the treatment that was heavily grazed which declined in legume content from 31% in 1978 to 19% in 1979. In Australia, McKeague et al (1978) have suggested that leaving a 10 cm stubble in July and August makes the best use of wet and dry season growth. In Thailand, early heavy grazing in the wet season and deferment in the late wet season is recommended to allow seed setting (Wilaipon and Humphreys, 1981; Humphreys, 1982).

CHAPTER 3

EXPERIMENT I: GROWTH PATTERN OF STYLOSANTHES HAMATA CV VERANO UNDER CONTROLLED ENVIRONMENT CONDITIONS

I. INTRODUCTION

There are few publications on the growth and development of Verano stylo (Stylosanthes hamata cv Verano). Gardener (1978) measured the relative growth rate and dry weight increments of a number of Stylosanthes species including Verano stylo over a period of six weeks after sowing. He found that relative growth rate and dry weight increments in Verano stylo were higher than those of perennial stylo species like Stylosanthes scabra but similar to that of S. humilis. However, the relative growth rate during this period was still low compared with that of C4 grasses (e.g. Panicum maximum) (Ludlow and Wilson, 1970). This could be a problem when Verano stylo is grown with such vigorous companion grasses. Gardener et al (1982) studied the changes in total dry weight and its components from a pure stand of Verano stylo over two growing seasons. Total dry weight production reached a peak at about 128 days after sowing. The contribution of the leaf fraction to dry matter yields was high during the early stages of growth, before declining throughout the wet season, with the subsequent major contribution coming from stem tissue.

This introductory experiment reports the uninterrupted growth and development of Verano stylo under conditions of adequate soil moisture and nutrients over a period of 131 days in the controlled environment of a growth room - and hence provides a desirable background and understanding of the species in question. It includes various aspects of plant morphological development, including branch numbers and plant height, and describes the increase and distribution of dry matter yield and leaf area development.

II. MATERIAL AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURES.

The experiment was carried out in the Controlled Climate Rooms at the Plant Physiology Division, DSIR, Palmerston North, New Zealand (Plate 1.1). Plastic pots of 16 cm diameter and 16 cm depth, with drainage holes at the base were filled with 5.5 kg of a mixture of peat, vermiculite and gravel (15 : 15 : 70). Stylosanthes hamata cultivar Verano (Verano stylo) seeds collected from North-Eastern Thailand were selected for similar size and scarified with concentrated sulphuric acid for 30 minutes, then washed thoroughly and dried. Seeds were incubated in a germinator for 48 hours at 20 - 30°C before planting. Ten germinated seeds were sown in each pot, covered with a thin layer of soil, and watered. Pots were placed directly in the controlled environment room. Environmental conditions imposed (detailed in Appendix 1) were:

Photoperiod	- 12 hours
Light intensity	- 160 Wm ⁻² (400 - 700 nm)
Temperature	- 30°C day and 24°C night
Humidity	- 70 day and 90 night
Carbon dioxide level	- 290 - 340 ppm

These environmental conditions were chosen, following reference to climatic records for the Central Plain region of Thailand, to simulate as closely as possible the climate prevailing during the growing season.

A complete nutrient solution (NCSU - Appendix 2) was applied twice daily for the first three weeks of planting. Watering frequency was then increased to four times per day until the end of the experiment. After three weeks of growth, some 'tip burn' was observed. To minimise this condition, pots were flushed through with deionized water every week to remove nutrients accumulating in the pot. Rhizobial bacteria (in agar form) were applied to the soil surface one week after sowing. Seedlings were thinned to three plants per pot, after two weeks and finally to one plant per pot.



Plate 1.1: General view of the Controlled Climate Room.

B. HARVESTING SCHEDULE

Harvests of the entire plant were made on days 7, 14, 21, 28, 39, 60, 67, 81, 88, 117 and 131 days after seedling emergence. Four plants were removed for dissection on each occasion.

C. PLANT MEASUREMENTS

At each harvest, plants were separated into leaf, stem and inflorescence. The samples were dried in a vacuum air oven for 48 - 72 hours and weighed. The number of leaves, branches and inflorescences were recorded. Leaf area was also measured using an electronic Leaf Area Meter (Model 3100 Area Meter). Soil was washed from the root system and the tap root (including large woody root) and fibrous roots were separated and weighed after drying.

III RESULTS AND DISCUSSION

Before presenting the data on the growth and development of Verano stylo, it is helpful to describe and explain its major morphological features. The following section describes the growth and development of intact plants of Verano stylo, from seedling emergence to full flowering at 131 days.

A. MORPHOLOGICAL FEATURES

A.1 Stage of Growth

Baldos and Javier (1976) recognised three sharply defined development phases in the growth of Townsville stylo (Stylosanthes humilis): juvenile, vegetative and reproductive. In contrast, Verano stylo, a quantitative short-day plant, had no sharp distinction between the vegetative and reproductive phase of development, as shown by Cameron and Mannetje (1977). The commencement of first flowering was also early compared with that of other tropical legumes like S. guianensis (Loch et al, 1976) and S. humilis (Baldos and Javier, 1976). Similar results were observed in the present

work and also showed that the juvenile and vegetative stages were difficult to distinguish. Thus, on morphological grounds, growth in this study was divided into two stages, viz pre-flowering and flowering. Pre-flowering covered both the so-called juvenile and vegetative stages while the flowering stage covered the period after the onset of flowering. In this study, the pre-flowering stage extended over the first 35 days of growth, which is shorter than that recorded under field conditions in Queensland (Skerman, 1977; Wilaipon and Humphreys, 1976). These authors reported the pre-flowering period to be about 60 - 67 days. However, under field conditions in Thailand Wilaipon and Humphreys (1981) found that Verano stylo had a somewhat shorter pre-flowering period of approximately 40 days from seedling emergence. Such variation may in part be explained by the differences in photoperiod. Under field conditions, daylength varied from month to month while in the controlled room a constant 12 hrs daylength was employed. Cameron and Mannetje (1977) found that under controlled conditions, Verano stylo flowered at all photoperiods tested, but it occurred much earlier in the shorter photoperiods of 10 and 11.5 hrs. In their experiment, Verano stylo flowered 32 days after sowing at 11.5 hrs photoperiod and 32°/24°C (day/night) - this is similar to the present experiment.

Plants at the pre-flowering stage had a slower rate of growth and produced fewer branches and leaves, accompanied by only small increments in plant height compared with the flowering stage. However seed germination was rapid and the production of the first trifoliate leaf was observed within 7 days (Plate 1.2A).

The major portion of dry weight accumulation during the life of the plant occurred after the onset of flowering and included vegetative and reproductive growth. This was also observed by Cameron and Mannetje (1977) and Wilaipon et al (1979). In this study, the flowering stage commenced approximately 35 days after seedling emergence and continued throughout the experimental period.

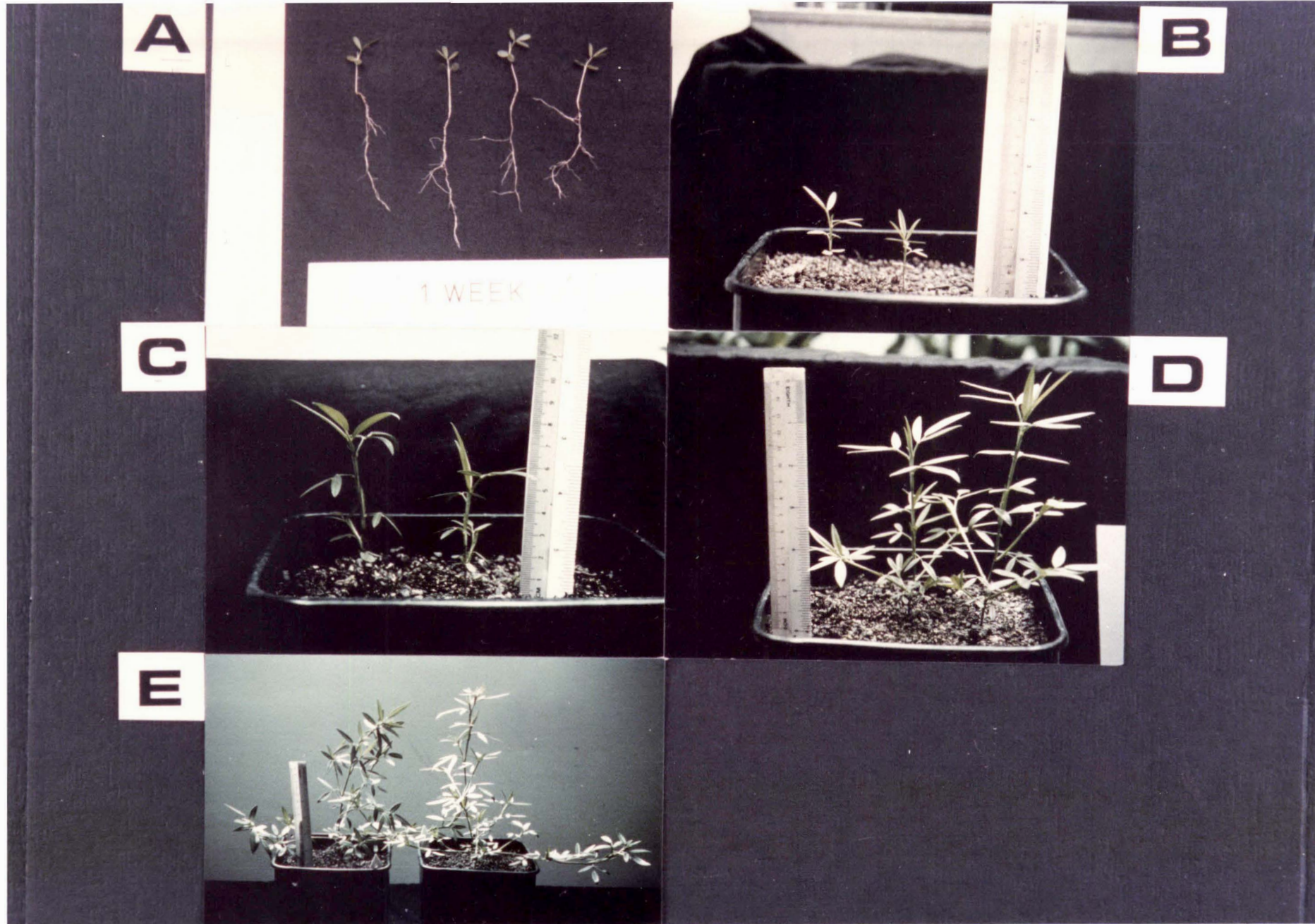


Plate 1.2: Growth and development of Verano stylo after seedling emergence up to first flowering appearance. A = 1 week; B = 2 weeks; C = 3 weeks; D = 4 weeks; E = 5 weeks.

A.2 BRANCH NUMBER

Branching of the main stem commenced in the axils of the cotyledons approximately 21 days after emergence (Plate 1.2C). Over a subsequent 2 - 3 week period, branch numbers increased only slowly at about 3 branches per week. At the onset of flowering, when secondary branch formation commenced, the rate of branch production rose sharply (Table 1.1). Branching progressed up the main stem and in this study, the terminal growing point developed an inflorescence after the formation of 11 nodes. This was similar to the figure given by Cameron and Mannetje (1977).

Branch numbers rapidly increased as primary, secondary and higher order branches appeared. As a result, the rate of branch appearance was highest between day 60 and 67 at 32 branches per day. Total branches per plant reached a maximum of 1823 at day 117. The decline in the number of branches at a later stage (day 131) was due to shedding of the small and older reproductive branches.

The results demonstrate that a high rate of branch differentiation continues during flowering in Verano stylo. It also shows that this cultivar is capable of producing large numbers of branches and greater, than some other tropical legumes. For example, with Townsville stylo, Baldos and Javier (1976) reported 845 branches/plant 168 days after sowing, with a maximum rate of branch appearance of 16 branches per day between day 112 and 140. Loch and Humphreys (1970), working with Townsville stylo, also reported a maximum rate of branch appearance of approximately 1.1 branches per day between days 89 and 104. For Verano stylo, Wilaipon et al (1979) reported that the maximum total branch density was 4980 branches/m² at 96 days after sowing, under glasshouse conditions. The high number of branches produced indicates that Verano stylo has a high potential for bud production for subsequent growth. A close relationship ($R = 0.952$ **) between branch numbers and plant dry weight, suggests that grazing or cutting management should aim at encouraging branch development.

Table 1.1 Number of branches per plant

Days after seedling emergence	Number of branches per plant
7	0
14	0
21	2 $\pm$ 0
28	6 $\pm$ 0.5
39 ¹	46 $\pm$ 12.6
60	317 $\pm$ 130.1
67	596 $\pm$ 148.5
81	1040 $\pm$ 190.6
88	1147 $\pm$ 206.8
117	1823 $\pm$ 666.7
131	1505 $\pm$ 348.0

¹ 50% of the plant population flowering.

A.3 LENGTH OF PRIMARY BRANCH

The first primary branches in the axils of the cotyledon were observed three weeks after seedling emergence. By the fourth week, another three branches (1.80, 3.90 and 1.83 cm in length respectively) had arisen from the axil of the first, second and third true leaves. All primary branches increased in length with the most marked increases occurring in the lower primary branches (Figure 1.1).

A.4 PLANT HEIGHT

The slow increase in plant height during the pre-flowering stage is shown in Table 1.2. However, there was a steep increase in plant height just before the plant flowered and a maximum height of 1.2 m was measured on day 131. This was similar to field values obtained for Verano stylo in Queensland by Clements (1980) under good growing conditions. The initial slow increase of plant height in Verano stylo compared with the more rapid increase in height of associated tropical grasses at the same stage of growth confers something of a competitive disadvantage on Verano stylo under mixed pasture conditions. (Gardener, 1978 and Udchachon, 1985).

B. GROWTH AND DEVELOPMENT

B.1 Growth Analysis

The relationship between total plant dry weight and time was tested using both the logistic and the cubic polynomial model (Evans, 1972). The results suggest that neither model describes the entire growth pattern of the legume accurately. The logistic growth model over-estimated total plant dry weight during the early stages of growth (Appendix 3A) while at the late stage (days 117 - 131) the model predicted an increase in plant dry weight with time. This contrasts with actual plant growth data (Figure 1.2A) where total plant dry weight dropped sharply at that time. Thus, maximum yield was unable to be obtained from the logistic curve. However, with

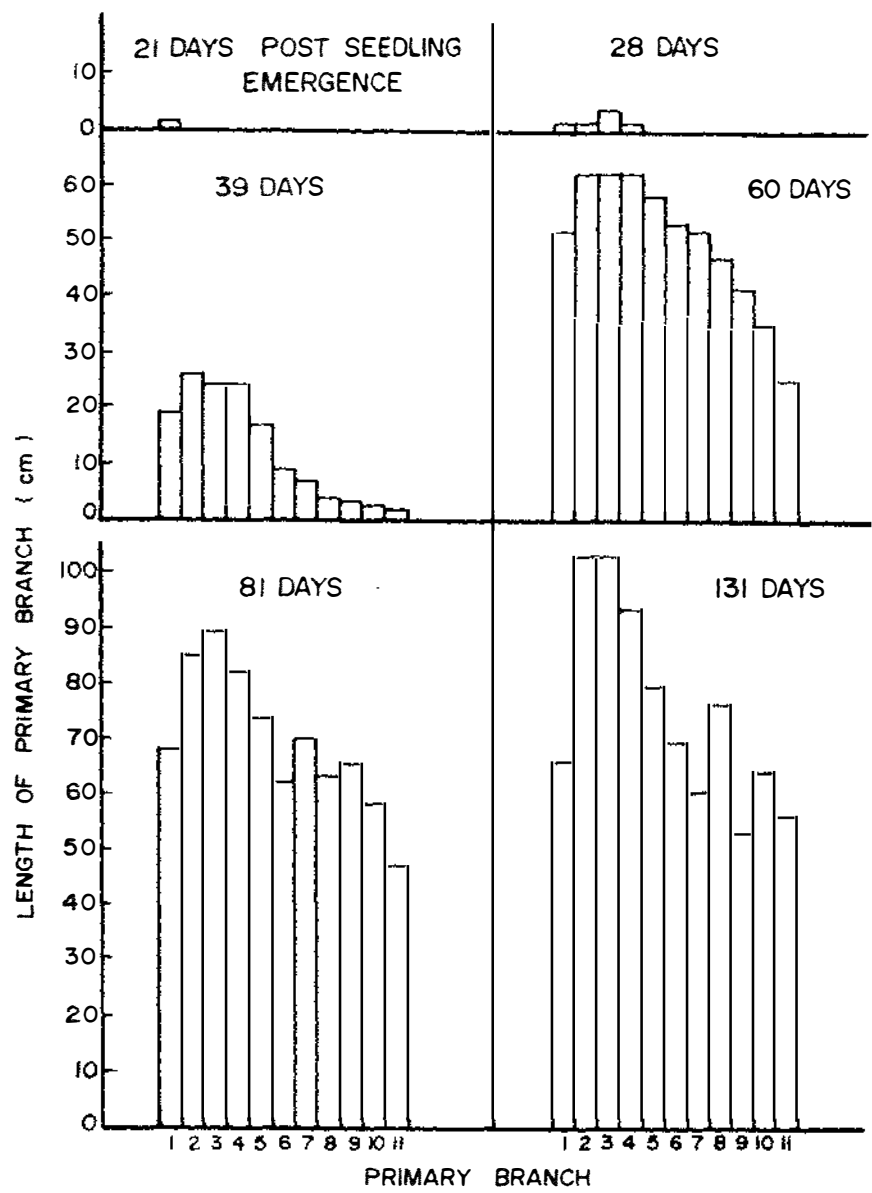


Figure 1.1: Length of primary branches along the main stem (cm)

Table 1.2 Plant height of Verano stylo

Days after seedling emergence	Plant height (cm)
7	2.6 ± 0.39
14	3.4 ± 0.85
21	4.7 ± 0.29
28	16.4 ± 0.54
39 ¹	28.9 ± 0.83
60	64.2 ± 0.79
67	72.7 ± 2.32
81	90.5 ± 6.81
88	92.6 ± 4.10
117	112.2 ± 4.78
131	114.9 ± 3.40

¹ 50% of the plant population flowering

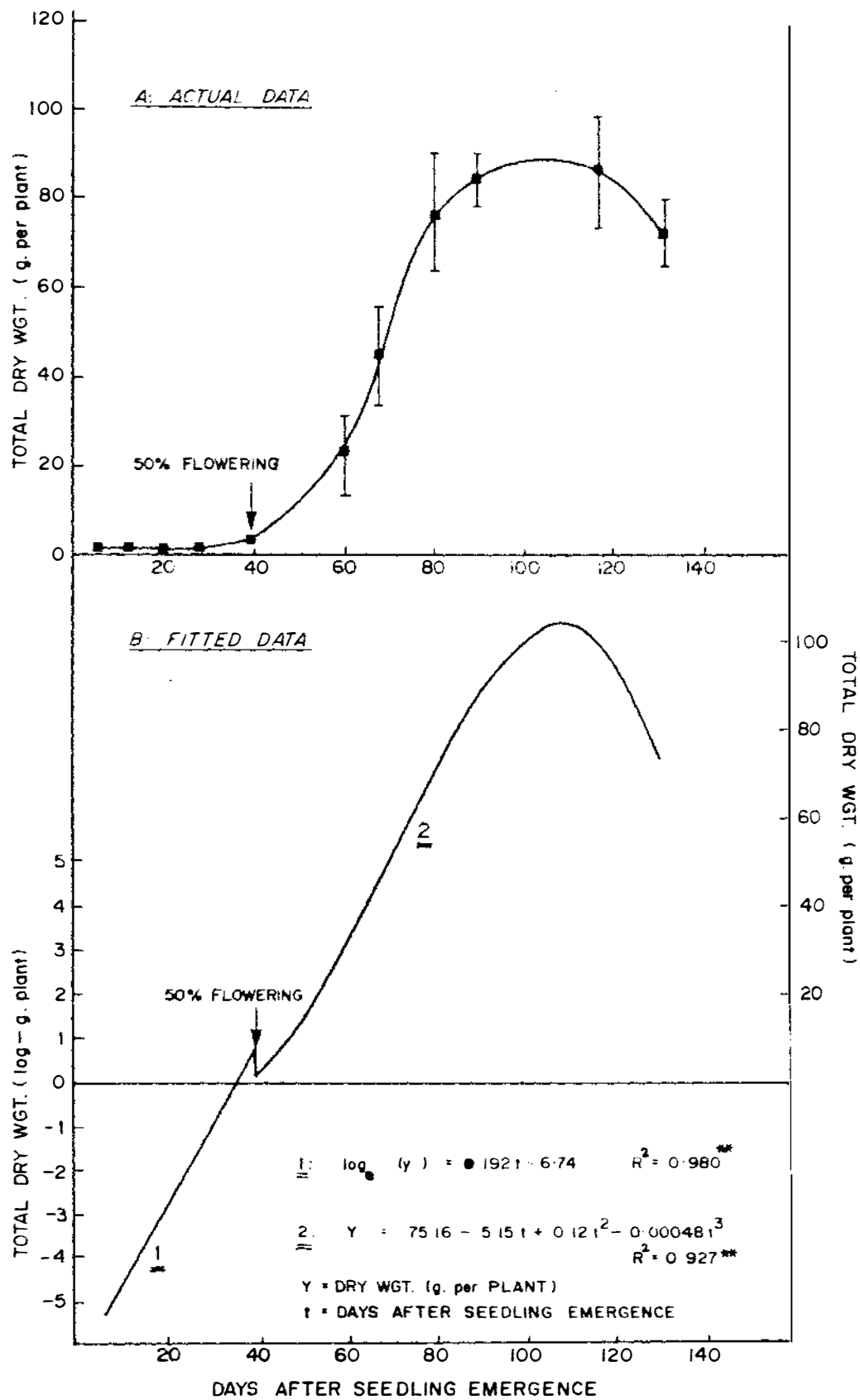


Figure 1.2: Changes in total dry weight with time:
A. Actual data; B. From fitted data;
1 and 2 represent line of best fit
between each phase of growth

the polynomial model (Appendix 3B), the growth of the plant was under-estimated during the early stages of growth (0 - 28 days). These led to the conclusion that the entire growth pattern of this species in the present experiment could not be described using only one model. Hunt and Parsons (1977) suggested that a lengthy and complex series of data should be approached by the segmentation of the growth curve.

The relationship between plant dry weight and time was therefore described using two equations. The first section of the data, up to 50% flowering (0 - 39 days), was best fitted with a linear equation (Figure 1.2B) while the remainder gave the best fit with a cubic polynomial (Figure 1.2B).

This latter equation was able to describe the rapid growth phase as well as the later decline in total plant dry weight.

To obtain more information on the growth pattern of *Verano stylo*, absolute growth rate was calculated at 10 day intervals using the above equations. The pattern of growth rate at the pre-flowering stage was slow and rapidly increased after the onset of flowering. The highest absolute growth rate occurred between 70 and 80 days after seedling emergence at 2.04 g per day (Figure 1.3). Maximum total plant dry weight of 105 g per plant was obtained 108 days after seedling emergence (Figure 1.2B) using the predicted growth curve. Absolute growth rate decreased rapidly to zero between 110 and 120 days. The relative growth rate calculated using the two equations, is shown in Figure 1.4. In common with the observation for most plant species, relative growth rate declined as the plant aged. This is related to the decreasing proportion of actively growing tissues.

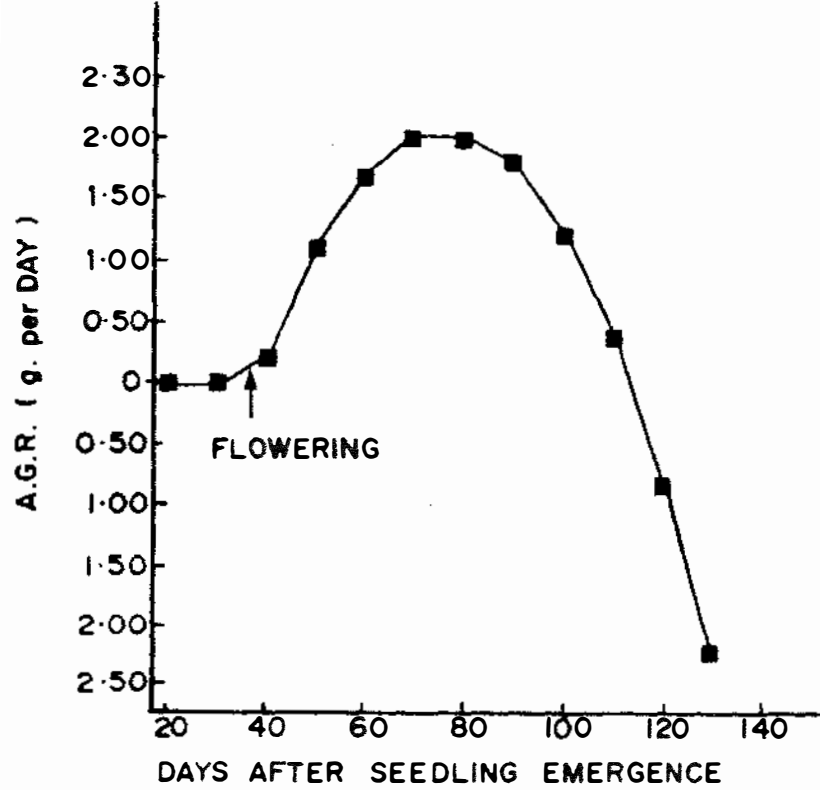


Figure 1.3: Absolute growth rate of Verano stylo calculated from fitted growth model (Figure 1.2B)

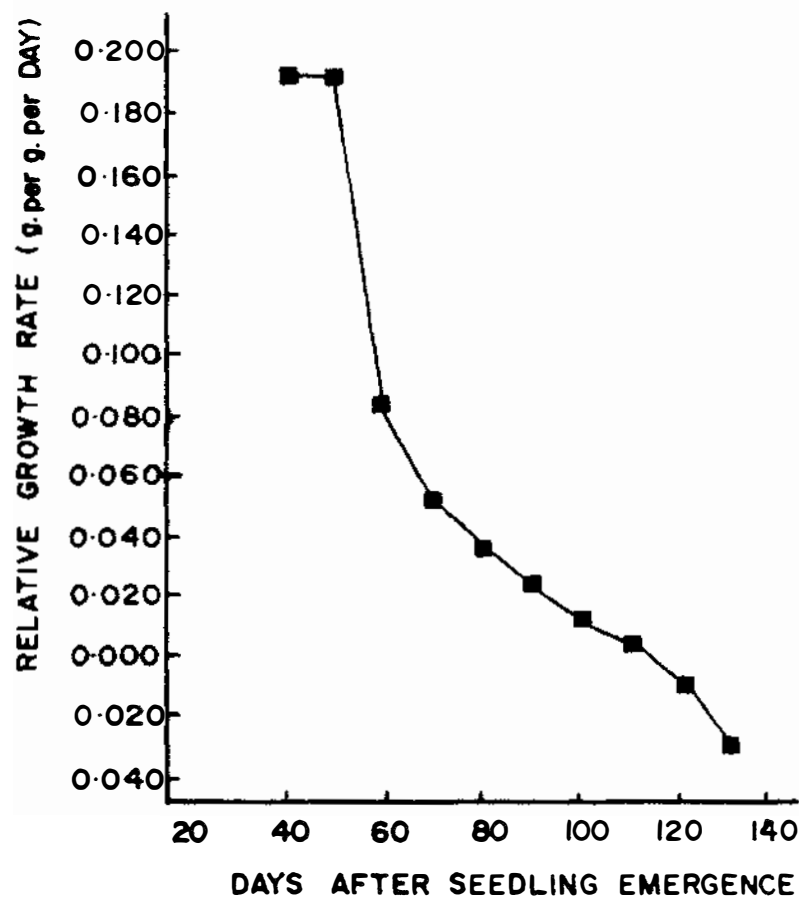


Figure 1.4: Relative growth rate of Verano stylo calculated from fitted growth model (Figure 1.2B)

B.2 DRY MATTER YIELD

The growth and development of plant components are presented in Figure 1.5. Leaf and stem fractions increased slowly during the pre-flowering stage (0 - 39 days). Then all components, including inflorescences, significantly increased with the onset of flowering, despite major differences in the rate of growth for each component. For example, during the first four weeks following the onset of flowering (i.e. to day 63 approximately), all components increased substantially with the maximum rate of increase occurring in the stem fraction, which continued to increase significantly. The leaf fraction increased at a much slower rate during the 4 weeks from flowering, as did the root fraction. After this time, both the leaf and root fractions remained relatively constant until the end of the experiment. All components reached a maximum dry weight by day 117, and then either remained constant or declined to the end of the experiment. Figure 1.5 clearly shows that stem is the main plant component, followed by the inflorescence fraction. The two contributed more than 50% of total plant dry weight.

Although Verano stylo had a high rate of leaf and branch differentiation after the onset of the flowering, total leaf dry weight (Figure 1.5) did not show the same trend as leaf number (Table 1.3) and branch number (Table 1.1) beyond day 67. This could be explained by reduced dry weight per leaf from day 39, by reduced specific leaf area from days 88 and through an observed increase in leaf senescence (leaf number) near the end of the experimental period (Table 1.3).

Branch number was also found to be closely correlated with inflorescence dry weight ($R = 0.978^{**}$), with stem dry weight ($R = 0.939^{**}$) and with total leaf dry weight ($R = 0.887^{**}$).

The inflorescence fraction dry weight was strongly related to inflorescence number ($R = 0.962^{**}$) rather than to the size of the individual inflorescence ($R = 0.453^{*}$) (Table 1.4). The decline in inflorescence dry weight over the final

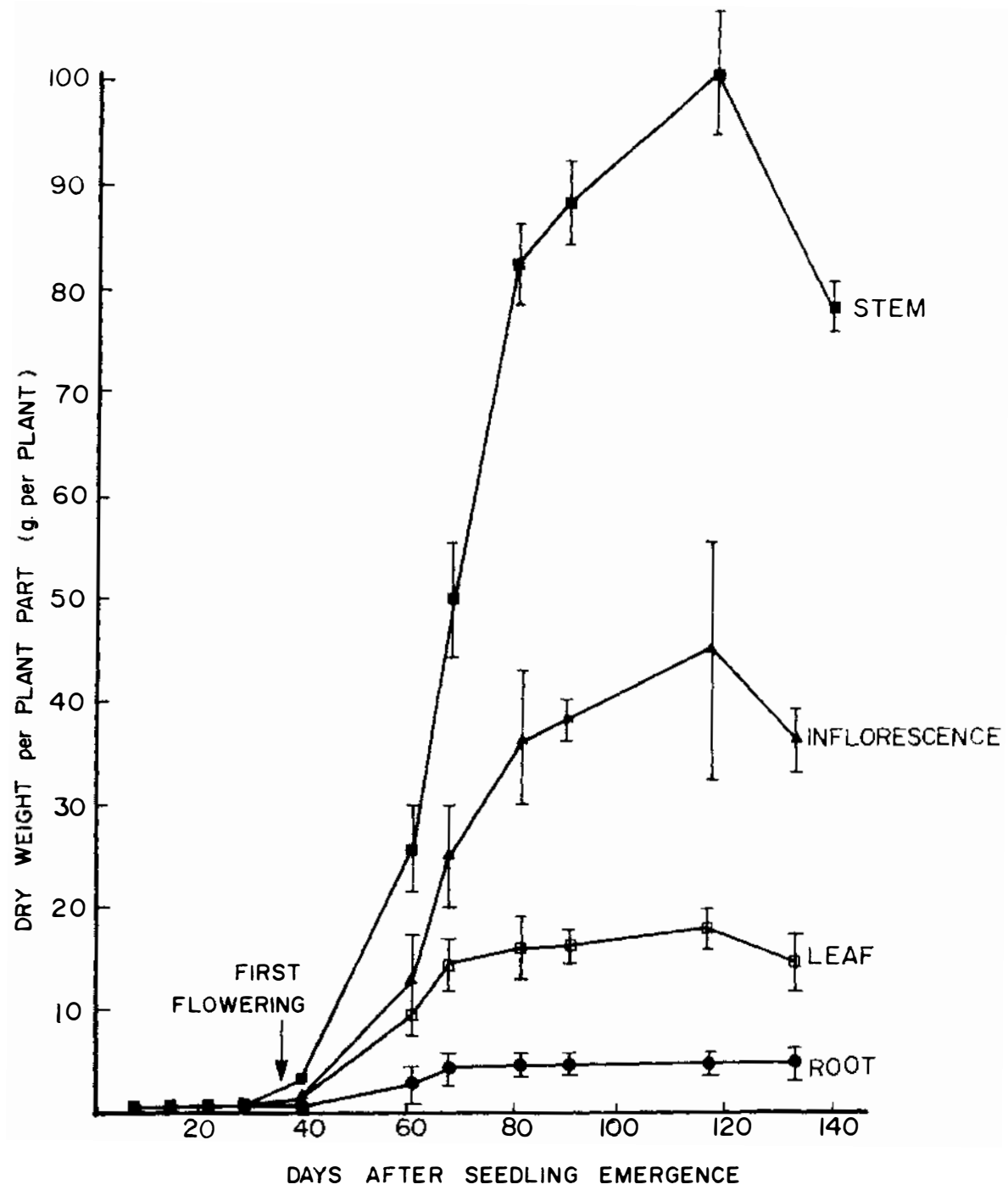


Figure 1.5: Dry matter yield of leaf, stem, inflorescence and roots of Verano stylo (g/plant)

Table 1.3 Leaf number, leaf size, dry weight per leaf and specific leaf area.

Days after seedling emergence	Number of leaves per plant ¹	Leaf size (cm ² /leaf)	Leaf dry weight (mg/leaf)	Specific leaf area (cm ² /g)
7	1	0.66	5	132.0
14	3	0.86	5	184.3
21	5	1.28	7	205.8
28	18	1.71	9	197.5
39 ²	107	3.15	15	210.1
60	538	2.78	12	227.6
67	984	2.39	11	227.0
81	1420	2.18	9	241.0
88	1424	2.10	8	254.3
117	1946	1.58	7	224.4
131	1634	1.32	7	202.2

¹ A trifoliate leaf.

² 50% of the plant population flowering.

Table 1.4 Inflorescence number and dry weight

Days after seedling emergence	Inflorescence number per plant	Dry weight (mg) per inflorescence
39	21	0.2
60	190	19.7
67	465	22.7
81	914	21.9
88	990	22.4
117	1777	15.2
131	1499	14.4

16 days is explained by the reduction in inflorescence number over this period (Table 1.4). In addition, shedding of older inflorescences could also be important, as demonstrated by Gardener et al (1982).

In the present study, the dry matter yield of all the components mentioned above arose mainly from the lower primary branches (branches 1 - 6) on the main stem (Figure 1.6). Only 30% of total dry matter yield came from the upper primary branches (branches 7 - 12) which originated from the sixth to eleventh nodes on the main stem. Once again, dry matter yield consisted mainly of stem tissue, particularly of the lower primary branches (Figure 1.6), with an increasing mass up to day 117. Beyond day 117 all components declined in weight, on both upper and lower branches, although the proportion of stem continued to rise.

Unlike the situation described by Torssell et al (1968) who showed that total leaf dry weight of the lower branches declined as stand height increased, total leaf dry weight of the lower branches in this experiment actually increased with plant height up to day 117 and only declined over the last 14 days.

In the present study the proportion of leaf and stem was similar in both the upper and lower branches and suggests that higher rates of leaf differentiation on the lower branches may compensate for loss of leaves through ageing, when the plant is grown under possibly ideal conditions.

Growth of roots during the seedling stage (0 - 28 days) was mainly due to elongation of tap root, but with few branch roots. A more rapid growth rate followed immediately after the onset of flowering (day 35) and significantly increased until day 67. Thereafter, root dry weight changed little throughout the experiment (Figure 1.5). As a result, the shoot to root ratio increased from 3 on day 7 to 22 on day 117.

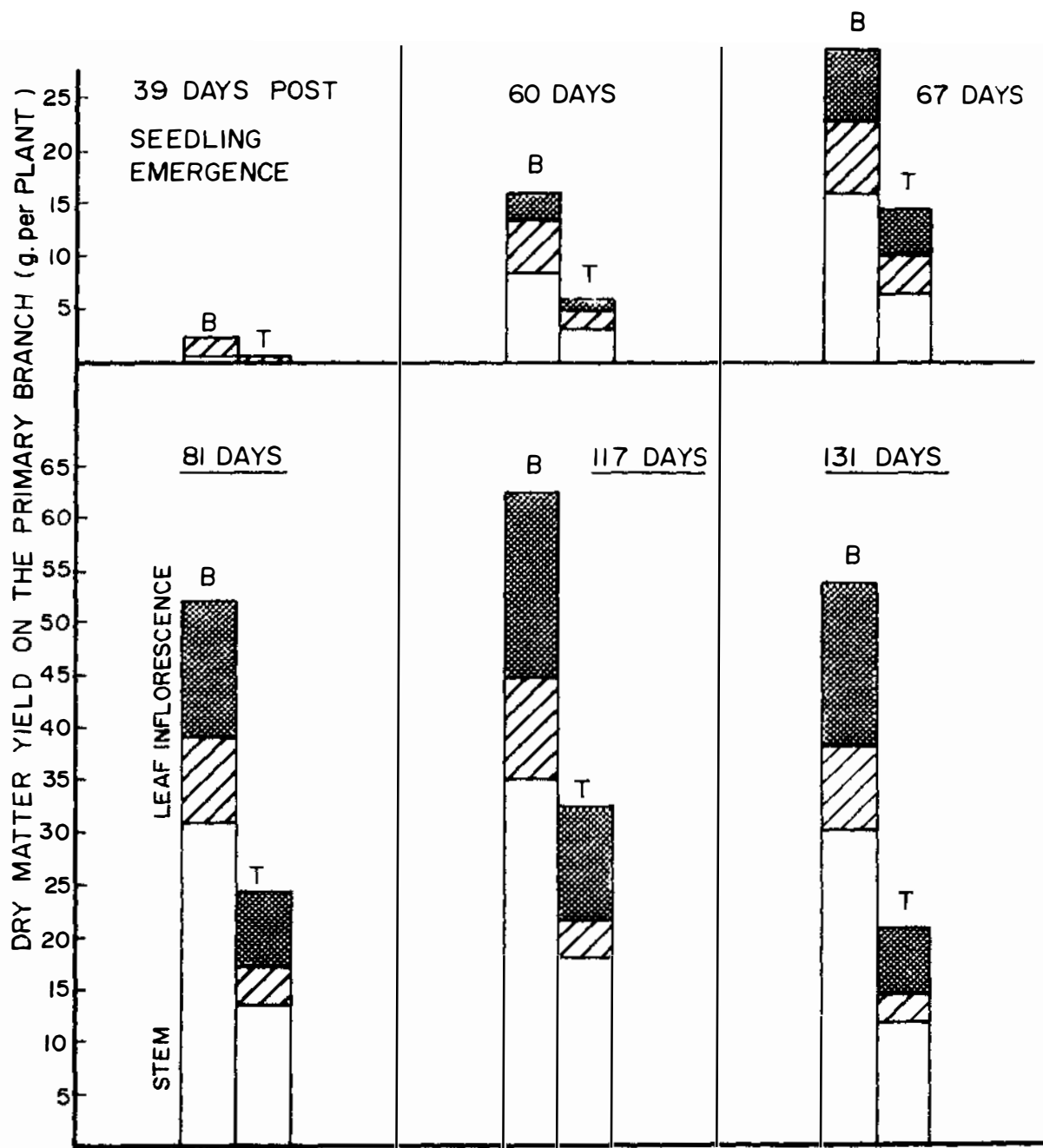


Figure 1.6: Distribution of dry matter yield on the primary branches of the main stem

B = lower primary branches (1 - 6)

T = upper primary branches (7 - 12)

B.3 LEAF AREA (CM²/PLANT), NUMBER OF LEAVES AND SPECIFIC LEAF AREA (CM²/G)

Leaf characteristics of Verano stylo plants are presented in Table 1.3 and Figure 1.7. The number of leaves and total leaf area did not increase significantly during the pre-flowering stage of growth. However, from the onset of flowering, the number of leaves increased rapidly from day 28 up to day 117. Leaf area also increased rapidly from day 28 but reached a maximum on day 81 - showing that attainment of maximum leaf area does not necessarily depend on leaf number, as leaf size and specific leaf area are also important in determining leaf area production. The reduction in leaf number from day 117, due presumably to leaf senescence, was probably the main contributor to the reduction in leaf area at that stage.

Although leaf area index could not be calculated, the maximum leaf area of 3097 cm/plant was noted on day 81. However, the maximum rate of leaf appearance of 63.2 leaves per plant per day was obtained between day 60 and day 67. The results of this study demonstrate that Verano stylo had a high rate of leaf differentiation following the onset of the flowering. Wilaipon et al (1979) also showed that a leaf density of 35500 per m⁻² occurred 96 days after sowing under glasshouse conditions. However, these results were not shown on a per plant basis.

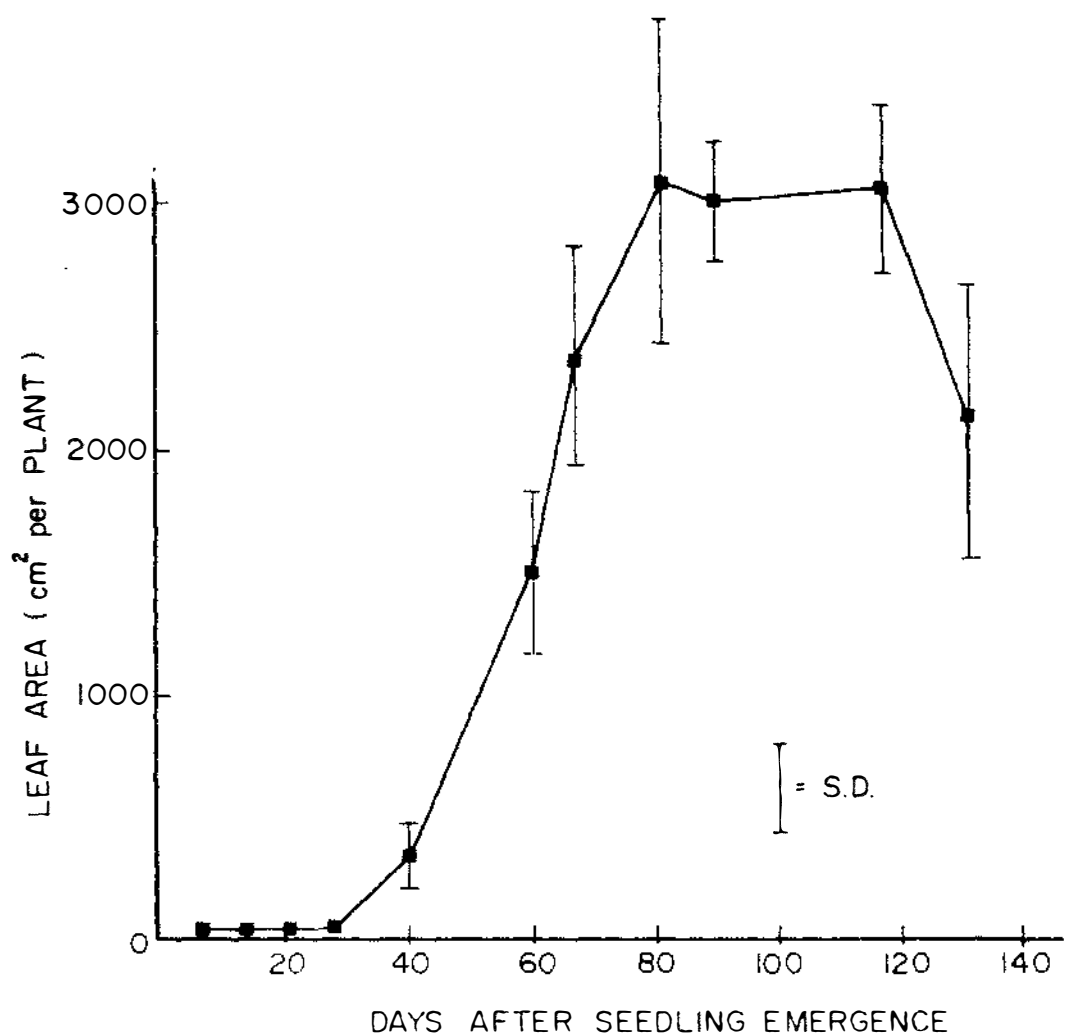


Figure 1.7: Changes in total leaf area of Verano stylo with time (cm²/plant)

CHAPTER 4

THE EFFECT OF DEFOLIATION ON THE GROWTH AND REGROWTH CHARACTERISTICS OF STYLOSANTHES HAMATA CV VERANO.

EXPERIMENT 2: STAGE OF GROWTH AND INTENSITY

I. INTRODUCTION

A necessary step in the development of management strategies for the long term persistence of legumes in grazed and cut pastures involves research into the effect of defoliation at critical periods in the plant's development. With Verano stylo under field conditions, evidence suggests that defoliation at an early stage of growth (first flower) does not affect the regrowth ability of the plant. However, grazing or cutting late in the growing season depresses yields (Wilaipon and Humphreys, 1976, 1981). In these experiments, Verano stylo was grown with volunteer grasses. In addition, the effects of late cutting were confounded with the unfavourable conditions at the end of the growing season. Thus, the effect of cutting per se could not be quantified.

Experiment 1 was designed to study the growth pattern of Verano stylo under controlled climatic conditions simulating those found in Thailand. The results indicated a worthwhile yield potential of this legume resulting from a high rate of branch and leaf differentiation over 131 days of the experiment. The next step was to examine the growth response pattern of the various plant components when the plant was subjected to different intensities of defoliation at different stages of growth and development.

II. MATERIAL AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURES

Environmental conditions and planting procedures were similar to the previous experiment (Experiment 1). After thinning to one plant per pot, all plants were blocked into four replications based on their uniformity of establishment. After treatments were imposed, pots of similar treatments were located together so that between treatment interference was minimised during regrowth.

B. TREATMENTS

There were two cutting intensities and two stages of growth in this experiment, as follows:-

- Stage of growth:
1. Early stage - when 50% of the plants commenced flowering (approximately 39 days after seedling emergence).
 2. Late stage - at approximately 88 days after seedling emergence (close to maximum growth rate).
- Cutting intensity:
1. Cut the main stem above node 5 (between nodes 5 and 6) and primary branch above node 4 (between nodes 4 and 5 along the branch).
 2. Cut the main stem above node 5 (between nodes 5 and 6) and primary branch immediately below node 1 (along the branch).
- Control: Uncut.

Therefore the five treatments (Figure 2.1) can be listed as follows:

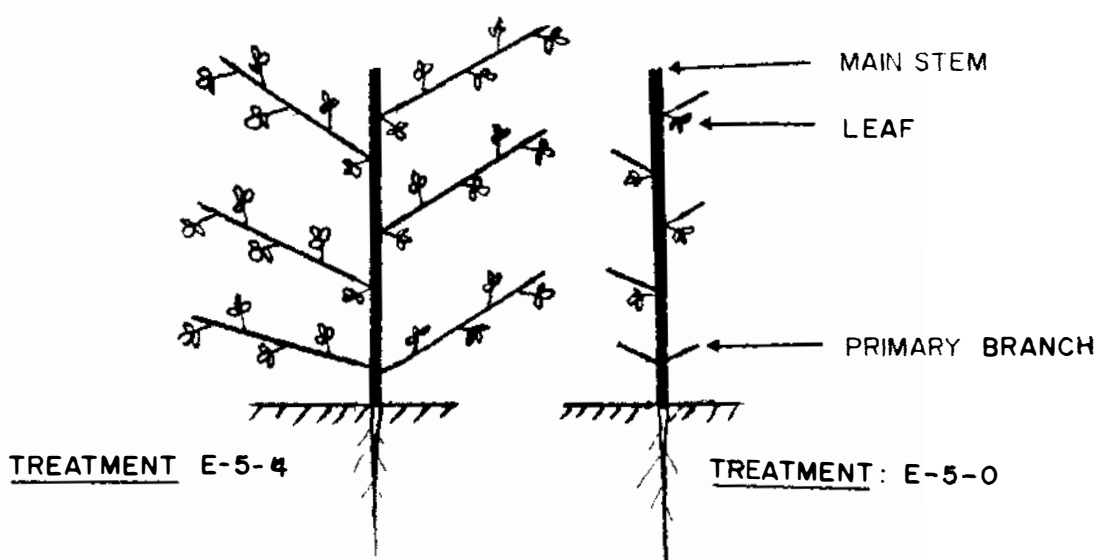
1. Control: Uncut.
2. E-5-4: Cut the main stem above node 5 (between nodes 5 and 6) and primary branch above node 4 (between nodes 4 and 5 along the branch) when 50% of the plants commenced flowering.
3. E-5-0: Cut the main stem above node 5 (between nodes 5 and 6) and primary branch immediately below node 1 (along the branch) when 50% of the plants commenced flowering.
4. L-5-4: Cut the main stem above node 5 (between nodes 5 and 6) and primary branch above node 4 (between nodes 4 and 5 along the branch) at 88 days after seedling emergence.
5. L-5-0: Cut the main stem above node 5 (between nodes 5 and 6) and primary branch immediately below node 1 (along the branch) at 88 days after seedling emergence.

The first cutting was according to the stage of growth and the second cut was imposed after a regrowth period of 42 days. A final cut was taken after a further regrowth period of 28 days, except the uncut control which was terminally sampled at 131 days after seedling emergence.

C. HARVESTING SCHEDULE

The harvesting schedule is given in Figure 2.2.

A: EARLY STAGE OF GROWTH (EARLY)



B: LATE STAGE OF GROWTH (LATE)

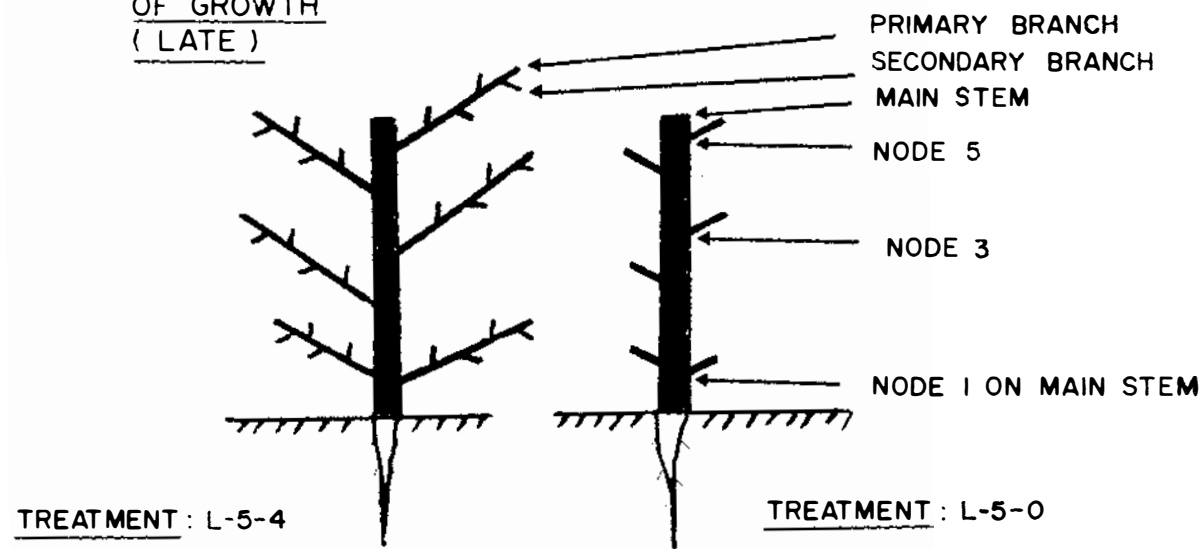
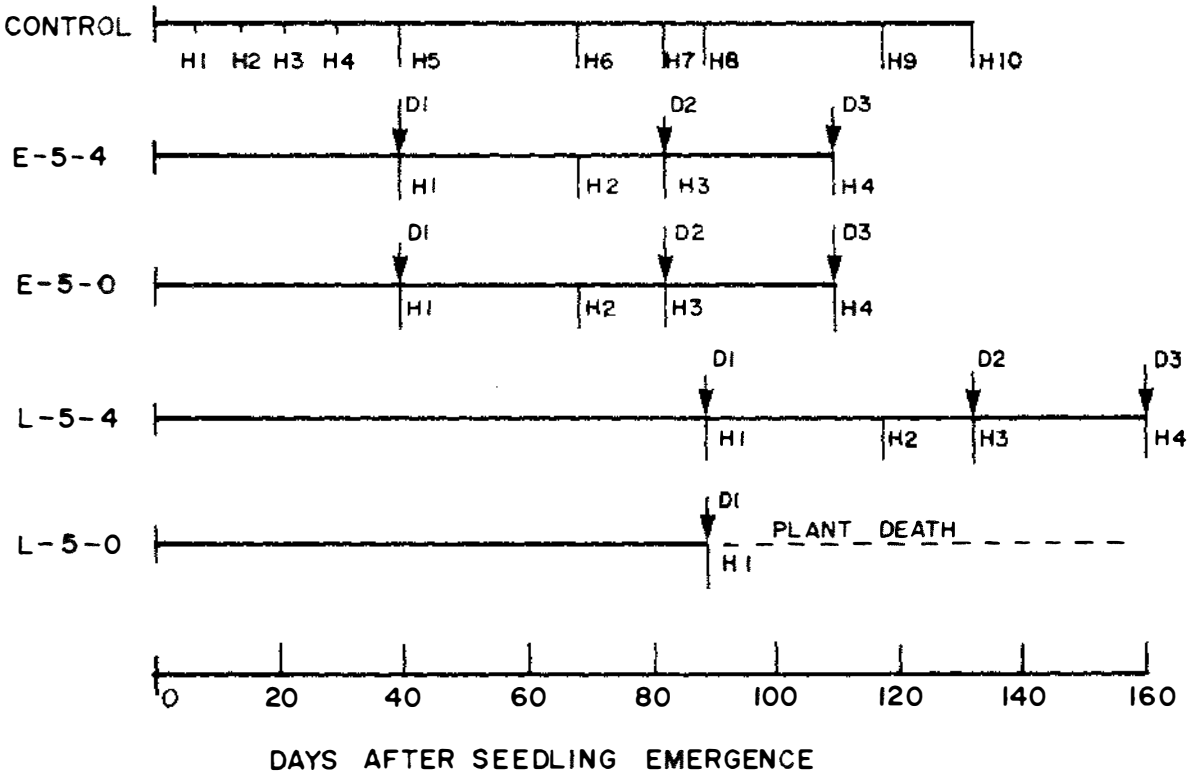


Figure 2.1: Diagrammatic illustration of the appearance of the plants after different intensities of defoliation.

