GROWTH STUDIES ON DEFOLIATED *LOTUS PEDUNCULATUS* cv. 'GRASSLANDS MAKU'.

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ABSTRACT

This thesis reports on a series of experiments designed to study the response of 'Grasslands Maku' to defoliation and thereby extend the understanding of growth and production of *Lotus pedunculatus*. Morphological structuring, production and nonstructural carbohydrate status of 'Grasslands Maku' were assessed for different defoliation regimes in two separate field experiments. The relative importance of several residual plant factors and assimilate partitioning in early shoot regrowth, was studied in controlled environmental conditions.

In the first field experiment, seasonal differences in the partitioning of growth were recorded, with the spring to mid-summer period being dominated by aerial shoot growth and the late-summer, autumn period by underground growth. Of the underground components, rhizome growth was the most responsive to seasonal and defoliation changes and it was this horizontal stem system that formed the basis of basal shoot initiation.

Canopy growth became increasingly dominated by rhizome shoots as cutting height and frequency decreased and stubble shoots, stubble and dead matter declined. Following defoliation, regrowth was consistently slow during the first two to three weeks, thus production increases were achieved where regrowth intervals were extended and subsequent, higher growth rates were allowed to be expressed. Higher cutting improved shoot regrowth, particularly in the stubble shoot pool, but increased within-canopy dry matter losses that were related to death and decomposition processes, resulted in little, if any improvement in net productivity.

Shoot regrowth responses resulting from higher cutting were primarily related to increases in the size of the residual shoot pools from which regrowth commenced. Residual shoot number and individual size were therefore important determinants of early regrowth. Any direct influence of residual nonstructural carbohydrate status on regrowth appeared to be principally confined to the rhizome shoot pool for the first few days of regrowth. The importance of accumulated starch would appear to be related to the provision of metabolic substrate for underground respiration during late autumn to early spring.

Where defoliation is incomplete, residual stubble would appear to be an important source of current and redistributed assimilates during early regrowth. Following defoliation, redistribution of carbon compounds to shoot growth was principally confined to the rhizome shoot pool. Total shoot growth increasingly dominated the partitioning of current assimilates as plants recovered from defoliation. Where defoliation is incomplete it is proposed that assimilate utilization is a more important limitation to early shoot regrowth than assimilate supply.

The defoliation responses recorded with 'Grasslands Maku' in these experiments are finally considered with regard to the role of *L. pedunculatus* in agriculture. Management guidelines are proposed and improved regrowth characteristics, necessary for any further extension of *L. pedunculatus* into grasslands farming, are suggested.

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CHAPTER 1. INTRODUCTION AND OBJECTIVES

In New Zealand, *Lotus pedunculatus* Cav. (syn: *Lotus uliginosus* Schk; *Lotus major* Scop. Sm.) has been an important pioneer legume in wet, infertile areas where other legumes have failed to establish or persist. It was considered to have been introduced into New Zealand between 1860 and 1870 (Thomson, 1922) and its early success as a component of seed mixtures oversown into unfertilized bush burn areas, was reported by Levy (1932). Levy (in MacDonald, 1946) further described the performance of *L.pedunculatus* in high rainfall, North Island areas as "splendid", particularly on loose textured hill country soils. By 1948, Saxby (1948) reported that the distribution of *L. pedunculatus* was widespread throughout high rainfall areas of New Zealand. At that time he recommended its use in moist, summer hill country where little or no topdressing was possible, and such a recommendation is still applicable.

L. pedunculatus has also been of value in the development of waterlogged, peat swamp lands in New Zealand (Levy, 1922). Saxby (1940) reported its use with *Holcus lanatus* L. in such conditions and more recently a similar pasture was advocated for the development of Westland Pakihi soils (During *et al*, 1964). In summarizing the place of *L. pedunculatus* in 'Grasslands of New Zealand', Levy (1970) considered its habitat to be soils of low to average fertility in very wet to average moisture conditions. He further considered it to be of good value on waterlogged, peat, heavy second class and wet hill land; moderate value on wet fertile land; little value on fertile and friable land; and useless on dry hill land.

In 1973, 'Grasslands Maku' tetraploid *L. pedunculatus* was released and placed on the New Zealand List of Acceptable Herbage Cultivars (Armstrong, 1974). With the release of this cultivar, and recent developments relating to soil fertility and insect problems, interest in *L. pedunculatus* , as a legume for both unimproved and improved pastures, has increased in New Zealand. The possibility of reduced phosphatic fertilizer inputs into grasslands farming has prompted interest in pasture plants better able to recover and/or efficiently use soil phosphate. The adaptability of *L. pedunculatus* to low

fertility conditions (Klapp, 1938; Crush, 1974; Nordmeyer & Davis, 1976) has been reported in the literature. Furthermore, *L. pedunculatus* has also been identified as being resistant to several insect pests, most notably grass grub *(Costelytra zealandica)* and porina *(Wiseana cervinata)* (Farrell & Sweeney, 1972, 1974). The possible use of this resistance in the development of pastures resistant to grass grub has been outlined by Kain and Atkinson (1975).

Because of these developments, it can be considered that the future role of *L. pedunculatus* in agriculture may extend further than that of being a pioneer legume. The ability of *L. pedunculatus* to successfully compete within defoliated, competitive pastures is poor however (Levy; in MacDonald, 1946), and recent work with 'Grasslands Maku' (Sheath *et al*, 1976; Brock & Charlton, 1977) confirms that the same problems of establishment and persistence still exist in mixed grazed swards on medium to high fertility soils. No published work has been specifically directed towards determining the growth pattern of *L. pedunculatus*, in order to identify the factors involved in its poor performance under these conditions. Similarly, in conditions where the relative competitive ability of *L. pedunculatus* is good, whole plant and/or herbage production responses to differential defoliation have not been determined. As such, there is little information upon which appropriate management schemes or breeding programmes can be based in order to achieve maximum persistence and/or productivity of *L. pedunculatus*. It was considered that to achieve these objectives, basic information on the response of *L. pedunculatus* to defoliation, was required.

This thesis reports on a series of experiments designed to determine the response of *L. pedunculatus* c v. 'Grasslands Maku' to defoliation. The objectives of this work were:

(i) To define the morphological characteristics of 'Grasslands Maku', and in terms of numbers and dry weights, determine the response of aerial and underground plant components to different defoliation regimes and seasonal changes.

(ii) To determine dry matter production levels and patterns in all aerial components during regrowth periods of several defoliation regimes.

(iii) To identify the principal plant factor(s) determining regrowth rates of 'Grasslands Maku' following defoliation.

(iv) To determine the pattern of assimilate partitioning between plant components of defoliated 'Grasslands Maku'.

The response of aerial and underground morphology and growth to different defoliation regimes and changing seasons was assessed in two field experiments involving pure 'Grasslands Maku' swards. From a pot experiment conducted in a controlled environment, more detailed information was provided as to the relative importance of residual leaves, shoots and nonstructural carbohydrates in early regrowth. Finally, C^{14} tracer techniques were used to determine the distribution and redistribution of carbon compounds following defoliation. In all experiments, plants that were studied possessed rhizomes and were therefore considered as established plants. Consequently, the results and discussions presented in this thesis are not relevant to establishing, non-rhizomatous seedlings.

CHAPTER 2. LITERATURE REVIEW

Literature pertaining to the nomenclature, morphology, breeding and agricultural importance and characteristics of *L. pedunculatus* is reviewed in the first section of this chapter. The extent of this information is limited however, and little of it specifically relates to the aspects considered in the series of experiments subsequently reported in this thesis. Therefore, literature that is relevant to the topics studied is reviewed in subsequent sections of this chapter with particular reference to other forage plants having similar growth characteristics to those of *L. pedunculatus*.

Patterns and relationships of plant component growth; defoliation management and dry matter production; nonstructural carbohydrates; and assimilate partitioning are aspects that are considered in these subsequent sections, particularly with regard to *Lotus corniculatus* L., *Medicago sativa* L. and *Coronilla varia* L. Considerable experimentation on the management of *L. corniculatus* has occurred in the past and as this legume is closely related to *L. pedunculatus*, literature on the former species is emphasised. Because of the extent of physiological experimentation and the understanding of shoot dynamics in *M. sativa*, this species is also reviewed in depth. Physiological and growth characteristics of *C. varia* appear to be intermediate between *L. corniculatus* and *M. sativa* and for this reason, appropriate literature on the former species is included.

2.1 *Lotus pedunculatus* (syn. *Lotus uliginosus*).

The Mediterranean basin was considered by Seaney and Henson (1970) to be the centre of origin of the genus *Lotus*, as it is in this region that the diversity of the eighty species within the genus, is greatest. Of these species, five were considered by MacDonald (1946) to be of agricultural importance, namely the annuals: *Lotus angustissimus* L. and *Lotus hispidus* Desf. and the perennials: *Lotus tenuis* Waldst., *Lotus corniculatus* L. and *Lotus uliginosus* Schk.

There has been, and still is considerable confusion surrounding the classification and nomenclature of *L. uliginosus* Schk. Workers in the early part of this century were reported by MacDonald (1946)

to have used *L. uliginosus* Schk. and *Lotus major* Scop. (Sm.) synonymously and more recently Clapham *et al.* (1962) and Healy (1976) considered that *L. pedunculatus* Cav. also referred to the same plant. In contrast, Ball (1968) in 'Flora Europaea' classified and discussed *L. uliginosus* Schk. and *L. pedunculatus* Cav. separately. He considered that the latter species was rare and confined to the Iberian peninsula, whereas *L. uliginosus* Schk. was distributed throughout Europe, the northern and eastern limits being 60^{o}N and 25^{o}E respectively.

Forde (1974) outlined the effect of this taxonomic confusion on nomenclature usage in New Zealand. 'Lotus major' has been the most popular common name and up until 1960, *L. uliginosus* Schk. was the specific name in use. Based on the principle of priority, *L. pedunculatus* Cav. was adopted subsequent to that date and it has persisted because of the uncertainty as to the existence of features that readily distinguish the two proposed species. At present *L. pedunculatus* Cav. is used in Australasia and North America, whereas *L. uliginosus* Schk. is used in Europe. Because of the general taxonomic uncertainty and current agronomic usage, *L. pedunculatus* Cav. will be used in a broad sense to include *L. uliginosus* Schk. Thus, the study plant reported in this thesis was considered as 'Grasslands Maku', *L. pedunculatus* Cav.

The most notable feature distinguishing *L. pedunculatus* from the remainder of the species in the genus *Lotus* is the initiation and growth of horizontal stems from an underground rootstock comprising a crown and taproot (MacDonald, 1946). Since this horizontal stem growth is predominantly underground, it is generally referred to as rhizome growth (Howell, 1948; Barnard, 1969; Levy, 1970). However, it is recognised that such growth can also occur above ground, particularly when associated with dense vegetation, and as such these stems have been referred to as stolons (Clapham *et al*, 1962; Barnard, 1969; Healy, 1976) or runners (MacDonald, 1946). This above ground form of lateral growth is most evident beneath matted, browntop growth or in mid-late summer beneath uncut lotus stands held for seed (Sheath, personal observation).

Branching rhizome systems, plus associated adventitious and nodal roots, result in a dense distribution of roots in the upper soil region (MacDonald, 1946) and leads to the turf forming habit of *L. pedunculatus* referred to by Howell (1948), Levy (1970) and Lambert *et al.* (1974). As well as continued rhizome branching from underground nodal sites, axillary shoot growth can also give rise to ascending stems (Howell, 1948) which can be described as decumbent within sparse vegetation but becoming more erect within dense growth (Barnard, 1969). While underground, these stems produce stunted scale-like leaves, but upon emergence from the soil, they develop the normal pentafoliate form (MacDonald, 1946). Within the genus *Lotus*, the number of leaflets per leaf varies from two to more than thirty (MacDonald, 1946). However, in *L. pedunculatus* there are five leaflets, three attached to the terminal, and two smaller ones to the base of the petiole. The stipules of this leaf system exist as small erect projections on the stem below the basal pair of leaflets. (MacDonald, *loc. cit.*; Heyn, 1976).

Axillary shoot growth can also occur at above ground nodal positions from the axils of expanded leaves and it is this habit which more clearly characterises the indeterminate, branching nature of growth in *L. pedunculatus*. From similar positions, under the stimulus of long days, reproductive organs develop (Thomas & Forde, 1967).

L. pedunculatus was recognised as a potential forage legume during the 18th and 19th centuries in Europe (MacDonald, 1946). However, active encouragement of its cultivation did not occur until the middle of last century when its use was advocated in the wetlands of France and Germany. Heddle and Ogg (1933) and Klapp (1938) reported that wet, acid, infertile soil conditions favoured the natural occurrence of *L. pedunculatus* in European pastures. In wet upland areas of Britain however, unsatisfactory performances of introduced *L. pedunculatus* have generally resulted from poor establishment and/or poor persistence due to heavy grazing or winter frosting (Thomas, 1935; Cowling, 1954; Copeman & Roberts, 1960; Davies, 1969). Only more recently has Charlton (1975) favourably reported on its potential usefulness when oversown into wet upland pastures of Scotland.

As in New Zealand, *L. pedunculatus* has been considered as a pioneer legume in the development of poorly drained, acid swamp areas in Australia (Filan, 1963; Macadam, 1966; Barnard, 1969). Barnard *(loc. cit.)* noted its ability to withstand prolonged submergence and its inability to tolerate drought. Thus, high rainfall and/or soil moisture were considered essential for satisfactory persistence and productivity.

On acid coastal soils of the N.W. Pacific region of North America, *L. pedunculatus* has persisted and produced in pastures of low pH and natural fertility where other legumes have failed (Howell, 1948). Similarly on wet, acid fragipan soils in Oregon, Heath (1969, 1970) reported the successful growth of *L. pedunculatus* in association with *Festuca arundinacea* Schreb. Under these conditions, Heath considered a more winter hardy ecotype had naturally developed, as cultivars suitable for coastal conditions had previously been winter killed in that locality. *L. pedunculatus* has also been used as a forage legume in Florida, although its susceptibility to diseases under moist, warm summer conditions has been a major limitation (Seaney & Henson, 1970).

O.E.C.D. acceptance of North American bred cultivars 'Columbia' and 'Beaver' occurred in 1967 (O.E.C.D., 1967) and more recently cv. 'Marshfield' was released (Billings & Swanson, 1974). This latter cultivar was recommended for use as a forage or stabilization legume on wet, fine textured, acid soils located in coastal uplands and grown in association with *Alopecurus pratensis* L., *Phleum pratense* L., or *Phalaris arundinacea* L.

Under low soil phosphate conditions, Brock (1973) recently identified *L. pedunculatus* as being more productive and better able to recover soil phosphate than 'Grasslands Huia' white clover. Similarly, superior phosphate uptake in *L. pedunculatus* has also been noted by Crush (1974) and he related this to greater root hair development relative to the other legumes studied. On acid soils, *L. pedunculatus* responds to lime less than white clover and although correction of soil pH may be beneficial, it is not essential for nodulation, establishment and growth of *L. pedunculatus* (Greenwood, 1961; Lowther, 1976). This greater tolerance of low pH soils would appear to be related to the acid tolerance of the alkali producing

Rhizobium lupini, specific to *L. pedunculatus* (Norris, 1965). Because of its adaptability to low phosphate and acid soil conditions, the use of *L. pedunculatus* has recently been advocated for the stabilization of acid subsoils (Nordmeyer & Davis, 1976) and the oversowing of acid tussock country (Lowther, 1976) in New Zealand.

Little experimental work reported in the literature specifically indicates the regrowth and production responses of *L. pedunculatus* to varying defoliation conditions. What relevant information there is available, generally develops indirectly from other forms of study or from general farming observations.

In pasture species evaluation work, Thomas (1935) reported that all established *L. pedunculatus* plants were lost under a hard grazing regime and in a similar situation Davies (1969) concluded that the regrowth ability of the species was poor. In a series of small cultivar evaluation trials, production was considered best when grazing pressure was low, particularly for the more vigorous, erect tetraploid cultivars (Barclay & Lambert, 1970). Lambert *et al.* (1974) made a similar statement based on improvements in lotus production that coincided with a change from set stocked to rotational sheep grazing. In another evaluation trial, Harris *et al.* (1973) were prompted to suggest that reductions in the tetraploid lotus component within their rotationally grazed swards were related to infrequent and then particularly severe defoliation. Cutting down to 2-3 cm, five to six times a year has also been suggested as being too severe to allow satisfactory regrowth and production of the *L. pedunculatus* cultivar, G4705 (Brock, 1973).

Howell (1948), when considering the use of this plant for wet acid conditions, stated that common management systems for *L. pedunculatus* involved pasturing in spring, followed by a silage and hay crop, with a return to pasturing in late autumn. Haying of spring growth and then grazing by beef cattle over the summer and autumn was also reported by Heath (1970) to encourage the spread and production of this legume. The management recommendations made for prostrate, *L. corniculatus* cultivars such as 'Empire', were considered to be appropriate for *L. pedunculatus* (Anon, 1967). Whereas continuous

grazing by cattle was considered unlikely to detrimentally affect stand production, the more selective and closer grazing habit of sheep necessitated the use of some deferred grazing system for this class of stock. However, with reference to wet, infertile situations where companion competition was likely to be minimal, Howell (1948) stated that even the closest pasturing by sheep over extended periods had not affected stand productivity.

The low competitive ability of *L. pedunculatus* was noted by Filan (1963) and he stressed the need to control companion growth when grown in mixed swards. Similarly, Bell (1940) indicated that ryegrass dominance during winter and early spring must be restricted to ensure the persistence of *L. pedunculatus* in mixed ryegrass swards. Maximum growth of *L. pedunculatus* was reported by Suckling (1960) and Levy (1970) to occur over summer, with little production occurring between late autumn and early spring, inclusive.

In New Zealand, a breeding and selection programme was instigated in 1951 to improve the agronomic performance of *L. pedunculatus* (Barclay , 1957). Its principal objectives were to extend cool season production, increase total dry matter yields and to increase seed size and therefore seedling vigor. Barclay (1959, 1960) reported on the progress of this programme and the final selections were outlined by Barclay & Lambert (1970).

Superior diploid New Zealand ecotypes were combined to produce 'G4701' and the colchicine treatment of this selection resulted in 'G4702', an autotetraploid with improved seed size and seedling vigour. Increased winter growth was based on the intervarietal hybridization of 'G4701' and winter active material from Caimbra, Portugal. Backcrosses of the F_1 hybrid to the New Zealand and Portugese parents resulted in 'G4703' and 'G4704' respectively. Finally an autotetraploid hybrid was produced by crossing 'G4702' (4N) with colchicine-treated Portugese material (4N) and then backcrossing to 'G4702'. From this backcross, thirteen élite plants were selected to form the nucleus of 'G4705', now named 'Grasslands Maku' tetraploid *Lotus pedunculatus* (Armstrong, 1974).

In the evaluation of these selections, Barclay & Lambert (1970) reported that seasonal production patterns principally reflected genetic parentage. Thus, as the Portugese content of the selections increased, summer growth was reduced and winter growth was improved. The development of tetraploid material doubled seed size and the resultant response in seedling vigor was most evident in 'G4705'. Growth of the tetraploid selections was also more erect and open relative to the dense diploid material, and it was considered that such a habit resulted in the poor persistence of the tetraploid selections when hard grazed under set stocked or severe, infrequent regimes (Harris *et al.* 1973; Lambert *et al.* 1974).

In 1973, 'G4705' was released as 'Grasslands Maku' and placed on the New Zealand List of Acceptable Herbage Cultivars. Armstrong (1974) referred to it as a hollow stemmed, sparsely hairy, non-bloating perennial legume that spreads by both stolons and shallow rhizomes. Compared with diploid material, leaves and stems are larger and the growth pattern is more erect and open. Because of this habit, it was stated that 'Grasslands Maku' produces maximum herbage when not exposed to heavy set stocking.

2.2 Plant Component Growth: Patterns and Relationships

In his review on the inter-relation of plant parts, Leonard (1962) presented the concept that once a plant has sufficient productive organs, most notably leaves, then it will concentrate on improving its supporting organs such as stems and roots. The ratio of shoot and root growth appears to be dependent on the relative supply of salts and water to the shoot and organic compounds to the root. Literature was cited where increased shoot/root ratios were reported in response to reduced light intensity, increased age, and increased mineral nutrition and moisture supply. Davidson (1969), following his work on differential temperatures, suggested that growth and subsequent root/shoot ratios were controlled by the supply of assimilates to the whole plant, and then by the relative activities of the two systems. As edaphic and aerial conditions change, then so do root and shoot activities, so maintaining a balanced economy of minerals and carbohydrates within the plant.

2.2.1 Growth of Shoots

2.2.1.1 *Lotus corniculatus*

Although *L. corniculatus* is described as having branched stems arising from a single crown, the habit of these stems varies such that two distinct forms exist within the range of agricultural genotypes (Seaney, 1975). The North American types, whose present cultivars are based on genotypes referred to in the early literature as var. *arvensis*, are more prostrate, indeterminate, finer stemmed and slower growing compared with the European types or var. *vulgaris*. Mac Donald (1946) described those plants of the var. *vulgaris* type as having stems arising from an above-ground crown region which, when in contact with the soil surface, become white and stoloniferous in appearance, but rarely root. The more prostrate forms are of a similar habit, but some stems do originate below ground, growing several inches before emerging. MacDonald *(loc. cit.)* stated that the white underground portion of these stems possessed reduced but recognisable foliage leaves and rarely root. However, Wassom & Barnett (1971) have observed nodal rooting and shoot formation on old woody prostrate stems in single spaced plants of *L. corniculatus*.

Morphological characteristics were reported by Nittler & Kenny (1965) to be influenced by environmental factors, with longer photoperiods and warmer temperatures resulting in more erect growth, especially for the prostrate cultivars. The critical photoperiod required to induce these changes was 14-15 hours, a similar period to that reported by McKee (1963) for the induction of flowering in *L. corniculatus*.

In uncut *L. corniculatus*, the first spring flush of shoots arises from the crown. However, from then until mid-autumn, when new crown shoots are initiated for the subsequent spring flush, the crown remains inactive as a shoot producing organ (Smith, 1962). During the intervening period, *L. corniculatus* exhibits an indeterminate growth habit with flushes of shoots developing from upper axillary buds at nodes on those stems first formed in spring. Nelson & Smith (1968a) suggested that it was reducing daylength and night temperatures associated with autumn that induced crown shoot activity.

With the cutting of stems formed from the first spring flush of crown shoots, Nelson & Smith *(loc. cit.)* found that shoot regrowth was almost entirely from upper axillary bud positions. Similarly, for subsequent regrowth periods few shoots arose from the crown or nodal sites at the base of cut stems. Langille & Calder (1971) further reported that increased cutting frequency and/or severity did not influence crown shoot numbers, but both practices increased side branching from nodes on the stubble.

2.2.1.2 *Medicago sativa* L.

Grove & Carlson (1972) considered that the crown in lucerne was a complex organ, consisting of the perennial portions of previous stem growth and the top of the taproot. It was from this combined region involving underground sites that Grandfield (1943) considered crown buds arose. These pink/white buds, as distinct from green, leafy buds at the base of the stubble, decreased in number and weight during the spring, such that few and only small crown buds existed in summer. During autumn their number and weight increased and these overwintered to produce the initial spring flush of growth. Few workers, however, classify crown buds as did Grandfield and most include axillary buds sited at aboveground nodes for an arbitrary length of aerial stem base.

As Grandfield noted, Nelson & Smith (1968a) reported that it was overwintered crown buds located at or below the soil surface that formed the first early spring flush of growth. When the first floral buds were visible, new buds were formed in axils of incomplete leaves at the base of these early stems and it was from these that regrowth almost exclusively developed if cutting occurred at this stage. Similarly, a third flush of stems developed at the basal nodes of the second flush and both combined to form regrowth in any subsequent cuts. This sequence of multibranching stem bases was also reported by Singh & Winch (1974a), who further noted that regrowing shoots originated mainly from the stubble of the most recently harvested stems. It was apparent that the younger and more viable the stubble stem, the more prolific it was as a producer of regrowth shoots.

For both young and established lucerne plants, the extent of crown bud formation was linked with overall assimilate production and carbohydrate accumulation at the crown (Cowett & Sprague, 1962). Thus, with increased light intensity, moisture, temperature and mineral nutrition, greater crown bud and stem production occurred. Cowett & Sprague (1963) further reported however, that light intensity and the penetration of light to the ground had no direct effect on crown development and subsequent stem production. Any affect that occurred was mediated through total plant vigour and crown size. Chatterton *et al.* (1974) also linked the extent and rate of crown shoot initiation with crown size and its associated carbohydrate levels.

With increasing cutting frequency, reductions in crown bud and shoot numbers were recorded by Cowett & Sprague (1962) and Hodgkinson (1973). Cutting height however, had little effect on crown shoot formation, although total shoot numbers were increased due to a greater stubble shoot pool. Leach (1968) also noted that by varying defoliation intensity and altering the number of potential shoot sites, the largest source of shoot number variation was related to the stubble shoot class. However, shoot numbers at the end of regrowth were not purely a reflection of potential shoot sites, as dominance did occur within shoot populations. Hodgkinson *(loc. cit.)* found that within two weeks of cutting, 50% of the crown and 70% of the stubble shoots were inhibited and grew no longer than 25 mm in length. Those shoots which were small and slow in initial growth rates were inhibited by their more rapid growing counterparts. The influence of this dominance was also noted by Singh & Winch (1974a), where final shoot numbers were often only 50% of that recorded at earlier peaks of shoot numbers.

Further variation in shoot origin can occur within those lucerne cultivars possessing the creeping rooted habit, characteristic of *Medicago falcata* (Avendo & Davis, 1966). Exogenous, adventitious buds arise at intervals along horizontally growing, branched lateral roots some 10-20 cm below ground (Murray, 1957). From these buds, aerial shoots can develop and may become independent units once their own associated root system develops. More severe and/or frequent defoliation reduced both shoot numbers and root weights

although shoot numbers per unit root weight increased (Carlson *et al.* 1964a). These workers also reported that warmer temperatures, but more importantly shorter days, increased the number of adventitious stem sites, this latter response being linked with hormonal relationships (Carlson *et al.* 1964b). In a further study on photoperiodic control of adventitious stem initiation, Carlson (1965) reported that shorter internodes, less apical dominance and more axillary shoot growth accompanied greater adventitious stem numbers under short day stimulation. He suggested that adventitious stem development was inhibited in long days by the apical dominance of rapidly developing stem apices, just as axillary buds are dominated.

Creeping rooted lucernes are distinct from rhizomatous lucernes in that rhizomes are only initiated from the original axis and can be considered purely as buried crown shoots (Murray, 1957). Somewhat similar to the prostrate *L. corniculatus* cultivars, stems may root while underground with their tips emerging from the soil as vegetative stems. It was proposed by Leach (1977) that these prostrate, slower growing rhizomatous lucernes had developed from wild populations that had been subjected to continuous grazing. Their greater persistence under severe grazing was considered to be related to a deeper crown and to less concentrated shoot flushes.

2.2.1.3 *Coronilla varia*

Like lucerne, *C. varia* (crown vetch) produces two or more distinct flushes of crown shoots (Langille & McKee, 1968). Following defoliation, regrowth can develop from the crown region or from upper axillary buds on cut stems, the extent of either depending on the stage of growth at cutting (Brann & Jung, 1974). Before flowering, crown buds are unexpanded and low in number, and if defoliated during this phase, regrowth is predominantly from axillary buds. Cutting at,or after flowering produces regrowth from crown buds. Brann & Jung proposed that crown vetch was intermediate in regrowth character between lucerne and *L. corniculatus* where crown and axillary bud development dominates regrowth respectively. They also reported that greater crown shoot production occurred under 7.5 cm rather than 15.0 cm cutting while Woodruff (1974) reported that greater axillary shoot development occurred within more prostrate, leafier canopies that were generated by frequent cutting.

2.2.2 Growth of Underground Organs

In reviewing the growth of underground organs, Troughton (1957) cited literature that reported a wide range in underground organ weights for different species, at different locations and under different managements. The full range was 560 to 35,800 kg D.M./ha, however the more common underground weights for grazed and cut swards varied between 3,360 to 6,720 kg D.M/ha.

2.2.2.1 Seasonal Effects on Underground Organs

Seasonal variations in lateral and nodal root weights are the net result of the initiation and growth of new roots and the cessation and death of old roots. Higher soil moisture (Garwood, 1968) and lower temperatures (Takeda & Agata, 1966; Beard & Daniel, 1966) improve nodal root initiation and as such initiation of new roots principally occurs during mid-autumn to early spring (Jacques & Edmonds, 1952; Caradus & Evans, 1977).

Growth of initiated nodal roots occurs during autumn and winter but is most rapid in early to mid-spring (Troughton, 1957; Garwood, 1968). Reduced growth and deterioration of old roots commences when plants begin to flower and the decay of roots continues through into the winter, generally giving a gradual decrease in total root weight over this period (Troughton, 1951, 1957; Jacques, 1956; Baker & Garwood, 1959).

When studying the rhizomatous growth of five grasses, Evans & Ely (1935) found that rhizome growth could occur at all times of the year when conditions were favourable for growth. However, development was most active in late summer and autumn, a period during which Arny (1932) with *Agropyron repens* L., and Sturkie (1930) with *Sorghum halepensis* L., also identified rhizome growth as being most active. With this latter species McWhorter (1961) reported increased rhizome growth after flowering when leaf growth was slow, which was in contrast to the pre-flowering period where rapid leaf growth accompanied slow rhizome growth.

Seasonal changes in taproot weights generally reflect changes in organic reserves as these organs are of a more permanent nature

than either rhizomes or nodal roots. Baker and Garwood (1959) reported that taproot weights of lucerne dropped during spring to a minimum of 2,800 kg D.M/ha by mid-summer, and then increased to a maximum of 5,600 kg D.M/ha by early winter. Autumn increases in organic reserves in lucerne were estimated by Willard (1951) to be equivalent to a 600 kg/ha increase in root dry weight. Greater taproot weights in lucerne have also been associated with lower ambient temperatures (Pearson & Hunt, 1972) and shorter days (Carlson *et al*. 1964a).

2.2.2.2 Defoliation Effects on Underground Organs

Defoliation of a plant reduces its root activity by retarding further initiation and growth, by promoting redistribution of organic compounds, or by advancing root maturity and death (Troughton, 1957). The magnitude of these changes induced by defoliation depends on: growth habit, stage of growth, defoliation severity and frequency and environmental conditions. As such, root initiation, elongation and viability decreases as defoliation frequency and severity increases (Jacques & Edmonds, 1952; Evans, 1971, 1973). In legumes, losses in both root and nodule tissue occur following defoliation, however the extent of these losses, and the replacement recovery, varies with species. Butler *et al*. (1959) reported that rapid nodule loss and replacement occurred with *Trifolium repens* L., which exhibited vigorous regrowth; slower losses and recovery occurred with the larger taprooted, but slower growing *Trifolium pratense* L.; and rapid losses plus slow recovery occurred with *L. pedunculatus*. These effects on root and nodule viability and growth can result in a poor exploitation of both root occupied and unoccupied soil volumes (Mitchell & Denne, 1967) and in reduced nitrogen fixation (Moustafa *et al*.1969).

Taproot weight reductions following defoliation generally involve the redistribution and utilization of organic compounds (May, 1960). Willard (1951) estimated that such losses of organic compounds in lucerne were equivalent to 200 kg/ha of root dry weight. For *L. corniculatus* and lucerne, increasing severity and/or frequency of cutting reduced root weights, although the former species was more responsive to cutting height and the latter to frequency (Smith &

Nelson, 1967). Reduced taproot weights with increasing cutting frequency has also been reported in lucerne by Dennis *et al* . (1959) and Langille & Warren (1962) and in *L. corniculatus* by Langille & Calder (1971).

2.3 Defoliation Management and Herbage Dry Matter Production

2.3.1 General Concepts

The concepts proposed by Watson (1947, 1958) relating crop growth rates with leaf area index (LAI) and net assimilation rate (NAR) have been extended into the analysis of pasture growth. Brougham (1956) and Donald & Black (1958) highlighted the relationships between LAI, light interception and pasture growth and as such, the latter authors stressed the need to maintain a LAI that would lead to maximum net photosynthesis. Based on LAI, growth rate relationships, Donald (1956) proposed that pastures should be managed whereby maximum dry matter (D.M.) increments can be expressed for as long as possible; either by rotational grazing or by continuous grazing where stock density is just sufficient to remove feed as it is produced. Results of Brougham (1959) supported these suggestions and the high annual yields obtained under specific grazing frequencies and intensities were related to the maximization of light interception.

It would appear however, that growth rates are not just a function of light interception. Watson (1958) reported a negative relationship between LAI and NAR as mutual shading of leaves increases, and the influence of falling NAR on growth rates, when reproductive development occurs towards the end of a regrowth period, has been illustrated by Brougham (1956) and Nelson & Smith (1968b). Furthermore, Hunt (1964) concluded that once complete light interception was achieved, then the rate of D.M. accumulation depended on tissue death and decay. Hunt (1970) considered that declining growth rates during later stages of regrowth were principally attributed to dry matter losses through tissue death and decay. Davidson & Birch (1972) proposed that where tissue readily decomposed and dead matter did not accumulate, then optimal LAI, growth rate relationships, as proposed by Donald & Black (1958), were likely to occur. In contrast, if senescence and/or decomposition was reduced, then non-optimal LAI,

growth rate relationships, similar to those reported by McCree & Troughton (1966) and Wilfong *et al.* (1967), were possible.

Due to within-canopy losses, there is often a discrepency between harvested yield and gross D.M. production and one is generally not an accurate reflection of the other, particularly under lax defoliation (Davidson & Birch, 1972). In a cutting experiment, Morris (1970) recorded the highest gross pasture production, but the lowest harvested yield, with frequent lax defoliation, a response which was the reverse to that for infrequent, severe cutting. Similarly, McLusky & Morris (1964) and Jackson (1974) recorded the highest harvested yields with infrequent, severe defoliation because all D.M. that was produced was harvested. Simons *et al.* (1972) measured no response to laxer defoliation because new growth and tissue death occurred below cutting height in the lax treatments. It was because of these within canopy morphological and D.M. changes that Ollerenshaw (1974) considered vertical cutting heights did not indicate the true nature of defoliation intensity.

Potential growth rates also depend on the meristematic activity of the canopy as it determines the plant's ability to utilize energy in growth processes (Blaser *et al.* 1966). For example in the regrowth of grasses, Lazenby & Rogers (1962) and Davies (1966) highlighted the importance of tiller density and Sheard & Winch (1966) and Jackson (1974), the importance of individual meristematic activity. In lucerne, the success of any management system largely depends on the presence of basal shoots at the crown region that can commence immediate regrowth following defoliation (Leach, 1967). Thus, shoot number and stage of development are critical in determining regrowth.

2.3.2 *Lotus corniculatus*

Depending on the growth habit involved, the response to defoliation differs between the various cultivars of *L. corniculatus*. The semi-erect 'Empire' types are more persistent and productive under intense defoliation than the erect European types and as such, are recommended for grazing (Seaney, 1975). The later types are readily defoliated and non-persistent under frequent, severe grazing and are therefore generally used for haying. When considering

haying regimes, 2 to 3 cuts per annum appears optimum as further increases in cutting frequency reduces production (Langille *et al.*, 1968; Langille & Calder, 1971). Production increases have been achieved by delaying the first cut and allowing the highly productive spring growth period to continue through to complete flowering (Parsons & Davis, 1961; Twamley, 1968). However, in order that subsequent spring growth is not impaired, late harvesting in the low producing autumn period should be avoided (Gasser & Lachance, 1969; Seaney, 1975).

Where infrequent cutting is employed, there is little or no yield response to increasing cutting height, although the size and health of the crown and root system may be improved (Pierre & Jacobs, 1953; Twamley, 1968). With more frequent cutting however, persistence and production responses do occur with increasing laxity of defoliation, particularly in association with the more erect cultivars (Duell & Gausman, 1957; Wall, 1957). Smith & Nelson (1967) proposed that these responses to higher cutting were related to the characteristically low carbohydrate reserves in *L. corniculatus* and the need to retain a self sufficient residual leaf complement.

Henson & Scoth (1962) considered that the use of a continuous grazing system should only be recommended for cattle grazing and semi-erect 'Empire' types, and even then pastures should be managed so that a minimum of 10 cm growth is present at all times. With sheep or erect cultivars, a deferred grazing system involving a 5-10 cm residual following grazing, was considered essential. Davis & Bell (1957); Van Keuren & Davis (1968); Van Keuren *et al.* (1969) have all highlighted the positive persistency and production responses of rotational versus continuous grazing, by both sheep and cattle.

Only in early spring is there a basal flush of shoots available for growth and any subsequent regrowth arises from axillary buds on residual stubble (Smith, 1962; Nelson & Smith, 1968a). Shoot extension from these sites is slow, particularly in autumn (Keoghan & Tassel, 1974) and following initial falls in LAI after cutting, Greub & Wedin (1971b) reported that one-two weeks were required to get a net accumulation of leaf. The inferior production of *L. corniculatus* compared with lucerne recorded by Nelson & Smith (1968b) and Greub & Wedin (1971a) related to poorer LAI values and hence, growth rates

over the initial regrowth periods. The former authors did report however, that *L. corniculatus* had a greater optimal LAI range than lucerne, as N A R was maintained for a longer period during flowering by continued flushes of upper canopy axillary growth. It was considered by Keoghan & Tassel (1974) that to improve the regrowth ability of *L. corniculatus* it would be necessary to provide flushes of large basal shoots that can commence immediate elongation after harvest, a more erect stem habit to improve light utilization and a more vigorous root system to help in initial regrowth.

The competitive ability of *L. corniculatus* is restricted by the nature of its slow regrowth and therefore a non-aggressive companion, particularly during establishment and early spring, is necessary for legume persistence (Chevette *et al*. 1960). The more competitive the companion, then the greater *L. corniculatus* suffers from the mismanagement of overgrazing (Wolf & Smith, 1964). MacDonald (1946) reported that the most suitable grass companions were those that produced an open sward such as *Phleum pratense*, *Dactylis glomerata* and *Poa pratensis* while Parsons & Davis (1961) found that a late rather than an early season *D. glomerata* cultivar was less competitive and hence more compatible with *L. corniculatus*.

2.3.3 *Medicago sativa*

In reviewing the early literature on lucerne management, Willard (1951) and Keoghan(1967) both indicated that frequency of cutting was a principal determinant of lucerne persistency and productivity. Two to three cuts per season, based on a stage of growth criterion, appears optimum for D.M. production. This stage of growth is indicated by the active extension of basal buds at the crown region in response to the physiological maturing of the previous shoot crop, and it is the periodicity of this that determines cutting frequency (Smith, 1962; Leach, 1967). Continued growth passed the stage where basal shoot extension has occurred may result in reduced yields, as senescence and decay processes become more important and the chance of new basal shoots being decapitated increases (Keoghan, 1967; Fuess & Tesar, 1968).

Highest yields are obtained when the number of shoots available for immediate regrowth are greatest and it is the rapid initiation and extension of these shoots that is essential for the quick restoration of an assimilatory leaf system (Leach, 1968; Hodgkinson, 1973; Chatterton *et al.* 1974). Shoot numbers and their initial growth activity, plus the subsequent initial accumulation of leaf area, have been considered as the main factors in obtaining D.M. accumulation (Smith *et al.*, 1964; Hodgkinson, *loc. cit.*). Leach (1968) reported that the number of shoots commencing regrowth within the first seven days accounted for more variation in final lucerne yield than did reserves or residual leaf area. In subsequent work, Leach (1969) concluded that total growth substances in roots and shoots were not the principal determinates of regrowth and that the number of shoots to commence immediate regrowth was more important. Regrowth was dominated by those shoots that commenced extension the earliest and Hodgkinson (1973) considered final lucerne yield variations were principally determined by the differences generated within the shoot populations during the first week of regrowth.

Where maximum production is desired and cutting is infrequent, the presence of greater residual leaf following laxer cutting does not improve production (Langer & Keoghan, 1970). Root reserves and shoot regrowth are high during initial regrowth in such a regime (Leach, 1967; Smith & Nelson, 1967) and residual leaf is of a senescent and photosynthetically inefficient nature (Brown *et al.*, 1966; Langer & Keoghan, 1970). Where defoliation is too frequent however, and does not coincide with basal shoot flushes and high carbohydrate reserves, then positive production responses occur with increasing cutting height (Kust & Smith, 1961; Langer & Steinke, 1965; Smith & Nelson, 1967; Silva, 1969). Lax defoliation was considered by Leach (1970) as being most beneficial in situations where initial regrowth is slow and/or the base of the plant is leafy. As such, improved regrowth through the retention of stubble leaves was greater at lower temperatures and for leafier, prostrate cultivars such as 'Rhizoma' (Leach, 1971).

In studies conducted by Hodgkinson *et al.*, (1972), the retention of stubble leaves following 15 cm, high cutting improved taproot dry weights and it was concluded that stubble leaf photosynthesis

replaced the need for redistribution of organic compounds from the taproot to new shoot growth and shoot respiration. Furthermore, photosynthates exported from the stubble leaves predominantly went to their associated axillary shoot and as a result, stubble shoot weights were enhanced. The photosynthetic efficiency of previously senescing residual leaves also increased with partial defoliation, a response that was considered to partly involve changes within photosynthetic processes at the enzyme level. Pearce & Lee (1966) also reported that marked photosynthetic adaptability of lucerne leaves was evident when they were switched between low and high light intensities. This type of adaptability to light intensities was considered by Bjorkman (1968) to be related to the levels of carboxylating enzymes.

Although extra sites for stubble shoot growth may result from higher cutting, this pool as a whole is of little importance under infrequent cutting (Langer & Keoghan, 1970; Leach, 1970). Where cutting is frequent however, positive production responses to increasing cutting height are achieved by greater stubble shoot growth (Hodgkinson, 1973) and it is in this situation that the responsiveness of the stubble shoot pool to defoliation, is most evident (Keoghan, 1967; Leach, 1968, 1970). It should be noted that under low density, spaced plant or controlled climate conditions, the viability and importance of residual leaf and stubble shoot growth increases (Langer & Keoghan, 1970).

2.3.4 *Coronilla varia*

Like lucerne, *C. varia* has two to three flushes of new crown shoots per annum and yields are maximized when cutting coincides with these flushes (Brann & Jung, 1974). Under a two to three cut regime there is little benefit from high cutting. However, as defoliation becomes more frequent, positive persistence and production responses occur with laxer management (Woodruff, 1974).

2.4 Nonstructural Carbohydrates

As well as an indicator of plant physiological status, non-structural carbohydrates (N C) can also be considered as a principal organic reserve that is often essential for plant survival and production following environmental and managerial stress periods

(Sheard, 1973). Constituents of the N C pool are variable, but they can be broadly classed as predominantly sucrose plus fructosans in temperate grasses, and sucrose plus starch in subtropical, tropical grasses and in members of the Leguminosae Family (Ojima Kunihiko and Takeshi Isawa, 1968; Smith, 1973a). Variation in plant NC status can be considered as the result of net energy balances between photosynthetic and respiratory processes. Therefore, whether NC are accumulating or declining depends on plant growth rates, the stage of plant development and the environment (White, 1973).

In general, changing NC levels can be considered as being inversely related to herbage growth (May, 1960; Sonneveld, 1962; Brown & Blaser, 1965). Restrictions of growth by nutrient deficiencies, water stress and low temperatures result in NC accumulation (Blaser *et al.*, 1966; White, 1973). In contrast, where respiratory responses exceed those of photosynthesis, such as with increased night temperatures, then NC may decline (Baker & Jung, 1968).

2.4.1 Seasonal Changes in Nonstructural Carbohydrates

Seasonal variations in NC are characteristic of climatic factors and of individual species, but generally late spring minimum and autumn maximum values occur (Weinmann, 1961). In uncut lucerne, total nonstructural carbohydrates (TNC) decline during spring until the first crop of stems begin to mature. Values then rise to a peak at flowering but again decline as a second flush of shoots develop from the crown region (Smith, 1962; Cooper & Watson, 1968). Subsequently, a further increase in TNC occurs and eventuates in an autumn maximum which is dominated by starch accumulation. During winter, starch is hydrolysed to sugars and as respiration continues, overall TNC levels decline (Jung & Smith, 1961).

