

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

A STUDY OF THE EFFECTS OF DIFFERENT FREQUENCIES OF DEFOLIATION  
ON THE RECOVERY GROWTH OF TWO VARIETIES OF  
LUCERNE (Medicago sativa L.)

\*\*\*\*\*

A thesis presented in partial fulfilment of the requirements  
for the Degree of Master of Agricultural Science

at

MASSEY UNIVERSITY

by

JOHN M. ABBOTT

1971

THIS THESIS IS DEDICATED TO MY

TWO SONS,

JOHN AND ROY.

## TABLE OF CONTENTS

1.	Introduction.	
2.	Review of literature.	
2.1.	The types and morphological variation of lucerne.	2
2.1.1.	Shoot growth.	3
2.1.2.	Crown growth.	4
2.1.3.	Root growth.	4
2.1.4.	Correlation of growth characteristics.	5
2.2.	The seasonal growth pattern of lucerne.	6
2.2.1.	Plant growth.	6
2.2.2.	Chemical composition of roots.	8
2.3.	The effects of defoliation frequency on lucerne.	
2.3.1.	The effects of defoliation frequency on the yield and chemical composition of lucerne.	
2.3.1.1.	The yield of shoots.	10
2.3.1.2.	Root growth.	15
2.3.1.3.	Chemical composition.	17
2.3.1.4.	Defoliation height.	19
2.3.1.5.	Defoliation by cutting and grazing.	19
2.3.2.	The effects of defoliation frequency on lucerne persistence.	20
2.3.3.	The growth form response of lucerne to different defoliation frequencies.	22
2.3.4.	The effect of defoliation frequency on lucerne growth rates.	24
2.4.	Factors controlling the yield and regrowth rate of lucerne.	
2.4.1.	Physiological factors.	
2.4.1.1.	The role of reserves.	25
2.4.1.2.	The role of lateral roots.	32
2.4.1.3.	The role of residual leaves.	34
2.4.1.4.	The interrelationship of the physiological factors.	36
2.4.2.	Morphological factors.	
2.4.2.1.	Basal shoot status in mature lucerne.	38
2.4.2.2.	Senescence.	39
2.4.2.3.	Shoot numbers and plant inter-shoot competition.	40

2.4.3.	Environmental factors.	
2.4.3.1.	Light transmission and interception in the lucerne canopy.	41
2.4.3.2.	The effect of temperature on lucerne growth.	44
2.5.	Lucerne varietal comparisons for defoliation and growth.	46
3.	The experiment and basic methods.	
3.1.	The aims and treatments.	51
3.2.	Experimental layout.	51
3.3.	The experimental site.	52
3.4.	Measurements and methods.	53
3.5.	Statistical analysis.	54
3.6.	Climatic conditions during the experiment.	55
4.	Crop production, composition and persistence.	
4.1.	Methods.	56
4.2.	Results.	
4.2.1.	Cumulative production.	58
4.2.2.	Botanical composition.	61
4.2.3.	Lucerne persistence.	63
4.3.	Discussion.	
4.3.1.	Production.	66
4.3.2.	Botanical composition.	69
4.3.3.	Lucerne persistence.	70
5.	The effect of defoliation frequency on the amount and nature of lucerne plant growth.	
5.1.	Methods.	
5.1.1.	Experimental.	72
5.1.2.	Statistical analyses.	75
5.2.	Results.	
5.2.1.	The growth yield of the lucerne plant.	
5.2.1.1.	Analysis by stage of growth comparison.	78
5.2.1.2.	Plant leaf growth.	79
5.2.1.3.	Plant shoot growth.	80
5.2.1.4.	Plant root and crown growth.	81
5.2.1.5.	Total plant growth.	81
5.2.1.6.	Plant shoot number.	82
5.2.1.7.	Plant growth rates.	83

5.2.2.	Within plant dry matter distribution and plant size variability.	86
5.2.3.	The nature of lucerne growth.	88
5.2.4.	The basal shoot growth of mature lucerne.	95
5.3.	Discussion.	
5.3.1.	Lucerne plant growth.	98
5.3.2.	Lucerne growth rates.	103
5.3.3.	Lucerne plant morphology and size.	104
5.3.4.	The nature of lucerne shoot growth.	106
5.3.5.	The basal shoot growth of mature lucerne.	108
5.3.6.	Defoliation criteria.	109
6.	Senescence, sward physiognomy and light transmission.	
6.1.	Method.	
6.1.1.	Experimental.	113
6.1.2.	Data preparation and statistical analysis.	114
6.2.	Results.	115
6.3.	Discussion.	118
7.	Organic reserves.	
7.1.	Methods.	123
7.2.	Results.	
7.2.1.	Organic reserve changes over time following different previous defoliation frequencies.	
7.2.1.1.	Root and crown dry weights.	125
7.2.1.2.	The percentage of total non-structural carbohydrates.	125
7.2.1.3.	The weight of total non-structural carbohydrates.	128
7.2.1.4.	The percentage of total nitrogen.	130
7.2.1.5.	The weight of total nitrogen.	130
7.2.1.6.	The total non-structural carbohydrates/total nitrogen weight ratios.	133
7.2.1.7.	Winter organic reserve changes.	135
7.2.2.	Treatment comparison.	135
7.2.3.	The dark growth of lucerne.	138
7.3.	Discussion.	
7.3.1.	The changes of organic reserves over time and their relative significances	139