TREATMENT:



KEY: H = HARVEST
D = DEFOLIATION

Figure 2.2: Harvesting schedules over the experimental period

D. PLANT MEASUREMENTS

D.1 Dry Matter Yield

Plant dry matter yields were measured by random sampling of the plant populations on week 0, 4, 6 and 10 after the first cut. On each harvest occasions, 4 plants per treatment were taken and separated into leaf, stem and inflorescence on each primary branch. Soil was washed from the root system and the tap (including large woody root) and fibrous roots separated. Dry matter yields were obtained by drying all samples in a vacuum oven for 72 hours.

D.2 Leaf Area and Leaf Number

Leaf area and number were measured at the same time as plant dry weight measurement. Leaf area was determined using the Electronic Leaf Area Metre (Model 3100 Area Meter).

D.3 Branch Number

Branch number was recorded on weeks 0, 1, 2, 3, 4, 6, 7, 8, 9 and 10 after the first cut. The numbers on control plants were determined on days 39, 67, 81, 88, 117 and 131 after seedling emergence. A branch is defined in this study as a shoot with at least one fully expanded trifoliate leaf.

D.4 The Number of Growing Points

The number of visible growing points arising from the stubble of the main stem and primary branches was determined 10 days after each cutting. A "growing point" is defined in this study as a bud from which a young leaf has started to emerge.

E. CHEMICAL MEASUREMENTS

E.1 Crude Protein

Nitrogen concentrations in each component were determined after semi-micro Kjeldahl digestion, using a Kjeltic Auto 1030 Analyser. Total nitrogen (including nitrate nitrogen) was determined according to Kjeltic Auto 1030 Analyser Manual and crude protein values calculated ($N \times 6.25$).

E.2 Total Non-structural Carbohydrate (TNC)

The analytical procedure used for determining soluble sugars and starch was that described by Haslemore and Roughan (1976). The levels of these two constituents were summed to give total non-structural carbohydrates (TNC).

E.3 Plant Material

Plant material analysed is shown in Table 2.1.

F. STATISTICAL ANALYSIS

Data were analysed according to the common procedure of a randomized complete block design for all plant characters (Little and Hills, 1975). The analysis was done by Genstat programme (Alvey et al 1977). The least significant difference at the 5% level was used to identify statistical differences. The symbols used to designate statistical significance are * ($P = 0.05$), ** ($P = 0.01$) and ns (not significant)..

Table 2.1 Plant components analysed

Time	Chemicals	Plant components				
		Stubble	Leaves	Stem	Inflor.	Root
1. At 1st cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
2. 4 wks after 1st cut	Protein	+	+	+	+	+
	TNC	-	-	-	-	-
3. 6 wks after 1st cut	Protein	+	+	+	+	+
	TNC	+	-	-	-	+
4. At 2nd cut	Protein	+	+	+	+	+
	TNC	+	-	-	-	+
5. 4 wks after 2nd cut (Final harvest)	Protein	+	+	+	+	+
	TNC	+	-	-	-	+

Plate 2.1: Uncut control treatment at early stage (39 days after seedling emergence).



Plate 2.2: Immediately after lax defoliation of the primary branches (E-5-4) at early stage (39 days after seedling emergence)



Plate 2.3: Immediately after hard defoliation of the primary branches (E-5-0) at early stage (39 days after seedling emergence)





Plate 2.4: Immediately after lax defoliation of the primary branches (L-5-4) at late stage of growth (88 days after seedling emergence). Note: L-5-4 (forward) and uncut control (backwards)



Plate 2.5: Immediately after hard cutting of the primary branches (L-5-0) at late stage of growth (88 days after seedling emergence).

III RESULTS

A. PHENOLOGICAL OBSERVATIONS

The plants grew very slowly during the establishment phase (0 - 4 weeks), as observed by many other workers (e.g. Wilaipon and Humphreys, 1983). During that period the plants developed noticeable "leaf tip burn" especially on the lower leaves, but by 5 to 6 weeks they had fully recovered and thereafter developed healthy and rapid growth.

The stage of "first flower" occurred 35 days from seedling emergence which was considerably earlier than in the field (Wilaipon and Humphreys, 1976; Skerman, 1977). With severe defoliation (L-5-0) at the late stage of growth, 85% of the plants died, whereas with early and lax defoliation there was no lethal effect on plants.

B. PLANT REGROWTH

B.1 Total Plant Dry Weight

Total dry weight per plant (cut to ground level) is presented in Figure 2.3 and Appendix 4. The early, lax cutting treatment (E-5-4) achieved almost as high a production level as the uncut control over the first 4 weeks of regrowth. However, the effect of the early defoliation became evident in the subsequent 2 weeks resulting in a significant reduction in dry matter yield over the 6 weeks regrowth compared with the uncut control.

A greater detrimental effect resulting from early, severe cutting (E-5-0) of the primary branches was clearly evident by the 4th week after defoliation and the effect continued to the end of the 6 weeks of regrowth. However, there was a relative improvement in these severely defoliated branches in the 4 to 6 week period (Figure 2.3).

Regrowth of the late and lax cut treatment (L-5-4) was relatively slow at first in spite of the greater amount of

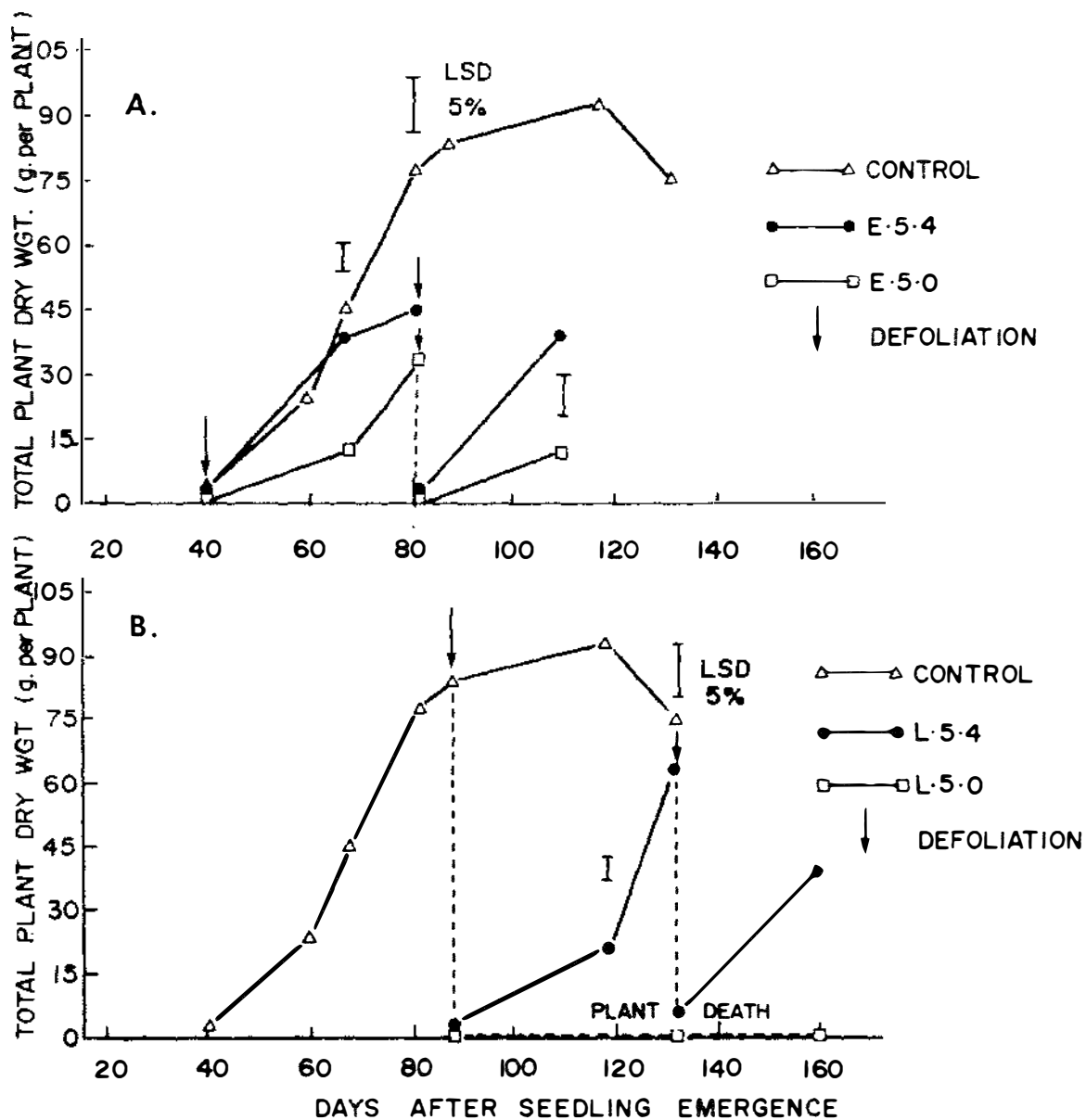


Figure 2.3: Total dry weight (cut at ground level)

A. Cut at early stage of growth (g/plant)

B. Cut at late stage of growth (g/plant)

residual stubble (Figure 2.4), but showed remarkably rapid growth in the last 2 weeks (4 - 6 weeks) and reached a yield little different from the control treatments and significantly higher than the early cut treatments (Appendix 4). The late and hard cut treatment was lethal to most of the plants so defoliated.

The different treatment effects on regrowth following the second cut six weeks later, were similar to those following the first cut. Intense and early cutting of the primary branches had a major depressing effect on production while intense late cutting caused further plant mortality.

In terms of the various plant component responses - of stem, leaf and inflorescence - to treatments, they generally showed trends very similar to total yield. The major exception was the root fraction which showed an early depression in response to hard cutting but after 6 weeks this effect was barely evident.

Regrowth in absolute terms (g/day) is presented in Figure 2.5 for the two successive growth periods. During the first four weeks after the first cut, plants in the early, lax cut treatment were superior to those in the other two cutting treatments and not significantly different from the uncut control. However, during the subsequent 2 weeks (4 - 6 weeks), plants in this early, lax cut treatment showed the slowest growth rate, while those in the late, lax cut treatment of the same intensity had the fastest growth rate.

Four weeks after the second cut (Figure 2.5), plants exposed to an early hard cut of primary branches showed the lowest growth rate, while those in the other two treatments were similar in response.

The data on the growth and development of the uncut plants (control) in this experiment have already been presented in Experiment 1. Thus, the relative growth rate which was obtained by using the predicted growth model (Experiment 1) is presented here to compare with the

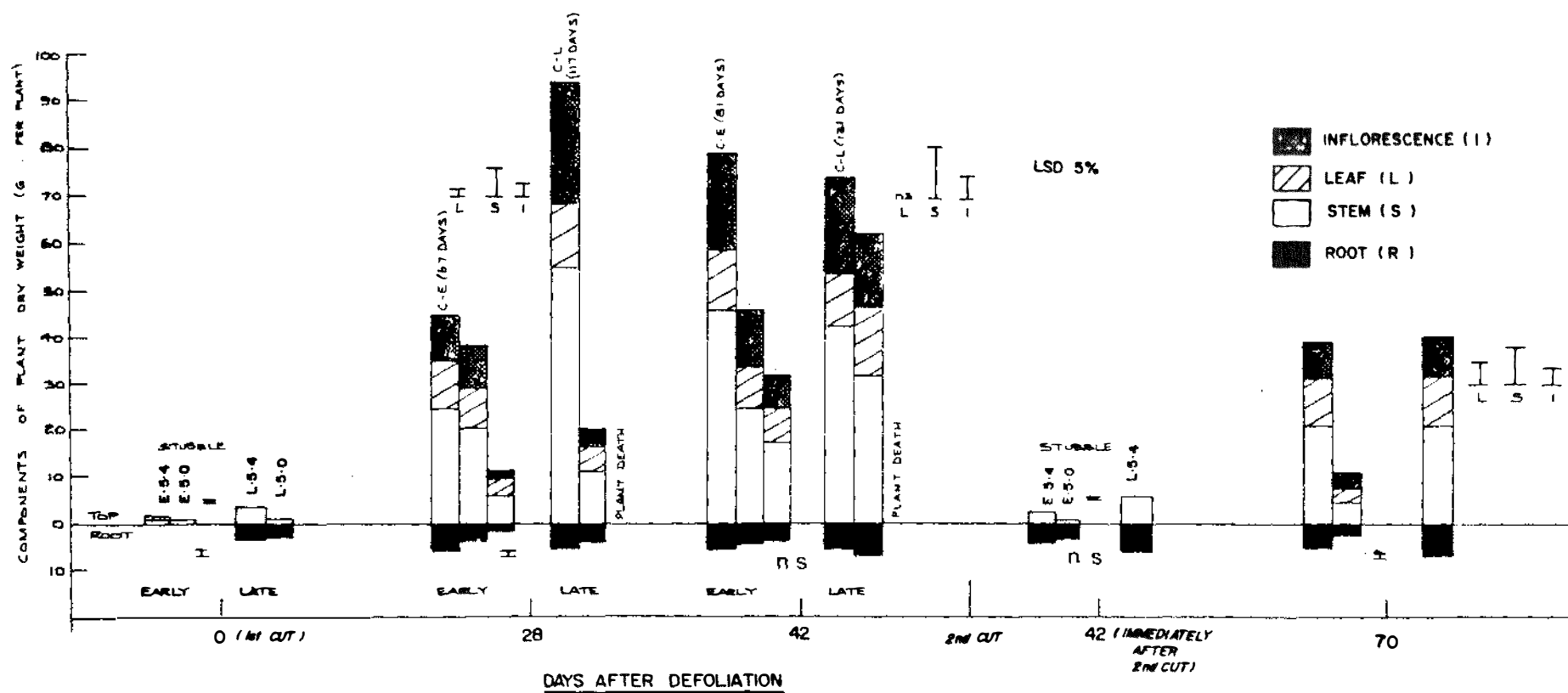


Figure 2.4: Effect of stage and intensity of defoliation on the components of plant dry weight (g/plant)

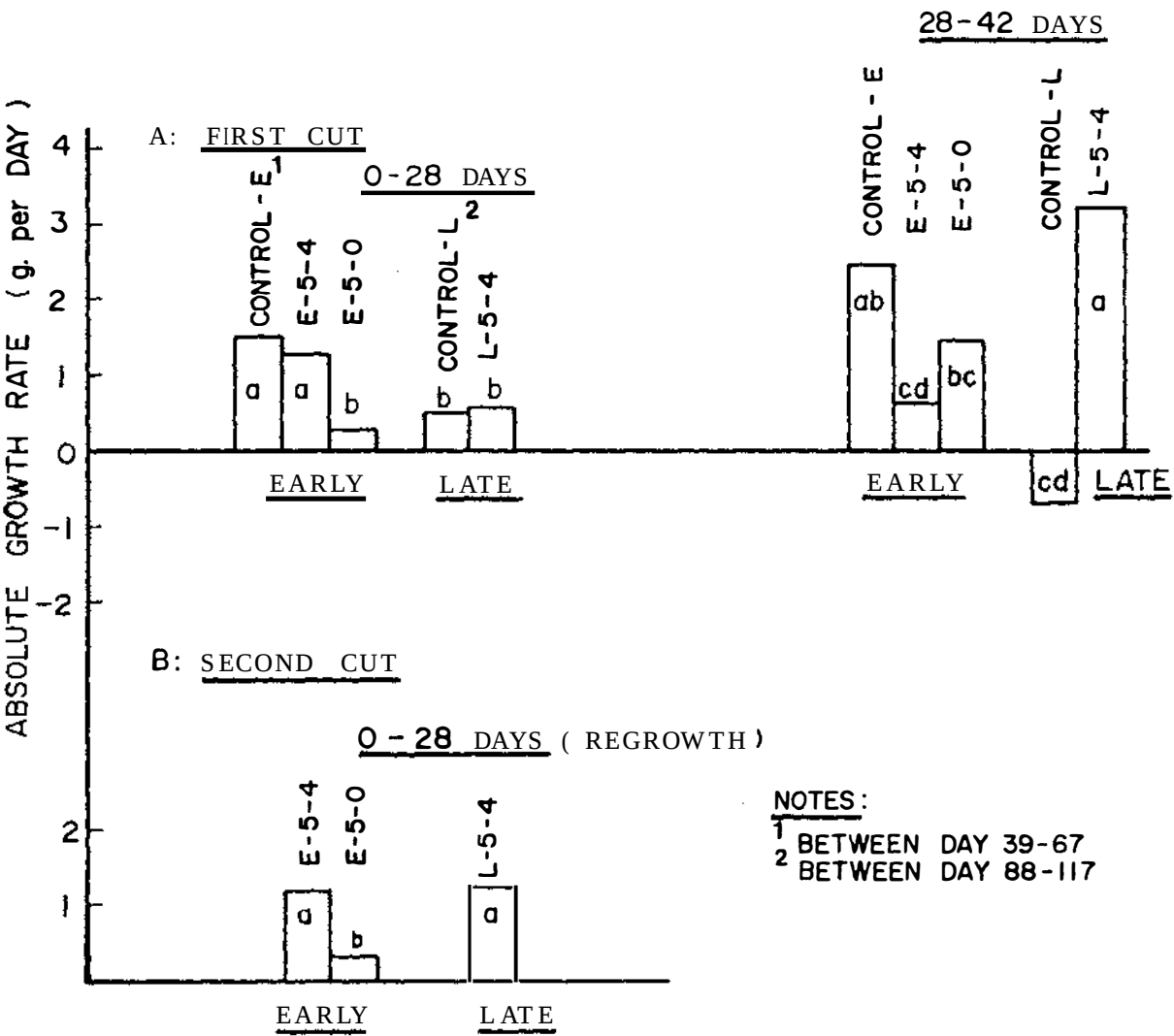


Figure 2.5: Effect of stage and intensity of defoliation on the absolute growth rate (g/day)

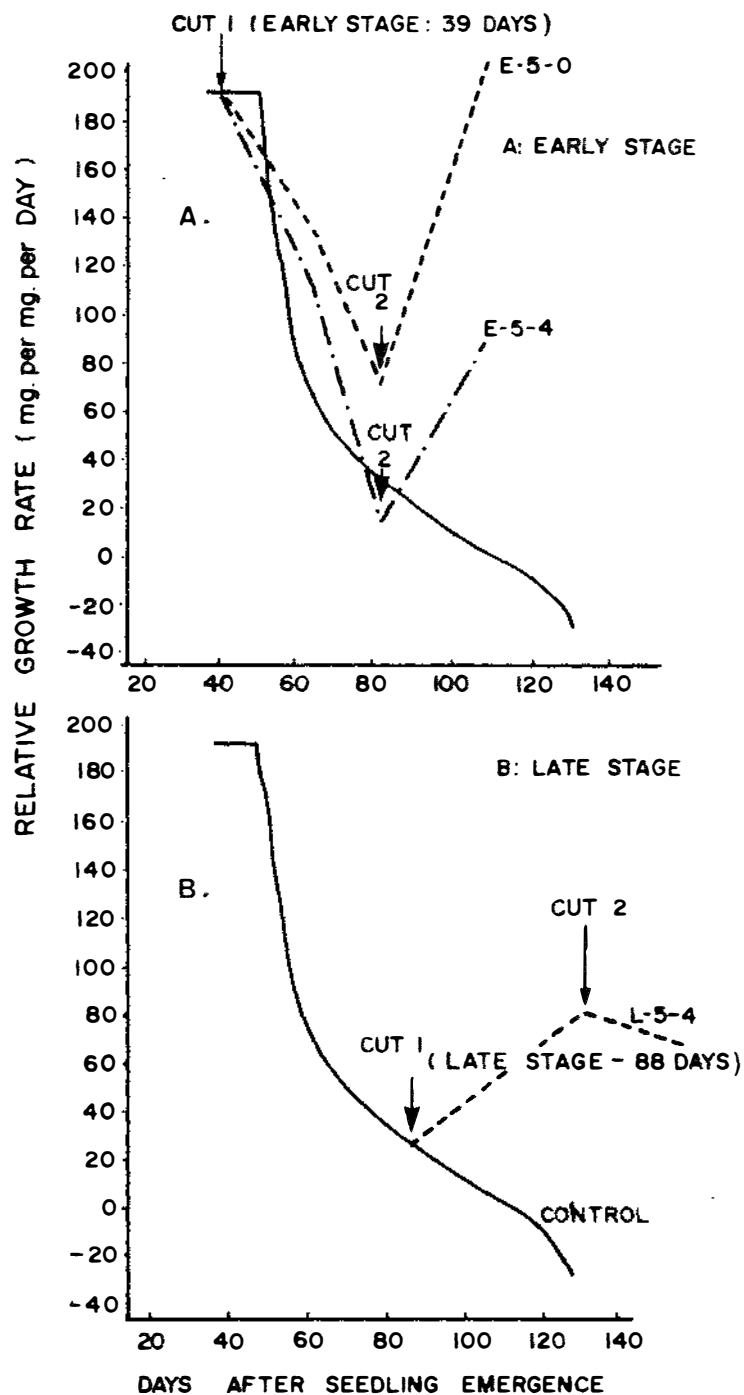


Figure 2.6: Effect of stage and intensity of defoliation on the relative growth rate (mg/mg/day)

defoliated treatments at the same time (Figure 2.6). Plants in defoliated treatments generally had higher relative growth rates than control plants, particularly with early, hard cutting. Initially, defoliation reduced relative growth rates in the early cut treatments compared with the control, but after 50 days they generally declined less rapidly than the control, particularly the early hard cut treatment, (E-5-0) through to the second cut (Figure 2.6A). In contrast, the late lax cut treatment (L-5-4) showed a marked increase in relative growth rate over the six weeks of regrowth following the first defoliation (Figure 2.6B).

Following the second cut, the early lax and early hard cut treatment produced a substantial increase in relative growth rate (Figure 2.6A). In contrast, plants in the late and lax cut treatment showed a slight decline in relative growth rate after the second cut, although the level was similar to that in the early, lax cut treatment and as expected much higher than that of the uncut control (Figure 2.6B).

Net regrowth yields over the experimental period are presented in Figure 2.7. There was no significant difference in net regrowth of leaf, stem or inflorescence for the two stages of defoliation at the same intensity (E-5-4- vs L-5-4). However, both intense cutting treatments significantly depressed the yield of all components.

B.2 Branch Number

The marked effects of the stages and intensities of cutting on the branch number per plant are shown in Table 2.2. Lax and especially hard defoliation caused a highly significant depression in branch number. However, the rapid build up in the number of branches, following early lax cutting, over the first 4 weeks and especially following late lax cutting over the 4 - 6 weeks period, was very evident.

The more rapid increase in branch number in the early lax cut treatment during the first four weeks of regrowth,

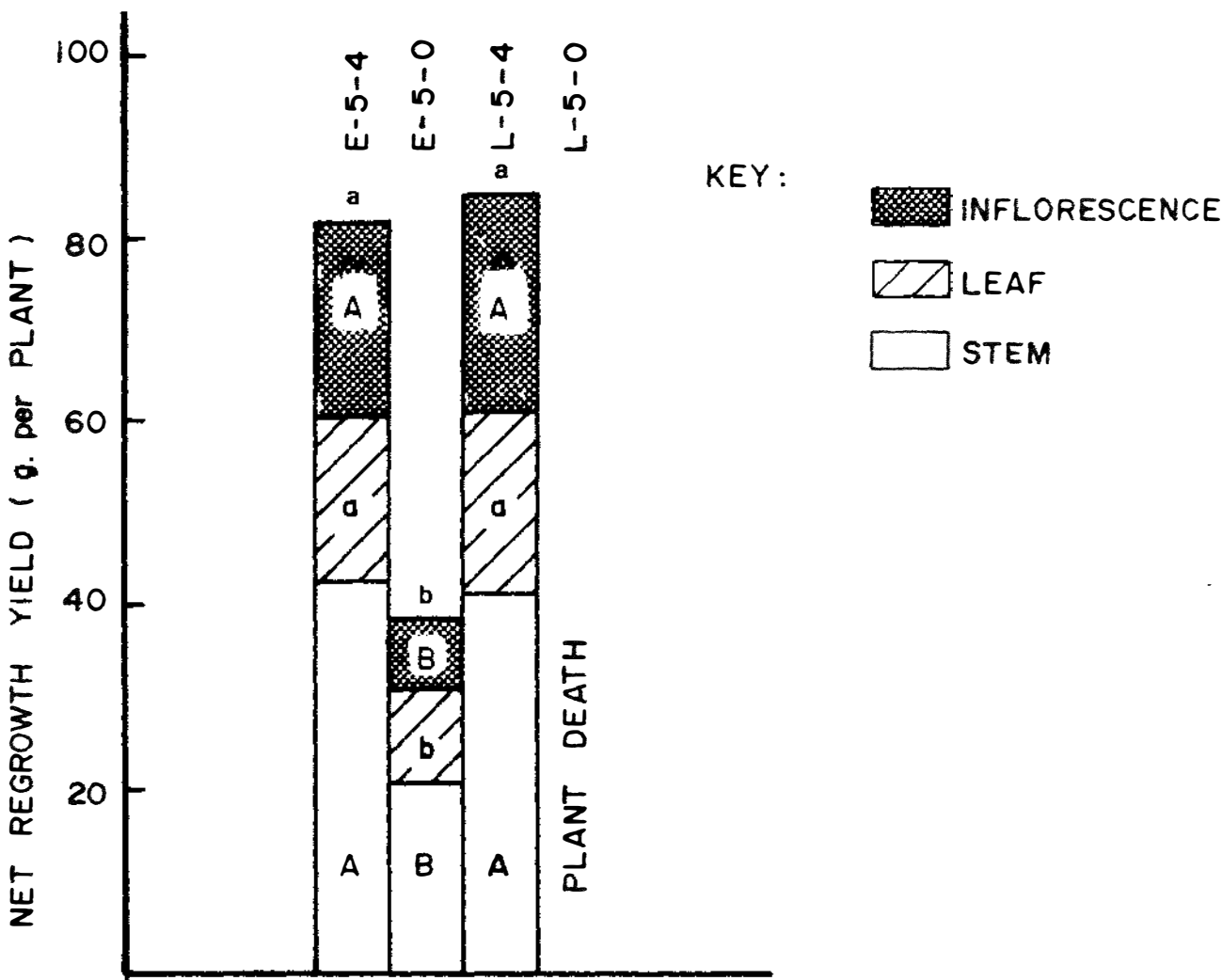


Figure 2.7: Effect of stage and intensity of defoliation on total net regrowth yield over ten weeks with two successive defoliations (g/plant)

Table 2.2 Effect of stage and intensity of defoliation on branch number per plant.

Treatment	Days after cutting					
	0	7	14	21	28	42
<u>After first cut</u>						
Early Control-E (Day 39)	46b ¹	NR ²	NR	NR	595b	1040ab
E-5-4	17c ³	69a	176a	423a	550b	670bc
E-5-0	3d	10b	29b	76b	166c	420c
Late Control-L (Day 88)	1147a	NR	NR	NR	1810a	1535a
L-5-4	2d	24a	48b	85b	242c	1080b
L-5-0	2d	-	-	-	-	-
Sig.	**	**	**	**	**	**
<u>After second cut</u>						
Early E-5-4	8a	35a	102a	234a	518a	-
E-5-0	2a	6b	23b	50b	129b	-
Late L-5-4	11a	47a	85a	165a	539a	-
L-5-0	-	-	-	-	-	-
Sig.	ns	**	**	**	**	

¹ Values in the same vertical column not followed by the same letter differ at p = 0.05

² Not recorded

³ Analysis based on log (x + 1)

may in part be explained by the higher number of "active" residual branches and the higher rate of branch appearance (Figure 2.8) in this treatment. This is in contrast to cutting at a later stage of growth (L-5-4) when most of the lower active branches had flowered or died due to shading. As a result, the rate of branch appearance was initially slow in this treatment. However, with additional time, (Table 2.2), plants in the late, lax cut treatment (L-5-4) subsequently (at 4 - 6 weeks) produced a real "flush" of branches, approaching 58 branches per day, during this later period of regrowth. By comparison the similar and earlier "flush" of branches recorded in the early lax cut treatment, had, by the 4th weeks, started to tail off.

The different treatment effects on branch development following the second cut showed a similar response under lax cutting but a major depression under hard cutting (Table 2.2).

B.3 Leaf Area and Leaf Number

As expected the greatest leaf area per plant remaining after cutting was from plants in the early lax cut treatment (Table 2.3). This probably accounted for the rapid and substantial leaf area development recorded four weeks later in these plants. In contrast, the leaf area remaining after late cutting, even when lax, was negligible and hence was reflected in slower leaf recovery. However by six weeks after cutting, all defoliated treatments (except the L-5-0 treatment) produced non-significant differences in leaf area.

Following the second cut, the residual leaf area of plants in all treatments were similarly low. However, after 4 weeks regrowth the early and late lax cut plants had developed a significantly greater leaf area than those of plants receiving early hard cutting.

The number of leaves per plants in the different treatments showed similar trends to the leaf area data except that numbers recorded six weeks after the first cut of the

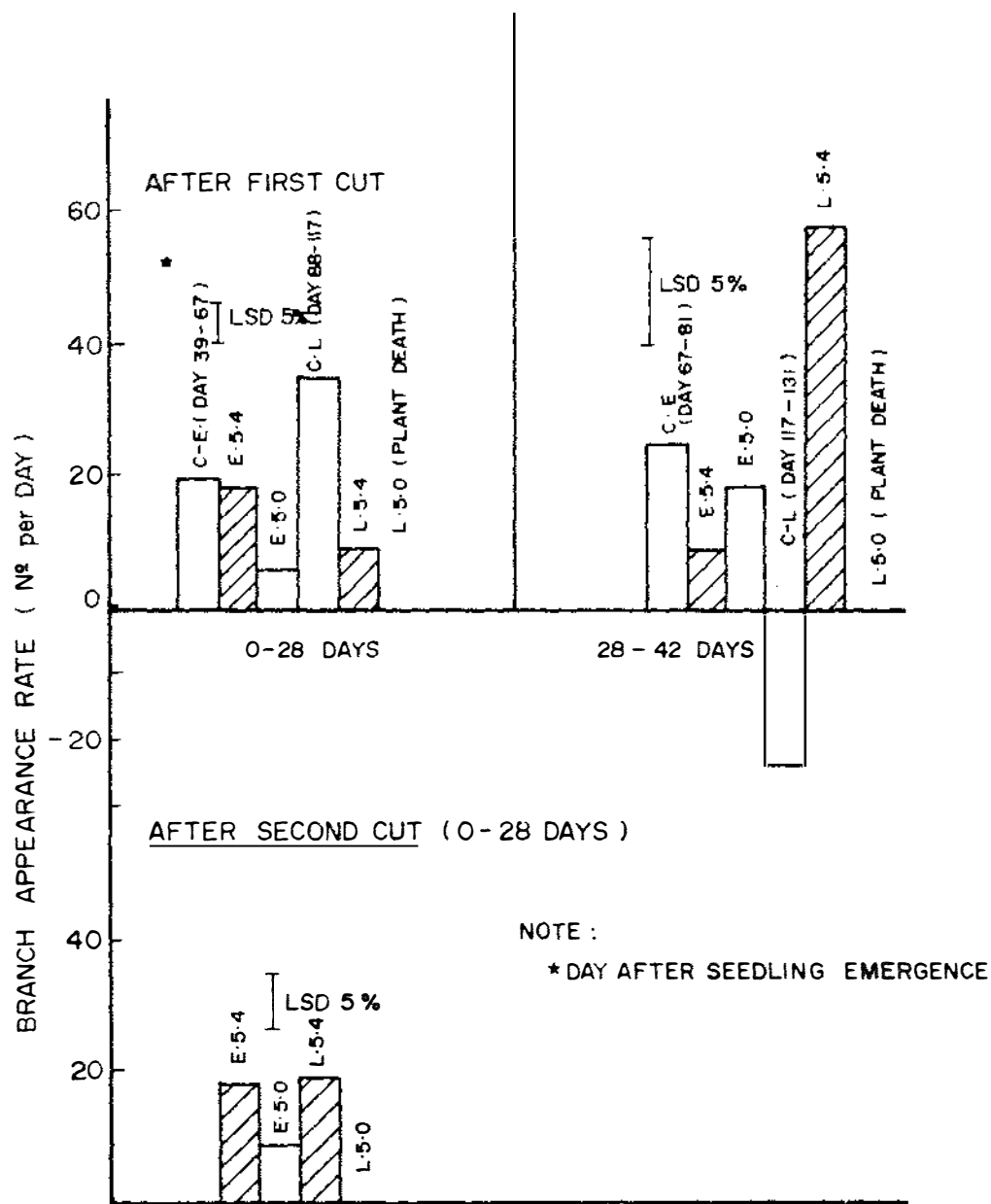


Figure 2.8: Effect of stage and intensity of defoliation on rate of branching (no/day)

Table 2.3 Effect of stage and intensity of defoliation on leaf area (cm²) (LA) and leaf number (LNO) per plant.

Treatment		Immediately after 1st cut		4 weeks after 1st cut		6 weeks after 1st cut	
		LNO	LA	LNO	LA	LNO	LA
Early	Control-E (Day 39)	107b ¹	337b	984b	2361b	1420ab	3094a
	E-5-4	64b	186c	848b	2041b	965bc	2220a
	E-5-0	7c	24d	329c	862c	775c	2123a
Late	Control-L (Day 88)	1424a	2996a	1923a	3077a	1642a	2127a
	L-5-4	6c	5d	502c	1192c	1371ab	3497a
	L-5-0	4c	5d	-	-	-	-
Sig.		**	**	**	**	**	ns

		Immediately after 2nd cut		4 weeks after 2nd cut	
		LNO	LA	LNO	LA
Early	E-5-4	3a	3a	907a	1975a
	E-5-0	5a	8a	281b	749b
Late	L-5-4	12a	29a	932a	2026a
	L-5-0	-	-	-	-
Sig.		ns	ns	**	**

¹ values in the same vertical column not followed by the same letter differ at P = 0.05

early, hard cut plants remained significantly depressed compared with most treatments (Table 2.3).

B.4 Number of Growing Points

The number of growing points on the stubble are shown in Table 2.4. Most of the growing points were located on the primary branch. Thus, hard cutting of the primary branches, either at early or late stages of growth, greatly and significantly reduced growing point numbers.

C. CHEMICAL COMPOSITION

C.1 Crude Protein

Crude protein concentrations are presented in Table 2.5. All cutting treatments caused a greater increase in crude protein than the uncut control for most of the plant components. In contrast, among the cutting treatments, the differences in crude protein were small, except in the residual stubble and roots following the first defoliation. However, there were large differences in the crude protein levels between plant parts. Crude protein concentration was highest in the leaf, also high in inflorescences, but much lower in the stem and particularly the tap root. Apart from the exception mentioned above, crude protein concentrations in the stubble (mainly stem) were consistently low.

When converted to a protein yield basis, the differences between treatments were highly significant and followed very much the plant weight responses presented earlier, i.e. protein yields were most depressed when both the main stem and the primary branches were defoliated (Figure 2.9). The effects of stage of cutting were shown only after 4 weeks' regrowth following the first defoliation.

The crude protein yields of the plant components were similarly affected by the different intensities of defoliation and stage of growth as for component dry weights (Figure 2.9). However, it is noteworthy that the yield of crude

Table 2.4 Effect of stage and intensity of defoliation on number of "growing points" on the stubble 10 days after cutting (no/plant)

Treatment	E-5-4	E-5-0	L-5-4	L-5-0	Sig.
<u>First cut</u>					
Main stem	6.3a ¹	6.0a	6.3a	- ²	ns
Primary branch	27.5a	-	14.5b	-	*
Total	33.8a	6.0c	20.8b	-	**
<u>Second cut</u>					
Main stem	6.0a	5.7a	5.7a	-	ns
Primary branch	16.3a	-	20.0a	-	ns
Total	22.3a	5.7b	25.7a	-	**

¹ Values in the same horizontal line not followed by the same letter differ at $P = 0.05$.

² Plant death

Table 2.5 Effect of stage and intensity of defoliation on crude protein concentration (% of dry matter) in leaf (L), stem (S), inflorescence (I) and root (tap (T) and fibrous (F)) components and in the residual stubble (R).

A. First Cut

	Treatments						
	Control-E (39 days)	E-5-4	E-5-0	Control-L (88 days)	L-5-4	L-5-0	Sig.
<u>Immediately after first cut</u>							
R		20.8a ¹	19.7a		5.3b	5.6b	**
T + F		21.4a	21.8a		10.1b	8.9b	**
<u>4 weeks after first cut</u>							
R	-	6.5a	7.1a	-	6.1a	-	ns
L	29.4a	29.4a	30.7a	25.1b	29.9a	-	**
S	12.8c	15.9b	16.5b	11.5c	18.2a	-	**
I	23.4b	25.7a	25.8a	22.5b	25.2a	-	**
T	8.0a	8.0a	7.3a	6.7a	8.1a	-	ns
F	14.0a	14.6a	14.8a	12.0a	14.8a	-	ns
<u>6 weeks after first cut</u>							
R	-	6.1a	6.8a	-	6.2a	-	ns
L	26.2b	27.8a	28.6a	26.2b	28.6a	-	**
S	9.5c	11.4b	13.8a	7.5d	13.8a	-	**
I	22.7b	23.4b	25.2a	25.3a	22.5b	-	*
T	7.6a	9.0a	7.2a	8.3a	6.9a	-	ns
F	14.8	14.7	16.6	13.7	15.6	-	ns

B. Second cut

	Treatments				
	E-5-4	E-5-0	L-5-4	L-5-0	Sig.
<u>Immediately after second cut</u>					
R	6.1a	6.8a	6.2a	-	ns
T	9.0a	7.2a	6.9a	-	ns
F	14.7a	16.6a	15.6a	-	ns
<u>4 weeks after second cut</u>					
R	6.8a	6.6a	7.5a	-	ns
L	31.4a	30.6a	31.1a	-	ns
S	15.9b	17.2a	15.5b	-	*
I	24.0a	23.5a	23.7a	-	ns
T	7.2a	7.8a	8.0a	-	ns
F	14.5a	16.4a	16.7a	-	ns

¹ Values in the same horizontal line not followed by the same letter differ at $P = 0.05$

protein from the leaf plus inflorescence fraction represented a significant amount especially in those treatments and plants receiving lax primary branch defoliation at both early and late stages of development. In contrast, only small quantities of crude protein were found in the roots.

C.2 Non-structural Carbohydrate Concentration and Yield

Plant residuals above and below ground immediately after the first and second defoliation and after 4 weeks of regrowth in the second cut, were analysed for non-structural carbohydrate (sugar and starch).

As presented in Figure 2.10, sugar concentrations in both tops and roots were low in all samples and showed non-significant differences between lax and hard defoliation. Only at the first defoliation did late cutting significantly depress sugar content compared with early cutting, otherwise no significant differences were recorded. It is therefore noteworthy that delaying cutting until the late stage of development did not improve sugar concentration in either top or roots. Sugar concentrations were generally much higher in the tap root than in the fibrous roots, but not greatly different between tap root and tops.

In terms of sugar yields, the differences recorded tend to reflect the different residual cutting treatments imposed. That is, plants exposed to lax cutting, at either the early or the late stage of growth, had significantly higher levels than those exposed to hard cutting of the primary branch (Figure 2.11).

Starch levels are also presented in Figure 2.10 and show that concentrations were extremely low in all residual parts and in all treatments. Starch yields are therefore not presented.

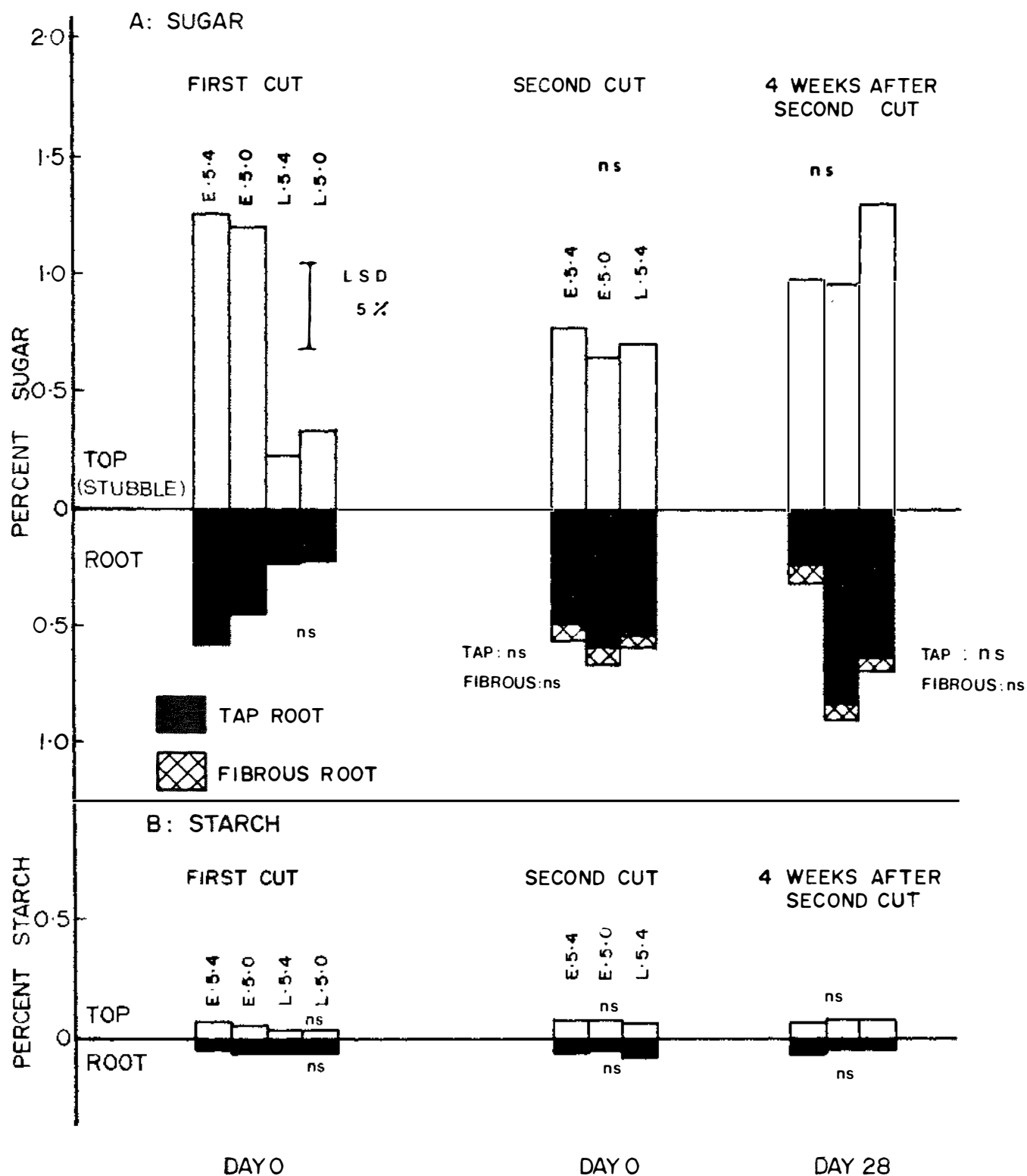
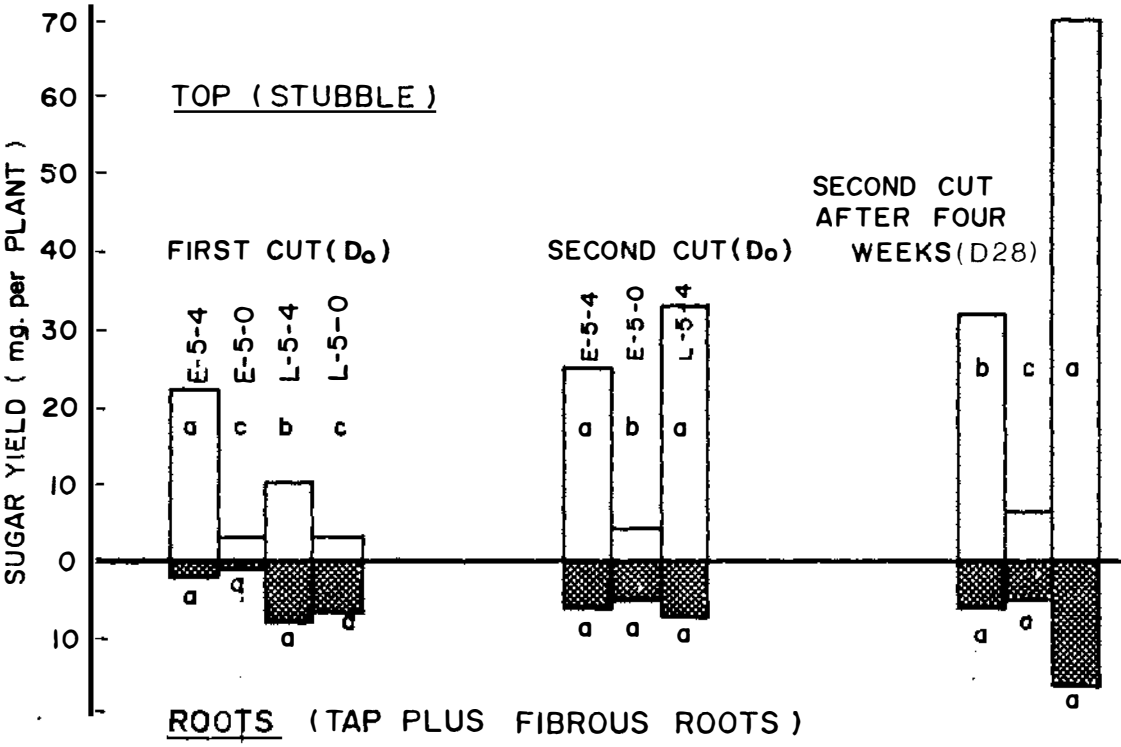


Figure 2.10: Effect of stage and intensity of defoliation on sugar and starch concentration in the residual top (stubble) and below ground (% of dry matter)



Figur2 2.11: Effect of stage and intensity of defoliation on sugar yield in the residual top (stubble) and below ground (mg/plant)

D. RELATIONSHIP BETWEEN REGROWTH AND RESIDUAL (STUBBLE)
PLANT VARIABLES

The relationship between regrowth yield and residual plant variables is presented in Table 2.6. Significant positive correlation was found for both cutting treatments. Following the first cut, the relationships of regrowth yield to residual variable of branch number, leaf area, leaf number, stubble to root ratio, the number of growing points and the amount of TNC in stubble, were positive and significant during the first four weeks of regrowth. When examined for the total 6 week regrowth period, however, no significant relationships for any of the variables with yield were recorded.

Following the second cutting, the relationships between regrowth yield and the residual variables of stubble dry weight, the number of growing points, stubble to root ratio, and the amount of non-structural carbohydrate were positive and significant.

E. RELATIONSHIP BETWEEN TOTAL PLANT DRY WEIGHT AND GROWTH
PARAMETERS (BRANCH NUMBER, LEAF NUMBER AND LEAF AREA
PER PLANT).

Highly significant and positive correlations were found between total plant dry weight and the main growth parameters (branch number, leaf number and leaf area) when compared at the 4 and 6 week sampling times, suggesting that these parameters are important in determining final yield (Table 2.7).

These results are in contrast to the lack of correlation between these parameters measured immediately after the second cut and the subsequent yield, as shown in Table 2.6. It appears that repeated cutting tends to emphasize the importance of other parameters, such as the number of growing points remaining after cutting, the stubble to root ratio, the residual dry weight and particularly the residual amount of carbohydrate in stimulating early recovery - and hence enable the development of these major contributors to subsequent yield, leaf area and branch number.

Table 2.6 Correlations of residual plant variables with net regrowth yield.

Residual plant variables	4 wks after 1st cut	6 wks after 1st cut	4 wks after 2nd cut
Branch number	0.852**	-0.055ns	0.410ns
Leaf area (cm ² /plant)	0.881**	-0.067ns	0.247ns
Leaf number (no/plant)	0.834**	0.033ns	0.262ns
Growing point (no/plant) ¹	0.895**	0.350ns	0.911**
Stubble to root ratio	0.900**	0.056ns	0.763*
Stubble dry weight (g/plant)	0.054ns	0.663ns	0.806**
Root dry weight	-0.304ns	0.541ns	0.609ns
% TNC in stubble	0.541ns	-0.417ns	0.453ns
% TNC in roots	0.527ns	-0.100ns	-0.186ns
TNC yield in stubble (mg/plant)	0.912**	-0.142ns	0.935**
TNC yield in roots (mg/plant)	-0.38ns	0.146ns	0.820**

¹ Determined 10 days after cutting

Table 2.7 Linear correlation coefficients between plant dry weight (DM) and main growth parameters (branch number (B), leaf number (LNO) and leaf area (LA))

	Parameters of growth		
	B	LNO	LA
4 weeks after first cut	0.960**	0.980**	0.936**
6 weeks after first cut	0.847**	0.907**	0.688**
4 weeks after second cut	0.946**	0.993**	0.976**

IV DISCUSSION

Significant plant mortality after late and intense cutting has been reported in many tropical legumes such as Stylosanthes humilis (Fisher, 1973), Crotalaria juncia (Kessler and Shelton, 1980). This also occurred in the present experiment (L-5-0). However, intense defoliation provided it is done at an early stage of growth (E-5-0) is not lethal but does result in a significant delay in regrowth. Similarly late defoliation, provided it is lax (L-5-4), will not kill plants but will cause an appreciable delay in recovery. In contrast early lax defoliation results in rapid recovery although a significant reduction in yield still occurs compared with no defoliation. Factors which are known to affect the rate of initial regrowth after defoliation are usually related to:

- 1) The carbohydrate reserves above and below ground.
- 2) The number of branches capable of regrowth.
- 3) The size of residual leaf area.
- 4) The number of growing points.

The importance of carbohydrate reserves to regrowth has been recognised by many workers (e.g. Yamada, 1975; Humphreys, 1978b). These authors suggested that reserve organic compounds are utilized during the early stages of regrowth and that later regrowth is dependent on leaf area and photosynthesis. The main reserves playing this role are suggested to be sugars and starch which are stored mainly in the stem base and roots (Yamada, 1975). In this experiment, the TNC (sugars and starch) concentrations were relatively low in both the stubble and roots in all treatments, and showed no difference between cutting treatments at a similar stage of growth. However, despite the low concentrations of TNC, the amounts (mainly sugar) were higher under lax cutting than under severe cutting of the primary branches (Figure 2.11) - presumably reflecting the greater stubble yield in the former treatment.

A significant positive correlation was also found between regrowth yield and the amount of TNC in the stubble, suggesting that the initial regrowth after cutting was dependent upon the amount of these reserves in the stubble (Table 2.6). This highlights the need to retain a greater size of primary branch after defoliation and thereby provide a larger supply of TNC for regrowth - and hence compensate for the low TNC concentration in the stubble and roots. This also may explain why Verano stylo was able to recover under late lax cutting despite lack of residual photosynthetic tissue. Low amounts of residual TNC under severe cutting of the primary branch, and low residual leaf area due to natural falling of the lower leaves, may have accounted for the mortality of these plants soon after the first cut.

The number of branches capable of regrowth after cutting was also found to be positively related to regrowth in some tropical legumes (Kessler and Shelton, 1980). The results of this study support this finding. In the early cut treatment (E-5-4), many branches capable of regrowth had already elongated on the primary branches, while in the later cut treatment, the branches capable of regrowth were low in number immediately after cutting (Table 2.2). Therefore, slow initial regrowth was observed in these late cut treatments due to slow build up in branch production.

The importance of residual leaf area and the number of growing points are supported by results obtained with other tropical legumes as indicated by the high correlation between regrowth yield and these parameters (Grof et al, 1970; Jones, 1974; Kessler and Shelton, 1980; Ludlow and Charles-Edwards, 1980). It is also relevant that plants which were cut at later stages of growth had lost all their lower leaves through natural leaf fall and were therefore lacking in photosynthetic tissue. The number of growing points was also significantly reduced under these treatments (E-5-0 and L-5-0). With the marked reduction in TNC amounts, as discussed earlier, plants had slow regrowth and many soon died, resulting from the photosynthate being insufficient to meet the demands for respiration and growth (Yamada, 1975). Thus

the high correlation obtained between regrowth yield and stubble to roots ratio was not surprising since defoliation is known to affect root growth (Kessler and Shelton, 1980) and death of root has frequently been reported (Bowen, 1959; Whiteman, 1970; Whiteman and Lulham, 1970). Furthermore, restricted supplies of water and nutrients because of root death may also account for slow regrowth and death of the plants.