Seasonal TNC patterns in *L. corniculatus* and *C. varia* differ from that of lucerne in that reaccumulation of starch following the spring decline does not occur until late summer (Smith, 1962; Langille & McKee, 1968; Woodruff, 1974). As a result, low TNC levels are present over most of spring and summer. Nelson & Smith (1969) considered that the delayed accumulation and low levels of TNC in *L. corniculatus* resulted from high respiratory demand at

high temperatures and from the continual growth of upper axillary shoots. Greub & Wedin (1971b) stated however, that reaccumulation commences when temperatures are highest and that it was unlikely to be linked to just one aerial growth factor. They proposed that photoperiod was the environmental stimulus that triggered the partitioning of carbohydrates to the crown and roots.

2.4.2 Defoliation Effects on Nonstructural Carbohydrates

When lucerne is defoliated, a cyclic pattern of utilization and accumulation of TNC is superimposed on the general seasonal pattern (Smith, 1962). For two to three weeks, net utilization of NC may occur and it is greater when respiration is high and/or when the attainment of a self sufficient leaf complement is delayed (Reynolds & Smith, 1962; Silva, 1969; Reynolds, 1971). The effects of repeated defoliations are cumulative, thus low TNC levels, resulting from prolonged negative energy balances and limited NC replenishment, occur with severe, frequent defoliation (May, 1960). Once low levels are reached, little cycling of NC is evident (Feltner & Massengale, 1965; Robinson & Massengale, 1968).

Similarly, when TNC levels are low in *L. corniculatus* and *C. varia* little cycling of NC occurs in response to defoliation (Nelson & Smith, 1968b; Greub & Wedin, 1971a). Only when defoliation occurs during the accumulating autumn period are TNC utilization, restoration patterns evident (Greub & Wedin, 1971b; Brann & Jung, 1974). Work by Nelson & Smith (1969) under controlled temperature conditions, showed that only at low temperatures, when TNC were accumulating, did TNC in *L. corniculatus* respond to defoliation.

Within a specific regrowth cycle, NC continue to decline until a sufficient leaf complement develops whereby current photosynthetic production is sufficient to satisfy the respiratory demands involved in the maintenance of existing, and the growth of new, plant tissue (White, 1973). Utilization of NC in regrowing plants is therefore influenced by the amount and efficiency of photosynthetic tissue remaining after defoliation, as it determines the adequacy or inadequacy of current photosynthesis to sustain plant respiratory processes.

Leafe *et al.* (1974) reported that in a grass sward the negative carbon balance and regrowth lag phase was less when more residual leaf was left and photosynthesis recovered more rapidly. In lucerne, Silva (1969) considered that the closer the residual leaf area was to that which provides current photosynthate self sufficiency then the less TNC becomes important. Booysen & Nelson (1975) found that current photosynthetic sufficiency was attained earlier in *F. arundinacea* following higher cutting and as a result, utilization of NC was reduced. Furthermore, leaf extension ceased being the dominant sink earlier, thereby allowing a greater expansion of other plant parts and reaccumulation of NC.

In defoliated lucerne, the absolute amount of NC used until the minimum value of the TNC cycle is attained, is proportional to plant size and associated respiration (Ueno & Smith, 1970). As such, these losses are greatest in large plants, although once independence of accumulated NC is achieved, it is these plants that restore leaf complement and TNC more rapidly. Earlier and more rapid accumulation of TNC is also a characteristic of plants more tolerant of frequent defoliation (Chatterton *et al.*, 1974). With the earlier mobilization of assimilates to, and starch accumulation in,the crown and taproot, basal shoot development is advanced and although the causal relationships are not known, these characteristics lead to more rapid regrowth.

2.4.3 Nonstructural Carbohydrates and Plant Regrowth

The actual role that NC plays in regrowing plants has been strongly debated. Graber *et al.* (1927) first proposed that elaborated organic carbon and nitrogen were stored then utilized following defoliation and as such,organic reserves were considered essential for plant viability and production. In subsequent reviews on organic reserves, Weinmann (1961) and Sonneveld (1962) supported these views but May (1960) questioned the emphasis that had been placed on organic reserves in determining regrowth and suggested that their function was primarily in the maintenance of respiratory processes.

More recent work involving C^{14} tracer techniques has provided more direct evidence as to the role of organic reserves in defoliated plants. In lucerne, Hodgkinson (1969); Silva (1969); Pearce *et al.*(1969); Smith & Marten (1970); and Singh & Winch (1974b), all reported high

respiratory losses of C^{14} initially located in the taproot and only low proportions of C^{14} incorporated into new top growth. They concluded that stored metabolizable compounds in the taproot of lucerne were used mainly as respiratory substrate and to a lesser extent in regenerating shoots.

The composition of plant organic reserves is generally considered to be dominated by nonstructural carbohydrates (Sheard, 1973), however work by Davidson & Milthorpe (1966b) with *D. glomerata* suggested that other labile organic compounds are also involved. Nitrogenous compounds were implicated in sustaining respiration and regrowth following defoliation. Smith & Silva (1969) reported that less than five percent of the compounds translocated from the roots to the tops in regrowing lucerne were nitrogenous compounds, however their methods of study take no account of *in situ* utilization within the root system. While nitrogenous compounds appear to be a potential energy source, White (1973) suggested that unlike NC, they are not alternately stored and utilized.

With *D. glomerata*, Ward & Blaser (1961) recorded superior absolute regrowth rates during the first twenty five days of regrowth in plants of an initially higher NC status. However, in reanalysing this same data, Davidson & Milthorpe (1966a) showed that after five days, relative growth rates were similar and independent of NC status. In their own work, they found that growth rates following defoliation depended first of all on the development of photosynthetic surfaces, the rate and extent of which were determined by the supply of carbohydrates to leaves capable of expanding. Initial leaf extension rates were positively related to carbohydrate status, but after two to four days, relative growth rates of low and high NC treatments were similar. Nevertheless, subsequent absolute growth rates were dependent on early leaf surface development, thus relatively small initial differences, resulting from higher NC status, were magnified so long as expotential growth continued. More rapid leaf expansion and greater regrowth rates were also measured by Alberda (1966) in *L. perenne* plants of a higher NC status. At lower levels there was less NC utilization, and NC reaccumulation and leaf regrowth was delayed (Alberda, 1970).

2.5 Carbon Partitioning in Plants

2.5.1 Carbon Distribution

The flow of carbon into or out of a leaf or shoot system, greatly depends on their physiological development as determined by age and stage of growth (Milthorpe & Moorby, 1969). Ho & Shaw (1977) considered that in young leaves, assimilated and imported carbon is incorporated into protein and structural polysaccharides and only when assimilates in excess of these requirements are produced, are sucrose and starch formed for subsequent translocation to other organs. As a generalization, Wardlaw (1968) stated that the transition from import to export of assimilates occurred when the leaf was a third to a half of full expansion. In soybeans, Thrower (1962) recorded this phase at 50 percent full leaf expansion, although during the transition, directional flow of assimilates was recorded. Milthorpe & Moorby (1969) considered that such bidirectional flow of assimilates would continue through until full leaf expansion due to amino acid importation.

Export patterns of C^{14} labelled assimilates are generally characterized by an initial rapid export period followed by one with a continuing but decreasing export rate (Wardlaw, 1968). Hofstra & Nelson (1969) reported that for a broad range of species this initial period lasted approximately 80 minutes, and it was during this time that species differences in export rates and proportional assimilate retentions were generated. In sugar beet, an early rapid loss of C^{14} from the leaf sucrose pool was reported by Joy (1964), although export continued at a decreasing rate for several days. In *Pisum sativum* L., Lovell *et al.* (1972) reported that export of C^{14} was mostly completed within 2 to 4 hours of fixation, and that which remained within the assimilating leaf was incorporated into structural tissue. Working with lucerne, Hodgkinson and Veale (1966) found that the rapid export phase lasted for 2 hours and that C^{14} losses were principally from the soluble ethanol pool. Over the same period, C^{14} in taproot tissue reached a maximum and then remained constant for the next 24 hours as leaves continued to export at a declining rate.

As a general pattern, lower exporting leaves tend to translocate assimilates to roots while those higher up the stem translocate to the shoot apex (Wardlaw, 1968). Under conditions of assimilate deficiency, expanding shoots appear to have priority over root and bud growth. The relative ability of these two latter components to obtain assimilates does vary however, with the root being a superior competitor when the stem apex is intact and conversely when the stem apex is removed. Wardlaw (1968) related this effect to growth substances and their influence on sink activities.

The direction and extent of assimilate export appears to be principally influenced by photosynthetic activity and the strengths of competing sinks as determined by the number, size and growth rates of the utilizing organs (Milthorpe & Moorby, 1969). Working with *P. sativum*, Lovell *et al.* (1972) found that export from expanded leaves was highest when assimilate sources were reduced by partial defoliation, but this was only so when the active apex sink was left intact. When the apex was removed, partial leaf defoliation did not significantly influence export patterns and in fact, assimilate export was reduced in plants with a full leaf complement. Where conditions are favourable for photosynthesis it would appear that assimilate export is controlled more by active sink utilization than assimilate production (Wardlaw, 1968; Milthorpe & Moorby, 1969).

When considering regrowing lucerne, it is evident that early shoot growth retains most of its own assimilate. As total plant assimilation increased over the first 14 to 21 days of regrowth, Pearce *et al.* (1969) found that shoot retention of assimilates remained high at approximately 80 percent. Thereafter, proportional retentions declined as assimilate distribution to root components, particularly the taproot, increased. This alteration in distribution coincided with the reaccumulation of nonstructural carbohydrates in the crown and taproot. Wolf (1967) also reported that during early stages of regrowth, assimilates were principally retained within the leaf and it was only when shoots were more mature and less active in growth that extensive C^{14} export to the taproot was evident. In contrast to these workers however, Hodgkinson (1969) recorded increasing shoot retentions with time, where after 6 days of regrowth, 71 percent of assimilates were retained as compared with 89 percent after 40 days of regrowth. These differences between workers may however, reflect the time differences between labelling and harvesting

which for Hodgkinson (1969) was 3 hours and for Pearce *et al.* (1969), 48 hours.

2.5.2 Carbon Redistribution

When all or nearly all leaf is removed during defoliation, it is inevitable that organic reserves are initially used for new leaf growth and respiratory processes in new and existing tissues. Following defoliation of lucerne, Hodgkinson (1969) found that labelled C^{14} organic compounds moved from residual plant parts into first formed leaves and new shoot stems during the first 20 days of regrowth and that this movement was greater under conditions that promoted more rapid shoot growth. However, of the losses associated with the net decline in C^{14} , particularly from the taproot, respiration accounted for 56 percent during the first 10 days of regrowth and 81 percent during the subsequent 10 days. In losing 50 to 66 percent of original taproot activity, it was considered that stored metabolizable compounds were principally used as respiratory substrate, and to a lesser extent in the regeneration of shoots.

Again with lucerne, Pearce *et al.* (1969) found that redistribution of C^{14} from the taproot to shoot regrowth, following cutting, was most active 3 to 15 days following defoliation, after which net increases in shoot C^{14} content ceased. After 28 days, 70 percent of original taproot activity was lost and 19 percent had been translocated to new top growth. Similar levels of C^{14} redistribution to new shoots were also reported by Silva (1969) for lucerne while Singh & Winch (1974b) reported that after 12 days, 80 percent of original taproot C^{14} was lost through respiration of which 20 percent had occurred in new shoots.

Following fractionation of residual C^{14} in lucerne, Smith & Marten (1970) reported that 90 percent was located in the starch pool. Of the original labelled nonstructural carbohydrates, 40 percent was incorporated into structural tissue, the remainder being respired and lost. High utilization of previously stored nonstructural carbohydrates was indicated by the 71% loss of activity within this pool and it was concluded that stored nonstructural carbohydrates in lucerne roots serve as a reservoir of carbohydrate

available to, and utilized by, the entire plant. In contrast, little net change with time in crown and stubble C^{14} was reported by Hodgkinson (1969) and as a result, it was considered that these components made little direct contribution to new growth of lucerne.

Where assimilate distribution is estimated by subsequently determining the location of C^{14} within the plant following exposure to C^{14} pulse(s), it is apparent that such estimates can be confounded by differential respiration losses and continued redistribution. In considering the carbon balance presented for *P. sativum* by Minchin & Pate (1973) the problems of interpretation are evident. Of the initial carbon fixed, 74 percent was exported from the assimilating tissues to below ground organs where roots and nodules consumed 7 and 5 percent respectively for growth, 35 and 12 percent in respiration and 15 percent was again returned to the shoot via the xylem as amino acids generated by nitrogen fixation. As a result of redistribution it was estimated that 37 percent of carbon involved in shoot growth came from carbon compounds re-exported from the root region. Respirational losses relative to carbon incorporation also varied between tissues and this is of importance when high and rapid C^{14} losses occur following assimilation. Of the original plant activity measured by Small & Leonard (1969) in *P. sativum* and *T. subterraneum*, slightly more than 40 percent was lost through respiration within 24 hours of labelling and for a similar time period Kyle & Powell (1974, 1975) reported a 25 percent decline in total plant activity in *Lolium* spp.

CHAPTER 3. MORPHOLOGICAL CHARACTERISTICS OF *LOTUS PEDUNCULATUS* CV. 'GRASSLANDS MAKU'

3.1 Introduction

As edaphic and aerial conditions change, then so does the relative growth of roots and shoots, thereby maintaining a balance of assimilated substrate within the plant (Davidson, 1969). Consequently, root initiation, growth, death and accumulation of organic compounds all respond to changing environmental conditions and defoliation intensities (Willard, 1951; Troughton, 1957; Baker & Garwood, 1959; May, 1960). Similarly, the pattern and structure of shoot growth differs for different seasons and defoliation regimes (Cowett & Sprague, 1962; Nelson & Smith, 1968a; Leach; 1968). Considerable variability can therefore occur in the morphological structuring of defoliated plants growing under different conditions.

Shoot growth in seedling *L. pedunculatus* initially consists of a primary stem and then subsequently, pairs of axillary shoots may develop from the cotyledonary node. As this node swells, a seedling crown is formed and it is from this region that rhizome growth may eventually occur. From observations made in the field in the lower North Island and South Island of New Zealand, it would appear that the initiation of such growth in establishing plants predominantly occurs in late summer to early autumn, but is delayed by increasing plant competition or slower growing conditions. It is proposed for this study that the development of rhizomatous growth marks the beginning of the established plant phase.

The dominant morphological feature of established *L. pedunculatus* was considered by MacDonald (1946) to be its rhizome growth. This growth, plus its associated roots, results in a turf forming habit and a dense distribution of roots in the upper soil profile. Axillary shoot growth from rhizome nodes gives rise to ascending stems and from these aerial stems further axillary growth may develop from above ground nodal positions (Howell, 1948). As a result, canopy growth of *L. pedunculatus* is of an indeterminate, branching habit.

A knowledge of the morphological characteristics, and their response patterns, was considered necessary in understanding the growth and production patterns of *L. pedunculatus*. As seasons change and defoliation managements differ, it was considered that variations in morphological structure would indicate changes in emphasis in the partitioning of growth between plant components. The influence of climatic conditions and agronomic management on shoot growth was also of importance, particularly in relation to their potential and actual numbers, growth patterns and place of origin.

During 1975-76, a field experiment was conducted in order to quantify above and below ground morphological characteristics of established *L. pedunculatus* cv. 'Grasslands Maku' and to show how these characteristics varied with different seasons and defoliation managements. This chapter presents and discusses the results of this experiment with regard to the pattern and structure of root, rhizome and shoot growth.

3.2 Experimental

On 19/11/74, 'Grasslands Maku' at 4.5 kg/ha (inoculated with rhizobium strain: CC814S) was disc drilled into the area on which the 1975-76 field experiment (Expt. I) was subsequently established. Herbicide spraying of 2,4DB (2,4-dichlorophenoxy butyric acid) at 2.8 l a.i./ha was conducted on 3/2/75 and 30% potassic superphosphate at 190 kg/ha, was broadcast on 21/3/75. During the summer-autumn period of establishment the area was lightly topped three times.

The experimental site was located on a Tokomaru silt loam (Cowie, 1972) at Massey University. Soil quick-test analyses of samples taken on 9/7/75 for the 0-7.5 cm and 7.5-15.0 cm depths were : pH - 6.1, 6.2; K - 5, 4; P - 9, 8. Gradwell (1974) reported the soil physical properties of this soil type. Appendix 1 presents weekly soil moisture determinations (% of oven dry weight) measured within the experimental area over the trial period, and Appendix 2 presents monthly climatic data recorded 1 km from the experimental area.

The most notable environmental features that occurred between the spring of 1975 and 1976, the period over which Experiment 1 was conducted, relate to low, late summer and autumn temperatures and soil moisture (Appendix 1 and 2). Except during January and more particularly February 1976, when temperatures were lower than would normally be expected, daily maximum, minimum and 10 cm soil temperatures were approximately similar to the appropriate mean monthly recordings. Although rainfall during February and March 1976, was not too dissimilar from the appropriate mean monthly rainfalls, there was a steady decline in soil moisture during these months. The minimum values reached at the peak of this stress period were below the -1 bar soil moisture equivalent of approximately 20% O.D.W., a point at which plant growth is restricted on this soil type (Scotter, pers. comm.). At the lowest soil depth sampled, values reached the 14% moisture level designated as wilting point by Gradwell (1974).

The six defoliation treatments of Experiment I were as follows:

SF: cutting down to 1.5 cm every three weeks
MF: " " " 5.0 cm " " "
LF: " " " 9.5 cm " " "
SI: " " " 1.5 cm " six "
MI: " " " 5.0 cm " " "
LI: " " " 9.5 cm " " "

The first and last cuts were made on 9/9/75 and 18/5/76 respectively, the last cut being determined by the failure of growth in LF and LI to exceed cutting height. Treatments were randomized within each of four blocks and each plot consisted of 2 x 2 m plus 2 x 5 m areas. From the former area all mown yield data were collected and the latter area provided sample sites for destructive harvesting. Cuts were made with a sickle-bar mower and defoliation was completed with a reel mower for the two, 1.5 cm cutting height treatments. All cut herbage from the 'non-destructive' area was collected, weighed, subsampled for dry matter determinations and then discarded along with the material from the remainder of the plot. Hand weeding, particularly the rogueing of volunteer white clover, was conducted throughout to maintain sample areas as pure 'Grasslands Maku'.

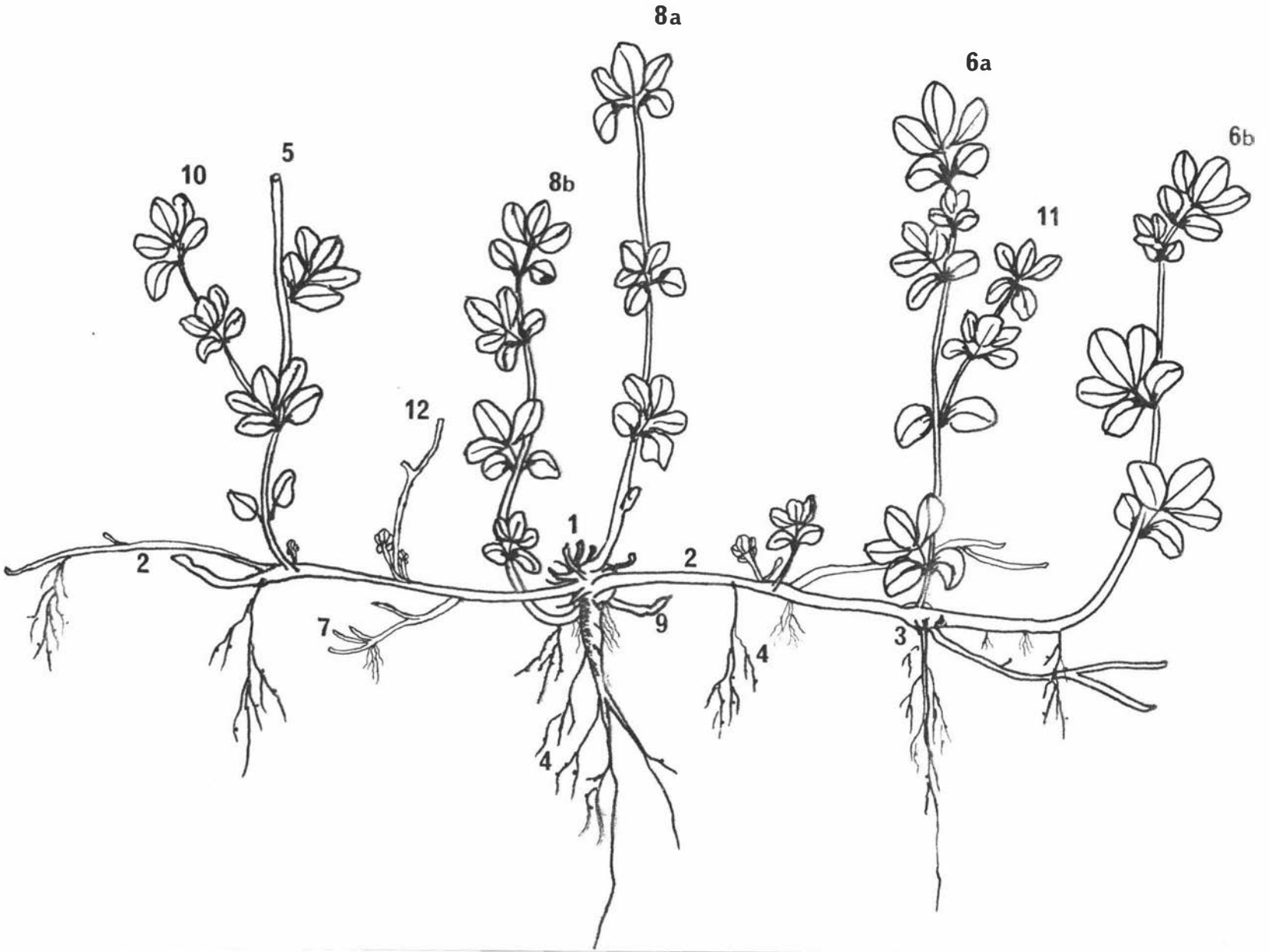
A grid pattern of 0.5 x 0.5 m was formed for the areas allocated to destructive subsampling and for each plot, three grid positions were randomly allocated to each sample date. Sod samples of approximately 30 x 30 x 20 cm were taken before and after each cut to provide material for final and residual plant component analyses respectively. Each sod was individually soaked in water for at least 15 minutes, washed free of soil and then disentangled. Within each sod sample all damaged plants and plant parts were discarded and the remainder were ranked in size. Five plants per sod were then selected on a systematic basis to represent the full plant size range. Both final and residual plant subsamples were then stored at $3^{o}C$ until dissection when all five subsample plants were bulked and mean values on a per plant basis recorded. Drying of all plant material for dry weight determinations was conducted in air dry ovens at $80^{o}C$ for 16 hours.

To minimize possible sampling effects on remaining plant growth, sods of 'Grasslands Maku' from outside the experimental area were transplanted into the sub-sampled areas. From the remaining grid position, a 0.1 m^2 quadrat cut to ground level was taken for determining residual dry matter and leaf area.

The division of plant parts used during dissections are represented diagramatically in Figure 1 and their nomenclature and definitions are as follows:

(1) Primary crown and taproot; the dominant crown and taproot system in a multi-crown plant; a composite organ consisting of an aggregate of indiscrete stem bases (crown) and an associated primary taproot.
(2) Rhizome; horizontally growing stems at, or predominately below the soil surface; supports adventitious and nodal roots; rhizome component ceases on an individual stem system at the last rooted node.
(3) Secondary crown and taproot; a swollen node within the rhizome system at which a woody root system develops.
(4) Fibrous root; adventitious and nodal roots; includes nodule tissue.
(5) Stubble; an above ground, living shoot without an intact terminal apex; excludes any intact subtending axillary shoots.

FIGURE 1: A diagramatic representation of the morphology of 'Grasslands Maku', *Lotus pedunculatus*.



(6) Rhizome shoot; a shoot developing from a rhizome axillary (6a) or terminal apex (6b) position at or below the soil surface; associated with nodal rooting; the apex is emergent above the soil surface.

(7) Rhizome shoot initial; an underground axillary shoot whose apex is below the soil surface and producing scale leaves; included as rhizome growth if its length exceeds 2 cm.

(8) Crown shoot; a shoot arising from indiscrete stem tissue of the crown; from a dorsal (8a) or lateral-ventral (8b) position on the crown.

(9) Crown shoot initial; as for (7) but arising from indiscrete stem tissue of the crown.

(10) Stubble shoot; an axillary shoot arising from an above ground position on a stem with the terminal apex removed.

(11) Secondary axillary shoot; as for (10) but the subtending stem has an intact terminal apex.

(12) Dead; stem and leaf tissue that was withered and brown.

Data were collected every three weeks for the frequently cut treatments (SF, MF, LF) and for all six treatments, every six weeks. Within each harvest date factorial analysis of variance tests indicated that interactions were common between cutting frequency and severity. For consistency of analysis and presentation, main effects were not considered and statistical analyses were based on a randomized block design for both three and six treatment harvests. Chi-square tests for homogeneity of error variances were separately conducted across harvest dates for three and six treatment analyses. A pooled analysis was then conducted on treatment and harvest date main effects and their interaction using "PHANIE", a statistical programme involving a random effects, split-plot in time model (Gordon, pers. comm.). Where homogeneity of variance did not exist across harvests, no treatment comparisons were made across harvest dates, although the general significance levels of the main effects and their interactions were considered sufficiently valid for comparative tests (Cochran, 1947).

For all plant components, data were collected every three and six weeks for the three and six-weekly cutting treatments respectively. However, for the more frequently cut treatments most data will only be presented for sampling dates common to the infrequently cut treatments, i.e.: on a six weekly basis. In all cases where the

intermediate three weekly data points are not presented, they would not have altered the general seasonal and treatment trends.

Unless specifically stated, plant component data were considered on a per plant basis. A plant unit was defined as a stem system involving above and below ground growth that was continuously linked with at least one crown and taproot. These continuous stem systems were at times multi-crown and taprooted but were nevertheless considered as one plant.

3.3 Results

3.3.1 Underground Plant Components

The crown, taproot, rhizome and fibrous root systems were collectively considered as forming total underground plant growth. The influence of season and treatment on the dry weight per plant of this total growth is shown in Figure 2 and two general trends are evident. On a seasonal basis, weight trends between treatments were variable during spring and early summer, showed a rapid increase from February through to May and then decreased during winter. On a treatment basis, the effects of cutting severity and frequency interacted. At a cutting height of 1.5 cm, weight increases were generally recorded with the longer regrowth interval; at 5.0 cm no general response was evident; and at a cutting height of 9.5 cm greater underground weights occurred with a three rather than six-weekly cutting interval. Nevertheless, there was a general increase in total underground weight per plant with increasing cutting height.

There was a significant treatment x harvest date interaction in underground weight per plant which was most obviously associated with the severe, more frequently cut treatment (SF). This treatment decreased in weight through until January and then showed a much reduced autumn recovery. In contrast, the total underground weight per plant of the three-weekly, lax cut treatment (LF) rose throughout spring, summer and autumn only to decrease over winter to a level similar to the previous spring. One further point to note was the delayed late summer/autumn recovery of the six-weekly cut treatments which showed a significant improvement only when, on 24/2/76, reproductive growth was removed by cutting.

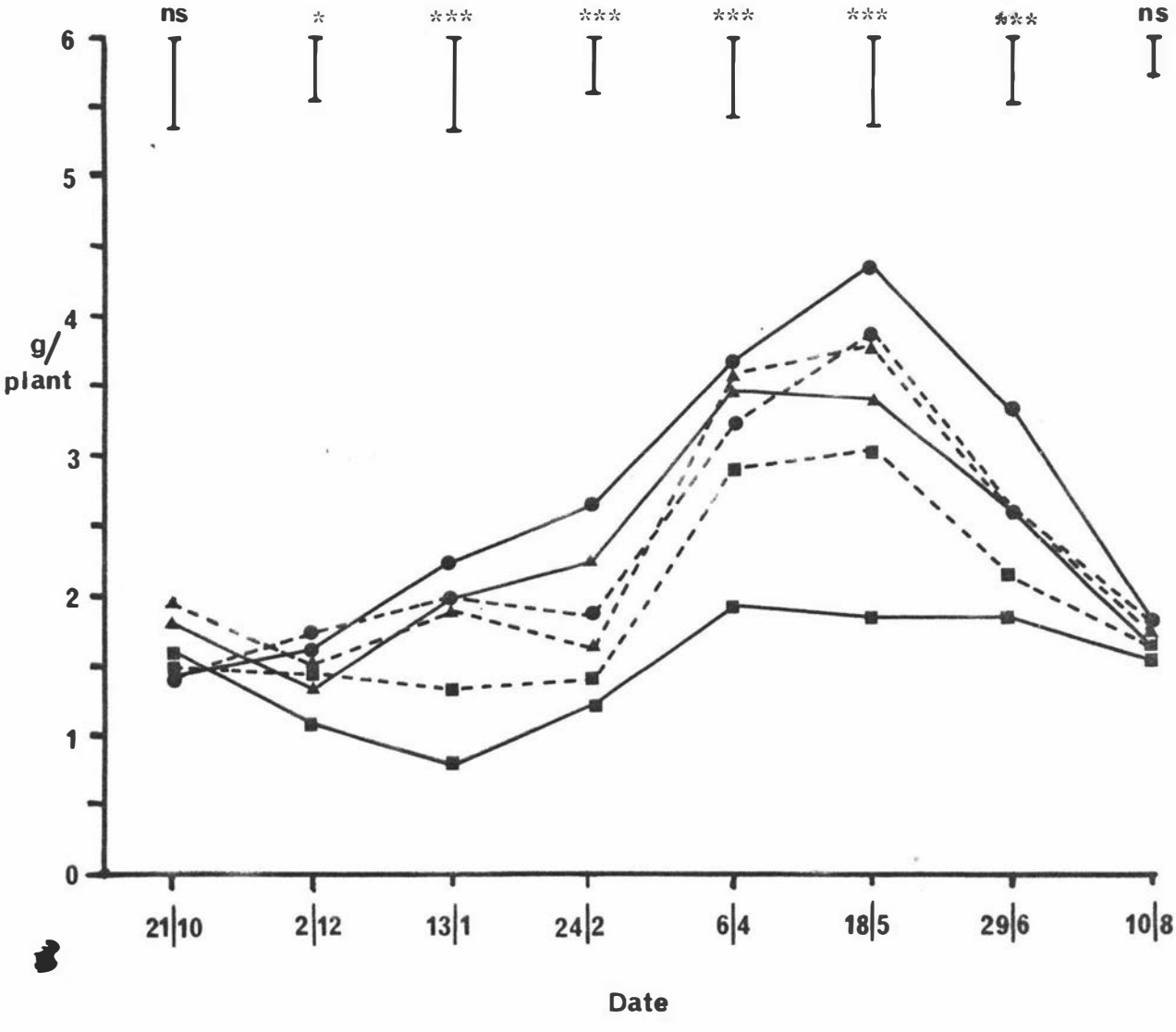


FIGURE 2: Total underground weight per plant at six-weekly harvest dates (g/plant)

—— Three-weekly cutting
---- Six-weekly cutting
I L.S.D. (5%)

■ 1.5 cm height
▲ 5.0 cm height
● 9.5 cm height

Treatment x Harvest Date Interaction: ***

The marked reduction in underground weight per plant over the winter was the result of two factors. Over this period there was a breakdown of the rhizome linkage within multicrown plants (Plate 1) which resulted in an increased plant number, as defined for this study, and an associated reduction in per plant size for the general population. The formation of new plant units was most obvious in those treatments with the largest total underground component at the end of autumn (Table 1). From duplicated, 0.1 m^2 sod samples, primary crown and taproot numbers were determined and counts made on the 5/9/76 indicated that following the increasing then decreasing underground growth phases of autumn and winter, there was a resultant increase in plant density at the higher cutting heights.

The second factor associated with decreasing per plant weights over the winter, was a definite decrease in absolute underground weights on a kg D.M./ha basis (Table 2). Absolute underground weights were estimated from known above ground herbage yields and above to below ground ratios determined from total plant dissections of final regrowth. For all six cutting treatments, weights peaked at the 18/5/76 harvest and thereafter, during the next six weeks, showed on average a 30% weight reduction. As with per plant weights, it was not until February that increasing total weights became evident with the seasonal response being most marked as cutting height increased. With values either falling or remaining static prior to this period of weight increases, there were contrasting seasonal fluctuations between treatments. Weights for the 1.5 cm treatments were low at all harvests and showed little seasonal variation. However, at a cutting height of 9.5 cm, particularly for LF, seasonal variation was considerable and the doubling of total underground weights between 13/1/76 and 18/5/76 was estimated to be equivalent to an approximate 4000-4500 kg D.M./ha increase.

3.3.1.1 Primary Crown and Taproot

The structure of this system was variable between plants in both form and size. Rhizome growth originating from the crown, developed from around its edge or undersurface and the number of stems involved varied from one to a counted maximum of nineteen. The taproot, although mainly consisting of one main root, was often forked with

TABLE 1. Plant densities for pre-autumn and post-winter samplings (plants per m^2).

Sample Date	13/1/76	5/9/76
Treatment		
SF	179	170
MF	170	217
LF	153	242
SI	155	182
MI	136	222
LI	159	225
Tmt. mean SE[a]	25.4	20.9
Signf. level[b]	NS	*
L.S.D. (5%)[c]		63

a - Standard error of treatment means within a harvest date

b - Significance levels : probability of statistical differences: * < .05; ** < .01; *** < .001

c - Least significance difference: based on two-tailed student t test at P < .05 (Snedecor & Cochran, 1967).

TABLE 2. Total underground dry weight (kg/ha)

Harvest Date	21/10	2/12	13/1	24/2	6/4	18/5	29/6
Treatment							
SF	3289	2725	2322	2427	2858	3159	2434
MF	3898	4114	3524	4399	5801	6498	4250
LF	3939	4853	4600	5445	8060	9276	6331
SI	2802	3014	2234	2552	4385	4502	3069
MI	4078	4160	2781	3229	4406	5975	3841
LI	3529	4193	3712	3720	5896	8023	5914
Tmt mean SE	414	322	311	326	465	543	228
Signf level	NS	***	**	***	***	***	***
L.S.D. (5%)		971	935	984	1402	1637	686

Treatment x Harvest Date Interaction: ***

Plate 1: A multicrown and taprooted plant linked by woody rhizome growth; considered as one plant unit.

Plate 2: Primary crown and forked taproot; pink crown shoot initials are also evident.

up to three lateral roots, arising from just below the crown, growing to a similar size as the principal root (Plate 2). Taproot lengths in excess of 20 cm were recorded in some sample plants.

The dry weight of the crown plus taproot varied with season and treatment in a similar pattern as did total underground weight (Table 3). Again there were late autumn peaks followed by late winter/spring troughs which resulted in weights being of a similar magnitude at the beginning and end of the experimental period. With the exception of SF, all treatments reached a peak weight approximately twice that of their initial weight. It was also treatment SF that was unable to maintain its crown plus taproot weight over the spring and as such, it had a significantly reduced value in mid-summer. Weights associated with the other low cut treatment (SI) were also low over January and February, however unlike the three-weekly cut treatment, autumn increases were evident. This response was the only significant one noted in regard to the influence of cutting frequency on crown and taproot weights.

3.3.1.2 Rhizome

This plant component consisted of horizontal stem growth at or below the ground surface and which terminated for individual stems at the last rooted node (Plates 3 and 4). It was predominantly a branching underground network of stems except in mid/late autumn when, under the laxly cut treatments, horizontal stem growth was sometimes in the form of rooted stolons on the soil surface.

The rhizome system was the most plastic of the underground components measured and varied considerably with season and treatment (Table 4). Again there were autumn peaks, late winter/early spring troughs, and with the exception of SF, an approximate three-fold difference over the seasonal weight range. Again it was the 1.5 cm cut treatments that were unable to maintain or improve their rhizome component during spring to late summer. In contrast, the more laxly defoliated treatments, particularly with three-weekly cutting (MF and LF), experienced a rapid and large expansion of their rhizome component. More obvious within the rhizome weight data was the delayed late summer improvement associated with the six-weekly cut treatments that were allowed to develop reproductive growth.

TABLE 3. Crown plus taproot dry weight (mg per plant)

Harvest Date:	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
Treatment								
SF	649	427	373	574	743	640	743	734
MF	894	451	926	975	1404	1327	1029	797
LF	515	695	987	1125	1373	1459	1277	781
SI	543	582	566	632	1166	1302	818	792
MI	807	631	738	834	1477	1217	1048	675
LI	795	705	886	984	1281	1440	1050	774
Tmt Mean SE	145.4	74.4	88.0	89.4	92.0	90.7	48.0	49.3
Signf level	NS	NS	***	***	***	***	***	NS
LSD (5%)			264	269	277	273	144	

Treatment x Harvest Date Interaction ***

TABLE 4. Rhizome dry weight (mg per plant)

Harvest Date	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
Treatment								
SF	611	476	342	717	1039	1121	1029	652
MF	746	634	849	1070	1797	2338	1429	711
LF	619	604	926	1296	2005	2688	1854	780
SI	699	634	538	496	1548	1562	1199	680
MI	608	668	871	632	1945	1892	1396	857
LI	712	720	879	688	1657	2160	1424	757
Tmt Mean SE	65.2	80.1	105.6	82.1	124.1	189.7	110.5	57.5
Signf level	NS	NS	***	***	***	***	***	NS
LSD (5%)			318	247	374	571	333	

Treatment x Harvest Date Interaction ***

Plates 3 and 4 (top to bottom): Rhizome components: non-woody rhizome; woody rhizome with a swollen nodal region and concentrated shoot locii; basal portion of a terminal rhizome shoot.

Swelling at nodal positions on some of the larger, woody rhizomes was observed in mid-summer and continued throughout the rest of summer and autumn. It was from these enlarged nodes that the majority of new rhizome growth originated. This new autumn rhizome growth, along with that originating from the primary crown, was readily distinguished from the old lignified rhizome system because of their white succulent stem growth. It was from the former woody rhizome component that the winter rhizome losses appeared to have occurred, for at the last harvest date on 10/8/76 the only lignified rhizome growth left was in the form of connecting linkages between the primary crown and swollen, shoot forming nodes.

3.3.1.3 Fibrous Root

This component consisted of non-woody roots arising from the crown and taproot, plus roots from nodal and adventitious positions along the rhizome system. The total weights of this fibrous root component also included associated nodules and are presented in Table 5.

TABLE 5. Fibrous root dry weight (mg per plant)

Harvest Date:	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
Treatment								
SF	361	232	81	113	121	99	79	149
MF	330	245	253	269	297	186	147	145
LF	322	324	375	275	295	333	208	174
SI	253	260	252	143	208	204	108	189
MI	404	314	348	147	270	301	179	227
LI	446	296	329	205	316	290	155	201
Tmt Mean SE	50.3	49.5	52.0	33.8	25.5	29.0	23.2	23.8
Signf level	NS	NS	*	*	***	***	*	NS
LSD (5%)			156	102	77	88	70	

Treatment x Harvest Date Interaction *

Fibrous root weights were consistently lower where 1.5 cm cutting occurred, particularly in treatment SF. Seasonal trends would appear to produce two low points, these being in January and February and again during winter. Following the mid-summer low, there was an increase in new white fibrous root growth associated with the expansion of new rhizome tissue. At the end of autumn, no brown fibrous roots arising from old woody rhizomes were evident and fibrous rooting was confined to the newly produced autumn rhizome system. It was on this new stem growth that fibrous rooting further developed in late winter to presumably reach a mid-spring peak similar to that recorded the previous year.

3.3.2 Final Canopy Components

The dissected components of those plants sampled at the end of each regrowth period were collectively considered as contributing to either above or below ground growth. Within the former group, stubble shoots, rhizome shoots, secondary axillary shoots, stubble and dead matter were considered to form final canopy growth. Because regrowth intervals varied and absolute weights of these components at the beginning of each regrowth period differed for the different defoliation treatments, absolute final weights of the canopy components at any specific harvest were of little significance. Therefore, the influence that defoliation and season had on these components was assessed by determining the proportional contribution they made to final canopy dry weight.

3.3.2.1 Final Shoot Growth

To be considered in the analysis of final shoot growth, stubble shoots had to possess at least one expanded leaf and exceed 3 mm in length, as only then were they considered to significantly contribute to final canopy yield. Similarly, rhizome shoots had to exceed 3 mm in length and possess a terminal apex that was above ground level and producing true leaves. If the terminal apex was below ground and producing scale leaves then the shoot was referred to as a rhizome shoot initial. Secondary axillary shoots developing on intact shoots were not separated and so they were included as part of the parent shoot.

TABLE 6. Percentage contribution of stubble and rhizome shoots[A] to final canopy weight

Harvest Date	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
				Stubble Shoots				
Treatment SF	23.1	15.9	16.1	17.9	7.2	9.6	[illegible]	3.7
MF	21.8	20.1	18.1	16.9	11.6	9.6	4.2	3.6
LF	22.5	22.8	19.5	10.7	5.7	10.4	2.7	2.4
SI	23.0	23.5	15.9	19.9	15.9	13.3	4.8	2.5
MI	12.6	17.7	14.6	22.6	11.9	8.8	3.4	3.2
LI	5.1	21.3	17.0	25.3	6.9	10.5	4.3	4.1
Tmt Mean SE	2.2	2.3	1.7	1.2	1.2	1.2	1.0	0.7
Signf level	***	NS	NS	***	***	NS	NS	NS
LSD (5%)	6.5			3.6	3.6			
				Rhizome Shoots[A]				
Treatment SF	28.4	32.9	33.4	30.4	14.0	36.7	49.7	68.3
MF	27.7	27.7	32.2	27.9	15.0	36.9	46.1	56.0
LF	31.5	14.1	18.7	29.0	14.7	40.5	48.2	57.6
SI	39.0	49.3	59.3	59.3	24.5	32.7	56.5	66.8
MI	52.5	50.1	46.7	44.6	22.9	33.4	50.6	61.9
LI	54.6	43.2	39.3	33.7	17.2	36.4	43.4	54.2
Tmt Mean SE	4.1	2.8	2.3	2.2	2.0	2.9	2.3	2.2
Signf. level	***	***	***	***	**	NS	*	***
LSD (5%)	12.3	8.4	6.8	6.5	6.1		6.8	6.5

A - Also includes the small contribution of crown shoots.

The percentage weight contributions of growing shoots to canopy dry matter at the end of individual regrowth periods are presented in Table 6. The most notable feature related to stubble shoot contributions, is the general consistency of the proportion involved at a common date within canopies of totally different sizes. The low values recorded for MI and LI on 21/10/76 were due to the development of considerable rhizome shoot growth during this first regrowth cycle. Nevertheless, the percentage values within and between harvests were generally of a similar value up until 24/2/76 when the dry autumn period began. For the remainder of the autumn, and then the winter, no consistent trends were obvious between treatments but within treatments there was a general, gradual decline in stubble shoot proportions.

The small contributions that crown shoots made to canopy structure were added to those of rhizome shoots and both have been collectively considered as the latter shoot class in Table 6. Prior to the regrowth cycle starting on 6/4/76, there was a consistent increase in the proportion of rhizome shoots present within the canopy when regrowth intervals were extended, a response that was not evident within the stubble shoot class. The high values recorded for MI and LI at the end of the first regrowth cycle were due to the presence of large intact shoots still remaining after the first cuts were imposed. Once shoot dominance was established within the various canopies, higher cutting tended to reduce rhizome shoot contributions, particularly for the six-weekly cut treatments and during the late spring, early summer period.

In the regrowth cycle following the dry March period, a resurgence in rhizome shoot growth occurred. Although the proportional contributions of rhizome shoots increased, there were no significant treatment differences during this recovery period. From the two subsequent sample dates, proportional values indicated a gradual increase in the contribution of rhizome shoots to canopy weight during winter. These increases were greater at the lower cutting heights.

3.3.2.2 Final Stubble and Dead Matter

The contributions of stubble and dead matter to final canopy weight are presented in Table 7. Whereas stubble proportions

TABLE 7. Percentage contribution of stubble and dead matter to final canopy weight.