From the above results, it appears that regrowth of Verano stylo following defoliation is dependent on the size of primary branches associated with several residual plant characteristics viz. the level of carbohydrate reserves in the stubble and roots, the residual number of branches, the residual number of growing points and the residual leaf area. The carbohydrate reserves although low, appeared to be of some importance in this respect as did the number of growing points, while residual leaf and branch number were only important after the first cutting. In contrast the total non-structural carbohydrate contained in the roots was only of value when the plants were older and bigger.

The response to cutting in terms of total plant dry weight was also related to the above factors as discussed earlier. Plant dry weight was not reduced under light cutting. This response was mainly through increase in stem, inflorescence, and to a lesser extent, increase in leaf dry weight (Figure 2.4). The result of this experiment demonstrated that all components of dry matter yield can be affected by defoliation, the stage at which the plant is cut, and the severity of cutting.

These results are contrary to the results of Wilaipon and Humphreys (1976, 1981) who reported that Verano stylo yields were reduced when grazing or cutting was delayed to late in the growing season. However, the reduction in yields in such an experiment appeared to be related to climatic conditions as well as to cutting. Since the cutting time was near the end of the growing season, temperature and moisture may have been restricting regrowth. It seems that lax

cutting or grazing at later stages of growth, although causing slow initial recovery, will not reduce regrowth ability under favourable conditions.

Plant dry weight was also related to the response of branch number to defoliation as indicated by the significant correlation between branch number and total dry weight. Branch production was markedly reduced when the primary branches were cut hard, particularly when cutting occurred at the late stage of development. This reduction in branch number corresponded to a reduction in dry matter yield. However, lax cutting of the primary branches at an early stage of growth rapidly increased branch production and hence the potential to achieve a higher plant dry weight than hard cutting of the primary branches. Similar effects were also found in another tropical legume, Townsville stylo (Fisher, 1973) and in the temperate legume Trifolium subterraneum (Rossiter, 1961). An increase in branch number was due to an increase in branching rate under lax cutting.

The present experiment also showed that lax cutting at the late stage of growth stimulated branch production over the six weeks of regrowth. The initial slow development of branches over the first four weeks was more than compensated for by the explosive development from the fourth to the sixth week. Although not statistically significant, leaf number and leaf area showed similar trends. This is indeed a most interesting finding, since it has also been shown that increased branch development can result in increased seed production (Rossiter, 1961; Fisher, 1973; Wilaipon and Humphreys, 1976). This may explain in part why Verano stylo can produce a similar dry matter yield to the control even under late defoliation. It suggests that when cutting is necessarily late, a period of at least 6 weeks should be left to allow the plant to produce new branches to compensate.

The number of leaves and leaf area were also affected by defoliation. The complete removal of the primary branches especially at the later stage of growth caused the slow build up in both number and area of leaves and hence a reduction in

growth rate, yield and also death of plants. In contrast, lax cutting of the primary branches especially at the early stage of growth enabled a rapid recovery of both number and area of leaves during the first four weeks - this recovery occurring 4 weeks later (during the 4th to 6th week) in the late lax cut treatment.

The results of this study demonstrate that Verano stylo has a high quality in terms of nutritive value for animal feeding. There was no significant effect of stage of growth and intensity of cutting on the crude protein content in the regrowth components. These levels of protein were higher than the critical level suggested by Milford and Minson (1966) at all stages of growth. Norman and Phillip (1970) have shown that animal production is proportional to the nitrogen content of the pasture. Thus, animal production from pasture containing this legume should be capable of achieving a relatively high level of performance (Gillard et al, 1980; Gillard, 1983).

As expected, leaf and inflorescence were higher in crude protein content than the stem fraction at all stages of growth. These crude protein levels decreased with prolonged regrowth conditions, but the decrease was less rapid in the leaf and inflorescence fractions than in the stem fraction. This phenomenon has been found in Townsville stylo (Fisher, 1969), Stylosanthes guianensis (Mufandaedza, 1976), Lucerne (Lee and Smith, 1972) and Verano stylo (Gardener et al, 1982).

Although the crude protein content was not greatly affected by cutting, there was a marked difference in crude protein yield between treatments. Hard cutting of the primary branches produced the lowest crude protein yield and reflected the low dry matter yields recorded. This is of some importance in terms of pasture management as the intake of animals is governed to a large extent by the amount of herbage present (Stobb, 1974).

Total crude protein yield in leaf plus inflorescence in the lax cutting, for both stages of growth, was high when compared with severe cutting (E-5-0). Observations in the field indicate that the inflorescence as well as the leaf is readily acceptable to the animal, even when the plants are mature (Gardener, 1980), and therefore an important source of protein.

The levels of non-structural carbohydrates (sugar and starch) were low and did not increase as the time of cutting was delayed. This is unlike the response obtained with lucerne, where advancing stage of growth greatly increased the available carbohydrate level (Nelson and Smith, 1968; 1969). With tropical legumes, Hunter et al (1970) reported that Glycine wightii (leaf), Greenleaf desmodium (leaf) and Silverleaf desmodium (stem) contained negligible quantities of starch at an early stage of development, but the more mature plants (at flowering) contained 1 - 2% starch in the dry matter. Jones (1974) reported that long cutting intervals (16 weeks) did not increase the carbohydrate in the roots of Siratro. However, these levels of carbohydrates reported were much higher than those in the present experiment. Unfortunately there are no specific data available on the concentration of carbohydrates in Verano stylo with which to compare the present results. However, the present data do indicate that most of the photosynthates were utilized for growth and not accumulated in the root and crown of the plant. Nelson and Smith (1968) also showed that in Birdsfoot trefoil, a temperate legume, the total non-structural carbohydrate was low during the growing season, and that most of the photosynthate was used for top growth.

EXPERIMENT 3: INTENSITY OF DEFOLIATION

I. INTRODUCTION

Intensity of cutting or grazing can have a major effect on yield and survival of the legume component of the pasture, especially when carbohydrate reserves are low from frequent cutting or other causes. Lax cutting can leave a greater photosynthetic surface and provide energy for initial regrowth after cutting, by comparison with close cutting (Smith and Nelson, 1967; Jones, 1974; Kessler and Shelton, 1980; Grof et al, 1970). Experiment 2 clearly showed that severe cutting of the primary branches, particularly at a late stage of growth, greatly reduced yield and even caused significant mortality of Verano stylo. However, lax cutting of the primary branches, at either early or late stages of growth, was advantageous in terms of dry matter yield and plant survival. Carbohydrate analysis indicated that this species contained very low levels in the residual components both above and below ground. However, with the larger residual from lax cutting, the greater amount of carbohydrate therefore available was considered to be important for initial regrowth, particularly following late defoliation. In Experiment 2, only two cutting cycles were studied and hence the long term effects of severe and lax cutting were not determined.

The present experiment was conducted to gain further information on the response of Verano stylo to different cutting intensities in terms of regrowth ability and chemical composition over 4 regrowth cycles.

II. MATERIAL AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURES

Environmental conditions and planting procedures were the same as reported for Chapter 3. After thinning to one plant per pot, all plants were blocked into three replicates based on plant uniformity. After cutting, pots containing plants undergoing similar treatments were located together so that interference between treatments was minimised during regrowth.

B. TREATMENTS

There were five cutting intensities as follows:

<u>Treatment</u>	<u>Detailed</u>
1. E-7-4:	Cut the main stem above node 7 (between nodes 7 and 8) and primary branches above node 4 (between nodes 4 and 5 along the branches)
2. E-7-0:	Cut the main stem above node 7 (between nodes 7 and 8) and primary branches immediately below node 1 (along the branch)
3. E-3-4:	Cut the main stem above node 3 (between nodes 3 and 4) and primary branches above node 4 (between nodes 4 and 5 along the branch)
4. E-3-0:	Cut the main stem above node 3 (between nodes 3 and 4) and primary branches immediately below node 1 (along the branch)
5. Control:	Non-defoliated plant

C. NUMBER OF CUTTING OCCASIONS

The first cutting occurred when 50% of the plant population commenced flowering and was repeated after six weeks' regrowth. Cutting was repeated 4 times over approximately 200 days giving four regrowth cycles (Figure 3.1).

D. HARVESTING SCHEDULE

Nine harvest occasions were taken as shown in Figure 3.1.

E. PLANT MEASUREMENTS

E.1 Plant Dry Weight

Measurements of dry matter yields and other phenological observations were obtained from 3 plants per treatment. Times of harvests are shown in Figure 3.1. Plants were separated for measurements as described in Experiment 1. Dry matter yields were obtained by drying all samples in a vacuum oven for 72 hours.

E.2 Leaf Area and Leaf Number

Leaf area (cm^2 per plant) and leaf number were recorded at the same time as dry matter yield was determined. Leaf area was measured using the Electronic Leaf Area Meter (Model 3100 Area Meter).

E.3 Branch Number

Branch number in each regrowth cycle was recorded at weekly intervals up to 4 weeks of regrowth and at 6 weeks immediately before cutting was repeated.

E.4 Number of Growing Points

The number of visible growing points arising from the stubble of the main stem and primary branches was recorded after ten days of regrowth in each cycle.

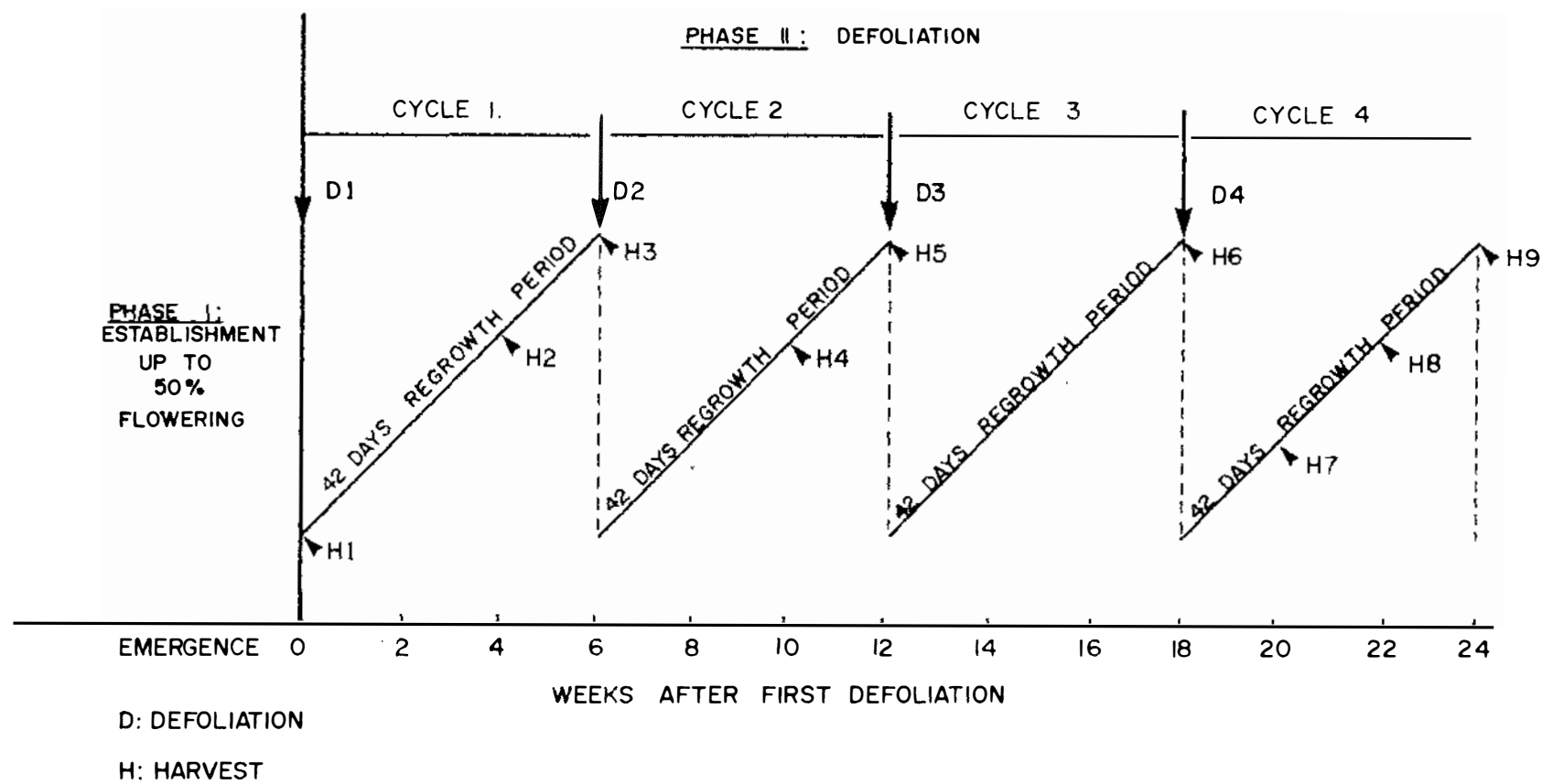


Figure 3.1: Planning of Experiment 3

F. CHEMICAL MEASUREMENTS

Crude protein and total non-structural carbohydrate (sugar and starch) concentrations were determined as described in Experiment 2. Plant fractions analysed are shown in Table 3.1.

G. STATISTICAL ANALYSIS

Data were analysed according to the common procedure of a randomized complete block design for all plant characters (Little and Hills, 1975). A factorial design was also used to analyse the main effect of cutting the main stem and primary branches on total net regrowth yields over the four regrowth cycles. The analysis was done by Genstat programme (Alvey et al, 1977). The least significant difference at the 5% level was used to identify statistical difference among the results. The symbols that were used to designate statistical significance were * ($P = 0.05$), ** ($P = 0.01$) and ns (not significant).

III. RESULTS

A. PHENOLOGICAL OBSERVATION

Plants grew very slowly during the establishment phase (0 - 28 days). There was the same temporary leaf 'tip burn' as observed in Experiment 2. After the establishment phase, the plants grew rapidly and reached the stage of 50% flowering on day 35.

The first plant deaths were recorded in the E-3-0 treatment following the second cut (2nd cycle). Plant mortality at this stage was 18.8% and increased at later cuttings. All plants in E-3-0 treatment died within one week after the fourth cut (4th cycle of regrowth). No plant deaths were recorded in the other treatments.

Table 3.1 Plant components analysed.

Time	Chemicals	Stubble	Plant components			
			Leaf	Stem	Inflor.	Roots
<u>Days after first cut</u>						
0	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
28	Protein	+	+	+	+	+
	TNC	-	-	-	-	-
42	Protein	+	+	+	+	+
	TNC	-	-	-	-	-
<u>Days after fourth cut</u>						
0	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
14	Protein	+	+	+	+	+
	TNC	-	-	-	-	-
28	Protein	+	+	+	+	+
	TNC	-	-	-	-	-
52	Protein	+	+	+	+	+
	TNC	+	-	-	-	+



Plate 3.3: The cutting treatments immediately after the third cut (for the symbol see Plate 3.1), showing that only a small number of leaves and branches remain under all treatments but the size of the residual stubble differs greatly between the E-3-0 (LH) and the E-7-4 (HL) treatment.



Plate 3.4: The cutting treatments immediately after the fourth cut (for the symbols see Plate 3.1), showing the negligible number of leaves or active branches along the primary branches.



Plate 3.1: The cutting treatments immediately after the first cut (LH = E-3-0; LL = E-3-4; HH = E-7-0; HL = E-7-4 and C = uncut control).

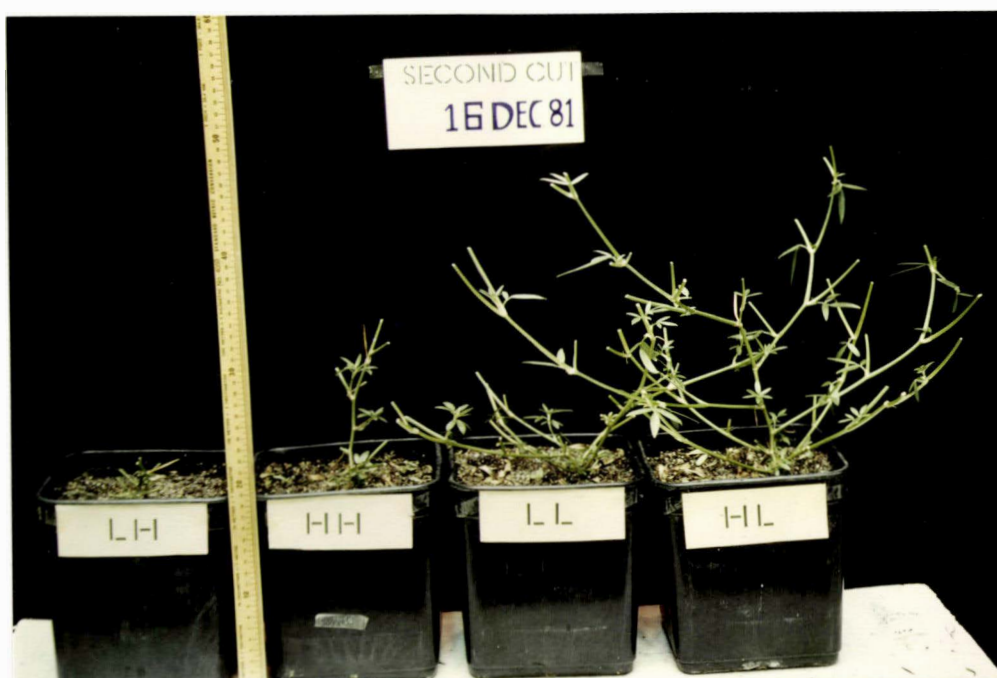


Plate 3.2: The cutting treatments immediately after the second cut (for the symbols see Plate 3.1), showing a greater number of leaves on plant HL (lightest cutting treatment: E-7-4).

B. PLANT REGROWTH

B.1 Plant Dry Weight

The total net regrowth for each treatment over the full experimental period is presented in Table 3.2. There was a marked effect of cutting on regrowth and the magnitude of this effect was dependent on the intensity of defoliation. That is, the more severe the intensity of defoliation, the poorer the regrowth.

Defoliating the primary branches also depressed regrowth more than defoliating the main stem (Figure 3.2), with intense defoliation of both the main stem and primary branches leading to significant plant mortality after only two cuts.

The regrowth patterns following each defoliation within the total experimental period are presented in Figure 3.3 (and Appendix 5). Once again it was the lax defoliation of primary branches, irrespective of the severity of defoliation of the main stem, that was prominent in ensuring good regrowth at every cycle. This effect, as might be expected, was more apparent when the main stem was also laxly defoliated. It is also significant that the different regrowth responses to different defoliation intensities were similar after each cut e.g. the regrowth yield achieved in approximately 6 weeks after the 4th cut was equal to that achieved 6 weeks after the 1st cut, except in the most severe cutting treatment (E-3-0) where plant death occurred.

Early regrowth in absolute terms (mg/day) also appeared to be influenced by the cutting treatments imposed, with the higher rate of regrowth being related to the laxer defoliation, particularly of the primary branches and hence higher residual dry weight. However, this effect was not evident in terms of relative growth rates (mg/mg/day) (Figure 3.4).

All the regrowth components, of inflorescence, leaf, stem and root, were similarly and significantly depressed by

Table 3.2 Effect of defoliation intensity on net regrowth yield over the experimental period (g/plant).

Treatment	Cycle 1	Cycle 2	Cycle 3	Cycle 4	Cycle 1-4
Control ¹	63.54	-	75.95	70.40	-
E-7-4	54.10a ²	51.40a	36.50a	70.54a	217.00a
E-7-0	23.50bc	22.10b	22.40b	31.20b	100.40c
E-3-4	32.40ab	56.80a	24.90b	61.40a	172.50b
E-3-0	13.60c	20.40b	15.60c	-	48.20d
Significance	**	**	**	**	**

¹ Not included in statistical analysis.

² Values in the same vertical column not followed by the same letter differ at P = 0.05.

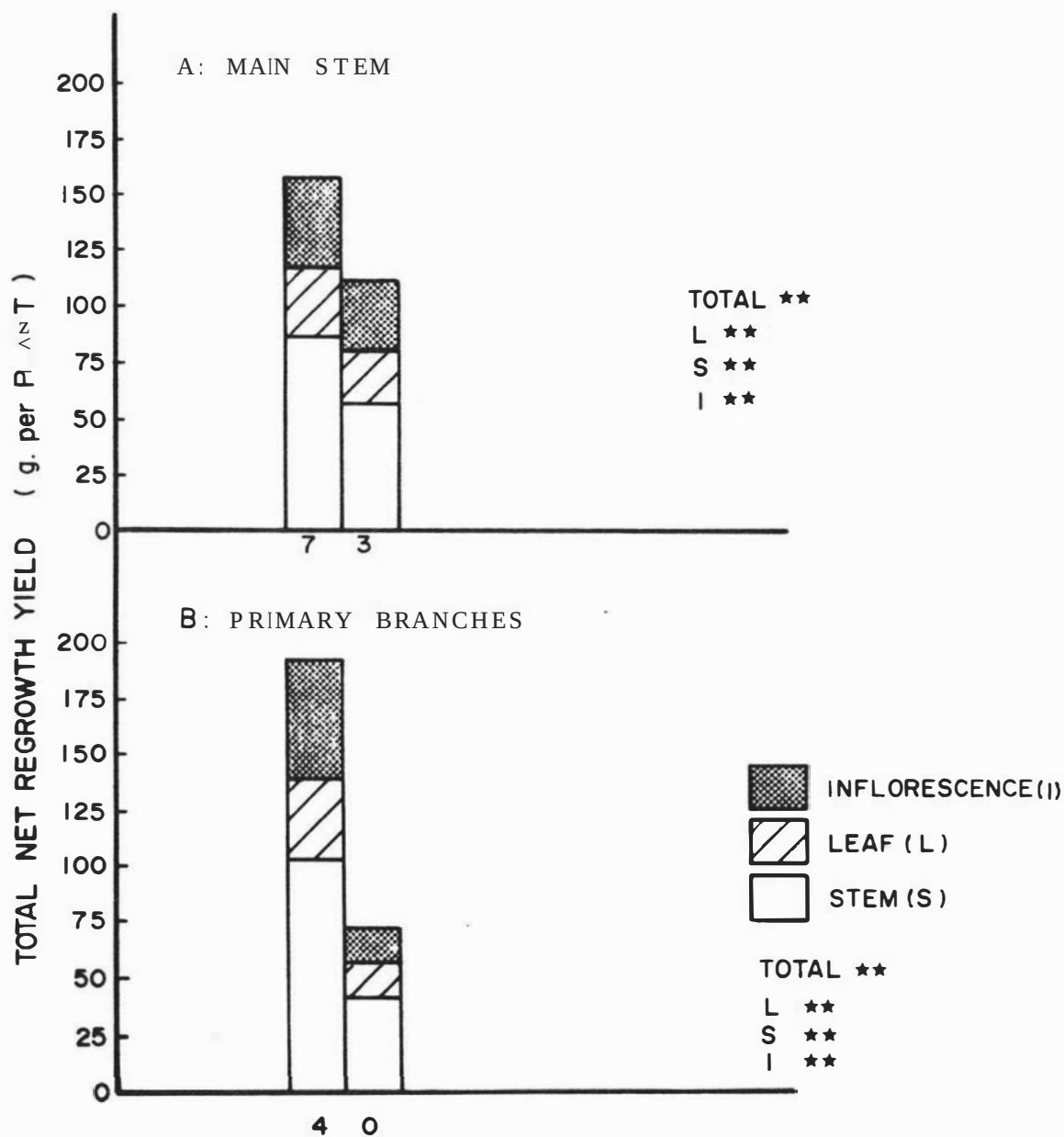


Figure 3.2: Main effect of defoliating the main stem (A) and the primary branches (B) on total net regrowth yield over the four regrowth cycles

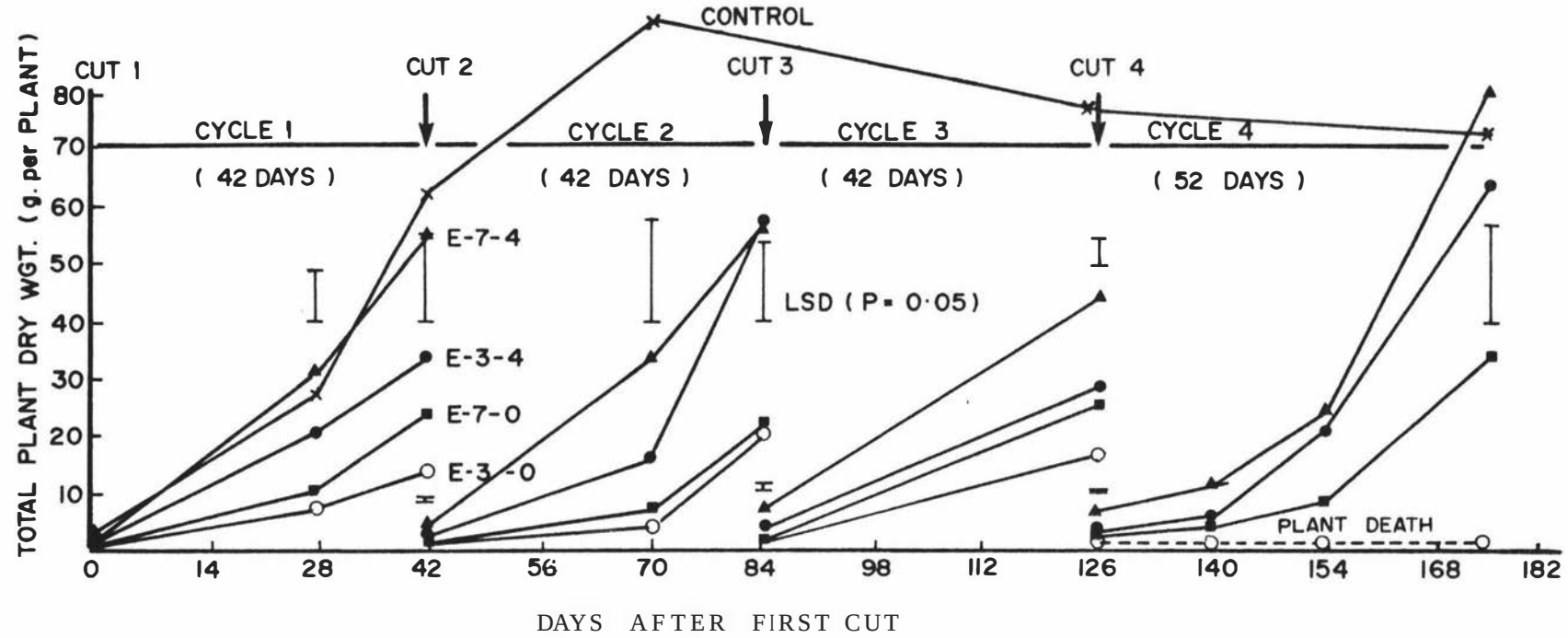


Figure 3.3: Effect of defoliation intensity on total plant dry weight at various cutting cycles (g/plant)

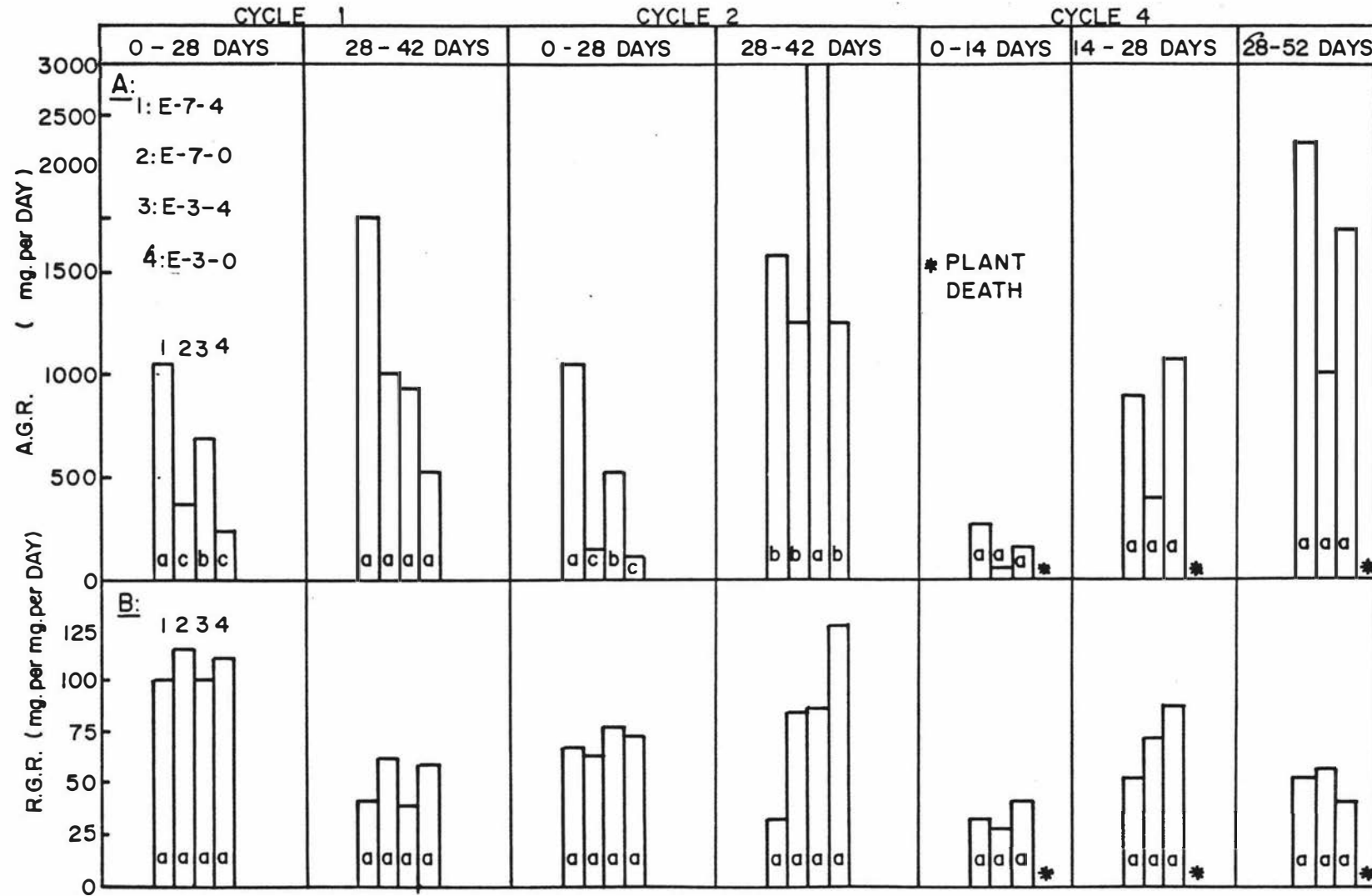


Figure 3.4: Effect of defoliation intensity on absolute (A) and relative (B) growth rate at various regrowth cycles.

cutting, as shown in Figure 3.5 and 3.6. The more depressing effect of primary branch removal compared with main stem removal on all components including roots; the initial slow rate of regrowth of all these components over the first 2 to 4 weeks followed by rapid regrowth; and the increasing proportion of stem developing over the experimental period, are all worthy of note.

B.2 Branch Number

The effects of defoliation on branch number per plant are presented in Figure 3.7. In the regrowth period of 6 weeks following the 1st cut, lax defoliation of both the main stem and primary branches (E-7-4) did not affect branch development (number of branches) compared with the uncut control. However, more intense defoliation, particularly of the primary branches, significantly depressed branch numbers. Of particular note was the relatively slow recovery, particularly of those plants suffering severe primary branch removal (E-7-0 and E-3-0) during the first 28 days followed by a general and substantial increase in branch numbers during the following 14 days (28 - 42 days) - and evident in all regrowth cycles.

B.3 Leaf Area and Number

Leaf area and leaf number per plant between treatments followed very similar patterns of development after each defoliation, with lax defoliation of the main stem and especially the primary branches encouraging significantly more leaf area and leaf numbers than intense defoliation (Figure 3.8).

Although the residual leaf areas following the 1st, 2nd and 3rd cut were significantly different, reflecting the defoliation intensities, these differences were small in actual area and number (Table 3.3). Nevertheless, the regrowth achieved over the 1st, 2nd and 3rd regrowth cycles did tend to reflect the residual leaf area per treatment and this may have contributed to such differences. However, in

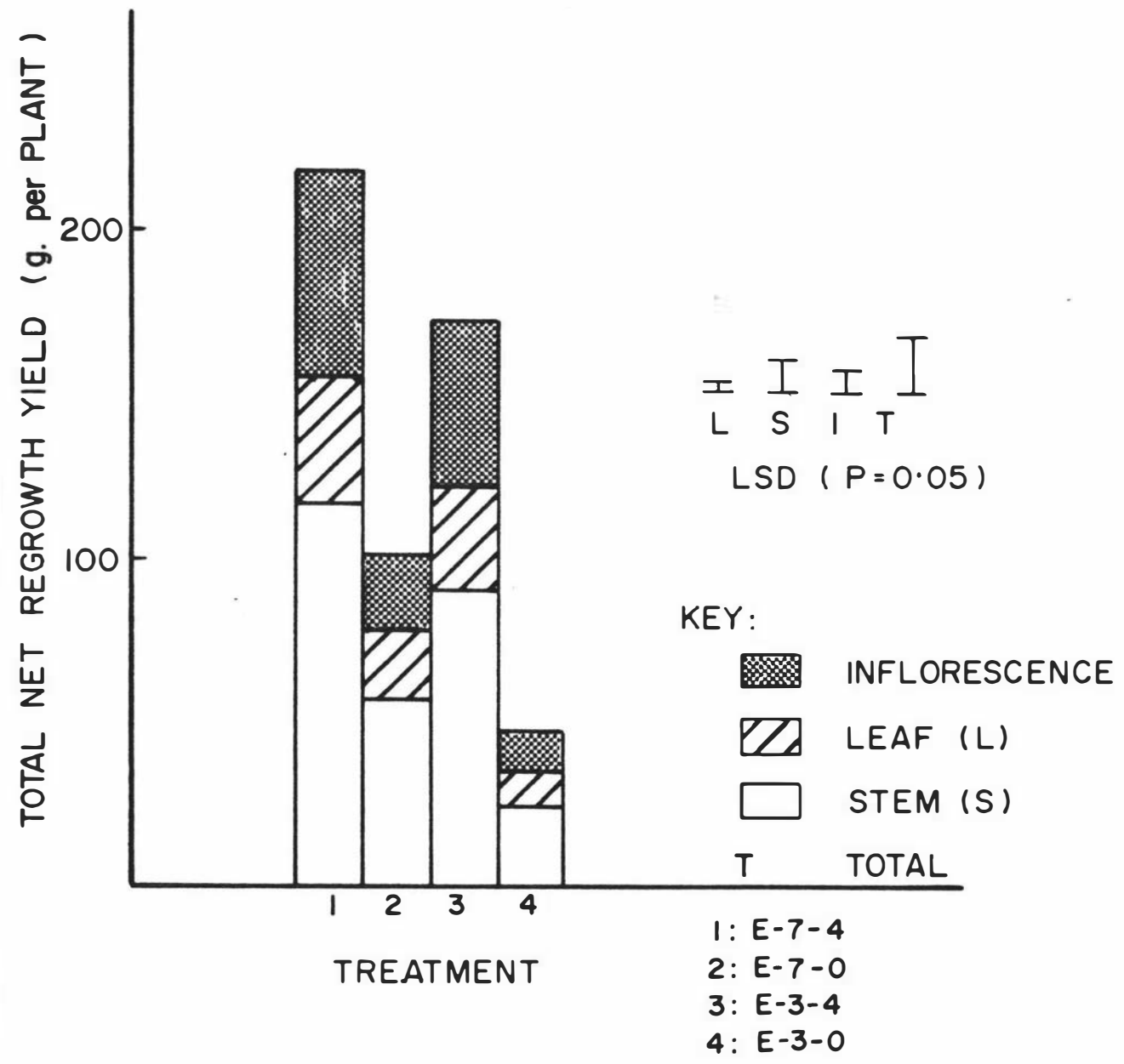


Figure 3.5: Effect of defoliation intensity on total net regrowth yield over the four regrowth cycles (g/plant).

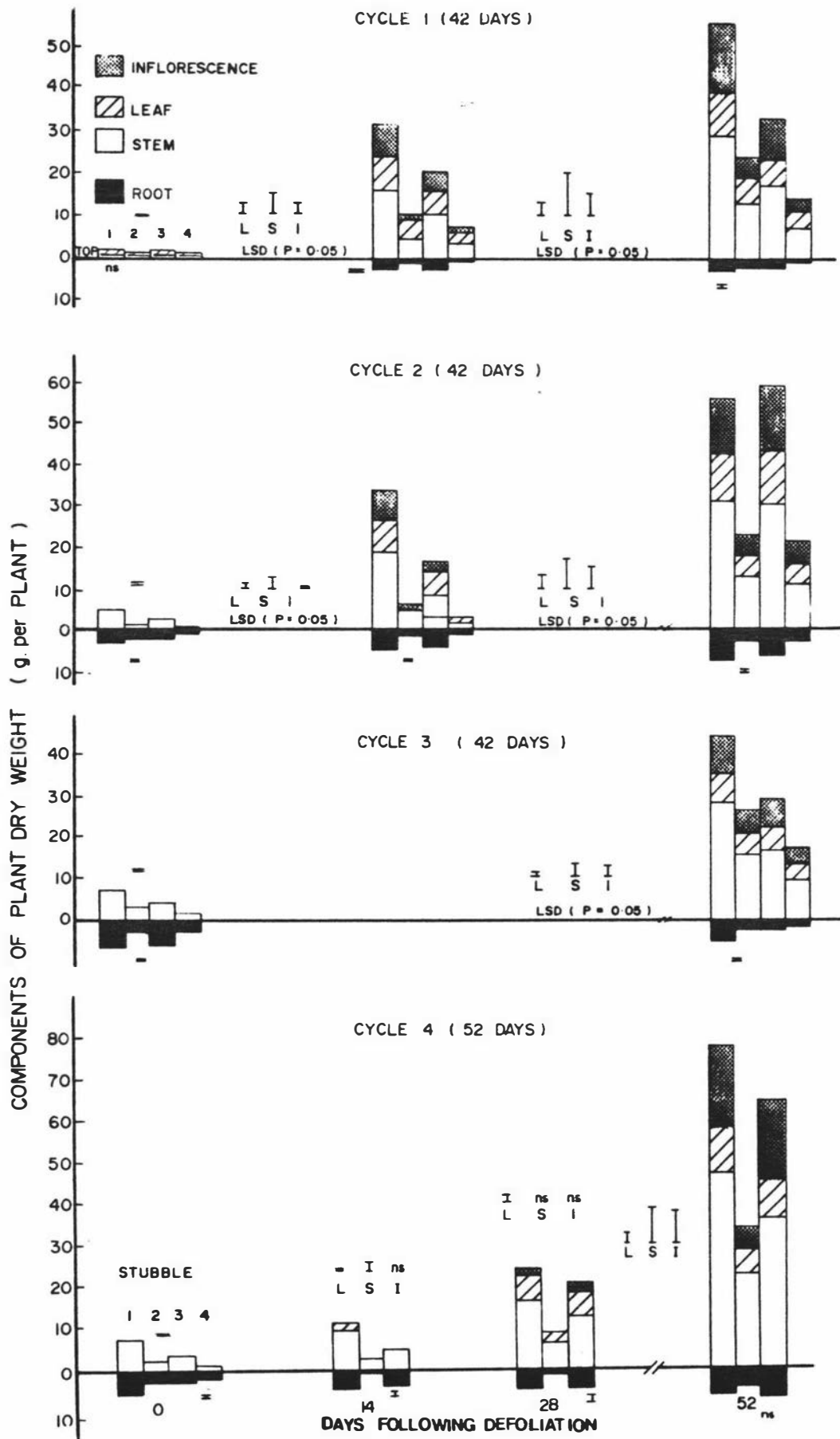


Figure 3.6: Effect of defoliation intensity on the components of plant dry weight (g/plant). Note: 1 = E-7-4, 2 = E-7-0, 3 = E-3-4 and 4 = E-3-0.

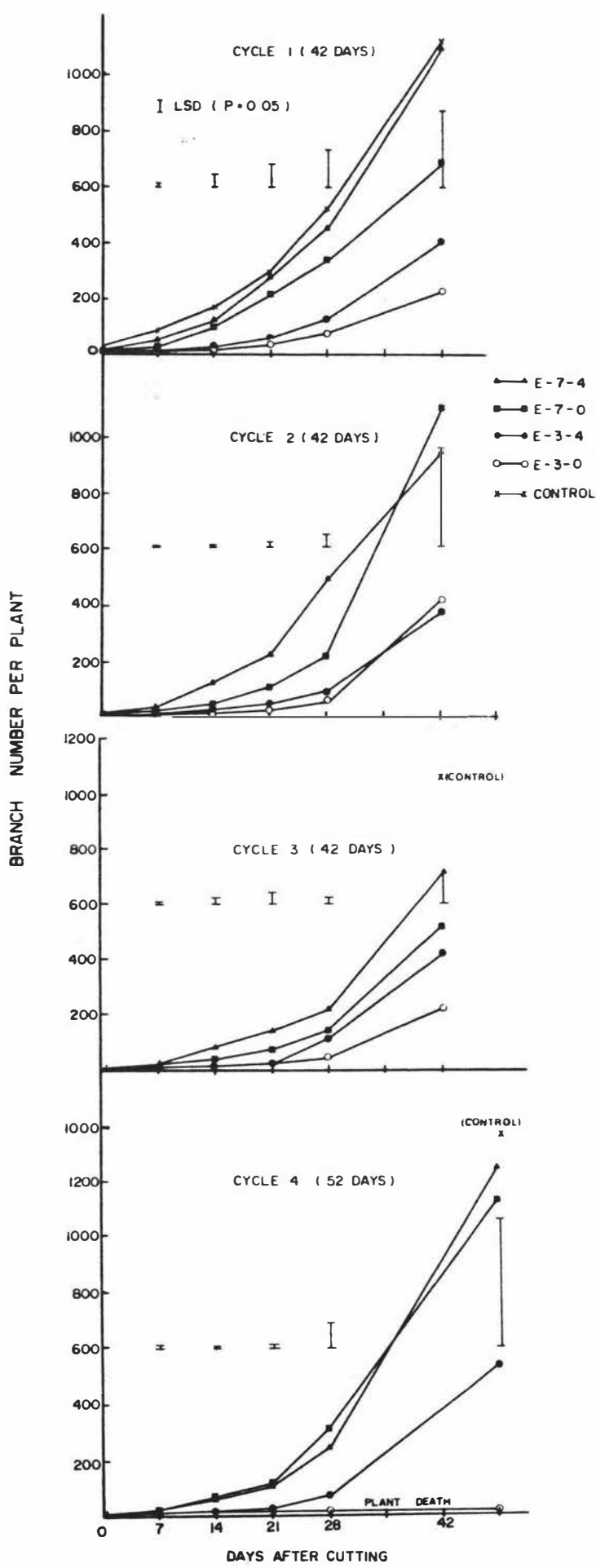


Figure 3.7: Effect of defoliation intensity on branch number per plant.

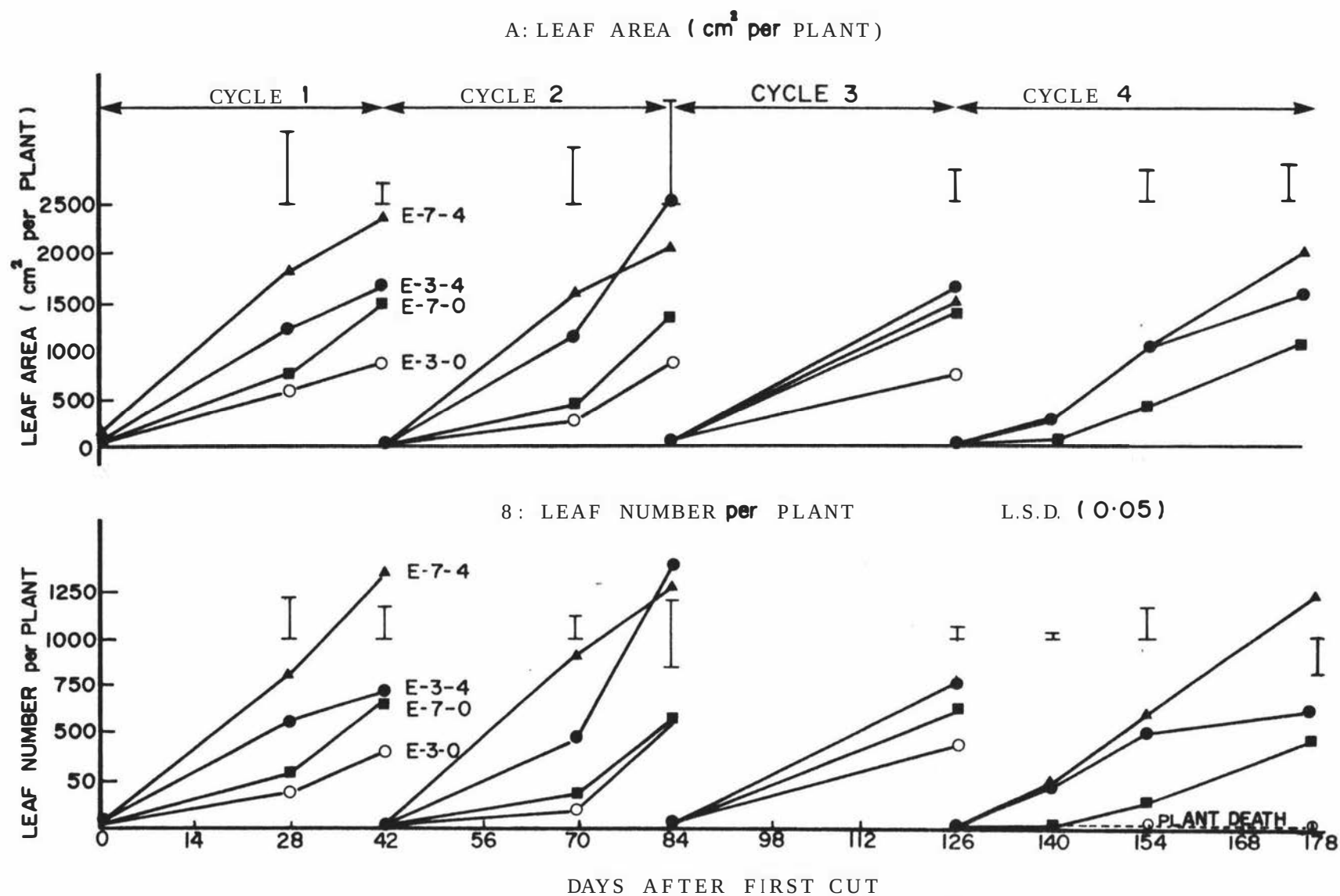


Figure 3.8: Effect of defoliation intensity on leaf area (cm^2) and leaf number per plant at all regrowth cycles.

Table 3.3 Effect of defoliation intensity on residual leaf area (LA)(cm²) and leaf number (LNO) per plant remaining immediately after each cut.

Treatment	Cycle 1		Cycle 2		Cycle 3		Cycle 4	
	LA	LNO	LA	LNO	LA	LNO	LA	LNO
E-7-4	197a ¹	68a	53a	37a	19a	34a	-	-
E-7-0	24c	11c	13b	10c	0c	0b	-	-
E-3-4	143b	54b	25b	24b	6b	10b	-	-
E-3-0	13c	10c	4b	6c	1c	4b	-	-
Sig.	**	**	**	**	**	**	-	-

¹ Values in the same vertical column not followed by the same letter differ at P = 0.05.

the 4th cycle, similar and significant treatment differences in regrowth occurred (Table 3.2) but purely from stem residuals (Table 3.3)

B.4 Number of Growing Points

As shown in Table 3.4, for all regrowth cycles, there was a marked effect of cutting on the number of growing points. Defoliation of the primary branches caused a much greater reduction in growing points than defoliation of the main stem. In fact, once the size of the primary branches had been severely reduced (i.e. from 4 to 0 nodes), the more intense defoliation of the main stem (i.e. from 7 to 3 nodes) made no further impact on the number of growing points present. However, the most severe defoliation treatment (E-3-0) did lead to total plant death by the 4th regrowth cycle. It was clearly evident from the results that the majority of growing points were on the primary branches and hence significantly affected by defoliation.

C. CHEMICAL COMPOSITION

C.1 Crude Protein

As shown in Table 3.5, for the two cycles analysed (1st and 4th), there was no significant effect of intensity of defoliation on the crude protein concentration of any of the plant components measured and differences were generally small. There were large differences, however, in the crude protein levels between the plant components. Crude protein concentration was highest in the leaf, also high in the inflorescences, but much lower in the stem and very low in the tap root and stubble.

When converted to a protein yield basis, the differences between treatments were highly significant and followed very much the plant weight responses presented earlier i.e. protein yields were depressed more by primary branch removal than by main stem removal and most by defoliation of both primary branches and the main stem (Figure 3.9).

Table 3.4 Effect of intensity of defoliation on number of "growing points" on the stubble 10 days after cutting.

Treatment	Regrowth cycles			
	1	2	3	4
E-7-4	43a ¹	39a	30a	29a
E-7-0	8c	8c	9b	15b
E-3-4	27b	23b	28a	31a
E-3-0	5c	5c	7b	-
Significance	**	**	**	**

¹ Values in the same vertical column not followed by the same letter differ at P = 0.05.

Table 3.5 Effect of defoliation intensity on crude protein concentration (% of dry matter) in leaf (L), stem (S), inflorescence (I), root (tap (T) and fibrous (F)) components and in the residual stubble (R).

Treatments	Control ²	E-7-4	E-7-0	E-3-4	E-3-0	Sig.
Cycle 1						
Day 0						
R	-	24.03a ¹	19.82b	23.99a	22.28a	*
T + F	23.73	21.98	21.98	21.68	21.68	ns
Day 28						
R	-	7.16	7.47	6.38	5.58	ns
L	26.72	27.32	28.35	27.51	31.04	ns
S	12.98	13.43	16.41	12.95	15.88	ns
I	23.41	22.62	25.00	24.36	22.86	ns
T	7.85	7.24	9.15	7.08	7.80	ns
F	15.86	16.99	17.57	14.38	16.08	ns
Day 42						
R	-	6.96	5.98	7.19	7.24	ns
L	-	26.92	28.67	26.62	28.80	ns
S	-	12.65	13.79	11.86	14.44	ns
I	-	22.87	23.17	24.72	24.95	ns
T	-	6.28	6.49	5.83	6.00	ns
F	-	14.69	15.99	14.36	18.01	ns
Cycle 4						
Day 0						
R	-	5.55	5.30	5.19	6.16	ns
T	7.60	5.81	6.68	6.66	7.10	ns
F	13.35	15.91	13.66	15.66	15.37	ns
Day 14						
R	-	5.27	4.74	5.36	-	ns
L	-	32.44	31.51	32.46	-	ns
S	-	18.10	19.22	21.01	-	ns
I	-	na	na	na	-	-
T	-	5.54	5.85	6.15	-	ns
F	-	12.47	13.38	11.77	-	ns
Day 28						
R	-	5.29	5.59	5.46	-	ns
L	-	30.40	29.31	30.12	-	ns
S	-	16.57	17.61	16.60	-	ns
I	-	22.47	-	22.03	-	ns
T	-	7.21	7.14	6.79	-	ns
F	-	14.25	16.03	14.31	-	ns
Day 42						
R	-	4.59	5.54	5.97	-	ns
L	20.40	26.38	30.18	26.42	-	ns
S	8.37	12.90	14.85	13.28	-	ns
I	20.56	23.44	23.78	22.61	-	ns
T	6.41	7.39	6.16	7.65	-	ns
F	11.74	13.53	11.69	12.71	-	ns

¹ Values in the same horizontal line not followed by the same letter differ at $P = 0.05$.

² Not included in statistical analysis.

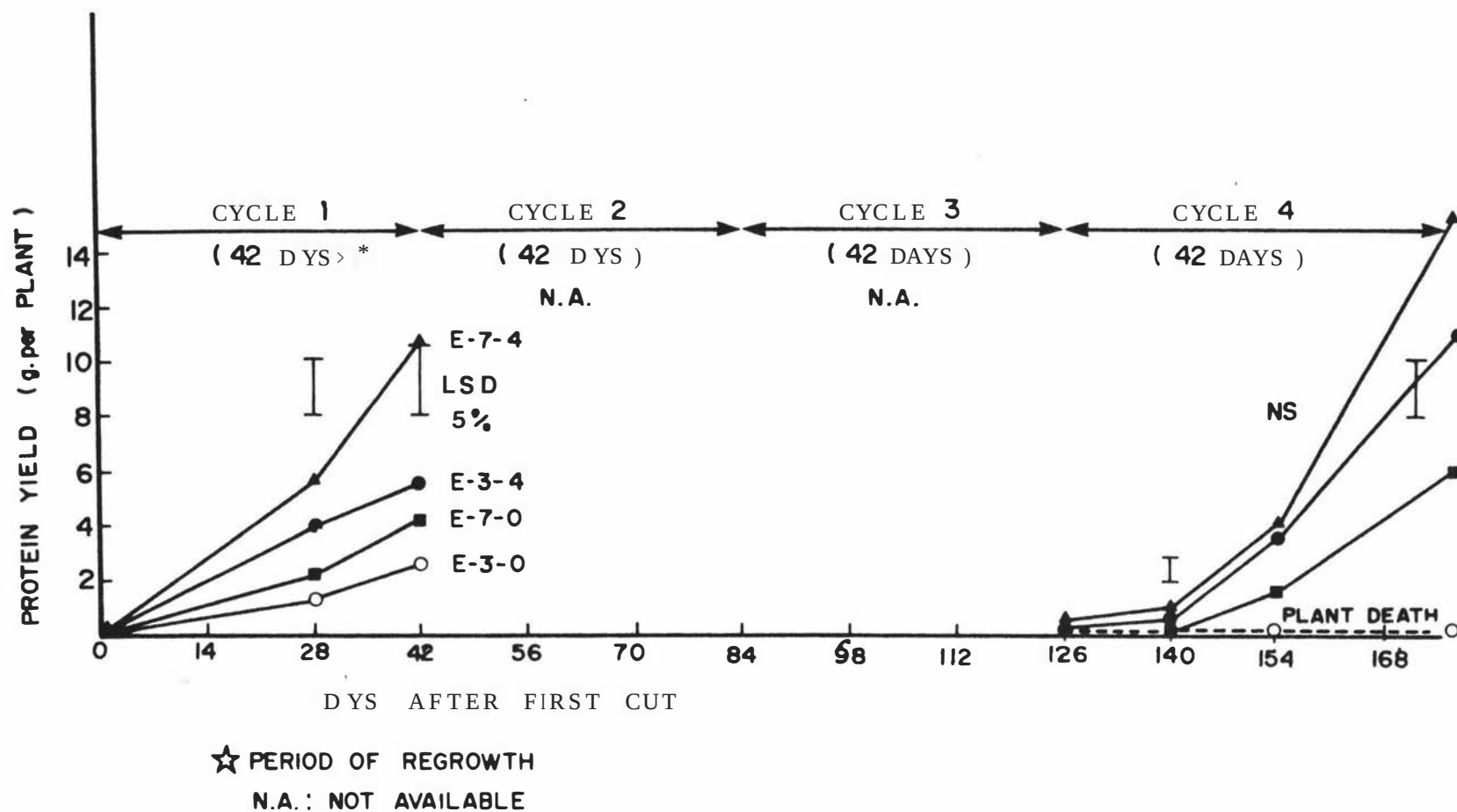


Figure 3.9: Effect of defoliation intensity on total crude protein yield at cycle 1 and 4 (g/plant)

The crude protein yields of the plant components were similarly affected by the different intensities of defoliation as were component dry weights (Figure 3.10). However, it is important to note that the yield of crude protein from the leaf plus inflorescence fraction represented a significant amount, especially in those treatments and plants receiving lax primary branch defoliation only. In contrast, only small quantities of crude protein were found in the roots.

C.2 Non structural Carbohydrate Concentration and Yield

Levels of non-structural carbohydrates (sugars and starch) were measured in the residual plants (above and below ground) immediately after the 1st and 2nd defoliation and after 52 days' regrowth in the 4th cycle.

As presented in Table 3.6, sugar concentrations in both the tops and roots were very low in all samples and showed non-significant differences between defoliation treatments. Sugar concentrations were generally much higher in the tap root than in the fibrous roots, but not greatly different between tap root and tops (above ground).

In terms of sugar yields (Figure 3.11), the differences recorded tended to reflect the different residual cutting treatments imposed. The exception, however, was the E-3-4 treatment at the end of the 4th cycle, suggesting that the sugar in the residual primary branches and even roots of those older plants, was significant in amount and greater than that in the residual main stem.

Starch levels are presented in Table 3.7 and show that concentrations were extremely low in all residual parts and in all treatments.

Table 3.6 Effect of defoliation intensity on sugar concentration (% of dry matter) in the residual above ground (stubble) and below ground (roots)

Treatments	Cycle 1 (day 0)	Cycle 2 (day 0)	Cycle 4 (day 52)
<u>A. Above ground residual - stubble</u>			
E-7-4	1.14	0.84	0.70
E-7-0	1.10	0.92	0.82
E-3-4	1.00	0.59	1.15
E-3-0	1.68	0.80	-
Significance	ns	ns	ns
<u>B. Below ground residual - roots</u>			
	Tap+Fibrous	Tap Fibrous	Tap Fibrous
E-7-4	0.73	0.72 0.04	1.32 0.04
E-7-0	0.73	0.60 0.03	0.71 0.04
E-3-4	0.79	0.44 0.03	1.41 0.04
E-3-0	0.79	0.59 0.04	- -
Significance	ns	ns ns	ns ns

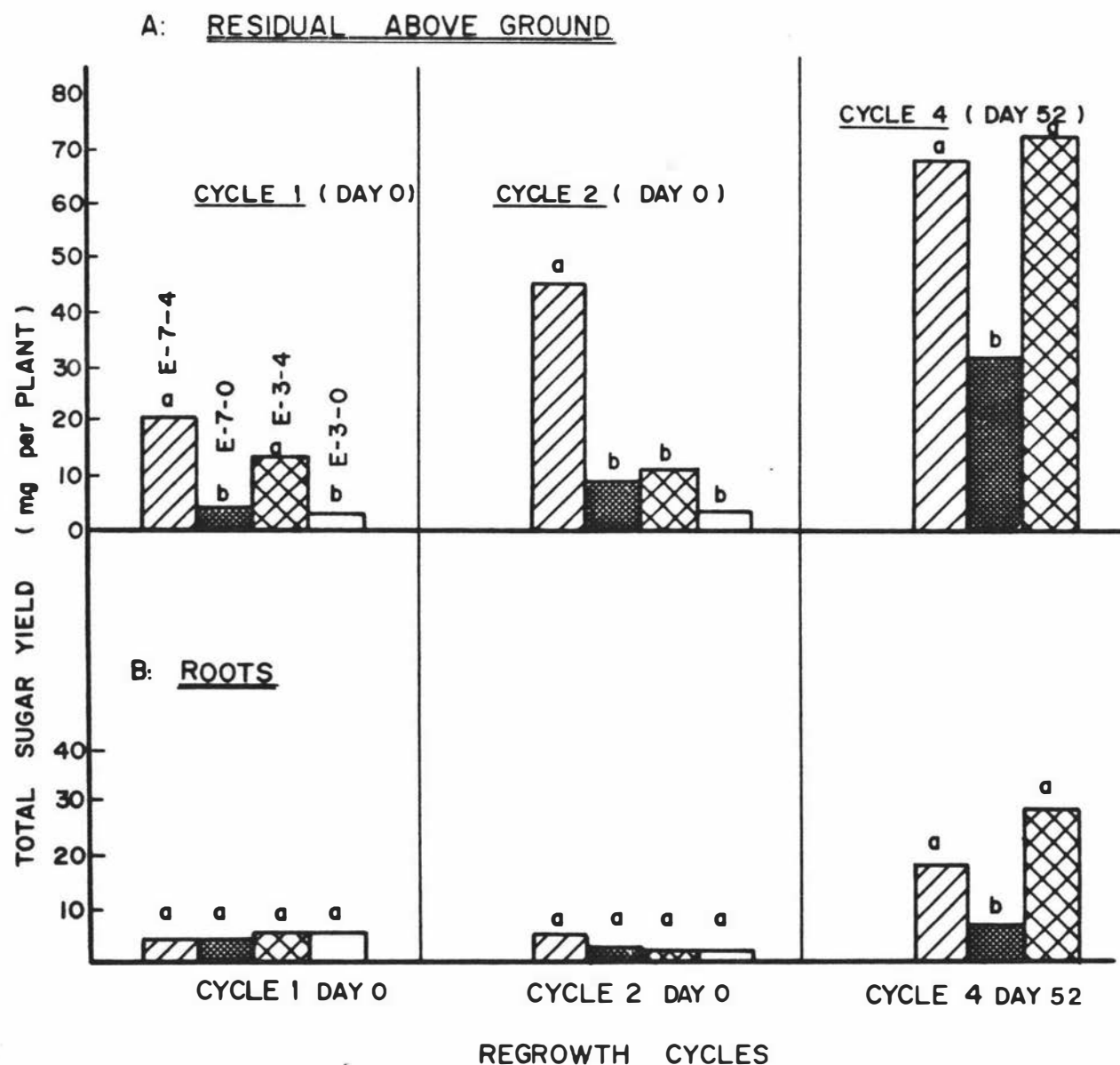


Figure 3.11: Effect of defoliation intensity on sugar yield in the residual top (stubble) and below ground (roots) (mg/plant)

Table 3.7 Effect of defoliation intensity on starch concentration (% of dry matter) in the residual above ground (stubble) and below ground (roots)

Treatments	Cycle 1 (day 0)	Cycle 2 (day 0)	Cycle 4 (day 52)
<u>A. Above ground Residual - stubble</u>			
E-7-4	0.06	0.02	0.11
E-7-0	0.03	0.04	0.10
E-3-4	0.02	0.03	0.14
E-3-0	0.01	0.02	-
Significance	ns	ns	ns
<u>B. Below ground residual - roots</u>			
	Tap+Fibrous	Tap Fibrous	Tap Fibrous
E-7-4	0.05	0.06 neg. ¹	0.09 neg.
E-7-0	0.05	0.04 neg.	0.05 neg.
E-3-4	0.02	0.04 neg.	0.11 neg.
E-3-0	0.02	0.05 neg.	- -
Significance	ns	ns	ns

¹ Neg. = negligible.

D. RELATION BETWEEN REGROWTH YIELD AND RESIDUAL
PLANT VARIABLES

The relationships between regrowth yield and the residual plant variables are presented in Table 3.8. Significant and positive correlations were found for all cuttings. Branch number, leaf area, leaf number, the number of growing points, residual top dry weight (stubble) and shoot to root ratio were all significantly and positively correlated with regrowth yield for most regrowth cycles. There was no significant correlation between regrowth yield and the concentration of TNC in stubble and roots for the regrowth cycles examined, except for a negative correlation for the 6 week period in cycle 1. However, the relationships between regrowth yield and the amount of TNC, particularly in the stubble, was significant and positive.

E. RELATIONSHIP BETWEEN TOTAL PLANT DRY WEIGHT AND THE MAIN
GROWTH PARAMETERS (BRANCH NUMBER, LEAF NUMBER AND
LEAF AREA)

Highly significant and positive correlations were found (Table 3.9) between plant dry weight and the main growth parameters (branch number, leaf number and leaf area) for almost all regrowth cycles, suggesting that these parameters are important in determining yield, as found in Experiment 2.

Table 3.8 Correlation of residual plant variables with net regrowth yield.

Residual plant variables immediately after cutting	Weeks after first cut		Weeks after second cut		Weeks after third cut		Weeks after fourth cut		
	4	6	4	6	4	6	2	4	6
Branch number	0.852**	0.735**	0.914**	0.718**	-	0.615*	0.909**	0.798	0.861**
Leaf number	0.788**	0.680**	0.890**	0.702**	-	0.729**	-	-	-
Leaf area (cm ² /plant)	0.780**	0.715**	0.881**	0.567	-	0.852**	-	-	-
Growing points (no./plant) ¹	0.898**	0.800**	0.979**	0.814**	-	0.776**	0.782	0.925**	0.820**
Stubble:root ratio	0.785**	0.852**	0.926**	0.620*	-	0.764**	0.882**	0.795	0.773*
Residual stubble dry wt. (g/plant)	0.774**	0.769**	0.926**	0.620*	-	0.828**	0.888*	0.485	0.830**
Root dry weight	-0.038	-0.180	0.837**	0.438	-	0.747**	0.581	-0.010	0.605
% TNC in stubble	0.308	0.586	-0.118	-0.442	-	-	-	-	-
% TNC in roots	-0.679	-0.908**	0.214	-0.146	-	-	-	-	-
TNC yield in stubble (mg/plant)	0.841**	0.773*	0.907**	0.429	-	-	-	-	-
TNC yield in roots (mg/plant)	0.096	-0.447	0.785*	0.241	-	-	-	-	-

¹ Determined 10 days after cutting

Table 3.9 Linear correlation coefficients between plant dry weight (DM) and main growth parameters (branch number (B), leaf number (LNO) and leaf area (LA))

	Parameters of growth		
	B	LNO	LA
<u>Cycle 1</u>			
4 weeks	0.973**	0.986**	0.973**
6 weeks	0.987**	0.901**	0.822**
<u>Cycle 2</u>			
4 weeks	0.994**	0.998**	0.928**
6 weeks	0.916**	0.952**	0.858**
<u>Cycle 3</u>			
6 weeks	0.969**	0.744**	0.635**
<u>Cycle 4</u>			
2 weeks	0.754 ^{ns}	0.884**	0.893**
4 weeks	0.897**	0.876**	0.880**
6 weeks	0.829**	0.854**	0.942**

IV DISCUSSION

Results of this experiment showed that severe and repeated cutting of Verano stylo was extremely deleterious to the plant as reflected in the death of 19% of the plants following the second cutting in treatment E-3-0. Yields from this treatment were greatly reduced and no regrowth occurred during the 4th cycle of regrowth (Table 3.2). Even when defoliation of the main stem was lax (E-7-0), the complete removal of the primary branch still had a dominant and detrimental effect on yield. This is in contrast to the effect of lax cutting of the primary branches (E-7-4 and E-3-4) which was much less harmful to yield even when the main stem was cut hard (Table 3.2). These results demonstrated that lax defoliation of the primary branches is of major importance in maintaining high forage production even if the main stem is severely defoliated.

The beneficial effects of lax cutting of the primary branches were related to the greater size and levels of residual plant variables following cutting, such as residual leaf area (Table 3.3), the number of branches capable of regrowth (Table 3.10), the number of growing points (Table 3.4) and the amount of stubble reserves (Figure 3.11). These parameters were all closely related to regrowth yields (Table 3.8) as also shown in Experiment 2.

The importance of residual leaf area in regrowth of Verano stylo is similar to results obtained with other tropical legumes (Grof et al, 1970; Jones, 1974; Akinola and Whiteman, 1975; Ludlow and Charles-Edwards, 1980). Jones (1967), Whiteman (1969) and Jones (1974) found that frequent cutting reduced yield and persistence of Siratro and this effect was attributed to a low leaf area remaining on the stubble. In another experiment with individual plants, when 0, 5 or 10 leaves were left on the stubble after cutting every four weeks, Jones (1974) found that dry weight of regrowth and stolon development were greatest when most leaves were left. There were no plant deaths when 5 or 10 leaves were left but two thirds of the plants died under

Table 3.10 Effect of defoliation intensity on number of residual branches per plant

Treatment	Cycle 1 (day 0)	Cycle 2 (day 0)	Cycle 3 (day 0)	Cycle 4 (day 0)
E-7-4	21a ¹	14a	11a	11a
E-7-0	4c	4b	3b	0c
E-3-4	17b	7b	6b	5b
E-3-0	4c	3b	2b	-
Significance	**	**	*	**

¹ Values in the same horizontal line not followed by the same letter differ at P = 0.05.

complete defoliation. A similar effect occurred in this experiment with Verano stylo, particularly under severe cutting when very little leaf was left after cutting and stubble and root reserves were low in both concentration and amount.

In this experiment, residual leaf areas were much greater under lax cutting than under severe cutting of the primary branches, when cutting was repeated at six weekly intervals (Table 3.3). Thus, under severe cutting of the primary branches, energy for initial regrowth must have come from the limited reserves in the main stem and roots, and hence lead to slow initial regrowth and, in the extreme treatment (E-3-0), even to death of the plant under repeated cutting.

Although TNC concentrations were generally low the actual amounts of reserve carbohydrates in the stubble and roots varied considerably according to cutting intensity, particularly of the primary branches and hence to residual plant dry weight. The severe cutting of the primary branches markedly reduced the plant's ability to rebuild its reserves of carbohydrates between cuts and when also subjected to severe cutting of the main stem lead to "carbohydrate exhaustion" and eventual death.

There has been considerable controversy concerning the relative importance of reserve carbohydrates and residual leaf areas in determining the rate of regrowth in pasture species. Ward and Blaser (1961) measured the regrowth rate of cocksfoot grass tillers previously subjected to short-term shading and to varying intensities of defoliation. They concluded that the regrowth of the apex blades was influenced by both carbohydrate reserves and residual L.A.I. The former predominated until day 25 and the latter was more influential thereafter. In their study it also appeared that the response to higher residual L.A.I. values in terms of dry matter production by apex blade, new tillers, and increase in apex blade length, was greater in the higher carbohydrate reserve treatments. This may also apply to the present work

as indicated by the higher growth rate under lax cutting (E-7-4 and E-3-4) during the first 4 weeks of the first two regrowth cycles examined (Figure 3.4). In contrast, in the last cycle in which initial regrowth was probably more dependent upon the reserve energy, due to an absence of residual leaves, regrowth was very slow during the first two weeks but increased steadily when the plants produced more leaves. This may suggest that in the situation where there are no leaves remaining on the plant after cutting, carbohydrate reserves do play an important role in early regrowth.

The number of branches capable of regrowth was high under lax cutting of the primary branches even when the main stem was severely defoliated (Table 3.10). The close association of the number of branches with regrowth yield confirmed the importance of this parameter in determining regrowth ability. This has also been reported in many legume species (Kessler and Shelton, 1980).

The advantage of lax cutting of primary branches was also related to the number of growing points remaining for regrowth. Regrowth of Verano stylo after cutting arose mainly from axillary buds located on the residual primary branches, with only a small number of growing points located on the main stem - as also reported in Experiment 2. Thus, intense cutting of the primary branches removed almost all of the growing points for regrowth, leading to slow initial regrowth in these treatments. The importance of growing points for regrowth has also been demonstrated in *Siratro* (Whiteman, 1969), *Stylosanthes guianensis* (Grof et al, 1970), *Desmodium intortum* (Imrie, 1971) and *Crotalaria juncia* (Kessler and Shelton, 1980).

From the above discussion, it appears that the response of Verano stylo to defoliation is dependent on the number and especially the size of primary branches, the number of growing points and the amount of stubble reserves immediately after defoliation. Although it was not possible to determine their relative importance, it does appear that these parameters assume differing levels of importance depending on the state and condition of the plant.

The response of total plant dry weight to lax cutting of the primary branches (i.e. to node 4) was mainly through an increase in the stem, and to a lesser extent, the inflorescence and leaf components (Figure 3.5 and 3.6).

The other main growth parameters such as branch number, leaf number and leaf area were also affected by cutting. Intense cutting of the primary branches (i.e. to node 0) especially in conjunction with the severe cutting of the main stem markedly depressed or delayed development of these parameters. This resulted in slow recovery, reduced vigour and even death of the plants. In contrast, lax cutting of the primary branches (i.e. to node 4) enabled a rapid recovery of branch number, leaf number and leaf area and hence high dry matter production, as reflected by a strong relationship between plant dry weight and these main growth parameters (Table 3.9).

Although one must be cautious in extrapolating the results of growth room studies into field situations, the data on crude protein concentrations from this experiment do, however, indicate the relatively high nutritive value of this species. The crude protein levels recorded were slightly higher than those reported by Gardener (1980) for Verano stylo and other tropical legumes by Hendy (1971), Ive (1974), Mufandaedza (1976) and Robertson et al (1976) and well above the level that would be expected to impair animal production - since Milford and Minson (1966) showed that intake is only reduced if crude protein of the forage is less than 8%. As shown for other tropical pasture species (Fisher, 1969, 1970; Robinson and Jones, 1972; McIvor, 1979; Gardener et al, 1982) leaves contained higher concentrations of crude protein than stem, and inflorescence generally had levels similar to leaves. By comparison concentrations in the stubble and tap root were consistently low. Cutting treatments did not affect the crude protein concentrations in any components, as also observed by Mufandaedza (1976) in S. guianensis and by Olsen (1973) in Desmodium intortum. However, a contrasting result was noted for S. humilis (Fisher, 1973).

Although the cutting intensity did not affect the crude protein levels, the total crude protein yield differed markedly between treatments (Figure 3.10). This was due to the difference in total plant dry weight. Crude protein yields under severe cutting of the primary branches was significantly lower than under lax cutting. This shows that such cutting intensity not only depresses net regrowth available for animal intake, but also depresses total protein available to the grazing animal. The high crude protein yield per plant recorded under lax cutting of both primary branches and main stem resulted from an increase in crude protein yield in the inflorescence fraction and to a lesser extent in the stem and leaf (Figure 3.10). This is of some importance in terms of its feeding value since the inflorescence fraction is acceptable to stock even when the plants are mature and hence can be utilized late in the season (Gardener, 1980).

Experiment 2 showed that total non-structural carbohydrates (sugar and starch) in the residual top and roots of Verano stylo were low (<2% of dry weight) and comprised mainly of sugar. The present work confirmed this finding and also showed that carbohydrate levels were independent of cutting intensity (total non-structural carbohydrate present, <2%). Unfortunately no reports could be found in the literature on the effects of defoliation on the carbohydrate status of Verano stylo for comparative purposes. However, the results of the present experiment were similar to those obtained with another tropical legume S. guianensis (Mufandaedza, 1976) where cutting intensity and frequency had no significant effect on total non-structural carbohydrates in the roots and stubble. In addition, he noted that the roots had a consistently higher total non-structural carbohydrate content than stubble, which was not the case in this study.

EXPERIMENT 4: FREQUENCY OF DEFOLIATION

I. INTRODUCTION

Numerous studies with other perennial legumes and grasses have shown that both intensity and frequency of cutting influence the yield and quality of forage production, root growth and survival of species (Jones, 1973, 1974; Murphy et al, 1977; Jones and Carabaly, 1981). These effects were also observed in Verano stylo in Experiment 3. In that experiment, the complete removal of the primary branches (i.e. to node 0) caused a significant reduction in yield and this effect was more accentuated when the main stem was also severely defoliated, and even lead to plant mortality. An examination of some of the factors affecting regrowth indicated the importance of photosynthetic areas, carbohydrate reserves, the number and size of primary branches and the number of growing points remaining after cutting (Experiment 3). While the effects of different cutting intensities were examined in Experiment 3, no assessment was made of the effects of cutting frequencies on plant productivity and survival. Under field conditions in Thailand, Topark-Ngarm and Akkasaeng (1978) found that the yield of Verano stylo under a four week cutting interval was significantly lower than under a six week cutting frequency. However, no assessment was made of the possible phenological responses, such as leaf area, carbohydrate levels etc.

The present experiment, therefore, was conducted to gain further information on the response of Verano stylo to 3 and 6 weekly cutting at three intensities of cutting of the main stem, in terms of regrowth and chemical composition.

II. MATERIAL AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURES

Environmental conditions and planting procedures were the same as reported for Chapter 3 (Experiment 1). After treatments were imposed, pots of similar treatments were located together to minimise the interference effects during regrowth.

B. TREATMENTS

Treatments replicated four times in a randomised block design were as follows:

<u>Treatment</u>	<u>Detailed</u>
1. E-7-4-3:	Cut the main stem above node 7 (between nodes 7 and 8) and primary branches above node 4 (between nodes 4 and 5 along the branch) every 3 weeks.
2. E-5-4-3:	Cut the main stem above node 5 (between nodes 5 and 6) and primary branches above node 4 (between nodes 4 and 5 along the branch) every 3 weeks.
3. E-3-4-3:	Cut the main stem above node 3 (between nodes 3 and 4) and primary branches above node 4 (between nodes 4 and 5 along the branch) every 3 weeks.
4. E-5-4-6:	Cut the main stem above node 5 (between nodes 5 and 6) and primary branches above node 4 (between nodes 4 and 5 along the branch) every 6 weeks.

The first defoliation was carried out when 50% of the plant population had commenced flowering and was repeated after three weeks' regrowth except in treatment E-5-4-6. Cutting was repeated 8 times with 8 regrowth cycles over approximately 200 days under 3-weekly defoliation and 4 times with 4 regrowth cycles under 6-weekly defoliation (Figure 4.1).

Nine harvests were taken in all treatments except treatment E-5-4-6 where only five harvests occurred.

C. PLANT MEASUREMENTS

C.1 Plant Dry Weight

Measurements of plant dry weights and other phenological observations were obtained from 4 plants per treatment. Plants were sampled at the end of each regrowth cycle (Figure 4.1) and separated for measurement as described in Experiment 1. At each sampling, roots were also washed and separated into tap and fibrous roots.

C.2 Leaf Area (cm²/plant) and Leaf Number

Leaf area and leaf number were recorded at the same time as plant dry weights were determined. Leaf areas were measured using the Electronic Leaf Area Meter (Model 3100 Area Meter).

C.3 Branch Number per Plant

Branch number per plant was recorded immediately after each regrowth cycle and before cutting was repeated, as described in Experiment 2.

C.4 Number of Growing Points

The number of visible growing points was recorded after 10 days of regrowth, as described in Experiment 2.

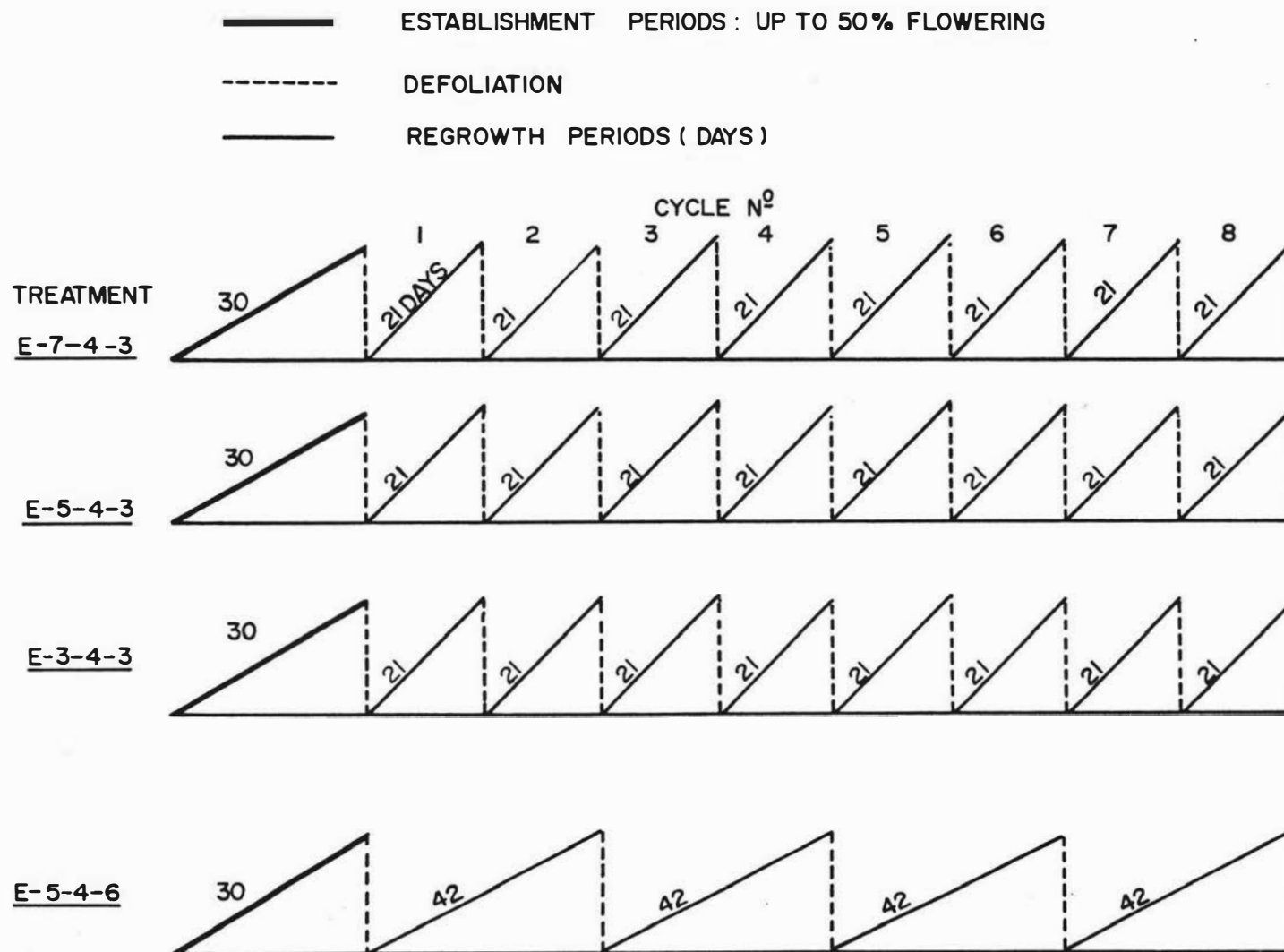


Figure 4.1: Planning of Experiment 4

D. CHEMICAL MEASUREMENTS

Crude protein and total non-structural carbohydrate (sugar and starch) concentrations were determined as described in Experiment 2. The plant fractions analysed are shown in Table 4.1.

E. STATISTICAL ANALYSIS

Data were analysed according to the common procedure of a randomized complete block design for all plant characters (Little and Hills, 1975). The analysis was done by Genstat programme (Alvey et al, 1977). The least significant difference at the 5% level was used to identify statistical differences. The symbols used to designate statistical significance were * ($P = 0.05$), ** ($P = 0.01$) and ns (not significant).

III. RESULTS

A. PHENOLOGICAL OBSERVATION

Growth and development during the establishment phase were the same as those reported in Experiment 1. The cutting treatments were first imposed when 50% of the plant population had commenced flowering and repeated at three-week intervals for treatment E-7-4-3, E-5-4-3 and E-3-4-3, and at six weeks for treatment E-5-4-6.

Under three weekly cutting, all treatments produced a dense mat of small new branches on the lower part of the main stem following the fifth cut. Flowering time was also delayed by at least 2 weeks in these treatments.



Plate 4.1: Comparison of Cutting Intensities and Frequency taken immediately prior to the third 3 weekly cutting and second 6 weekly cutting.
(Note: Greater production under 6 weekly versus 3 weekly cutting; greater production under lax versus severe cutting of the main stem).

Time and Treatment	Chemical	Plant Components				
		Stubble	Leaves	Stem	Inflor.	Root
A. E-7-4-3, E-5-4-3 and E-3-3-4.						
1. Immediately after First Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
2. Immediately after Third Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
3. 3 Weeks after Eighth Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
B. E-5-4-6						
1. Immediately after First Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
2. Immediately after Second Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+
3. 6 Weeks after Fourth Cut	Protein	+	-	-	-	+
	TNC	+	-	-	-	+

B. PLANT REGROWTH

B.1 Plant Dry Weight

The total net regrowth for each treatment over the full experimental period is presented in Figure 4.2. There was a marked effect of cutting intensity and frequency on the total net regrowth. With a cutting interval of three weeks, net regrowth yields obtained under the heavy (E-3-4-3) and moderate (E-5-4-3) cutting treatments were similar, but both lower in yield than that achieved under lax cutting (E-7-4-3)

Total net regrowth yield under 6 weekly cutting was double that obtained under 3 weekly cutting at the moderate intensity of cutting (E-5-4-6). It was also clear that cutting frequency had a relatively greater effect on plant growth than cutting intensity.

The regrowth patterns following each defoliation are presented in Figure 4.3. All treatments under 3 weekly cutting showed a decline in yield at the 3rd and 4th cutting particularly under hard (E-3-4-3) and moderate (E-5-4-3) intensities of defoliation. Thereafter, the effects of defoliation intensity remained relatively constant throughout subsequent cuttings. The regrowth pattern of the plants defoliated every 6 weeks showed a similar decline in yield to the 4th cut.

All regrowth components, of inflorescence, leaf, stem and root were similarly and in most cases significantly depressed by cutting intensity and frequency as shown in Figure 4.4. However the depression resulting from the most intense defoliation (E-3-4-3) was not significantly different from that resulting from moderate defoliation (E-5-4-3). As might be expected, the more frequent cutting treatment (3 weekly) markedly depressed inflorescence development compared with less frequent cutting (6 weekly).

The absolute growth rates (mg/day) were also depressed by cutting intensity but not always significantly and to a much lesser degree than by cutting frequency (Table 4.2).

B.2 Branch Number

The effects of defoliation on branch number per plant are presented in Figure 4.5. Moderate and hard cutting significantly decreased branch numbers compared with lax cutting, while the difference between moderate and hard cutting was not significant.

Cutting more frequently (3 weekly) depressed branch numbers significantly compared with cutting less frequently (6 weekly).

B.3 Leaf Area and Number

Leaf area (Figure 4.6) and leaf number (Figure 4.7) per plant followed very similar patterns of development after each cut, with the most lax or infrequent cutting generally encouraging significantly more leaf area and leaf number than intense and frequent cutting.

Although there was no significant effect of the residual leaf area on leaf development following the first cutting, leaf area and leaf number of plants undergoing different cutting intensities increased in proportion to the leaf area and number remaining in the subsequent regrowth cycles (Table 4.3 and 4.4). Delaying cutting to six weeks in the moderate intensity treatment (E-5-4-6) had a nil or depressing effect on residual leaf area. Nevertheless, the regrowth achieved over 4 regrowth cycles in this treatment was significantly greater than in the frequent cutting treatment.

B.4 Number of Growing Points

The number of growing points was significantly reduced by cutting intensity but only during the first four cycles of regrowth. Again, there was no significant difference in this respect between moderate and hard defoliation. However, all cutting treatments showed an increase in the number of growing points with time, particularly under moderate and severe cutting, leading to a similar number between treat-

ments in subsequent cycles (Table 4.5). The reason for this lack of response to lax defoliation over the later cuttings is difficult to explain, but observations indicated an increasing concentration of new shoots arising from the lower primary branches on the main stem with repeated cutting.

Delaying cutting to six weeks significantly depressed the number of growing points, while frequent cutting led to a substantial increase as the experiment progressed.

C. CHEMICAL COMPOSITION

C.1 Crude Protein

As shown in Table 4.6 for the four cycles (1st, 2nd, 7th and 8th) analysed, there was virtually no significant effect of intensity and frequency of defoliation on the crude protein concentration of any of the plant components measured and differences were generally small. However, there were large differences between the plant components. Crude protein concentration was highest in the leaf, also high in the inflorescences, but lower in the stem and very low in the roots, especially the tap root (Table 4.6).

Total yields of crude protein were markedly affected by cutting frequency (Figure 4.8) and to a lesser extent by cutting intensity and tended to reflect the same trends as shown in regrowth yields.

It is interesting to note that leaves tended to be the major contributor to total protein yield particularly under frequent cutting.

C.2 Non-structural Carbohydrate Concentration and Yield

As presented in Table 4.7, sugar concentrations in both the stubble and roots were very low in all samples and showed non-significant differences between defoliation treatments. Sugar concentrations were generally much higher in the stubble than in the tap root and virtually absent in the fibrous roots.

Starch levels are presented in Table 4.8 and show that concentrations were extremely low in all residual parts.

In terms of TNC yields in the stubble (Figure 4.9) the treatment differences tended to reflect the different cutting treatments imposed. For example, sugar in the residual of laxly defoliated plants was significantly greater than that of severely defoliated plants. This was very evident by the end of the 8th cycle (day 21) (Figure 4.9). Frequency of cutting had no significant effect on either sugar or starch yields.

The amount of starch present in the stubble of all treatments and on each measurement occasion was consistently low and much less than sugar yields.

D. RELATIONSHIP BETWEEN PLANT DRY WEIGHT AND THE MAIN GROWTH PARAMETERS (BRANCH NUMBER, LEAF NUMBER AND LEAF AREA)

Highly significant, positive correlations were found between plant dry weight and the main growth parameters for almost all regrowth cycles (Table 4.9), suggesting that these parameters are important in determining yield, as found in Experiments 2 and 3.

IV. DISCUSSION

This experiment showed that moderate (E-5-4-3) and severe (E-3-4-3) defoliation of the main stem reduced yield by approximately 28% compared with lax defoliation over a period of approximately 28 weeks and involving 8 cuts. This difference occurred within the first 2 cuts and thereafter remained relatively constant. Severe defoliation however was no more detrimental to regrowth than moderate defoliation.

It is suggested that the superior regrowth ability of the lax defoliation (E-7-4-3) treatment was related to the greater amount of stubble (Figure 4.4) and hence the greater amount of TNC available for regrowth (Figure 4.9) and the greater residual leaf area. The response in terms of total plant dry weight was mainly through an increase in the stem and to a lesser extent in the leaf fractions (Figure 4.2).

Total net regrowth yield from 6 weekly cutting was twice that achieved from 3 weekly cutting at the moderate intensity of defoliation imposed. The increase in dry matter yield recorded under less frequent cutting was also reported with the same species by Topark-Ngarm and Akkasaeng (1978) in their field experiment and with other pasture legumes such as Siratro (Jones, 1967), Desmodium (Jones, 1973; Ludlow and Charles-Edward, 1980) and Psoralea eriantha (Gutteridge and Whiteman, 1975). Much of this increase in yield was due to a substantial development of the stem fraction and to a lesser extent the inflorescence and leaf components.

The other main growth parameters such as branch number, leaf number and leaf area were also affected by cutting intensity and frequency. The severe and moderate removal of the main stem significantly depressed or delayed development of these parameters and hence lead to lower dry matter production. These growth parameters were also markedly depressed under frequent cutting in spite of a greater number of growing points present. This resulted in low dry matter yield as reflected by a strong relationship between total dry matter and these main growth parameters (Table 4.9). Further-

more, frequent cutting may reduce yield due to the inability of the legume to build up these growth parameters over such short intervals between cutting when compared with longer cutting intervals.

From a practical point of view, it is important to graze or cut Verano stylo laxly when under frequent defoliation. If defoliation is severe then stubble is reduced and regrowth severely impaired, especially if the removal of the primary branches is also severe as demonstrated in Experiment 3. Furthermore, if the legume is in association with a grass, as is normally the case, then the deleterious competitive effect can lead to further restriction on legume regrowth and hence low yield.

The percentage of crude protein in Verano stylo did not change markedly as a result of varying the cutting intensity. Similarly there was little effect on crude protein concentration from cutting frequently or infrequently, although there was some evidence of depression in the stem fraction under infrequent cutting. Differences in crude protein yields were largely a reflection of the changes in dry matter yield. With the severe (E-3-4-3) and the moderate (E-5-4-3) removal of the main stem, the crude protein yield response was similar but differed significantly from lax cutting (E-7-4-3) of the main stem (Figure 4.8). The major contributor to this response was the crude protein yield in the stem and to a lesser extent in the leaf components. Delayed cutting to 6 weeks greatly increased the crude protein yield of the stem and to a lesser extent the leaf and inflorescence fractions.

There is little information in the literature on the effect of cutting frequency on carbohydrate reserves in Verano stylo. However, in Stylosanthes guianensis, Alferez (1974) found that under infrequent cutting (90 day interval) there was greater accumulation of total non-structural carbohydrates in the roots than under a 30 or 60 day cutting interval. In addition, total root dry weights were reduced by frequent cutting. In contrast, Jones (1974) found that nitrogen and soluble carbohydrates in the roots of Siratro

(Macroptilium atropurpureum) were reduced under infrequent cutting (16 weeks) compared with frequent cutting (4 and 8 weeks). Young and Robinson (1963) also found that under light defoliation (20% of top growth removed every two weeks) and heavy defoliation (60% of top growth removed every two weeks) there was a large increase in the percentage of carbohydrates in Siratro compared with the undefoliated control. In the present study, cutting frequency had no significant effect on either concentrations or amounts. However, the level of total non-structural carbohydrate in the roots and stubble under both frequent and infrequent cutting were lower than that recorded in Siratro (Jones, 1974). The specific growth conditions such as optimum temperature for growth (Ludlow and Wilson, 1970), and the unlimited water and nutrient supply, are considered to be largely responsible. On the other hand, cutting intensity did affect carbohydrate yields, reflecting dry matter responses, with lax defoliation providing a significantly greater residual of reserves in the stubble than moderate or severe defoliation.

CHAPTER 5

EXPERIMENT 5: EFFECT OF WATER STRESS AT DIFFERENT DEFOLIATION LEVELS ON REGROWTH CHARACTERISTICS OF STYLOSANTHES HAMATA (VERANO)

I. INTRODUCTION

The performance and yield of a pasture species is the genotypic expression as modulated by the continuous interactions with the environment. Among the environmental factors, one of the most widely limiting for pasture growth is water. Within tropical areas, a period of drought, either short term or long term, commonly occurs during the growing season. This is the major determinant of pasture yield. Although there is an increasing understanding of drought response in many crop plants, few attempts have been made to measure these responses in pasture plants, specifically in tropical legumes. Much effort has been expended in order to maintain a grass-legume association without knowing the water requirements and relationships. The plants' response to this sort of hazard should be investigated in order to understand the dynamics of the associated plants in sown pastures.

II. MATERIALS AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURES

The experiment was carried out in the Climate Controlled Rooms of the Plant Physiology Department, DSIR, Palmerston North, New Zealand. Verano stylo was grown in plastic pots (15 cm diameter by 40 cm deep) filled with 7 kg of "Opiki loam" and sand mixture (70 : 30 v/v). Appropriate fertilizers were also added. Sowing procedures were similar to the previous experiment. The conditions in the controlled environment room were:

temperature - 30^o/24^oC (day/night),
humidity - 70/90 RH (day/night)
photoperiod - 12 hours

CO₂ level was monitored during the experiment and it ranged from 290 - 350 ppm during day conditions, and from 320 - 390 during night conditions.

A complete nutrient solution (NCSU - Appendix 1) was applied four times daily until 50% of the plant population commenced flowering. The solution was added to each pot to completely saturate the soil. At least 200 ml of the solution added drained out of the bottom of each pot overnight and the pot was weighed at the start of the light period. This was recorded as the field capacity. Pots were left until the water reached stress 1 and 2, (see below) when the cutting treatments were then imposed.

At the start of the water stress period, the soil surface in the pot was covered with plastic and gravel to reduce water loss. Pots were weighted at random every day before the beginning of the light period. Plastic tube and syringe were used to replace the water (deionized) that was lost through transpiration. Correction for plant weight was made every time plants were harvested and watering adjusted to maintain the two levels of water stress achieved, as shown in Table 5.1 After 84 days of water stress, all plants then received full watering over the recovery period of three weeks to the end of the experiment.

B. TREATMENT

The two levels of water stress imposed were:

Stress 1 (Mild Stress - W1): Leaves on the main stem become yellow and plant slightly wilted (11 days after water withdrawn - Plate 5.1).

Stress 2 (Severe Stress - W2): Leaves on the main stem start to fall off, lower leaves become yellow and plant severely wilted (18 days after water withdrawn - Plate 5.2).

As seen in Table 5.1 the two levels of water stress proposed were satisfactorily achieved and maintained. When the plants reached Stress 1 and 2 - 11 and 18 days, respectively after cessation of watering - defoliation was imposed as follows:-

1. Cut the main stem above node 7 (between nodes 7 and 8) and primary branches above node 4 (between nodes 4 and 5 along the branch)(C1)
2. Cut the main stem above node 5 (between nodes 5 and 6) and primary branches above node 4 (between nodes 4 and 5 along the branch)(C2)
3. Cut the main stem above node 3 (between nodes 3 and 4) and primary branches above node 4 (between nodes 4 and 5 along the branch)(C3)



Plate 5.1: Plant under mild water stress compared with non-stressed plant immediately before the cutting treatment was imposed (Note: Plant is slightly wilted under mild water stress).

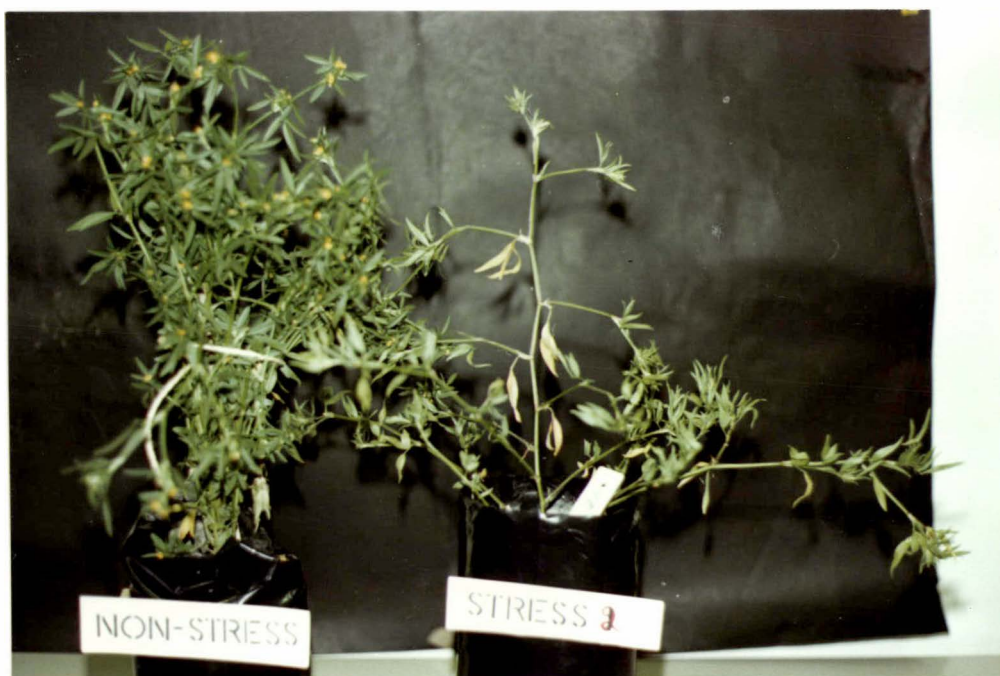


Plate 5.2: Plant under severe water stress compared with non-stressed plant immediately before the cutting. (Note: Death and significant wilting of leaves on the main stem under severe water stress).

The experiment therefore comprised two levels of water stress, with three intensities of defoliation and can be listed as follows:-

- W1C1: Cut the main stem above node 7 (between nodes 7 and 8) and primary branches above node 4 (between nodes 4 and 5 along the branch) at mild stress level.
- W1C2: Cut the main stem above node 5 (between nodes 5 and 6) and primary branches above node 4 (between nodes 4 and 5 along the branch) at mild stress level.
- W1C3: Cut the main stem above node 3 (between nodes 3 and 4) and primary branches above node 4 (between nodes 4 and 5 along the branch) at mild stress level.
- W2C1: Cut the main stem above node 7 (between nodes 7 and 8) and primary branches above node 4 (between nodes 4 and 5 along the branch) at severe stress level.
- W2C2: Cut the main stem above node 5 (between nodes 5 and 6) and primary branches above node 4 (between nodes 4 and 5 along the branch) at severe stress level.
- W2C3: Cut the main stem above node 3 (between nodes 3 and 4) and primary branches above node 4 (between nodes 4 and 5 along the branch) at severe stress level.

C. MEASUREMENTS

C.1 Water Status

C.1.1. Soil water status

Soil moisture content was measured at the day of harvesting. As previously stated, the two levels of water stress proposed were satisfactorily achieved and maintained (Table 5.1).

C.1.2. Plant water status

During the water stress period and after re-watering, leaf relative water content (%RWC) was determined on day 0, 14, 28, 42, 63, 70, 84 and 105 after cutting. On each occasion, five newly expanded leaves were taken in order to provide leaves of a similar physiological age. The leaf samples were then weighted to determine fresh weight and floated in distilled water for three hours until they became fully turgid. Turgid weight was determined and dry weight was recorded after vacuum air oven drying for 6 hours. Relative water content of leaf was calculated as follows:-

$$\%RWC = \frac{\text{Fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \times 100$$

As seen in Figure 5.1, the two levels of water stress proposed were generally achieved and maintained.

C.2 Plant Measurements

C.2.1. Plant dry matter yield

Measurements of dry weight and phenological observations were obtained from a total of 3 plants per treatment. Plants were separated for measurements as described in Experiment 1. Dry matter yields were obtained by drying all samples in a vacuum oven for 72 hours.

C.2.1. Leaf area and leaf number

Leaf area (cm²/plant) and leaf number were measured on day 0, 42, 63, 84 and 105 after cutting. The area of leaf was determined in the same manner as reported in a previous experiment (Experiment 1).

C.2.3. Branch number (no/plant)

Branch numbers were recorded on day 0, 14, 28, 42, 63, 84, 91 and 105 after cutting.



Plate 5.5: Plants under mild water stress nine weeks after cutting.



Plate 5.6: Plants under severe water stress nine weeks after cutting. (Note: Maintenance of fresh green leaves and stems under mild water stress compared with grey-green leaves and reddish-purple stems under severe water stress).



Plate 5.3: A general view of the plants under the mild water stress six weeks after cutting. (Note: significant retain of leaves)



Plate 5.4: A general view of the plants under severe water stress six weeks after cutting. (Note: Large number of leaves senesced and fall off).



Plate 5.9: The cutting treatments of plants under previous mild water stress three weeks after re-watering (Note: Significant increase in plant size and in number of branches and leaves).
(E-6-4 = W1C1, E-4-4 = W1C2 and E-2-4 = W1C3).



Plate 5.10: The cutting treatments of plants under previous severe water stress three weeks after re-watering (Note: Significant increase in plant size and in number of branches and leaves).
(E-6-4 = W2C1, E-4-4 = W2C2 and E-2-4 = W2C3).



Plate 5.7: The cutting treatments of plants under mild water stress twelve weeks after cutting. (Note: Clusters of small branches along the primary branches). (E-6-4 = W1C1, E-4-4 = W1C2 and E-2-4 = W1C3).



Plate 5.8: The cutting treatments of plants under severe water stress twelve weeks after cutting. (Note: Fewer clusters of branches along the primary branches compared with plants under mild water stress, Plate 5.7). (E-6-4 = W2C1, E-4-4 = W2C2 and E-2-4 = W2C3).

C.3 Chemical Compositions

The chemical compositions (crude protein and TNC) were determined in the same manner as reported in Experiment 2. Plant parts and time of harvesting are shown in Table 5.2.

D. STATISTICAL ANALYSIS

Data were analysed according to the procedure of a factorial design (Little and Hills, 1975). The analysis was done by Genstat programme (Alvey et al, 1977). The least significant difference at the 5% level was used to identify statistical differences. The symbols used to designate statistical significance were * ($P = 0.05$), ** ($P = 0.01$) and ns (not significant).

III RESULTS

A. PHENOLOGICAL OBSERVATIONS

After a relatively slow establishment phase of 28 days, the plants grew rapidly and 50% of the plant population were flowering by day 35.

During the drought period, plants under mild stress maintained green leaves and stem surfaces (Plate 5.5), whereas under severe stress the plant stems developed a reddish purple colour (Plate 5.6). All plants in all treatments shed their leaves, particularly those under severe stress, and the new leaves produced were smaller, thicker and a darker green colour. New branches were also smaller and had very short internodes and tended to display a cluster of branches (Plate 5.7 and 5.8).

During the recovery period, plants previously under both mild and severe stress displayed leaf turgor within 24 hours. New leaves were noticeably bigger in size and the plants grew very rapidly during the recovery period. New branches also had longer internodes (Plate 5.9 and 5.10).

Table 5.2 Plant components analysed.

Weeks after cutting	Chemicals	Plant components				
		Stubble	Leaves	Stem	Inflor.	Roots
0	Protein	+	+	+	+	+
	TNC	+	+	+	+	+
6	Protein	+	+	+	+	+
	TNC	+	+	+	+	+
12	Protein	+	+	+	+	+
	TNC	+	+	+	+	+
15	Protein	+	+	+	+	+
	TNC	+	+	+	+	+

B. PLANT REGROWTH

B.1. Plant Dry Weight

The results presented in Table 5.3 show the main effects of water stress and cutting on plant dry weight during the drought and recovery periods. Under severe water stress total plant dry weight was significantly lower than under mild water stress throughout the drought period. Also hard cutting of the main stem significantly depressed yield compared with the moderate and light cutting (Table 5.3).

The response of Verano stylo to cutting under both mild and severe water stress showed similar trends (Figure 5.2). Under both levels of water stress, hard cutting generally depressed plant dry weight compared with lax and moderate cutting, this effect being more apparent under mild water stress. While plants under mild water stress showed a steady increase in dry weight from the commencement of regrowth, plants under severe water stress showed little increase for the first 42 days and then only a small increase in weight to the end of the drought period.

During the recovery period (12 - 15 weeks), in all cutting treatments under previous mild and severe stress, the growth of plants increased substantially. As a result, at the end of the recovery period, all cutting treatments, now at the same moisture regime, showed no significant differences in total plant dry weight (Figure 5.2). However, mean total plant dry weight (over all cuttings) in the severe water stress treatment remained significantly lower than that in the mild water stress treatment (Table 5.3). Although the absolute growth rates were similar between cutting treatments, plants under severe water stress were lower in absolute growth rate during both drought and recovery periods (Table 5.4).

Table 5.3 Main effect of water stress and defoliation on total plant dry weight during drought and recovery periods (g/plant).