Harvest date		21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
					Stubble				
Treatment	SF	39.7	33.9	27.0	35.0	30.8	22.9	14.0	5.7
	MF	39.4	41.6	34.3	39.1	27.2	18.6	8.5	11.1
	LF	42.4	51.7	48.6	39.1	25.3	13.4	6.7	11.7
	SI	29.9	17.5	8.6	9.3	18.2	21.5	9.7	6.6
	MI	30.6	20.0	16.4	11.0	26.9	23.2	7.7	7.8
	LI	33.7	28.0	23.5	13.8	33.2	13.8	8.7	7.6
Tmt Mean SE		3.5	2.9	3.2	1.3	0.9	2.0	1.3	1.0
Signf level		NS	***	***	***	***	**	*	**
LSD (5%)			8.8	9.7	4.0	2.8	5.9	3.9	3.1
					Dead Matter				
Treatment	SF	8.8	17.3	23.5	16.7	48.0	30.8	30.3	22.3
	MF	11.1	9.6	15.4	16.1	46.2	35.0	41.2	29.3
	LF	3.6	11.4	13.2	21.2	54.3	35.7	42.4	28.3
	SI	8.1	9.7	16.3	11.5	41.4	32.0	28.8	24.1
	MI	4.9	12.2	22.3	21.8	38.3	34.6	38.3	26.1
	LI	6.6	7.5	20.2	27.2	42.7	39.3	43.6	34.1
Tmt Mean SE		1.5	1.8	3.0	1.8	2.7	2.7	2.8	1.9
Signf level		*	*	NS	***	***	NS	**	**
LSD (5%)		4.5	5.3		5.3	8.2		8.3	5.7

in the three-weekly cut treatments were relatively stable during spring and summer, they gradually fell in the less frequently cut treatments as growth rates increased. Through until 6/4/76, the proportional weight of stubble within the canopy increased with increasing cutting height and frequency. Thereafter however, treatment responses were much less consistent and the most notable feature was the decline in the proportion of stubble present during the late autumn/winter period.

From observations made during dissections, it was evident that stubble tissue death predominantly occurred above the highest node supporting an actively growing stubble shoot. Such growth appeared necessary to maintain stubble tissue viability. Where no stubble shoot growth existed, the stubble stem generally died back to the first rooted node of the rhizome system.

The marked increase in dead matter during the dry March spell and then the continued high levels over the remainder of autumn and then winter, would be the most significant features of the contribution dead matter made to final canopy weights (Table 7). From the 24/2/76 harvest onwards, there was a general increase in dead matter as cutting height increased for both frequencies. Throughout the experiment period however, there was no evidence of cutting frequency consistently influencing the proportions of dead matter.

3.3.3 Final Shoot Numbers and Characteristics

The classification of those shoots considered in the analysis of final shoot numbers was the same as that outlined for final shoot growth (3.3.2.1).

3.3.1 Stubble Shoots

The general trend of higher final stubble shoot numbers with more severe and/or frequent cutting was most evident during the productive spring and summer period (Table 8). Despite lower absolute numbers during the dry period following the 24/2/75 harvest and then the subsequently cooler period of April and May, similar treatment responses did continue in relation to cutting height but not cutting frequency. Over this period of poor growth, final stubble shoot numbers were similar for both cutting frequencies. Following the last cut, which was made on 18/5/76, the two winter samples both recorded increasingly lower stubble shoot numbers and eventually no treatment responses.

Although most stubble shoots developed at nodes subtended by leaves there was an increasing proportion developing at non-subtended nodes on the stubble when cutting was more lax and/or infrequent and when the early autumn dry period was experienced. Although up to three axillary buds, generally at different stages of development, were

TABLE 8. Number of final stubble shoots (per plant)

Harvest Date	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
Treatment								
SF	14.6	20.2	19.0	31.0	12.4	14.3	8.3	2.4
MF	12.7	19.5	21.4	25.3	13.9	12.4	4.5	2.3
LF	11.0	14.3	21.5	13.7	6.2	11.7	3.1	1.7
SI	9.5	13.8	16.4	12.2	16.8	18.3	5.9	2.5
MI	6.6	10.5	16.5	12.1	14.5	11.5	4.0	2.7
LI	6.5	8.8	11.6	9.4	8.8	10.5	2.8	2.6
Tmt Mean SE	1.40	1.74	2.87	1.39	1.24	1.45	0.86	0.50
Signf level	***	**	*	***	***	**	**	NS
LSD (5%)	4.2	5.2	8.6	4.2	3.7	4.4	2.6	

Treatment x Harvest Date Interaction ***

TABLE 9. Number of final rhizome shoots (per plant)

Harvest Date	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
Treatment								
SF	9.5	20.0	15.6	20.7	12.0	22.3	21.9	14.5
MF	5.8	9.5	11.4	10.7	12.0	15.9	17.5	10.3
LF	7.3	4.4	6.1	7.4	6.9	19.6	18.3	10.8
SI	8.7	11.4	12.9	12.6	16.4	21.2	19.2	14.2
MI	7.2	10.0	12.3	9.0	13.4	17.8	16.8	12.8
LI	5.0	4.4	7.8	7.0	8.0	16.6	15.4	11.6
Tmt Mean SE	0.83	1.22	0.93	0.97	0.92	1.23	0.90	0.69
Signf level	NS	***	***	***	***	***	*	**
LSD (5%)		3.68	2.80	2.93	2.77	3.99	2.68	2.07

Treatment x Harvest Date Interaction ***

observed at stubble nodes, it was rare to find more than one stubble shoot developing in each node (Plate 5). This was in contrast to the multishoot nodes found within the rhizome system.

During early regrowth stubble and rhizome shoots of a similar size differed markedly in their leaf and stem complements (Plate 6 and also see Chapter 6.3.3). Stubble shoots were initially more leafy but as regrowth proceeded and rhizome shoots dominated, stubble shoot leaves, and eventually the shoots themselves, died. It was generally observed that the further the supporting node was located from the first ground level, rooted node of the rhizome system, the more likely it was that stubble shoot death occurred.

3.3.3.2 Rhizome Shoots

The pattern of increased rhizome shoot numbers occurring with increased cutting severity continued through the experimental period until the 6/4/76 harvest (Table 9). During the subsequent regrowth period, involving the recovery from dry conditions, there was a general flush of rhizome shoots, particularly in association with the most laxly defoliated treatments. These shoot numbers were maintained during early winter but had fallen by the time of the last sample on 10/8/76. The greater numbers recorded for SF, compared with SI, up until the beginning of the early autumn dry period was the only consistent response to cutting frequency.

For both the severely cut treatments, and in particular SF, rhizome shoots predominantly arose from sites on the upper surfaces of rhizomes, especially at swollen nodal positions. In contrast, rhizome shoots in the remaining treatments frequently arose from the sides or undersurfaces of nodes within the rhizome system and often the basal portion of their stems indicated that up to 2-3 cm of underground, horizontal growth had initially occurred before the shoot became emergent (Plates 7 and 8).

Prior to the autumn dry period, rhizome shoot numbers, relative to those recorded for stubble shoots, were generally of a similar (SF and SI) or reduced (MF, MI, LF and LI) order. Following this dry period however, the situation was reversed and rhizome shoots were predominant in all treatments.

Plate 5: A stubble node possessing three axillary shoots at different stages of development.

Plate 6: Contrasting leaf and stem complements in rhizome shoots (left) and stubble shoots (right) during early regrowth.

Plate 7: A rhizome shoot characteristically dominating two stubble shoots (left) and a rhizome shoot with a basal underground portion (arrowed, right).

Plate 8: Two rhizome shoots and several rhizome shoot initials at different stages of development.

3.3.3.3 Rhizome Shoot Initials

In plant samples taken before the 3/2/76 and after the 18/5/76 harvests, rhizome shoot initials were recorded, but no treatment differences were evident and absolute numbers were low with an overall mean of 0.8 per plant. Between these two dates however, there was a general increase in absolute numbers and marked treatment responses, the most notable occurring with treatments MF and LF (Table 10). Rhizome shoot initials in SF were consistently lower in number than those of the other three-weekly cut treatments and furthermore, unlike the remaining cutting heights, numbers were not consistently reduced when less frequent cutting was employed.

TABLE 10. Number of rhizome shoot initials (per plant)

Harvest Date	3/2	24/2	16/3	6/4	27/4	18/5
		Normal				
Treatment						
SF	1.4	0.9	1.4	1.9	2.5	4.3
MF	4.3	4.1	4.5	4.6	5.2	5.7
LF	9.4	4.5	3.9	6.0	4.5	5.9
SI		2.7		1.2		5.9
MI		2.2		1.6		4.7
LI		2.3		3.1		5.4
Tmt Mean SE	0.64	0.47	0.51	0.56	1.11	0.95
Signif level	***	***	***	***	NS	NS
LSD (5%)	2.2	1.4	1.8	1.7		

Treatment x Harvest Date Interaction : *

		Abnormal				
Harvest Mean	-	1.6	1.5	1.3	1.0	-
Harvest Mean SE	-	0.17	0.18	0.12	0.14	-

Underground axillary shoots were present after 18/5/76, however, those that had not become orthotropic and formed aerially growing shoots (Plate 9) were generally in excess of 2 cm in length and therefore classified as part of the rhizome system. Swollen nodes were the predominant sites for both single and multi-initiation of rhizome shoot initials, although lateral branching of a single rhizome, giving rise to initials, did occur.

The initials referred to as abnormal in Table 10, developed during the middle part of this active period when the terminal apex on some initials died and the remaining stem tissue became swollen (Plate 10). No statistically significant differences were recorded between treatments or harvest dates, thus only harvest means and associated standard errors are presented. Following the dry autumn period, new rhizome shoot initials developed from axillary positions on these stubs.

3.3.3.4 Crown Shoots and Crown Shoot Initials

During mid-summer/autumn, there was a general increase in crown shoot numbers, particularly as cutting height increased (Table 11). Outside this period however, they were low in number and at times, absent. Crown shoots principally originated from the side or undersurface of the crown (lateral-ventral) and very few arose from the upper surface (dorsal).

Crown shoot initials, which always arose from lateral-ventral positions, increased in number over the same period as did rhizome shoot initials (Table 11). Again the largest increases were recorded with MF and LF cutting treatments. These initials formed the basis of new rhizome growth from the crown and/or the basis for lateral-ventral crown shoots.

3.3.4 Residual Shoot Numbers (Table 12)

The classification and division of residual shoots was similar to that outlined for the analysis of final plant shoots. However, in order that the residual shoot determinations would indicate the potential number of shoots available for immediate growth following a cut, the size of shoots included in each class did vary between pre- and post-cut samples. All intact shoots showing signs of growth, such as

Plate 9 (left to right): Early rhizome shoot development ranging from a leafy orthotropic rhizome shoot to an underground rhizome shoot initial.

Plate 10 (right to left): Stages of abnormal rhizome shoot initials; apical death; subtended axillary bud development; resumed rhizome shoot initial growth.

TABLE 11. Number of final crown shoots and crown shoot initials (per plant)

	Crown shoots						
Harvest Date	21/10	2/12	3/1	24/2	6/4	18/5	29/6
Treatment							
SF	0.1	0	0.9	0.6	0.7	0.3	0.1
MF	0.1	0	2.4	1.6	1.2	0.6	0.2
LF	0.1	0	3.1	2.4	2.1	0.7	0
SI	0.4	0	0.6	1.3	2.5	1.1	0.1
MI	0.5	0	0.3	0.7	3.1	0.7	0.1
LI	0.2	0	1.1	1.6	2.4	1.2	0.3
Tmt Mean SE	0.12		0.31	0.40	0.45	0.37	0.11
Signif level	NS		***	*	*	NS	NS
LSD (5%)			0.9	1.2	1.3		

	Crown Shoot Initials					
Harvest Date	3/2	24/2	16/3	6/4	27/4	18/5
Treatment						
SF	0.3	0.7	0.2	0.3	0.7	0.7
MF	1.1	1.7	1.2	0.9	1.3	0.9
LF	2.7	2.6	2.3	1.5	0.9	1.0
SI		0.6		0.5		0.6
MI		0.3		0.3		1.1
LI		1.1		0.9		0.9
Tmt Mean SE	0.22	0.29	0.16	0.32	0.29	0.21
Signif level	***	***	***	*	**	NS
LSD (5%)	0.7	0.9	0.5	0.9	0.4	

TABLE 12. Residual shoot numbers (per palnt)

Harvest Date	9/9	21/10	2/12	13/1	24/2	6/4	18/5
			Stubble Shoots				
Treatment							
SF	5.6	11.5	16.1	18.0	16.3	21.1	26.7
MF	15.2	15.0	14.3	12.8	21.7	21.7	27.4
LF	30.0	15.7	9.4	15.6	19.9	15.2	23.4
SI	8.8	11.0	5.5	10.9	7.9	11.2	18.9
MI	13.2	13.9	6.6	11.4	10.7	13.0	21.6
LI	26.1	10.6	4.7	10.8	7.3	18.8	25.1
Tmt Mean SE	2.17	1.25	1.30	1.05	1.38	1.23	1.56
Signif level	***	**	***	***	*	***	*
LSD (5%)	6.6	3.8	4.1	3.2	4.2	3.7	4.7
			Rhizome Shoots				
SF	8.3	9.2	12.9	15.0	11.9	21.6	30.0
MF	10.3	9.6	6.0	11.7	17.2	36.8	32.4
LF	17.2	10.7	4.1	16.7	21.8	38.4	32.0
SI	10.1	10.5	3.2	13.4	12.2	19.9	25.6
MI	9.9	11.1	4.1	8.4	12.3	23.9	28.0
LI	15.0	6.4	2.0	7.6	10.3	32.6	30.4
Tmt Mean SE	1.64	1.43	0.59	0.89	1.12	2.09	2.09
Signif level	*	NS	***	**	*	***	NS
LSD (5%)	4.9		1.8	2.7	3.4	6.3	
			Crown Shoots				
Harvest Mean	0.5	0.1	0.1	1.2	1.3	2.4	1.4

Harvest Mean SE : 0.13 Harvest Mean LSD (5%): 0.35

expanded leaves or stem extension, were included in residual shoot determinations. Therefore within this classification, shoot initials were included as residual rhizome or crown shoots provided stem extension was obvious. Axillary buds showing no sign of expansion were excluded as it was considered that they, along with all nodal positions, may form a potential pool for new shoot growth but were not avilable for immediate regrowth.

3.3.4.1 Residual Stubble Shoot Numbers

Residual stubble shoot numbers left after the first cut indicate the increase in residual shoots obtainable by increasing the cutting height within a similarly structured plant canopy. However, in subsequent harvests, once different canopy structures had been determined, no consistent differences in residual stubble shoot numbers between cutting heights were evident. This is in contrast to the consistent negative relationship between final stubble shoot numbers and cutting height previously reported.

There was a general decrease in residual stubble shoots with less frequent defoliation and this was particularly evident in residual plants following cuts made during rapid growth periods such as January and February.

3.3.4.2 Residual Rhizome Shoot Numbers

Marked seasonal fluctuations in residual rhizome shoot numbers were recorded for all treatments, particularly in those involving lax defoliation. Low values were recorded in mid-spring/early summer, with peak values occurring towards the end of autumn. The interaction of treatments with harvest dates was highly significant ($P<.001$) and is indicated by the negative relationship in numbers with cutting height in late spring/early summer and the positive relationship in autumn.

Only during the initial stages of the late summer/autumn improvement did residual numbers in the six-weekly fall behind the three-weekly cutting treatments and only then for the intermediate and lax cutting heights.

3.3.4.3 Residual Crown Shoot Numbers

There were no significant treatment differences recorded, thus only harvest means are presented. However, a significant variation between harvests was measured and although numbers were much lower, the seasonal pattern was similar to that reported for residual rhizome shoots. Again values were low during spring, started to increase during January and February, and peaked in mid-autumn.

3.4 Discussion

3.4.1 Underground Plant Components

The general increase in the activity of underground organs during late summer and autumn was in direct contrast to the spring and early summer period when vertical, aerial shoot growth dominated plant growth. Seasonal changes in crown, taproot and rhizome weights were of a similar pattern as those reported for lucerne root weights (Acker & Garwood, 1959) and rhizome weights in *A. repens* (Arny, 1922) and *S. halepense* (Sturkie, 1930). Increasing rhizome shoot and crown shoot activity during autumn was also similar to that which has been reported for crown shoot activity in *L. corniculatus* (Smith, 1962; Smith & Nelson, 1968a) and lucerne (Grandfield, 1943).

The physiological mechanisms involved in the seasonal partitioning of the growth of 'Grasslands Maku' can only be speculated upon, although there would appear to be both internal and external factors involved. During spring, the predominance of vertical aerial extension of shoots is positively related to long days and lower winter temperatures (Thomas, unpublished data) which would suggest a relationship with reproductive activity. This is further supported by the delay in rhizome expansion experienced with the six-weekly cutting regimes where reproductive activity was allowed to develop. More erect growth was reported to occur in prostrate cultivars of *L. corniculatus* after exposure to long photoperiods and warm temperatures (Nittler & Kenny, 1965). Conversely, reducing daylength and night temperatures associated with autumn have suggested by Nelson & Smith (1968a) to induce increased crown and root activity in *L. corniculatus* and this may also occur in *L. pedunculatus*.

The resurgence of underground activity first became evident in February 1976 for Experiment 1 and in March 1977 for Experiment 2 (see Chapter 4). For both years, improvements coincided with the start of reducing air and soil temperatures, and underground growth then continued to expand through the increasingly cooler autumn months. Whether temperature influences underground growth directly and/or indirectly by modifying the extent of above-ground growth is not certain but it should be noted that over the dry then cold period, while rhizome expansion was proceeding at its greatest rate, poor above-ground herbage production occurred (see Chapter 4.3.1.1). Troughton (1957) did state that maximum underground growth often coincided with minimum above-ground herbage growth and that rarely did maximum growth of these two collective plant components coincide.

The wide range in estimated absolute underground weights resulting from varied seasonal and managerial factors does indicate the plasticity of growth that exists in this region of the plant. Although the peak underground weights achieved under the laxly defoliated treatments during autumn were not greatly superior to those reported for agricultural swards (Troughton, *loc. cit.*), it should be noted that at such peaks during April and May, underground growth represented, on average for all treatments, 71% of total plant growth at the end of their appropriate regrowth intervals.

The nature of the above-ground canopy definitely influenced underground growth as was illustrated by the differences generated in the various defoliation regimes. The positive relationships between underground growth, increased cutting height and increased regrowth intervals are well known (Troughton, 1957) and the principles involved would appear to be related to total plant photosynthesis and photosynthate distribution (Leonard, 1962). It is interesting to note therefore, the interaction between cutting height and frequency during late summer/autumn and that only under severe defoliation was there a consistent increase in underground weight in response to less frequent cutting. The higher residual and subsequent leaf complements that occurred with higher cutting (Appendix 6) would appear to have sufficiently compensated any benefits associated with longer regrowth intervals in so far as underground growth was concerned.

The weight losses that occurred in underground organs during winter can partly be associated with general respiratory losses involving the utilization of stored starch (see Chapter 5.3.1). A further contributor to these losses was the death of old rhizome tissue which appeared to be closely related to disease factors. Lesions on rhizome tissue, especially on the older stems, became common during late autumn and winter and isolation of the involved pathogens indicated a soil fungal complex existed that involved *Rhizoctonia*, *Phytophthora* and *Colletotrichum destructivum* (Laundon, pers. comm). Henson & Scoth (1962) have also reported *Rhizoctonia solani* as an important disease of underground organs and basal portions of aerial stems in *L. pedunculatus*.

3.4.2 Crown and Taproot

The primary crown and taproot can be considered as the central organ of a plant unit, in that it links the network of peripheral stem growth that dominates the growth habit of *L. pedunculatus*. Although there was no obvious retraction in the length of this central system at any time, its weight did show marked seasonal variation and the manipulation of above-ground growth by cutting, did influence the extent and pattern of these seasonal weight changes. Probably of greatest importance were the relatively low weights recorded where severe and frequent cutting was employed, particularly as the reductions were most noticeable during summer. This response has important implications in relation to plant persistence under conditions of summer moisture stress and stocking managements involving continuous grazing. Levy (1970) does refer to *L. pedunculatus* as being intolerant of dry conditions and the reduction in the size of the taproot system under intense defoliation may in part form the basis for such a comment.

The pattern and extent of crown shoot initiation, as influenced by season and management, were similar to those recorded for crown and taproot weights. However, within a plant containing a rhizome system, the crown is of little relative importance as a shoot producing organ and tends only to provide the basis for initial rhizome expansion. Of those crown shoots that did develop, nearly all arose from lateral/ventral positions growing initially as horizontal shoot initials and then as vertical aerial shoots. This tendency to grow away from the plant's centre and produce few dorsal crown shoots is well illustrated by the hollow plant centre in above-ground growth, frequently observed in single spaced plants of *L. pedunculatus*.

3.4.3 Rhizome

The development of a rhizome system is probably the most important feature in the morphological structuring of 'Grasslands Maku' and as stated by MacDonald (1948), it is the most notable feature distinguishing it from the remainder of the species in the genus *Lotus*. Variations in the general appearance of plants were principally determined by the extent of rhizome expansion and this was particularly noticeable where different cutting heights occurred. As cutting became less severe and rhizome expansion increased, plant growth changed from a compact to a more open, spreading habit (see Plates 11-13).

Although variations in rhizome weights followed similar seasonal and treatment trends to those of the crown and taproot, the magnitude of the changes was much greater. The more responsive nature of the rhizome system to growing conditions, or opportunities, would suggest that it is a more transient, temporary structure relative to the crown and taproot. Following the winter losses of rhizome tissue, the majority of the rhizome system consisted of new non-woody stems initiated in the previous autumn. Old woody rhizome tissue only existed as linkages between major rhizome shoot loci. This pattern of growth would suggest that in its endeavour to spread and colonize, *L. pedunculatus* possesses an approximate annual replacement cycle of rhizome tissue. The responsive nature of rhizome growth to seasonal and managerial factors has also been highlighted with *P. pratensis* (Graber & Ream, 1931; Brown 1943) and *S. halepensis* (Sturkie, 1930).

As an alternative to the crown region, the rhizome system was the dominant underground shoot forming region. Nodal regions distant from the crown were the sites from which shoot initiation occurred within this system, particularly swollen nodes which were situated 1-10 cm from the primary crown and taproot (Plate 14).

3.4.4 Fibrous Root

The weight of fibrous root was the net measurement of two processes; the formation of new and the death of old roots, both of which showed different seasonal patterns. The formation of new roots, particularly at nodal positions on rhizome growth, commenced in autumn and continued through to late spring. In contrast the death of old roots on older, woody rhizome tissue commenced in summer and continued through autumn

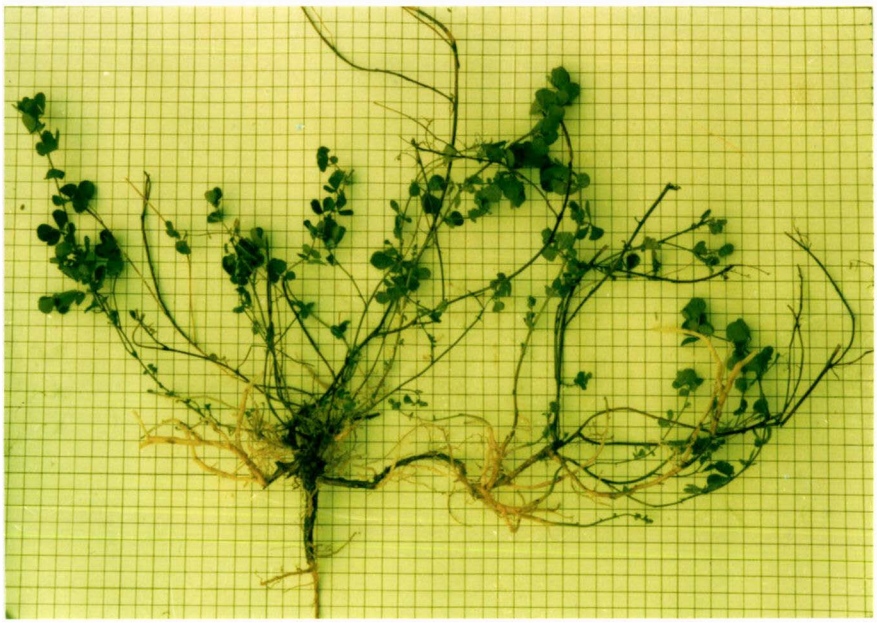


Plate 11: A spreading, open plant habit typical of 9.5 cm cutting (LF) where underground growth was extensive.

Plate 12: Intermediate plant habit of 5.0 cm cutting (MF).

Plate 13: A compact plant habit resulting from 1.5 cm cutting and reduced rhizome expansion. (SF)

Plate 14: A dorsal view indicating concentrated shoot loci at swollen rhizome nodes distant from the crown.

and winter. Soper (1959) reported that the decay of root structures was generally restricted to the oldest roots of autumn harvested *L. pedunculatus* plants, although even then, root decay was much less than that of white clover. Similar seasonal patterns of nodal root growth and decay to those observed in this experiment were reported in other pasture plants by Jacques & Edmonds (1952), Troughton (1957) and Caradus & Evans (1977).

Downward vertical growth of fibrous roots from nodal positions was uncommon and generally failed to extend below a depth of 5 cm from the soil surface. This tendency to grow more horizontally, combined with the extensive nature of the supporting rhizome tissue, resulted in a dense superficial rooting habit similar to that reported by MacDoanld (1946) and Ozanne *et al*. (1965) for *L. pedunculatus*. The presence of large lacunae in the root cortex of *L. pedunculatus* (Soper, 1959), combined with this dense and shallow fibrous rooting system, may in part explain its ability to survive and produce under waterlogged conditions (Barnard, 1969). Furthermore, the high concentration of roots in the superficial layers of the soil profile may also relate to the ability of *L. pedunculatus* to efficiently recover soil phosphate under low fertility conditions, as it is in this organic zone that plant available phosphate predominantly exists under such conditions (Walker & Adams, 1959).

3.4.5 Stubble Shoots

With lower cutting heights, above-ground growth became more prostrate in habit and shoot internode lengths were reduced. As a result of these morphological modifications within the canopy, increased cutting height did not improve residual stubble shoot numbers and in fact, greater final stubble shoot numbers within a common regrowth period generally occurred with the more severely cut treatments. It was apparent that greater stubble shoot numbers were generally associated with smaller canopies, a fact that was further supported by the lower numbers generally recorded where canopy growth was extended by increasing regrowth times. Along a stem, and also within a cutting treatment, the development of stubble shoots did appear to be more numerous at nodal sites subtended by leaves. This would be consistent with the treatment responses where lower residual and final numbers were recorded on the poorer leaved stubble of the six-weekly cutting treatments. With *L.corniculatus* , Langille &

Calder (1971) reported that with both increasing frequency and severity of cutting, side branching from nodes on the stubble increased and Greub & Wedin (1971a) found that of the axillary shoots remaining after infrequent cutting, few were subtended by leaves.

The reduction in stubble shoot growth associated with the early autumn dry period would indicate that moisture stress and desiccation strongly influences the extent to which subtending axillary shoots on stubble can develop. Because of the poor viability of this shoot system under stress conditions, it would appear that little benefit would be gained from a management system purely designed to encourage their growth during dry conditions. Similarly, the viability of stubble and associated shoots was poor during winter frosting. Under such conditions there would again appear to be little benefit in establishing and retaining high stubble and stubble shoot numbers within a winter canopy purely on the basis of stubble shoot growth. Stubble shoot vigour and viability has also been noted to be poor in regrowing lucerne (Leach, 1968, 1970), particularly the further the shoot is from the crown region.

3.4.6 Rhizome Shoots

The importance and the plasticity of the rhizome system was further illustrated by the number of shoots developing from nodal sites at or under the soil surface. Through the influence of cutting height, large differences in rhizome shoot numbers participating in aerial growth were generated. During spring and early summer, residual and final rhizome shoot numbers were generally lower where higher cutting occurred and this was reflected in the low contributions rhizome shoots made to final canopy weights. Towards late summer there was a general increase in rhizome shoot initiation, as indicated by the increased number of rhizome shoot initials and residual shoots. This increase continued through autumn, particularly under lax defoliation, however there was no comparable increase in the number of rhizome shoots actually participating in aerial growth until after the dry period in autumn ended. It was apparent, and increasingly so with laxer defoliation, that axillary shoots from rhizomes were not developing into aerially growing, leafy shoots but were remaining underground as horizontally growing, fleshy rhizome shoot initials.

Following the dry period in which stubble shoot death occurred there was a general flush of aerially growing rhizome shoots, particularly with laxer cutting. Most of the new shoots possessed up to 2 to 3 cm of white, fleshy growth at their base which would suggest a transition had occurred with shoot initials developing into leaf forming, aerial shoots. This release of initials to aerial growth, combined with the greater tendency to produce leafy rhizome shoots under severe defoliation, indicates that the size and vigor of the above-ground canopy greatly influences the number and destiny of rhizome based shoots. Furthermore, the increase in rhizome shoot initials that had lost apical activity and then subsequently resumed growth from subtended axillary buds following the dry period, further indicates that determining processes exist which differentially control the role of rhizome shoots depending on the growth activities of both above and below ground plant components.

The transition of axillary shoots from horizontally growing rhizomes to leafy orthotropic shoots which is apparent in 'Grasslands Maku' also occurs in *Solanum tuberosum* (Wareing & Phillips, 1970) and *Solanum andigenum* (Woolley & Wareing, 1972). Such responses in these two latter species can result from the removal of aerial meristems and/or the application of exogenous hormones and as such, these two manipulations have been linked in interpreting the transition mechanism involved. Although the growth of axillary buds would appear to be ultimately controlled by hormones, the functional control mechanisms would seem to involve the active competition between regions of plant growth for substrates such as assimilates, nutrients and water (McIntyre, 1971; Jewiss, 1972; Langer 1974). In *S. halepense*, Beasley (1970) reported that axillary bud development was influenced by the dominance of above-ground herbage and both parent and lateral rhizome apices. As indicated by the variation in final shoot numbers, the extent to which axillary shoot development was dominated, related positively to cutting height and interval. Whether this increasing dominance was due to the presence of greater amounts and more active stubble herbage with increasing cutting height or larger and more rapidly growing shoots with both increasing cutting heights or interval, cannot confidently be determined from this experiment.

Although rhizome based shoots became the predominant aerial component within the canopy as winter progressed, apical dominance within these shoots was low and secondary axillary shoots became numerous. On the older, poorly leaved rhizome shoots, secondary axillary shoot development was generally at nodes not subtended by leaves and towards the top of the parent stem. In contrast, secondary shoot development on newly emerged, thick stemmed rhizome shoots was found at more basal nodes and it was these new rhizome shoots and associated axillary shoots that dominated new spring growth. Because of the few rhizome shoot initials present at the 29/6/76 harvest, it would appear that the thick stemmed shoots present in spring had developed from rhizome shoot initials that had emerged by mid-winter.

In summary, it was apparent that the emphasis in the partitioning of plant growth differed markedly throughout the year, with aerial shoot growth dominating the spring/early summer period and underground growth dominating the late summer/autumn period. The rhizome system was the most notable plant component studied as it was a large and highly responsive component that principally determined total plant growth habit. It was also a region of active axillary shoot initiation from which rhizome shoots developed. Viability of stubble shoots during dry summer or cold winter conditions was poor and as a result, canopy growth at these times was dominated by rhizome shoots.

CHAPTER 4: DEFOLIATION MANAGEMENT AND HERBAGE DRY MATTER PRODUCTION OF *LOTUS PEDUNCULATUS* cv. 'GRASSLANDS MAKU'

4.1 Introduction

The supply of assimilates to, and the demand of assimilates by, respiratory processes involved in the maintenance and formation of plant tissue, strongly influences the extent of regrowth of defoliated pasture plants. Assimilate supply depends on the development of photosynthetic processes in previous and current regrowth periods which are in turn influenced by the frequency and severity of defoliation (Donald, 1956; Brougham, 1956; May, 1960). The presence of meristematic regions in sufficient numbers and at sufficiently active stages of development to utilize assimilate supplies, also influences the ability of plants to regrow. Thus, the physiological state of the plant, as determined by environmental factors and defoliation intensity, becomes important (Leach, 1967; Jackson, 1974).

L. pedunculatus has frequently been referred to as being intolerant of hard grazing and this has been particularly so for erect, tetraploid cultivars (Thomas, 1935; Davies, 1969; Armstrong, 1974; Lambert *et al.* 1974). Only where competition from companion species is minimal, such as in wet, infertile soils, does it seem likely that *L. pedunculatus* can withstand severe defoliation (Howell, 1948; Charlton, 1975). Within defoliated, competitive swards its poor regrowth ability, persistence and hence production has been noted by Levy (in MacDonald, 1946); Filan (1963); Sheath *et al* . (1976); and Brock & Charlton (1977). There has however, been no detailed reference to the patterns and extent of *L. pedunculatus* regrowth that allow these general defoliation responses to be explained.

Yield data collected from the 1975/76 field experiment, which has in part been presented in Chapter 3, provided some information on the production responses of *L. pedunculatus* cv. 'Grasslands Maku' to different frequencies and severities of defoliation. To further extend this regrowth information, several more cutting treatments were evaluated in a separate field experiment during 1976/77. The production levels, rates and composition of pure 'Grasslands Maku' measured in these field experiments are presented and discussed in this Chapter. For both

seed on 31/10/75. Previously, the area had been cultivated out of a grass-clover pasture and then fallowed for 18 months. At sowing, 375 kg/ha superphosphate fertilizer was broadcast and for the control of broad-leaved weeds, 2,4,DB (2,4-dichlorophenoxy butyric acid) at a rate of 2.8 l a.i./ha was sprayed when seedling 'Grasslands Maku' plants possessed 2-3 stems. To restrict white clover growth, ethofumisate at 5.0 l a.i./ha was applied in August, 1976 and in an endeavour to maintain a pure 'Grasslands Maku' stand, hand weeding of the area on which Experiment 2 was located continued throughout the experimental period. Plant numbers, as defined in Chapter 3, were counted from duplicate, 0.1 m^2 sod samples taken on 30/11/76 and the mean plant density plus its standard error was 299 ± 80 per m^2, respectively.

The experimental area was located on a Tokomaru silt loam (Cowie, 1972) for which a mean soil moisture value of 20% O.D.W. in the top 30 cm of the soil profile was considered to be approximately equivalent to -1 bar soil moisture tension (Scotter, pers. comm.). Weekly soil moisture determinations were made within the experimental area and when these levels approached 20% O.D.W. for the top 30 cm, overhead watering was conducted. On the 18/12/76, 23/1/77, 15/2/77 and 28/3/77 applications of approximately 40 - 45 mm of water were made, such that soil moisture in at least the top 30 cm was restored to field capacity as defined by Gradwell (1974) for this soil type.

The experimental area was not defoliated during the autumn and winter of 1976 and when the cutting treatments of Experiment 2 were first imposed on 7/9/76, total canopy weight was 3780 ± 302 kg D.M./ha. The cutting treatments were as follows:

RS : cutting down to 1.5 cm when over 50 percent of those major shoots with growth in the upper 5.0 cm layer, possessed reproductive bud development.

SAS : cutting down to 1.5 cm when over 50 percent of those major shoots with growth in the upper 5.0 cm canopy layer, possessed growing secondary axillary shoots at their upper nodes.

6S : cutting down to 1.5 cm every six weeks.

6L : cutting down to 9.5 cm every six weeks.

SAL : as for SAS but cutting down to 9.5 cm.

LS : alternation of SAS and cutting down to 9.5 cm when over 50 percent of those major shoots with growth in the upper 5.0 cm canopy layer

were of sufficient height such that their shoot apex was removed.

Treatments were randomly located within four blocks and the appropriate cuts were made over the entire 2 x 5 m plot areas with a rotary mower. For each plot a ground level, 0.1 m^2 quadrat cut, randomly located within a plot grid, was taken before and after each cut and thereafter at approximately three-weekly intervals. Following determinations of percent dry matter and leaf area, as detailed for Experiment 1, residual, intermediate and final dry matter yields plus appropriate leaf area indices were estimated.

From a central position within each quadrat, a ground level subsample was separately taken and kept for canopy structure determinations. The dissection components, as defined in Chapter 3, were : dead matter, stubble, stubble shoots, rhizome shoots and secondary axillary shoots. The dead component included all brown and withered tissue; all leaf and stem that had fallen to the ground; and all tissue left attached to the plant following cutting that had been damaged and therefore considered to have little value in plant regrowth.

For dissection, only shoots showing stem extension or leaf expansion and exceeding 3 mm in length were considered to significantly contribute to canopy dry weight. Shoot numbers as an indicator of potential regrowth sites following cutting would therefore have underestimated the true value. Those shoots within the subsample that were not located at the node of other stem tissue were assumed to have arisen from an underground origin and to have been cut at ground level. As such, it should be noted that within this group, classified as rhizome shoots, some would have originated from the crown region. Data presented in Chapter 3 does indicate however, that the number of shoots originating from the crown region is negligible within the general pool of shoots arising from sites located at, or under the soil surface. Thus, for clarity of presentation this basal pool will be referred to as rhizome shoots. From the counts of shoots within each class and the dry weight of individual components, determined after drying at 80°C for 16 hours, component shoot numbers and dry matter yields, on an area basis, were determined for each cut.

Due to low temperatures (Appendix 2) and slow growth during late April and May, the quadrat cuts taken on 17/5/77 were considered as the last for determining the herbage production of the cutting treatments.

Thus, total net herbage production for each treatment was considered as the cumulative difference between the residual and final dry matter of individual regrowth cycles during the 7/9/76 to 16/5/77 period. Except for treatment RS, which was cut on 16/5/77, all other canopies were left intact and quadrat cuts were made on 18/6/77 and 9/9/77 to indicate component changes within varyingly structured canopies over the winter.

Analysis of variance tests conducted in both field experiments were based on a randomized, complete block design involving four replicates.

4.3 Results

4.3.1 Experiment 1:

Absolute herbage dry matter values (D.M.) and leaf area indices (LAI) present at the beginning and end of each regrowth period are presented in Appendices 3 and 4. Within a cutting height, residual DM and LAI were consistently lower when six rather than three-weekly cutting was employed. Obvious reductions in DM and LAI levels during the dry then cool autumn period were evident in all treatments.

4.3.1.1 Net Herbage Production

As no consideration was given to weight changes occurring within the canopy below cutting height, mown D.M. was considered invalid in determining production differences between treatments. As residual D.M. decreased during spring and summer, mown D.M. exaggerated production and conversely, as canopy weight accumulated below cutting height during autumn, mown D.M. underestimated actual production. The magnitude of these discrepancies increased as cutting heights increased and therefore it was considered more valid to assess net production as the cumulative value of the differences between final and residual D.M. of each regrowth cycle.

Net herbage production, as defined above, is presented in Table 13 for three periods approximately representing spring, summer and autumn. During the spring period, significantly lower production was recorded at each cutting height when regrowth intervals were reduced and within both frequencies when the low, 1.5 cm cutting height was employed. For the summer period, there was again a consistent, positive response

(Figure 3). This initial delay was most marked for the 9.5 cm cutting height,although similar net production was eventually attained for all three treatments. The individual nature of regrowth cycles was well illustrated where more frequent cutting occurred, particularly at the high cutting level. For treatment LF, the alternation of high then low net regrowth was common and is also evident in Appendix 3A. Similarly for treatment SF contrasting regrowth patterns were recorded for the two cycles of this spring period. Slow regrowth occurred in the first cycle whereas initial regrowth was rapid in the second cycle.

As with D.M. accumulation, significant delays in attaining net leaf area accumulation were also evident during many of the spring regrowth cycles (Table 14). However, it is interesting to note the continually high LAI present in LF throughout both cycles and the decline from approximately 7.5 in LAI values towards the end of the regrowth cycles of the higher, six-weekly cut treatments.

(ii) Summer Regrowth Cycle (13/1 to 24/2)

For the less frequently cut treatments, the initial delays in net regrowth that were evident in the spring period, were of a much smaller magnitude during the summer regrowth cycle (Figure 4). For this period, net regrowth curves of the three, infrequently cut treatments were distinctly different. Initial delays in regrowth were greater for the 1.5 cm cut and the overall rate of increase in net proudction was more gradual for the 9.5 cm cut. For the more frequently cut treatments, summer regrowth rates were greater than those in spring, however the alternation of high then low net regrowth, at the 9.5 cm cutting height, was still evident.

Differences in LAI between the six-weekly cut treatments were much less than those recorded in spring. All showed a similar pattern of increasing to a maximum LAI of approximately 5.5 - 6.5, then falling towards the end of the regrowth period (Table 14). Differences in LAI values were also less marked between the more frequently cut treatments and they too showed signs of levelling off during the first regrowth cycle at the higher cutting heights.

4.3.2 Experiment 2

The cumulative net growth of each of the three shoot classes measured

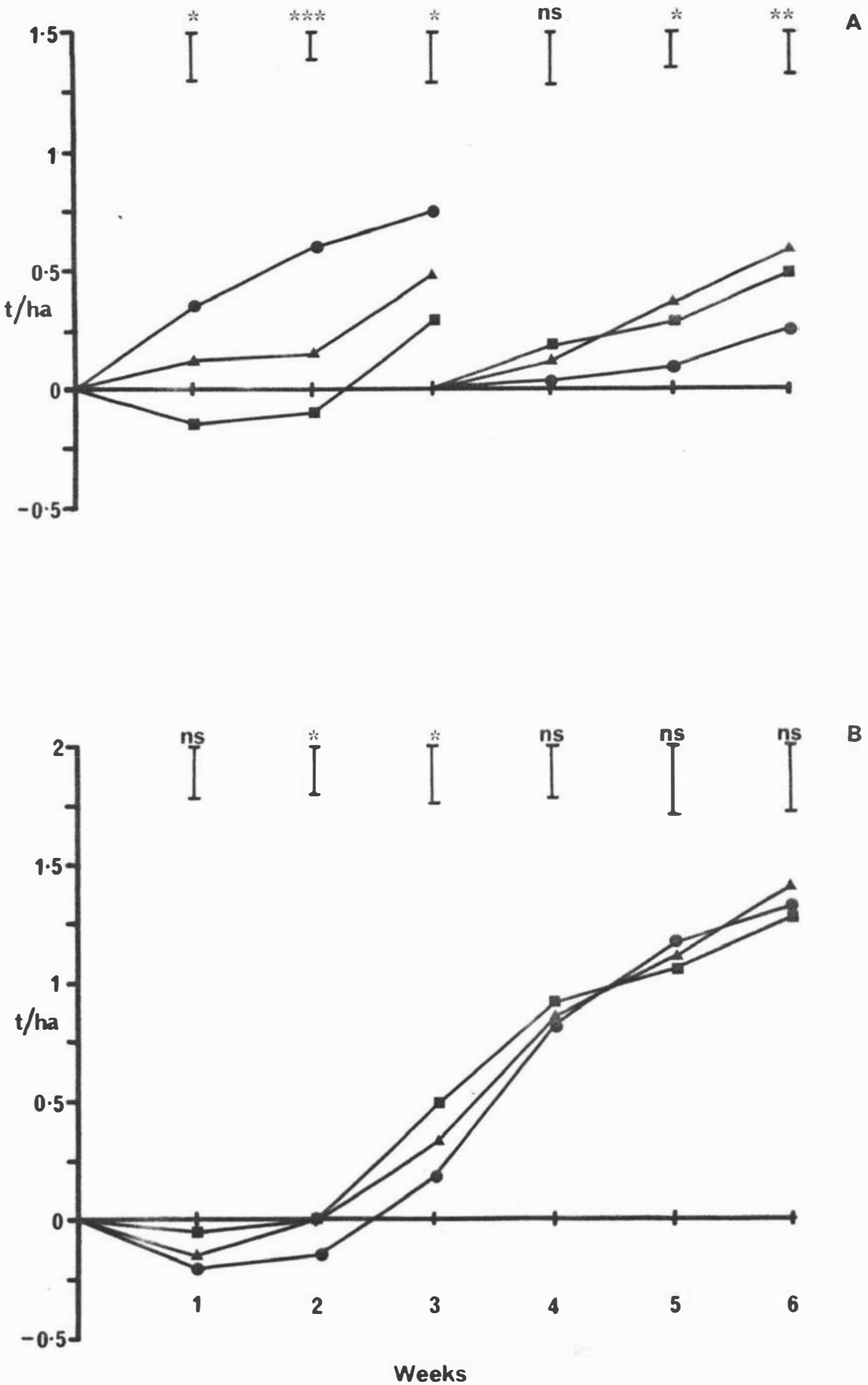


FIGURE 3: Net herbage production (tonnes D.M./ha) during a six week spring period in Experiment 1 for 3 weekly (A) and 6 weekly (B) cutting at 1.5 cm (■), 5.0 cm (▲) and 9.5 cm (●) cutting heights.

Table 14: Leaf area indices during a spring and summer regrowth cycle of Experiment 1.