Treatments	During drought period				Recovery from drought
	Days after cutting				
	0	42	63	84	21 days
<u>Water stress</u>					
W1	4.07	7.57	9.26	12.40	43.30
W2	4.09	4.48	5.49	5.79	30.20
Significance	ns	**	**	**	**
<u>Defoliation</u>					
C1	4.84a ¹	7.00a	8.40a	9.74a	36.60
C2	4.27a	6.44b	7.95a	9.80a	39.60
C3	3.12b	4.63c	5.77b	7.74b	34.20
Significance	**	**	**	**	ns
Interaction (W x C)	ns	**	ns	ns	ns

¹ Values in the same vertical column not followed by the same letter differ at $P = 0.05$

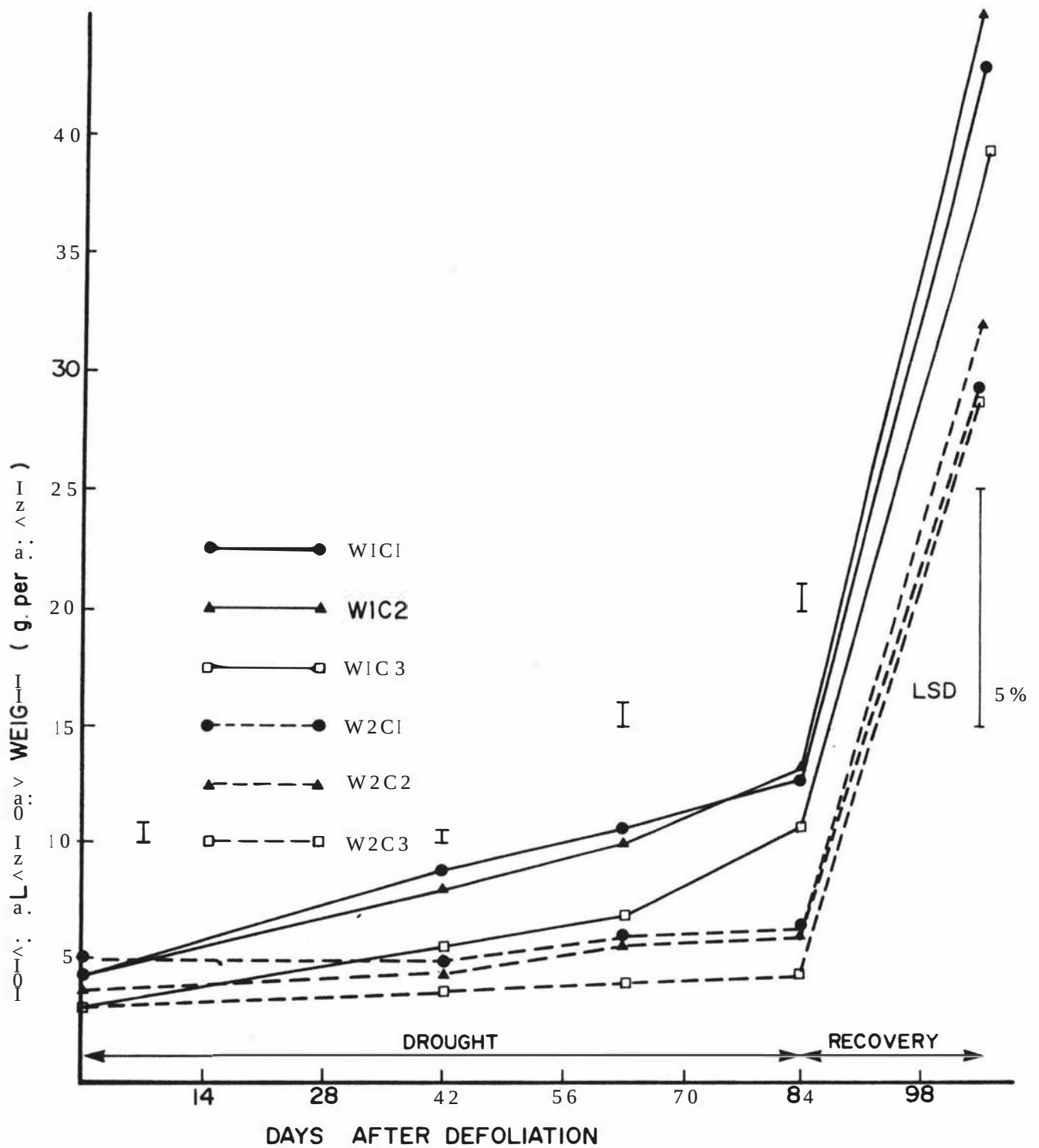


Figure 5.2: Effect of water stress and defoliation on total plant dry weight (g/plant)

The greater reduction in growth rate with severe cutting under mild water stress compared with severe water stress caused a significant interaction between water and cutting during 0 - 42 days after cutting (Table 5.4).

Relative growth rate (Table 5.4) was also lower under severe water stress but such plants were superior in relative growth rate during the recovery period. There was no effect of cutting on relative growth rate and no interaction between water and cutting during both drought and recovery periods.

During the drought period, all the regrowth components, of inflorescence, leaf, stem and root, were affected by water stress (Figure 5.3). Under mild water stress, the stem fraction increased in dry weight throughout the drought period whereas leaf increased only slightly. In contrast, inflorescence dry weight declined. Under severe water stress, the stem was the only component that increased in weight throughout the total drought period.

Cutting was also shown to have a significant effect on plant components (Figure 5.3). Hard cutting of the main stem significantly depressed the inflorescence and particularly the stem fraction compared with moderate and light cutting. Leaf and root fractions were not significantly affected by cutting during the drought period.

There was a significant interaction between water and cutting due to the greater depressive effect of hard cutting under mild water stress on the component dry weights of leaf, stem and inflorescence compared with those under severe moisture limitation (Figure 5.4). For leaf, this effect was only apparent during the first 42 days, but continued up to 63 days for stem and up to 84 days for inflorescence.

On re-watering, all components of leaf, stem and inflorescence markedly increased. However, the mean overall effect of water stress showed that the leaf and stem fractions under previous mild water stress were significantly greater in dry weight than under previous severe water stress (Figure 5.3).

Table 5.4 Effects of water stress and defoliation on absolute growth rate (A) and relative growth rate (B) during drought and recovery period

Treatments	During drought period			Recovery
	Days after cutting			from drought
	0 - 42	42 - 63	63 - 96	0 - 21 days
A. Absolute growth rate (mg/day).				
W1C1	105a ¹	80a	113a	1443a
W1C2	86ab	88a	159a	1604a
W1C3	59b	73a	176a	1372a
W2C1	-3c	53a	15b	1112a
W2C2	17c	56a	17b	1229a
W2C3	13c	35a	11b	1149a
Significance	**	ns	**	ns
Interaction (W x C)	*	ns	ns	ns
B. Relative growth rate (mg/mg/day).				
W1C1	17a	4a	5a	57b
W1C2	14a	5a	7a	60b
W1C3	14a	6a	10a	61b
W2C1	0b	5a	1b	72a
W2C2	4b	5a	2b	78a
W2C3	4b	4a	1b	86a
Significance	*	ns	*	*
Interaction (W x C)	ns	ns	ns	ns

¹ Values in the same vertical column not followed by the same letter at P = 0.05

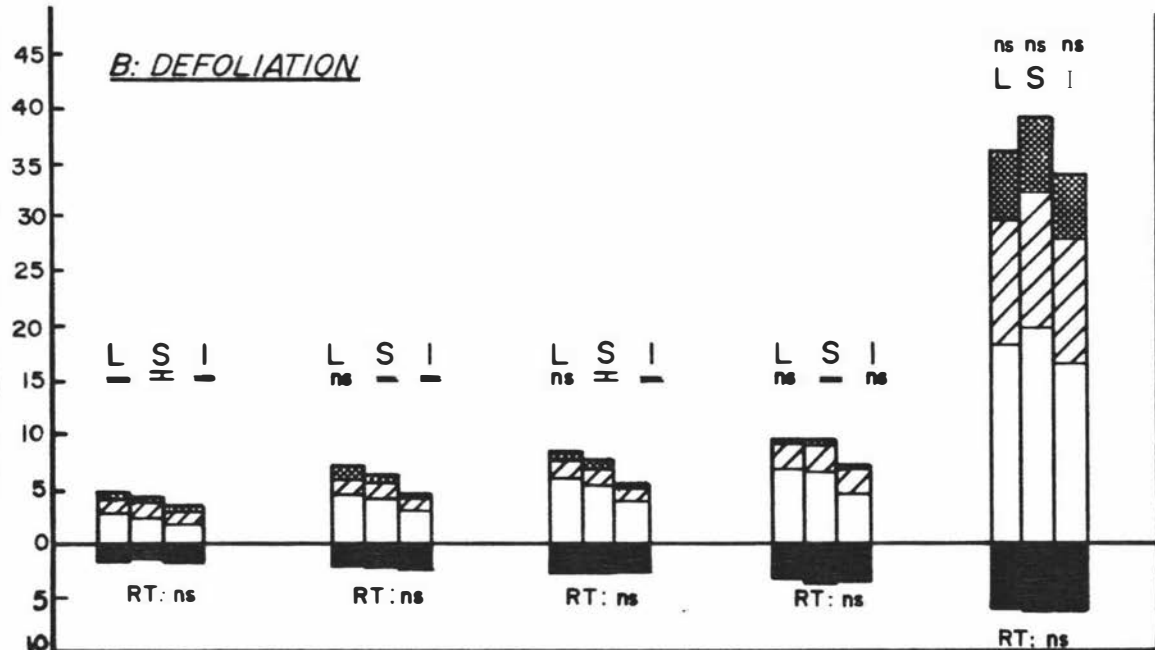


Figure 5.3: Main effect of water stress (A) and defoliation (B) on plant components dry weight (g/plant)

B.2 Branch Number

During the first 14 days after cutting, plants under mild and severe water stress showed similar branch numbers. Thereafter, the increase in branch number was more rapid in the mild water stress treatment (Figure 5.5)

There was no significant difference due to cutting under severe water stress (Figure 5.5). However, under mild water stress, the W1C1 and W1C2 treatments maintained significantly higher branch numbers than the W1C3 treatment up to day 63. The greater depressive effect of hard cutting on branch number in the mild water stress treatment compared with that in the severe water stress caused the significant interaction recorded between water stress and cutting at this stage. However, this effect had disappeared by the end of the drought period on day 84, by which time the number of branches in the hard defoliation treatment (W1C3) had rapidly increased and attained a level that was not significantly different from the other two treatments.

During the recovery period, branching was stimulated in all cutting treatments under previous mild and severe water stress conditions (Figure 5.5). However, the main effect of the earlier water stress was still apparent at the end of the recovery period of 21 days i.e. plants previously under severe water stress were significantly lower in branch number than those previously under mild water stress. In contrast, the effect of previous cutting was apparent only during the first 7 days of the recovery in the mild water-stressed treatment as shown by a lower branch number under the hard cutting compared with the moderate and light cutting. This effect failed to reach significance during the last 14 days of recovery as shown by the non-significant difference in branch number between cutting treatments at the final harvest. In the severe water-stressed treatments there were no significant effects due to cutting intensity (Figure 5.5).

In terms of branching rates, the main effect of cutting had no significant influence during the drought period (Table

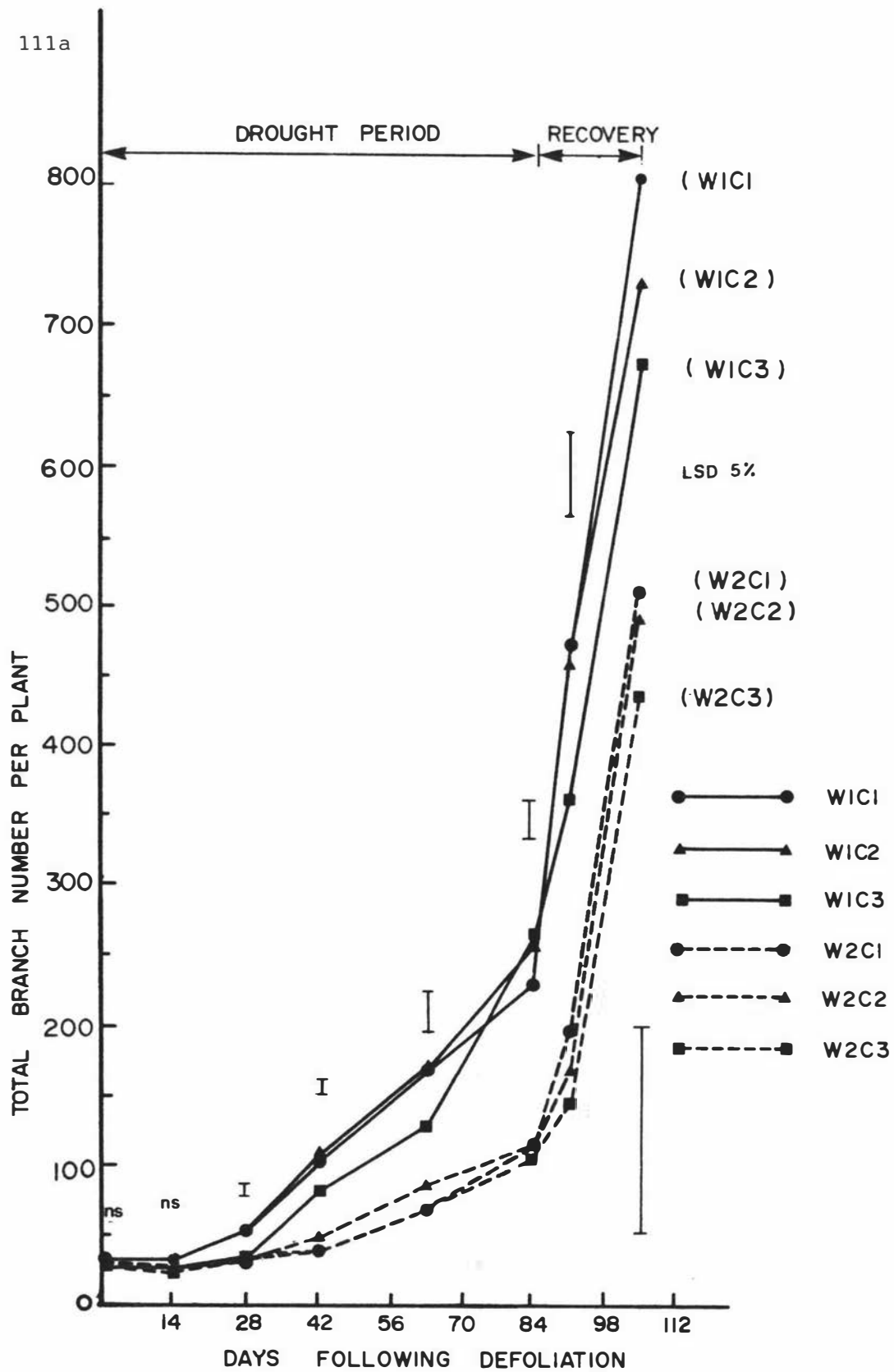


Figure 5.5: Effect of water stress and defoliation on total branch number per plant during drought and recovery period

5.5). In contrast, the main effect of water stress was most evident. Plants under severe water stress had a significantly lower branching rate than those under mild water stress throughout the entire drought period. However, in the mild water stress treatment, all cutting treatments produced new branches with the plants under hard cutting (W1C3) branching at relatively low rates for the first 4 weeks. During the following two weeks the rate of branching increased rapidly and then maintained this relatively high and similar rate to the end of the drought period (Table 5.5). In the severe water stress treatments, cutting intensity had little effect on branching rate.

On re-watering, the branching rate was increased substantially. Plants previously under severe water stress branched at relatively low rates for the first 7 days (Table 5.5) but thereafter, increased rapidly to reach a similar rate to plants previously under mild water stress. Cutting intensity also had an effect during the early stage of recovery (0 - 7 days) but disappeared during the last 14 days of recovery. Once again, in the previous mild water stress treatment, the plant under previous severe cutting branched at relatively low rates for the first 7 days, but thereafter increased rapidly (Table 5.5). In the previous severe water stress treatments, previous cutting intensity had no effect on branching rates, but the branching rate in these treatments was still significantly depressed by the previous drought for the first 7 days. However by day 21 all treatments increased their rate of branching to a similar level.

Table 5.5 Main effects of water stress and defoliation on rate of branching during drought and recovery period (no/plant/day).

Treatments	During drought period					Recovery from drought	
	Days after defoliation					(days)	
	0-14	14-28	28-42	42-63	63-84	0-7	7-21
<u>Water stress</u>							
W1	0.15	1.00	3.71	2.78	4.53	26.00	21.60
W2	-0.08	0.40	0.71	1.59	1.79	8.60	22.10
Sig.	ns	**	**	*	**	**	ns
<u>Defoliation</u>							
C1	0.19	0.80	2.00	2.28	2.60	23.30a ¹	20.40
C2	-0.04	0.81	2.70	2.23	2.79	18.60a	24.00
C3	-0.05	0.46	1.96	1.94	4.10	10.10b	21.30
Sig.	ns	ns	ns	ns	ns	**	ns
<u>Interaction (W x C)</u>							
W1C1	0.38	1.26	3.74	3.06	3.00	34.70	18.30
W1C2	-0.07	1.33	4.10	2.89	4.17	29.10	24.60
W1C3	0.14	0.40	3.31	2.38	6.43	14.30	22.00
W2C1	0.00	0.31	0.26	1.49	2.21	12.00	22.40
W2C2	0.00	0.29	1.26	1.78	1.40	8.00	23.30
W2C3	-0.24	0.52	0.62	1.49	1.76	5.90	20.70
Sig.	ns	ns	ns	ns	ns	ns	ns

¹ Values in the same vertical column not followed by the same letter differ at P = 0.05.

B.3 Leaf Area and Number

The effects of water stress and cutting on leaf area per plant (cm^2) are presented in Figure 5.6. It clearly shows that cutting had less effect on leaf area than water stress. Severe moisture limitation restricted the leaf area development compared with mild water stress throughout the drought period.

Plants in all cutting treatments under both mild and severe water stress showed a decrease in leaf area during the first 42 days of drought (Figure 5.6A), with a substantial decrease under light and moderate defoliation at both stress levels. Over the subsequent 42 days of drought, leaf area in all cutting treatments under severe water stress continued to maintain a relatively low level to the end of the drought period (day 84) and showed no significant difference between cutting intensities. In contrast the leaf area of plants in all cutting treatments under mild water stress, showed a small but steady increase over this later period, with hard cutting resulting in a significantly higher leaf area than light and moderate cutting by the end of the drought (day 84). The greater increase in leaf area through hard cutting under mild water stress conditions compared with that under severe water stress conditions (Figure 5.6A) caused a significant interaction between water stress and cutting.

During the recovery period (21 days), all plants were greatly stimulated by the application of adequate water (Figure 5.6A). As a result, by the end of the recovery period, all plants produced a large area of leaf. However, the main effect of water and cutting were still apparent during this recovery period. Plants previously under mild water stress produced significantly greater leaf area than those previously under severe water stress. Previous light (W1C1) and moderate (W1C2) defoliation produced greater leaf area than hard defoliation (W1C3) in those treatments previously under mild water stress. However, plants under previous severe water stress continued to show no significant effect of previous cutting intensity on leaf area production.

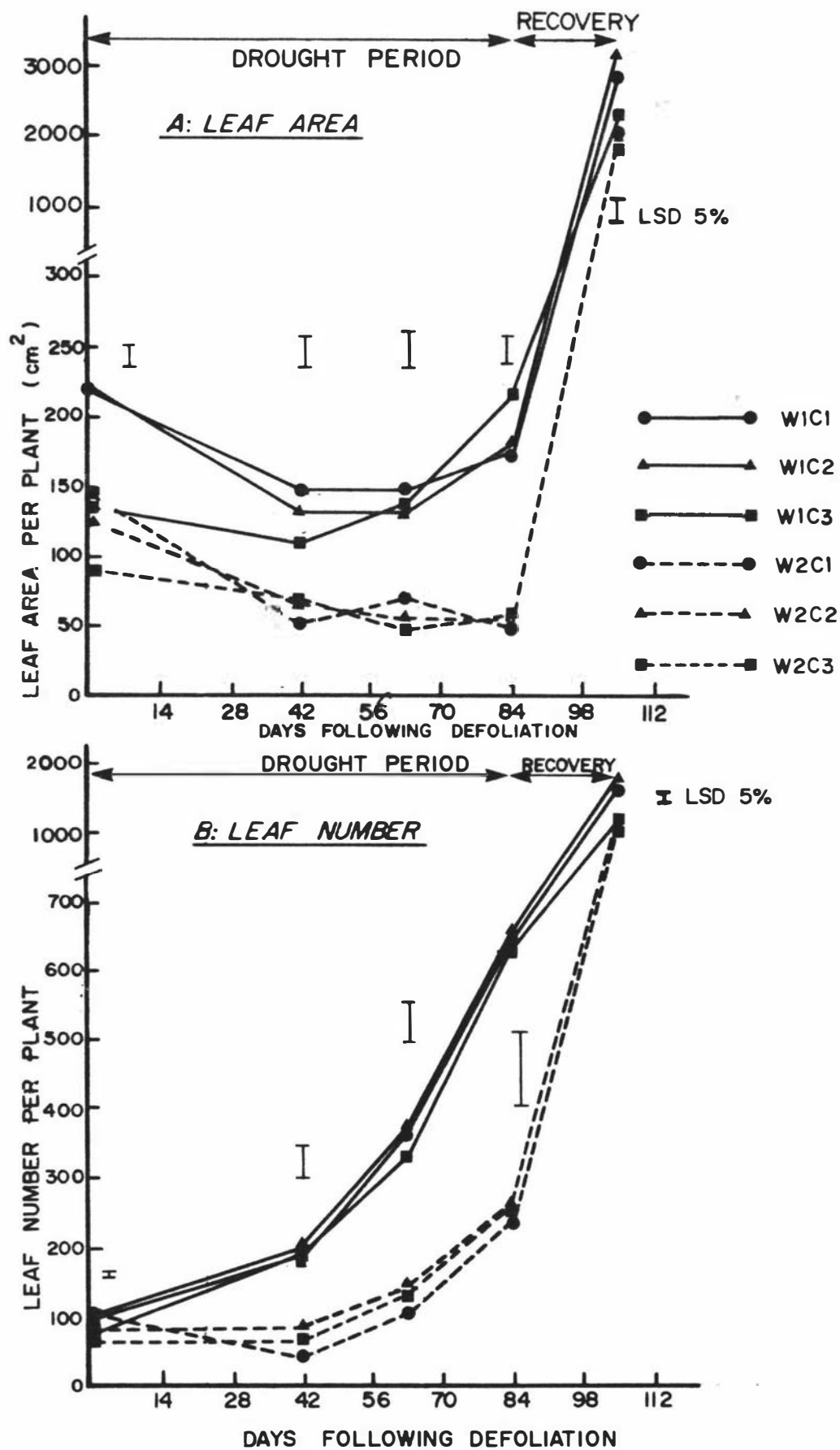


Figure 5-6: Effect of water stress and defoliation on leaf area (cm^2) and leaf number per plant during drought and recovery period

Hence the greater depressive effect of previous hard cutting on leaf area in the previous mild water stress treatment compared with that in the severe water stress again caused a significant interaction between water stress and cutting.

Leaf number per plant did not follow the leaf area pattern. The main effect of water was evident throughout the experimental period (Figure 5.6) with plants in the mild water stress treatment showing greatly increased leaf number, an effect which occurred within 20 days of defoliation and continued throughout the experimental period. In contrast, plants under severe water stress showed little effect on leaf number for the first 42 days, but thereafter, increased steadily until the end of the drought period.

There was no significant difference due to cutting under both mild and severe water stress throughout the drought period (except immediately after defoliation) (Figure 5.6).

On re-watering, leaf number in both the previously mild and severe water stress treatments (Figure 5.6) was greatly stimulated, with the previous mild water stressed plants attaining higher leaf number than the previous severely water stressed plants. However, the more notable response was the much greater increase in leaf number recorded in the latter treatment during the recovery period.

The effect of previous cutting was also apparent during this period, with previous light (W1C1) and moderate (W1C2) defoliation producing significantly more leaves than hard defoliation under previous mild water stress (Figure 5.6). In the severe water stressed treatments there were no significant effects due to cutting intensity (Figure 5.6).

Leaf appearance rate was lower under severe water stress compared with mild water stress through to the end of the drought but both treatments showed a similar, steady increase over this period (Table 5.6). By comparison, cutting intensity had no significant effect on leaf appearance rate at either water stress level.

Table 5.6 Effect of water stress and defoliation on leaf appearance rate (no/plant/day)

Treatments	During drought period			Recovery from drought	
	Days after defoliation			0-21 days	Main effect
	0 - 42	42 - 63	63 - 84		
W1C1	2.11a ¹	8.71	13.44	48.10ab	
W1C2	2.51a	8.06	13.22	51.30a	
W1C3	2.68a	7.13	14.38	28.30d	42.60
W2C1	-1.35b	2.87	6.44	40.10bc	
W2C2	0.10b	2.87	5.76	39.30bc	
W2C3	0.11b	2.30	6.06	31.20cd	36.90
Interaction (W x C)	*	ns	ns	**	ns

¹ Values in the same vertical column not having the same letter differ at P = 0.05

Table 5.7 Effect of water stress and defoliation on leaf size (cm²/leaf)

Treatments	During drought period				Recovery from drought
	Days after defoliation				21 days
	0	42	63	84	
W1C1	2.28a ¹	0.80b	0.40a	0.27b	1.73
W1C2	2.23a	0.65c	0.35a	0.28b	1.86
W1C3	1.85b	0.61c	0.41a	0.34a	1.76
W2C1	1.41c	1.08a	0.68a	0.20c	1.48
W2C2	1.50c	0.77b	0.39a	0.21c	1.87
W2C3	1.42c	1.01a	0.33a	0.21c	2.02
Interaction (W x C)	**	**	*	*	ns

¹ Values in the same vertical column not having the same letter differ at P = 0.05

On re-watering, leaf appearance rates were greatly increased in all treatments but failed to show any significant main effect due to previous water stress. However, hard cutting under both mild and severe water stress depressed leaf appearance rate compared with the moderate and lax defoliation, this effect reaching significance under mild water stress.

The size of the individual leaves in the various treatments varied greatly and somewhat erratically through the experimental period but became increasingly smaller with time. However on rewatering there was a marked increase to a similar size in all treatments (Table 5.7).

Specific leaf area was also affected by drought on most occasions (Table 5.8). Both mild and severe water stressed plants reduced their specific leaf area with time, resulting from an increase in their thickness as the stress progressed. During the recovery period there was a substantial increase but the plants previously under severe water stress had a greater specific leaf area than those previously under mild water stress.

The intensity of cutting had a significant effect on specific leaf area by the end of the drought and during the recovery period (Table 5.8). By day 84 hard cutting (C3) had significantly increased specific leaf area compared with light cutting (C1) but during the recovery period those plants previously under light cutting showed a substantial and greater increase in specific leaf area than those plants previously cut hard.

There was also a significant interaction in terms of specific leaf area between water stress and cutting due to a greater decrease in such parameters under hard cutting in the severe water stress conditions compared with that under mild water stress conditions on day 63. During the recovery period, previous hard cutting under previous mild water stress significantly depressed specific leaf area while this effect was not observed in the severe water stress - resulting in a significant interaction between water stress and cutting by the end of the recovery period.

Table 5.8 Main effect of water stress and defoliation on specific leaf area (cm²/g)

Treatments	During drought period				Recovery from drought
	Days after cutting				
	0	42	63	84	21 days
<u>Water stress</u>					
W1	161	93	73	56	189
W2	109	104	79	48	218
Sig.	**	**	ns	**	**
<u>Defoliation</u>					
C1	132	96	82	49	223
C2	133	95	70	52	205
C3	139	103	75	56	183
Sig.	ns	ns	ns	*	*
<u>Interaction (W x C)</u>					
W1C1	157	94	71bc ¹	51	192bc
W1C2	161	90	66c	54	210b
W1C3	165	93	80ba	62	165c
W2C1	108	99	93a	46	253a
W2C2	104	99	74bc	49	199b
W2C3	114	113	69bc	50	201b
Sig.	ns	ns	*	ns	*

¹ Values in the same vertical column not followed by the same letter differ at P = 0.05

C. CHEMICAL COMPOSITION

C.1 Crude Protein

As shown in Table 5.9, during the drought period there were significant effects from water stress and cutting on the crude protein concentration for all of the regrowth components, with roots (including tap and fibrous roots) having the highest concentration and stubble the lowest. Differences were generally small between water stress levels and cutting treatments, but there was a tendency for the above ground parts (leaf, stem and inflorescence) to have higher protein concentrations under severe water stress and hard defoliation. The effects of water stress and defoliation levels on the protein concentrations in the stubble and roots were even more variable and showed no clear or consistent responses.

During the recovery period, all plant components except the stubble and root, increased in crude protein concentrations, particularly in the leaf and inflorescence. However, the main effect of previous water stress levels on protein concentration was still apparent but only in the stubble, leaf and fibrous root. The concentration of crude protein in the stubble and leaf of previously mild water stressed plants was significantly lower than that of previously severe water stressed plants. This contrasted with the crude protein concentration in the fibrous root which was higher under previous mild than severe water stress.

An effect of previous cutting on crude protein concentration during the recovery period was also recorded in the stubble, stem and fibrous root fractions. Lax cutting tended to result in a lower concentration in the stubble and stem but a higher concentration in the fibrous root fraction.

There was also a significant interaction in terms of crude protein concentration between water and cutting but only during the first half of the drought period. This interactive effect was recorded only in the stubble, leaf and

Table 5.9 Main effects of water stress and defoliation on crude protein concentration in the leaf, stem, inflorescence, stubble and tap and fibrous root components (% of dry matter).

Treatments	During drought period				Recovery from drought
	0	Days after cutting			21 days
		42	63	84	
A. Stubble					
W1	16.14	8.76	-	12.44	6.53
W2	16.38	8.76	-	10.77	8.27
Significance	**	ns	-	**	**
C1	16.22a ¹	8.75	-	11.70	6.54b
C2	14.35b	9.09	-	12.16	8.18a
C3	15.21ab	8.45	-	10.95	7.48ab
Significance	*	ns	-	**	*
Interaction (WxC)	ns	*	-	ns	ns
B. Leaf					
W1	-	16.73	-	15.70	25.88
W2	-	17.81	-	18.37	28.08
Significance	-	**	-	**	**
C1	-	16.37b	-	17.01	26.74
C2	-	17.49a	-	16.51	26.99
C3	-	17.43a	-	17.59	27.22
Significance	-	**	-	ns	ns
Interaction (WxC)	-	**	-	ns	ns
C. Stem					
W1	-	12.81	-	12.00	16.22
W2	-	14.98	-	13.11	16.27
Significance	-	**	-	**	ns
C1	-	13.90	-	13.00	14.84c
C2	-	13.75	-	12.17	16.53b
C3	-	14.05	-	12.50	17.38a
Significance	-	ns	-	ns	**
Interaction (WxC)	-	ns	-	ns	ns
D. Inflorescence					
W1	-	17.32	-	15.76	22.78
W2	-	19.49	-	15.37	22.98
Significance	-	**	-	ns	ns
C1	-	17.52b	-	13.81c	22.59
C2	-	18.45a	-	15.98b	22.85
C3	-	19.25a	-	16.91a	23.15
Significance	-	**	-	**	ns
Interaction (WxC)	-	ns	-	ns	ns
E. Roots					
E.1. Tap root					
W1	9.76	15.70	-	19.18	13.72
W2	10.04	13.38	-	18.58	13.60
Significance	ns	**	-	ns	ns
C1	10.27	14.53	-	18.73	13.56
C2	10.16	15.28	-	19.00	13.94
C3	9.28	13.80	-	18.90	13.53
Significance	ns	ns	-	ns	ns
Interaction (WxC)	ns	ns	-	ns	ns
E.2. Fibrous roots					
W1	13.15	19.37	-	19.01	17.37
W2	13.56	17.36	-	20.19	15.78
Significance	ns	**	-	ns	**
C1	12.98	18.30b	-	19.91	18.26a
C2	13.83	19.77a	-	18.87	16.35b
C3	13.26	17.03c	-	20.03	15.11c
Significance	ns	**	-	ns	**
Interaction (WxC)	ns	**	-	ns	ns

¹ Values in the same vertical column not followed by the same letter differ at P = 0.05

fibrous root fractions (Figure 5.7). In the stubble and especially the fibrous roots, this was due to the greater depressive effect of hard cutting under mild water stress compared with that under severe water limitation. In the leaf, lax cutting decreased protein concentration under mild water stress but not under severe water limitation.

When converted to a protein yield basis, the differences between treatments were highly significant and followed the plant dry weight trends (Table 5.10) i.e. protein yields were depressed more by severe water stress and intense cutting. Re-watering increased protein yield considerably in all treatments, with the effect of previous severe water stress still being apparent, but with no carry-over effect from the previous cutting treatments.

The crude protein yields of the plant components were also depressed by water stress (Figure 5.8). During the dry period, stem plus root fractions represented a significant amount of crude protein for all treatments. However, by the end of the recovery periods, leaf and inflorescence showed a remarkable increase in crude protein particularly of those plants previously under mild water stress, while the previous cutting treatments failed to have any significant influence on crude protein yields during this recovery period.

There was a significant interaction in terms of total crude protein yield (leaf + stem + inflorescence + stubble) between water stress and cutting intensity during the drought period at day 42 but not during the recovery period (Figure 5.8). This was due to the greater effect of hard cutting under mild water stress compared with that under severe water stress and was associated mainly with the stem fraction (Figure 5.8).

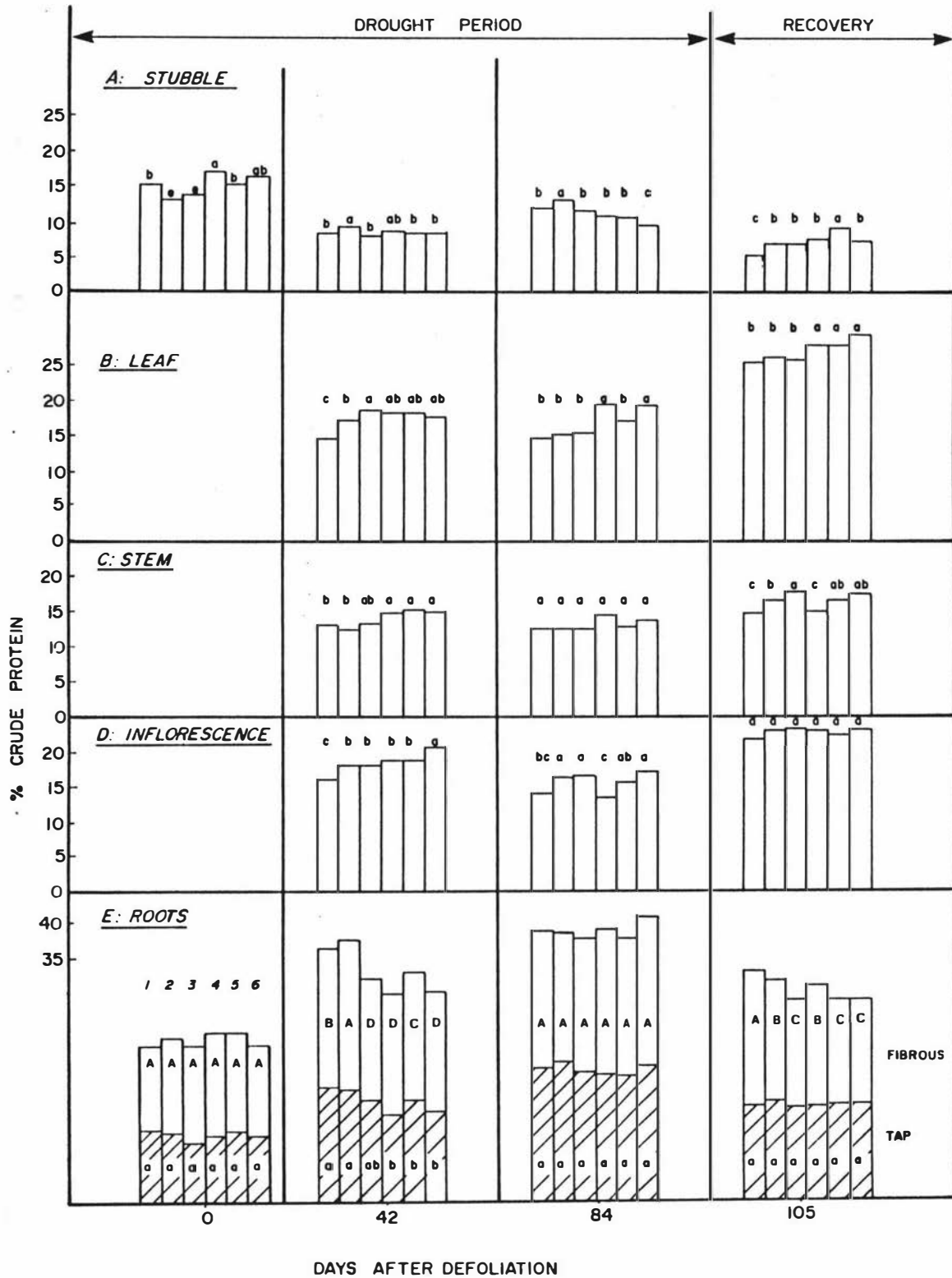


Figure 5.7: Effect of water stress and defoliation on crude protein concentration in the plant components (% of dry matter). **Note:** 1 = W1C1, 2 = W1C2, 3 = W1C3, 4 = W2C1, 5 = W2C2 and 6 = W2C3.

Table 5.10 Main effects of water stress and defoliation on total crude protein yield (leaves + stem + stubble + inflorescence) during drought and recovery period (mg/plant).

Treatments	During drought period		Recovery from drought
	42 days after cutting	84 days after cutting	21 days
<u>Water stress</u>			
W1	955	1684	8318
W2	572	759	6047
Significance	**	**	**
<u>Defoliation</u>			
C1	842a ¹	1270a	6656
C2	830a	1327a	7859
C3	618b	1068b	7032
Significance	**	**	ns
Interaction (W x C)	*	ns	ns

¹ Values in the same vertical column not followed by the same letter differ at $P = 0.05$

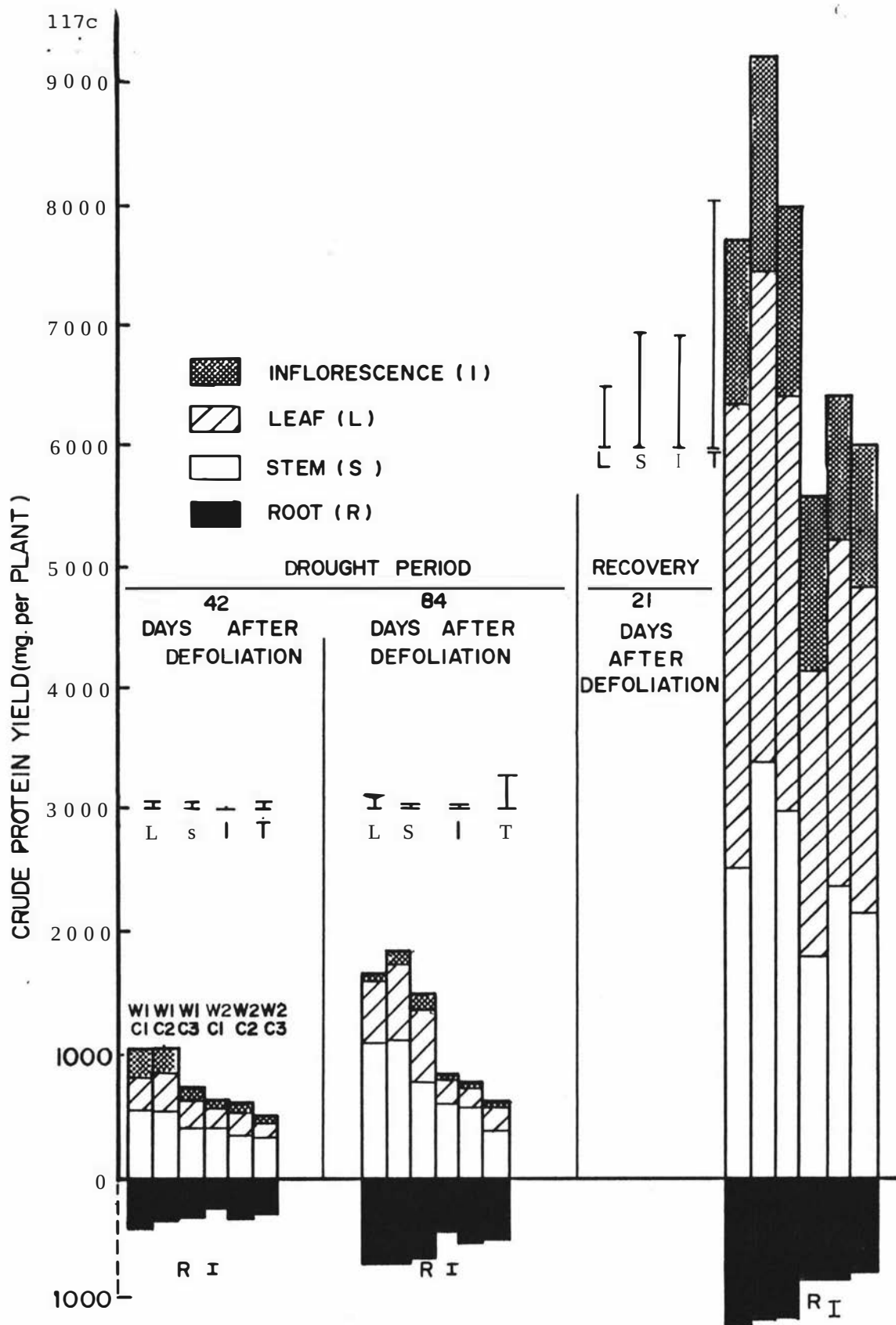


Figure 5.8: Effect of water stress and defoliation on crude protein yield in the plant components (g/plant)

C.2 Non-structural Carbohydrate Concentration and Yield

Both the sugar and starch, and hence the TNC concentrations of the plant components markedly increased during the drought period. However, there was no significant effect of level of water stress on the sugar and starch concentration of the stem and stubble (except immediately after cutting) throughout the entire drought period (Figure 5.9). This contrasted with the sugar and starch concentrations in the inflorescence where severe water stress significantly depressed sugar and starch concentration relative to mild water stress by the end of the drought period. In the leaf, this effect was recorded only in the starch fraction.

The main effects of cutting intensity on sugar and starch of the plant components were observed during the drought period but were only apparent in the stubble and inflorescence fractions (Figure 5.9). Severe and moderate defoliation (C2 and C3) depressed sugar concentrations in the stubble significantly compared with light defoliation (C1) and continued through to the end of the drought (day 84). At this stage (day 84) the starch fraction in the stubble was also depressed viz. the more severe the cutting intensity the lower the starch concentration. In the inflorescence, both starch and sugar, and hence TNC were also depressed by the severe and moderate cutting (C1 and C2).

During the recovery period, all regrowth components showed a considerable decrease in both sugar and starch. There was no effect of previous water stress on sugar and starch in all plant components, except the stubble where sugar concentration showed a greater increase in previously severely stressed plants compared with mildly stressed plants. Cutting intensity had no effect on sugar and starch in all plant components (Figure 5.9), except the stubble where starch concentration was depressed by the severe and moderate cutting under previously severe water stress (Appendix 6)

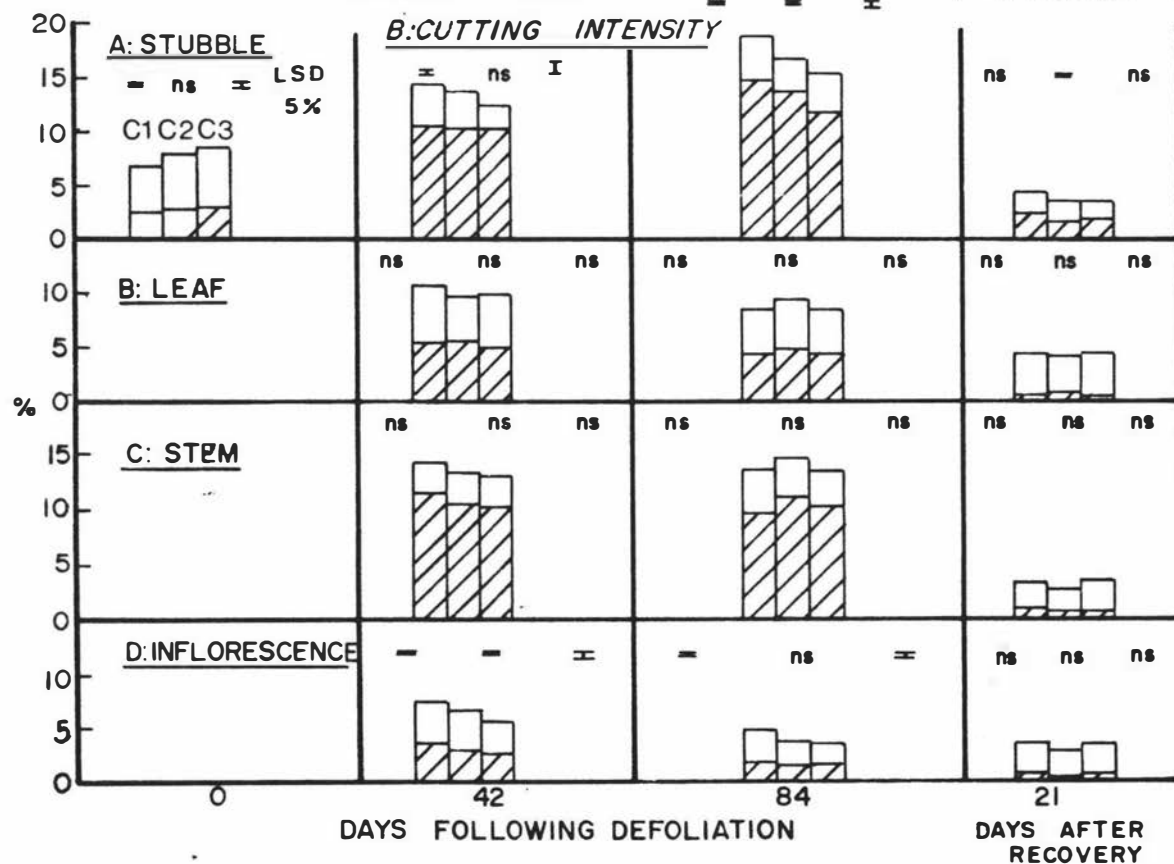
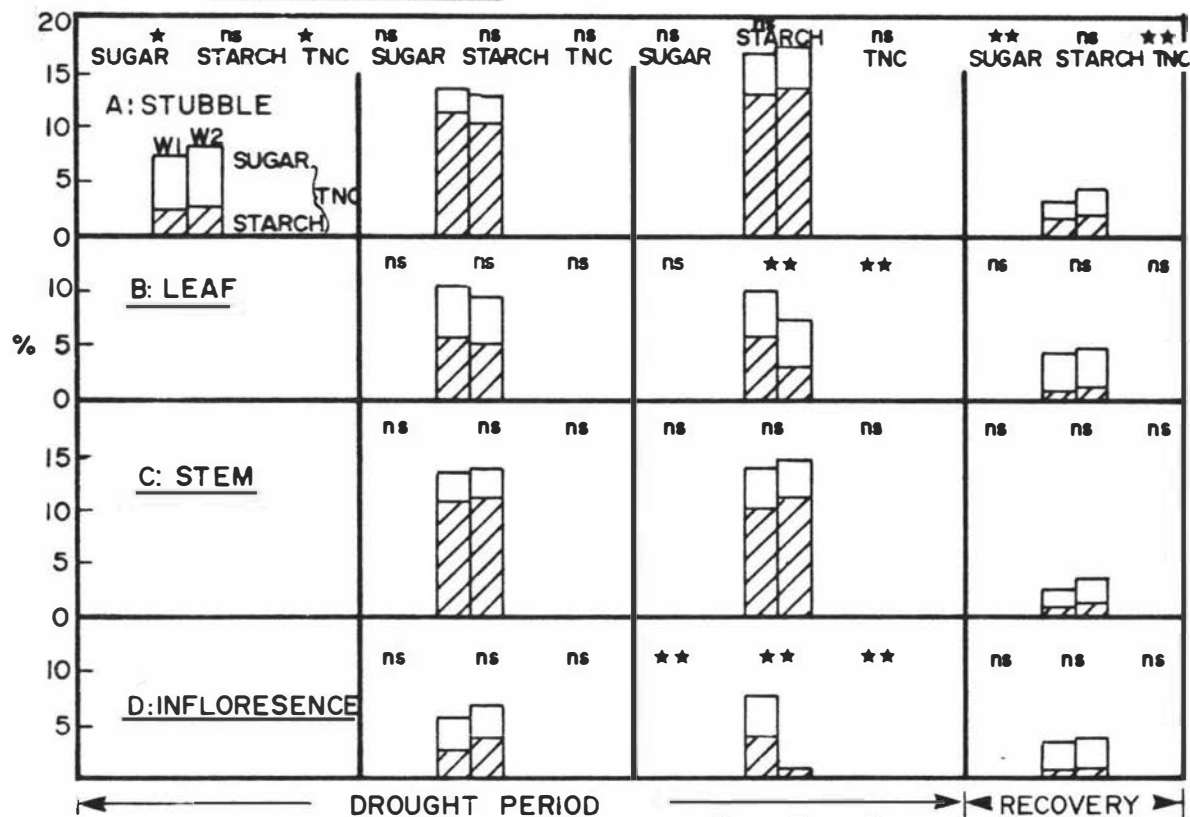
A: WATER STRESS

Figure 5.9: Main effect of water stress (A) and defoliation on carbohydrates concentrations in the plant components (% of dry matter)

In terms of the carbohydrate concentration in the root fraction, sugar was found in both the tap and fibrous roots but was not significantly affected by cutting or water stress throughout the entire drought period. Nevertheless the sugar concentration was much higher in the tap root than in the fibrous roots during the first half of the drought (Figure 5.10). Thereafter, both tap and fibrous roots had similar sugar levels. In contrast, starch was predominant in the tap root but negligible in the fibrous roots. Thus, the difference between treatments in TNC levels was due mainly to the starch fraction. There was no effect of cutting on TNC concentration in the fibrous roots. In contrast, severe cutting depressed TNC, and particularly starch, in the tap root significantly. The effect of water stress was also apparent throughout the entire drought period but only in the tap root where severe moisture limitation increased TNC concentration significantly over mild water stress. However, on re-watering, TNC levels decreased significantly, particularly the starch fraction, and were negligible in the tap and fibrous roots. Sugar was also negligible in the fibrous roots and at only low levels in the tap root.

When converted to TNC yields, the differences between treatments during the drought period were highly significant and followed the plant weight responses presented earlier, i.e. TNC yields were lower under severe than under mild water stress and were increasingly depressed with increasing levels of cutting (Figure 5.11). These responses were similar in both the sugar and starch fractions (Figure 5.12 and 5.13).