Spring Cycle

Sample Date	21/10	28/10	4/11	11/11	11/11	18/11	25/11	2/12
Treatment								
SF	1.2	0.8	1.6	2.2	1.2	1.2	1.9	3.0
MF	2.6	2.5	3.1	3.4	2.2	2.9	3.6	4.5
LF	4.6	5.8	5.9	5.5	3.4	4.3	4.7	4.7
Tmt Mean SE	0.15	0.13	0.18	0.24	0.18	0.17	0.17	0.14
SI	1.0	0.6	1.1	2.0		4.5	5.0	5.7
MI	2.2	1.8	2.2	3.4		6.6	7.4	6.7
LI	3.3	2.4	2.6	4.8		7.1	7.5	7.0
Tmt Mean SE	0.24	0.11	0.19	0.19		0.28	0.27	0.26

Summer Cycle

Sample Date	20/1	27/1	3/2	10/2	10/2	17/2	24/2	2/3
Treatment								
SF	2.5	2.4	3.6	4.3	1.3	1.4	2.1	2.0
MF	2.8	2.6	5.4	5.0	2.0	2.5	3.0	3.7
LF	3.9	3.5	4.6	4.7	2.7	3.1	3.2	3.7
Tmt Mean SE	0.21	0.15	0.17	0.20	0.18	0.17	0.18	0.16
SI	0.7	0.6	1.9	4.0		5.3	6.7	5.8
MI	0.9	0.8	1.9	5.2		5.5	6.4	4.5
LI	1.8	1.8	2.9	4.5		5.8	6.3	4.5
Tmt Mean SE	0.16	0.07	0.16	0.17		0.09	0.23	0.21

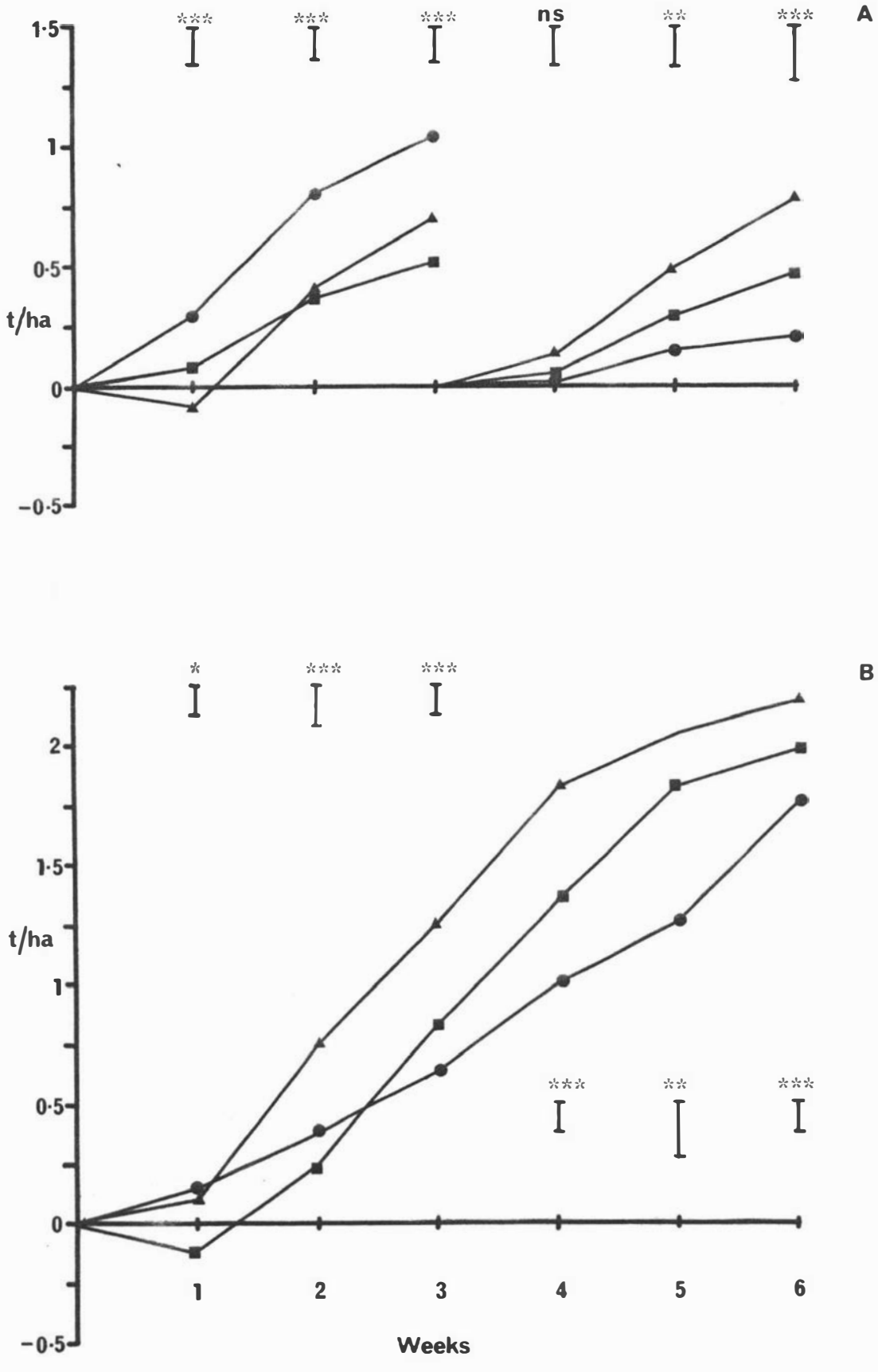


FIGURE 4: Net herbage production (tonnes DM/ha) during a six week summer period in Experiment 1, for 3 weekly (A) and 6 weekly (B) cutting at 1.5 cm (■), 5,0 cm (▲) and 9.5 cm (●) cutting heights.

in this experiment was summed to give total net shoot production for the period 7/9/76 to 16/5/77 (Table 15). Net D.M. production for the canopy as a whole was considered as the cumulative difference between residual and final D.M. levels of each regrowth cycle, thereby taking into account D.M. losses resulting from the death and disappearance of plant material within the canopy.

Table 15: Total and component dry matter production in Experiment 2 (kg/ha)

	Stubble Shoots	Rhizome Shoots	Secondary Axillary Shoots	Total Net Shoot	Total Net Canopy
Treatments					
RS	311	11334	858	12503	10513
SAS	291	12139	881	13311	10955
6S	1626	9249	590	11465	8451
6L	4208	8492	1012	13712	9567
SAL	5160	8257	796	14213	9017
LS	3719	8033	699	12451	8244
Tmt Mean SE	204	172	66	182	209
Signif Level	***	***	**	***	***
LSD (5%)	614	519	200	548	629

Total net shoot production was highest in those two treatments (6L, SAL) that were consistently cut at the 9.5 cm level. Whether cutting was based on the extent of secondary axillary development or on a six-weekly basis, increasing the cutting height from 1.5 to 9.5 cm, increased total shoot production. Within both cutting heights the use of secondary axillary development as a criterion for cutting improved production relative to the six-weekly cuts. At the 1.5 cm cutting height, longer regrowth periods resulted in increased total net shoot production for SAS compared with 6S. However, there was no further improvement for treatment RS even though a further extension in regrowth interval resulted from the use of reproductive development as a criterion for cutting. Where lax then severe cutting was alternated, total shoot production was superior to only that of treatment 6S.

From the dry matter production values it was apparent that the stubble shoot class was very responsive to different intensities of defoliation. Where 9.5 cm cutting occurred, stubble shoot production

was strongly encouraged, even when this was alternated with low, 1.5 cm cutting. Within the more severely cut treatments, a greater amount of stubble shoot production occurred with the more frequently cut 6S. Nevertheless, rhizome shoot production in 6S still dominated that of the other two shoot classes involved in regrowth. This dominance occurred for all the low cut treatments and with regard to the rhizome shoot class, production levels were significantly higher when cutting to 1.5 cm was consistently employed. The extended physiological development allowed within 6L during the summer resulted in increased secondary axillary shoot production being recorded for that treatment. Overall however, production from secondary axillary shoots was generally variable and of little importance.

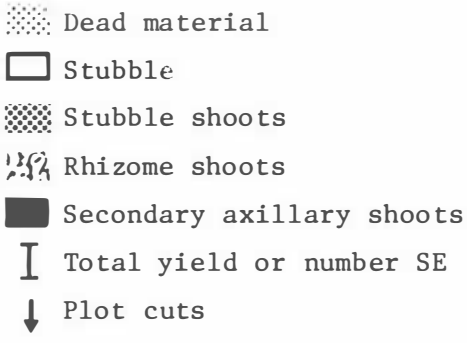
When dry matter losses within the canopy are taken into consideration, treatment patterns in total net canopy production were different from those for total shoot production. In contrast to total shoot production values, highest net canopy production was recorded for the two less frequent, severely cut treatments. The lower net canopy production values recorded for the more laxly cut treatments resulted from D.M. losses of 30-37 percent within the canopy. Of the low cutting heights, 6S produced the lowest net canopy D.M., a response which was also partly related to a high proportion of within-canopy losses. Similarly with low shoot production and large losses, the alternating lax, severe cutting treatment recorded, along with 6S, the lowest net canopy production levels.

The dynamics of dry matter changes within each canopy differed between treatments and regrowth cycles within treatments. As a result, consistent generalized comments on regrowth patterns are difficult to make, thus each treatment will be considered individually.

4.3.2.1 Treatment RS (Figure 5A)

The dominant form of shoot growth was undoubtedly that from the rhizome shoot class which, during periods of maximum growth, exceeded production rates of 600 kg D.M./ha/wk (Appendix 5). To achieve growth rates of this magnitude it did appear that rhizome shoot densities of 2500-3500 per m^2 were required (Figure 6A). Within three weeks such numbers were present for regrowth cycles 2 and 3.

FIGURE 5 and 6: Component dry matter yields (tonnes/ha), shoot numbers ($x10^3/m^2$) and LAI of residual, intermediate and final harvests in individual regrowth cycles of treatments RS (A) and SAS (B).



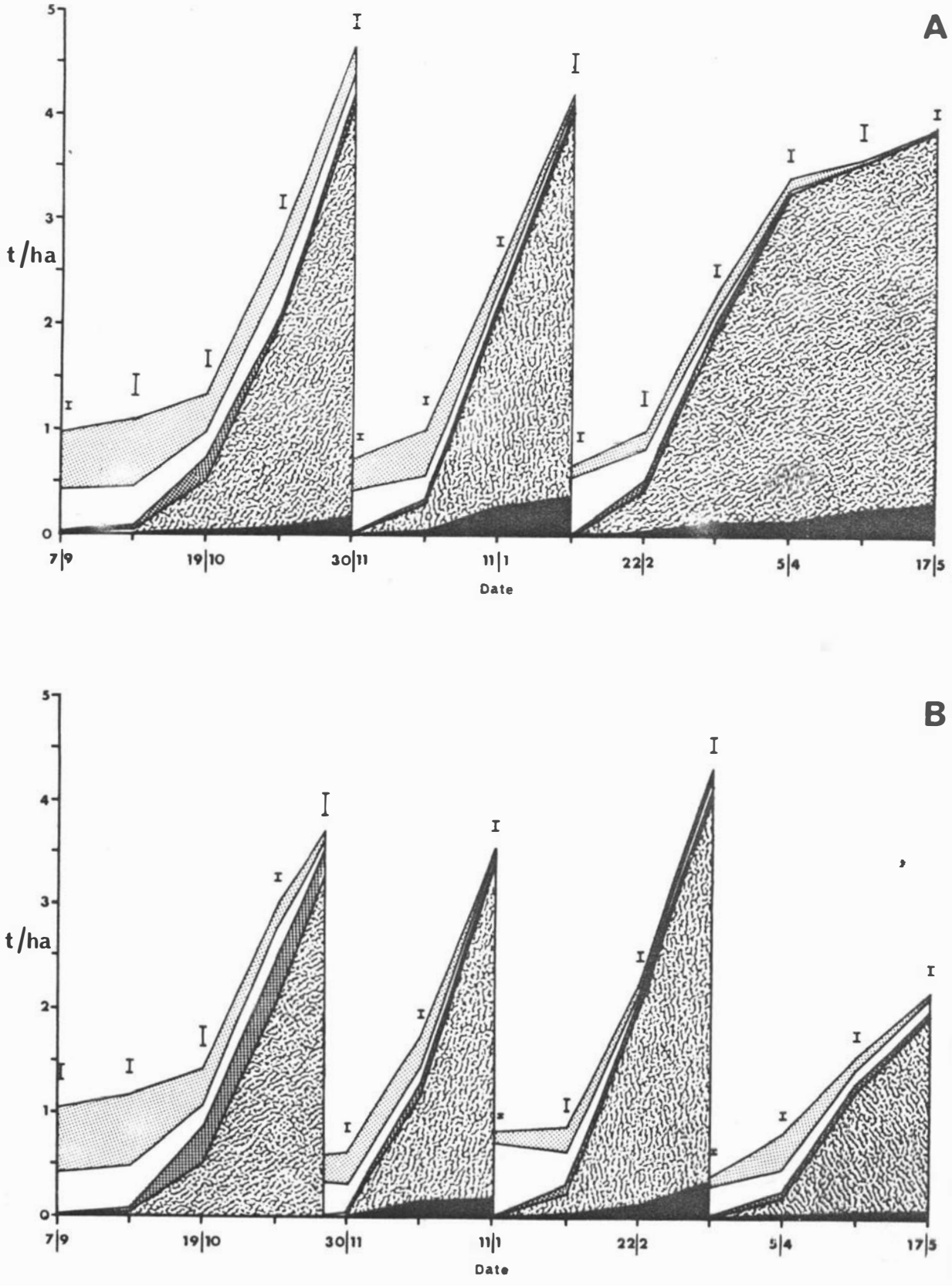


FIGURE 5: Component dry matter yields for treatments RS (A) and SAS (B). (tonnes/ha).

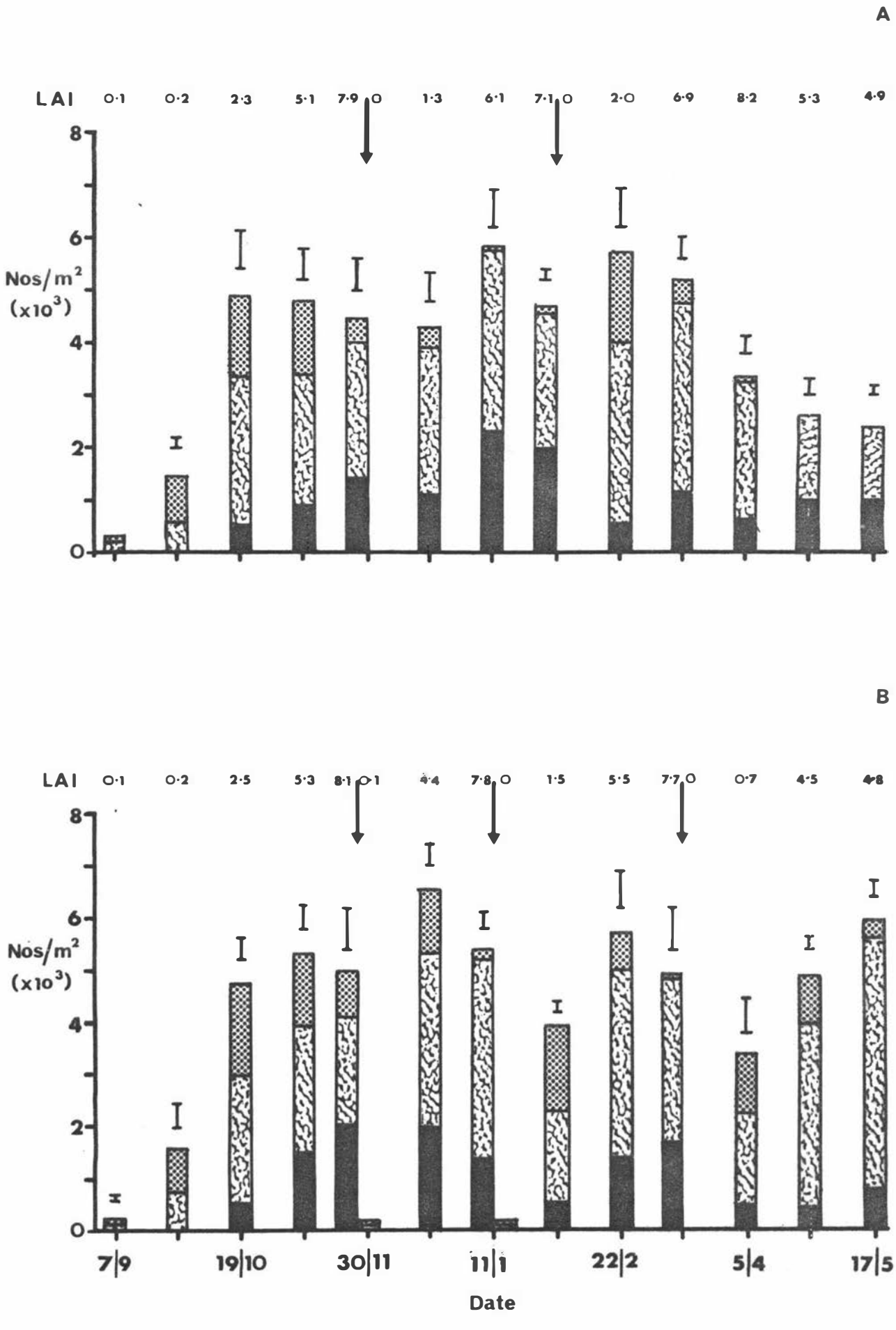


FIGURE 6: Shoot numbers and LAI for treatments RS (A) and SAS (B).

However, in the first cycle, rhizome shoot numbers increased slowly and may in part explain the very slow initial three weeks regrowth in this cycle.

Stubble shoot production was minimal and tended to be related to initial stages of regrowth. During such periods, stubble shoot numbers increased to approximately 1500 per m^2, but then declined as rhizome shoot growth rates rapidly increased and stubble shoot growth rates decreased. Nevertheless, even at maximum numbers, stubble shoots still contributed very little to overall shoot production.

Within all three regrowth cycles, secondary axillary shoot numbers and production values increased with time and developed to the greatest extent during the second cycle. However, even during this cycle,when their numbers peaked at 2330 per m^2, the mean growth rates for this component over two, three-week periods were only 76 and 33 kg DM/ha/wk.

The severity of low cutting following extended regrowth periods was indicated by low and often non-existent residual shoot numbers and leaf areas. The influence of this on shoot regrowth was particularly evident during the cool initial stages of cycle 1, but was less so during the significantly faster growing initial periods of cycles 2 and 3 (see paired t-tests, Appendix 5). It should be noted however, that during initial regrowth in all three cycles, the lower 95% confidence limits placed on net canopy growth rates were below that which represents zero growth rate.

An earlier defoliation during the third regrowth cycle would probably have improved total production levels for this treatment, as during the last six weeks lodging of rhizome shoots became evident. With this, there was an associated fall in rhizome shoot numbers, growth rates and total canopy leaf area.

4.3.2.2 Treatment SAS (Figure 5B)

The increase in total net shoot production (Table 15) of the four-cut, SAS treatment,compared with the three-cut RS treatment, was due to the extra production recorded in SAS during the autumn. However, as a result of the extra cut and associated death and disappearance

of plant matter, greater D.M. losses occurred within SAS and as a result net canopy production was similar for the two treatments. Such losses tended to occur more during the earlier stages of regrowth and they do in part contribute to initial net canopy growth rates in cycles 1 and 3 not being significantly different from zero growth rate (Appendix 6).

As with RS, regrowth in treatment SAS was dominated by rhizome shoots which reached maximum growth rates in excess of 600 kg DM/ha/wk and shoot numbers of approximately 3000-3500 per m^2 (Figure 6B). The slow build up in total shoot numbers during the first regrowth cycle was again in evidence and also became apparent in the last cycle. Nevertheless, it was during this last cycle, when temperatures and growth rates were falling, that rhizome numbers reached 4800 per m^2, the highest value recorded throughout the experiment.

Associated with stubble shoot number increases during the early stages of regrowth, were low but positive growth rates. However, with time, numbers consistently fell and stubble shoot growth rates became negative.

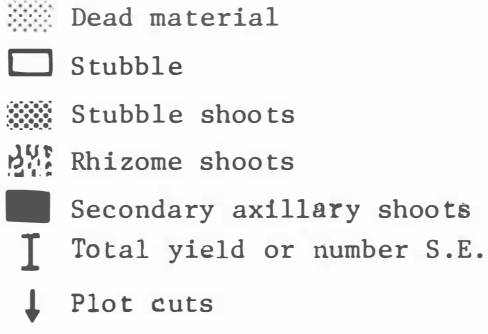
4.3.2.3 Treatment 6S (Figure 7A)

As with treatments RS and SAS, where cutting to 1.5 cm was employed, rhizome shoot production dominated regrowth in 6S, particularly within the second three weeks of each cycle. During these periods, rhizome shoot growth rates were at their highest (Appendix 7) while rhizome shoot numbers continued to increase to maximum values of 4000-4500 per m^2 (Figure 8A).

In contrast, the pattern of stubble shoot regrowth was more variable. In cycles 2-5, stubble shoot numbers quickly reach a maximum of 4000-5000 per m^2 during the first three weeks of regrowth and then declined, a pattern which was similar to that of stubble shoot growth rates. However, during the slower growing cycles, 1 and 6, stubble shoot numbers and growth rates continued to increase throughout both cycles. Under such conditions, stubble shoot contribution to shoot production was at its greatest.

The different regrowth patterns in cycles 3 and 4 illustrate the influence of differing residuals on subsequent regrowth. The eventual

FIGURE 7 and 8: Component dry matter yields (tonnes/ha), shoot numbers ($x10^3/m^2$) and LAI of residual, intermediate and final harvests in individual regrowth cycles of treatments 6S (A) and 6L (B).



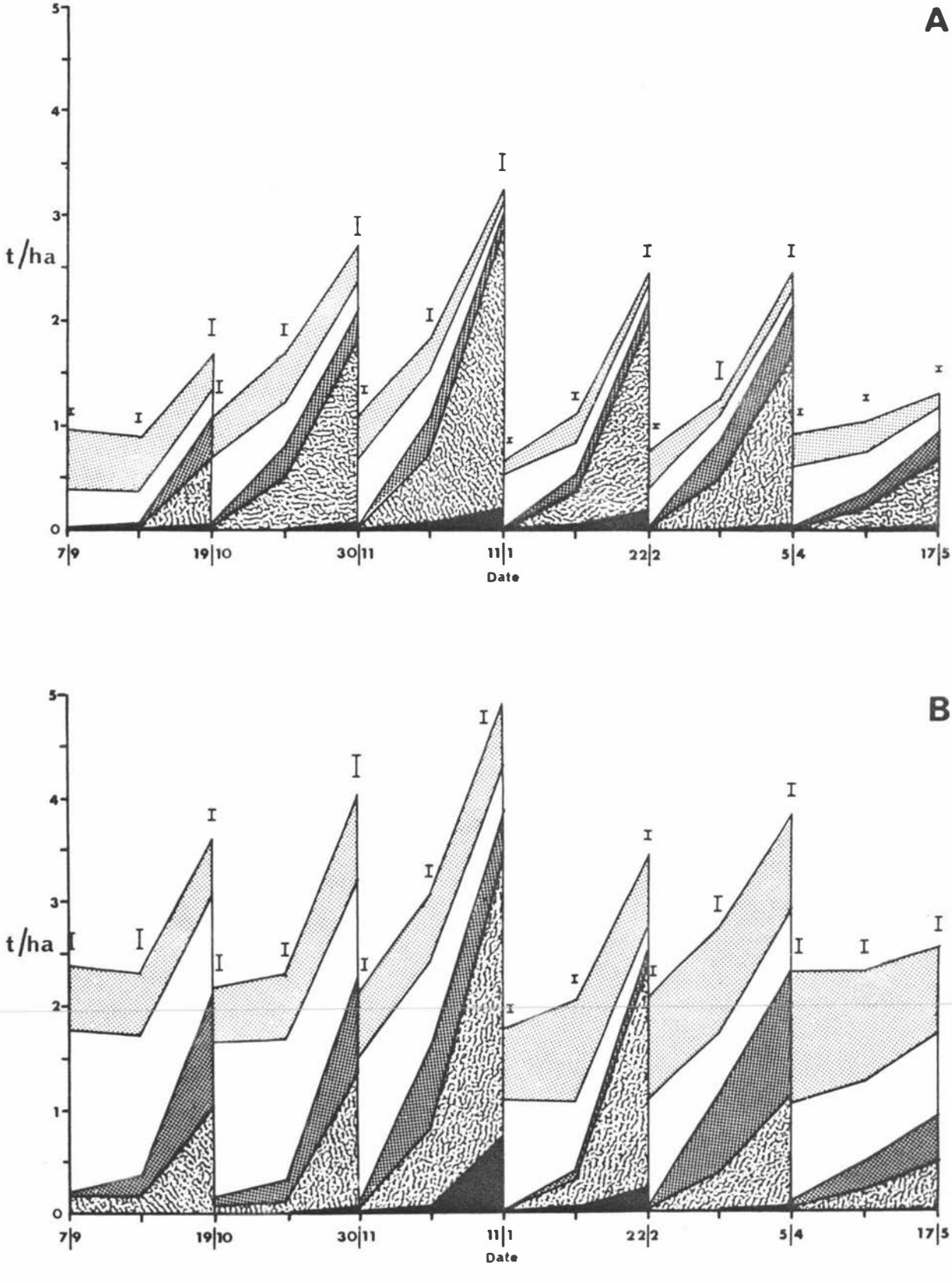


FIGURE 7· Component dry matter yields of treatments 6S (A) and 6L (B) (tonnes/ha).

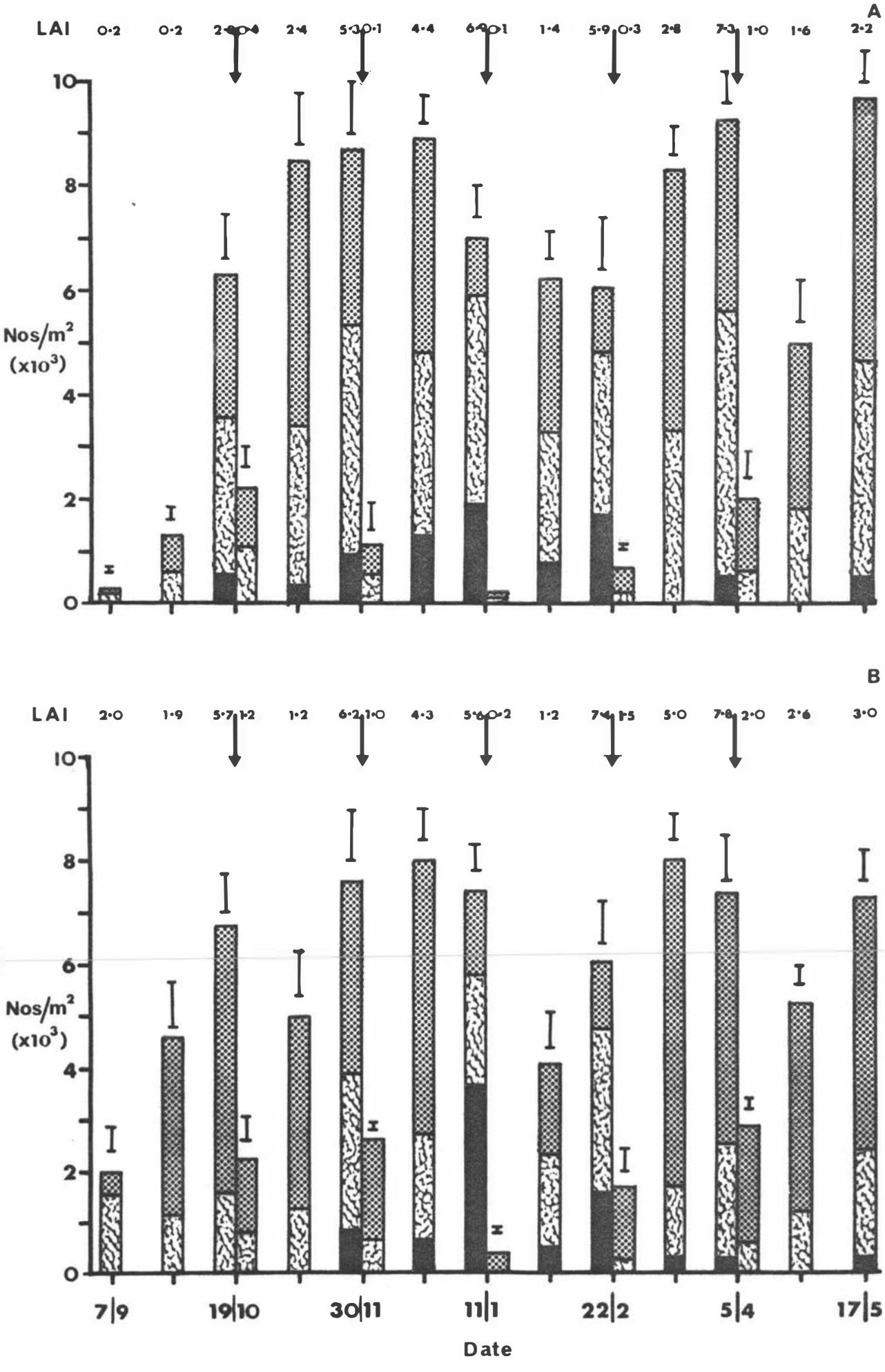


FIGURE 8: Shoot numbers and LAI of treatments 6S (A) and 6L (B).

size of the canopy in cycle 3 was the largest measured for this treatment and following cutting down to 1.5 cm, the lowest residual shoot numbers and leaf area within this treatment, were recorded. The initial accumulation of shoot numbers and leaf area in cycle 4 was lower than for the corresponding three-week period in cycle 3 and accompanying this slow recovery were significantly lower total shoot and net canopy growth rates (paired t-tests, Appendix 7).

The type of residual, and subsequent regrowth pattern, recorded in cycle 4 was very similar to that recorded in cycle 3 of the less frequently cut SAS treatment. Comparisons between the initial three-week periods of cycles 3 and 5 in treatment 6S and cycles 2 and 3 in treatment RS, also indicate the sensitivity of regrowth to residual characteristics. With similar cutting heights, but on canopies of a smaller size, treatment 6S possessed greater residual leaf areas, shoot numbers and subsequent dry matter increases.

Except for cycles 1 and 6, where initial growth rates were poor, initial net canopy growth rates in the remaining cycles were significantly greater than zero; this was in direct contrast to the less frequent, severely cut SAS and RS. However, with more frequent cutting in 6S, continuation of high rhizome shoot growth rates was restricted and this, combined with greater dry matter losses within the canopy, led to lower total net canopy production relative to the other severely cut treatments, SAS and RS.

4.3.2.4 Treatment 6L (Table 7B)

Relative to treatment 6S, the significantly higher total net shoot production recorded in 6L was associated with improved stubble shoot production (Table 15). Stubble shoot numbers were generally greater in the more laxly defoliated treatment, particularly during the earlier stages of regrowth in each cycle (Figure 8B). Only when rapid growth in cycle 3 occurred, did stubble shoot numbers significantly fall from a peak and growth rates become negative (Appendix 8). In the remaining cycles, stubble shoot numbers and growth rates remained constant or improved with time. Relative to the rhizome shoot pool, growth rates from stubble shoots were similar, if not significantly greater during cooler and/or initial regrowth periods and only in the latter

half of cycles 2 to 4 did the production rates of rhizome shoots dominate those of the stubble shoot pool.

Except for cycle 4, rhizome shoot densities of only 2000 per m^2 were achieved in 6L (Figure 8B). Nevertheless, even with these lower numbers, rhizome shoot growth rates were significantly lower than those of treatment 6S in only the second and fifth cycles.

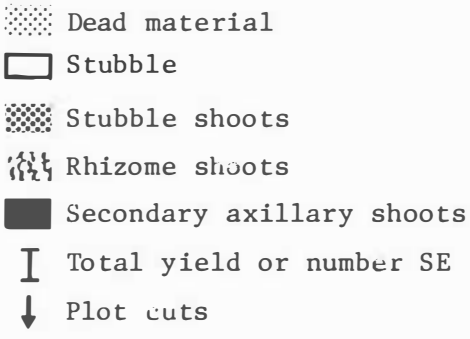
With the exception of cycle 2, net shoot growth rates during the first half of each cycle in treatment 6L were similar to, or greater than those in 6S. However, due to larger within-canopy losses in 6L over these periods, net canopy growth rates of this treatment were never significantly greater than those of 6S. For the second half of each cycle, where rhizome shoot growth rates were generally similar in both treatments, it was the added production resulting from an improved survival of stubble shoots that generally increased net shoot and canopy production of 6L over that of 6S.

Following the large growth recorded in cycle 3 even lax cutting to 9.5 cm resulted in low residual leaf areas and shoot numbers. Subsequent regrowth, particularly that of the stubble shoot pool, was poor and the regrowth pattern was very similar to that of 6S for the same period. In contrast, where residual shoot numbers and leaf area were greater, as in cycle 5, initial net shoot and canopy regrowth was significantly greater and notably associated with rapid stubble shoot regrowth.

4.3.2.5 Treatment SAL (Figure 9A)

Total rhizome shoot production (Table 15) and rhizome shoot numbers (Figure 10A) in treatment SAL were similar to those of treatment 6L. However, in contrast to the latter treatment, rhizome shoot production in SAL predominantly occurred during the cooler, less frequently cut periods rather than during the shorter regrowth, summer periods. The high stubble shoot production recorded in SAL also resulted from extended regrowth intervals during cooler periods and from the continued growth of stubble shoot pools that were maintained by more frequent cutting during the rapidly growing summer period.

FIGURE 9 and 10: Component dry matter yields (tonnes/ha), shoot numbers (x $10^3/m^2$) and LAI of residual, intermediate and final harvests in individual regrowth cycles of treatments SAL (A) and LS (B).



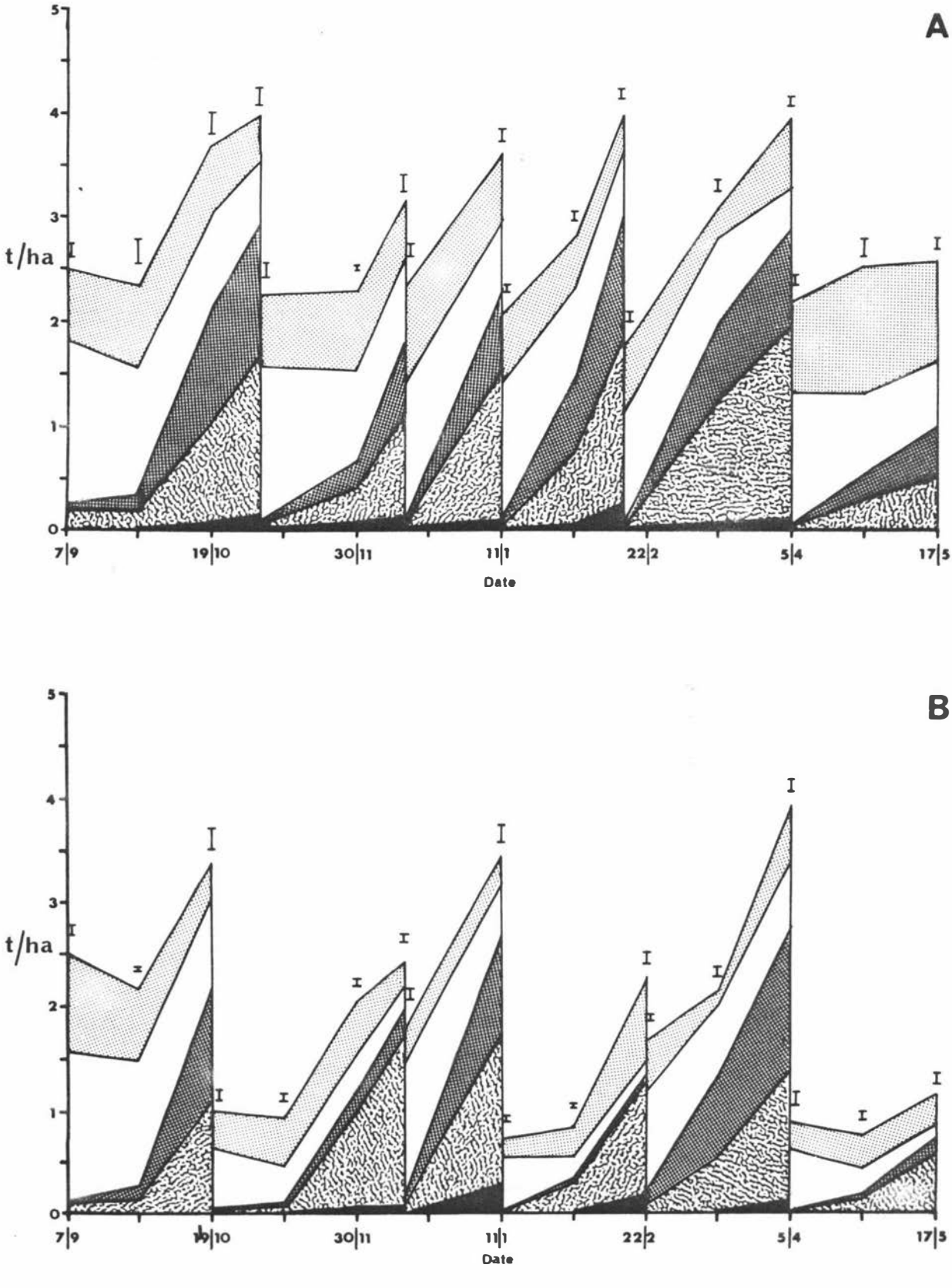


FIGURE 9: Component dry matter yields of treatments SAL (A) and LS (B) (tonnes/ha)

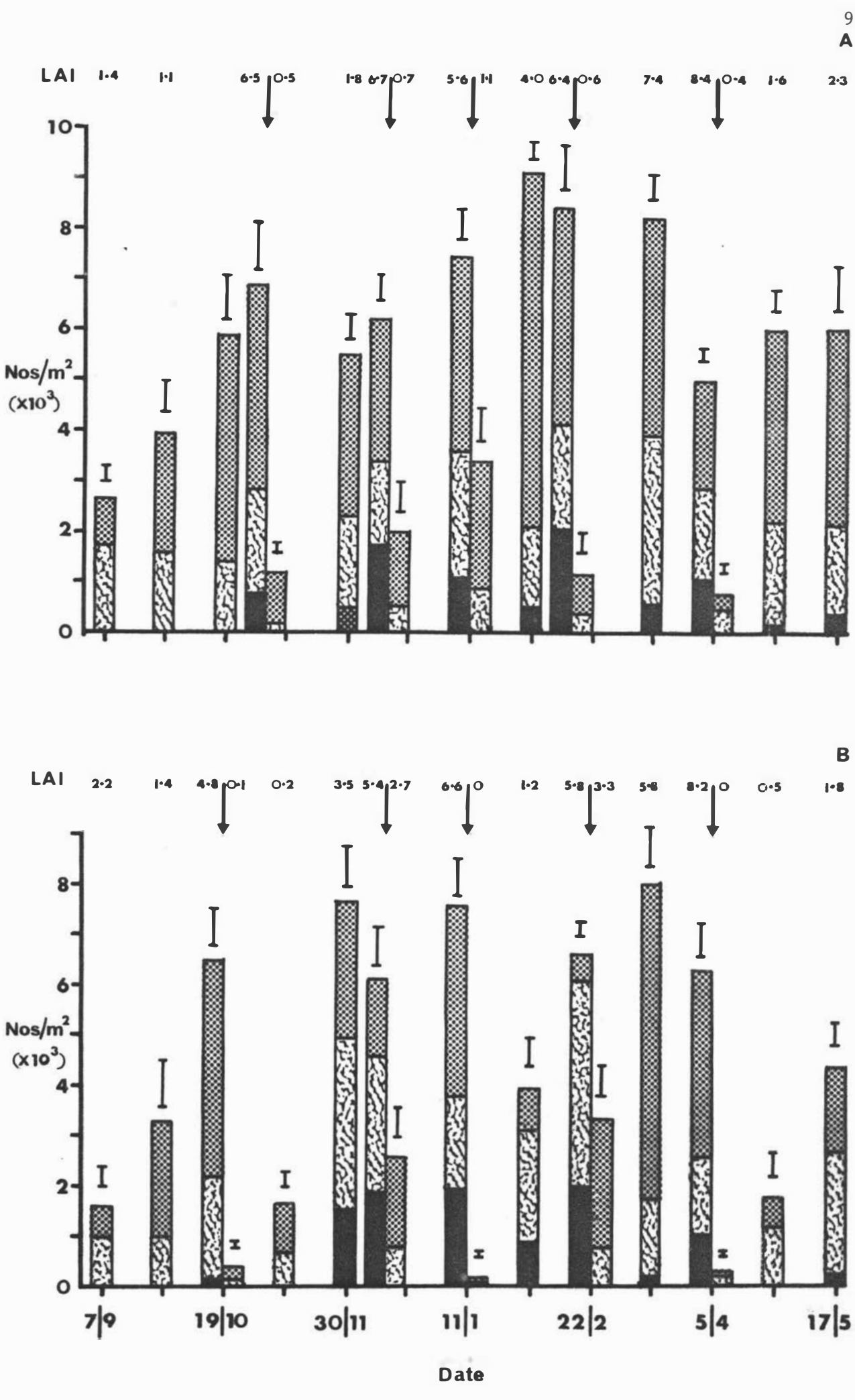


FIGURE 10: Shoot numbers and LAI of treatments SAL (A) and LS (B).

In cycle 4, treatments 6L and SAL were cut to the same height, however the residual resulting from the cutting of the smaller SAL canopy contained, and then accumulated, more leaf area and growing shoots. For the first three weeks of regrowth, net canopy and total shoot growth rates were significantly higher in SAL (Appendix 9). In the subsequent period total shoot growth rates were similar in both treatments, although contributions from the shoot pools differed markedly.

The depressing effects of longer regrowth, severe cutting and low residual leaf areas and shoot numbers on initial regrowth were again illustrated between the third and fourth cycles of treatments SAS and SAL, respectively. Similarly in the second three weeks of cycle 1 and in the first period of the last cycles, shoot growth rates were significantly higher in SAL than SAS, primarily as a result of greater stubble shoot production.

4.3.2.6 Treatment LS (Figure 9B)

As with treatment SAL, regrowth patterns in LS were strongly influenced by large dry matter losses within the canopy which primarily occurred during the initial regrowth stages of the severely cut cycles. Due to such losses, plus slow total shoot regrowth, net canopy growth rates over the first three weeks of cycles 1, 2, 4 and 6 were not significantly greater than zero (Appendix 10).

The severe cutting of a large canopy, resulted in regrowth patterns for cycles 2, 4 and 6 being similar to the initial stages of treatments RS and SAS. Residual leaf areas and shoot numbers were low and following slow initial regrowth periods, production was subsequently dominated by rhizome shoots whose number peaked at approximately 2500-3000 per m^2 (Figure 10B). Stubble shoot participation in the regrowth of these cycles was minimal.

In contrast, the lax defoliation of rapidly growing canopies produced high residual LAI and shoot numbers. As with those cycles in 6L and SAL possessing these residual characteristics, initial shoot growth rates were high and much of this can be attributed to the stubble shoot pool. The higher initial growth rates recorded in cycles 3 and

5 in LS, compared with the third of SAL and fifth of 6L respectively, were primarily the result of greater stubble shoot production in the former treatment, even though stubble shoot numbers involved were similar.

4.3.3 Winter Production of Experiment 1 and 2

In Experiment 1, only D.M. production recorded up until 18/5/76 was considered valid for treatment comparisons in total net canopy production. At this and subsequent dates, insufficient growth was present to impose the 9.5 cm cutting treatments, thus no further treatment cuts were conducted. However, for the different sized canopies that remained after the 18/5/76 harvest, net canopy dry matter changes that occurred during the winter of 1976 were assessed by taking ground level cuts on 7/9/76. For both cutting frequencies, net canopy D.M. production over the sixteen week period was negatively related to previous cutting heights (Table 16). Although consistently lower, net production of those treatments previously cut every six weeks was not statistically different from those cut more frequently when within cutting height comparisons were made. When considering the dry weight of the canopy present at the beginning of this production period (see Appendix 3) it is evident that its size was negatively related to subsequent net canopy production recorded over the winter.

Table 16: Net dry matter production during winter in Experiment 1 and 2 (kg/ha).