Also in terms of the plant components both the sugar and starch, and hence the total TNC yields of all plant components, were similarly depressed by water stress. In contrast, the main effect of cutting on TNC yields in the leaves and including both sugar and starch fraction were not affected. However, TNC yields in the stem and including both sugar and starch were increasingly depressed with increasing levels of cutting intensity. The main effect of cutting intensity on TNC, sugar and starch yields in the inflorescence was evident only during the first 42 days of

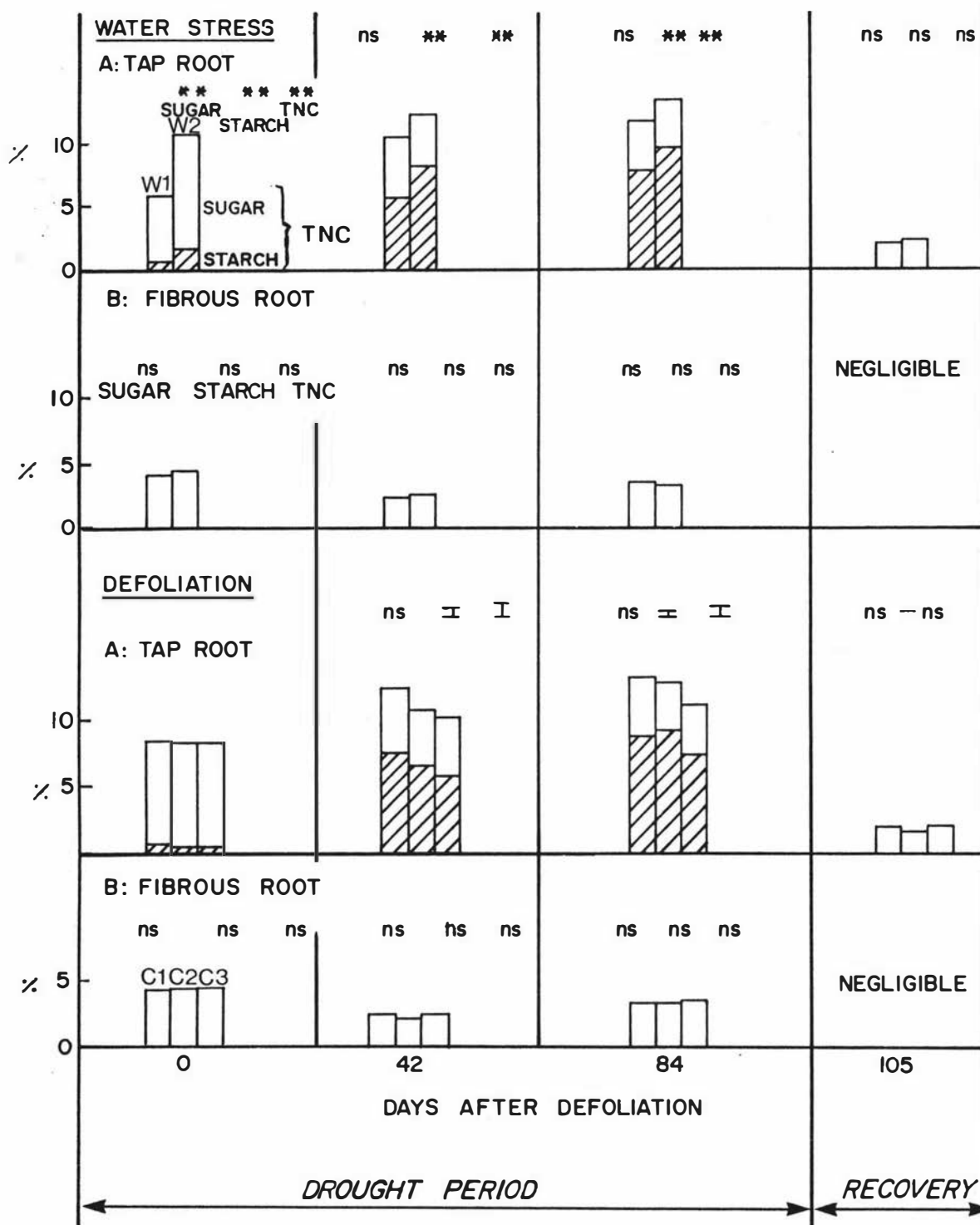


Figure 5.10: Main effect of water stress (A) and defoliation (B) non-structural carbohydrates concentration in the tap and fibrous roots. (% of dry matter)

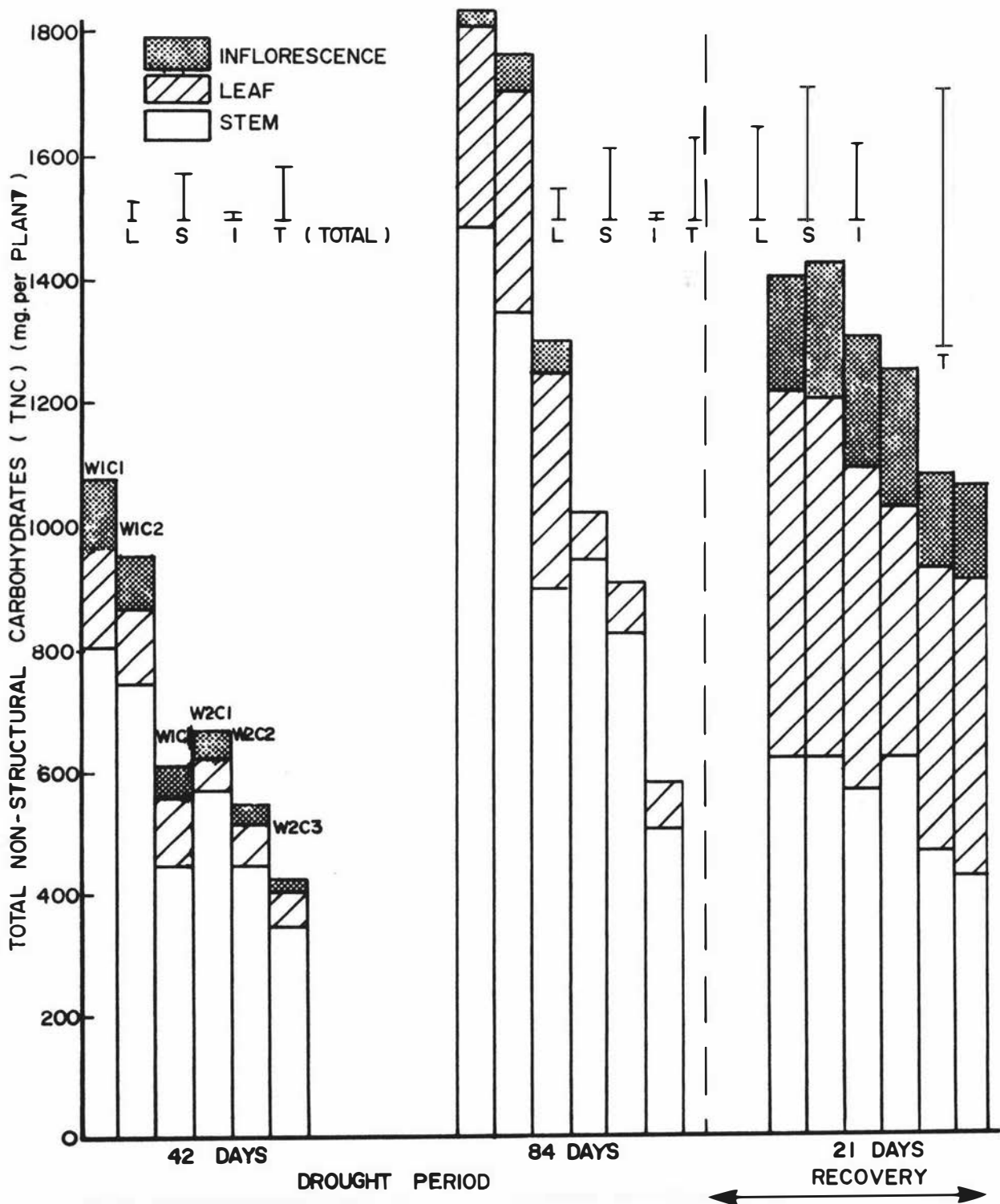


Figure 5.11: Effect of water stress and defoliation on total non-structural carbohydrates (TNC) yields (mg/plant)

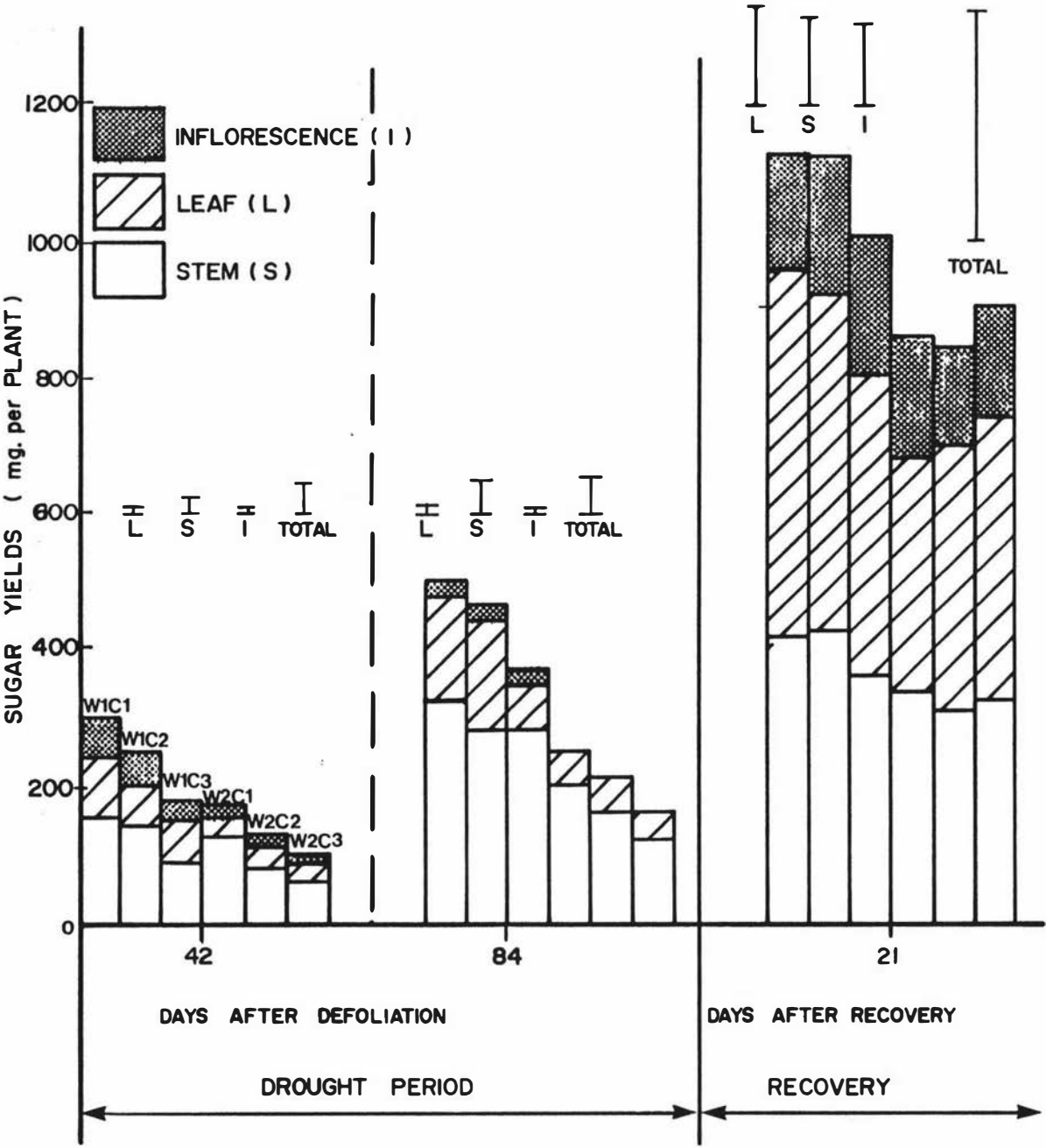


Figure 5.12: Effect of water stress and defoliation on sugar yields of the plant components (mg/plant)

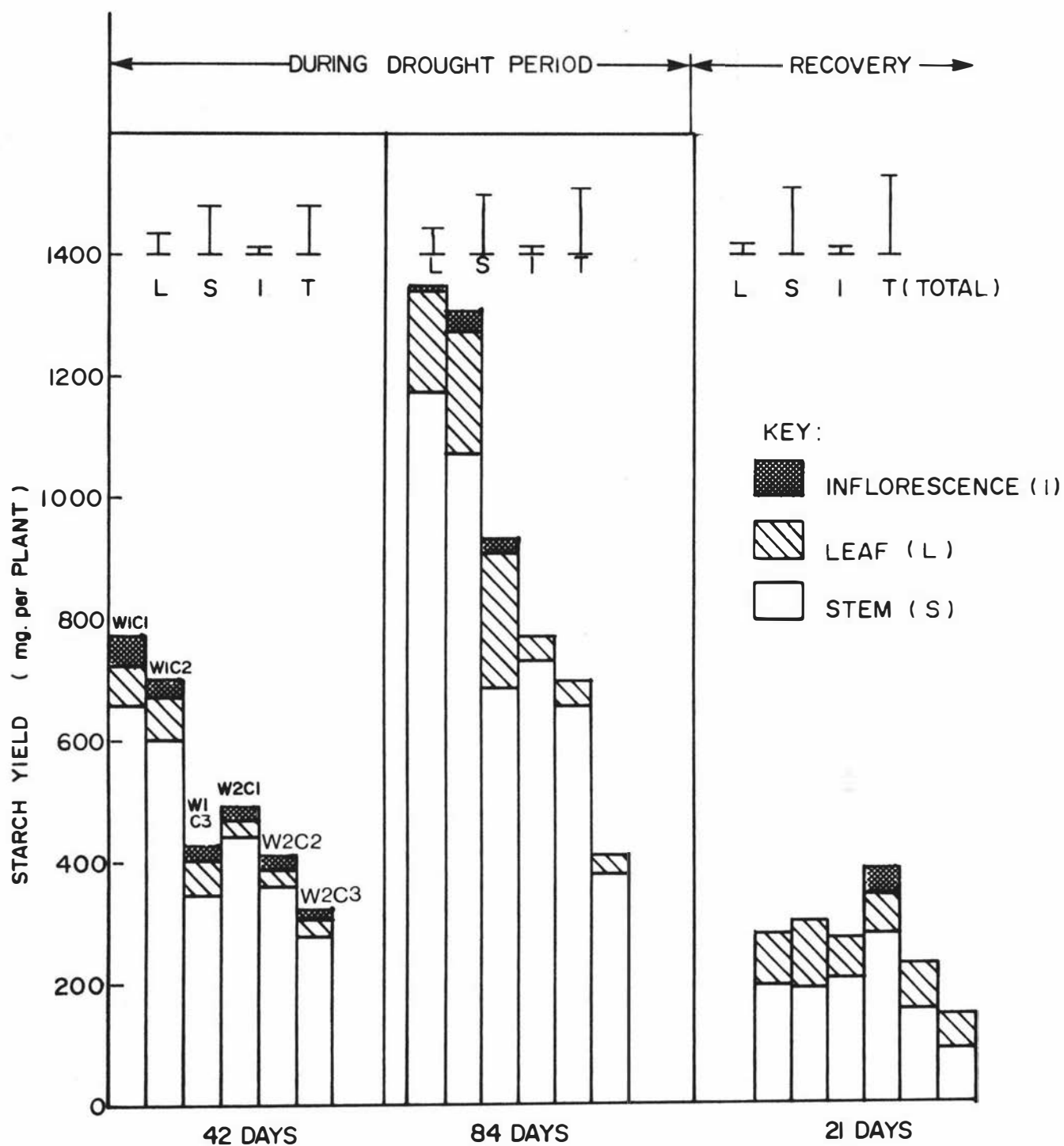


Figure 5.13: Effect of water stress and defoliation on starch yields of the plant components (mg/plant)

regrowth. This effect was dependent on the severity of cutting, i.e. the more severe the cutting the lower the TNC, sugar and starch yields in the inflorescence.

The greater effect of hard cutting on total starch and TNC yield of the stem and inflorescence components under mild water stress compared with that under severe water stress caused a significant interaction between water and cutting but only on day 42. This effect had disappeared by the end of the drought (day 84) by which time the total starch and TNC yield under both mild and severe water stress were similarly depressed by hard cutting relative to the moderate and lax cutting (Figure 5.11 and 5.13). This interaction was not apparent in terms of sugar yields.

During the recovery period, although the concentrations of TNC were low, there was a substantial increase in sugar yields in all treatments (Figure 5.12). This was greater in those plants previously under mild water stress (W1) than under severe water stress (W2), and particularly in the leaf and inflorescence components. By contrast, starch yields declined appreciably over this period and continued to show the depressing effect of cutting but only under previous severe water stress (Figure 5.13).

In terms of the yields of TNC, sugar and starch in the root fraction of the various treatments they were relatively low in the first half of the drought period but increased noticeably by the end of the period (Figure 5.14). By this time yields of both sugar and starch were generally higher under mild water stress than under severe water stress and in terms of starch significantly depressed under hard cutting.

During the recovery period, TNC levels dropped appreciably with the complete absence of starch, only half the previous quantity of sugar and with no difference between previous treatments (Figure 5.14).



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D. RELATIONSHIP BETWEEN TOTAL PLANT DRY WEIGHT AND THE MAIN
GROWTH PARAMETERS (BRANCH NUMBER, LEAF NUMBER AND
LEAF AREA

Highly significant and positive correlations were found between plant dry weight and the main growth parameters (branch number, leaf number and leaf area) for all harvests (Table 5.11) suggesting that these parameters are important for determining yield, as found in the non-water stress experiments (Experiments 2, 3 and 4).

IV DISCUSSION

Soil moisture is the most frequent and major limitation to plant growth (Whiteman, 1980) and can reduce dry matter accumulation and the expansion of plant parts significantly (Waikakul, 1983). However, the severity of this effect is dependent upon the degree of this limitation as shown in the present experiment. Severe soil moisture limitation resulted in a considerable reduction in plant size and plant dry weight compared with mild water stress (Table 5.3). This was also reflected in the lower absolute and relative growth rate recorded (Table 5.4). As a result, the accumulation of total plant dry weight showed little increase under severe water stress throughout the drought period. The effects of water stress on plant dry weight were expressed mainly through the stem fraction and to a lesser extent the leaf and inflorescence components (Figure 5.3).

The same response was reflected in the number of branches (Figure 5.5), number of leaves and leaf area (Figure 5.6) and the highly significant and positive correlations between these parameters and plant dry weight (Table 5.11). Thus, it is not surprising that the poorer response of these parameters recorded under severe water stress resulted in lower dry matter yield compared with those plants under mild moisture limitation.

Table 5.11 Linear correlation coefficients between plant dry weight (DM) and main growth parameters (branch number (B), leaf number (LNO) and leaf area (LA))

Weeks from defoliation	Parameters of growth		
	B	LNO	LA
6 (during drought period)	0.913**	0.754**	0.863**
9 (during drought period)	0.909**	0.846**	0.843**
12 (during drought period)	0.863**	0.939**	0.888**
15 (during recovery period)	0.945**	0.885**	0.803**

All growth parameters mentioned above (plant dry weight, branch number, leaf number and leaf area) were increased substantially during the recovery period in both the previously severe and mild water stress treatments but the effect of the previous intensity of water limitation was still evident i.e. plants previously under severe moisture limitation produced significantly lower yields than those previously under mild water stress (Table 5.3). One of the more interesting responses on re-watering was the remarkable recovery in all growth parameters, especially in leaf number and leaf area, of those plants previously under severe water stress (Figure 5.6). Slatyer (1973) stated that developing tissues appear to enter a rejuvenating phase, and when the water stress is eliminated, the relative growth rates of such plants may be more rapid than in the control (non-stressed) plants. Fisher and Campbell (1977) showed that only at early vegetative growth stages did the water stress reduce the growth rate of Townsville stylo but when the stress was eliminated, a period of rapid growth ensued which compensated for the loss. Thus, the rapid increase in the growth of all plant parameters can possibly be attributed to the younger physiological state of the previously severely stressed plants compared with those under previous mild moisture limitation. Ludlow and Ng (1977) also found rapid extension growth on re-watering after drought in Panicum maximum and they concluded that the stimulated rates resulted from the rapid expansion of cells accumulated during the stress period, as cell division is less sensitive to water stress than cell expansion.

It is also of interest to note that in the one parameter that was increased during the recovery period (at 7 days) viz. number of branches, there was an immediate rapid increase in the previous mild water stress treatment but a delay in the previous severe stress treatment (Figure 5.5). However, once over this initial delay, by the end of the first week, branch number on the previously severely water stressed plants increased at a similar rate to that of the previously mildly water stressed plants. Presumably the early advantage shown by the previously mildly water stressed

plants was due to their greater reserve of carbohydrates (Figure 5.11), greater leaf area and leaf number (Figure 5.6) and possibly even greater root weight for better nutrient uptake (Figure 5.3).

During the drought period crude protein concentrations in the leaf, stem and inflorescence were higher under severe than under mild water stress (Table 5.9), as also reported by Carvalho (1978). However, this increase in crude protein concentration was not sufficient to compensate for the reduction in the amount of protein when converted to a yield basis. Mildly water stressed plants still produced a significantly higher crude protein yield than did severely water stressed plants (Table 5.10) - reflecting the greater dry weight of the mildly stressed plants, as discussed earlier. The major contributor to this response was the crude protein yield in the stem and to a lesser extent in the leaf and inflorescence components (Figure 5.8). Similar results have been recorded by Bennett et al (1964) for sudan grass, millet and sorghum.

On re-watering, the crude protein concentrations markedly increased in the stem and especially in the leaf and inflorescence components due possibly to the translocation of crude protein from the stubble and roots under both previous mild and severe water stress. The differences in concentrations between treatments were generally small but differed markedly in the crude protein yields and followed the plant dry weight response - lower under previous severe than under mild water stress.

In turning now to the carbohydrate levels, there are several reports which state that water stress increases the carbohydrate concentration in forage e.g. of cocksfoot and tall fescue by Brown and Blaser (1970), of rye grass by Norris and Thomas (1982a, 1982b), of green panic, buffel and spear grass by Ford and Wilson (1981) but, in contrast, this trend was not observed in Siratro by Ford and Wilson (1981). The result of the present work indicated that a mild intensity of water stress also increased carbohydrate

concentration, particularly that of starch, but only in the leaf and inflorescence (Figure 5.9). However, severe moisture limitation depressed the carbohydrate level in the leaf and inflorescence significantly but continued to increase it in the tap root. Of the total carbohydrate fraction, starch maintained a much higher concentration than sugar in all treatments throughout the drought period, particularly in the stem and stubble (Figure 5.9).

In terms of the amounts of carbohydrate reserves, there were large differences due to water stress with the severely water stressed plants accumulating only half the reserves of the mildly water stressed plants during the drought period. This reduction was particularly noticeable in the leaf and inflorescence components, relative to the stem (Figure 5.11) and roots (Figure 5.14). Under both mild and severe water stress the stem was the major accumulator of these reserves, particularly the starch fraction (Figure 5.12 and 5.13).

During the recovery period, although carbohydrate yields were high due to high dry matter production, concentrations were low, particularly of starch, and probably reflected their use in the production of new leaf and new branches (Alberda, 1957; May, 1960; Davidson and Milthorpe, 1966; Norris and Thomas, 1982a, 1982b). It is interesting to note the differences between sugar and starch in terms of both concentrations and amounts immediately prior to the re-watering period and after 3 weeks of adequate watering. Starch concentration and yield, particularly in the stem and stubble, showed a substantial drop in the "recovery" period, presumably being used for early regrowth, while the sugar fraction showed much less change. However, owing to the lack of intensive measurements during the re-watering period, it is not possible to detect the dynamics of these reserves, particularly of the sugar fraction.

Turning now to the effects of cutting, the results clearly showed that total plant dry weight during the water stress period was reduced under hard defoliation, especially when plants were subjected to mild moisture limitation

(Figure 5.2). This effect was evident throughout the drought period. The major contributors in this regard were the stem and to a lesser extent the leaf fractions.

Branch production was also depressed by cutting, but again only under mild moisture limitation, as indicated by the significant interaction between water stress and cutting. When under severe moisture stress - which in itself depressed plant weight and branch number significantly - plants showed no further depression from light, moderate or hard cutting. These results tend to conflict with the statement of Jantii and Heinonen (1957) who recommended light or moderate defoliation when plants are under severe moisture stress. Perhaps the difference between their work and the current study is due to the relative levels of water stress imposed i.e. the current findings could support their recommendation if their co-called severe water stress equated with our mild water stress.

Cutting had no significant effect on leaf number throughout the drought period, except immediately after cutting, but did depress leaf area. However, this depression only occurred during the first 6 weeks when cutting was hard and under mild water stress (Figure 5.6). Thereafter, this treatment showed a substantial increase resulting in a significantly higher leaf area than light and moderate cutting by the end of the drought period (day 84). In contrast, there was no effect due to cutting under severe moisture limitation, except immediately after cutting, throughout the drought period.

On re-watering, the effects of previous cutting on all growth parameters tended to be relatively minor compared with the effects of previous water stress and differences were often non-significant. The exception was the previous hard defoliation treatment under mild water stress which showed a small but significant increase in leaf area and leaf number (Figure 5.6). However, one of the more interesting responses on re-watering was the remarkable recovery in leaf area and especially leaf number in all the cutting treatments particu-

larly under previous severe water stress - as also mentioned earlier following water stress. Apparently even hard defoliation followed by an extended period of water stress did not prevent the plant from responding dramatically to the application of adequate water, particularly in terms of leaf area and leaf number, over the subsequent three weeks.

In terms of the crude protein concentration in the various plant components, the effects of cutting were generally small although sometimes significant. Hard cutting tended to increase crude protein concentration under both mild and severe water stress particularly in the leaf and inflorescence (Figure 5.7). However, this increase in crude protein concentrations was not sufficient to compensate for the reduction in the amount of protein when converted to a yield basis. The greater the severity of cutting especially under mild water stress, the lower the total crude protein yields.

Crude protein concentrations and amounts in the leaf, stem and inflorescence were all markedly increased during the recovery period, particularly in the leaf and inflorescence fractions.

In terms of carbohydrate levels in the plant components, the effects of cutting during the drought period were only evident in the stubble, inflorescence and tap root fractions - the levels declining with increasing intensity of defoliation, particularly of the starch fraction (Figure 5.9). However, the concentration of TNC (sugar plus starch) was much higher than that found in Experiments 3 and 4 which were conducted with adequate water supply. This suggests that under conditions where soil moisture is limiting and growth rate reduced, carbohydrates may be able to accumulate to a greater extent than under conditions of rapid continuous growth, as also reported by Brown and Blaser (1970), particularly in the stem, stubble and tap root.

Although total TNC concentration in the leaf was not as high as in the apparent storage components of stubble, stem

and tap root, it did, nevertheless, contain a higher proportion of sugar relative to starch - whereas starch was by far the major fraction in the former components. It was this starch fraction in the stubble, stem and especially in the tap root that almost totally disappeared during the rapid recovery phase following re-watering - presumably used in regrowth - as discussed earlier. This supports the findings of Fisher and Ludlow (1984) who showed that the sugar concentrations in the leaves of Verano stylo tend to increase under water stress - and presumably enabled, in this experiment, the appreciable build-up of starch in the stubble, stem and tap root during the water stress period which was subsequently used during the recovery phase.

Returning to the effect of cutting on carbohydrates, it was apparent that during the drought period hard cutting significantly depressed the concentration and accumulation of sugar and starch mainly in the stubble and in terms of yield, especially under mild water stress. In the roots only the starch fraction was so affected. Similarly during the recovery period, previous hard cutting again depressed both carbohydrate concentration and yield, particularly in those plants under previous severe water stress - but only in terms of the starch fraction.

CHAPTER 6

EXPERIMENT 6: EFFECT OF GRAZING MANAGEMENT ON STYLOSANTHES HAMATA PRODUCTION AND SURVIVAL

I. INTRODUCTION

Although the number of dairy cattle in Thailand has substantially increased over the past ten years, the main feeding systems for these cattle have shown little change. Large amounts of money are still being spent on concentrate feeding during the dry season and even during the rainy season for milk production. (Thai Dairy Promotion and Organization, 1984). The recognised alternative of using cultivated grasses with selected legumes, such as Siratro (Macroptilium atropurpureum), Centrosema (Centrosema pubescens) and Stylo (Stylosanthes guianensis) as a means of reducing this dependency on concentrates still lacks acceptance and adoption due to inadequate information on good grazing or cutting management practices.

The successful establishment and persistence of Verano stylo (Stylosanthes hamata cv Verano) under grazing has been reported from the northeastern part of Thailand (Wilaipon and Humphreys, 1981; Wilaipon, 1985). As such the potential for using this legume to improve feeding quality of improved pastures for dairy production is of real practical significance.

Under intensive studies in the Controlled Climate Rooms at the Plant Physiology Division, DSIR, Palmerston North, New Zealand, it has been clearly shown that Verano stylo has a real potential to produce acceptable yield and quality under an appropriate defoliation system. Early cutting, for example, when 50% of the plant population reaches the flowering stage, results in rapid recovery although subsequent yield is depressed, while late cutting results in slow recovery of growth and may lead to a reduction in yield. The extent of this reduction depends on the severity of cutting and in particular the number and size of the residual

primary branches left after cutting. In the subsequent study comparing frequency and intensity of cutting, it was also shown that grazing management should aim at allowing the plants to retain at least 7 nodes on the main stem (approximately 7 - 8 primary branches) and at least 4 nodes along the primary branches after defoliation to achieve high yield and survival. However, these experiments were conducted under artificial growth room and cutting conditions and therefore it was considered essential to test this hypothesis under realistic field conditions. Hence a field experiment was conducted in Thailand under grazing conditions, to study the effect of selected grazing management practices on the productivity and persistence of a Verano stylo sward.

II MATERIAL AND METHODS

A. ENVIRONMENTAL CONDITIONS AND PLANTING PROCEDURE

The experiment was conducted at the Thai Dairy Promotion and Organisation of Thailand, located at Muaklek, 180 Km Northeast of Bangkok. In the area selected, Guinea grass (Panicum maximum) and other native grasses were initially sprayed with ^{Glyphosate} (Roundup) and left for 7 days to achieve a good kill, and then ploughed, cultivated and subsequently sown to Stylosanthes hamata cv Verano (Verano stylo) at 20 kg/ha. A basal fertilizer of superphosphate (250 kg/ha) and **muriate** of potash (125 kg/ha) was applied immediately before sowing; no nitrogen fertilizer was added. The soil type was described by the Department of Land Development (1979) as a fine textured silty clay loam with poor structure in both the A and B horizons and with a pH of 6.5.

Climatic conditions at the experimental site are monsoonal with the rainy season extending from May to October with peak precipitation in September and averaging 1,012 mm annually. From November to April the weather is relatively dry with little rain occurring in this period. Mean maximum and minimum temperatures are 34.18 and 18.7°C respectively, with a relative humidity averaging 77%. Details of the



Plate 6.1: A general view of the experimental site, showing the well prepared seed-bed before sowing.



Plate 6.2: The area was irrigated after sowing to ensure good germination.

climatic conditions for the past ten years are given in Figure 6.1. However, during the experimental period, soil moisture at sowing, on 29th April 1983, was low. As there was little rain following sowing, irrigation was applied to ensure good seed germination and establishment. Only light showers continued throughout May and much of June and it was not until late June that good heavy rains occurred, with some minor flooding in August. Good rainfall continued through September, October and into early November when pasture growth began to be restricted by lower temperatures. There was also some slight evidence of an Anthracnose infection which might also have affected growth towards the end of the growing season.

Plant establishment was excellent and the relatively few weeds appearing were removed by hand.

B. TREATMENTS

The pasture was first grazed at an early stage of growth viz. when 50% of plants began flowering. Thereafter, two grazing management treatments were imposed viz. at first flower (approximately 4 weekly intervals) and at full flowering (approximately 8 weekly intervals) (Figure 6.2). The pasture was grazed down to the 6th - 7th node (from the ground) on the main stem for both treatments which was equivalent to cutting above node 7 of the main stem (E-7-4) under the previous controlled room experiment. Dry cows were used for grazing which extended over a 48 - 72 hour period. The number of animals used was dependent on the amount of herbage present. Mowing with an Auto scythe was carried out after each grazing to achieve a uniform residual plant height (6th - 7th node), approximately 12 cm above ground level.

The design of this experiment was a randomised complete block with 4 replications. This totalled 8 paddocks with each paddock being 20 x 20 m and fenced separately.

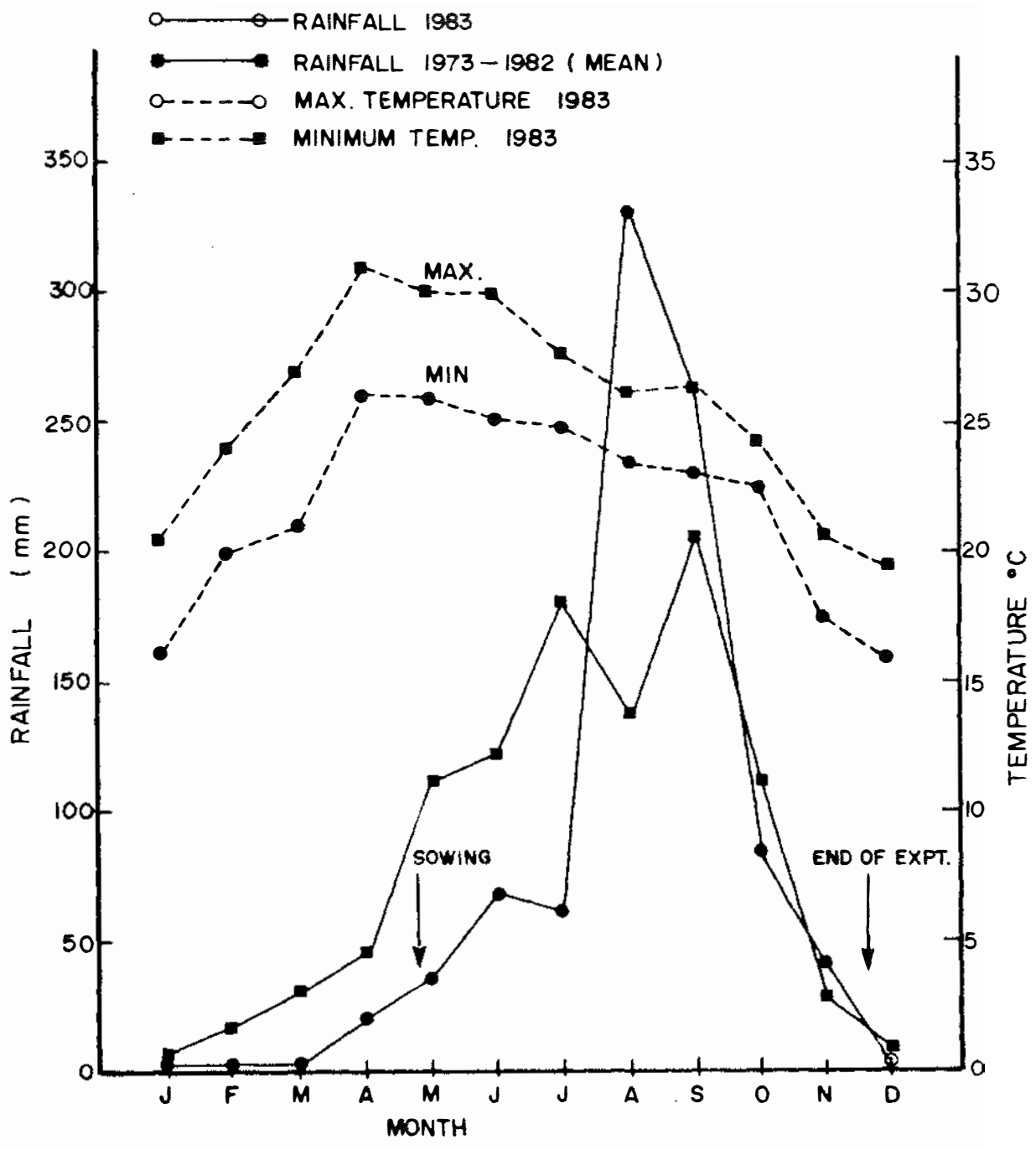


Figure 6.1: Monthly rainfall and maximum and minimum temperatures at Muaklek, Thailand

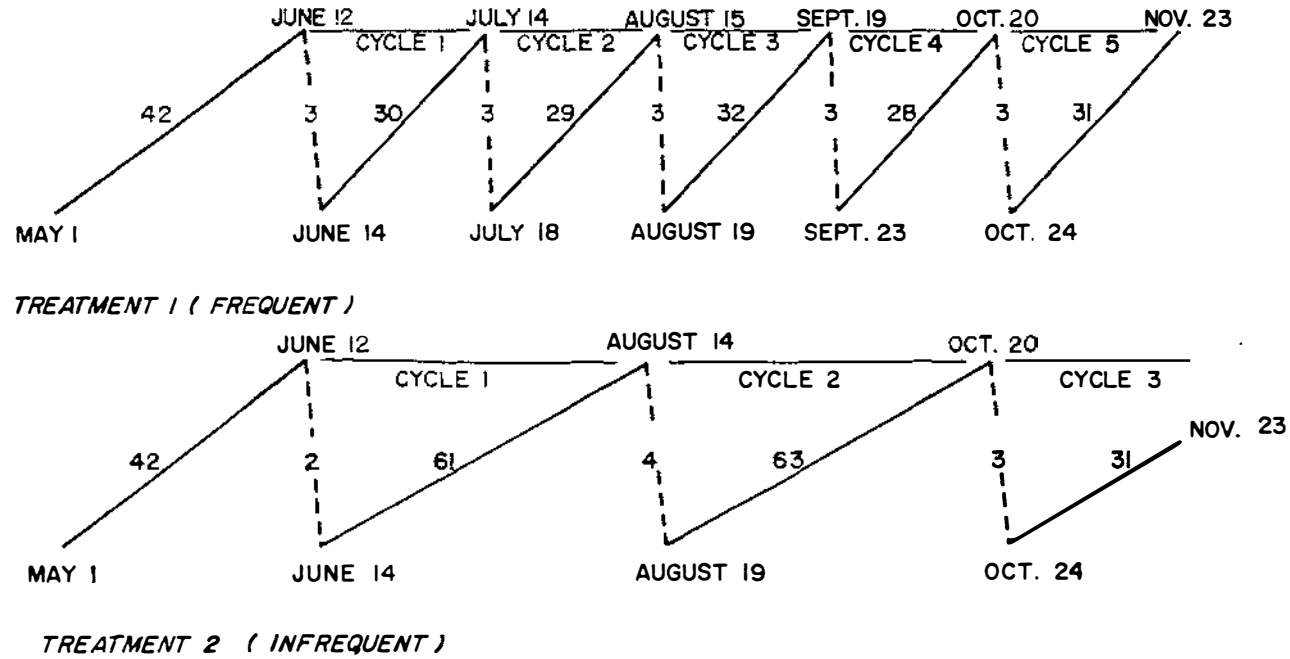


Figure 6.2: Timing of grazing and regrowth period throughout the experiment

C. MEASUREMENTS

Seedling establishment and survival of the sown plants (Verano stylo) was recorded on 12th June, 1st July, 14th July, 3rd August, 14th August, 19th September, 20th October, 9th November and 23rd November 1983, approximately 0, 2, 4, 6, 8, 12, 16, 18 and 20 weeks after first grazing, by taking twelve quadrats (50 x 50 cm) per plot on each occasion.

Dry matter yields were measured immediately before and after each grazing and on some occasions during the regrowth period (approximately 2, 4, 6, 8, 12, 16, 18 and 20 weeks after first grazing). Ten quadrats (50 x 50 cm) were taken at random in each paddock and cut to ground level, care being taken to avoid sampling the same quadrat area twice. The cut samples were then bulked, weighed and subsampled to determine dry matter percentage. Drying was for 72 hours at 90°C. A further subsample, comprising at least 10 plants, was also taken for detailed measurements of plant components (stem, leaf and inflorescence), leaf area and branch number.

Additional measurements of branch numbers were made between dry matter yield determinations, to give weekly counts, from normally 20 random plants per plot.

III RESULTS

A. SEEDLING ESTABLISHMENT

Seed germination and seedling establishment, although slow initially, was excellent and by 12th June a count of 178 plants/m² was recorded. First flowers appeared 32 days after sowing and the first grazing commenced on 12th June 1983 (42 days after sowing). As shown in Figure 6.3, plant density for both treatments declined with time but to a much greater extent under infrequent grazing. Only 12% of the plants survived under infrequent grazing compared with 39% under frequent grazing (Table 6.1). These differences were also reflected in the dry matter yields (kg/ha) presented in Figure 6.4.

Phenological observation also showed that plants in the infrequently grazed plots grew taller in height, were less branched and had a leaf canopy concentrated on the upper 40 cm of the sward. This was apparent by the end of the first eight weeks following the first grazing. Many plants died after the second grazing and the survivors regrew only slowly. On the other hand, fewer plants died in the frequently grazed plot and those remaining regrew vigorously. Plants in the frequently grazed plot also produced many fine branches near ground level, forming a dense mat of relatively prostrate stems and leaves.

B. PLANT REGROWTH

B.1 Plant Dry Weight and Production

Total net regrowth yields for both treatments over the full experimental periods are presented in Figure 6.4 on an area basis (Kg/ha). There was a marked difference between treatments with the frequently grazed treatment producing a significantly higher dry matter yield ($P = 0.01$) than the infrequently grazed treatment. In terms of dry matter production during the experimental period, the superiority of the frequently grazed treatment was clearly evident (Figure

Table 6.1 Plant density on the day before first grazing and at the end of the experiment (plants/m²)

Treatments	At first grazing (12/6/83)	At the end of the experiment (23/11/83)	% survival
Frequent	159	62	38.99
Infrequent	174	20	11.49
Significance	ns	**	

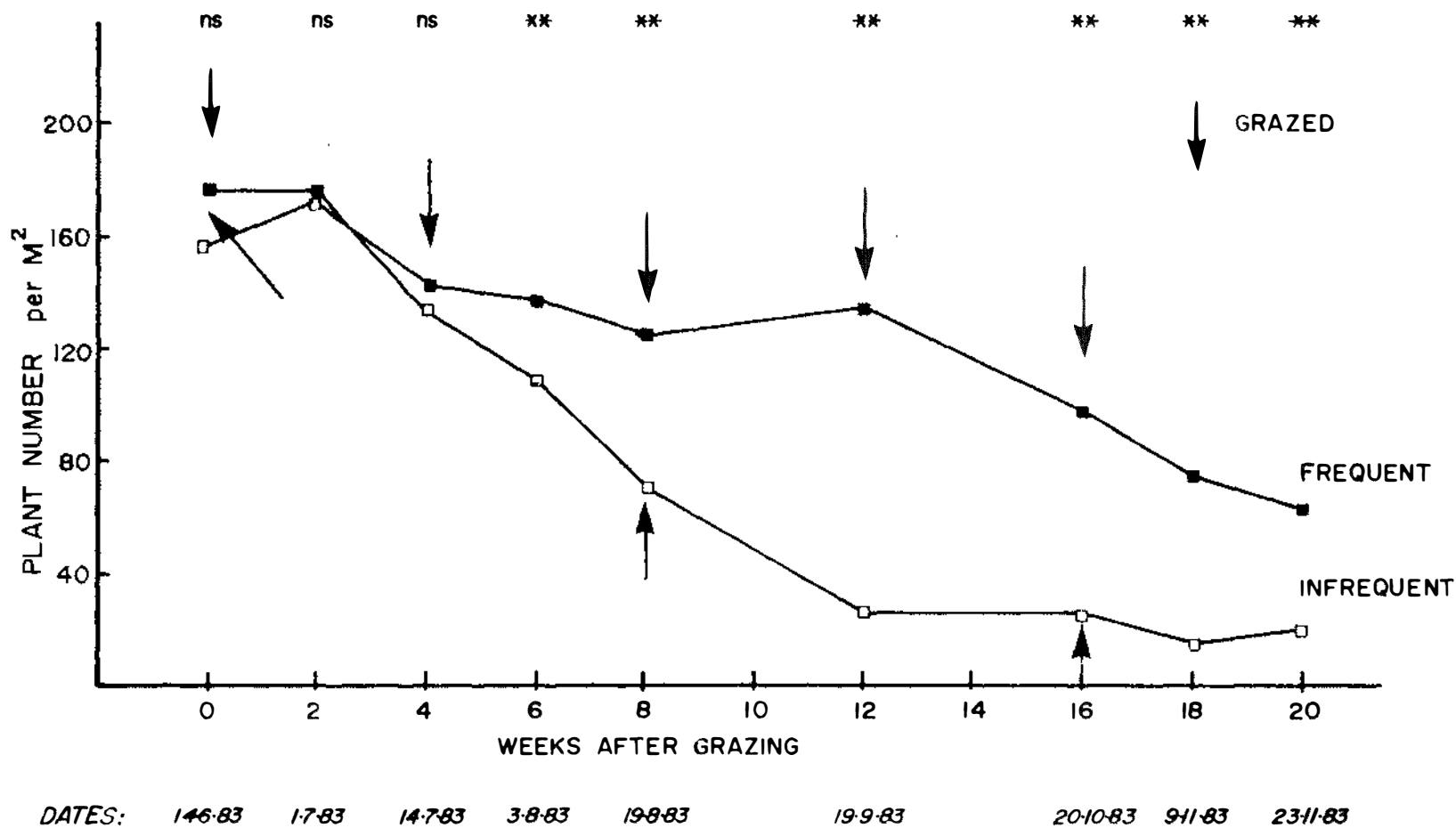


Figure 6.3: Changes in legume plant density with time (number/m²)

6.5). The infrequently grazed treatment showed a marked peak in production to the first eight-week defoliation in mid-August but thereafter showed poor recovery and regrowth. In contrast the frequently grazed treatment maintained relatively high production up to the 4th defoliation and then declined somewhat over the remaining two regrowth periods. This decline may well have been a reflection of the drop in plant numbers over this period, as shown in Figure 6.3, together with the onset of the dry and cooler season.

. The regrowth pattern on a per plant basis (g/plant) under the two grazing managements is shown in Figure 6.6. A changing pattern of plant regrowth in the infrequently grazed treatment was again most evident, with a marked peak in plant dry weight on the 15th of August, after which the yield declined sharply. In contrast, plant dry weight achieved in the frequently grazed treatment was relatively constant over the experimental period.

The components of plant dry weight are shown in Figure 6.4 and 6.7 on a total unit area basis, and on a per plant basis, respectively. Stem was the major component in both treatments but with a considerably higher proportion and amount of leaf per plant being produced under frequent grazing than under infrequent grazing.

B.2 Branch Number

As shown in Figure 6.8, rapid branch development (no /plant) was recorded in the frequent grazing treatment after every grazing. In contrast, branch development under infrequent grazing was markedly depressed following the first eight week defoliation in mid August. However, branch production was encouraged during the last four weeks of the experiment in both treatments. This was possibly due to an increase in reproductive branches as the plant responded to lower temperature and shorter day-length.

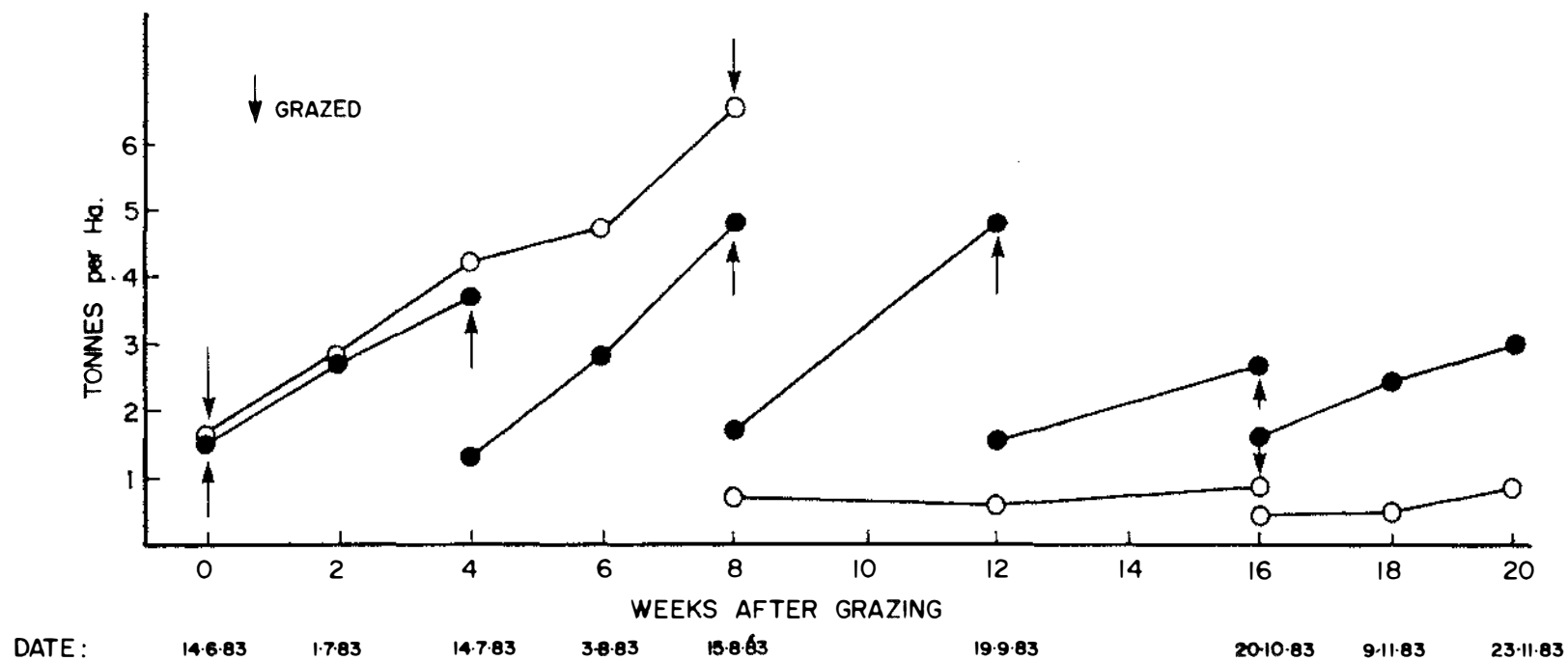


Figure 6.5: Effect of grazing management on dry matter production (ton/ha)

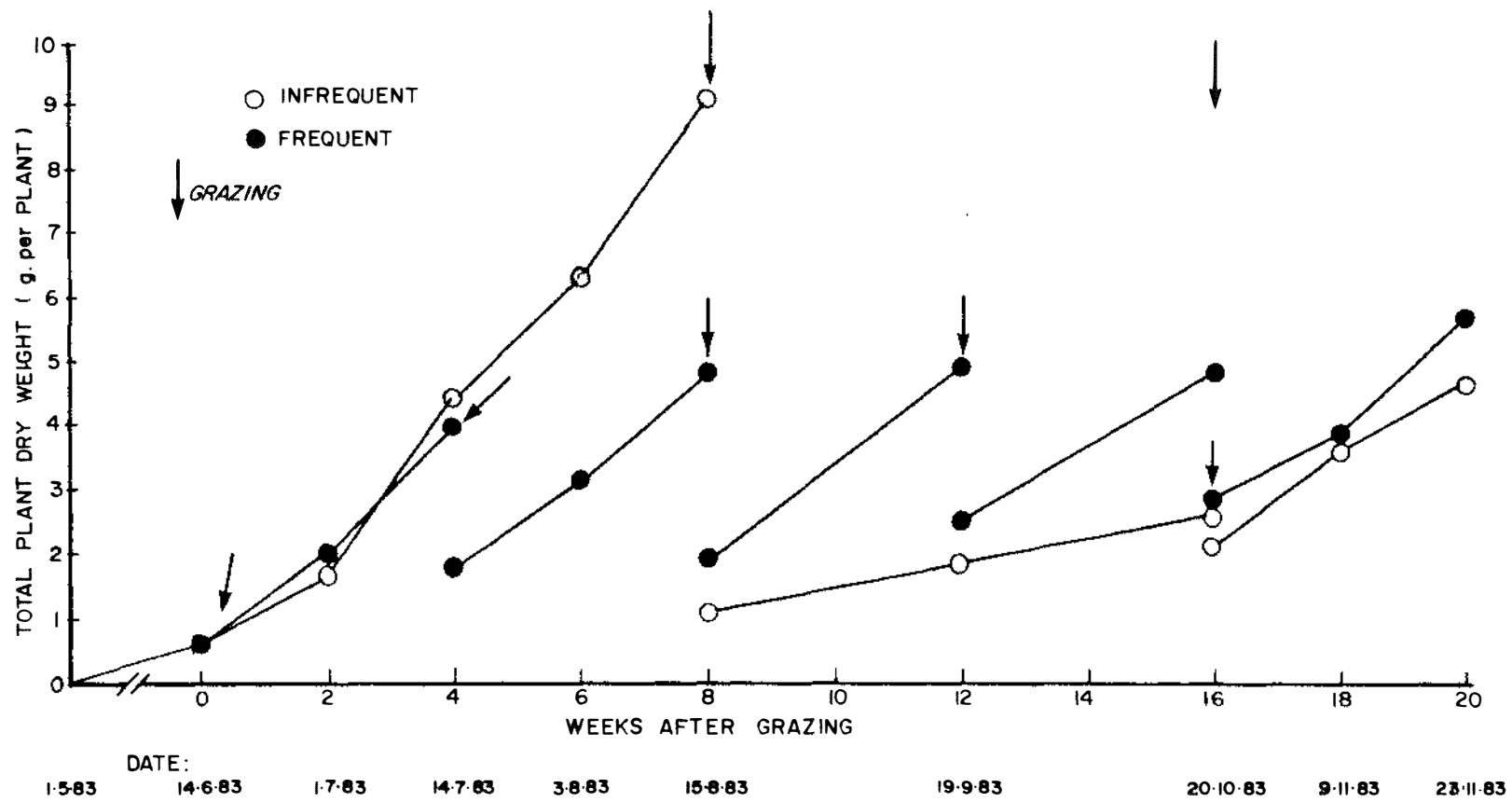


Figure 6.6: Total plant dry weight (g/plant)

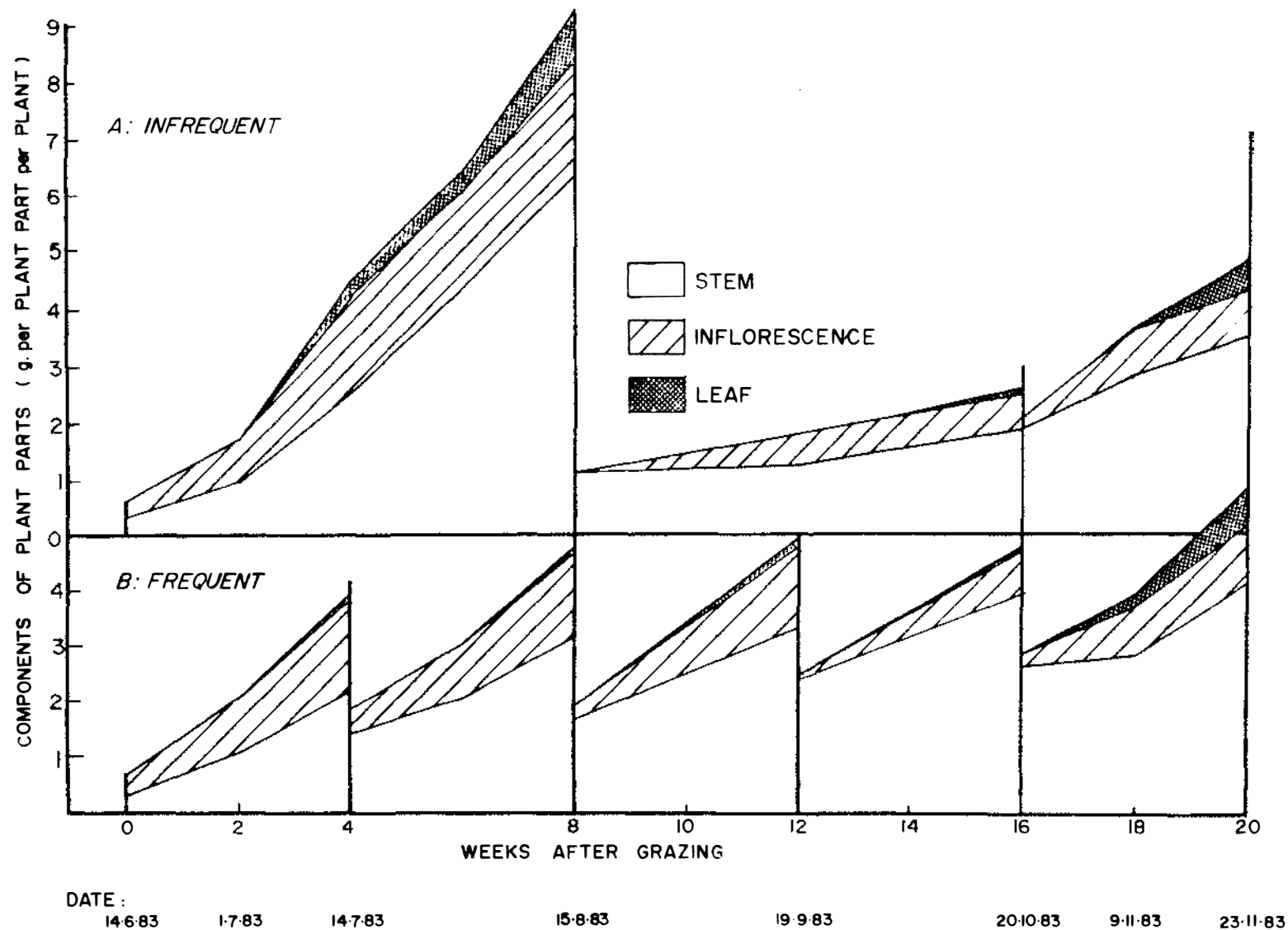


Figure 6.7: Effect of grazing management on the plant components dry weight (g/plant)

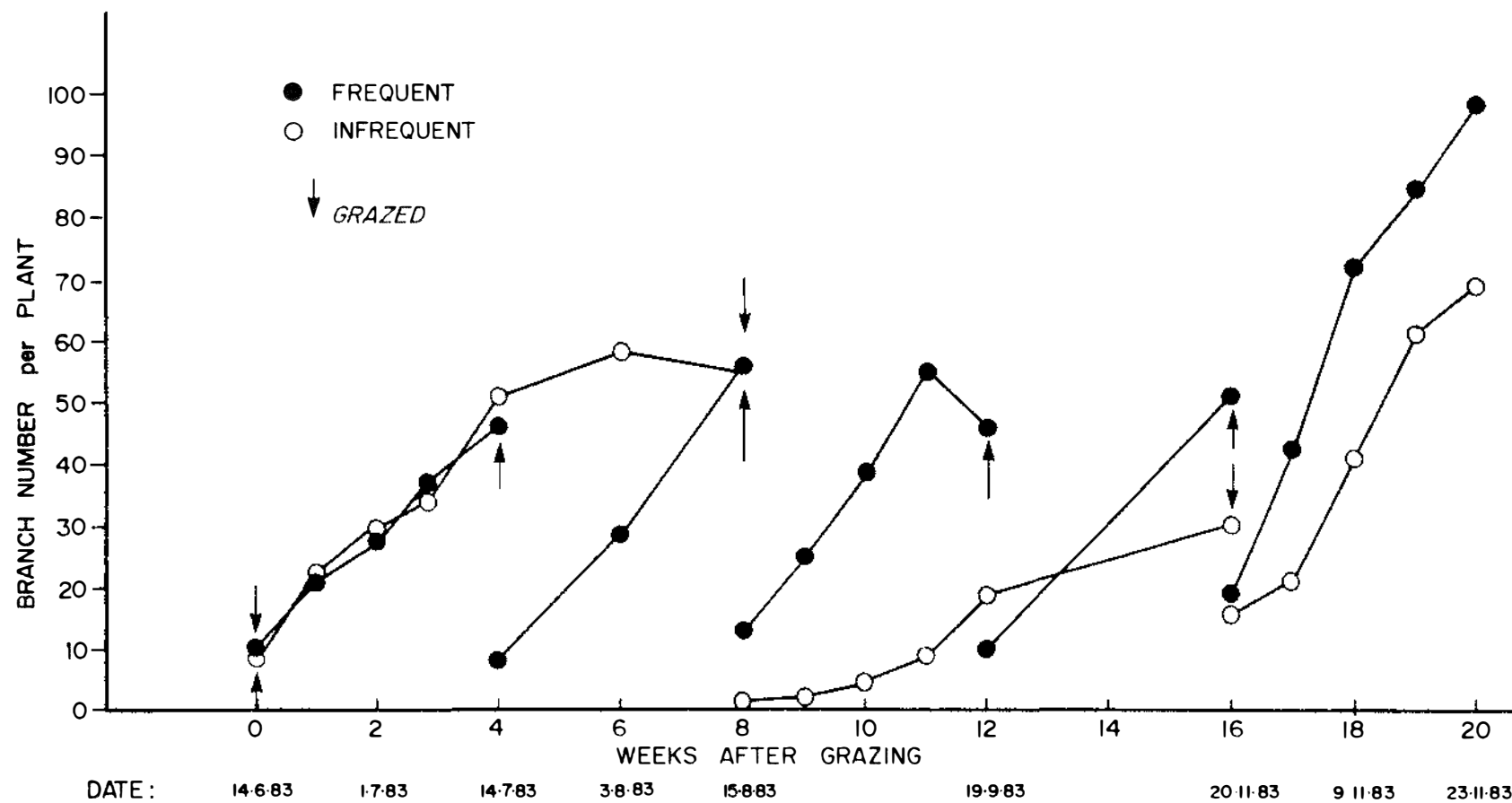


Figure 6.8: Effect of grazing management on branch number per plant

B.3 Leaf Area and Leaf Number

As shown in Figure 6.9, leaf area (cm^2/plant) was encouraged by frequent grazing management following the first three grazings but thereafter leaf area development was substantially reduced. Under infrequent grazing leaf area development tended to be slower following grazing and with little increase after the first four weeks of regrowth. This slower rate of recovery was probably a reflection of the negligible leaf area remaining after grazing, which was particularly noticeable after the second grazing.

Leaf numbers followed a similar trend to leaf area production, with a notably constant and rapid rate of increase following the first three grazings under frequent grazing.

C. WEED CONTENT

During the establishment phase, weeds were removed from the plot and were negligible in amount at the first grazing (Figure 6.10). However, the percentage of weeds increased with time in both treatments but reached significantly greater proportions under infrequent compared with frequent grazing. The weeds were mainly Panicum maximum and Amaranthus spp. (pigweed).

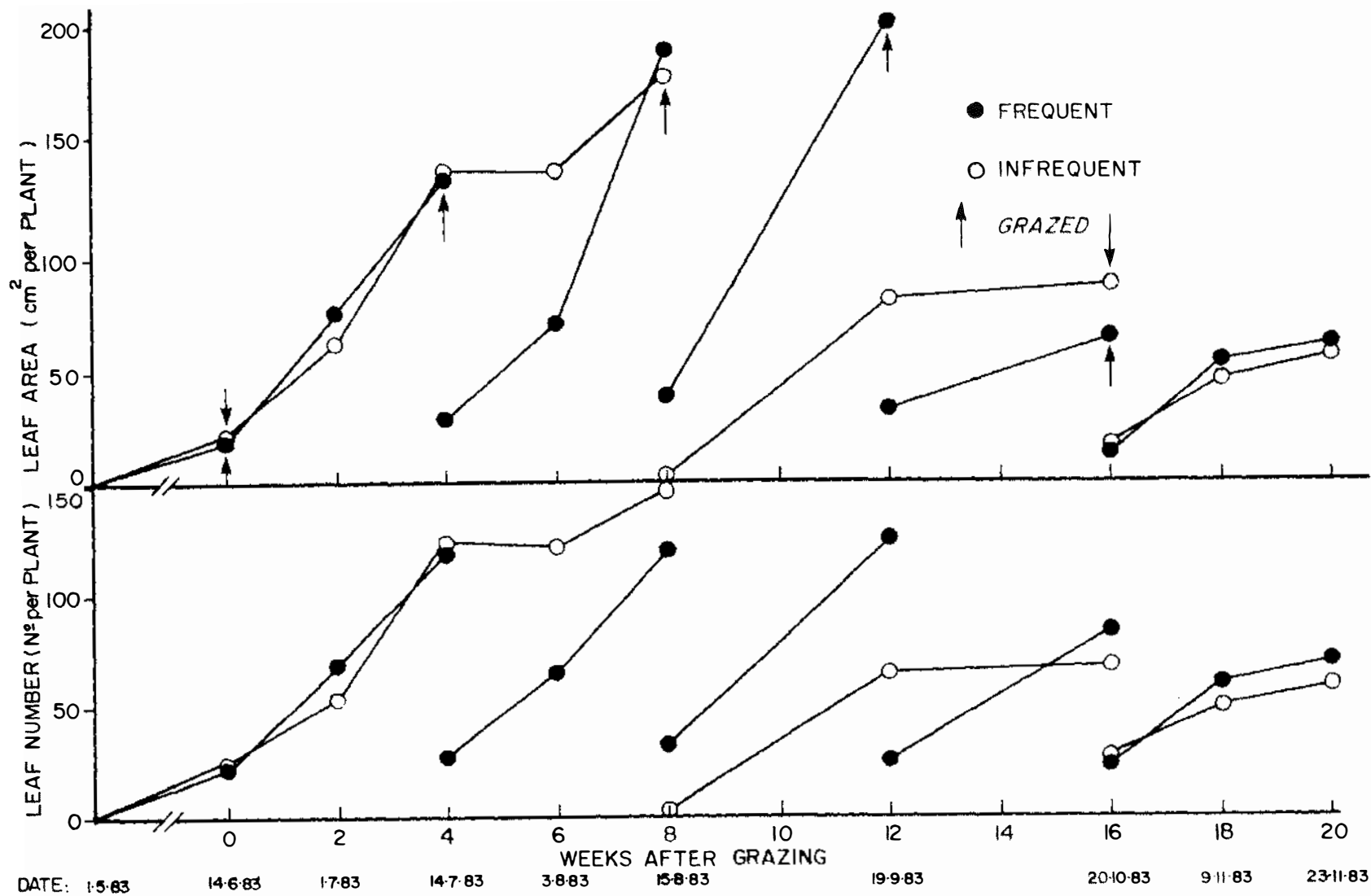


Figure 6.9: Effect of grazing management on leaf area (cm²) and leaf number per plant

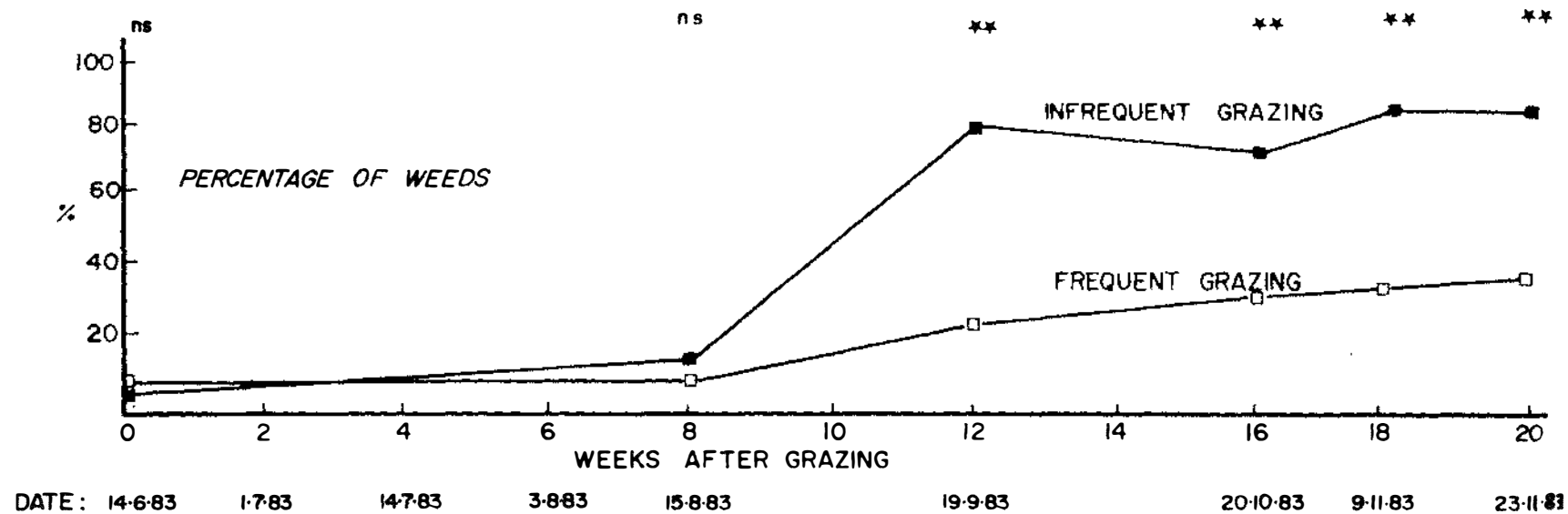


Figure 6.10: Percentage of weeds during the experimental period



Plate 6.5: Dry cows on Verano stylo at first grazing.
(Note: Ready acceptance by grazing animals).



Plate 6.6: Immediately after first grazing - plant height approximately 12-15 cms.



Plate 6.3: A general view showing good Verano stylo establishment.



Plate 6.4: Immediately before first grazing when approximately 50% of plants begin to flower - approximately 30-35 cms in height.



Plate 6.9: During second grazing at eight weekly interval and third grazing at four weekly interval. (Note: Ease of prehension of four weekly grazing and severe wastage of eight weekly grazing).



Plate 6.7: Immediately before third grazing of four weekly intervals. (Note: Large number of green leaves and branches close to ground).



Plate 6.8: Immediately before second grazing at eight weekly intervals. (Note: Negligible number of green leaves and branches close to the ground).

IV DISCUSSION

The reduction in plant density for both treatments from the beginning of the wet season to the end of the growing season, agrees with the findings of Gillard et al (1980) and Wilaipon and Humphreys (1981). However, mortality was much greater under the longer spelling interval. The majority of plant deaths also occurred much earlier under infrequent grazing, leading to a major drop in production. Obviously plant competition was more intense under the longer spelling interval leading to greater death of plants, compared with the shorter spell between grazings.

The importance of residual leaf area remaining after grazing was also evident in achieving rapid recovery of leaves and branches for regrowth. Under the controlled climate room studies, it was shown that Verano stylo had low levels of carbohydrate reserves even under adequate water supply, so that the primary branches were needed to compensate for the lack of the residual leaf areas and thereby to provide the flush of new buds. In the present experiment, the plants were grazed and mown to a similar intensity to treatment E-7-4 in Experiment 2 (Chapter 4). However, under the controlled climate room conditions, the plant was better able to withstand cutting several times, probably due to the greater number of growing points remaining below cutting height. In the field conditions, under long spelling intervals, the elevation of growing points above the grazing and cutting height was probably a factor contributing to subsequent plant mortality. Similar effects have been reported in Townsville stylo (Stylosanthes humilis) (Robertson et al, 1976), where they recorded a 53% mortality of Townsville stylo plants under an 8 week cutting interval compared with 2% under a 2 week cutting regime. This they considered to be due, mainly, to the elevation of the growing points above cutting height. Trampling by cattle may also have been a factor in causing plant mortality in the present study, as discussed by Watkin and Clements (1978).

In contrast, under the shorter spelling interval, Verano stylo develop a more prostrate habit with many branches and



Plate 6.10: Four weekly grazing treatment at end of experimental period. (Note: Maintenance of relatively dense and clean stand of Verano stylo).



Plate 6.11: Eight weekly grazing treatment at end of experimental period. (Note: Relatively low density of Verano stylo and subsequent ingress of weeds).

leaves growing close to the ground and hence less susceptibility to prehension and removal by animal or machine. With other tropical legumes, Fisher (1973) also noticed the difference in plant and sward morphology under frequent and infrequent cutting in S. humilis.

The death of plants under frequent grazing occurred mainly after the fourth grazing. It is difficult to explain whether this was due to the limited longevity of the plant or to the treatments imposed. Verano stylo is a short-lived perennial plant (Humphreys, 1980a) and under grazing conditions, Gardener (1981) found that the majority of Verano stylo plants died in their seeding year. He recorded only 0.03% survival to the end of the third year. Wilaipon and Humphreys (1981) also reported a similar result under grazing conditions in Thailand. They also noticed that grazing late in the wet season increased the number of perennating plants. Although this decline in plant numbers did occur in the present experiment, it is encouraging to note the relatively high number and percentage of plants present in the frequently grazed treatment, at the end of the season.

The longer spelling interval also reduced plant size and branch recovery, particularly after the second grazing. The infrequently defoliated plants took a longer time to build up their branch numbers compared with the more frequently defoliated plants. Weeds, mainly Guinea grass (Panicum maximum), were therefore able to invade and increased from 20% to 80% by the second and third grazing respectively.

The results of this field experiment, although only covering one year's production, clearly support and substantiate the results obtained from the controlled climate room studies. Although the carbohydrate reserves were not determined in this field work, the slower recovery of the infrequently grazed plants was considered to be due to the lack of residual leaf area, growing points and branches capable of regrowth, as demonstrated in the controlled room studies. Primary branches on the main stem are also essential to achieve high yield and survival as stated earlier.

CHAPTER 7

GENERAL DISCUSSION

A. GROWTH AND DEVELOPMENT

Verano stylo has become increasingly important in recent years because it has shown a potential for high yields of good quality feed (Gardener, 1980; Wilaipon, 1985) in conjunction with rapid or moderately rapid recovery after cutting or grazing throughout a wide range of conditions (Edye et al, 1975a; Bishop et al, 1980; Gillard et al, 1980; Gardener, 1981). It has a reputation for being a drought resistant forage legume (William and Gardener, 1984; Fisher and Ludlow, 1984) which, although highly productive under high rainfall (Bishop et al, 1980), is also well suited to areas of low (500 mm) or erratic rainfall (Edye et al, 1975b). These characteristics have been clearly demonstrated in the controlled environment studies (Experiments 1 - 5) under a wide range of defoliation and water stress regimes.

Growth and development of Verano stylo in the controlled environment clearly showed the highly productive capacity of the species over the experimental period of 131 days. However, early growth in terms of dry matter yield, leaf area, plant height and number of branches, was relatively slow up to the onset of flowering. This trend was also observed under field conditions in Thailand (Experiment 6). Nevertheless, growth of the plant increased rapidly after the onset of flowering (Figure 1.2) and reached a maximum absolute growth rate around day 80 which closely approximated the attainment of maximum leaf area. Maximum dry matter production of 105g/plant based on the predicted growth model, occurred on day 108 after seedling emergence. This increase in plant dry weight was mainly through the stem and inflorescence fractions and to a lesser extent the leaves - as also reflected in an increase in the number of branches and leaves. Beyond the 108 day period production noticeably declined due to ageing processes with the stem fraction, remaining the dominant component, as also reported by Gardener et al (1982).

B. DEFOLIATION AND PLANT GROWTH

High yields of good quality feed in conjunction with the adaptability to low soil fertility has led to a rapid and growing use of Verano stylo throughout the tropics. However, the widespread adoption of this legume in farm practice has been constrained by its failure to persist. This is in part due to a lack of understanding not only of the management which must be applied to ensure the persistence of the legume but also of the appropriate method of utilization to achieve satisfactory legume growth as well as maintain plant vigour and stand longevity, and of the appropriate pathway of plant replacement. Work in the controlled environment study has clearly shown the possibility of achieving at least some of these goals through correct cutting and grazing management, as illustrated in Experiment 2 - 6.

As one might expect, the results from the controlled environment studies clearly showed that the greater the intensity of defoliation the greater the depression of regrowth (Experiment 4). However, this effect was very different depending on whether it was defoliation of the main stem or the primary branches (Experiment 3). Reducing the size of the primary branches had a greater detrimental impact on plant regrowth than defoliating the main stem and hence reducing the number of primary branches. For example, a reduction in the number of primary branches from node 7 to node 3 on the main stem (i.e. from 8 branches to 4 branches) reduced total yield by approximately 30% while a reduction in the size of primary branches from node 4 to node 0 (along the branch) reduced yield by over 60% (Figure 3.2). The most severe cutting treatment of both the main stem and the primary branches (E-3-0) resulted in the maximum reduction in yield and on several occasions resulted in significant plant death. This highlights the importance of controlled grazing to ensure a residual of an adequate number and particularly size of primary branches and hopefully a greater residual leaf area for regrowth. In view of the strong relationship between number of branches and plant weight it is perhaps not surprising that defoliation practices which lead to a marked

depression or delay in new branch development results in slow recovery and often low dry matter production.

The effect of reducing the size of the primary branches was even more apparent when defoliation was delayed to the later stage of growth (Experiment 2). In this situation, virtually complete removal of the primary branches (i.e. to node 0) resulted in extensive plant death after only a single cut whereas retaining some length of primary branches (up to node 4) assisted plants to survive and regrow at a slow but steady rate and subsequently achieve a total dry matter yield not too dissimilar from that of the uncut control six weeks after defoliation (Figure 2.3). This indicates that severe grazing of *Verano* stylo at this late stage may lead to a severe reduction in subsequent yield through an insufficiency of sites for regrowth as well as through plant mortality. Such effects on plant mortality after both late and intense cutting has also been reported in other tropical legumes such as *Stylosanthes humilis* (Fisher, 1973) and *Crotalaria juncea* (Kessler and Shelton, 1980).

When total dry matter yield was examined in terms of its components, it was found that the differences in yield were largely due to changes in the stem, and to a lesser extent the inflorescence and leaf fractions. The importance of the stem as a major component of yield was also apparent under infrequent grazing - as the increase in yield from six weekly versus three weekly cutting was largely through an increase in the stem and to a lesser extent the inflorescence components.

The beneficial effect of retaining an adequate number and especially size of the primary branches after defoliation is obviously associated with the greater number of sites in terms of active "growing points" (potential new branches) and branches, the amount of carbohydrate reserves and the residual leaf area remaining for initial regrowth after cutting, as revealed in the high and significant correlation of these parameters with subsequent regrowth. Removal of the primary branches (i.e. to node 0) greatly reduced all these

parameters. Thus, growth of these plants in terms of dry matter, the number of branches, leaf number and leaf area was slow to recover as reflected in the slow rate of growth (Figure 3.4), resulting in low dry matter production. In contrast, the presence of primary branches resulted in a rapid increase in all these parameters especially in those plants having the greatest residual after defoliation even under repeated cutting.

It was also interesting to note that when cutting was delayed to the later stage of growth and then subjected to only a lax intensity - hence more residual sites for new branch development (Table 2.4) - initial plant recovery was slow due to lack of residual leaf area but subsequently produced a real "flush" of branches and leaves during the later period of growth. This slow initial recovery growth particularly under hard cutting warrants emphasis as it was a common reaction in all the experiments and reflected the time required for adequate leaf and especially branch development to occur - often a period of 3 to 4 weeks. However, once achieved then subsequent growth was generally rapid over the following 2 to 3 weeks.

Root weights were also significantly depressed by the removal of the primary branches especially when the main stem was also severely defoliated (Figure 3.6). Such an effect must also limit the plants' ability to obtain soil nutrients and moisture for regrowth.

Humphreys (1981) also highlighted the importance of new shoot development by stating that a high rate of shoot replacement after cutting or grazing is necessary to ensure high yield and persistence under grazing or cutting. Grazing management that leads to complete loss of the primary branches may not only reduce growth in terms of dry matter, green leaf number and number of branches but also in terms of the legume longevity.

The frequency of cutting was also important in determining yield. In fact frequency of defoliation had a

much greater impact on yield than intensity of defoliation. Many workers have clearly demonstrated the advantage of cutting infrequently rather than frequently (e.g. Topark-Ngarm and Akkasaeng, 1978). Experiment 4 showed that growth in terms of dry matter, number of branches, leaf number and leaf area was significantly depressed under frequent cutting in spite of a greater number of growing points present. Presumably the 3-weekly cutting was too short an interval to permit the full exploitation and development of leaf from the greater number of sites. Brown and Blaser (1968) have shown the importance of high levels of canopy light interception for maximum growth rate. Thus, the growth rate of plants under infrequent cutting was greater than under frequent cutting (Table 4.2), resulting in higher dry matter production. However, the results from the field experiment in Thailand were quite different from the growth room study - this will be discussed later.

C. WATER STRESS AND PLANT GROWTH

The results from the controlled environment study confirmed that Verano stylo is a dehydration tolerator (Fisher and Ludlow, 1984) and showed that the plant is able to survive a prolonged moisture limitation without seriously impairing its ability to recover. This dehydration tolerance is associated with a reduction in leaf area through leaf senescence and a reduction in leaf expansion. An increase in specific leaf weight due to leaf thickening, and an increase in chlorophyll concentration as observed in the dark green colour of the leaves during the stress period, were also noted (Plate 5.7 and 5.8). These phenomena are considered as morphological mechanisms of adaptation which assist plant survival (Peak et al, 1975; Fisher, 1983; Waikakul, 1983; Fisher and Ludlow, 1984). In addition, an increase in the carbohydrate concentrations in the leaves is also regarded as a physiological mechanism of the plant (Wilson et al, 1980). This mechanism is known as osmotic adjustment, which is the process by which leaf osmotic potential decreases and offsets the lowered water potential, and hence fully or partially

maintains turgor. Maintenance of turgor is necessary for shoot and root growth, stomatal opening, and many metabolic processes (Ludlow, 1980a, 1980b; Fisher and Ludlow, 1984). These phenomena are found in many species of Stylosanthes and Centrosema but not in Macroptilium atropurpureum cv. Siratro (Ludlow et al, 1983; Fisher and Ludlow, 1984).

Under field conditions, it was also found that Verano stylo displays deep-rootedness (Gutteridge, 1982) and paraheliotropic leaf movements which reduce absorption of solar radiation, and hence leaf temperature and water loss (Fisher and Ludlow, 1984). Verano stylo is therefore well adapted to a dry monsoonal environment where drought during growth is a common occurrence.

The results from the controlled environment study (Experiment 5) indicated that mild and severe water deficit resulted in a reduction in plant growth in terms of dry matter, number of green leaves and number of branches when compared with well watered plants (Experiment 3). The severity of this effect was related to the degree of water deficit i.e. the more severe the water deficit the greater the reduction in these plant structures. For example, at the end of the drought (day 84), total dry matter yield, green leaf number and branch number under severe water stress were only 44%, 45%, and 40% of these respective parameters under mild water stress. However, enhanced growth and yield were obtained following re-watering in both previously mild and severe water stressed treatments - especially in the former treatment. Although it was not possible to establish whether there was any compensatory growth following rewatering of the previously stressed plants, they nevertheless displayed a remarkable ability to recover from a significant period of water stress - this is of considerable practical importance.

The most striking effect of water deficit was on total leaf area (Figure 5.6). For any crop, the leaf area is determined by the number of leaves produced and the size and rate of development of these new leaves. In this study (Experiment 5) the total number of leaves per plant (Figure

5.6) and the rate of new leaf appearance (Table 5.6) were the major contributors to the differences in total leaf area recorded and showed marked reductions under severe water stress. By comparison individual leaf size appeared less sensitive to stress and in fact showed both a positive and negative response on occasions (Table 5.7). The paramount importance of leaf area on the productivity of plants has been repeatedly emphasized (Watson, 1947). During the recovery period, total leaf area was markedly increased through a rapid increase in leaf number and at a similar rate in both the previously mild and severe stress treatments - although the total leaf area achieved over the three weeks of re-watering was greater in the former treatment (Figure 5.6). In this respect, it is important to note that mild stressed plants had higher amounts of total TNC at the end of the drought than did the severely stressed plants (Figure 5.11). It is suggested that these higher reserves of carbohydrate may well have assisted the early recovery growth of the previously mild stressed plants (Davidson and Milthorpe, 1966) leading to their greater production of leaf area (Figure 5.6) and dry matter (Table 5.3).

Dry matter yields throughout the drought and recovery periods were greater in the mild stress treatment than in the severe stress treatment largely due to an increase in the stem fraction and to a lesser extent in the leaf and inflorescence fractions (Figure 5.3). This sensitivity of stem elongation to water stress has also been reported by Williams and Gardener (1984).

As in the previous experiments, the number of branches per plant was strongly correlated to plant dry weight, with the severely stressed plant producing significantly fewer branches than mildly stressed plants. This difference in branch number and hence plant dry weight established during the drought period was maintained through into the recovery period in spite of a greater increase in the rate of branching of those plants previously under severe water stress (Table 5.5).

As cell division is reported to be less sensitive to water stress than cell expansion (Hsiao, 1973), it is possible that under mild stress cell division and hence branch initiation occurred but cell expansion was restricted. With the removal of water stress there was a rapid expansion of these cells resulting in massive branch development - as recorded during the first 7 days following re-watering. In contrast, those plants that were previously under severe water stress showed slower branch development suggesting that both cell division and cell expansion were severely restricted during the drought period and hence slower in recovery following re-watering (Table 5.7). As discussed in the experimental section (page 121), this response is probably closely linked to the differences in carbohydrate reserves, leaf area, leaf number and root weights of the respective treatments.

Defoliation shortly after the onset of drought stress caused a significant depression in subsequent yield particularly when severe and if the plant was under mild water stress. This effect was evident throughout the drought period but was not significant following re-watering. It suggests therefore that hard grazing during the dry season should be avoided and preference given to merely "taking the top" off the legume and thereby ensuring an adequate number and size of residual primary branches. Although there were no significant differences in root weights between cutting treatments made at the onset of the drought period, it is nevertheless suggested that lax rather than severe defoliation prior to the dry season (Experiment 3) may be important in encouraging deeper root development as an aid to plant survival through the drought.

D. HERBAGE QUALITY

Although the results from the cutting experiment have limited application to grazed pasture where defoliation is usually incomplete and may be of higher frequency, it can still be used as a guide for quality prediction.

As shown in Tables 2.5, 3.5, 4.6 and 5.9, Verano stylo generally contained sufficient crude protein to meet animal requirements. These data also show that the content of crude protein in these studies varied (1) with stage of growth, (2) with cutting management (3) in different organs and (4) with the watering regime.

Regarding the first aspect the results of a number of studies (Fisher, 1969, 1970; Winter et al, 1977; Gardener et al, 1982) have shown that the crude protein is highest in young tissue at the early part of the growing season, and declines with advancing plant maturity. These changes were also observed with Verano stylo in the uncut control treatment (Tables 2.5 and 3.5). However the rate of decline with maturity varies between plant parts with the leaf and inflorescence having a higher crude protein concentration than the stem at all stages of maturity. The changes in leaf and stem values with time may be associated with translocation of nitrogen to the seeds as demonstrated by Robinson and Jones (1972) with Townsville stylo.

The crude protein concentration in all plant parts was increased by defoliation especially in the stem fraction (Tables 2.5, 3.5 and 4.6) as also reported in Townsville stylo (Hendy, 1971; Ive, 1974). However, the differences between the treatments as a result of varying the cutting intensity and frequency were generally small. Crude protein was also slightly higher in the stem of the frequently cut plants (every three weeks) compared with the stem of infrequently cut plants (every six weeks). Similar effects were reported by Mufandaedza (1976) who found that the crude protein level in several strains of S. guianensis increased with more frequent cutting. Robertson et al (1976) working in Thailand, also reported an increase in crude protein levels of S. humilis under more frequent cutting.

Leaf and inflorescence contained higher concentrations of crude protein than stem at all cutting intensities and frequencies (Tables 2.5, 3.5 and 4.6). In contrast, stubble had the lowest crude protein level in all cutting treatments.

The concentrations of these plant components mentioned above respond differently under water stress. Leaf and inflorescence were depressed in crude protein level relative to well watered plants in Experiments 2, 3 and 4, and appeared to be due to the redistribution of nitrogen from leaves and inflorescence to the root fraction. This in part supports the results obtained by Fisher (1980) working with S. humilis, who found that the plant redistributed its nitrogen and phosphorus to the roots primarily in response to water stress rather than maturity. This transfer of nitrogen appeared to be less apparent under severe than under mild water stress (Table 5.9).

Although the crude protein percentage in different plant parts and for different cutting intensity and frequency and for different watering regimes was small, the amounts per plant (Figures 2.9, 3.9, 4.8 and 5.8) were largely due to the large and significant difference obtained in dry weights between the different treatments.

The effect of defoliating the main stem on crude protein yields followed a similar pattern to that of plant dry weight viz. defoliating to node 5 or node 3 significantly depressed yield compared with defoliating to node 7, with little difference between medium (to node 5) and severe (to node 3) defoliation (Figure 4.8). However, reduction in the size of the primary branches again had a greater impact on crude protein yield than reduction in the number of primary branches - with the greatest depression resulting from the defoliation of both the main stem and the primary branches. The importance of size of primary branches on crude protein yield was also apparent even when cutting was delayed to the later stage of growth. Increasing the frequency of cutting from 6 to 3 weekly intervals decreased the crude protein yields of all above ground components in spite of the slight increase in nitrogen concentration in the stem under frequent cutting.

The effect of water stress on crude protein yield again reflected the dry matter responses. At 42 days after cutting

the depression from severe cutting was only significant under mild water stress, but by day 84 the effect of severe cutting resulted in a reduction in crude protein yield under both mild and severe stress. Of perhaps greater significance was the fact that cutting, even when severe, had less effect on crude protein yields than water deficiency (Figure 5.8), and was reflected in all plant components. Also, mildly stressed plants produced substantially greater crude protein yields than severely stressed plants.

The results of these experiments clearly show that the complete removal of the primary branches especially in conjunction with the hard cutting of the main stem is detrimental to both quantity and quality of production. While lax cutting of the primary branches may not be too damaging to dry matter yield and quality under adequate soil moisture, this may not apply during periods of soil moisture limitation. Figure 5.8 clearly shows that even under mild water stress crude protein yields were greatly reduced but were nevertheless capable of rapid recovery following adequate rainfall.

It is interesting to note in Experiment 3 that although the stem was the major contributor to total dry matter under lax cutting, the crude protein yield arose largely from the inflorescence. In fact the crude protein yield of leaf plus inflorescence represented more than 50% of the total and indicates the high quality of this species even under infrequent cutting. This was also illustrated in the uncut control treatment of Experiment 2 (Figure 2.9) and suggests that cutting for hay at a later stage of growth can achieve high dry matter of high quality. However, in Experiment 5, where plants were subjected to water stress, results showed that the increase in crude protein in mildly stressed plants arose mainly from the stem and to a lesser extent the leaf, while the inflorescence which was severely reduced in development contributed only a small amount to the total crude protein yield. However, on re-watering the crude protein yield of the leaf and the inflorescence showed a marked increase during the recovery period.

E. MANAGEMENT RECOMMENDATIONS

The findings from this study suggest that Verano stylo is capable of producing acceptable dry matter yields of high quality under cutting or grazing in tropical monsoonal climates such as that of Thailand, provided that an adequate number and size of primary branches is retained. The results also indicate a high tolerance to water stress and an ability to recover from drought.

In order to achieve good establishment of the legume it is important to ensure good seedbed preparation, appropriate fertilizer application, weed and insect control and correct inoculum. Since Verano stylo has a relatively high percentage of hard seed, scarification using sand paper or soaking in hot water at 80°C for 10 minutes is necessary and effective.

Verano stylo should also be sown early in the wet season when soil moisture is adequate for germination and emergence. Although it was not a consideration in this study, Verano stylo is normally sown in a mixture with appropriate tropical grasses and subsequently cut for feeding directly or for storage as hay or grazed in situ.

E.1 Cutting

In a "cut and carry" system, Verano stylo can achieve relatively high production of high quality provided it is cut laxly at approximately 6 weekly intervals. From the current experiments, it is possible to recommend a cutting intensity down to the 7th node on the main stem to achieve this level of production. However, in the field under practical conditions, such a requirement is somewhat academic. Nevertheless in view of the evenness of the stand, as found in the field experiment at Muaklek (Plate 6.3 and 6.4), it may well be possible for the farmer to cut within an acceptable range of the optimum - between the 6th and the 8th node - and still achieve high yields.

Results also highlighted the importance of retaining primary branches of adequate size for regrowth. From a practical stand point the recommendation of cutting to a mean level approximating the 7th node on the main stem should also ensure this residual of adequate branch size. Those primary branches projecting into the upper regions of the canopy at later cutting will certainly be defoliated but should also retain the residual size recommendation (i.e. at least 4 nodes remaining).

Under a cut and carry system it also appears possible to achieve even higher dry matter production under relatively lax cutting when the plant is defoliated at a much later stage of growth - approximating maximum yield. Although quality (crude protein) is still relatively high the extra production is largely due to greater stem production which may be less palatable to stock. The major limitation to such late and also to infrequent cutting is the slow initial recovery - of 3 to 4 weeks. Nevertheless provided the cutting is lax and adequate time is allowed for recovery high yields and quality can be achieved.

In marked contrast to the plant responses recorded under adequate soil moisture, the reaction of plants to similar defoliation under soil moisture stress was almost nil. This suggests that under such climatic conditions, the farmer is able to adopt a much more flexible cutting practice without affecting production - a flexibility that he can even maintain up to 3 weeks of recovery growth e.g. the first cut, following good rains.

E.2 Grazing

Possibly the most important finding in this series of experiments is the completely opposite plant response obtained depending on the method of defoliation. Under cutting, 6 weekly defoliation produced significantly higher yields than 3 weekly defoliation, whereas under grazing, 4 weekly defoliation was markedly superior in yield to 8 weekly defoliation.

It is well known that grazing is a very different form of defoliation from cutting - as it can be highly selective between plants and plant parts, it includes the animal impacts of treading and excreting and it is more difficult to impose precise intensities and frequencies of defoliation - compared with cutting.

A further factor associated with grazing is the ability of the plant to modify its growth form in response to animal prehension. This reaction was strikingly evident in the field study, where the more frequently grazed sward (approximately 4 weekly) developed a more prostrate habit of growth while the infrequently grazed sward (approximately 8 weekly) maintained an erect and semi-erect habit. With more frequent removal of the main stem under 4 weekly grazing, the primary branches became more abundant and productive as they grew at a more acute angle closer to the ground and hence better able to avoid total prehension by the grazing animal. In contrast the more erect growth under 8 weekly grazing suffered more complete defoliation at grazing leaving a rather "nude" main stem with fewer residual branches and buds for regrowth.

A further factor contributing to the relatively poor productivity of the infrequently grazed sward was the much greater decline in Verano stylo plant density with time. From an initial and very similar plant density of approximately 170 plants/m^2 at the first grazing, the frequently grazed sward ended the season 20 weeks later with 62 plants/m^2 while the infrequently grazed ended with only 20 plants/m^2 (Table 6.1). It is suggested that the various factors of plant competition were more damaging to plant density under infrequent grazing than under frequent grazing. This "opening up" of the sward, particularly under infrequent grazing, obviously accounted for the significant ingress of weeds recorded in the treatment by the end of the season - approximately 80% compared with approximately 40% under frequent grazing (Figure 6.10).

In terms of the practical recommendation to farmers, it is clear that frequent rather than infrequent grazing should be encouraged on the grounds of both quantity and quality of

dry matter and the probable improvement in forage acceptability and intake due to the greater amount of leaf produced.

Again, the difficulty and very practical question of grazing intensity must be faced - and it is recommended that grazing intensity should be adjusted to leave approximately 7 residual nodes on the main stem after grazing. As stated earlier, this may well be feasible in view of the relative evenness of sward that can be established - and if necessary, maintained by mechanical trimming. Obviously farmers must not allow the sward to become rank as it will lead to lower production and more rapid sward deterioration through legume death and ingress of weeds.

In terms of the recommendations relating to the grazing management of Verano stylo at the early stage of the drought period, it appears that farmers may be able to graze these stands to a lower level (e.g. down to the 5th node rather than the 7th node) without causing a significant reduction in regrowth during the remainder of the drought and without restricting recovery following the onset of the early wet season rains. On the other hand severe grazing (down to the 3rd node) during the early drought period will depress regrowth significantly during the remaining drought period - at a time when even small additions of quality feed may be highly important. However, such a practice does not appear to effect recovery growth detrimentally with the subsequent onset of rains.

This series of experiments did not attempt to address the question of management of mixed legume/grass pastures generally found in practice. Hence caution must be shown in attempting to extrapolate these current findings from pure Verano swards to Verano/grass pastures. Nevertheless it is argued that in view of the paramount importance of legumes in tropical pastures, the productivity and persistency of the legume component should be favoured. Such an emphasis could well lead to tropical Verano/grass pastures of high animal performance through the production and maintenance of feed of high quality, high acceptability and high digestibility, even though this may be at the expense of some dry matter production.

Appendix 1 Controlled environment conditions.

Temperature:	30/24 $\pm$ 0.5°C	day/night
Humidity:	70/90 $\pm$ 5% RH	day/night
	13/2 mb VPD	
Lighting:	12 hour photoperiod	
	W m ⁻² PAR* pre 159	uE.m ⁻² .sec ⁻¹ 742
	post 135	640
	mean 147	691

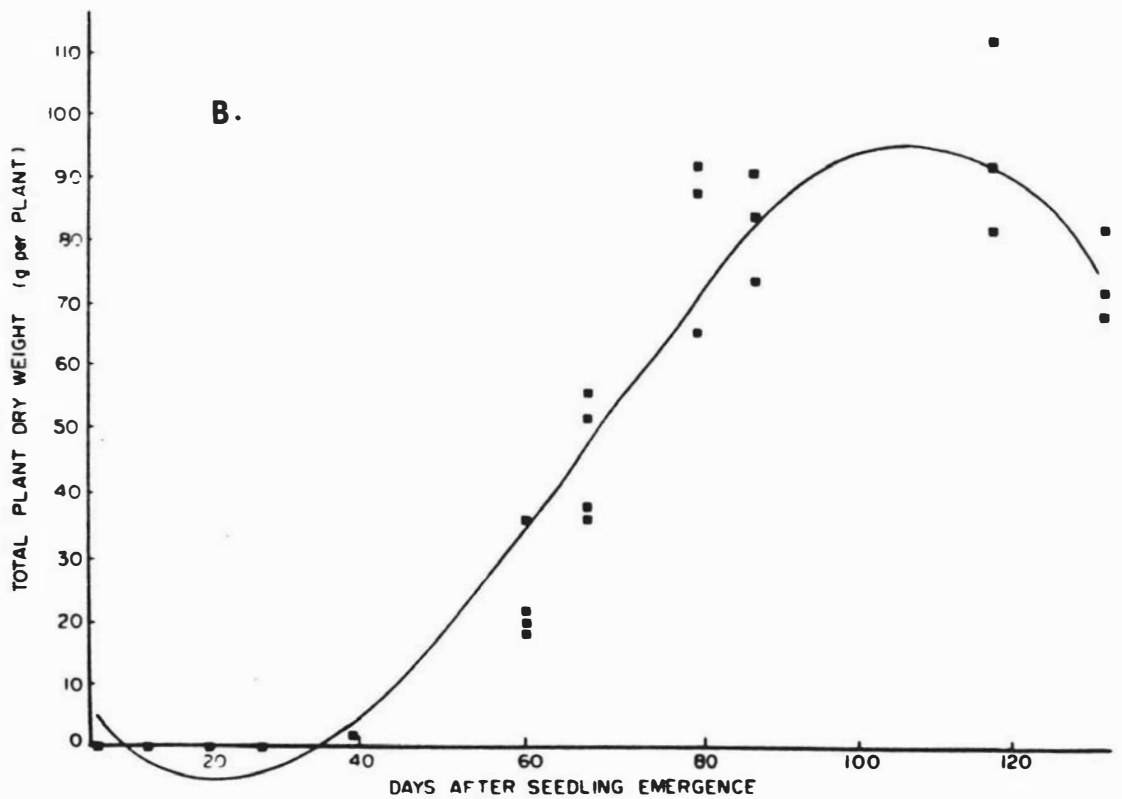
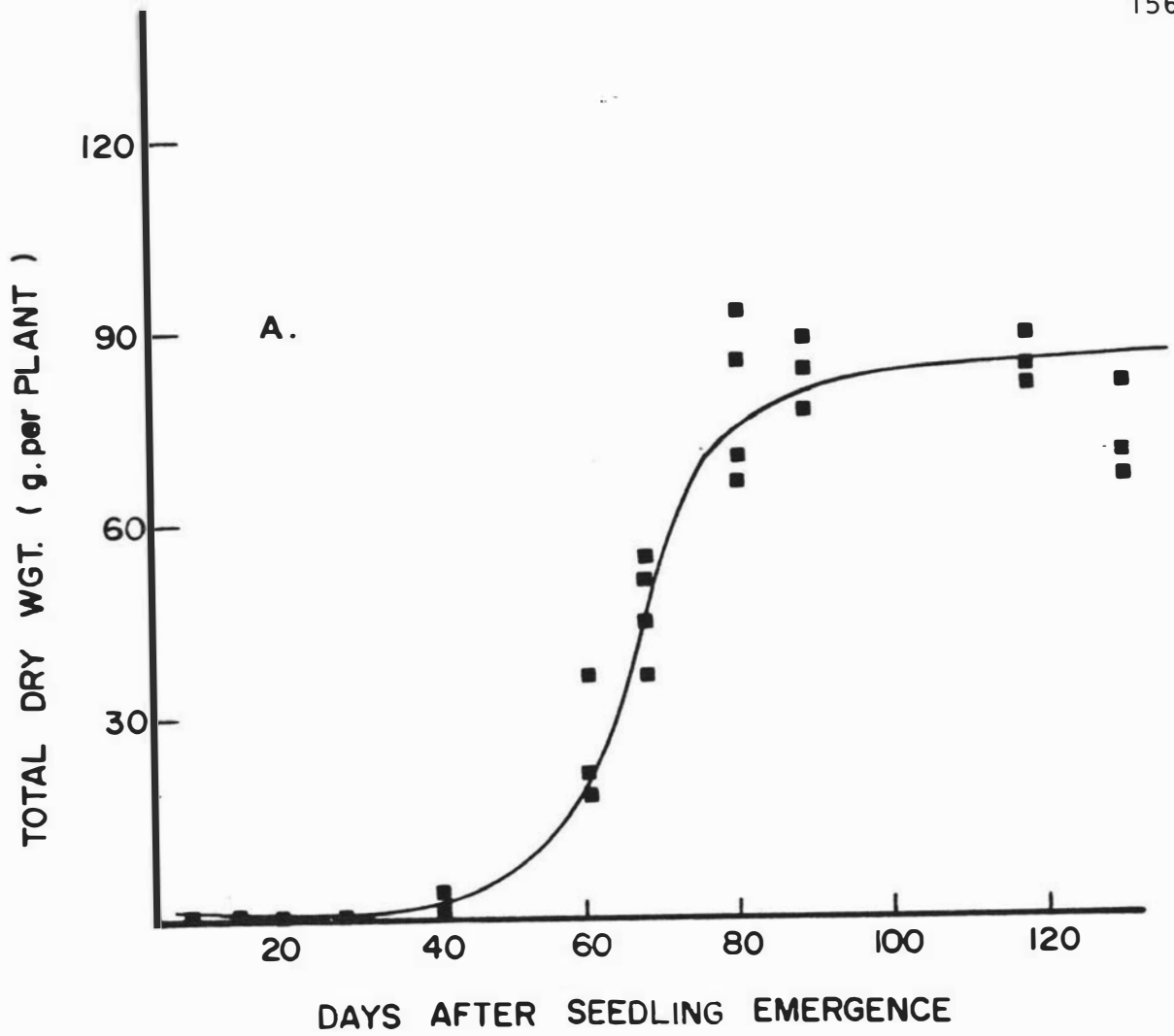
* 400 - 700 nm photosynthetically active radiation.

Appendix 2 Climate laboratory - N.C.S.U. Phytotron nutrient

	2 ml A + 2 ml B/ litre water					
	grams/litre					
	Molecular weight (g)	Conc.	Final soln.		PPM	
<u>Stock solution A</u>						
Ammonium nitrate						
NH ₄ NO ₃	80.2	80.05	.1601	N	56.05	
Calcium nitrate				Ca	54.06	
Ca(NO ₃) ₂ x 4 H ₂ O	236.15	159.25	.3185	N	37.79	
Sequestrene 330				Fe	5.96	
10% DTPA Na Fe	468.20	29.8	.0596	Na	2.93	
<u>Stock solution B</u>						
Potassium phosphate				K	7.18	
KH ₂ PO ₄	136.08	12.5	.025	P	5.69	
Potassium phosphate				K	4.94	
K ₂ HPO ₄	174.17	5.5	.011	P	1.96	
Potassium nitrate				K	49.42	
KNO ₃	101.11	63.9	.1278	N	17.71	
Magnesium sulphate				Mg	6.08	
MgSO ₄ x 7H ₂ O	246.50	30.81	.06162	S	8.02	
Sodium sulphate				Na	22.98	
Na ₂ SO ₄	142.05	35.5	.071	S	16.03	
Zinc sulphate				Zn	0.011	
ZnSO ₄ x 7H ₂ O	287.55	0.025	.00005	S	0.006	
Manganese chloride				Mn	0.144	
MnCl ₂	197.92	0.26	.00052	Cl	0.186	
Copper sulphate				Cu	0.005	
CuSO ₄ x 5H ₂ O	249.68	0.01	.00002	S	0.003	
Boric acid						
H ₃ BO ₃	61.82	0.35	.0007	B	0.123	
Sodium molybdate				Na	0.001	
NaMoO ₄ x 2H ₂ O	241.93	0.0027	.0000054	Mo	0.002	

Nutrient	PPM	um	Nutrient	PPM	um
N	111.55	NH_4 2200 NO_3 6130	B	0.123	BO_3 11.39
P	7.65	PO_4 6.8	Mn	0.144	2.55
K	61.54	80	Cu	0.005	0.08
S	24.06	SO_4 750	Zn	0.011	0.17
Ca	54.06	1280	Mo	0.002	0.02
Fe	5.96	125	Cl	0.186	5.36
Mg	6.08	250	Na	25.911	1125

pH of final solution = 6.5 - 7.5



Appendix 3: Changes in total dry weight with time.

A. Fitted with Logistic growth model

B. Fitted with Polynomial growth model (0-131 days after seedling emergence)

Appendix 4 Effects of defoliation on total dry weight
(g/plant).

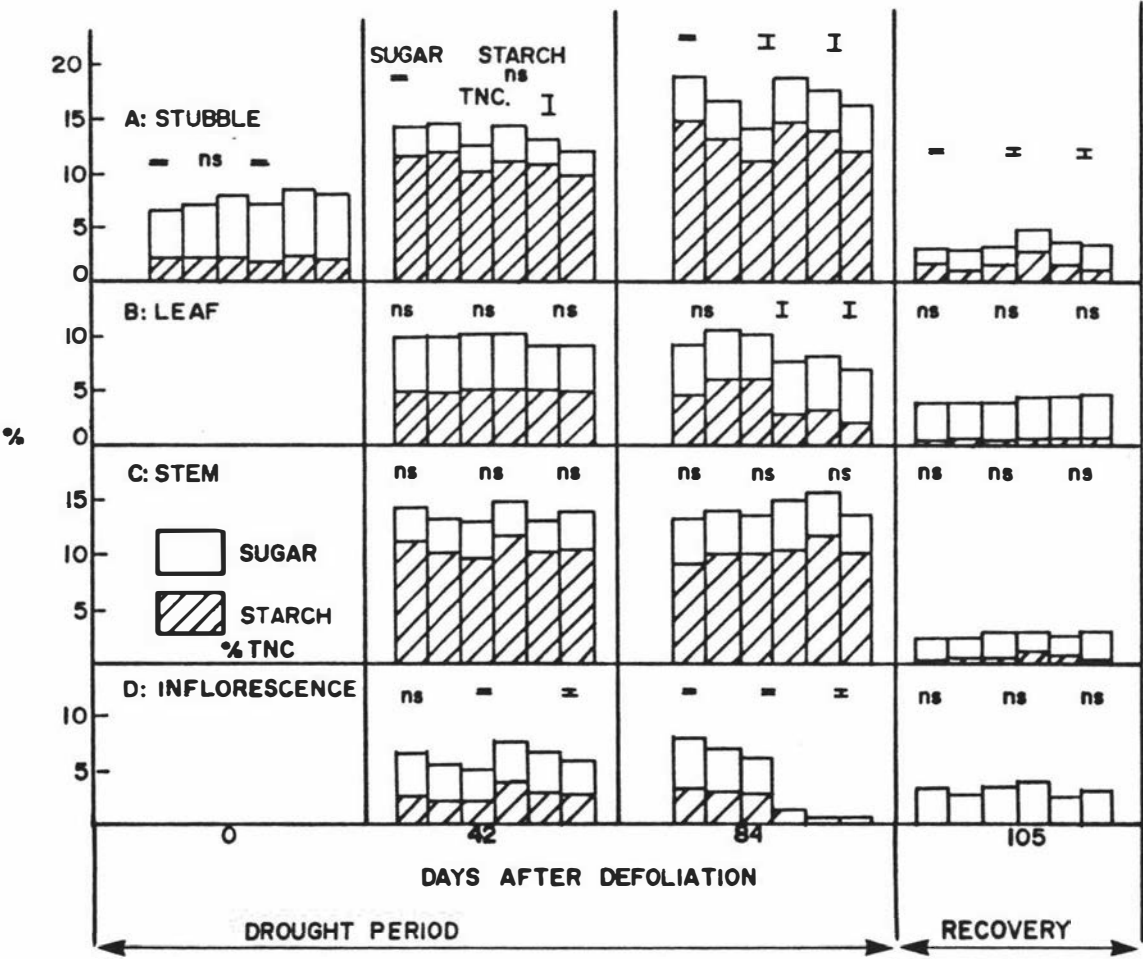
Treatment		Weeks after cutting		
		0	4	6
<u>After first cut</u>				
Early	Control-E	2.81b	45.77b	79.10a
	E-5-4	1.59c	37.64b	45.56bc
	E-5-0	0.29d	11.33c	31.57c
Late	Control-L	84.20 ¹	94.17a	73.80a
	L-5-4	3.65a	19.58c	64.50ab
	L-5-0	0.96d		
Sig.		**	**	**
<u>After second cut</u>				
Early	E-5-4	3.32	38.52a	
	E-5-0	0.69	10.70b	
Late	L-5-4	6.05	39.34a	
	L-5-0	-	-	
Sig.		**	*	

¹ Not included in statistical analysis.

Appendix 5 Effect of defoliation on total plant dry weight (g/plant).