Experiment 1 - 1976			Experiment 2 - 1977				
Net Canopy			Stubble Shoot	Rhizome Shoot	Secondary Axillary Shoot	Total Shoot	Net Canopy
SF	1247	RS	58	1691	166	1916	1413
MF	754	SAS	-5	554	136	685	651
LF	486	6S	-232	1628	123	1519	1200
SI	1052	6L	-257	1730	142	1615	805
MI	635	SAL	-421	1707	248	1535	886
LI	332	LS	-130	1837	166	1873	1555
Tmt Mean SE	68.2		21.3	59.7	25.7	57.3	64.4
Signif level	***		***	***	**	***	***
LSD (5%)	198		64	180	77	173	194

In Experiment 2 similar consideration was given to net D.M. changes within different structured canopies between 16/5/77 and 9/8/77. The components of the various canopies at the beginning of this period can, with the exception of RS, be established from data presented for the last harvest date in Figures 5, 7 and 9. Only treatment RS was cut on this date and the residual canopy of 753 kg DM/ha consisted of only stubble and dead matter. The amount of stubble shoot growth present at the 9/8/77 harvest was negligible in all treatments and thus the magnitude of negative net stubble shoot production depended on the amount present at the start of the winter period. This was greatest where lax or more frequent cutting had previously been employed (Table 16). Rhizome shoot production dominated canopy D.M. changes and it was only in treatment SAS, where initial rhizome shoot growth was equivalent to 1920 kg DM/ha, that substantially lower net rhizome shoot production was recorded. Where initial rhizome shoot growth was below 750 kg DM/ha, then similar net production occurred. Although the absolute amount of secondary axillary shoot growth increased over the winter, its overall contribution to total shoot growth and response to variable canopy structures was minimal.

Total net shoot growth was highest where initially low rhizome and stubble shoot components existed. As losses from the stubble shoot pool increased or net rhizome shoot growth decreased, then so did total net shoot production decrease. The difference between net shoot and canopy production indicates the D.M. losses that were incurred from the stubble and dead matter components. Such losses were greatest where previously lax defoliation had occurred and a large stubble, plus dead pool, initially existed. Net canopy production for 6L and SAL was therefore low. However, it was treatment SAS, with low total shoot production, that recorded the lowest net canopy production. With initially small canopies, where superior rhizome shoot production and reduced within-canopy losses were measured, net canopy production was greatest.

4.4 Discussion

When comparing the two field experiments, consideration must be given to two experimental factors that differed. Firstly, the rotary mower used in Experiment 2 was more severe in defoliation than the

sickle-bar mower used in Experiment 1. In the former situation lower residual dry matter and leaf area generally resulted, particularly at the 9.5 cm cutting height. The nature of the residual canopy in Experiment 2 following a 9.5 cm cut could be considered as being intermediate between the 5.0 and 9.5 cm cuts of Experiment 1. It was because of such differences that Ollerenshaw (1974) cautioned the use of vertical cutting heights as indicating the severity of defoliation treatments. Secondly, the application of water to Experiment 2 to correct soil moisture deficiencies undoubtably influenced the different absolute production levels recorded for the two experiments. Nevertheless, although these differences existed, the regrowth patterns and relative responses generated from the two experiments were complimentary to one another. It is important to remember when discussing the results of both experiments however, that all the work was conducted on pure 'Grasslands Maku' swards and that competition from other plant species was eliminated by regular hand weeding.

4.4.1 Stubble Shoots

As Leach (1968) reported with lucerne, it was the stubble shoot pool of 'Grasslands Maku' that was most responsive to changes in defoliation patterns. Where similar cutting heights were employed, stubble shoot numbers and their contribution to total shoot regrowth increased with more frequent cutting. As indicated in Experiment 2, stubble shoot regrowth followed a basic pattern, whereby growth rates initially increased but then declined as rhizome shoots began to dominate regrowth. The extent of these initial increases was positively related to cutting frequency, as was the delayed decline in the vigor of the stubble shoot pool.

The influence that cutting frequency had on stubble shoot growth was principally determined through altering the size of the canopy prior to cutting and thereby determining the nature of the residual canopy. Where regrowth intervals were extended and larger final canopies produced, residual canopies following cutting were lower in potential stubble shoot sites and leaf area and appeared less conducive to stubble shoot regrowth. Similar responses occurred in treatments with a fixed cutting height and frequency where seasonal effects influenced final canopy size. This was apparent following the large growth experienced in the

third cycles of 6S and 6L in Experiment 2 and only through more frequent cutting during this rapid growth period, as with treatment SAL, was final canopy size restricted and stubble shoot growth improved. Jones (1973) working with *Desmodium intortum* also reported that pre-cut canopy size influences the nature of the residual canopy and then, subsequent regrowth.

Where cutting height was the only treatment variable, potential stubble shoot numbers may have been increased with higher cutting but the number of stubble shoots actually participating in regrowth were generally lower in Experiment 1 and only slightly improved in Experiment 2. Nevertheless, even with limited improvements in shoot numbers, stubble shoot growth rates and contributions to growth increased with laxer defoliation. This production response may relate to the larger and more actively growing nature of individual stubble shoots remaining after such a cut. The possible improvements in initial stubble shoot growth rates due to the presence of larger, more actively growing shoots within a residual canopy was also evident in cycles 3 and 5 of treatment LS. High stubble shoot growth rates were recorded when lax defoliation of a previously low cut, but rapidly regrowing canopy was employed. In lucerne, Leach (1968, 1970) and Hodgkinson (1973) have shown that initial shoot size is positively related to initial regrowth rates, shoot viability and contribution to overall production.

Relative to the rhizome shoot pool, a notable feature of the changing stubble shoot populations was the rapid and often large increase in shoot numbers initially involved in early regrowth. During later stages of regrowth however, stubble shoot numbers often declined, whereas only during the last prolonged regrowth cycle of RS in Experiment 2, was this evident for the rhizome shoot pool. The timing and extent of stubble shoot losses appeared to be positively related to rhizome shoot growth rates, a relationship that suggests inter-shoot competition was operative. In lucerne, Leach (1970) and Hodgkinson (1973) have proposed that crown shoot dominance over stubble shoots, particularly during rapid regrowth, is related to inter-shoot competition for mineral nutrients. Such a relationship may also occur in 'Grasslands Maku', as it was those shoots growing from rooted rhizome nodes that dominated regrowth.

4.4.2 Rhizome Shoots

Although it was the stubble shoot population that was the more responsive to different defoliation patterns, total shoot growth within most regrowth cycles was dominated by rhizome shoots, particularly under more severe defoliation. Absolute rhizome shoot production, and more noticeably its contribution to total shoot production, increased with more severe and/or infrequent cutting.

In most regrowth cycles, initial rhizome shoot numbers and growth rates were low. Under no treatments, even when cutting was delayed until reproductive development, was there any indication of a basal cluster of rhizome shoots developing in the canopy in response to plant physiological maturity. Even though a large potential for rhizome shoot growth exists within the rhizome system (see Chapter 3.3.3) there appears to be no plant process that generates shoots to a state whereby rapid, immediate rhizome shoot growth can commence once the canopy is defoliated. One of the principal factors in the success of correctly managed lucerne is the development of a basal flush of crown shoots which can commence early, rapid regrowth following defoliation (Leach, 1967; Keoghan, 1967) and it is the formation of such a shoot pool that Keoghan and Tassel (1974) considered was essential for any further improvement in the production potential of *L. corniculatus*.

The slow build-up in rhizome shoot numbers following cutting must in part be due to the slow release of axillary buds from rhizome nodes, particularly during spring. Furthermore, the need to activate a transition of underground shoot initials into a vertically growing, leafy form may also add to the delays in the establishment of an actively growing shoot population. In Experiment 1, rhizome shoot development was found to be low during spring/early summer and to include a horizontal underground component during autumn (see Chapter 3.3.3).

The initial development and growth of rhizome shoots may be further retarded by their basal location within the canopy. Undoubtedly while underground, they are dependant on the supply of growth substrates from other regions. Heinricks *et al*. (1977) related the slow regrowth of creeping rooted lucernes to the underground origin of shoots and the dissipation of energy required to form them. Increases in rhizome

shoot numbers and growth rates were also found to be poorer during cool regrowth periods and this may be related to low ground temperatures. Leach (1971) reported that shoot initiation in lucerne was delayed with lower temperatures and that earlier stages of regrowth had higher optimum temperature requirements. The ability of newly emerged rhizome shoots to conduct rapid, independant growth must also be restricted by poor light levels at the canopy base and the low leaf complement of the rhizome shoots themelves. Compared with stubble shoots that develop higher in the canopy, the leaf complement of newly emerged rhizome shoots was low (see Chapter 3.3.3), a difference that is likely to be related to light quality and/or quantity (Brougham, 1962).

Rhizome shoots were undoubtably the major potential source of shoot production in 'Grasslands Maku', yet the realization of this potential through the manipulation of defoliation strategies was difficult. With lax defoliation it was possible to retain larger and more actively growing rhizome shoots within the residual canopy but such a system reduced rhizome shoot numbers participating in regrowth. As a result, positive rhizome shoot production responses to higher cutting did not occur and furthermore, an association of lower rhizome shoot numbers and growth rates was evident during late spring where cutting was high.

Increases in rhizome shoot numbers generally occurred with more frequent cutting, but rarely were these increases reflected in improved rhizome shoot growth. Under such a regime, expression of potentially high rhizome shoot growth rates did not occur. Where regrowth intervals were extended, high growth rates eventually developed and rhizome shoot production was improved. However, this led to defoliation of large canopies which in turn resulted in poor residual rhizome and stubble shoot populations and slow early regrowth. Undoubtably the presence of an excess number of actively growing rhizome shoots at the time of cutting would be the ideal situation for encouraging rhizome shoot production. This regrowth feature was not apparent in 'Grasslands Maku' and it could not be generated by defoliation management in these experiments.

4.4.3 Secondary Axillary Shoots

The development of axillary buds at above-ground nodes on shoots with an intact apex appeared to occur most frequently when the growth

of that apex was least active. Thus, secondary axillary shoots were most noticeable at the beginning and end of each regrowth cycle and during cool winter periods. Following a severe cut, growth of axillary buds in the lower leaf axils of rhizome shoots was common and they accounted for most if not all of the initial secondary axillary shoot production that was recorded in Experiment 2. However, as the growth rates of the supporting rhizome shoots increased, further growth of these secondary axillary shoots ceased and few, if any of them, became successfully established within the canopy. Towards the later stages of regrowth a further flush of secondary axillary shoots generally developed and the most marked occurred during the third cycle of treatment 6L where physiological maturity was allowed to advance to flower formation. In the latter part of this cycle, growth rates of 202 kg DM/ha/wk were recorded for this shoot class, although much of this can be attributed to reproductive growth which was included within this dry matter pool. A more valid indication of the potential production of secondary axillary shoots was seen in the severe but infrequently cut treatments, RS and SAS, where maximum growth rates of only 75 kg DM/ha/wk were recorded. Even at these rates the contribution of secondary axillary shoots to total shoot growth was low.

4.4.4 Stubble and Dead Matter

With the removal of the terminal shoot apex, the residual tissue of such a shoot has, in itself, little capacity for further expansion. As stubble, it can support stubble shoot growth; supply growth substrates from assimilatory and remobilization processes; and eventually die, thereby entering into the dead matter pool.

Stubble dry matter losses predominantly occurred during the initial stages of regrowth and tended to be most rapid during warmer regrowth periods. Such losses were generally greater in treatments continually defoliated under a lax regime where greater absolute and relative stubble components were generated within the canopy. Undoubtedly, it was the stubble component that was the major source of plant material for the dead component of the canopy, particularly where lax defoliation occurred.

The transfer of stubble tissue to the dead pool, and then the loss of dry matter through decomposition, formed a process within the

canopy whereby large dry matter losses were incurred. When more frequent, but more particularly lax cutting was employed, a larger stubble component existed within the canopy and these dry matter losses were greater. The differences between net canopy and total shoot growth rates presented in Appendices 5-10 indicated the extent of the dry matter losses during regrowth in Experiment 2. For the severely cut treatments maximum losses were approximately 150 kg DM/ha/wk and they occurred during the three week period subsequent to that period where stubble tissue losses peaked. In contrast, dry matter losses within the more laxly defoliated canopies were consistently high throughout most of the regrowth cycles and maximum losses were in the range of 230-260 kg DM/ha/wk. High within-canopy D.M. losses have also been reported by Morris (1970), Davidson and Birch (1972), Jackson (1974) and Simons *et al*. (1972) where large residual canopies of other pasture swards were generated by lax defoliation.

4.4.5 Leaf Area

As cutting became less frequent and/or more severe, residual leaf areas decreased and the overall degree of leaf senescence increased. Net leaf area losses occurred during the first and often second week of regrowth, and these losses were greater and more prolonged with less frequent and/or more severe cutting, particularly during slow regrowth conditions. This slow accumulation of leaf area during the initial stages of regrowth was a notable characteristic of 'Grasslands Maku' following defoliation. Slow leaf area increases during early regrowth have also been reported in *L. corniculatus* (Nelson & Smith, 1968b; Greub & Wedin, 1971a,b), *Macropitilium atropurpureus* (Jones, 1967, 1974a,b) and *D. intortum* (Jones, 1973) and all of these legumes are characterized by slow regrowth and a poor competitive ability in defoliated mixed swards.

In Experiment 1, maximum LAI were approximately 7.5 during spring and 6.5 in summer when growth was more erect and stemmy. Maximum LAI values in Experiment 2 ranged between 8.0 and 8.5, and the patterns LAI followed were similar to those of total shoot growth rates. During later stages of regrowth, decreasing LAI values were recorded in both experiments. However, it was observed that senescence of basal leaves on actively growing shoots rarely occurred before LAI values of 5.5 to 6.0 were achieved. This delay in leaf senescence probably

accounts for the high LAI values that were frequently recorded in these experiments and it also illustrates the shade tolerant nature of *L. pedunculatus* that has previously been referred to by Levy (1932, 1970).

4.4.6 Net Canopy Growth

When these various growth components are considered together, the overall response of 'Grasslands Maku' to a defoliation system can be explained more confidently. The slow initial net regrowth that was first recorded in Experiment 1, and which seems to be the principal 'weak link' in regrowth, is the summed response of both positive and negative growth factors which operate within the canopy at different rates depending on defoliation management. Where cutting is severe, total shoot regrowth is slow and dry matter losses within the canopy occur. With increasing laxity, initial shoot regrowth rates may increase but net canopy D.M. changes will still be small, if not negative, due to even greater stubble and dead matter losses. As regrowth proceeds, increasing total shoot growth rates gradually dominate dry matter losses which may themselves, decrease as the stubble component declines in size.

Under severe defoliation initial shoot growth rates are improved with increasing cutting frequency due to the added regrowth of an increased, but still temporary stubble shoot pool. Where regrowth is more reliant on the rhizome shoot pool, as with less frequent cutting, then initial regrowth is slower, particularly during cooler conditions. However, with increased regrowth intervals, the high growth potential of rhizome shoots is given a greater opportunity to be expressed, and as a result dry matter production in both experiments was positively related to increasing cutting interval. Nevertheless, it would appear that there is little benefit to be gained by extending the regrowth interval until reproductive development occurs. The growth potential of secondary axillary shoots appears to be low and there was no evidence that delaying cutting until reproductive development provided shoots which could give an immediate flush of regrowth.

By increasing the laxity of cutting, greater initial total shoot growth rates occur as a result of an improved stubble shoot growth component. This increased stubble shoot component is maintained for a longer period during regrowth following lax cutting, and when combined with rhizome shoot growth it leads to increased total shoot production. If total shoot growth is an indication of the competitive ability of a canopy, then lax defoliation would improve the persistence and hence production of 'Grasslands Maku' within a competitive mixed sward. However, even though total shoot production may be substantially improved with laxer defoliation, this may not be so marked in the case of net canopy production due to the large within-canopy D.M. losses incurred. Where lax, then severe cutting is alternated, the opportunity for high stubble and dead matter losses exist and periods of slow regrowth occur following each severe defoliation. As a result, both shoot and canopy production are low. McLusky and Morris (1964), Morris (1970) and Jackson (1974) have all reported that lax defoliation of mixed swards maximize gross aerial production, but it is a severe, infrequent defoliation regime that normally gives maximum harvested yield.

Net canopy production would also seem to be related to assimilate partitioning patterns within the plant. It should be noted that during the dry then cool autumn period of Experiment 1, when net canopy production was low, considerable increases in underground dry weights occurred (see Chapter 3.3.1). The partitioning of dry matter appeared to have favoured underground growth during this period, a feature that was not evident during spring. In Experiment 2, soil moisture was maintained above -1 bar by irrigation and February/March temperatures were warmer (Appendix 2). No general autumn slump in production was recorded in this experiment although it was not until early March, approximately one month later than in Experiment 1, that rhizome expansion was observed to commence. Only towards the last half of cycle 3 in treatment RS was there an obvious association of poor canopy growth and underground expansion.

Lambert *et al.* (1974) ranked autumn growth of G4705, *L. pedunculatus* behind that of summer and spring and in *L. corniculatus* slow autumn regrowth has been reported by Gasser & Lachance (1969); Nelson &

Smith (1968a); and Keoghan & Tassel (1974). Similarly in lucerne, Smith *et al* . (1964) suggested that the low emphasis of photosynthate partitioning to expanding shoots during autumn was related to competition from pre-wintering processes such as carbohydrate storage. Certainly in Experiment 1, the autumn production slump coincided with a period of rapid nonstructural carbohydrate accumulation in underground organs (see Chapter 5.3.1).

4.4.7 Proposed Management

When considering the responses of 'Grasslands Maku' to defoliation, it is tempting to propose a general management outline that might be considered optimum for *L. pedunculatus*. The formation of such a proposal is difficult however, as the requirements for maximizing net productivity and competitiveness, as indicated by total shoot production patterns, appear to conflict. If persistence and subsequent productivity of the lotus component within a mixed competitive sward is to be maintained or enhanced, then net productivity may have to be sacrificed. It is with this in mind that the following outline has been formulated, as it is likely that in most situations, *L. pedunculatus* will be considered as part of a mixed, competitive, grazed sward rather than as a hayed pure stand.

Under cool conditions recovery from defoliation is slow, thus regrowth intervals should be lengthened in order that eventual high growth rates can operate for a greater time period. However, regrowth intervals need not be extended past a stage of development where growth of secondary axillary shoots occurs on the majority of large rhizome shoots within the canopy. Any defoliations over such a period should be lax and although this may encourage greater within-canopy losses, the extra stubble shoot growth that eventuates will improve initial and subsequent total shoot growth rates. The regrowth benefits resulting from lax defoliation will be less during winter frosting conditions, as rhizome shoot growth dominates and stubble shoot viability becomes negligible. However, the maintenance of a larger canopy will provide a better basis for more rapid initial spring growth.

As temperatures and/or the potential for growth increases, secondary axillary shoot development is still a satisfactory criterion for defoliation time. Thus, its continued use would require increased defoliation frequency. If moisture availability is sufficient for growth over these warmer periods, and continuous growth within the canopy is required, then lax defoliation should be maintained throughout, even though considerable within-canopy dry matter losses will occur. If on the other hand soil moisture availability is low, or higher net production from the canopy is required, then defoliation can become more severe. This change will result in reduced canopy losses and the inferior shoot growth rates that generally associate with more severe defoliation, particularly during the initial stages of regrowth, will be less marked under warmer conditions.

In summary, it would appear that the principal component of potential regrowth is associated with the rhizome shoot pool and that the stubble shoot pool exists as a more superficial, temporary growth component. The failure of the rhizome shoot pool to quickly recover from defoliation and show rapid initial regrowth would seem to be the major factor limiting the competitiveness and production of 'Grasslands Maku' under defoliation.

were determined in two separate field experiments which have previously been detailed in Chapters 3 and 4.

5.2 Experimental

In Experiment 1, the plant material used for determining residual plant TNC status was the same as that used for residual shoot numbers (see Chapter 3.3). As diurnal variation in TNC levels occurs (Lechtenberg *et al.* 1971), sod sampling was confined to between 1100 and 1200 hours on the day of cutting and once washed, plants were stored at 3C until shoot counting and dissection. When shoot counts were completed, plant parts were separated into two groups:

(a) Central System : primary crown plus taproot.

(b) Peripheral System : rhizome, stubble and shoot tissue.

The tissue of all five subsample plants was bulked into these two groups for each plot and then frozen within 8 hours of sod sampling. It was considered that dead material was of little importance in regrowth, thus it was discarded and only live residual plant tissue was analysed for TNC status. Similarly, fibrous roots were discarded as accurate dissection of this component would have prolonged potential respiratory TNC losses. For sample dates, 29/6/76 and 10/8/76, no field cuts were conducted, however the remainder of the sampling procedure was similar to that outlined above.

In Experiment 2, sod samples were taken on 30/11/76 and 25/4/77 from 0.1 m^2 areas where ground level quadrat cuts had previously been taken for yield determinations. As in Experiment 1, five plants were systematically selected to represent the full size range and these were then dissected, bulked and frozen as two groups for each plot, namely crown plus taproot tissue and rhizome tissue. Thus, only underground growth was analysed for TNC levels and again dead and fibrous root tissue was discarded.

Within 48 hours of sampling, the frozen, dissected material was placed in a vacuum oven (1.0 mm Hg) fitted with a refrigerator coil (-25 C) and drying continued for at least 72 hours. Freeze drying was considered by Smith (1973b) as the most reliant drying procedure with regard to TNC determinations of legume tissue. After drying, weights were recorded for each bulked system and the tissue was then ground to pass through a 0.5 mm mesh. Nelson & Smith (1972) reported that

interconversion of carbohydrates can be minimized by drying and storing tissue at low temperatures, low tissue moisture levels and for minimum time periods. Therefore, ground tissue was stored in sealed vials at -3 C and analyses were conducted within four weeks of the initial field sampling.

The analytical procedure used for determining TNC levels was essentially that described by Haslemore & Roughan (1976). The principal steps involved and the slight modifications used are outlined in the following section.

(a) Sugar:

Plant material (50-60 mg) was extracted with 5 ml, 62.5% (v/v) methanol at 55C for 15 minutes. A 4 ml aliquot of this extract was taken, from which non-carbohydrate, interfering materials (pigments, phenols) were precipitated by the addition of 0.1 ml saturated lead acetate while lipids were removed by shaking with 5 ml chloroform. Soluble sugars were retained within an upper aqueous, methanol layer and the amount present in a 50 µl aliquot was determined by the phenol-sulphuric procedure (Dubois *et al.* 1956). Standards of 2.5 and 5.0 µg sucrose were also processed and absorbances read at 490 nm. In this extraction some short chain fructosans would have been included (Haslemore & Roughan, 1976) although their levels in leguminous tissues are generally low (Smith, 1973a).

(b) Starch:

Following the 62.5% methanol extraction, plant tissue was washed twice with 100% methanol and then boiled as an aqueous suspension for 60 minutes. Hydrolysis of the resultant, gelatinized starch was then achieved by incubation with 0.1 ml of an amyloglucosidase preparation (purified from Agidex Liquid Concentrate - see Haselmore & Roughan, 1976) at 55C for 60 minutes. Free glucose in 100 µl of the diluted starch hydrolysate was then determined by the glucose oxidase method (Kilburn & Taylor, 1969), as were standards of 25 and 50 µg glucose. A magenta colour was produced by adding 5 ml, 18N sulphuric acid and absorbances were read at 540 nm. Four, 8 mg starch standards were processed in the same way for each analytical run and the mean recorded starch yields ranged from 93 to 98 percent. Plant tissue starch levels were appropriately adjusted to represent 100 percent starch yields. Similar procedures involving the enzyme hydrolysis of poly-

saccharides and disaccharides to glucose monomers have proved to be satisfactory in the determination of TNC in starch-accumulating legumes and C_4 grasses (Smith, 1969, 1973a).

Statistical analyses for both experiments were based on a randomized block design and for Experiment 1 data were further considered with a split-block in time analysis as outlined in Chapter 3.2. Experimental and treatment details for Experiments 1 and 2 have been outlined in Chapters 3 and 4, respectively.

5.3 Results

5.3.1 Experiment 1

In this experiment TNC were determined on residual plant material that was sampled immediately following each cut. However, results of these determinations are only presented on a six-weekly basis and therefore TNC values of the three-weekly cut treatments only relate to every second harvest date which was common to the six-weekly cut treatments. Omission of the intermediate data points did not influence treatment or seasonal TNC patterns for the more frequently cut plants.

The TNC levels of the separately analysed central and peripheral plant systems, as defined in the experimental section, were calculated by summing the appropriate 62.5% methanol extracted sugar levels and the enzyme hydrolysed starch levels. By weighting the TNC of both systems, on a dry matter basis, total residual plant TNC levels were determined. These latter values, which do not include dead or fibrous root tissue, are presented in Figure 11 as a percentage of analysed dry weight. Marked seasonal trends in total residual plant percent TNC were evident and all treatments showed a somewhat similar seasonal pattern. During spring, concentrations declined to a December minimum and then steadily rose over summer and autumn to peak during April and May. Values again declined over winter to levels that were somewhat similar to those of the previous spring.

There was however, a significant treatment by harvest date interaction ($P < .001$) which indicated that the basic seasonal pattern was differentially modified by varying defoliation regimes. The spring

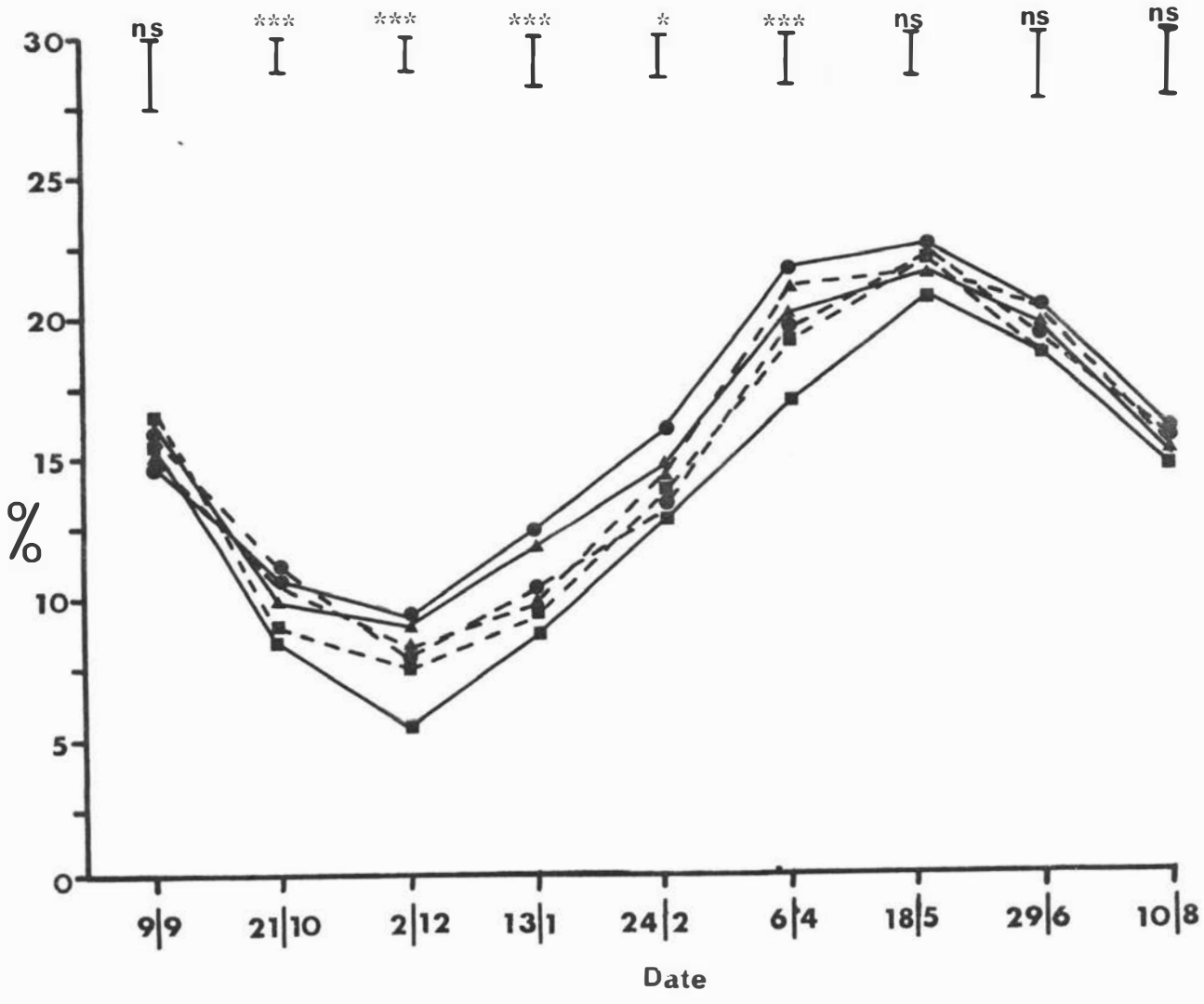


FIGURE 11: T.N.C. status of residual plants following cutting (% of dry weight).

—— Three-weekly cutting
- - - Six-weekly cutting
I L.S.D.(5%)

■ 1.5 cm height
▲ 5.0 cm height
● 9.5 cm height

decline was most rapid in treatment SF and because of the low minimum level attained, percent TNC were significantly lower than those of MF and LF until the late autumn peak. In contrast to the positive relationship between percent TNC and cutting height in this more frequently cut regime, no such relationship was evident within the six-weekly cut treatments. The increasing percent TNC phase was also delayed with these latter treatments, although similar peak values to those of the three-weekly cut treatments were eventually attained. General trends indicated that with 1.5 cm cutting, TNC concentrations increased with longer regrowth intervals. In contrast, no consistent response to cutting frequency was recorded for the 5.0 cm cutting height treatments and where 9.5 cm cutting was employed, TNC levels and regrowth intervals were negatively related.

5.3.1.1 Central System Total Nonstructural Carbohydrates

Sugar concentrations in the crown plus taproot were not significantly influenced by defoliation management but marked seasonal variations were evident (Table 17). Concentrations declined during spring and summer and reached minimum values in April. Over late autumn sugar levels again increased to attain maximum winter values. Within the starch pool, concentrations also fell during spring, particularly for the 1.5 cm cut treatments. A phase of increasing starch concentrations then commenced in December and January and continued until April. Initial increases were most marked for treatments MF and LF and for the latter treatment this superiority continued through to the mid-autumn peak. For the more laxly defoliated treatments, starch concentrations decreased during late autumn and these decreases continued for all treatments over the subsequent winter.

The absolute weights of TNC that are presented in Table 17 for the central system were determined from the dry weight and percent TNC values of the crown plus taproot components. Absolute TNC dropped during spring until December and then recovered to attain a peak in late autumn. The extent of this recovery was least where 1.5 cm cutting was employed and most marked for treatment L.F. The peak weights recorded in late autumn were positively related to cutting height, however these differences gradually disappeared as TNC levels decreased during winter. Where treatment differences occurred in absolute TNC

Table 17: Nonstructural carbohydrate status of the central plant system in Experiment 1.

Harvest Date	9/9	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
				Sugar (% of dry weight)					
Harvest Mean	4.2	2.4	2.4	1.6	1.4	1.3	2.6	3.6	6.4
			Harvest Mean SE: 0.04			Harvest Mean LSD (5%): 0.10			
Treatment				Starch (% of dry weight)					
SF	15.2	9.8	4.9	11.8	16.8	23.7	23.6	16.8	11.8
MF	16.7	12.4	8.0	15.8	17.4	26.7	23.3	18.3	12.5
LF	16.6	13.4	8.1	19.9	18.7	28.3	23.2	17.9	10.7
SI	16.3	9.0	7.3	11.0	16.5	22.8	22.8	15.4	11.7
MI	13.2	11.7	8.3	12.2	17.1	26.1	23.4	18.3	10.6
LI	15.0	13.3	7.3	14.3	16.4	26.8	23.7	18.4	12.1
Tmt Mean SE	0.81	0.70	0.61	0.68	0.65	1.27	0.68	0.66	0.66
Signif level	NS	***	*	***	NS	**	NS	*	NS
LSD (5%)		2.1	1.8	2.1		3.8		2.0	
				TNC Weight (mg per plant)					
SF	139	71	41	78	121	197	209	183	104
MF	87	92	57	124	157	372	329	220	181
LF	118	67	64	225	294	525	361	196	146
SI	104	71	53	67	162	220	292	168	151
MI	86	107	63	128	207	396	378	204	169
LI	121	169	74	136	174	425	367	207	149
Tmt Mean SE	14.9	11.7	9.9	21.0	22.6	51.3	18.5	15.4	19.0
Signif level	NS	*	NS	***	*	***	***	NS	NS
LSD (5%)		35		63	68	155	56		

levels, the principal factor involved was that of crown and taproot dry weight variation (see Chapter 3.3.1.1).

5.3.1.2 Peripheral System Total Nonstructural Carbohydrates

The peripheral plant system consisted of underground rhizome growth and above-ground stubble plus residual shoot growth. Whereas rhizome dry weights were indirectly influenced by defoliation, the composition and quantity of the aerial residual was directly determined by both cutting height and frequency (see Chapter 3). Although the tissue composition of this bulked peripheral system varied with different cutting heights and frequencies, no significant treatment effects were recorded in relation to sugar concentration (Table 18). Seasonal differences did exist however, and as with the central plant system, sugar concentrations peaked in winter and then declined through spring and summer to minimum values in April.

Although percent starch levels were much lower than those of the central plant system, similar seasonal and treatment trends were recorded. Following decreases during spring, starch levels started to rise in December and reached peak values in May. These percentage increases would have been due to increasing starch storage as well as to an increasing proportion of storage rhizome tissue relative to above-ground growth. Increases were again most notable in treatments MF and LF, although at the late autumn peak, and over the subsequent decreasing winter phase, treatment means were not significantly different.

As the residual aerial component remained relatively constant with time, seasonal variation in absolute TNC followed changes in TNC concentration and changes in the dry weight of the rhizome system. As a result, decreases in TNC weight were recorded in winter and spring while TNC accumulation occurred during summer and autumn (Table 18). With increasing cutting height, the dry weight of the peripheral system increased as a result of a larger residual canopy and a more expansive rhizome system. Thus, absolute TNC levels were higher and the commencement of the accumulating phase was earlier where cutting height was increased.

As the last cut was made on 18/5/76, the losses of TNC per plant over the winter, as indicated by the two winter samplings, were not related to defoliation. The concentration of TNC declined over this

Table 18: Nonstructural carbohydrate status of the peripheral plant system in Experiment 1

Harvest Date	9/9	21/10	2/12	13/1	24/2	6/4	18/5	29/6	10/8
				Sugar (% of dry weight)					
Harvest Mean	7.9	4.3	3.6	2.2	2.8	2.0	4.3	4.9	6.7
	Harvest Mean SE: 0.09				Harvest Mean SE: 0.24				
Treatment				Starch (% of dry weight)					
SF	6.2	3.5	2.2	4.7	9.2	11.5	14.8	12.3	6.5
MF	7.1	4.0	3.2	7.7	9.9	14.8	15.6	14.7	7.1
LF	6.5	4.5	2.9	7.6	10.8	15.7	16.1	13.9	7.0
SI	7.5	3.3	2.6	5.8	9.0	14.3	16.5	12.8	7.5
MI	6.2	5.5	3.2	5.6	9.6	14.6	16.4	14.5	6.6
LI	6.1	4.8	2.1	5.0	8.8	14.2	16.8	13.9	6.9
Tmt Mean SE	0.44	0.18	0.26	0.40	0.52	0.75	0.51	1.01	0.50
Signif Level	*	***	*	***	NS	*	NS	NS	NS
LSD (5%)	1.3	0.5	0.8	1.2		2.2			
				TNC Weight (mg per plant)					
SF	147	113	61	77	141	219	402	284	145
MF	178	134	85	153	265	561	618	354	196
LF	263	133	111	315	406	719	609	405	173
SI	185	113	57	95	226	262	512	366	180
MI	152	213	87	127	307	461	726	387	213
LI	294	282	109	200	289	582	718	426	196
Tmt Mean SE	30.3	31.3	12.5	24.4	38.6	75.6	48.8	42.4	20.3
Signif Level	*	**	*	***	*	***	***	NS	NS
LSD (5%)	91	94	38	73	116	227	147		

period and organ dry weights were reduced as a result of rhizome decomposition and the production of smaller plant units from vegetative propagation (see Chapter 3.3.1).

Higher absolute TNC levels were recorded within the peripheral rather than the central plant system and the extent of this difference was most evident within the more laxly cut treatments and in late autumn when rhizome growth and TNC accumulation had peaked. Just as cutting frequency had little consistent influence on absolute TNC levels within both systems, the relative importance between the storage regions did not appear to respond to varied regrowth intervals.

For the 6/4/76 sampling, the peripheral system was further separated and TNC status of the rhizome and aerial residual components were separately determined (Table 19). In the above-ground tissue, sugar concentrations were higher than those recorded within the rhizome system and these were in turn higher than the values recorded within the central plant system at the same sampling date. In contrast, starch concentrations were markedly higher within the rhizome fraction of the peripheral system although they were still lower than those recorded in the crown plus taproot. Because of the high starch concentrations within the rhizome tissue, it was this component that principally determined TNC levels of the peripheral system.

Table 19: Nonstructural carbohydrate status of the rhizome and above-ground fractions of the peripheral system sampled on 6/4/76 (% of dry weight)

	Above-ground Fraction		Rhizome Fraction	
Treatment	% Sugar	% Starch	% Sugar	% Starch
SF	2.5	4.8	1.5	14.3
MF	2.8	5.7	1.8	18.1
LF	2.9	5.9	1.8	18.8
SI	2.8	4.6	1.7	17.7
MI	2.6	5.6	1.8	18.9
LI	2.9	5.1	1.9	18.3
Mean SE	0.16	0.43	0.11	0.95
Signif Level	NS	NS	NS	*
LSD (5%)				2.8

5.3.2 Experiment 2

5.3.2.1 Spring Sampling

All six treatments were sampled on 30/11/76 at various stages of regrowth and then subsequently, sugar and starch levels were determined for the rhizome and crown plus taproot components. The two carbohydrate fractions were summed to give percent TNC and these values, along with component dry weights are presented in Table 20. In all treatments, and for both components, percent TNC values were low and of a similar magnitude to those previously recorded in the late spring of Experiment 1. The sugar fraction at this sampling, as a mean of all six treatments, was 1.3 percent of dry weight for both rhizome and crown plus taproot tissue.

There was no evidence of enhanced TNC in association with extended regrowth intervals and only treatment SAS, which was cut to 1.5 cm one week prior to sampling, had a significantly reduced TNC concentration. No significant treatment differences in underground organ weights were recorded and as a result, absolute TNC levels were not significantly different between treatments.

5.3.2.2 Autumn Sampling

Percent TNC recorded in the autumn sampling (26/4/77; Table 20) were markedly higher than those measured in late spring and this is in agreement with the seasonal trends recorded in Experiment 1. The sugar fractions of the TNC values did not differ significantly between treatments and were approximately 3.5 percent of dry weight for both storage regions. Although TNC concentration was greater in the crown plus taproot than in the rhizome tissue, it was the least responsive to the defoliation treatments imposed. Highest TNC concentrations and dry weights in the crown plus taproot were recorded for treatment RS where, prior to sampling, regrowth had occurred for twelve weeks. Between the remaining treatments however, there were few significant treatment differences which was in contrast to the rhizome system, particularly in relation to dry weights.

Table 20: TNC concentrations (% dry weight) and dry weights (mg /plant) of underground organs during late spring and autumn in Experiment 2.

Treatment	LR[a]	Rhizome %TNC	Rhizome Dry Wt.	Crown plus Taproot % TNC	Crown plus Taproot Dry Wt	Total Underground %TNC
		Late Spring (30/11/76)				
RS	12	5.4	146	6.9	366	6.5
SAS	1	4.1	122	5.4	397	5.2
6S	6	5.4	152	7.5	401	6.9
6L	6	5.9	141	8.8	366	7.9
SAL	4	5.2	126	6.7	341	6.2
LS	6	4.8	110	6.6	371	6.3
Tmt Mean SE		0.40	12.9	0.49	60.4	0.46
Signif Level		NS	NS	**	NS	*
LSD (5%)				1.5		1.4
		Autumn (26/4/77)				
RS	12	22.1	1005	26.1	952	23.9
SAS	6	18.0	561	21.9	783	20.5
6S	3	16.0	231	23.4	560	21.2
6L	3	20.0	571	24.7	867	22.7
SAL	3	17.4	600	24.1	623	20.8
LS	3	15.7	455	22.7	751	20.0
Tmt Mean SE		0.96	38.3	0.78	75.6	0.63
Signif Level		***	***	*	*	***
LSD (5%)		2.9	1.15	2.3	22.8	1.9

LR[a] - length of regrowth period (wks) from the time of cutting to the sampling date.

Within the rhizome system, short term effects of the imposed defoliation treatments were evident in the different TNC concentrations recorded for the autumn sampling. Higher concentrations were recorded where regrowth intervals were extended (Treatment RS) and where previous defoliation was lax (Treatment 6L). Where 1.5 cm cutting occurred only three weeks before sampling (Treatments 6S and LS) lower TNC levels were measured. Long term treatment effects were apparent with regard to rhizome dry weights and where cutting had continuously been low, there was a positive dry weight response to increasing cutting interval. A response in TNC concentration to lax defoliation was also evident, as values after a similar regrowth period were higher in treatment 6L compared with 6S.

Although the combined TNC concentrations of the underground components were significantly different, the magnitude of the differences was minimal compared with those of organ dry weights. It was principally due to this latter factor that absolute TNC levels were highest in treatments RS and 6L. Where the expansion of the rhizome system was poor, as in treatment 6S, the lowest weight of underground TNC was recorded.

5.4 Discussion

In terms of percentage unit changes, starch was the more responsive carbohydrate fraction and the seasonal pattern it followed, principally determined TNC seasonal patterns. Concentrations of both carbohydrate fractions were influenced to a greater extent by season than defoliation, however the seasonal patterns they followed differed considerably. Whereas starch levels fell during late autumn and winter, sugar levels increased. Increasing sugar and declining starch concentrations, as starch is hydrolysed to sugars, have also been reported for lucerne (Jung & Smith, 1961), *L. corniculatus* (Nelson & Smith, 1968b) and red clover (Smith, 1950) during late autumn to early spring. Declining TNC values in 'Grasslands Maku' over this same period indicated a net usage of accumulated carbohydrate. Whether this usage relates to respiration in underground organs and/or to the remobilization of carbohydrates to aerial shoot growth, cannot be conclusively determined from these experiments. However, in other forage legumes declining TNC over similar periods have been related to root respiration (Weinmann, 1961).

The greater partitioning of assimilates to stored starch between December and May in Experiment 1 coincided with the expansion of underground organs. It is unlikely that the accumulation of TNC was the causal factor in underground growth, as its expansion was greater and more prolonged than that of starch storage. More likely, a common environmental trigger stimulated greater assimilate partitioning to underground organs and resulted in both improved storage and growth. In *L. corniculatus*, Greub & Wedin (1971a) proposed that this stimulus was related to photoperiod although Nelson & Smith (1969) also found that the accumulation of TNC was limited by high temperatures.

A resurgence in crown and rhizome shoot numbers also coincided with the accumulation of TNC in Experiment 1. Whether this relationship was indirectly linked to a common stimulus or more directly to increased partitioning of assimilates to underground organs again, cannot be conclusively determined. In lucerne, Cowett and Sprague (1962) positively linked crown TNC, shoot numbers and shoot vigor and Chatterton *et al*. (1974) stated that their data indicated that high crown carbohydrate levels not only provided energy required for growth processes, but also functioned in the initiation and activation phase of bud development.

Although TNC concentrations were highest within the crown plus taproot, it was the principal storage organ only when rhizome growth was limited. Where expansion of the rhizome system was encouraged by lax and/or infrequent defoliation, then the relative importance of the central plant system declined. It was also apparent that whereas time influenced both TNC concentration and storage organ dry weights, the effect of differential defoliation was more confined to varying organ size. It is interesting to note therefore, that at any one time TNC concentrations were generally similar and seemed to be determined by seasonal factors, thus the variation in absolute TNC was principally an expression of defoliation effects on underground organ expansion. Langille *et al*. (1968), working with *L. corniculatus* also found that seasonal patterns dominated TNC concentrations and that the effects of different cutting regimes were primarily reflected in the size of the crown and taproot.

In the spring sampling of Experiment 2, TNC concentrations and storage organ weights showed little variation between treatments, yet when nonstructural carbohydrates were accumulating at the autumn

sampling, TNC concentrations, and more particularly organ weights, responded to lax and infrequent defoliation. In terms of absolute TNC, this contrast suggests that it is defoliation over the autumn period that is most critical in determining TNC accumulation. Greub & Wedin (1971b) working with *L. corniculatus* also showed that only during the accumulating autumn period did TNC concentration respond to differential defoliation. For the same species, Nelson & Smith (1969) reported that only under cool temperatures, that allowed TNC to accumulate, did TNC concentrations cycle in response to defoliation.