Treatment	Weeks after cutting			
	0	2	4	6
<u>Cycle 1</u>				
Control	2.73a ¹	-	27.40ab	63.54a
E-7-4	1.76b	-	31.40a	55.90a
E-7-0	0.38d	-	10.40c	23.90bc
E-3-4	1.17c	-	20.40b	33.60b
E-3-0	0.28d	-	6.70c	13.90c
Significance	**		**	**
<u>Cycle 2</u>				
Control	-	-	92.64a	-
E-7-4	4.93a	-	34.50b	56.40a
E-7-0	1.02c	-	6.25c	23.10b
E-3-4	2.22b	-	16.47c	58.90a
E-3-0	0.40d	-	3.80c	20.70b
Significance	**		**	**
<u>Cycle 3</u>				
Control	-	-	-	75.95a
E-7-4	7.75a	-	-	44.27b
E-7-0	1.42c	-	-	25.86c
E-3-4	3.88b	-	-	28.79c
E-3-0	0.92c	-	-	16.48d
Significance	**			**
<u>Cycle 4</u>				
Control	-	-	-	70.40a
E-7-4	7.64a	11.58	24.10	78.20a
E-7-0	2.57c	3.43	9.20	34.10b
E-3-4	3.59b	5.99	20.80	65.00a
E-3-0	1.50d	-	-	-
Significance	**	ns	ns	**

¹ Values in the same vertical column not followed by the same letter differ at $P = 0.05$



Appendix 6: Effect of water stress and defoliation on total non-structural carbohydrate concentration of the plant components (% of dry matter).

REFERENCES

- Adegbola, A. (1966). Preliminary observations on the reserve carbohydrate and regrowth potential of tropical grasses. Proc. Xth Int. Grassld. Congr., Helsinki, Finland: p. 93.
- Akinola, J.O. and Whiteman, P.C. (1975). Agronomic studies on pigeon pea (Cajanus cajan (L.) Millop). III. Responses to defoliation. Aust. J. Agric. Res. 26: 67.
- Alberda, T. (1957). The effects of cutting, light intensity and night temperature on growth and soluble carbohydrate content of Lolium perenne L. Plant and Soil 8: 199.
- Alferez, A.C. (1974). Effect of temperature and cutting treatments on dry matter yields and carbohydrate accumulation in stylo (Stylosanthes gracilis H.B.K.). Cited in Herb. Abstr. 44: 458.
- Alvey, N.G. et al (1977). Genstat: a general statistical programme. Rothamstead Experimental Station.
- Andrew, C.S. (1966). A kinetic study of phosphate absorption by excised roots of Stylosanthes humilis, Phaseolus lathyroides, Desmodium uncinatum, Medicago sativa and Hordeum vulgare. Aust. J. Agric. Res. 17: 611.
- Andrew, C.S. and Norris, D.O. (1961). Comparative responses to calcium of five tropical and four temperate pasture legume species. Aust. J. Agric. Res. 12: 40.
- Andrew, C.S. and Pieters, W.H.J. (1970). Effect of potassium on the growth and chemical composition of some pasture legumes. III. Deficiency symptoms of 10 tropical pasture legumes. C.S.I.R.O. Aust. Div., Trop. Past. Tech. Paper No. 5.

- Andrew, C.S. and Robins, M.F. (1969). The effect of phosphorus on the growth and chemical composition of some tropical pasture legumes. I. Growth and critical percentage of phosphorus. *Aust. J. Agric. Res.* 20: 665.
- Baldos, D.P. and Javier, E.Q. (1976). The growth and development of Townsville stylo (Stylosanthes humilis H.B.K.). *Philipp. J. Crop Sci.* 1: 209.
- Begg, J.E. and Torrsell, B.W.R. (1974). Diaphotonastic and parahelionastic leaf movements in Stylosanthes humilis H.B.K. (Townsville stylo). In Mechanisms of Regulation of Plant Growth. Eds. R.L. Bieleski, A.R. Ferguson and M.M. Greswell. *Bull. 12. R. Soc. N.Z.*, Wellington: pp. 277.
- Begg, J.E. and Turner, W.C. (1976). Crop water deficits. *Adv. Agron.* 28: 161.
- Bennett, O.L., Doss, B.D., Ashley, D.A., Kilmer, V.J. and Richardson, E.C. (1964). Effects of soil moisture regime on yield, nutrient content, and evapotranspiration for three annual forage species. *Agron. J.* 56: 195.
- Bishop, H.G., McIvor, J.G. and Rutherford, M.T. (1980). Yield and persistence of perennial Stylosanthes species on the Mackay west coast. *Trop. Grassld.* 14: 57 - 62.
- Black, J.N. (1957). The influence of varying light intensity on the growth of herbage plants. *Herb. Abstr.* 27: 89.
- Black, J.N. (1963). The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (Trifolium subterraneum L.). *Aust. J. Agric. Res.* 14: 20.
- Blunt, C.G. and Humphreys, L.R. (1970). Phosphate response of mixed swards at Mt. Cotton, south-eastern Queensland. *Aust. J. Exp. Anim. Husb.* 10: 431.

- Bogdan, A.V. (1977). Tropical Pastures and Fodder Plants. Longman, London.
- Bowen, G.D. (1959). Field studies on nodulation and growth of Centrosema pubescens Benth. Qld. J. Agric. Sci. 16: 253.
- Brolmann, J.B. and Sonoda, R.M. (1981). Note on response of various Stylosanthes hamata accessions to two levels of nitrogen. Trop. Agric. 58: 133.
- Brougham, R.W. (1958). Interception of light by the foliage of pure and mixed stands of pasture plants. Aust. J. Agric. Res. 9: 39.
- Brougham, R.W. (1960). The relationship between critical leaf area, total chlorophyll content and maximum growth rate of some pasture and crop plants. Ann. Bot. (N.S.) 24: 463.
- Brown, R.H. and Blaser, R.E. (1968). Leaf area index in pasture growth. Herb. Abstr. 38: 1.
- Brown, R.H. and Blaser, R.E. (1970). Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (Dactylis glomerata). Crop Sci. 10: 213.
- Bryan, W.W. (1969). Lotononis bainesii Baker - a legume for subtropical pastures. Aust. J. Exp. Agric. Anim. Husb. 1: 4.
- Burt, R.L. and Miller, C.P. (1975). Stylosanthes - a source of pasture legumes. Trop. Grassl. 9: 117.
- Burt, R.L. and Reid, R. (1976). Exploration for, and utilization of, collections of tropical pasture legumes. III. The distribution of various Stylosanthes species with respect to climate and phytogeographic region. Agro-Ecosystems 22: 319.

- Burt, R.L., Cameron, D.G., Cameron, D.F., Mannetje, L.'t and Lenne, J. (1983). *Stylosanthes*. In: The Role of Centrosema, Desmodium and Stylosanthes in improving Tropical Pastures. Eds. R.L. Burt, P.P. Rotar, J.L. Walker and M.W. Silvey. Westview Tropical Agriculture Series, No. 6: pp. 141 - 181.
- Burt, R.L., Edye, L.A., William, W.T., Grof, B. and Nicholson, C.H.L. (1971). Numerical analysis of variation patterns in the genus *Stylosanthes* as an aid to plant introduction and assessment. *Aust. J. Agric. Res.* 22: 737.
- Burt, R.L., Edye, L.A., Williams, W.T., Gillard, P., Grof, B., Page, M., Shaw, N.H., Williams, R.J. and Wilson, G.P.M. (1974). Small-sward testing of *Stylosanthes* in northern Australia: preliminary considerations. *Aust. J. Agric. Res.* 25: 559.
- Butler, G.W., Greenwood, R.M. and Soper, K. (1959). Effects of shading and defoliation on the turnover of root and nodule tissue of plants of *Trifolium repens*, *Trifolium pratense* and *Lotus utiginosus*. *N.Z. J. Agric. Res.* 2: 415.
- Cameron, D.F. and Mannetje, L.'t. (1977). Effects of photoperiod and temperature on flowering of twelve *Stylosanthes* species. *Aust. J. Exp. Agric. Anim. Husb.* 17: 417.
- Campbell, M.H. (1969). Aerial sowing of pastures on the central tablelands of N.S.W. *Agric. Gaz. N.S.W.* 79: 644.

- Carvalho, L.J.C.B. (1978). The effect of water stress on growth and herbage quality of Stylosanthes hamata cv Verano and Stylosanthes guyanensis cv Schofield. M.S. Thesis, University of Florida, Gainesville, Fl. U.S.A.
- Carvalho, M.M.de, Edwards, D.G., Andrew, C.S. and Asher, C.J. (1981). Aluminium toxicity, nodulation and growth of Stylosanthes species. Agron. J. 73: 261.
- Carvalho, M.M.de, Andrew, C.S., Edwards, D.G. and Asher, C.J. (1980). Comparative performance of six Stylosanthes species in three acid soils. Aust. J. Agric. Res. 31: 61.
- Clements, R.J. (1980). Personal communication.
- Clements, R.J., Williams, R.J., Grof, B. and Hacker, B. (1983). Centrosema. In: The Role of Centrosema, Desmodium and Stylosanthes in improving Tropical Pastures. Eds. R.L. Burt, P.P. Rotar, J.L. Walker and M.M. Silvey. Westview Tropical Agriculture Series, No. 6: pp 69 - 96.
- Cook, S.J. (1984). Establishment of four pasture grasses and Siratro from seed oversown into dense and open spear-grass pastures. Aust. J. Exp. Agric. Anim. Husb. 24: 360.
- Crider, R.J. (1955). Root growth stoppage resulting from defoliation of grass. U.S. Dep. Agric. Tech. Bull. 1102.
- Crowder, L.V. and Chheda, H.R.C. (1982). Tropical Grassland Husbandry. Tropical Agriculture Series. Longman, London and New York.
- Date, R.A., Chandler, M. and Roughley, R.J. (1980). Herb. Abstr. 50: 458.

- Davidson, J.L. (1978). Root systems - the forgotten component of pastures. In: Plant Relations in Pastures. Ed. J.R. Wilson, C.S.I.R.O., Melbourne: pp. 86 - 94.
- Davidson, J.L. and Donald, C.M. (1958). The growth of subterranean clover with particular reference to leaf area. Aust. J. Agric. Res. 9: 53.
- Davidson, J.L. and Milthorpe, F.L. (1966). The effect of defoliation on the carbon balance in Dactylis glomerata. Ann. Bot., N.S., 30: 185.
- Department of Land Development (1979). Land Development Report. Land Development, Soil Survey Division, Bangkok, Thailand. No. 245 (in Thai).
- Donald, C.M. and Black, J.N. (1958). The significance of leaf area in pasture growth. Herb. Abstr. 28: 1.
- Douglas, N.H. (1965). Tropical legumes on a blady grass burn. Qld. Agric. J. 91: 36.
- Dovrat, A. and Cohen, Y. (1970). Regrowth potential of Rhodes grass (Chloris gayana Kunth.) as affected by nitrogen and defoliation. Proc. XIth Int. Grassld. Congr., Surfers Paradise: pp. 552.
- Dowling, P.M., Clements, R.J. and McWilliam, J.R. (1971). Establishment and survival of pasture species from seeds sown on the soil surface. Aust. J. Agric. Res. 22: 61.
- Edye, L.A. and Grof, B. (1983). Selecting cultivars from naturally occurring genotypes: evaluating Stylosanthes species. In: Genotypic Resources of Forage Plants. Eds. J.G. McIvor and R.A. Bray, C.S.I.R.O.: pp. 217.
- Edye, L.A., Field, J.B. and Cameron, D.F. (1975a). Comparison of some Stylosanthes species in the dry tropics of Queensland. Aust. J. Exp. Agric. Anim. Husb. 15: 655.

- Edye, L.A., Burt, R.L., Williams, W.T. and William, R.J. (1973). A preliminary agronomic evaluation of Stylosanthes species. Aust. J. Agric. Res. 24: 511.
- Edye, L.A., Burt, R.L., Nicholson, C.H.L., William, R.J. and Williams, W.T. (1974). Classification of the Stylosanthes collection 1928 - 1969. C.S.I.R.O. Div. Trop. Agron. Tech., Paper No. 15: 28 pp.
- Edye, L.A., Field, J.B., Bishop, H.G., Hall, R.L., Prinsen, J.H. and Walker, B. (1976). Comparison of some Stylosanthes species at three sites in central Queensland. Aust. J. Exp. Agric. Anim. Husb. 16: 715.
- Edye, L.A., Williams, W.T., Burt, R.L., Grof, B., Stillman, S.L. and Winter, W.H. (1977). The assessment of seasonal yield using some Stylosanthes guyanensis accessions in humid tropical and sub-tropical environments. Aust. J. Agric. Anim. Husb. 17: 425.
- Edye, L.A., Williams, W.T., Anning, P., Holm, A.McR., Miller, C.P., Page, M.C. and Winter, W.H. (1975b). Sward tests of some morphological agronomic groups of Stylosanthes accessions in dry-tropical environments. Aust. J. Agric. Res. 26: 481.
- Evans, G.C. (1972). The quantitative analysis of plant growth. I. Studies in ecology. Blackwell Scient. Publ., Oxford.
- Evans, S. (1964). The herbicidal control of broad-leaved and grass weeds in established grassland. J. Br. Grassld. 19: 205.
- Eyles, G.O., Shelton, H.M., Buranviriyakul, S. and Suksri, A. (1973). Fertilizer studies on forage legumes in Northeast Thailand. Thai. J. Agric. Sci. 6: 35.-

- Falvey, J.L., Gibson, T.A. and Andrew, A.C. (1984). Animal production from improved pastures in the Thai highlands. *World Animal Reviews* 49: 13.
- Fisher, M.J. (1969). The growth and development of Townsville stylo (*Stylosanthes humilis*) in ungrazed swards at Katherine, N.T., Australia. *Aust. J. Exp. Agric. Anim. Husb.* 9: 196.
- Fisher, M.J. (1970). The effect of super phosphate on the growth and development of Townsville lucerne (*Stylosanthes humilis*) in pure ungrazed sward at Katherine. *Aust. J. Exp. Agric. Anim. Husb.* 10: 716.
- Fisher, M.J. (1973). Effect of time, height and frequency of defoliation on growth and development of Townsville stylo in pure ungrazed swards at Katherine, N.T. *Aust. J. Exp. Agric. Anim. Husb.* 13: 389.
- Fisher, M.J. (1980). The influence of water stress on nitrogen and phosphorus uptake and concentrations in Townsville stylo (*Stylosanthes humilis*). *Aust. J. Exp. Agric. Anim. Husb.* 20: 175.
- Fisher, M.J. (1983). Responses of Siratro to water stress. *J. Aust. Inst. Agric. Sci.* 49: 161.
- Fisher, M.J. and Campbell, N.A. (1977). The influence of water stress on the growth and development of Townsville stylo (*Stylosanthes humilis*) in pure, ungrazed sward at Katherine, Northern Territory. *Aust. J. Exp. Agric. Husb.* 17: 598.
- Fisher, M.J. and Ludlow, M.M. (1982). Responses of Siratro (*Macroptilium atropurpureum*) to water stress. *Proc. XIV Int. Grassld. Congr. 1981, Lexington, KY, USA.* Westview Press, Boulder, Colorado. Pp. 396 - 398.

- Fisher, M.J. and Ludlow, M.M. (1984). Adaptation to water deficits in Stylosanthes. In: The Biology and Agronomy of Stylosanthes. Eds. H.M. Stace and L.A. Edye. Academic Press, Australia: pp. 163 - 179.
- Ford, C.W. (1982). Accumulation of o-methyl-inositols in water-stressed Vigna species. Phytochemistry 21: 1149.
- Ford C.W. and Wilson, J.R. (1981). Changes in levels of solute during osmotic adjustment to water stress in leaves of four tropical pasture species. Aust. J. Plant Physiol. 8: 77.
- Gaff, D.F. (1980). Protoplasmic tolerance of extreme water stress. In: Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J. Kramer. Wiley-Interscience, New York: pp. 207 - 230.
- Gardener, C.J. (1975). Mechanisms regulating germination in seed of Stylosanthes. Aust. J. Agric. Res. 26: 281.
- Gardener, C.J. (1978). Seedling growth characteristics of Stylosanthes. Aust. J. Agric. Res. 29: 803.
- Gardener, C.J. (1980). Diet selection and liveweight performance of steers of Stylosanthes hamata - native grass pastures. Aust. J. Agric. Res. 31: 379.
- Gardener, C.J. (1981). Population dynamics and stability of Stylosanthes hamata cv Verano in grazed pastures. Aust. J. Agric. Res. 32: 63.
- Gardener, C.J., Megarrity, R.G. and McLeod, M.N. (1982). Seasonal changes in proportion and quality of plant parts of nine Stylosanthes lines. Aust. J. Exp. Agric. Anim. Husb. 22: 391.

- Gates, C.T. (1968). Water deficit and growth of herbaceous plants, in: Water Deficit and Plant Growth, Vol II, Ed. T.T. Kozlowski: pp. 135 - 190.
- Gates, C.T. (1974). Nodule and plant development in Stylosanthes humilis H.B.K.: symbiotic responses to phosphorus and sulphur. Aust. J. Bot. 22: 45.
- Gilbert, M.A. and Shaw, K.A. (1980). The effect of superphosphate application on establishment and persistence of three Stylosanthes spp. in native pasture on an infertile Duplex soil near Mareeba, North Queensland. Trop. Grassld. 14: 25.
- Gillard, P. (1983). The dry tropics - the kangaroo story. in: The Role of Centrosema, Desmodium and Stylosanthes in Improving Tropical pastures. Eds. R.L. Burt, P.P. Rotar, J.L. Walker and M.W. Silvey. Westview Tropical Agriculture Series, No. 6: pp. 23 - 27.
- Gillard, P. and Fisher, M.J. (1978). The ecology of Townsville stylo based pastures in Northern Australia. in: Plant Relations in Pastures, Ed. J.R. Wilson, C.S.I.R.O., Australia: pp. 340 - 352.
- Gillard, P., Edye, L.A. and Hall, R.L. (1980). Comparison of Stylosanthes humilis and S. hamata and S. subsericea in the Queensland dry tropics: effects on pasture composition and cattle liveweight gain. Aust. J. Agric. Res. 31: 205.
- Graber, L.F., Nelson, N.T., Luckel, W.A. and Albert, W.B. (1927). Organic food reserves in relation to the growth of alfalfa and other perennial herbaceous plants. Wisconsin Agricultural Experiment Station, Bulletin No. 80.

Grof, P., Harding, W.A.T. and Woolcock, R.F. (1970).

Effects of cutting on three ecotypes of Stylosanthes guianensis. Proc. XIth Int. Grassld. Congr., Surfers Paradise, Australia: pp. 226 - 230.

Gutteridge, R.C. (1978). Effect of phosphorus and sulphur fertilizers on the growth of Stylosanthes species on five soil types in northern Thailand. Pasture Improvement Project Ann. Rept., Khon Kaen University: pp. 78 - 79.

Gutteridge, R.C. (1982). The productivity and pathways of persistence of legumes sown in grazed native pasture situations in northeast Thailand. Ph.D. Thesis, University of Queensland, Australia.

Gutteridge, R.C. and Whiteman, P.C. (1975). Effect of defoliation frequency on growth and survival of four accessions of Psoralea eriantha. Aust. J. Exp. Agric. Anim. Husb. 15: 493.

Hall, R.L. (1971). The influence of potassium supply on competition between Nandi setaria and Greenleaf desmodium. Aust. J. Exp. Agric. Anim. Husb. 11: 415.

Hall, T.J. (1979). Initial evaluation of Stylosanthes spp. on two soils of Mayvale land system, North-west Queensland. Trop. Grassld. 13: 9.

Hare, M.D. (1985). Tropical Pasture Seed Production for Village Farmers in South-east Asia. DSIR, Palmerston North, New Zealand. 41 pp.

Hare, M.D. (1986). Personal communication.

Harris, W. (1978). Defoliation as a determinant of the growth, persistence and composition of pasture, in: Plant Relations in Pastures, Ed. J.R. Wilson. CSIRO, Melbourne: p. 67.

- Haslemore, R.M. and Roughan, R.G. (1976). Rapid chemical analysis of some plant constituents. *J. Sci. Fd. Agric.* 27: 1171.
- Hatrlick, A.A. and Bowling, D.J.F. (1973). A study of the relationship between root and shoot metabolism. *J. Exp. Bot.* 24: 607.
- Hendy, K. (1971). The performance of a pangola grass/Townsville stylo pasture near Darwin. *J. Aust. Inst. Agric. Sci.* 37: 65.
- Henzell, E.F. (1977). Nitrogen nutrition of tropical pasture, in: Tropical Forage Legumes, Ed. P.J. Skerman. F.A.O., Rome. Pp. 86 - 102.
- Hodgkinson, K.C. and Williams, D.W. (1978). Adaptation to grazing in forage plants. In: Genetic Resources of Forage Plants, Eds. J.G. McIvor and R.A. Bray: pp. 85 - 100.
- Hodgson, J. (1979). Nomenclature and definition in grazing studies. *Grass and Forage Science* 34: 11.
- Hsiao, T.C. (1973). Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24: 519.
- Humphreys, L.R. (1966a). Pasture defoliation practice - a review. *J. Aust. Inst. Agric. Sci.* 32: 92.
- Humphreys, L.R. (1966b). Sub-tropical grass growth. 2. Effects of variation in leaf area index in the field. *Qld. J. Agric. Anim. Sci.* 23: 337.
- Humphreys, L.R. (1967). Townsville lucerne: history and prospect. *J. Aust. Inst. Agric. Sci.* 35: 3.
- Humphreys, L.R. (1978a). Pasture research in Thailand: an Australian role. *J. Aust. Inst. Agric. Sci.* 44: 180.

- Humphreys, L.R. (1978b). Tropical Pasture and Fodder Crops. Longman, London.
- Humphreys, L.R. (1980a). A Guide to better Pasture for the Tropics and Sub-tropics. 4th edn. Wright Stephenson Sydney.
- Humphreys, L.R. (1980b). Deficiencies of adaptation of pasture legumes. Trop. Grassld. 14: 153.
- Humphreys, L.R. (1981). Environmental Adaptation of Tropical Pasture Plants, Macmillan, London.
- Humphreys, L.R. (1982). Perspectives on the adaptation of pasture legumes to tropical farming systems. Outlook on Agriculture 11: 144.
- Humphreys, L.R. (1984). Global ventures in Stylosanthes V. South-East Asia. In: The Biology and Agronomy of Stylosanthes, Eds. H.M. Stace and L.A. Edye. Academic Press: pp. 529 - 534.
- Humphreys, L.R. and Robinson, A.R. (1966). Subtropical grass growth. I. Relationship between carbohydrate accumulation and leaf area in growth. Qld. J. Agric. Anim. Sci. 23: 211.
- Hunt, R. and Parsons, I.T. (1977). Plant growth analysis: further applications of a recent curve-fitting program. J. App. Ecol. 14: 965.
- Hunter, R.A., McIntyre, B.L. and McIlroy, R.J. (1970). Water soluble carbohydrates of tropical pasture grasses and legumes. J. Sci. Fd. Agric. 21: 400.
- Hutton, E.M. (1970). Tropical Pastures. Adv. Agron. 22: 1.
- Hutton, E.M. and Beal, L.B. (1977). Breeding of Macroptilium atropurpureum. Trop. Grassld. 11: 15.

- Imrie, B.C. (1971). The effects of severity of defoliation and soil moisture stress on Desmodium intortum. Aust. J. Exp. Agric. Anim. Husb. 11: 521.
- Imrie, B.C., Jones, R.M. and Kerridge, P.C. (1983). Desmodium. In: The Role of Centrosema, Desmodium and Stylosanthes in Improving Tropical Pastures. Eds. R.L. Burt, P.P. Rotar, J.L. Walker and M.W. Silvey. Westview Tropical Agriculture Series, No. 6: pp. 97 - 140.
- Ive, J.R. (1974). Effect of mechanical defoliation on botanical composition and yield of a Townsville stylosabi grass sward. Aust. J. Exp. Agric. Anim. Husb. 14: 758.
- Jacques, W.A. and Edmond, D.B. (1952). Root development in some common New Zealand pasture plants. V. The effect of defoliation and root pruning on cocksfoot (Dactylis glomerata) and perennial ryegrass (Lolium perenne). N.Z. J. Sci. Technol. 34: 231.
- Jantii, A. and Heinonen, R. (1957). Effect of defoliation and soil moisture on grassland re-growth. J. Brit. Grassld. Soc. 12: 56.
- Jantii, A. and Kramer, P.J. (1957). Regrowth of pastures in relation to soil moisture and defoliation. Proc. VII Int. Grassld. Congr., pp. 33 - 42.
- Jantakool, S. (1983). A study of the effects of plant spacing and irrigation on seed production and seed development in Siratro. Ph.D. Thesis, Massey University, Palmerston North, New Zealand.
- Jameson, D.A. (1963). Response of individual plants to harvesting. Bot. Rev. 29: 532.
- Jehne, W. (1984). Mycorrhizas and Stylosanthes. In: The Biology and Agronomy of Stylosanthes. Eds. H.M. Stace and L.A. Edye. Academic Press, Australia: p. 227.

- Jones, C.A. and Carabaly, A. (1981). Some characteristics of the regrowth of 12 tropical grasses. Trop. Agric. (Trinidad) 58: 37.
- Jones, R.J. (1965a). Nutrient requirements of improved pasture on podzolic soil developed in phyllite at North Deep Creek. Trop. Grassld. Soc. Aust. Proc. No. 6: 23.
- Jones, R.J. (1965b). The use of cyclodiene insecticides as liquid seed dressings to control bean fly (Melanagromyza phaseoli) in species of Phaseolus and Vigna marina. Aust. J. Exp. Agric. Anim. Husb. 7: 157.
- Jones, R.J. (1967). Effects of close cutting and nitrogen fertilizer on growth of Siratro (Phaseolus atropurpureus) pasture at Samford, southeastern Queensland. Aust. J. Exp. Agric. Anim. Husb. 7: 157.
- Jones, R.J. (1972). The place of legumes in tropical pastures. ASPAC Fd. Fertil. Technol. Cent. Tech. Bull. No. 9.
- Jones, R.J. (1973). The effect of frequency and severity of cutting on yield and persistence of Desmodium intortum cv. Greenleaf in a subtropical environment. Aust. J. Exp. Agric. Anim. Husb. 13: 171.
- Jones, R.J. (1974). Effect of previous cutting interval and of leaf area remaining after cutting on regrowth of Macroptilium atropurpureus cv. Siratro. Aust. J. Exp. Agric. Anim. Husb. 14: 343.
- Jones, R.J. and Jones, R.M. (1971). Agronomic factors in pasture and forage crops production in tropical Australia. Trop. Grassld. 5: 229.
- Jones, R.J., Griffiths, D. and Waite, R.B. (1967). The contribution of some tropical legumes to pasture yields of dry matter and nitrogen at Samford, Southeast Queensland. Aust. J. Exp. Agric. Anim. Husb. 7: 57.

- Jones, R.K. (1974). A study of phosphorus response of a wide range of accessions from the genus Stylosanthes. Aust. J. Agric. Res. 25: 847.
- Jones, R.M. (1973a). Dynamics of Siratro. Annual Report, C.S.I.R.O., Div. Trop. Agron. 1972 - 1973: p. 14.
- Jones, R.M. (1973b). Seedling death of Desmodium intortum in the Queensland wallum with special reference to potassium chloride fertilizer. Trop. Grassld. 7: 269.
- Kessler, D.J. and Shelton, H.M. (1980). Dry season legume forages to follow paddy rice in N.E. Thailand. III. Influences of time and intensity of cutting on Crotalaria juncea. Expl. Agric. 16: 207.
- Keya, N.C.O., Olsen, F.J. and Holliday, R. (1971). The role of superphosphate in the establishment of oversown tropical legumes in natural grasslands of Western Kenya. Trop. Grassld. 5: 109.
- Keya, N.C.O., Olsen, F.J. and Holliday, R. (1972). Comparison of seed beds for oversowing of Chloris gayana (Kunth.) Desmodium uncinatum (Jacq.) mixture in Hyparrhenia grassland. E. Afri. Agric. For. J. 37: 286.
- Lee, C. and Smith, D. (1972). Changes in the concentration of nitrogenous fractions in alfalfa herbage with advancing maturity. Agron. J. 64: 326.
- Lenne, J.M. and Sonoda, R.M. (1979). The occurrence of Colletotrichum spp. on Stylosanthes spp. in Florida and the pathogenicity of Florida and Australian isolates Stylosanthes spp. Trop. Grassld. 13: 98.
- Leach, G.J. (1967). The growth of the lucerne plant after cutting: the effects of cutting at different stages of maturity and at different intensities. Aust. J. Agric. Res. 19: 517.

- Little, T.M. and Hills, F.J. (1975). Statistical Methods in Agricultural Research. University of California: Davis. P. 242.
- Ludlow, M.M. (1980a). Stress physiology of tropical pasture plants. Trop. Grassld. 14: 136.
- Ludlow, M.M. (1980b). Adaptive significance of stomatal responses of water stress. In: Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J.Kramer. Wiley-Interscience, New York: pp. 123 - 38.
- Ludlow, M.M. and Charles-Edwards, D.A. (1980). Analysis of the regrowth of a tropical grass/legume sward subjected to differing frequencies and intensities of defoliation. Aust. J. Agric. Res. 31: 673.
- Ludlow, M.M. and Ibaraki, K. (1979). Stomatal control of water loss in Siratro (Macroptilium atropurpureum (DC) Urb), a tropical pasture legume. Ann. Bot. 43: 639.
- Ludlow, M.M. and Ng, T.T. (1976). Effect of water deficit on carbon dioxide exchange and leaf elongation rate of Panicum maximum var. trichoglume. Aust. J. Pl. Physiol. 3: 401.
- Ludlow, M.M. and Ng, T.T. (1977). Leaf elongation rate in Panicum maximum var. trichoglume following removal of water stress. Aust. J. Plant Physiol. 4: 263.
- Ludlow, M.M. and Wilson, G.L. (1970). Growth of some tropical grasses and legumes at two temperatures. J. Aust. Inst. Sci. 36: 43.
- Ludlow, M.M., Chu, A.C.P., Clements, R.J. and Kerslake, R.G. (1983). Adaptation of species of Centrosema to water stress. Aust. J. Plant Physiol. 10: 119.

- Loch, D.S. and Humphreys, L.R. (1970). Effects of stage of defoliation on seed production and growth of Stylosanthes humilis. Aust. J. Exp. Agric. Anim. Husb. 10: 577.
- Loch, D.S., Hopkinson, J.M. and English, B.H. (1976). Seed production of Stylosanthes guyanensis. I. Growth and development. Aust. J. Exp. Agric. Anim. Husb. 16: 218.
- Mackay, J.H.E. (1975). Register of Australian herbage plant cultivars. B. Legume: 12. Stylo. J. Aust. Inst. Agric. Sci. 41: 271.
- Mannetje, L.'t (1969). Rhizobium affinities and phenetic relationships within the genus Stylosanthes. Aust. J. Bot. 17: 553.
- Mannetje, L.'t (1978). The role of improved pastures for beef production in the tropics. Trop. Grassld. 12: 1.
- Mannetje, L.'t (1984). Considerations on the taxonomy of the genus Stylosanthes. In: The Biology and Agronomy of Stylosanthes. Eds. H.M. Stace and L.A. Edye. Academic Press, Australia: pp. 1 - 21.
- Mannetje, L.'t, O'Connor, K.F. and Burt, R.L. (1980). The use and adaptation of pasture and fodder legumes. In: Advances in Legume Science. Eds. R.J. Summerfield and A.H. Bunting. Royal Botanical Garden, Kew, London: pp. 537 - 551.
- May, L.H. (1960). The utilization of carbohydrate reserves in pasture plants after defoliation. Herb. Abstr. 30: 239.
- McCown, R.L., Gillard, P. and Edye, L.A. (1974). The annual variation in yield of pastures in the seasonally dry tropics of Queensland. Aust. J. Exp. Agric. Anim. Husb. 14: 328.

- McIlroy, R.J. (1967). Carbohydrates of grassland herbage. Herb. Abstr. 37: 79.
- McIvor, J.G. (1976). Germination characteristics of seven Stylosanthes species. Aust. J. Exp. Agric. Anim. Husb. 16: 723.
- McIvor, J.G. (1979). Seasonal changes in nitrogen and phosphorus concentrations and in vitro digestibility of Stylosanthes species and Centrosema pubescens. Trop. Grassld. 13: 92.
- McKeague, P.J. and Holmes, A.E. (1979). 21 months of grazing stylo in the dry tropics. Qld. Agric. J. 105: 109.
- McKeague, P.J., Hiller, C.P. and Anning, P. (1978). Verano stylo - a new stylo for the dry tropics. Qld. Agric. J. 104: 31.
- McLeod, C.C. (1962). Pasture renovation and crop establishment with aid of chemicals. N.Z. J. Agric. 104: 479.
- Middleton, C.H. (1973). Oversowing legumes into grass swards. Qld. Agric. J. 99: 217.
- Milford, R. (1967). Nutritive values and chemical composition of seven tropical legumes and lucerne grown in subtropical south-eastern Queensland. Aust. J. Exp. Agric. Anim. Husb. 7: 540.
- Milford, R. and Minson, D.J. (1966). The feeding value of tropical pastures. In: Tropical Pastures. Eds. W. Davies and C.R. Skidmore. Faber and Faber, London: p. 106.
- Miller, H.P. (1967). The effect of pre-treatment of native pasture and sowing rate on establishment of Townsville lucerne on Trippera clay loam at Katherine, N.T. Aust. J. Exp. Agric. Anim. Husb. 7: 515.

- Miller, H.P. and Perry, R.A. (1968). Preliminary studies on the establishment of Townsville lucerne (Stylosanthes humilis) in uncleared native pasture at Katherine, N.T. Aust. J. Exp. Agric. Anim. Husb. 8: 26.
- Milthorpe, F.L. and Davidson, J.L. (1966). Physiological Aspects of Regrowth in Grass in the Growth of Cereals and Grasses. Eds. F.L. Milthorpe and J.D. Ivins. Butterworths Scientific Publications, London. Pp. 357.
- Minson, D.J. and McLeod, M.N. (1970). The digestibility of temperate and tropical grasses. Proc. XIth Int. Grassl. Congr., Surfers Paradise, Austr: p. 719.
- Mohlenbrock, R.H. (1958). A revision of the genus Stylosanthes. Ann. Mo. Bot. Gard. 44: 299.
- Mott, J.J. (1979). High temperature contact treatment of hardseed in Stylosanthes. Aust. J. Agric. Res. 30: 847.
- Mott, J.J. McKeon, G.M. and Moor, C.J. (1976). Effect of seedbed conditions on the germination of four Stylosanthes species in the Northern Territory. Aust. J. Agric. Res. 27: 811.
- Mott, J.J., McKeon, G.M., Gardener, C.J. and Mennetje, L.'t (1981). Geographic variation in the reduction of hard seed content of Stylosanthes seed in the tropics and subtropics in northern Australia. Aust. J. Agric. Res. 32: 861.
- Mufandaedza, O.T. (1976). Effects of frequency and height of cutting on some tropical grasses and legumes. II. Stylosanthes guianensis (Anbl.) S.W. Rhod. J. Agric. Res. 14: 79.
- Murphy, W.M., Scholl, J.M. and Baretto, I. (1979). Effects of cutting management on eight sub-tropical pasture mixtures. Agron. J. 69: 662.

- Murray, R.M. (1983). Plant-animal relationships. In: The Role of Centrosema, Desmodium and Stylosanthes in Improving Tropical Pastures. Eds. R.L. Burt, P.P. Rotar, J.L. Walker and M.W. Sivey. Westview Tropical Agriculture Series, No. 6: pp. 227 - 229.
- Murtagh, G.J. (1963). Herbicides as an aid to the establishment of sod-sown Glycine javanica. Aust. J. Exp. Agric. Anim. Husb. 3: 173.
- National Academy of Science (1977). Leucaena. Promising Forage and Tree Crop for the Tropics. Washington D.C.
- Nelson, C.J. and Smith, D. (1968). Growth of Birdsfoot trefoil and alfalfa. III. Changes in carbohydrate reserves and growth analysis under field conditions. Crop Sci. 8: 251.
- Nelson, C.J. and Smith, D. (1969). Growth of Birdsfoot trefoil and alfalfa. IV. Carbohydrate reserve levels and growth analysis under two temperature regimes. Crop Sci. 9: 589 - 591.
- Noble, A. and Lowe, K.F. (1974). Alcohol soluble carbohydrates in various tropical and temperate pasture species. Trop. Grassld. 8: 179.
- Norman, M.J.T. (1962). Response of native pasture to nitrogen and phosphate fertilizer at Katherine, N.T. Aust. J. Exp. Agric. Anim. Husb. 2: 27.
- Norman, M.J.T. (1965). Postestablishment grazing management of Townsville lucerne on uncleared land at Katherine, N.T. J. Aust. Inst. Agric. Sci. 31: 311.
- Norman, M.J.T. and Phillips, L.J. (1970). Wet season grazing of Townsville stylo pasture at Katherine, N.T. Aust. J. Exp. Agric. Anim. Husb. 16: 710.

- Norris, I.B. and Thomas, H. (1982a). Recovery of ryegrass species from drought. *J. Agric. Sci., Camb.* 98: 623.
- Norris, I.B. and Thomas, H. (1982b). The effects of cutting on regrowth of perennial ryegrass selections exposed to drought conditions. *J. Agric. Sci., Camb.* 99: 547.
- Olsen, F.J. (1973). Effects of cutting management on a Desmodium intortum/Setaria sphacelata mixture. *Agron. J.* 65: 714.
- Olsen, F.J. and Moe, P.G. (1971). The effect of phosphate and lime on the establishment, productivity, nodulation and persistence of Desmodium intortum, Medicago sativa and Stylosanthes gracilis. *E. Afri. Agric. For. J.* 37: 29.
- O'Reilly, M.V. (1975). Better Pastures for the Tropics. Arthur Yates and Co. Pty. Ltd. 1st Edition: pp. 60.
- Oswalt, D.L., Bertrand, A.R. and Teel, M.R. (1959). Influence of nitrogen fertilization and clipping on grass roots. *Soil Sci. Soc. Am. Proc.* 23: 228.
- Pearen, J.R. and Koeghan, J.M. (1982). A review of factors influencing successful pasture renovation. *Trop. Agric.* 59: 179.
- Probert, M.E. (1984). The mineral nutrition of Stylosanthes. In: The Biology and Agronomy of Stylosanthes. Eds. H.M. Stace and L.A. Edye. Academic Press. Pp. 203 - 226.
- Peake, D.C.I., Stirk, G.D. and Henzell, E.F. (1975). Leaf water potentials of pasture plants in a semi-arid environment. *Aust. J. Exp. Agric. Anim. Husb.* 15: 645.
- Pongsakul, V., Wiliaipon, B. and Gutteridge, R.C. (1982). Undersowing upland crops with pasture legumes. II. Kenaf with Stylosanthes hamata cv Verano. *Thai J. Agric. Sci.* 15: 7.

- Reid, R.L., Post, A.J., Olsen, F.J. and Mugerwa, J.S. (1973).
Studies on the nutritional quality of grasses and legumes in Uganda. I. Application of in vitro digestibility techniques to species and stage of growth effects. Trop. Agric. (Trinidad) 50: 1.
- Ritson, J.B., Edye, L.A. and Robinson, P.J. (1971).
Botanical and chemical composition of a Townsville stylo spear grass pasture in relation to conception rate of cows. Aust. J. Agric. Res. 22: 993.
- Robertson, A.D. (1978). Terminal Report: Northeast Livestock Development Project, Tha Phra, Thailand.
- Robertson, A.D., Humphreys, L.R. and Edwards, D.G. (1976).
Influence of cutting frequency and phosphorus supply on the production of Stylosanthes humilis and Arundinaria pusilla at Khon Kaen, Northeast Thailand. Trop. Grassld. 10: 33.
- Robinson, P.J. (1983). Comparative edaphic requirements.
In: The Role of Centrosema, Desmodium and Stylosanthes in Improving Tropical Pastures. Ed. R.L. Burt, P.P. Rotar, J.L. Walker and M.W. Silvey. Westview Tropical Agriculture Series No. 6. Pp. 189 - 195.
- Robinson, D.W. and Jones, R.J. (1972). The effect of phosphorus and sulphur fertilization on the growth and distribution of dry matter, nitrogen, phosphorus and sulphur in Townsville stylo (Stylosanthes humilis). Aust. J. Agric. Res. 23: 633.
- Rossiter, R.C. (1961). The influence of defoliation on the components of seed yield in swards of subterranean clover (Trifolium subterraneum L.). Aust. J. Agric. Res. 12: 821.

- Ruaysoongnern, S. (1978). An examination of nitrogen fixation by accessions of Stylosanthes hamata with native rhizobium in two upland soils. Pasture Improvement Project Annual Report, Khon Kaen University: pp. 89 - 93.
- Shaw, N.H. (1961). Increased beef production from Townsville lucerne (Stylosanthes sundiaca Taub.) in the spear grass pastures of central coastal Queensland. Aust. J. Exp. Agric. Anim. Husb. 1: 73.
- Shaw, N.H. and Bissett, W.J. (1955). Characteristics of a Bunch Spear grass (Heteropogon contortus (L.) B canv.) pasture grazed by cattle in sub-tropical Queensland. Aust. J. Agric. Res. 6: 539.
- Shelton, H.M., Gutteridge, R.C., Wilaipon, N., Wickham, B., Kratzing, D.C. and Waring, S.A. (1979). Nutrient studies on pasture soils of North-eastern Thailand. Thai J. Agr. Sci. 12: 235.
- Sheriff, D.W. and Kaye, P.E. (1977). Responses of diffusive conductance to humidity in a drought avoiding and a drought resistant (in terms of stomatal response) legume. Ann. Bot. 41: 653.
- Sheriff, D.W. and Ludlow, M.M. (1984). Physiological reactions to an imposed drought by Macroptilium atropurpureum and Cinchrus ciliaris in a mixed sward. Aust. J. Plant Physiol. 11: 23.
- Skerman, P.J. (1977). Tropical Forage Legumes. F.A.O., Rome.
- Slatyer, R.O. (1973). In: Plant Response to Climatic Factors. Ed. R.O. Slatyer, UNESCO, Paris: pp. 177 - 191.
- Smith, C.J. (1967). Sowing dryland pastures. Rhodesia Agric. J. 64: 69.

- Smith, D. (1973). The nonstructural carbohydrates. In: Chemistry and Biochemistry of Herbage. Eds. G.W. Butler and R.W. Bailey. Academic Press. Vol. I. Pp. 105 - 156.
- Smith, D. and Nelson, C.J. (1967). Growth of birdsfoot trefoil and alfalfa. I. Responses to height and frequency of cutting. Crop Sci. 7: 130.
- Staples, B. (1981). The technology of Townsville stylo (Stylosanthes humilis): a continuing need? J. Aust. Inst. Agric. Sci. 47: 200.
- Stern, W.R. and Donald, C.M. (1962). The influence of leaf area and radiation on the growth of clover in swards. Aust. J. Agric. Res. 13: 615.
- Stobbs, T.H. (1974). Rate of biting of Jersey cows as influenced by the yield and maturity of pasture swards. Trop. Grassld. 8: 81.
- Stonard, P. (1969). Effect of sowing depth on seedling emergence of three species of Stylosanthes. Qld. J. Agric. Anim. Sci. 26: 65.
- Teitzel, J.K. (1975). Maintenance fertilizer strategies for tropical pastures. In: Refresher Course Management of Improved Tropical Pasture. Univ. of Qld: pp. 123 - 132.
- Thai Dairy Production and Organization (1984). Thai Dairy Promotion and Organization of Thailand. Annual Report, 1984 - 1985.
- Topark-Ngarm, A. and Akkasaeng, R. (1978). Effects of seeding rate and cutting frequency on forage yields of four Stylosanthes species. Annual Report, Khon Kaen University Pasture Improvement Project, Khon Kaen, Thailand: p. 14.

- Topark-Ngarm, B., Aitken, R.L., Hughes, J.D. and Soonthonsorn, S. (1979). Annual Report, Khon Kaen University Pasture Improvement Project, Khon Kaen, Thailand: p. 99.
- Torrsell, B.W.R. (1973). Patterns and Processes in the Townsville stylo-annual grass ecosystem. *J. Appl. Ecol.* 10: 463.
- Torrsell, B.W.R. and McKeon, G.M. (1976). Germination effects on pasture composition in a dry monsoonal climate. *J. Appl. Ecol.* 13: 593.
- Torrsell, B.W.R., Ive, J.R. and Cunningham, R.B. (1976). Competition and population dynamics in legume-grass swards with Stylosanthes hamata (L.) Taub. (sens. lat.) and Stylosanthes humilis (H.B.K.). *Aust. J. Agric. Res.* 27: 71.
- Torrsell, B.W.R., Begg, J.E., Rose, C.W. and Bryne, G.F. (1968). Stand morphology of Townsville lucerne (Stylosanthes humilis) seasonal growth and root development. *Aust. J. Exp. Agric. Anim. Husb.* 8: 533.
- Troughton, A. (1957). The underground organs of herbage grasses. Bull. No. 44, C'wealth Bur. Pastures and Field Crops, Hurley, U.K.
- Tudsri, S. (1980). Principles of Tropical Pasture Science. Aksornasian Publishing, Bangkok. 450 pp. (in Thai).
- Tudsri, S. and Whiteman, P.C. (1977a). The effect of cultural treatments on establishment of Macroptilium atropurpureum cv. Siratro oversown in a Setaria anceps sward. *Trop. Grassld.* 11: 49.

- Tudsri, S. and Whiteman, P.C. (1977b). Effects of initial and maintenance of phosphorus levels on the establishment of four legumes oversown into Setaria anceps swards. Aust. J. Exp. Agric. Anim. Husb. 17: 629.
- Turner, W.C. (1974). Stomatal response to light and water under field conditions. Royal Soc. of N.Z. Wel. Bul. 12: 423.
- Turner, W.C. and Begg, J.E. (1978). Responses of pasture plants to water deficits. In: Plant Relations in Pastures. Ed. J.R. Wilson, C.S.I.R.O., Melbourne: pp. 50.
- Udchachon, S. (1985). M. Agr. Sci. Thesis, Massey University.
- Ueno, M. and Smith, D. (1970). Growth and carbohydrate changes in the root wood and bark of different sized alfalfa plants during regrowth after cutting. Crop Sci. 10: 396.
- Vickery, P.J. (1981). Pasture growth under grazing. In: Grazing Animals. Ed. F.H.W. Morley, Elsevier Scientific Publishing Co., Amsterdam-Oxford-New York: pp. 55 - 57.
- Vinijsanond, T. and Topark-Ngarm, A. (1978). A study of the reaction of Stylosanthes sp. to Colletotrichum gloeosporioides. Annual Report, Khon Kaen University Pasture Improvement Project, Khon Kaen, Thailand: p. 26.
- Waikakul, P. (1983). A study of the effects of water and cutting on seed production of Verano stylo (Stylosanthes hamata) and Siratro (Macroptilium atropurpureum). Ph.D. Thesis, Massey University, Palmerston North, New Zealand.
- Ward, C.Y. and Blaser, R.E. (1961). Carbohydrate food reserves and leaf area in regrowth of orchardgrass. Crop Sci. 1: 366.

- Watkin, B.R. and Clements, R.J. (1978). The effects of grazing animals on pastures. In: Plant Relations in Pastures. Ed. J.R. Wilson, C.S.I.R.O., Melbourne: pp. 273 - 289.
- Watson, D.J. (1947). Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot. (Lond.)* 11: 41.
- Watson, D.J. (1952). The physiological basis of variation in yield. *Adv. Agron.* 4: 101.
- Weinmann, H. and Goldsmith, E.P. (1948). Underground reserves of Cynodon dactylon. In: Better Turf through Research. African Explosives and Chemical Ind. Ltd.
- White, J.G.H. (1972a). Pasture Establishment in Pastures and Pasture Plants. Ed. R.H.M. Langer. A.H. and A.W. Reed Ltd., Wellington-Sydney-London.
- White, R.E. (1972b). Studies on mineral ion absorption by plants. I. The absorption and utilization of phosphate by Stylosanthes humilis, Phaseolus atropurpureus and Desmodium intortum. *Pl. Soil* 36: 427.
- Whiteman, P.C. (1969). The effects of close grazing and cutting on the yield, persistence and nitrogen content of four tropical legumes with Rhodes grass at Samford, south-eastern Queensland. *Aust. J. Exp. Agric. Anim. Husb.* 9: 287.
- Whiteman, P.C. (1970). Seasonal changes in growth and nodulation of perennial tropical pasture legumes in the field. II. Effects of controlled defoliation levels on nodulation of Desmodium intortum and Phaseolus atropurpureus. *Aust. J. Agric. Res.* 21: 207.

- Whiteman, P.C. (1978). Tropical pastures - Australia's contribution to regional pasture research and development. ASPAC Fd. Fertili. Technol. Cent. Ext. Bull. No. 118.
- Whiteman, P.C. (1980). Tropical Pasture Science. Oxford University Press.
- Whiteman, P.C. and Lulham, A. (1970). Seasonal changes in growth and nodulation of perennial tropical pasture legumes in the field. I. The influence of planting date and grazing and cutting on Desmodium uncinatum and Phaseolus atropurpureus. Aust. J. Agric. Res. 21: 195.
- Wilaipon, B. (1980). Effect of fencing and cultivation on the establishment and growth of five forage legumes on private and commercial grazing areas in north-east Thailand. Annual Report, Khon Kaen University Pasture Improvement Project, Khon Kaen, Thailand: p. 34 - 37.
- Wilaipon, B. (1985). Establishment, cutting and grazing management and nutritive value of Stylosanthes hamata cv Verano. Memoirs of the Tokyo University of Agriculture 26: 135.
- Wilaipon, B. and Humphreys, L.R. (1981). Influence of grazing on the seed production of Stylosanthes hamata cv Verano. Thai J. Agric. Sci. 14: 69.
- Wilaipon, B. and Humphreys, L.R. (1983). Grazing effects on a mixed pasture in the year of planting. Thai J. Agric. Sci. 16: 27.
- Wilaipon, B. and Pongskul, V. (1983). Pasture establishment in the farming systems of northeast Thailand. ASPAC Ext. Bull. No. 199.

- Wilaipon, B., Gigir, S.A. and Humphreys, L.R. (1979). Apex, lamina and shoot removal effects on seed production and growth of Stylosanthes hamata cv. Verano. Aust. J. Agric. Res. 30: 293.
- Wilaipon, B., Gutteridge, R.C. and Chutikul, K. (1981). Undersowing upland crops with pasture legumes. I. Cassava with Stylosanthes hamata cv Verano. Thai J. Agric. Sci. 14: 333.
- Wilaipon, N., Aitken, R.L. and Hughes, J.D. (1981). The use of apical tissue analysis to determine the phosphorus status of Stylosanthes hamata cv Verano. Plant Soil 59: 141.
- Wilaipon, N., Gutteridge, R.C., Simpson, G.H., Homehurn, S. and Rogers, B. (1978). A salinity microsurvey on an Udon series soil and effect of differing soil salt concentrations on growth of pasture legumes. Thai J. Agric. Sci. 11: 297.
- Wilaipon, P. and Humphreys, L.R. (1976). Grazing and mowing effects on the seed production of Stylosanthes hamata cv Verano. Trop. Grassld. 10: 107.
- William, C.H. and Andrew, C.S. (1970). Mineral nutrition of pastures. In: Australian Grasslands. Ed. R.M. Moore. Aust. Nat. Press, Canberra: pp. 321 - 338.
- Williams, J. and Gardener, C.J. (1984). Environmental constraints to growth and survival of Stylosanthes. In: The Biology and Agronomy of Stylosanthes. Eds. H.M. Stace and L.A. Edye. Academic Press, Australia: pp. 181 - 201.
- Wilson, J.R. (1981). Effect of water stress on herbage quality. Proc. XIV Int. Grassld. Congr. Lexington, USA. Westview Press. P. 447.

- Wilson, J.R. (1983). Effects of water stress on in vitro dry matter digestibility and chemical composition of herbage of tropical pasture species. Aust. J. Agric. Res. 30: 377.
- Wilson, J.R. and Muchow, R.C. (1983). Effect of water stress on dry matter digestibility and concentrations of nitrogen and phosphorus in seven tropical grain legumes. J. Aust. Inst. Agric. Sci. 49: 167.
- Wilson, J.R. and Ng, T.T. (1975). Influences of water stress on parameters associated with herbage quality of Panicum maximum var. trichoglume. Aust. J. Agric. Res. 26: 127.
- Wilson, J.R., Ludlow, M.M., Fisher, M.J. and Schulze, E.D. (1980). Adaptations to water stress of leaf water relations characteristics of some tropical forage grasses and a legume in a semi-arid environment. Aust. J. Plant Physiol. 7: 207.
- Winkworth, R.E. (1969). Germination of Townsville lucerne (Stylosanthes humilis H.B.K.) in relation to weather at Katherine, N.T. J. Aust. Inst. Agric. Sci. 35: 201.
- Winter, W.H., Edye, L.A., Megarritty, R.G. and Williams, W.T. (1977). Effect of fertilizer and stocking rate on pasture and beef production from sown pastures in northern Cape York Peninsula. Aust. J. Exp. Agric. Anim. Husb. 17: 66.
- Yamada, T. (1975). Growth physiology of pasture plants and fodder crops. FFTC APAC Ext. No. 46.
- Young, N.D. and Robinson, A.R. (1963). Defoliation effects on legume growth and nitrogen uptake. Proc. IIIrd Aust. Grassld. Conf., C.S.I.R.O., Melbourne, Australia.