From the nonstructural carbohydrate determinations conducted in these experiments, it is difficult to conclusively establish the importance and extent of TNC depletion and restoration processes in the regrowth of 'Grasslands Maku'. In Experiment 1, higher TNC concentrations were frequently recorded for plants that had regrown for three rather than six weeks prior to sampling. If TNC concentrations were strongly influenced by defoliation it might be expected that lower levels would have occurred with more frequent cutting. This did not occur.

Lower nonstructural carbohydrate usage in respiration and growth may have been reflected in the higher absolute TNC levels recorded in lax rather than severely cut plants. However, these cutting height responses may also indicate an earlier, or even uninterrupted, partitioning of assimilates to underground organs which was expressed as greater storage organ weights and TNC accumulation. This latter relationship would seem more likely as it was organ size rather than TNC concentration that principally responded to higher cutting. *L. corniculatus* (Nelson & Smith, 1968b; Greub & Wedin, 1971a), *C. varia* (Langille & McKee, 1968; Woodruff, 1974) and *O. viciifolia* (Cooper & Wilson, 1968) have similar seasonal TNC patterns to that of 'Grasslands Maku' and all show limited TNC cycling in response to defoliation.

Regrowth characteristics of 'Grasslands Maku' would suggest that residual TNC was not of major importance in determining regrowth rates and production. In Experiment 1, canopy production was high in late spring/early summer when TNC levels were at their lowest and conversely, production was low in autumn when TNC levels were high (Chapter 4.3.1.1). Furthermore, it is possible that autumn TNC accumulation may well have played a part in limiting the partitioning of assimilates to, and

growth of, aerial herbage. In Experiment 2, initial regrowth rates were again highest in late spring and summer when TNC values would have been at their lowest levels. Within the same experiment, initial regrowth rates were not improved when the regrowth interval of severely cut treatments were lengthened even though greater absolute TNC levels would have been present. The role of higher absolute TNC levels in determining the positive shoot production responses to lax defoliation is difficult to ascertain as this response is confounded by increased residual shoot numbers, shoot size and leaf area. However, on a net canopy production basis there was no apparent initial advantage to lax defoliation and higher TNC levels.

In terms of a direct function in early regrowth and herbage production, accumulated TNC would appear to be of limited value where defoliation is incomplete. The importance of accumulated TNC is more likely to be associated with providing a substrate for underground respiration during late autumn,winter and early spring and hence maintain a basis for shoot initiation and herbage production.

CHAPTER 6: THE IMPORTANCE OF SEVERAL RESIDUAL PLANT FACTORS IN DETERMINING EARLY REGROWTH IN *LOTUS PEDUNCULATUS* cv. 'GRASSLANDS MAKU'

6.1 Introduction

Accumulated organic reserves in defoliated plants can serve as a substrate for both respiratory and growth processes (Hodgkinson, 1969; Pearce *et al.* 1969; Smith & Marten, 1970; Singh & Winch, 1974b). However, their direct influence on regrowth would appear to be confined to only a few days following defoliation (Davidson & Milthorpe, 1966a) and this becomes of less importance as the associated leaf complement increases (Silva, 1969; Leafe *et al.* 1974; Booysen & Nelson, 1975). Furthermore, regrowth is not only determined by the capacity of the plant to supply energy, but also by the capacity to utilize it, as determined by the stage of development and number of meristems (Blaser *et al.*, 1966; Sheard, 1973). In lucerne residual shoot size and number have been shown to be principal determinants of regrowth (Leach, 1968, 1969, 1970; Hodgkinson, 1973).

Previous field work involving *Lotus pedunculatus*, cv. 'Grasslands Maku', (see Chapters 3-5), has indicated that season, rather than defoliation, is the dominant factor in determining TNC variation. Furthermore, there was little evidence that positively related regrowth with residual plant TNC status. In contrast however, defoliation height markedly influenced regrowth rates and patterns, but as leaf area, shoot size and shoot number all varied, the operative factors were not conclusively identified. Early regrowth of 'Grasslands Maku' in the field is characteristically slow, however the rates and patterns of regrowth depend on the extent to which the various shoot pools participate. Therefore, the origin and growth characteristics of residual and subsequent shoot populations are important factors in determining regrowth.

This chapter presents and discusses the results of an experiment (Experiment 3) designed to provide more detailed information on the response of *L. pedunculatus* cv. 'Grasslands Maku' to defoliation when grown under controlled environmental conditions. During a 28 day regrowth period, relationships were sought between shoot regrowth and several residual plant factors, namely: total nonstructural carbohydrates (TNC), leaf area, shoot number and shoot size.

6.2 Experimental

On 3/1/76, sods of pure 'Grasslands Maku' were taken from an area previously described in Chapter 3 and adjacent to Experiment 1. Plants were washed and separated and following the removal of stem growth, crown plus taproots were graded into various size ranges. Those that fell within an approximate dry weight range of 500 to 800 mg were subsequently transplanted into a soil mix at three per pot. The soil used was a sterilized mix of 70 percent Opiki silt loam and 30 percent Manawatu sandy silt and prior to potting the equivalent of 8 mg of 30 percent potassic superphosphate per pot, was added. The three transplants were arranged in a line within each five litre plastic pot, with the two peripheral transplants being placed against opposite sides of the pot. Once transplanting was completed, Rhizobium strain CC 814S was applied in water.

Plants were then grown under glasshouse conditions, being watered daily and cut every two weeks. Where individual transplants failed or were slow to establish, the pot was discarded. On 9/5/76, one day prior to entering the growth room, 120 pots were blocked into five replicates based on their uniformity of establishment. As blocks, these plants were then grown under controlled climate room conditions (see Appendix 11: Experiment 3) and were cut twice, down to 2 cm, at weekly intervals. Pots were randomly allocated to four treatments and six sample dates on 3/6/76 and then half were cut down to 2.0 cm and the other half to 5.0 cm.

To create plants of lower TNC status, half the pots of both cutting heights from three blocks were placed in a 25C day/20C night environment on 8/6/76. Light was excluded by enclosing the layered trolleys containing the pots with black polythene sheeting. The following day the remaining two blocks were similarly treated. Air was pumped through tubing into each enclosed system and each day, plants were exposed to ten minutes of light. After 48 hours of dark pretreatment, plants were removed, and along with those from the appropriate blocks which had remained in the original environment, they were again cut down to 2.0 or 5.0 cm height. Thus, the treatments imposed were:

L.L.	low nonstructural carbohydrate	2.0 cm cutting height
H.L.	high "	2.0 " " "
L.H.	low "	5.0 " " "
H.H.	high "	5.0 " " "

Although allocated randomly into five initial blocks, pots of similar treatments, when returned to the growth room, were located together so that between treatment interference was eliminated during regrowth. It is unlikely that any environmental bias occurred with this layout as pots within trolleys and trolleys within the room were rotated every two days.

Following the final cut, those plants allocated to day 0 analyses were washed free of soil and separated. The central plant of each pot was retained and stored in darkness at 3 C until dissection, while the remaining two were discarded. Dissected components were: stubble shoots, rhizome shoots, stubble, rhizome, crown plus taproot, fibrous root and dead material and their classification was similar to that outlined in Chapter 3.2. The aerial components were separately subsampled and dissected into leaf and stem and then leaf area determinations were made as described in Chapter 4.2. Dissected material was stored at 3C until vacuum oven drying (16 hours, 2.0 mm Hg, 40C) and then dry weights were recorded. Appropriate pots were removed at 0800 hours on regrowth days 3, 7, 13, 20 and 28, and similar determinations were made.

Dried stubble shoots, rhizome shoots, stubble, rhizome and crown plus taproot were separately ground to pass through a 0.5 mm sieve. Ground samples were then stored at -3C in sealed glass vials for subsequent sugar and starch analyses. Analyses were conducted on a three replicate basis as tissue from the appropriate treatments in replicates two and three were bulked, as were those of four and five. The analytical procedures used for determining sugar and starch percentage levels were similar to those outlined in Chapter 5.2.

Data were statistically analysed by a 2 x 2 factorial analysis of variance. However, as treatment main effects frequently interacted, only treatment means are presented in the text. Following $\log_{10}$ transformation, shoot dry weight data were fitted to the linear equation

$$\log_{10} \text{D. Wt} = b \times \text{days} + a$$

for regrowth days : 0 to 7 and 7 to 28. Relative growth rates (R.G.R.) were calculated for both individual and collective shoot dry weights in accordance with the equation

$$\text{R.G.R.} = \frac{\log \text{D.W.}_2 - \log \text{D.W.}_1}{t_2 - t_1}$$

6.3 Results

6.3.1 Shoot Regrowth

On a per plant basis, total shoot dry weights were considered as being the sum of stubble and rhizome shoot dry weights (Table 21). On day 0 significant differences in shoot dry weights only existed between cutting heights and in absolute terms these differences continued to increase with time. As such, net regrowth in both shoot classes over the 28 day period was greater where higher cutting was employed, particularly where initial TNC levels were higher.

Where cutting to 2.0 cm was employed, total shoot weights were consistently higher for those plants that had an initially higher TNC status, however these differences were not statistically significant ($P<.05$). More marked were the responses to higher TNC where plants were cut to 5.0 cm, particularly from day 7 onwards. It is evident when considering the two shoot classes, that the response in total shoot dry weight to TNC status for the 2.0 cm cut, was almost completely related to the rhizome shoot pool. Where higher cutting occurred, again rhizome shoot growth was more responsive to the TNC treatment, particularly over the last two weeks of regrowth.

When considering the contribution of the two shoot classes to total shoot regrowth, it should be noted that from day 13 onwards the rhizome shoot pool became dominant. As a result of the more responsive nature of this component, this dominance did appear to be greater at the higher TNC and/or cutting level.

Table 21: Total, stubble and rhizome shoot dry weights (mg per plant)

Days of Regrowth	0	3	7	13	20	28
			Total Shoots			
LL	53	94	260	765	1846	3483
HL	71	150	358	930	2049	4674
LH	269	393	741	1460	2590	5425
HH	258	501	1006	1816	3332	7498
Tmt Mean SE	16.4	39.0	53.3	66.4	94.9	403.3
Signif Level	***	***	***	***	***	***
L.S.D. (5%)	51	120	164	205	293	1243
			Stubble Shoots			
LL	28	56	139	421	787	1221
HL	37	80	174	428	750	1361
LH	143	242	439	681	1165	2015
HH	154	313	534	865	1310	2701
Tmt Mean SE	9.4	23.1	35.4	44.9	76.6	157.9
Signif Level	***	***	***	***	***	***
L.S.D. (5%)	29	71	109	138	236	487
			Rhizome Shoots			
LL	25	39	121	343	1059	2262
HL	34	70	183	501	1299	3313
LH	125	151	301	779	1425	3409
HH	104	188	471	951	2021	4791
Tmt Mean SE	9.2	17.5	25.0	43.5	59.0	325.9
Signif Level	***	***	***	***	***	***
L.S.D. (5%)	29	54	77	134	182	1005

Relative growth rates (RGR) of the collective total, stubble and rhizome shoot pools, calculated on a dry weight basis, are presented in Figure 12. Data points are located at the mid-point of each appropriate regrowth period. Where 2.0 cm cutting occurred, total and rhizome shoot RGR were greater in higher TNC plants for the first three days of regrowth, but thereafter they were similar or lower than those of low TNC plants. Where plants were cut to 5.0 cm, both stubble and rhizome shoot pools of higher TNC status had greater RGR for the first 3 and 7 days of regrowth, respectively. As a result, total shoot RGR were greater in higher TNC plants for the first 7 days, but thereafter there were no marked treatment differences between the two TNC levels.

Except for the last eight days of regrowth, shoot RGR were consistently lower where high cutting was employed. These reductions were most marked where TNC levels were low. For all treatments, RGR of the stubble shoot pool declined with time, whereas in the rhizome shoot pool, with the exception of treatment HL, values increased to a maximum during days 3 to 7, and then declined. This latter pattern, again with the exception of HL, was also evident for total shoot regrowth.

The relationships of $\log_{10}$ shoot dry weight to regrowth days were determined with linear regression analysis for total, stubble and rhizome shoot regrowth during days 0 to 7 and 7 to 28 (Table 22). The regression slopes (b values) of these relationships represent the predicted average RGR during appropriate regrowth periods, while the constants (a values) represent, for the fitted regression, projected shoot dry weights at the start of the appropriate regrowth period. For the regrowth period, day 0 to 7, regression slopes were always greater with low cutting, but the differences were only statistically signifiant for low TNC status plants. Only with 5.0 cm cutting were regression slopes greater for higher TNC plants and significant differences were confined to rhizome and total shoot regrowth.

For the 7 to 28 day regrowth period, regression slopes were not significantly different between TNC treatments within each cutting height and shoot class. However, in all shoot classes and for both TNC levels, significantly lower regression slopes and higher intercepts were recorded where 5.0 rather than 2.0 cm cutting occurred. Significantly greater regression constants for plants of higher TNC status were

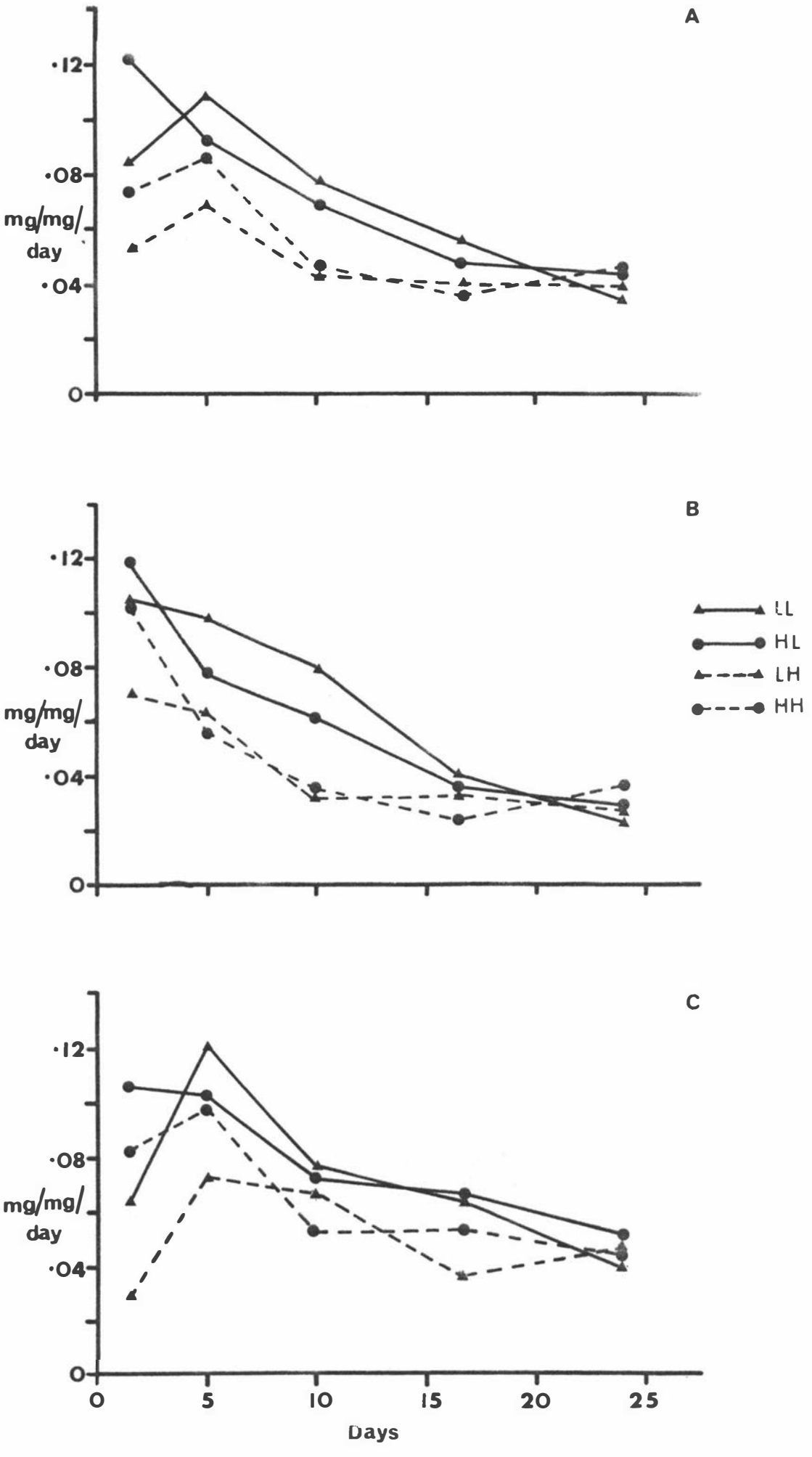


FIGURE 12: RGR of collective total (A), stubble (B) and rhizome (C) shoot pools.

Table 22: Shoot dry weight relationship with regrowth time. (log D.Wt = b x days + a; for days 0-7 and 7-28)[A]

	Regrowth Period, 0-7 Days					Regrowth Period, 7-28 Days				
	b value	SE_b	a value	SE_a	R^2	b value	SE_b	a value	SE_a	R^2
	Stubble Shoots					Stubble Shoots				
LL	.103	.0137	1.454	.0978	.841	.044	.0038	1.934	.0718	.879
HL	.097	.0140	1.598	.0861	.788	.041	.0033	2.009	.0614	.898
LH	.069	.0095	2.152	.0729	.806	.033	.0022	2.380	.0412	.925
HH	.075	.0091	2.211	.0741	.841	.033	.0022	2.486	.0409	.927
	Rhizome Shoots					Rhizome Shoots				
LL	.108	.0130	1.399	.0898	.895	.061	.0034	1.695	.0630	.949
HL	.107	.0111	1.507	.0931	.878	.060	.0025	1.882	.0464	.970
	.058	.0120	2.044	.0845	.861	.052	.0023	2.074	.0423	.967
HH	.089	.0108	1.930	.0861	.792	.048	.0020	2.343	.0376	.969
	Total Shoots					Total Shoots				
LL	.105	.0147	1.690	.0892	.807	.053	.0032	2.113	.0600	.939
HL	.102	.0119	1.858	.0821	.850	.052	.0026	2.229	.0478	.959
LH	.064	.0083	2.406	.0751	.789	.043	.0019	2.531	.0362	.964
HH	.084	.0079	2.397	.0742	.898	.041	.0017	2.709	.0318	.970

A - Significance levels were determined on a paired t-test basis

confined to rhizome shoot regrowth and total shoot regrowth where 5.0 cm cutting occurred.

Average individual shoot weights were calculated for each shoot class by dividing the appropriate shoot dry weights per plant with shoot numbers (Table 23). Where 2.0 cm cutting occurred, individual stubble and rhizome shoot dry weights were consistently higher in plants of an initially higher TNC status, but the differences were statistically non-significant. For the 5.0 cm cut treatments, individual shoot weights were again greater for higher TNC treatments and these were statistically significant within the rhizome shoot pool. Individual shoot sizes at the end of the experimental regrowth period were higher within the rhizome shoot pool and where 5.0 rather than 2.0 cm cutting was used.

RGR for individual shoot dry weights were calculated for both shoot pools and these are shown in Figure 13. Within the stubble shoot class, individual shoot RGR within both cutting heights responded inconsistently to TNC status. With 5.0 cm cutting the response pattern was similar to that of total stubble shoot RGR (see Figure 12), however at 2.0 cm the pattern differed in that initial values were lower for higher TNC treatments. Individual rhizome shoot RGR responded to different TNC levels in a similar pattern to that for the collective rhizome shoot pool, although the positive response was more prolonged where 5.0 cm cutting occurred.

Where 5.0 cm rather than 2.0 cm cutting was employed individual shoot RGR were generally lower and this was particularly so for the lower TNC treatments. Contrasting trends of RGR with time occurred between the shoot classes. Whereas values showed a rapid initial decline in the stubble shoot pool, only after seven days of regrowth did a gradual decline become evident within the rhizome shoot class.

6.3.2 Shoot Numbers

Over the initial seven days of regrowth, shoot numbers tended to increase more rapidly, and were therefore generally greater, in higher TNC treatments (Table 24). However, for both cutting heights and both shoot pools these responses were not statistically significant

Table 23: Individual stubble and rhizome shoot dry weights (mg per shoot)

Days of Regrowth	0	3	7	13	20	28
			Stubble Shoots			
LL	0.7	1.3	2.1	3.6	6.4	11.5
HL	1.1	1.6	2.1	4.2	6.6	13.0
LH	2.3	3.3	4.7	6.3	10.3	21.0
HH	2.4	4.0	5.1	8.0	12.3	22.8
Tmt Mean SE	0.13	0.20	0.21	0.45	0.51	1.37
Signif Level	***	***	***	***	***	***
LSD (5%)	0.4	0.6	0.6	1.4	1.6	4.2
			Rhizome Shoots			
LL	1.1	1.4	2.5	6.1	13.7	33.8
HL	1.5	2.1	3.3	7.4	16.3	41.0
LH	3.6	4.4	6.3	11.5	23.2	54.4
HH	3.5	4.9	7.9	16.1	32.8	74.1
Tmt Mean SE	0.29	0.28	0.32	0.81	0.81	3.97
Signif Level	***	***	***	***	***	***
LSD (5%)	0.9	0.9	1.0	2.5	2.5	12.2

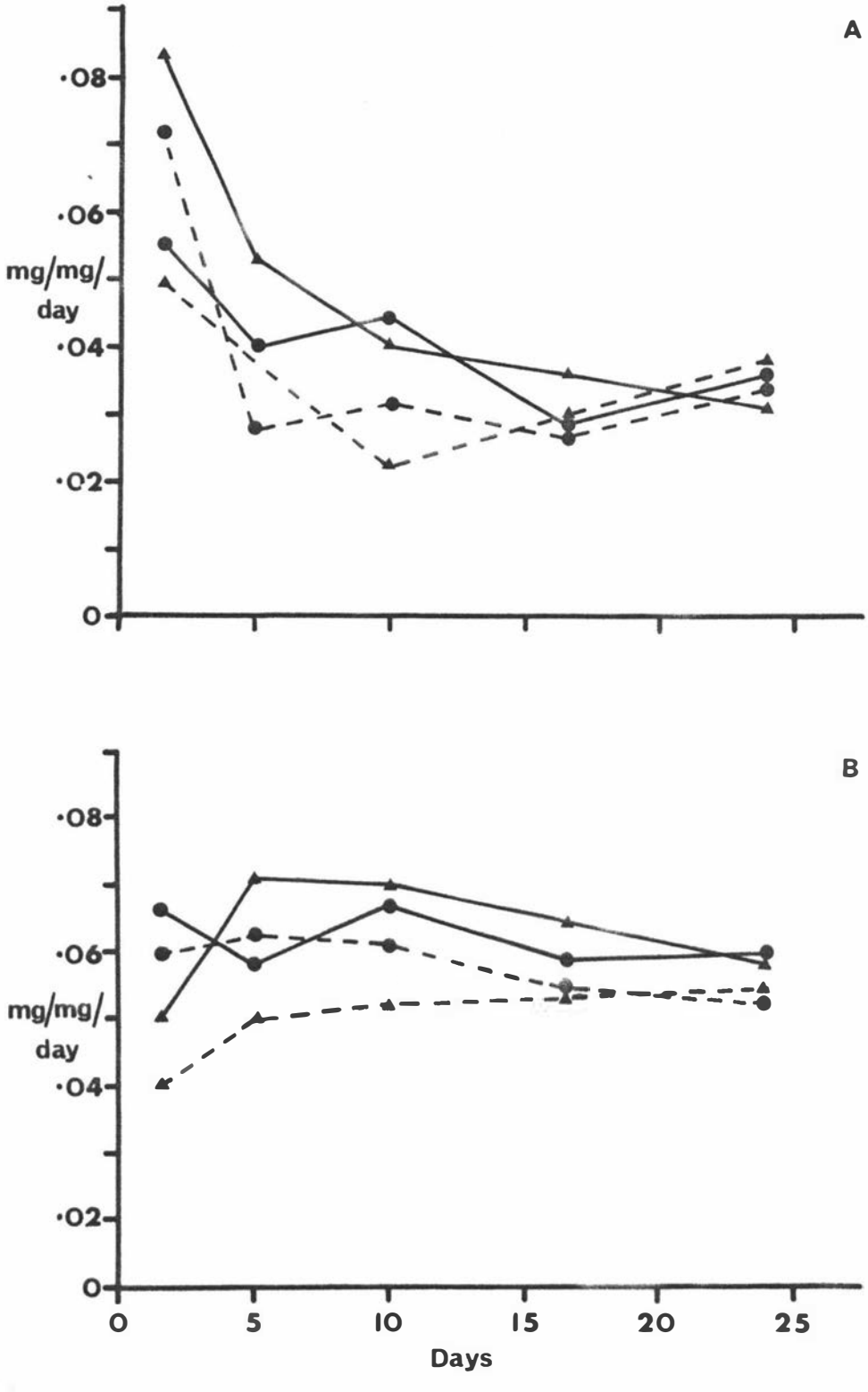


FIGURE 13: RGR of individual stubble (A) and rhizome (B) shoots.

Table 24: Stubble and rhizome shoot numbers (per plant)

Days of Regrowth	0	3	7	13	20	28
			Stubble Shoots			
LL	38	45	67	115	124	106
HL	32	50	84	101	115	107
LH	61	73	95	108	113	97
HH	64	78	104	110	106	118
Tmt Mean SE	4.0	5.2	7.3	6.5	8.2	7.3
Signif Level	***	***	*	NS	NS	NS
LSD (5%)	12	16	22			
			Rhizome Shoots			
LL	23	29	48	56	78	67
HL	23	33	56	70	80	81
LH	36	35	49	68	61	64
HH	30	39	60	60	70	64
Tmt Mean SE	2.6	2.3	5.5	5.5	5.8	4.4
Signif level	**	NS	NS	NS	NS	NS
LSD (5%)	8					

($P<.05$). With lower cutting, initial shoot numbers were reduced, but after seven and thirteen days for the respective rhizome and stubble shoot classes, any such affects had disappeared. Generally from day thirteen onwards shoot numbers had stabilized, although in absolute terms, shoot number increases had been markedly greater within the stubble shoot pool.

6.3.3 Residual Leaf Area, Stubble Weight and Underground Weight

Following the final cut, the majority of the residual leaf area was associated with the stubble component, particularly for the 2.0 cm cut treatments (Table 25). As regrowth proceeded, the relative importance of this leaf pool decreased, although even at day 7 it contributed approximately one half and one third of the total plant leaf area for the 2.0 and 5.0 cm treatments, respectively. Generally, higher stubble leaf area resulted and persisted with the higher cutting level, although over the last rapidly regrowing period, stubble leaf area showed a sharp decline in the 5.0 cm cut treatments.

Within both shoot pools, leaf areas were consistently greater where TNC were initially higher and this was particularly so with 5.0 cm cutting. However, often these differences failed to reach statistical significance. As with shoot dry weights, leaf areas in both classes positively responded to higher cutting but in contrast, the rhizome shoot pool did not dominate final plant leaf area as it did shoot regrowth on a dry weight basis.

Leaf to stem dry weight ratios for stubble, stubble shoot and rhizome shoot growth, are presented in Appendix 12. The most notable feature was the markedly higher leaf to stem ratios recorded in the stubble shoot pool compared with the rhizome shoot pool, particularly during the early stages of regrowth.

Stubble dry weight showed little response to differences in either initial TNC status or cutting height (Table 26). This lack of variation must in part be a reflection of the previously common cutting procedure imposed on all plants prior to the final two cuts. The most obvious trend in stubble dry weight was the general decline that continued throughout the regrowth period. No consistent trends

Table 25: Leaf area of stubble, stubble shoots and rhizome shoots (cm^2 per plant)

Days of Regrowth	0	3	7	13	20	28
			Stubble			
LL	76.0	55.2	73.0	58.0	80.6	81.2
HL	105.0	72.2	68.8	72.2	78.8	88.0
LH	157.6	138.4	101.8	109.0	128.4	84.0
HH	178.2	144.8	117.4	104.6	138.0	96.4
Tmt Mean SE	19.7	15.6	9.9	7.4	10.7	16.2
Signif Level	***	***	***	***	***	NS
LSD (5%)	60.8	48.2	30.7	22.9	33.0	
			Stubble Shoots			
LL	6.2	10.0	33.8	106.6	290.2	414.2
HL	9.2	22.0	49.6	108.6	269.8	510.2
LH	44.8	70.6	118.6	190.2	403.8	696.2
HH	45.6	73.4	153.2	240.6	469.8	930.4
Tmt Mean SE	4.1	7.5	12.7	12.3	27.0	73.1
Signif Level	***	***	***	***	***	***
LSD (5%)	12.8	23.3	39.2	37.8	83.2	224.5
			Rhizome Shoots			
LL	5.4	9.2	25.0	85.6	333.6	666.0
HL	5.6	15.6	37.6	131.4	365.6	709.4
LH	40.2	44.4	80.4	183.8	389.6	913.0
HH	30.0	49.2	128.6	220.2	557.2	1071.2
Tmt Mean SE	2.9	3.8	5.3	13.8	29.5	70.9
Signif Level	***	***	***	***	***	***
LSD (5%)	8.9	11.6	16.3	42.5	90.9	218.4

Table 26: Stubble and total underground dry weight (mg per plant)

Days of Regrowth	0	3	7	13	20	28
			Stubble			
LL	1020	991	1001	800	808	753
HL	1071	1072	928	767	723	748
LH	1179	1036	1091	787	987	831
HH	1039	1088	975	1024	994	882
Tmt Mean SE	92.0	121.8	111.2	61.9	66.8	53.6
Signif Level	NS	NS	NS	**	*	NS
LSD (5%)				190	206	
			Total Underground			
LL	2822	2822	3426	2562	2477	3034
HL	2721	3056	3247	2767	2786	2864
LH	3418	2825	2732	2869	2788	3593
HH	2875	2898	2734	2764	2810	3762
Tmt Mean SE	263.2	268.0	228.7	254.6	187.3	242.9
Signif Level	NS	NS	NS	NS	NS	**
LSD (5%)						747

with time were evident in total underground dry weight and the only notable variation was an increase in this component during the last regrowth period of the 5.0 cm cut treatments. Of all plant components, it was those located underground that were the most variable, particularly with regard to fibrous root growth which appeared to be greater where a larger rhizome and/or a smaller crown plus taproot system occurred.

6.3.4 Nonstructural Carbohydrate Status

Stubble shoot, rhizome shoot and stubble TNC concentrations were considered as the sum of their respective 62.5 percent methanol extracted sugar and enzyme hydrolysed starch levels (Figure 14A,B,C). Percent stubble shoot TNC significantly differed between treatments only

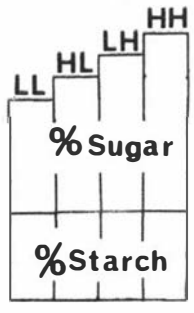
at day 0, immediately following the dark pretreatment. Sugar levels were lower in treatments LL and LH, however by day 3 they had recovered to values comparable with those of the remaining two treatments. Over this three day period there was a general increase in both sugar and starch fractions but thereafter, TNC remained at a relatively stable level of 6.0 to 7.0 percent. If variations did occur they were principally related to the starch fraction.

Within the rhizome shoot pool the lower sugar and TNC levels evident at day 0, in those plants that were pretreated in darkness, were still apparent on the third day. Thereafter however, treatment differences were inconsistent. Rhizome shoot TNC levels continued to increase as regrowth progressed and other than during the first three days of regrowth, these increases were principally related to the starch fraction.

In those treatments that had been dark pretreated, percent TNC were significantly lower in the stubble component at the start of regrowth. By day 3 these differences had disappeared and in fact were reversed on the seventh day. Thereafter, there was a gradual increase in the starch fraction, particularly where 5.0 cm cutting had occurred. As a result, significantly higher TNC concentrations were recorded in the higher cut treatments for the last two regrowth periods. Nonstructural carbohydrate status in the stubble was much lower than that of both shoot pools and this was particularly so with regard to the sugar fraction.

The TNC status of the rhizome and crown plus taproot components were considered in a similar manner as were those of the aerial plant components (Figure 14D,E). TNC levels in rhizome tissue gave no indication that the one differential cut given prior to day 0 had any affect on TNC status. Pretreatment in the dark did however, reduce starch and TNC levels and these reductions were still consistently evident on the third regrowth day. During the first thirteen days of regrowth, TNC levels were similar to their original values, but thereafter they increased as starch accumulated, particularly where 5.0 cm cutting had occurred.

FIGURE 14: Nonstructural carbohydrate levels (% dry weight) in stubble shoots (A); rhizome shoots (B); stubble (C); rhizome (D) and crown plus taproot (E).



I LSD(5%) for TNC levels

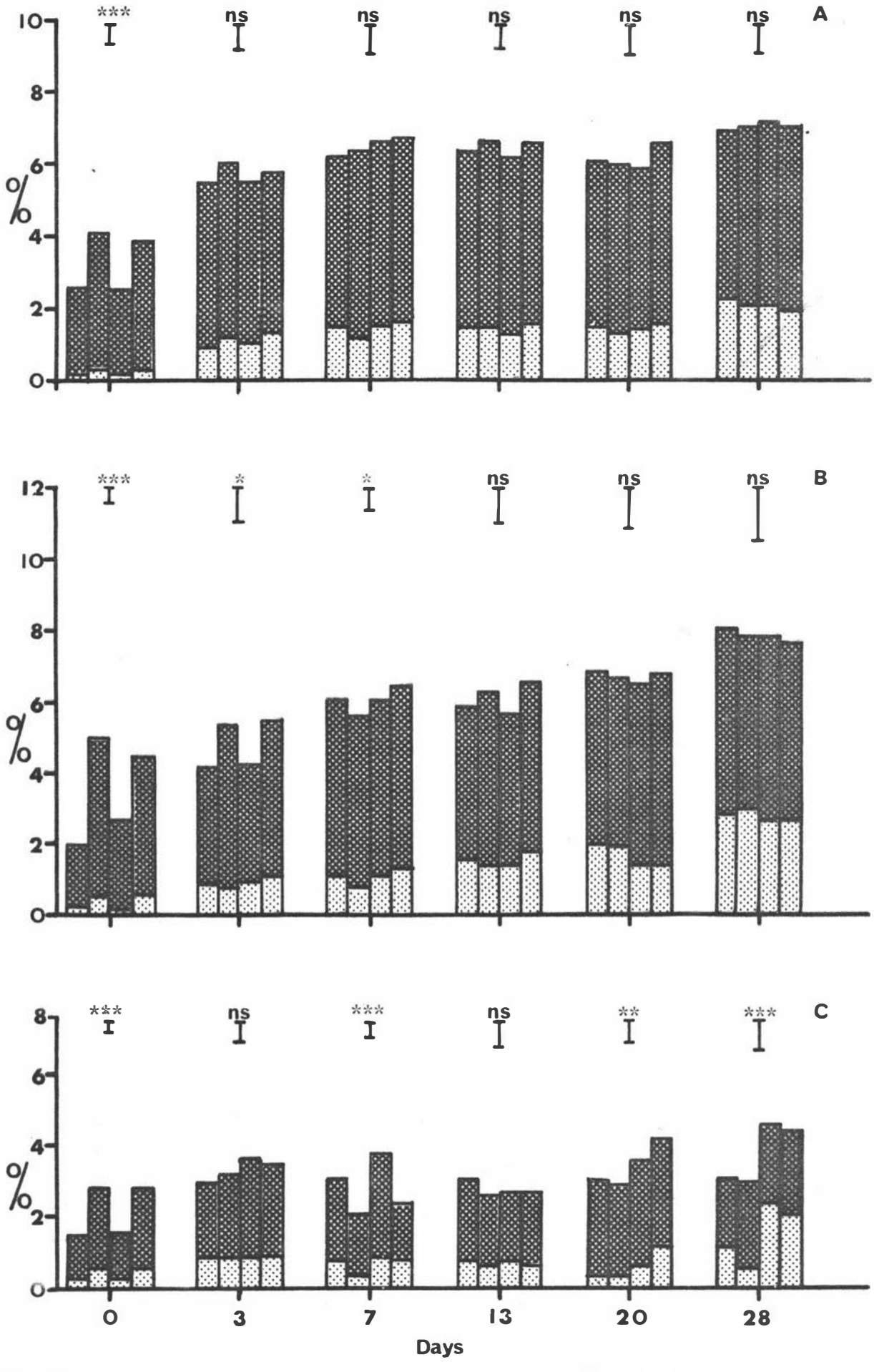


FIGURE 14 A,B,C: Nonstructural carbohydrate levels in stubble shoots, rhizome shoots and stubble.

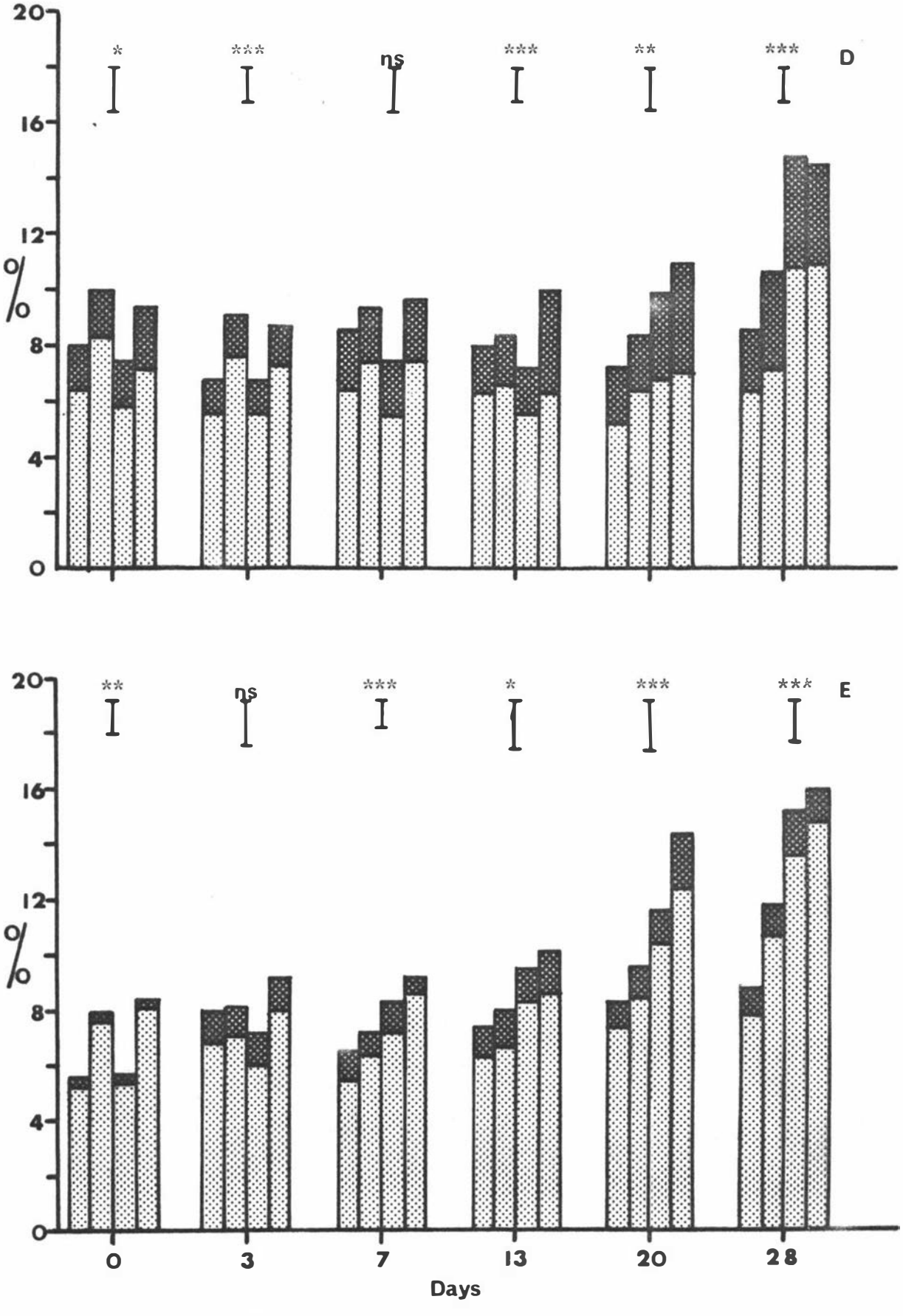


FIGURE 14 D, E: Nonstructural carbohydrate levels in rhizome and crown plus taproot

On all sample dates there was evidence of reduced crown plus taproot starch and TNC levels in treatments that were initially pretreated in the dark. Subsequent to day 3, cutting height affects were further superimposed. Increasing starch and TNC levels became most evident after day 13 and these increases were most marked where 5.0 cm cutting and/or higher TNC were the initial treatments. TNC patterns and levels were somewhat similar in both underground components, although TNC in the crown plus taproot tissue consisted of a greater starch fraction.

6.4 Discussion

In terms of absolute growth rates and net regrowth, treatment responses in this experiment were most evident where cutting heights differed. As in the field experiments (see Chapter 4.3), shoot growth rates and net shoot production were greater where higher cutting occurred. However, these production responses were not related to the presence of shoots or shoot pools with higher RGR potentials. Shoot RGR appeared to be inversely related to their weights, thus even with greater residual leaf areas, shoot RGR were lower in higher cut plants. Consequently, the regrowth advantage of higher cutting was to increase the weight of the residual shoot pools from which regrowth commenced. This highlights the importance of residual shoot size and number in determining regrowth potential, a relationship which has also been reported in lucerne by Leach (1968, 1969, 1970) and Hodgkinson (1973).

In this experiment, as in field Experiment 2 (see Chapter 4.3.2), improved regrowth was apparent where individual, residual shoots were larger. In the latter experiment, responses to initially larger shoots were most evident in the stubble shoot pool where growth was prolonged and production enhanced with higher cutting. However, in this pot experiment both stubble and rhizome shoot pools responded equally to higher cutting in terms of absolute weights. It is likely that shoot dominance was not as great in Experiment 3, where spaced plants were grown in an artificial environment, and as such the relative benefits of higher cutting and larger residual shoots in the stubble shoot pool would not have been as marked as in the field.

The importance of residual shoot numbers in determining the size of the residual shoot pool, and hence early regrowth rates, was apparent in both the field and this pot experiment. However, one contrasting feature between these experiments was the increase in residual shoot numbers, particularly rhizome shoots, that occurred with higher cutting in Experiment 3,but not in the field experiments. Because only one pre-treatment cut was employed in the former experiment, it is unlikely that any morphological adaptation of the canopy could occur, in response to cutting height, as it did in the field experiments. However, increased residual shoot numbers recorded in this pot experiment did add another dimension to cutting height responses and again illustrated their importance in determining the size of the residual shoot population and subsequent regrowth, particularly in the rhizome shoot pool.

Regrowth characteristics of stubble and rhizome shoots, whether on an individual or collective basis, were quite different. Individual shoot RGR were initially higher in the stubble shoot pool and then values rapidly declined with time. In contrast, individual rhizome shoot RGR showed only a gradual decline with time and as a result higher values were recorded within this pool during the last two weeks of regrowth. When comparing both shoot pools on a collective basis, thereby involving shoot numbers, differences in RGR patterns were still evident, but less marked. The rapid decline in individual stubble shoot RGR was partially compensated by a more rapid increase in stubble shoot numbers as compared with the rhizome shoot pool. Nevertheless, RGR of the rhizome shoot pool were greater over the last two weeks of regrowth and as a result it was this component that eventually dominated aerial growth.

Similar patterns involving rapid early stubble shoot regrowth, followed by rhizome shoot dominance, were also recorded in field Experiments 1 and 2 (see Chapter 4.3). Furthermore, the lower RGR of rhizome shoots, and the slower increase in their number during early regrowth, again illustrate the delayed nature of regrowth in this shoot pool.

The increases in RGR between day 3 and 7, that were a feature of the rhizome shoot pool, can only be partly explained by individual shoot RGR. The lower RGR values recorded during the first three days of regrowth were also a reflection of low increases in rhizome shoot

number. This fact, combined with differences in RGR trends between the two shoot classes over the first seven days, suggests that shoot number, as a regrowth factor, is more restrictive and of greater importance in rhizome shoot regrowth.

The greater regrowth response to higher TNC status that was recorded when cutting was to 5.0 cm rather than 2.0 cm, must in part be explained by the relative size of the residual shoot pools. It is likely that the larger shoot pool generated with higher cutting was able to exploit more fully the RGR responses that occurred during the first few days of regrowth where TNC levels were initially higher.

Differences in shoot regrowth that were generated by different initial TNC levels were more evident within the rhizome shoot pool than the stubble shoot pool. With 2.0 cm cutting, any absolute regrowth advantage gained by the stubble shoot pool in higher TNC plants during the first three days, was subsequently lost as RGR values declined below those of low TNC plants. Due to individual shoot responses, greater rhizome shoot RGR were also recorded for higher TNC plants until the third day. However, unlike the stubble shoot pool, this early advantage was maintained and resulted in greater absolute shoot dry weights and growth rates for higher TNC plants.

At the 5.0 cm cutting height, greater stubble shoot weights and growth rates in higher TNC plants principally depended on the initial advantage gained by higher individual and collective shoot RGR during the first three days. Within the rhizome shoot class, individual and collective shoot RGR showed a response to TNC up until the day 7 harvest and as a result it was this component that was most responsive to TNC in terms of absolute weights and growth rates.

It is likely that the limited response of stubble shoots to initial TNC status is the result of a more favourable supply of current photosynthates to this shoot pool. By being located in the axil of stubble leaves they are in close proximity to an immediate source of carbohydrate following defoliation and this source, during the first week of regrowth, was a major component of the total leaf complement. In lucerne, Hodgkinson *et al.* (1972) reported that stubble shoots were a major recipient of exported stubble leaf photosynthates.

By being located higher within the canopy and by having a greater leaf complement, stubble shoots may also have a greater capacity to produce assimilates as compared with rhizome shoots. An earlier attainment of stable sugar levels within the stubble shoot pool following cutting would lend support to this proposal.

In contrast, the immediate supply of photosynthates to rhizome shoots is likely to be more restricted due to their basal location and poorer leaf complement. The positive response of rhizome shoot regrowth to higher initial TNC status may suggest a direct involvement of TNC accumulated in those organs from which rhizome shoots developed. However, if this is so, the amount of redistributed TNC is likely to be small as there was no indication of a depletion pattern in rhizome TNC levels. Furthermore, the delay in attaining comparable sugar levels in rhizome shoots, that differed in initial TNC status, would also suggest that the buffering capacity of accumulated underground TNC may be limited in terms of shoot regrowth.

In this experiment, differences in residual TNC were artificially created by dark pre-treatment. It was apparent that any direct effect these differences had on regrowth was confined to the first seven days. Thereafter, absolute weight and growth rate responses were related to the different amounts of shoot growth that had been generated during the initial stages of regrowth. Residual plant TNC was therefore a determining factor of shoot regrowth in this experiment, however whether this is so under normal field conditions is another matter. It should be noted that residual shoots which were not pre-treated in darkness had initially lower TNC levels than those at which they eventually stabilized. This probably reflects their previously shaded and dominated history. However, accumulation of sugar in these shoots (HL, HH) was such that by day 3 sugar levels were not significantly different from those at subsequent samplings. This would indicate that residual shoots were sufficiently strong enough 'sinks' to rectify initially low assimilate levels. Under field conditions where defoliation is incomplete, as in this experiment, it is unlikely that residual TNC is a major determinant of early regrowth.

The low TNC levels recorded in rhizome and crown plus taproot tissue on day 0 would be a reflection of the low and frequent cutting procedure used prior to the experimental regrowth period and of transferring the plants from an autumn to an artificial spring environment. Following the final cut there was no indication of net TNC utilization in these organs and this may in part be a function of the low absolute TNC levels involved. Nelson & Smith (1968b, 1969) and Greub & Wedin (1971b) reported that utilization and accumulation patterns were only evident within the taproot of *L. corniculatus* when TNC levels were high.

However, the absence of TNC utilization trends in this experiment may also be related to the fact that defoliation was not complete and considerable leaf remained within residual canopies, particularly in association with the stubble component. With such a residual leaf complement a greater proportion of respiratory demands would have been met by current photosynthesis, thereby reducing the need to utilize accumulated TNC. The non-expansive nature of, and the low levels of accumulated TNC in stubble tissue would indicate that the stubble component was not a highly active assimilate sink (Wareing & Patrick, 1975), yet a major proportion of total leaf area was associated with this same component during early regrowth. It is therefore likely, that stubble leaf was an important source of assimilates for early growth and respiration in other plant parts. Hodgkinson *et al* (1972) considered that stubble leaf photosynthesis in partially defoliated lucerne replaced the need for redistribution of organic compounds from the taproot to new shoot growth and respiration. Silva (1969) with lucerne, and Greub & Wedin (1971 a,b) with *L. corniculatus*, have also reported low net TNC utilization following incomplete defoliation.

Accumulation of TNC during the last two weeks of regrowth was principally confined to rhizome, crown and taproot tissue. The extent to which the starch fraction increased over this period was apparently related to absolute aerial growth as the increases were greatest in those plants that responded to higher initial TNC and/or cutting levels. Earlier and more rapid reaccumulation of TNC has also been reported by Alberda (1970) and Booysen & Nelson (1975) for plants that regrew and re-established leaf area more quickly following cutting.

In summary, it would appear that the nature of the residual shoot population is a principal determinant of 'Grasslands Maku' regrowth. In partially defoliated plants any direct influence that TNC may have on shoot regrowth appears minimal and confined to the first few days of regrowth.

CHAPTER 7: THE PARTITIONING OF C^{14} LABELLED ASSIMILATES IN DEFOLIATED *LOTUS PEDUNCULATUS* cv. 'GRASSLANDS MAKU'

7.1 Introduction

The partitioning of carbon compounds between various plant parts is the net result of the distribution of current, and the redistribution of previously fixed assimilates. The distribution of current photosynthates is principally determined by the relative activities of utilizing organs, thus the number, size, growth rate, age and physiological status of these sinks become important (Wardlaw, 1968; Milthorpe & Moorby, 1969). Redistribution of organic compounds is continual (Minchin & Pate, 1973) and it becomes more marked when current assimilate deficiencies occur. Following defoliation therefore, organic compounds may be remobilized for respiration processes and for the partial support of new leaf growth (Marshall & Sagar, 1968; Hodgkinson, 1969; Pearce *et al.*, 1969; Smith & Marten, 1970; Singh & Winch, 1974b; Ryle & Powell, 1975).

In current studies with *L. pedunculatus* cv. 'Grasslands Maku', greater shoot production and larger underground dry weights were recorded where higher cutting occurred (see Chapters 3-6). It was proposed that a principal factor in determining shoot production was the size of the residual shoot population that could commence immediate regrowth following defoliation. Shoot regrowth also responded to differing residual plant TNC levels (see Chapter 6.3.1), however there was no evidence to suggest that such responses were directly linked to the redistribution of organic compounds. Early regrowth in 'Grasslands Maku' is characteristically slow, yet it is during the first one to two weeks of regrowth that these treatment and production differences establish themselves. Whether these responses ultimately resulted from different assimilation rates or from different partitioning patterns could not be conclusively determined from these experiments.

This chapter reports on two experiments that were conducted to assess the pattern of assimilate partitioning during the early stages of regrowth in *L. pedunculatus* cv. 'Grasslands Maku'. The important sources and sinks of assimilates were identified and considered with regard to dry weight changes of above and below ground plant components

following cutting to two different heights. Current assimilate distribution was assessed by the fixation and subsequent location of C^{14} at three separate stages of regrowth (C^{14} Distribution experiment). Redistribution of organic compounds during the first 14 days of regrowth was estimated by determining activity levels in the various components of sequentially harvested plants that had assimilated and distributed C^{14} prior to cutting (C^{14} Redistribution experiment).

7.2 Experimental

On 6/9/76, inoculated seed (Rhizobium strain, CC814S) of 'Grasslands Maku' was sown into a sterilized Opiki silt loam, Manawatu sandy silt (1:1) soil mix to which the equivalent of 2 g, per 1.2 litre pot, of 30 percent potassic superphosphate had been added. Plants were grown under glasshouse conditions (25C maximum; 15C minimum) and were thinned to one per pot by 26/10/76. Until 13/12/76 aerial growth was cut to 2.0 cm every week. On this latter date, plants were selected and then separately grouped for either the C^{14} Redistribution or Distribution experiments. Within each experimental group, five blocks were formed and within each block, plants were randomly allocated to two cutting height treatments and to four and three sampling dates respectively. To encourage aerial growth in the central region of each pot, plastic mesh (1.7 mm gauge) was placed around the perimeter of individual pots and each mesh cylinder was raised or lowered in accordance with cutting and regrowth schedules. Plants continued to grow under glasshouse conditions and each week they were cut to a height of 2.0 or 7.0 cm according to their treatment allocation.

Plant material that was used in the C^{14} Redistribution experiment was transferred to a controlled climate room (See Appendix 11: Experiment 4.) on 31/1/77. Seven and eight days later, plants of three and two replicates respectively, were exposed to C^{14} O_2 and two days after exposure, all were cut to their appropriate 2.0 or 7.0 cm heights. Those ten plants allocated to regrowth day 0 were subsequently washed free of soil and dissected, as were further sets of plants on the third, seventh and fourteenth regrowth day.

Plants used in the C^{14} Distribution experiment were transferred to the same growth room on 14/2/77 and five days later were cut to their appropriate 2.0 or 7.0 cm heights. Two days after cutting, ten

plants were exposed to $C^{14}O_2$ and 24 hours later they were washed and dissected. Two further sets of ten plants were similarly treated on the sixth and thirteenth day of regrowth. A relative time scale summarizing the time sequence of both experiments is presented in Appendix 13A.

Radioactive $C^{14}O_2$ was generated in a sealed trap by reacting aqueous $Na_2C^{14}O_3$ with 2N H_2SO_2. Batches of 1.25 m Ci, $C^{14}O_2$ were separately produced and placed in a 25 ml air column from which 1 ml subsamples of the radioactive gaseous mix were subsequently taken. Adjustable mercury columns maintained atmospheric pressure within this air column and ensured consistent subsample volumes and activities. Single plants were sealed in glass chambers (14 litre volume; 3mm thick glass) that were located in the controlled climate room, and they were then exposed to $C^{14}O_2$ by injecting a 50μ Ci subsample through a neoprene seal. Throughout the 30 minute exposure period, the atmosphere in the chamber was mixed by a rotating fan located adjacent to the plant canopy. Temperatures within the chambers increased from 17C to approximately 23C during the exposure periods. Exposure of plants to $C^{14}O_2$ was confined to between 12.00 and 16.00 hours, a period that represented six to ten hours of previous growth room irradiance. Once exposure was completed, residual $C^{14}O_2$ remaining within the glass chamber was removed by pumping its gaseous contents through two aqueous NaOH traps via an outlet tube system.

On the appropriate regrowth day, those plants required for growth analysis were removed from the growth room at 13.00 hours and once washed free of soil, they were stored in darkness at 3 C until dissected. The dissected components were: stubble shoot, rhizome shoot, stubble, rhizome, crown plus taproot and fibrous root as defined in Chapter 3.2. Dissected material was stored at 3C until drying in a vacuum dry oven 2.0 mm Hg, 40C, 16 hr). Once dry weights were determined, all components were spearately ground to pass through a 0.5 mm sieve and then stored at -3C in sealed glass vials.

Besides those involved in the experimental treatments, two further plants were allocated to each sample day in order to estimate background

radioactivity within the controlled climate room. Other than not being exposed to $C^{14}O_2$ within a glass chamber, these plants were handled in a similar manner to that of the treatment plants, with one being cut down to 2.0 cm and the other to 7.0 cm at the beginning of the appropriate experimental period. At no harvest did total radioactivity levels within these check plants exceed 3 percent of the total within the corresponding treatment plants. Estimates of plant leaf area at each sample date, were also determined from these plants as described in Chapter 4.2.

A liquid combustion procedure, similar to that outlined by Shimshi (1969), was employed to release C^{14} from the ground experimental plant material. Approximately 50 mg of plant tissue was weighed into a 100 ml screw top glass jar into which a 15 ml glass vial containing 10 ml, 1N NaOH was also placed. To the larger, outer jar, 20 ml of cold saturated chromic acid ($K_2Cr_2O_7$ + 18N H_2SO_4) was then added and immediately, the combustion system was sealed with a rubber lined screw lid. Combustion proceeded for 3 hours at 105°C. Following a one hour cooling period, at room temperature, the inner NaOH trap was removed and its volume was again made up to 10 ml by the further addition of 1N NaOH. Combustion efficiency was estimated with each combustion run by including two standard radioactive tissue samples. In Appendix 13B, activity levels in a standard C^{14} tissue sample are presented for the outlined method and other tissue, chromic acid combinations.

A 0.5 ml subsample was taken from the NaOH-$Na_2C^{14}O_3$ trap and added to 10 ml of a liquid scintillation cocktail that consisted of a two to one toluene scintillation solution (0.5% P terphenyl -C_6H_5. C_6H_4. C_6H_5), Triton X-100 detergent mix, plus 10 percent distilled water (Patterson & Greene, 1965). Radioactive measurements were made in a Beckman L5350 liquid scintillation spectrometer with a gain setting of 490 and a window setting of 50 to 1,000. For each sample, counts were integrated over a 10 minute period giving mean counts per minute (c.p.m.) with standard errors that ranged from 1 to 3 percent. Previously determined blank activities were subtracted and individual sample c.p.m. values were then corrected by a quench factor, (65-73%) based on a standard C^{14} quench curve, to give disintegrations per minute (d.p.m.).

Data were statistically analysed as a randomized block design within each sample date and a pooled analysis was conducted across sample dates as described in Chapter 3.2.

7.3 Results

7.3.1 C^{14} Distribution Experiment

Component dry weights recorded on regrowth days 3, 7 and 14 are presented in Table 27 for the 2.0 cm (L) and 7.0 cm (H) cut treatments. Other than rhizome shoot initials, all component dry weights were significantly greater where higher cutting occurred. Dry weights in non-shoot components tended to be lower in those plants sampled on day 14 but generally, trends with time, were inconsistent. Estimated leaf areas for sampled plants, i.e. one day after $C^{14}O_2$ exposure, are presented in Appendix 14. All aerial growth was confined to within the plastic mesh aprons, thus LAI were determined on the basis of pot surface area. For this experiment, leaf areas were generally high and even for the low cut treatment, after only three days regrowth, a LAI of 1.1 was measured.

Specific activities of plant components sampled on regrowth days 3, 7 and 14, one day after exposure to $C^{14}O_2$, are presented in Table 28. On day 3 all component specific activities were lower in those plants where high cutting had previously occurred. At subsequent sample dates, relative treatment differences were smaller in all aerial components but were maintained in underground growth. High specific activities were recorded in stubble shoots and rhizome shoots, the former pool being consistently higher for all treatments and sample dates.

Absolute activity levels in underground organs were generally lower in treatment H, but for most situations the differences between high and low cutting were not statistically significant (Table 29). On an individual and collective basis, activity in underground components showed no consistent trend with time. The extent and duration of activity changes differed between aerial components during regrowth. Whereas values declined within the stubble, activity in both shoot pools increased as regrowth continued. Therefore, increases in total plant activity at successive labellings were related to the shoot components of aerial growth. Where higher cutting had previously occurred, greater leaf areas were present at the time of $C^{14}O_2$ exposure, however corresponding increases in total plant activity were not evident at any of the three sampling dates.

Table 27: Dry weights of plant components during regrowth in the C^{14} Distribution experiment (mg per plant)

	Regrowth Day		
	3	7	14
Stubble shoots			
L	193 (**,25)[A]	390	821 (***, 14)
H	402	754	1314
Rhizome shoots			
L	155 (*,26)	396 (***,40)	907 (*,86)
H	329	828	1445
Stubble			
L	2136 (***,49)	1836 (***,102)	1790 (***,61)
H	4568	4150	3959
Rhizome shoot initials			
L	76 (NS, 22)	101 (NS, 16)	41 (*,6)
H	140	104	74
Rhizome			
L	938 (**,55)	981 (NS, 85)	774 (*, 31)
H	1243	1065	906
Crown plus taproot			
L	632 (*,53)	657 (**,30)	467 (***,30)
H	966	1054	894
Fibrous root			
L	824 (*, 99)	792 (*,52)	854 (*,56)
H	1376	1187	1193

A: significance level, treatment mean SE.

Table 28: Specific activity of plant components in the C^{14} Distribution experiment (d.p.m. x 10^3 per mg dry weight)

	Regrowth Day		
	3	7	14
Stubble shoots			
L	13.9 (**, 1.2)	13.5 (**, 0.7)	8.6 (NS, 0.9)
H	6.3	8.2	6.5
Rhizome shoots			
L	11.4 (**, 1.0)	10.4 (* 0.8)	7.8 (NS, 0.7)
H	4.7	5.3	5.6
Stubble			
L	3.1 (**, 0.2)	2.4 (*,0.2)	1.2 (NS, 0.1)
H	1.2	1.4	0.9
Rhizome initials			
L	7.5 (NS, 1.1)	5.6 (NS, 0.6)	7.6 (*, 0.6)
H	4.5	4.6	3.5
Rhizome			
L	2.4 (**, 0.2)	1.7 (**, 0.1)	2.3 (NS, 0.3)
H	1.0	1.2	1.7
Crown plus taproot			
L	1.6 (**, 0.1)	1.1 (*, 0.1)	1.7 (NS, 0.2)
H	0.7	0.8	1.1
Fibrous root			
L	1.8 (**, 0.1)	1.8 (NS, 0.2)	2.9 (*, 0.2)
H	0.8	1.2	1.6

Table 25: Absolute activity components in the C^{14} Distribution experiment (d.p.m. x 10^6 per plant)

	Regrowth Days 3	7	14
Stubble shoots			
L	2.68	5.21	7.09
	(NS, 0.33)[A]	(NS, 0.31)	(NS, 0.78)
H	2.53	6.16	8.55
Rhizome shoots			
L	1.76	4.08	7.04
	(NS, 0.40)	(NS, 0.32)	(NS, 0.68)
H	1.54	4.36	8.20
Stubble			
L	6.69	4.46	2.05
	(NS, 0.70)	(NS, 0.51)	(*, 0.26)
H	5.57	5.78	3.41
Aerial components			
L	11.13	13.74	16.18
	(NS, 1.25)	(NS, 0.85)	(NS, 1.63)
H	9.64	16.30	20.17
	*, 2.54 [B]		
Rhizome shoot intials			
L	0.56	0.56	0.31
	(NS, 0.17)	(NS, 0.07)	(NS, 0.05)
H	0.63	0.47	0.26
Rhizome			
L	2.24	1.71	1.79
	(**, 0.11)	(NS, 0.14)	(NS, 0.28)
H	1.28	1.25	1.56
Crown plus taproot			
L	1.01	0.75	0.81
	(NS, 0.09)	(NS, 0.05)	(NS, 0.12)
H	0.70	0.81	1.01
Fibrous root			
L	1.45	1.39	2.41
	(NS, 0.17)	(NS, 0.11)	(NS, 0.20)
H	1.16	1.44	1.89
Underground components			
L	5.26	4.40	5.32
	(NS, 0.41)	(NS, 0.28)	(NS, 0.49)
H	3.77	3.97	4.72
	NS, 0.81		
Total plant			
L	16.39	18.14	21.50
	(NS, 1.56)	(NS, 1.05)	(NS, 2.06)
H	13.41	20.27	24.89
	*, 3.08		

( )[A] : significance level for between treatment comparisons, treatment mean SE.

| |[B] : significance level for between harvest comparisons of the component means, L.S.D. (5%)

In plants sampled on day 3, i.e. one day after exposure to $C^{14}O_2$, approximately 40 percent of total plant radioactivity was located within the stubble component (Table 30 and Figure 15). Proportional values for this component, and for the remaining components at the day 3 sample, were very similar for both cutting heights. At this stage of regrowth, slightly more than 30 percent of total plant activity had been translocated to underground organs, the majority of which was located in rhizome and fibrous root tissue. Within the shoot pools, a greater percentage of total activity was located in stubble shoots rather than rhizome shoots.

Table 30: Percentage distribution of total plant activity between components in the C^{14} Distribution experiment

	Regrowth Day		
	3	7	14
Stubble shoots			
L	16.0	28.8	32.7
	(NS, 1.0)	(NS, 0.6)	(NS, 1.2)
H	18.9	30.4	34.3
Rhizome shoots			
L	10.6	22.3	32.5
	(NS, 0.6)	(NS, 1.5)	(NS, 1.0)
H	11.5	21.5	33.0
Stubble			
L	41.6	24.7	9.6
	(NS, 1.5)	(NS, 1.6)	(**, 0.4)
H	41.5	28.5	13.7
Rhizome shoot initials			
L	3.3	3.0	1.3
	(NS, 1.1)	(NS, 0.3)	(NS, 0.3)
H	4.7	2.3	0.9
Rhizome			
L	14.0	9.4	8.3
	(*, 1.0)	(*, 0.6)	(NS, 0.8)
H	9.6	6.2	6.3
Crown plus taproot			
L	6.2	4.2	3.9
	(NS, 0.9)	(NS, 0.3)	(NS, 0.6)
H	5.2	4.0	4.0
Fibrous root			
L	8.8	7.6	11.7
	(NS, 0.4)	(NS, 0.3)	(**, 0.4)
H	8.6	7.1	7.7

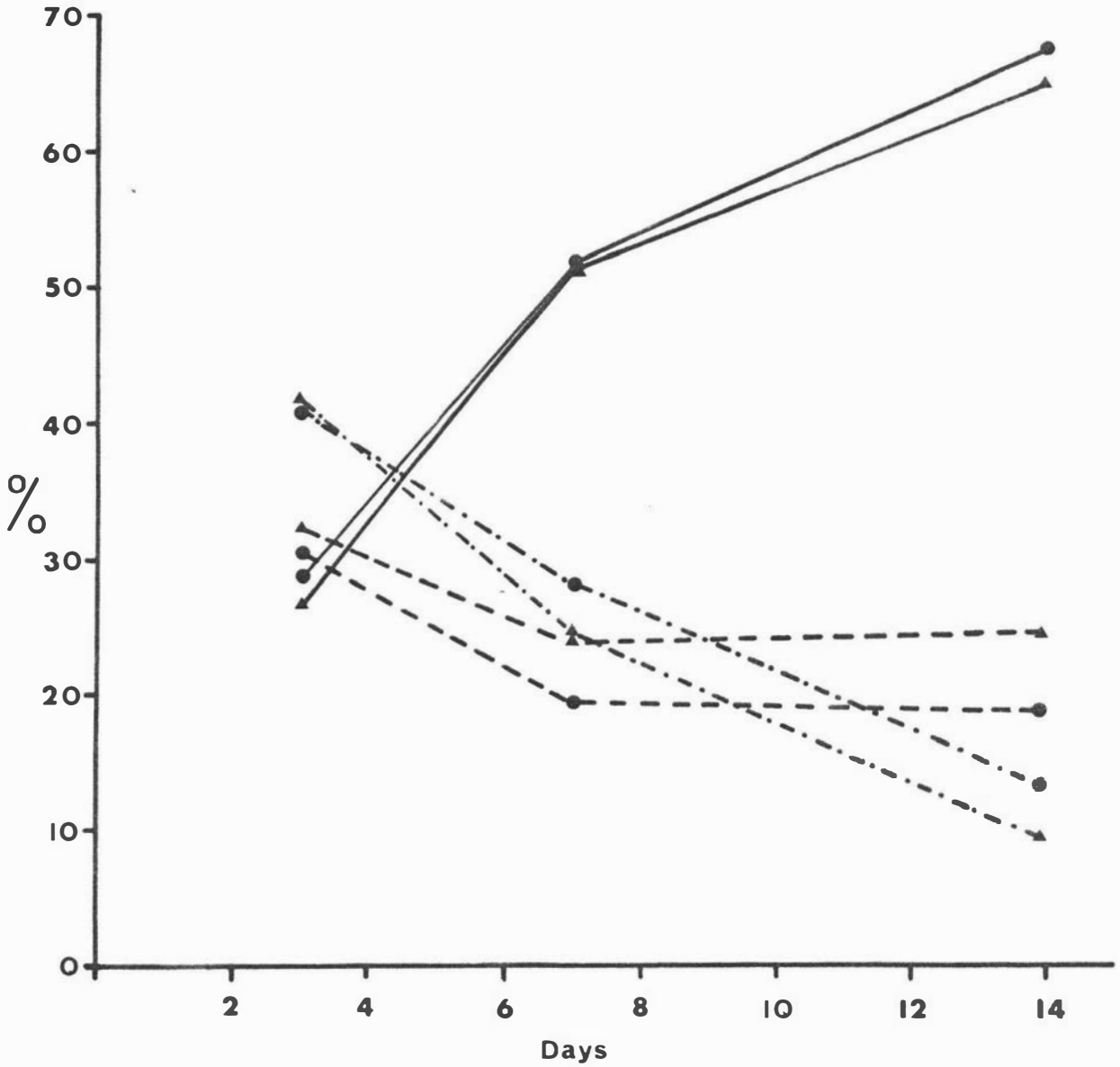


FIGURE 15: Percentage distribution of total plant activity in collective components of high (●) and low (▲) cut plants in the C^{14} Distribution experiment.

—— Total shoot growth
– – – Total underground
—·—·— Stubble

(A) - LSD (5%) for between harvest mean comparisons within each designated component.

At subsequent labellings, proportional values followed similar patterns for both treatments but they differed markedly between the various plant components. On days 7 and 14, slightly more than 50 and 65 percent of total plant activity was respectively located in total shoot growth. Within the stubble shoot pool proportional increases, with time, were less rapid than those of the rhizome shoot pool and as a result similar values were recorded for both pools of the day 14 sample plants. As regrowth continued the proportion of activity located in the stubble declined with successive labellings and only 10 to 15 percent was recorded for the last sample date. Between the first and second label-sample periods, proportional activity in individual and collective underground components also declined, although for the last period, values had stabilized.

7.3.2 C^{14} Redistribution Experiment

Two days after exposure to $C^{14}O_2$, all plants were cut down to either 2.0 (L) or 7.0 (H) cm and the residual and subsequent plant component dry weights that were recorded, are presented in Table 31. Of the aerial components, both stubble and stubble shoot dry weights were greater where higher cutting occurred, however it was not until day 14 that a significant treatment difference was evident within the rhizome shoot class. The long term effect of eight weeks differential cutting was evident in all underground components, and for all sampling dates, cutting height and dry weights were positively related. Within each non-shoot component, no consistent dry weight changes were recorded in either treatment during the fourteen day regrowth period. Similarly, rhizome and crown plus taproot TNC concentrations varied little with time, although higher values were recorded in the high cut plants (Appendix 15).

The generally lower specific activities of residual plant components in treatment H, must in part reflect a dilution of C^{14} throughout a larger plant system (Table 32). Specific activities were highest within the two shoot classes, although it was within these same rapidly growing components that the decline in specific activity, with time, was most rapid. Nevertheless, even within the less expansive components, declining specific activities were also recorded.

Table 31: Dry weights of plant components during regrowth in the C^{14} Redistribution experiment (mg per plant)

	Regrowth			
	0	3	7	14
Stubble shoots				
L	66	118	230	685
	(**, 18)	(**, 21)	(**, 34)	(*, 66)
H	217	293	500	1031
Rhizome shoots				
L	58	170	343	815
	(NS, 8)	(NS, 31)	(NS, 30)	(*, 51)
H	77	243	455	1083
Stubble				
L	1584	1823	1704	1654
	(***,72)	(***, 102)	(***,87)	(***, 64.8)
H	3600	3891	3648	3735
Rhizome shoot initials				
L	56	45	55	105
	(NS, 12)	(***,6)	(*, 14)	(NS, 18)
H	65	95	138	113
Rhizome				
L	643	832	842	763
	(*, 53)	(*, 65)	(NS, 70)	(NS, 56)
H	983	1184	1088	912
Crown plus taproot				
L	393	473	518	465
	(*, 44)	(*, 57)	(***, 14)	(***, 26)
H	816	837	867	774
Fibrous root				
L	801	895	904	975
	(*, 67)	(**, 30)	(NS, 85)	(*, 51)
H	1050	1104	1086	1201

Table 32: Specific activity of plant components in the C^{14} Redistribution experiment (d.p.m. x 10^6 per mg dry weight)

	Regrowth Day			
	0	3	7	14
Stubble shoots				
L	5.8	3.0	1.4	0.4
	(NS, 0.6)	(*, 0.2)	(NS, 0.2)	(NS, 0.1)
H	3.5	2.0	1.4	0.5
Rhizome shoots				
L	7.9	3.6	1.7	0.6
	(*, 0.8)	(*, 0.2)	(NS, 0.2)	(NS, 0.1)
H	3.1	2.6	1.5	0.6
Stubble				
L	2.0	1.1	1.0	0.5
	(*, 0.2)	(**, 0.04)	(**, 0.1)	(0.06)
H	0.9	0.7	0.6	0.4
Rhizome shoot initials				
L	6.7	4.0	2.3	1.3
	(*, 1.4)	(NS, 0.5)	(NS, 0.5)	(NS, 0.1)
H	2.9	2.9	1.6	0.9
Rhizome				
L	2.3	1.7	1.4	1.1
	(NS, 0.3)	(NS, 0.2)	(*, 0.1)	(*, 0.1)
H	1.5	1.3	1.0	0.7
Crown plus taproot				
L	2.0	0.9	0.8	0.7
	(*, 0.3)	(NS, 0.1)	(*,0.04)	(NS, 0.05)
H	0.8	0.7	0.6	0.5
Fibrous root				
L	3.1	1.7	1.4	1.0
	(*, 0.2)	(NS, 0.1)	(*, 0.07)	(NS, 0.08)
H	1.7	1.4	1.0	0.7

Immediately following cutting, residual C^{14} levels were highest in the stubble, a component that would have principally consisted of the residue of those shoots that were previously exposed to $C^{14}O_2$, but subsequently defoliated (Table 33). Total underground activity was greater than that of any other collective pool on day 0 and this relative ranking was maintained throughout the fourteen day regrowth period. Activity levels in stubble and all underground components were progressively lower at successive sample dates. Underground dry weights responded positively to cutting height, but consistently higher activities were not evident in treatment H for these organs. For both shoot classes, low residual activity levels were recorded, however during subsequent regrowth, activity patterns differed. Whereas activity within the stubble shoot pool declined with time, levels within the rhizome shoot pool increased between day 0 and 3 and then declined gradually or remained stable.

As total plant activity declined, there was little variation in the proportion of total plant C^{14} recorded within individual or composite underground components (Table 34 and Figure 16). At all four sample dates, approximately 55 percent of total plant activity in treatment L was recorded in underground growth and only on day 3, did values notably vary from approximately 45 percent in treatment H. Rhizome and fibrous root growth dominated underground activity with rhizome shoot initials and the crown plus taproot being only minor components. In both treatments, the percentage of total plant activity located in the stubble declined with time and this decrease was more marked where 2.0 cm cutting occurred. Higher proportional values were recorded in the stubble and stubble shoot pools with 7.0 cm cutting, a response that reflected the greater weight of both components. The percentage of total activity located in total shoot growth increased at successive harvests and as values remained relatively constant within the stubble shoot class, these increases were principally related to the rhizome shoot pool, particularly for treatment H.

Activity levels recorded on regrowth day 3, 7 and 14, expressed as a percentage of those originally recorded on day 0 are presented in Table 35. Although not statistically significant, total plant percentage values were consistently lower throughout the fourteen day regrowth period where low cutting occurred. For both treatments, approximately half of the original total plant activity was lost during

Table 33: Absolute activity of plant components in the C^{14} Redistribution experiment (d.p.m. x 10^6 per plant).

	Regrowth Day			
	0	3	7	14
Stubble shoots				
L	0.39	0.36	0.32	0.28
	(*, 0.08)	(*, 0.04)	(NS, 0.09)	(NS, 0.07)
H	0.76	0.57	0.68	0.50
Rhizome shoots				
L	0.46	0.62	0.58	0.47
	(NS, 0.06)	(NS, 0.06)	(NS, 0.08)	(NS, 0.10)
H	0.23	0.60	0.66	0.65
Total shoots				
L	0.85	0.97	0.90	0.74
	NS, 0.13)	(NS, 0.08)	(NS, 0.17)	(NS, 0.16)
H	0.99	1.17	1.35	1.15
		NS, 0.25		
Stubble				
L	3.24	1.97	1.71	0.83
	(NS, 0.24)	(NS, 0.17)	(NS, 0.19)	(*, 0.14)
H	3.34	2.61	2.28	1.43
		*, 0.47		
Rhizome shoot initials				
L	0.37	0.18	0.14	0.13
	(NS, 0.09)	(NS, 0.04)	(NS, 0.03)	(NS, 0.01)
H	0.19	0.28	0.23	0.09
Rhizome				
L	1.50	1.42	1.23	0.78
	(NS, 0.07)	(NS, 0.17)	(NS, 0.08)	(NS, 0.03)
H	1.50	1.60	1.05	0.65
Crown plus taproot				
L	0.77	0.45	0.43	0.31
	(NS, 0.06)	(NS, 0.12)	(NS, 0.03)	(*, 0.02)
H	0.64	0.57	0.52	0.38
Fibrous root				
L	2.44	1.51	1.21	0.95
	(NS, 0.25)	(NS, 0.10)	(NS, 0.06)	(NS, 0.10)
H	1.82	1.53	1.03	0.87
Total underground				
L	5.08	3.56	3.00	2.17
	(NS, 0.37)	(NS, 0.26)	(NS, 0.14)	(NS, 0.12)
H	4.15	3.98	2.84	2.00
		*, 0.40		

Table 34: Percentage distribution of total plant activity between components in the C^{14} Redistribution experiment

	Regrowth Day			
	0	3	7	14
Stubble shoots				
L	4.0	5.4	5.8	7.3
	(*, 0.9)	(*, 0.4)	(*, 1.2)	(NS, 1.1)
H	9.0	7.3	10.4	10.8
Rhizome shoots				
L	4.8	9.5	10.3	12.2
	(*, 0.4)	(NS, 0.6)	(NS, 0.9)	(NS, 1.2)
H	2.7	7.7	10.3	14.1
Stubble				
L	34.3	30.5	29.9	22.2
	(NS, 2.1)	(NS, 2.1)	(NS, 2.5)	(**, 1.2)
H	39.4	33.6	35.4	30.9
Rhizome shoot initials				
L	4.0	2.8	2.3	3.5
	(NS, 0.7)	(NS, 0.5)	(NS, 0.3)	(NS, 0.5)
H	2.2	3.6	3.4	2.2
Rhizome				
L	16.7	22.0	21.9	21.7
	(NS, 0.9)	(NS, 1.6)	(*, 1.0)	(*, 1.4)
H	17.7	20.6	16.4	14.5
Crown plus taproot				
L	8.3	6.8	7.6	8.2
	(NS, 0.6)	(NS, 1.4)	(NS, 0.4)	(NS, 0.77)
H	7.5	7.3	8.0	8.4
Fibrous root				
L	27.8	22.9	22.3	25.0
	(NS, 2.7)	(NS, 1.9)	(NS, 1.8)	(**, 0.8)
H	21.5	19.7	16.0	19.1

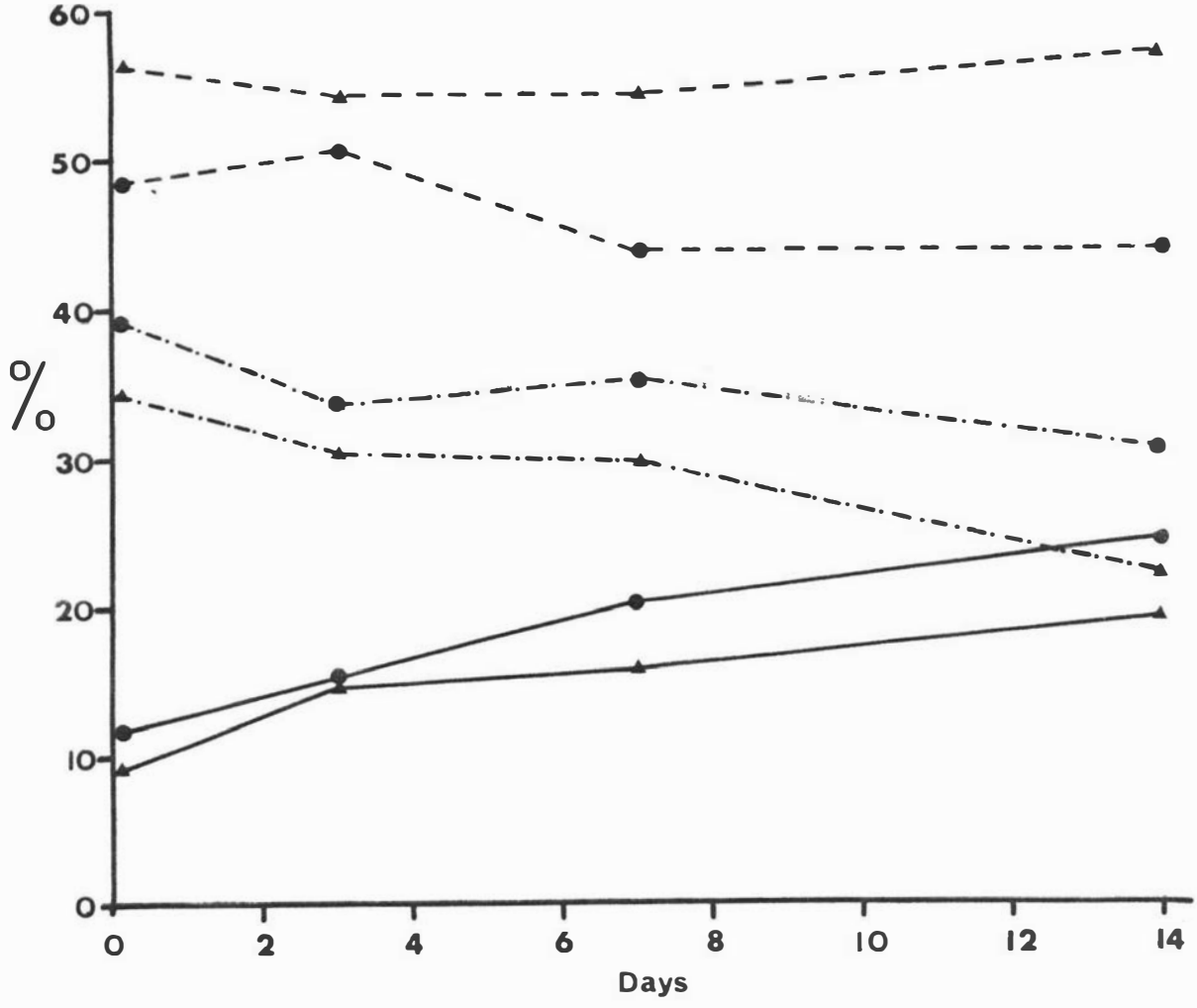


FIGURE 16: Percentage distribution of total plant activity in collective components of high (●) and low (▲) cut plants in the C^{14} Redistribution experiment

		A
——	Total shoot	*
- - -	Total underground	ns
-·-·-	Stubble	*

(A)-LSD (5%) for between harvest mean comparisons within each designated component.

Table 35: Activity levels of plant components, as a percentage of their original activity on day 0, in the C^{14} Redistribution experiment.

	Regrowth Day		
	3	7	14
Stubble shoots			
L	95.3	82.1	74.3
	(NS, 10.6)	(NS, 12.8)	(NS, 9.7)
H	76.0	88.9	66.3
Rhizome shoots			
L	135.8	128.1	103.3
	(*, 23.0)	(*, 19.8)	(*, 23.1)
H	261.8	288.4	281.4
Stubble			
L	63.8	54.2	24.7
	(NS, 7.7)	(NS, 6.2)	(NS, 5.9)
H	79.3	69.0	41.9
Rhizome shoot initials			
L	49.2	36.7	34.9
	(NS, 43.2)	(NS, 30.1)	(NS, 13.8)
H	149.5	125.7	49.1
Rhizome			
L	95.3	83.5	50.9
	(NS, 16.3)	(NS, 4.7)	(NS, 5.2)
H	104.2	73.0	43.2
Crown plus taproot			
L	59.4	54.8	40.1
	(NS, 17.3)	(NS, 14.9)	(NS, 11.2)
H	88.7	80.2	58.4
Fibrous root			
L	61.3	50.1	37.8
	(NS, 13.5)	(NS, 8.0)	(NS, 6.0)
H	85.1	58.6	48.2
Total plant			
L	72.9	62.4	42.1
	(NS, 7.4)	(NS, 4.3)	(NS, 5.2)
H	90.5	77.2	53.1

the experimental period. The relative patterns of net activity changes differed markedly between the various plant components. Of those located underground, activity losses were eventually of a similar relative magnitude, although they were initially more rapid within crown plus taproot and fibrous root tissue. Data associated with rhizome shoot initials were highly variable and may have reflected their transformation to aerially growing rhizome shoots.

The greatest decline in C^{14}, relative to day 0, was recorded within the stubble component and this was particularly so for treatment L where, at the end of the experimental period, only 24.7 percent of the original activity remained. Combining the two treatments, losses in the stubble shoot class accounted for only 30 percent of their original activity, and within the rhizome shoot pool net activity gains were made. The larger, relative increases that were recorded in rhizome shoots of treatment H may in part reflect the low dry weights and total activities of this pool on day 0. However, the stable nature of activity in this component differed markedly from that of the other components. In treatment L, increases in rhizome shoot activity losses were less rapid than those of the stubble and underground components.

7.4 Discussion

7.4.1 C^{14} Distribution Experiment

Irrespective of size and photosynthetic capacity, each plant in the C^{14} Distribution Experiment was exposed to 50μ Ci, $C^{14}O_2$. Consequently, absolute levels of photosynthetically assimilated C^{14} did not indicate the true photosynthetic activity of the treatment plants. Furthermore, it is likely that during each exposure within the sealed glass chambers, CO_2 levels quickly became a limiting factor in photosynthesis. As a result, plants with a greater leaf canopy would not have been able to fully exploit their photosynthetic potential. This was most obvious at each exposure-sample period where total plant activities did not differ significantly between the two cutting height treatments. The fact that total activity increased at successive labellings in this experiment does indicate however, that as new shoots grew and dominated

older stubble tissue, a more efficient photosynthetic canopy developed. It is unlikely that the C^{14} distribution patterns, recorded in plants 24 hours after C^{14} assimilation, would have been greatly influenced by these experimental short-comings, as they would have occurred for only a short period within the 14 hour day photoperiod under which the plants were grown.

Translocation of C^{14} from assimilating organs is generally rapid over the first 1 to 2 hours following fixation and then it continues at a slower rate (Hodgkinson & Veale, 1966; Hofstra & Nelson, 1969). Therefore, it is obvious that C^{14} distribution patterns will vary as the time from exposure to sampling changes. A 24 hour delay was selected for use in the C^{14} Distribution experiment reported in this chapter, as it was considered that such a period enabled the incorporation of C^{14} into structural tissue, and the translocation of C^{14} to other components, to be virtually completed.

Activity levels recorded in aerial components, 24 hours after $C^{14}O_2$ exposure, would have been the net result of assimilatory, respiratory, import and export processes. It is unlikely that the decline in C^{14} retained within the stubble at successive labelling times resulted from increased respiration or export to underground organs. More likely the decline reflects reduced rates of assimilation as shoot regrowth progressively shaded the more basal stubble component.

Where defoliation is incomplete and frequent, stubble leaf is a major component of residual plant leaf area in 'Grasslands Maku'. In Experiment 3, where environmental conditions were similar to those of this experiment, stubble leaf accounted for 88 percent and 65-70 percent of residual plant leaf area following 2.0 cm and 5.0 cm cutting, respectively (Table 25). During the early stages of regrowth in this C^{14} Distribution experiment, stubble leaf would appear to have been a major source of current photosynthates. Assimilate retention in young expanding shoots is high (Wolf, 1967; Pearce *et al.*, 1969), therefore most, if not all, of the underground activity recorded at day 3 sample of the C^{14} Distribution experiment would have originated from stubble rather than shoot assimilation. As activity levels present in underground organs on that day were similar to those for

subsequent labellings, it would appear that during early regrowth the stubble component was an equally satisfactory source of assimilates for underground organs as subsequent canopies comprising more new shoot growth. This may partly explain why there is little evidence of declining underground dry weights and nonstructural carbohydrates following incomplete defoliation in this experiment and in Experiment 3 (Chapter 6.3).

Approximately 40 percent of total plant activity still remained within the non-expanding stubble component of day 3 sample plants. High specific activities indicated that shoots were strong, active sinks and it is unlikely that retained stubble C^{14} would have been so high if more rapidly growing organs were deficient in assimilate. It would therefore appear that where stubble leaf is a major assimilate source, early shoot regrowth is not limited by assimilate supply. More likely it is the ability of the plant to use assimilates in regrowth that is the important, initial limitation. As regrowth continued, assimilate distribution was increasingly dominated by the two shoot pools. This would indicate that it is not until adequate shoot populations are established that current photosynthate supply may become a limiting regrowth factor.

It should be noted however, that in this experiment, where an artificial environment was employed, the apparent importance of stubble leaf assimilation may have been overestimated. Stubble leaf viability was obviously enhanced under the light regime and highly favourable growth room environment to which they were exposed. In lucerne, Langer & Keoghan (1970) also reported that the abundance and longevity of basal leaves tended to be greater in spaced plants, especially in controlled environments.

Prior to Day 0 of the C^{14} Distribution experiment, plants were cut to two different heights on a weekly basis and as a result greater underground dry weights occurred where higher cutting was employed. During the fourteen day regrowth period in this experiment there was no evidence that suggested a greater proportion of assimilated carbon was partitioned to underground organs where 7.0 rather than 2.0 cm cutting occurred. Therefore, it would seem that the larger underground weights recorded in this experiment with high cutting, principally

reflected greater absolute assimilation rates. Nevertheless, it is possible that the proportional distribution of assimilates to underground components may have increased, as shoot growth rates declined, if the experimental period had been extended. In Experiment 3, where environmental conditions were similar to this experiment, an increasing emphasis in the partitioning of assimilates to underground organs, as indicated by the accumulation of TNC, did not occur until the third and fourth week of regrowth (Chapter 6.3.4.)

Of the plant components analysed in this experiment it was fibrous root growth that was the most atypical and this probably reflected pot conditions where adequate moisture, low soil compaction and minimal top to root temperature differentials occurred. The relatively large dry weights recorded for this component probably indicate a greater level of assimilate utilization by fibrous root growth in these experiments than would normally be expected in field conditions.

7.4.2 C^{14} Redistribution Experiment

Initial total and proportional activity levels recorded on day 0 of the C^{14} Redistribution experiment reflect the experimental procedures employed. As in the C^{14} Distribution experiment, the greater leaf canopies of high cut plants were unable to fully exploit their photosynthetic potential and as a result, similar underground activities were recorded for the two treatments. In fact, proportional underground activity levels were lower where high cutting occurred, as greater levels of residual acitivity were left within the aerial components. Nevertheless, activity changes between and within components, following day 0 cutting, indicated C^{14} redistribution patterns that resulted from respiratory, import and export processes.

The decline in total plant activity measured during the fourteen day regrowth period of the C^{14} Redistribution experiment would have principally resulted from respiratory losses. This decline was greater within the low cut treatment, indicating that a greater use of previously assimilated carbon was made by those plants. In either treatment however, this usage was not at the net expense of previously accumulated underground nonstructural carbohydrates.

As total plant activity declined with time, only the stubble showed a consistent decline in the proportional distribution of total plant activity between the various components. This decrease may have resulted from the net export of C^{14} and/or from relatively greater respiratory losses, although the latter is less likely due to the non-expansive nature of the stubble component. Export of labelled organic compounds to stubble shoots was probable and may in part explain the slower decline in total activity recorded for this shoot pool. However, redistribution of C^{14} from stubble to underground organs may also have occurred. During the first three days, when the decline in stubble activity was most rapid, there was little change in rhizome activity levels. Of the underground organs, this latter component would have been the most closely linked with the stubble pool, and its initial activity pattern contrasts with those of the remaining underground components.

The constant proportion of total activity recorded in the underground components during regrowth, indicated that C^{14} losses followed a similar pattern to that of the total plant. This might suggest that respiration accounted for much of the losses. There was no evidence of a large net export of organic compounds from underground organs and this may have resulted from minimal redistribution and/or simultaneous importing from the stubble. Certainly, large exports of organic compounds from underground tissue, as reported for more completely defoliated lucerne (Hodgkinson, 1969; Pearce *et al.*, 1969; Smith & Marten, 1970), were not evident in this experiment with 'Grasslands Maku'. Again residual leaf canopies appeared to produce sufficient assimilate to satisfy respiratory and growth demands.

Activity increases within the rhizome shoot pool during the first three days of regrowth did indicate the entry of labelled organic compounds into this component. This increase may have involved the importation of C^{14} labelled compounds from the rhizome pool and/or the transformation of previously labelled rhizome shoot initials into aerially growing rhizome shoots during early regrowth. These initial increases were most marked for the high cut treatment and probably reflected the small residual rhizome shoot population that resulted from defoliation of a previously rapid, regrowth cycle. The limited decline in rhizome shoot activity was in contrast with the remaining

components and may have resulted from the continuing entry of C^{14} into this pool and/or the previous incorporation of C^{14} into more stable structural tissue. It was evident from the redistribution patterns that rhizome shoots, rather than stubble shoots, were more involved in the importation of previously assimilated carbon. In Experiment 3 (see Chapter 6.3.1) regrowth rates also indicated that the rhizome shoot pool was more responsive to residual plant TNC levels.

In summary, it would appear that where defoliation of 'Grasslands Maku' is incomplete, residual stubble is initially a major potential source of previously and currently assimilated carbon. Importation of accumulated organic compounds appears most likely to occur in the rhizome shoot pool, although the total amount of carbon would be minimal to that involved in respiratory losses. The continual loss of previously assimilated carbon indicates the continual turnover of organic compounds. During the early stages of regrowth, shoots increasingly dominate the distribution of current photosynthates and it would seem that following partial defoliation, it is the ability to utilize assimilates rather than produce them, that limits regrowth. Cutting height responses, in terms of underground dry weights, were not related to different partitioning patterns, therefore it is likely that such differences were related to the absolute supply of assimilates as determined by the photosynthetic capacities of the aerial canopies.

CHAPTER 8: GENERAL DISCUSSION

In determining the response of 'Grasslands Maku' to defoliation, the series of experiments reported in this thesis considered plant morphology, canopy dry matter production, nonstructural carbohydrates, residual plant factors as determinants of early regrowth and assimilate partitioning following defoliation.

Under field conditions, regrowth rates in defoliated 'Grasslands Maku', at times, exceeded 100 kg DM/ha/day, yet recovery was consistently characterized by slow regrowth during the first two to three weeks after defoliation. When grown as a pure sward, or where competition from companion species is low, this slow phase will lead to reduced canopy production but it is unlikely to be critical in relation to the persistence of the lotus component. In contrast however, where rapidly growing companions can express their growth potential, the failure of 'Grasslands Maku' to rapidly regrow following defoliation is likely to result in its poor persistence and production, similar to that reported by Sheath *et al*. (1976) and Brock & Charlton (1977).

As in many legumes such as *M. sativa* (Leach, 1967), *L. corniculatus* (Smith & Nelson, 1967), *C. varia* (Brann & Jung, 1974) and *M. atropurpureus* (Jones, 1974b), actively growing apices in 'Grasslands Maku' were readily removed during defoliation and as such, initial regrowth was highly dependent on the nature of the residual shoot population. Where defoliation was severe and residual shoot numbers were low, mean regrowth rates for the first three weeks following defoliation rarely exceeded 90-100 kg DM/ha/wk. The size and the number of shoots available for, and eventually participating in early regrowth, were important residual plant factors in this context.

Early regrowth and shoot production were enhanced where the growth of the stubble shoot pool was encouraged (Chapter 4.3.2). The presence of this shoot pool increased the number of shoots participating in early regrowth and this in turn led to these regrowth improvements. However, this pool was more superficial than the rhizome shoot pool and negative stubble shoot growth rates were recorded towards the end of some regrowth cycles. Furthermore, stubble shoot growth was encouraged by frequent and/or lax defoliation which respectively, limited production and increased within-canopy dry matter losses.

Delays in the formation of adequate shoot populations were most evident in the rhizome shoot pool and this was critical in regrowth for it was this same shoot pool that eventually provided the bulk of shoot growth (see Figure 5). Possible reasons for this delay have been outlined in previous discussion sections, but they principally involve the initiation and location of rhizome shoot initials. At no time during these studies was there any evidence of a distinct flush of leafy shoots developing in the basal region of the canopy, yet it is such a flush, if it coincided with defoliation, that could provide a basal shoot population able to commence immediate regrowth. Where residual canopies contained a large number of actively growing shoots, early regrowth rates increased two to three fold and ranged between 200-300 kg DM/ha/wk.

The coincidence of defoliation with basal shoot flushes is the key to maximizing lucerne production (Keoghan, 1967) and the development of such an association in *L. corniculatus* was considered by Keoghan & Tassel (1974) to be a major step in the possible improvement of that species' production potential. Similarly in *L. pedunculatus*, the development of plants that concentrate the release of shoots from basal sites would appear necessary if satisfactory early regrowth is to be achieved. However, such a plant would require special management, as in the case of lucerne, if its persistence and productivity was to be maintained. Whether this approach is feasible will depend on the characterization of growth habit and regrowth in other *L. pedunculatus* genotypes, in order to identify appropriate plant material.

In severely grazed mixed swards, diploid *L. pedunculatus* cultivars have performed better than 'Grasslands Maku' (Harris *et al.*, 1973; Lambert *et al.*, 1974). It is likely that this improved performance relates to the greater ability of these more prostrate plants to maintain larger residual rhizome shoot and stubble shoot populations that can commence immediate regrowth following defoliation. On the basis of persistence, and hence productivity, prostrate diploid material may well be more suited to severe and/or frequent grazing conditions where the production potential of 'Grasslands Maku' is unable to be expressed. However, this does mean that growth habit and potential productivity conflict (Armstrong, 1974).

Because of the need to re-establish a new, actively growing shoot population following defoliation, *L. pedunculatus* is at a distinct disadvantage relative to traditional pasture plants such as *L. perenne* or *T. repens* where actively growing meristems are not readily removed during grazing. This disadvantage would appear to be the key to the poor regrowth and competitive ability of *L. pedunculatus*. Unless the regrowth characteristics of *L. pedunculatus* , or pasture management, are radically changed,it would therefore seem unlikely that it will become an important legume component of grazed, mixed swards where the relative competitive ability of *L. pedunculatus* is not favoured by edaphic or climatic conditions.

Detailed growth analyses in Experiment 3 indicated that both shoot number and individual shoot weights were important in determining the size of the residual shoot pool following defoliation (Chapter 6.3.1). In the field, cutting frequency strongly influenced residual shoot numbers in 'Grasslands Maku' by determining the extent of canopy regrowth. Defoliation of large canopies resulted in low residual shoot populations, thus residual shoot numbers were least, and often absent, where severe, infrequent cutting occurred (Figure 6). With higher cutting, canopy development became more open and erect and rhizome shoot numbers decreased. Because of these morphological adaptations in the field, shoot numbers showed little response to different cutting heights.

Higher cutting did provide greater initial shoot weights and although RGR of the shoot pools were lower, absolute growth rates and net shoot production were increased (Chapter 6.3.1). In the field, production responses to lax defoliation were most obvious within the stubble shoot pool where initially larger shoots were able to maintain higher growth rates for a longer period during regrowth. It was principally through the encouragement of growth in this pool that total shoot production was improved by up to 2.0 - 3.0 t D.M./ha with laxer defoliation. However, it should also be noted that within-canopy dry matter losses, amounting to approximately 30 percent of total shoot production, occurred with high cutting and that these losses generally nullified any net canopy production benefits gained by increased shoot regrowth (Table 15). Nevertheless, where management practices provide larger residual shoots, it is apparent that shoot regrowth and hence, the competitive ability of 'Grasslands Maku', will be improved.

By extending regrowth intervals from three to six weeks in Experiment 1, and by reducing the number of cuts from six to four in Experiment 2, net canopy production in both situations was improved by at least 2.0 t DM/ha. The extent of these responses indicated that a deferred grazing system would be necessary if the potential performance of 'Grasslands Maku' is to be realized under grazing conditions. Furthermore, the very slow early regrowth, already mentioned, would also indicate the potential limitations of continuous or frequent grazing in terms of canopy dry matter production.

No benefit in dry matter production was achieved by prolonging regrowth past the stage where secondary axillary shoots were released and developed in the upper axils of dominant shoots within the canopy. Furthermore, long regrowth intervals also lead to large canopies and poor residual shoot populations if lenient defoliation can not be implemented. It would therefore seem that the most appropriate regrowth interval for 'Grasslands Maku' is that which enables the greatest expression of high shoot growth rates that occur in later regrowth, but still provides sufficient residual shoots that can commence rapid immediate regrowth.

Lax, rotational grazing would appear to be the most appropriate management that would provide the regrowth criteria necessary for the persistence and production of 'Grasslands Maku' in grazed swards and this may be best achieved with cattle rather than sheep. As in treatment SAL of Experiment 2 (see Chapter 4.3.2), such a management may maximize early regrowth, total shoot production and the competitive ability of the lotus component. However, it will also result in low utilization and high dry matter losses within the canopy.

Canopy structure and net production was an integrated function of different shoot regrowth patterns and within-canopy dry matter losses. Although increases in stubble shoot numbers and weights were often greater than for the rhizome shoot pool during early regrowth, it was the latter pool that increasingly dominated canopy growth as regrowth continued. This dominance resulted from the inability of stubble shoots to maintain RGR at a level similar to that of rhizome shoots (Figure 14). Thus, the dominance of the rhizome shoot pool

over stubble shoots was enhanced as regrowth intervals increased, although it was delayed when higher cutting produced residual stubble shoots of greater initial dry weights. Stubble death and subsequent decomposition resulted in dry matter losses within the canopy of up to 150 kg DM/ha/wk where low cutting occurred and up to 250 kg DM/ha/wk where high cutting was employed. Because of the extent of these losses, they were an important determinant of net canopy production patterns, particularly during early regrowth when stubble was a major component of canopy structure.

Where defoliation was severe and infrequent, residual leaf area was low, if not absent, and generally of a senescent nature (Figure 6). However, where defoliation was less complete; studies involving C^{14} partitioning and nonstructural carbohydrate determinations indicated that residual leaf can be a satisfactory source of assimilates for respiratory and growth demands during early regrowth. In such canopies, which were encouraged by lax and/or frequent defoliation, stubble leaf appeared to be an important early source of current and previously fixed assimilates. Where management practices ensure satisfactory residual shoot populations, then residual leaf area should also be high.

Following defoliation, previously fixed assimilates were redistributed to the rhizome shoot pool (Chapter 7.3.2) and it was this same shoot pool that also responded to residual nonstructural carbohydrate levels. However, there was never any evidence of large net nonstructural carbohydrate usage following incomplete defoliation and at no time did nonstructural carbohydrates have a greater influence on regrowth rates, than did the size of the residual shoot pools. While shoot populations were re-establishing following cutting, it appeared that assimilate utilization, rather than supply, was the more important limitation in regrowth.

Because of their apparent minimal involvement in shoot regrowth, accumulation of nonstructural carbohydrates may be considered as inefficient in terms of shoot production. However, stored starch would appear to be an important respiratory substrate for underground organs during winter and early spring and as such it plays an important part in maintaining a basis for shoot initiation and production. Concentrations of TNC appeared to be principally determined by seasonal factors with

underground values falling from late autumn peaks, of 25 to 30 percent, to late spring troughs, of 5 to 10 percent. In contrast, defoliation frequency, but more particularly severity, influenced the size of storage organs and this was most noticeable during the accumulating autumn period and within the rhizome system.

The underground crown and taproot of 'Grasslands Maku' acted as a central link between a network of underground and aerial stems. However, in comparison to the stem system that it linked, this region was of little significance as an initiator of new growth in established plants. Only during late summer/autumn did new stem growth arise from the crown and this generally continued in the form of rhizomes. Nevertheless, under stress conditions the relative importance of the crown as an initiator of new stem growth is likely to improve, as the primary crown plus taproot appears to be a less transitory component than its associated peripheral stem system. In previous work, the author has observed this to occur as a result of severe summer moisture stress or winter frosting and a similar situation is also possible where rhizome development is restricted by severe defoliation and/or competition.

In these studies, the dominant feature of underground growth was the expansive nature of the rhizome system and its importance as a region of shoot initiation. Rhizome expansion during late summer and autumn involved a large accumulation of dry matter, much of which was dissipated over the subsequent winter and spring as multicrown plants fragmented. At the end of this expansion period, total underground dry weights of up to 8.0 to 9.0 t/ha were estimated for some defoliation treatments and following the breakdown of multicrown plants, densities increased by 70 to 80 plants per m^2 in the more expansive treatments. This initial expansion and then vegetative propagation highlights the colonizing nature of *L. pedunculatus*. The ability to spread, combined with its dense superficial rooting habit (MacDonald, 1946), acid tolerance (Levy, 1970) and efficient phosphate uptake (Brock, 1973) must form the basis of the success of *L. pedunculatus* in the stablization of acid subsoils (Nordmeyer & Davis, 1976). Because of these same characteristics, *L. pedunculatus* can also be considered as a potential legume for colonizing inter-tussock areas of poorly

developed high country grasslands. Lowther (1976) has already highlighted the potential usefulness of 'Grasslands Maku' in such situations, although Scott *et al.* (1974) and Musgrave (1976) have reported its susceptibility to dry summer and freezing winter conditions.

Expansion of underground growth mainly occurred during late summer and autumn and was further encouraged during this period by less frequent and/or less severe defoliation. It would therefore seem that if they were required, improvements in rooting depth and in the spread of the rhizome system would be best achieved by limiting intensive defoliation over this period.

It is possible that by acting as a large competitive sink for assimilates, the expansion of underground organs may restrict aerial dry matter production and thereby impinge on the agricultural performance of the plant. In Experiment 1, net canopy production in autumn ranged from 500 to 900 kg DM/ha while underground dry weight increases over the same period were estimated to be as much as 3.0 to 4.0 t/ha for the more expansive treatments. Development of plant material less likely to promote rhizome growth, as is evident in the *Lotus corniculatus* x *Lotus pedunculatus* hybrid cv. 'Grasslands 4712', may reduce the competitiveness of underground growth. However, such a development would only be successful if the crown satisfactorily replaced the rhizome system as a shoot producing organ. This is unlikely, as crown activity in both *L. pedunculatus* and *L. corniculatus* (Smith, 1962; Nelson & Smith, 1968b) would appear to be low and seasonally determined. Even if the rhizome system in 'Grasslands Maku' is a competitive sink, it does at least provide a basis for shoot formation such that, unlike *L. corniculatus*, it does not solely depend on stubble shoots for the majority of its regrowth following defoliation.

In conclusion, it would appear that rapid, early regrowth of 'Grasslands Maku' is primarily dependent on the presence, within the residual canopy, of a shoot population that contains intact, actively expanding individuals. The retention of such a shoot population is best achieved by lax defoliation and by ensuring severe defoliation of large canopies does not occur. If the residual shoot population is unsatisfactory, early regrowth will be poor, and in grazed mixed

swards this is likely to lead to low persistence and production levels. Selection for rapid early regrowth, particularly with reference to the productive rhizome shoot pool, would appear to be essential in the development of a more appropriate *L. pedunculatus* plant for grazed situations.

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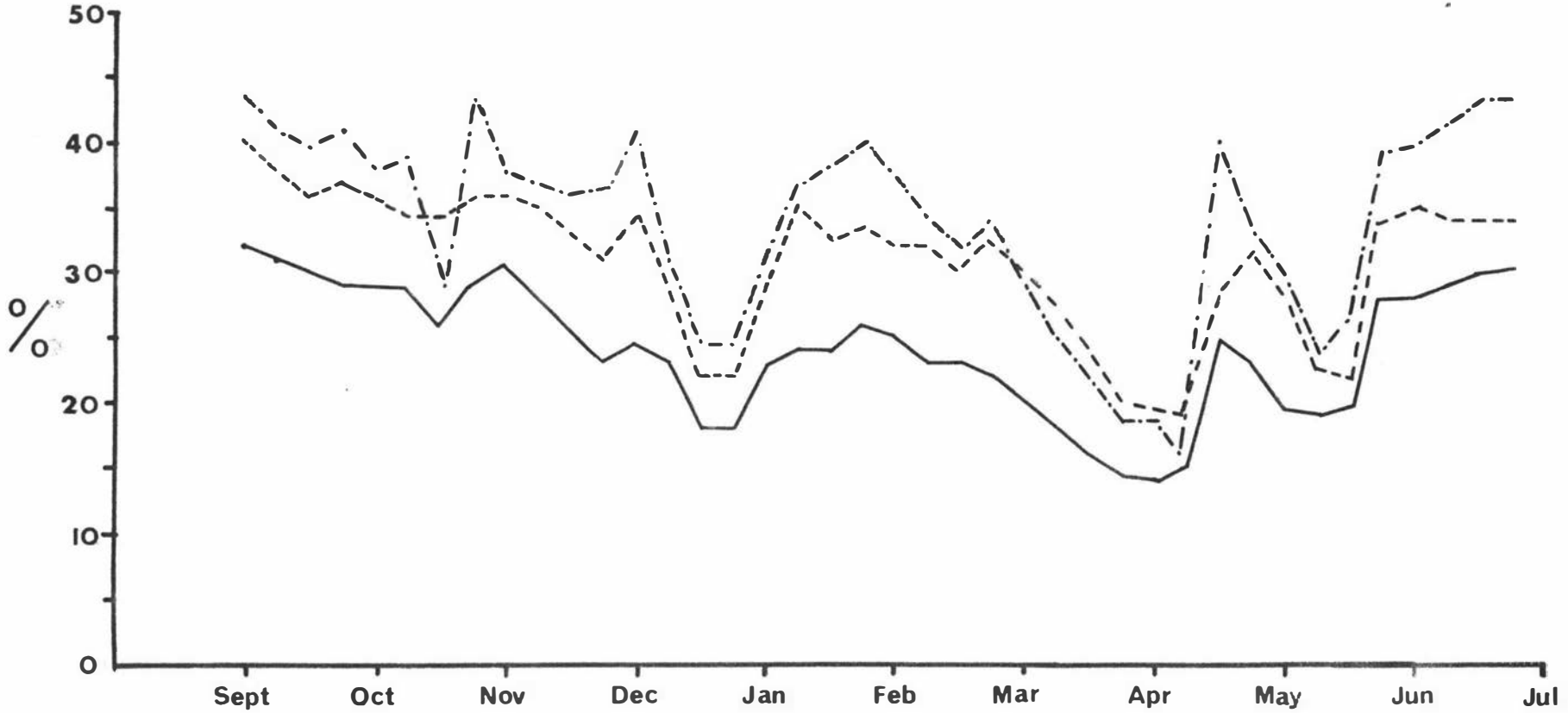
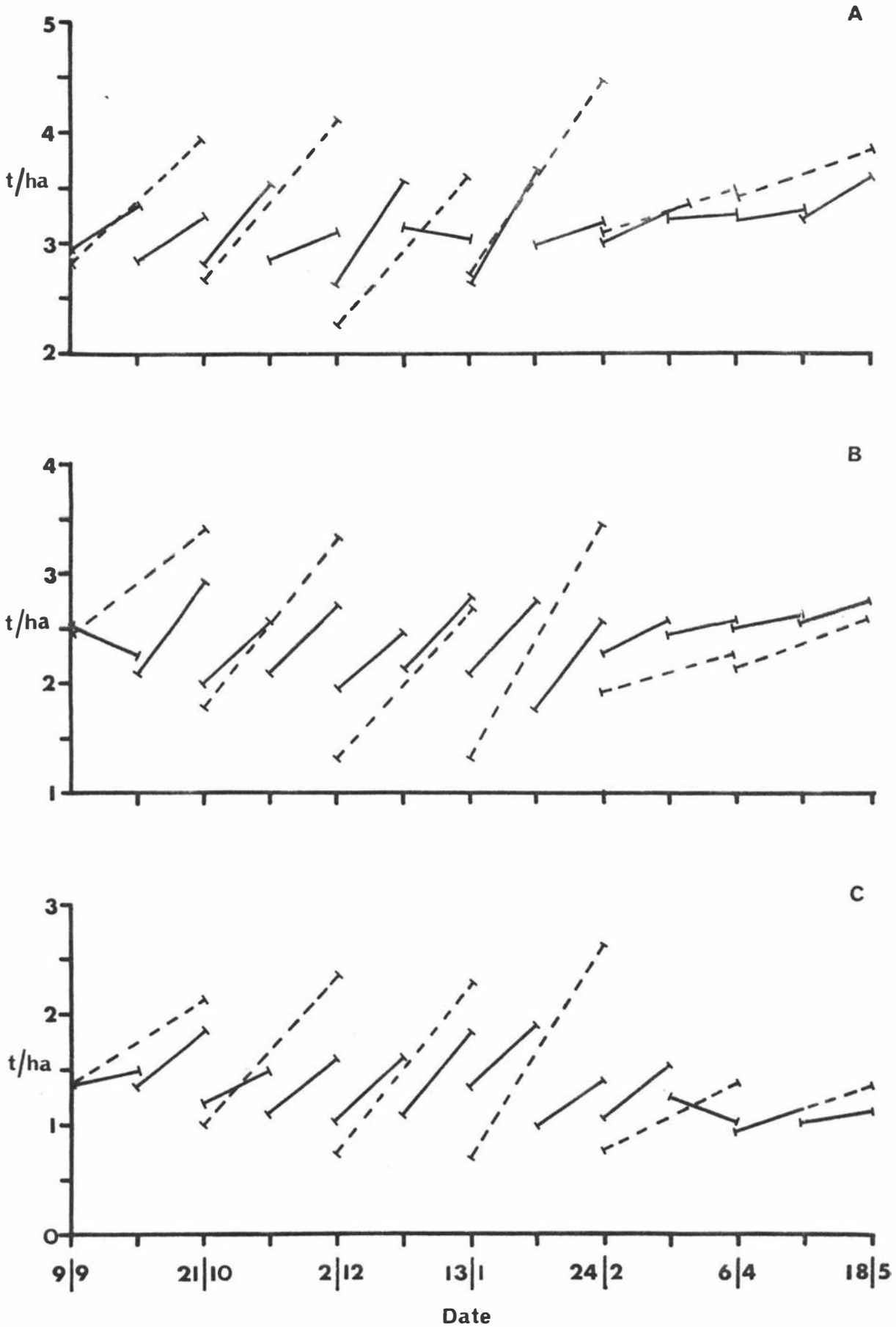


APPENDIX 1: Percentage soil moisture during 1975/76 for 0-5 cm (-·-·-), 5-15 cm (- - -) and 15-30 cm (——) depths.

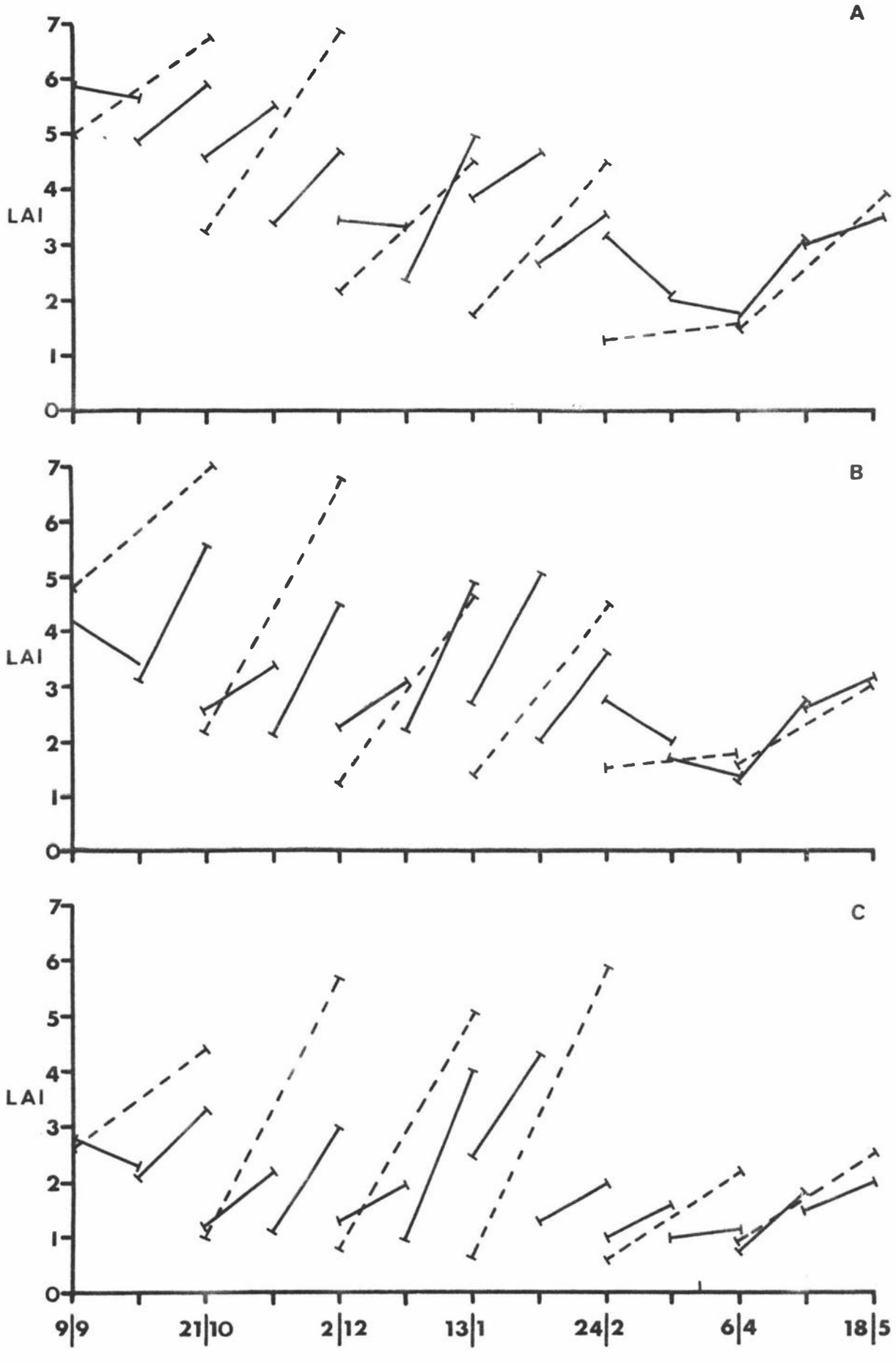
APPENDIX 2: Meteorological Measurements, DSIR, Palmerston North

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Rainfall (mm)												
1928-75 Mean	81	70	67	79	89	97	87	89	73	87	76	94
1975	38	26	51	73	124	69	124	160	54	83	53	103
1976	89	61	79	51	109	215	120	132	78	140	65	75
1977	67	45	52	67	113	109	80	53	107	47	75	93
Daily Max. Temp (^{o}C)												
1928-75 Mean	22.0	22.4	20.9	18.2	15.0	12.6	11.9	13.1	14.8	16.6	18.6	20.6
1975	24.9	24.1	22.2	18.9	15.7	12.3	11.9	13.3	14.4	16.7	17.0	19.3
1976	20.9	19.0	21.2	18.2	14.3	11.9	11.7	13.2	14.3	16.1	17.3	20.2
1977	20.2	22.4	22.1	18.1	13.3	12.3	12.4	13.1	12.6	15.7	17.7	19.5
Daily Min.Temp (^{o}C)												
1928-75 Mean	12.7	12.8	11.6	9.5	6.8	4.6	3.9	4.9	6.6	8.3	9.8	11.6
1975	15.4	14.9	13.9	10.4	9.2	4.3	3.5	6.0	7.0	9.8	9.5	11.1
1976	14.0	10.4	11.9	10.4	6.4	4.4	4.6	7.1	7.1	7.9	8.7	12.8
1977	12.3	12.8	12.2	9.4	4.9	5.5	5.1	6.5	4.9	8.1	9.4	10.9
10 cm Soil Temp ^{o}C												
1940-75 Mean	18.7	18.3	16.4	13.2	10.2	7.7	6.6	7.6	9.9	12.5	15.2	17.5
1975	19.5	18.3	16.8	13.1	11.0	6.7	5.8	7.7	9.5	12.7	13.5	15.4
1976	17.6	14.8	14.5	13.0	9.2	6.9	7.0	8.5	9.4	12.2	13.1	16.0
1977	15.9	17.1	15.8	12.6	7.7	7.2	6.6	7.9	9.7	11.8	13.1	15.4

APPENDIX 3: Residual and final dry matter levels of Experiment 1 (tonnes/ha)



APPENDIX 4: Residual and final leaf area indices of Experiment 1.



Appendix 5: Growth rates in treatment RS (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2°Axillary Shoots	Net Canopy	Total Shoot
1:1[a]	9,[b]5[c]	9,3	0,	30,45	18,7
1:2	81,31	138,32	8,6	79,37	227,51
1:3	-5,30	499,86	15,20	518,47	509,94
1:4	-16,40	687,101	36,21	613,38	707,71
2:1	5,3	81,15	16,2	92,27	102,11
2:2	8,13	571,94	76,22	522,23	655,26
2:3	0,	599,51	33,45	568,52	632,50
3:1	32,22	130,20	16,10	106,61	178,20
3:2	-6,7	607,69	30,29	568,74	631,84
3:3	-17,16	331,66	-7,12	255,61	307,77
3:4	-8,10	55,33	42,26	85,21	89,60
3:5	0,	72,10	28,11	77,51	100,37

a:- regrowth period within cycle 1

b:- mean growth rate

c:- standard error of mean growth rate

Total Shoot:

RS:1:1 <RS:2:1 $t = 6.46^{***}$

RS:1:1 <RS:3:1 $t = 7.55^{***}$

Appendix 6: Growth rate in treatment SAS (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2° Axillary Shoots	Net Canopy	Total Shoot
1:1	9,10	15,18	0,	45,36	24,28
1:2	83,28	150,22	7,6	81,44	240,52
1:3	41,40	506,19	33,7	537,62	580,54
1:4	-75,31	516,93	75,7	357,80	516,112
2:1	32,4	256,20	40,15	288,36	328,28
2:2	-26,4	772,63	10,21	609,50	756,56
3:1	23,7	92,11	8,4	46,47	123,8
3:2	-2,14	577,52	35,20	461,25	610,29
3:3	-22,11	651,32	77,39	707,37	706,37
4:1	21,10	70,12	5,3	147,22	96,17
4:2	2,5	332,30	6,3	252,29	340,16
4:3	-16,15	237,43	10,7	174,40	231,28

Appendix 7: Growth rates in treatment 6S (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2°Axillary Shoots	Net Canopy	Total Shoot
1:1	8,12	3,6	0,	-53,34	11,7
1:2	119,33	231,25	7,7	260,31	357,40
2:1	93,15	155,15	4,6	206,48	262,29
2:2	-9,19	433,84	21,12	346,45	445,73
3:1	112,12	221,13	25,14	253,35	358,12
3:2	-59,31	664,91	39,15	491,49	644,82
4:1	41,3	107,11	12,7	142,22	160,19
4:2	15,2	504,44	52,16	470,18	571,51
5:1	115,19	167,22	0,	170,31	282,27
5:2	10,11	380,27	14,10	417,45	404,42
6:1	33,18	64,10	0,	42,13	97,15
6:2	39,33	153,39	12,5	89,30	204,30

Stubble Shoot

6S:2:1 > 6S:2:2	t = 4.63**
6S:3:1 > 6S:3:2	t = 2.85*
6S:4:1 > 6S:4:2	t = 7.22***
6S:5:1 > 6S:5:2	t = 4.78**

Net Canopy

6S:3:1 > 6S:4:1	t = 2.71*

Total Shoot

6S:3:1 > 6S:4:1	t = 8.30***
6S:3:1 > RS:2:1	t = 9.45***
6S:5:1 > RS:3:1	t = 3.10*

Appendix 8: Growth rates in treatment 6L (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2°Axillary Shoots	Net Canopy	Total Shoot
1:1	60,16	-3,24	0,	-30,21	57,21
1:2	303,37	291,71	0,	432,57	594,50
2:1	42,12	9,24	0,	38,51	51,34
2:2	239,35	403,48	19,17	579,73	661,94
3:1	230,24	270,18	21,16	315,22	521,50
3:2	-105,43	676,65	202,29	629,65	773,51
4:1	26,28	91,28	12,3	92,29	129,36
4:2	35,26	611,49	69,26	479,41	715,57
5:1	242,40	110,22	6,6	228,41	358,38
5:2	147,31	254,28	2,11	376,15	403,91
6:1	72,12	57,16	0,	-1,20	129,32
6:2	56,20	93,17	6,4	75,26	155,30

Rhizome Shoot

6L:2:1 < 6S:2:1 $t = 5.16^{**}$

6L:5:2 < 6S:5:2 $t = 3.24^{*}$

Total Shoot

6L:4:1 < 6L:5:1 $t = 2.49^{*}$

Net Canopy

6L:4:1 < 6L:5:1 $t = 2.71^{*}$

Appendix 9: Growth rates in treatment SAL (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2°Axillary Shoot	Net Canopy	Total Shoot
1:1	31,22	-10,17	0,	-58,63	21,12
1:2	333,32	289,16	0,	445,73	623,15
1:3	72,71	264,31	67,7	153,24	403,49
2:1	50,20	93,13	3,1	5,33	146,33
2:2	218,81	629,56	87,38	853,76	934,101
3:1	184,30	361,10	27,17	311,47	572,41
4:1	249,31	188,31	18,8	253,29	455,89
4:2	186,81	491,97	107,42	598,49	784,99
5:1	180,8	296,21	13,11	339,49	489,22
5:2	70,59	229,50	11,19	289,16	310,101
6:1	74,14	94,21	2,4	104,32	170,22
6:2	93,36	57,49	4,1	-23,33	154,53

Total Shoot

SAL:2:1 < SAL:3:1	t = 8.02***
SAL:4:1 > 6L:4:1	t = 3.60*
SAL:1:2 > SAS:1:2	t = 7.08***
SAL:6:2 > SAS:4:1	t = 2.66*

Appendix 10: Growth rates in treatment LS (kg D.M./ha/wk)

Regrowth Cycle	Stubble Shoots	Rhizome Shoots	2°Axillary Shoots	Net Canopy	Total Shoot
1:1	34,16	13,14	0,	-130,28	47,27
1:2	331,56	308,64	13,7	412,70	652,32
2:1	21,6	17,7	0,	-30,28	38,12
2:2	68,13	284,21	26,6	381,29	378,19
2:3	-1,29	374,48	6,5	197,22	321,63
3:1	216,25	366,30	75,41	429,64	657,39
4:1	12,6	95,13	10,3	40,26	117,14
4:2	7,13	522,50	56,18	489,39	585,51
5:1	323,14	154,24	6,5	267,42	483,35
5:2	86,28	372,56	26,13	498,15	484,62
6:1	10,5	44,10	0,	-39,23	54,20
6:2	43,10	109,15	6,5	119,27	158,19

Total Shoot

LS:3:1 > SAL:3:1 t = 2.50*

LS:5:1 > 6L:5:1 t = 2.47*

Appendix 11: Environmental details of the controlled climates in Experiment 3 and 4

	Experiment 3	Experiment 4
Temperature (^{o}C) : Day	18	17
Night	13	11
Relative humidity (%) : Day	65	65
Night	80	80
Vapour pressure deficit (-bars):		
Day	6.7	6.3
Night	2.8	2.4
Mean light irradiance [a] (W m^{-2})	165	155
Daylength (hrs)	14	14
Commencement of irradiance (hrs)	0000	0600
Daily nutrient feed [b] (ml/pot)	250	150
Lag duration [c] (hrs)	4	4

[a] Photosynthetically active range: 400-700 nm

[b] Hoagland nutrient solution; minus N

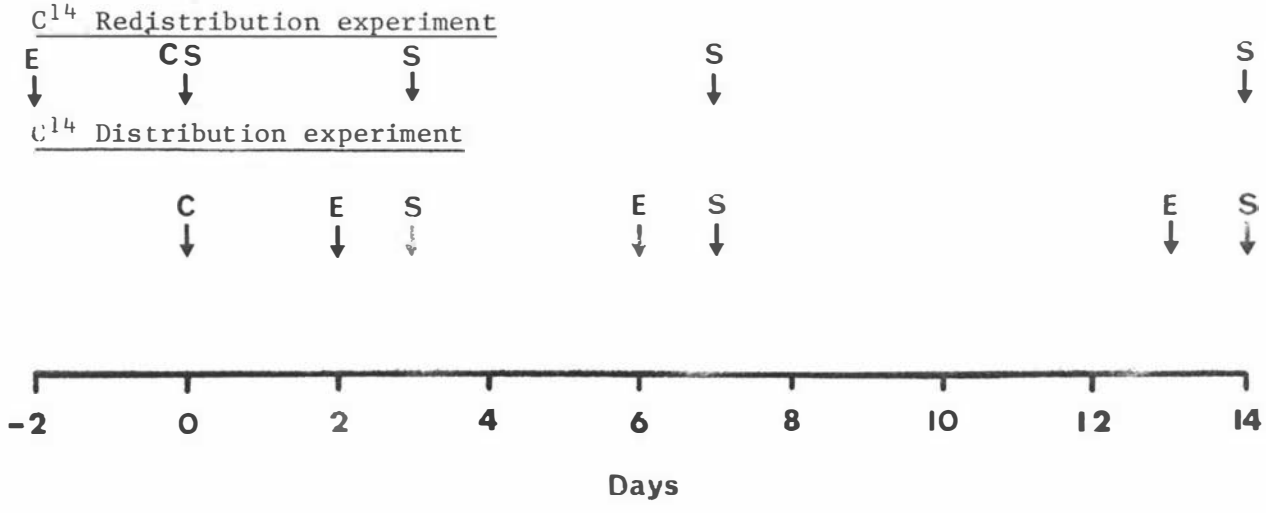
[c] Time duration over which temperatures changed

APPENDIX 12: Leaf to stem dry weight ratios of stubble, stubble shoots and rhizome shoots

Days of Regrowth	0	3	7	13	20	28
			Stubble			
LL	0.23	0.26	0.29	0.27	0.27	0.21
HL	0.34	0.28	0.28	0.38	0.34	0.24
LH	0.56	0.43	0.54	0.57	0.36	0.19
HH	0.57	0.47	0.52	0.53	0.39	0.18
Tmt Mean SE	0.04	0.04	0.05	0.03	0.05	0.04
Signif Level	***	*	***	***	NS	NS
LSD (5%)	0.11	0.13	0.15	0.10		
			Stubble Shoots			
LL	2.54	1.96	2.62	3.29	2.54	1.66
HL	2.31	2.21	3.20	3.05	2.73	2.00
LH	3.32	3.21	2.75	2.64	2.30	1.88
HH	3.09	2.62	3.17	2.87	2.36	1.80
Tmt Mean SE	0.34	0.19	0.20	0.21	0.14	0.18
Signif Level	NS	***	NS	NS	NS	NS
LSD (5%)		0.58				
			Rhizome Shoots			
LL	1.14	1.02	1.23	2.33	2.37	1.50
HL	1.02	1.40	1.31	2.23	2.01	1.37
LH	1.44	1.42	1.66	1.90	1.85	1.42
HH	1.58	1.41	1.92	2.10	2.05	1.09
Tmt Mean SE	0.15	0.09	0.10	0.11	0.22	0.07
Signif Level	NS	*	***	NS	NS	**
LSD (5%)		0.29	0.32			0.22

APPENDIX 13: Experimental details of the C^{14} Redistribution and Distribution experiments.

(A) Relative time scale of C^{14} experiments.



E - exposure to C^{14} O_2.

C - cutting down to 2.0 or 7.0 cm.

S - sample harvest.

(B) Standard tissue activity for several tissue, chromic acid combinations (d.p.m. per mg dry weight)

		mean[b]	standard error
(1)	50 mg tissue + 20 ml chromic acid[a]	1232	52
(2)	25 mg tissue + 20 ml chromic acid	1298	63
(3)	10 mg tissue + 20 ml chromic acid	1273	59

a - a recombustion of the residue of this procedure yielded the equivalent of 81 ± 20 d.p.m. per mg tissue.

b - mean of six replicates.

APPENDIX 14: Total plant leaf area in the C^{14} Distribution experiment (one day after exposure; cm^2 per plant)

Treatment	Regrowth Day 3	7	14
L (2.0cm)	174 (1.1)[A]	398 (2.6)	592 (3.8)
H (7.0 cm)	580 (3.8)	992 (6.4)	1334 (8.7)

A: leaf area expressed as leaf area indices (pot area:154 cm^2)

APPENDIX 15: Rhizome and crown plus taproot TNC in the C^{14} Redistribution experiment (% of dry weight)

		Regrowth Day 0	3	7	14
Rhizome	L	10.2	10.9	9.4	9.1
		(*,0.3)	(**,0.2)	(*,0.4)	(**,0.5)
	H	11.9	13.8	12.0	12.8
			| NS, 1.0 |		
Crown plus taproot	L	8.9	8.9	8.3	7.1
		(*,0.5)	(*,0.7)	(*,0.5)	(***,0.5)
	H	11.8	12.1	11.3	12.2
			| NS, 1.3 |		