7.3.2.	The influences of different defoliation frequencies on organic reserves at harvest.	142
7.3.3.	The winter changes of organic reserves.	144
7.3.4.	The use of dark regrowth to estimate the carbohydrate reserve status.	145
8.	Early spring temperature/shoot growth correlations.	147
9.	A reversal study of the extreme defoliation treatments.	
9.1.	Method.	149
9.2.	Results.	
9.2.1.	Plant numbers.	150
9.2.2.	Top growth and yield composition.	151
9.2.3.	Growth rates.	154
9.2.4.	Root and crown weight.	156
9.2.5.	Organic reserve levels.	157
9.3.	Discussion.	162
10.	Discussion.	
10.1.	Experimental.	167
10.2.	Varieties.	169
10.3.	Lucerne yield and growth.	173
11.	Summary and conclusions.	178
12.	Bibliography.	183
13.	Acknowledgments.	204
14.	Appendices.	
1A	A summary of the original experiment.	206
2A	Data of the climatic parameters during the experimental period.	211
3A	Data.	213
4A	Statistical Analysis.	261
5A	Computer programs.	290
6A	Light meter description.	305
7A	Organic reserve analyses.	307
8A	Sample of root weight adjustment calculation.	312

Symbols and abbreviations used.

Treatment abbreviations are as in table 3.1.

C Chanticleer variety

W Wairau variety

RTCR root plus crown

TNC total non-structural carbohydrates

TN total nitrogen

LSD Least significant difference

ANOVA analysis of variance

P = 0.01 the percentage significance

F the F-ratio value

r correlation coefficient

R<sup>2</sup> coefficient of multiple determination

## CHAPTER 1.

### INTRODUCTION

In recent years there has been increasing interest in the use of lucerne in the farming systems in localities other than those which have "traditionally" grown lucerne. Much of the North Island, including the Manawatu is involved with this developing interest. To contribute to the information needed to support this, a field experiment studying the effects of different frequencies of grazing lucerne was established in 1965 at Massey University. Pure sowings of two varieties were used. These were New Zealand certified Chanticleer and New Zealand certified Wairau, with treatments ranging from continuous grazing through to hay stage defoliation. This experiment is discussed in more detail in appendix 1A.

By the spring of 1969 at the commencement of the author's study, treatment differences were apparent. The author's study continued selected treatments and measured their differences of spring growth. The initial interest was in the treatment yield differences, volunteer species ingress, lucerne persistence and the associated interaction, if any, between the defoliation treatments and the spring climatic parameters.

Further more detailed work considered the lucerne plants' response to these treatments; the differences of their size, growth form, growth efficiency and organic reserve content. During the last half-decade, several intensive studies have been made of the nature of lucerne regrowth (Leach, 1968a, 1969a; Keoghan, 1970) and the physiology of lucerne regrowth (Hodgkinson, 1967; Smith and Silva, 1969; Keoghan, l.c.; Smith and Marten, 1970) after defoliation. Verification of some of these results was attempted in the field environment, at the same time using this information to explain other observations made.

Along with all these aspects, the responses of the two varieties were compared.

While there is considerable information on the agronomic aspects of lucerne and the lucerne sward's productive response to defoliation frequency, there is little information on the nature of the individual lucerne plant's response in the sward environment. The recently increased knowledge of the nature and physiology of the lucerne plant's regrowth is increasingly in need of verification in the more rigorous and competitive sward environment. This information needs to be further extended to circumstances of continued treatment application. This study considers some aspects of these requirements.

## CHAPTER 2

### REVIEW OF LITERATURE

As well as considering lucerne defoliation this thesis includes a lucerne variety comparison and measurements in a late winter/spring growth period. To satisfy these latter aspects, this review initially considers the origin and the morphological variation between lucerne varieties and the seasonal growth of lucerne. The bulk of the review considers the response of lucerne to different defoliation frequencies, supported by a review of the physiological, morphological and some selected environmental factors involved in lucerne growth after defoliation. Concluding the review is a consideration of the variatal influence on the response of lucerne to defoliation.

Several reviews associated with this thesis topic have been recently compiled and were available as theses. Defoliation of pure lucerne (Keoghan, 1967), lucerne growth after defoliation (Keoghan, 1970), the physiology of lucerne regeneration (Hodgkinson, 1967) and others of an older and more general nature (Willard, 1951; May, 1960). Where pertinent, reference will be made to studies on species other than lucerne.

#### 2.1. The Types and Morphological Variation of Lucerne.

Iversen and Meijer (1967) reviewed the known types of lucerne identifying two main species; 1. Medicago sativa, native of a temperate climate; 2. M. falcata, originating in the colder climate of Siberia. Hybridisation between M. falcata and M. sativa species has resulted in the M. media species of rather variable type. Brief descriptions of each group have been compiled from their observations and those of Bolton (1962).

M. sativa is a plant native to an arid mainly low land environment, where it has developed an erect growth habit, few thick stems, large long leaves and a deep almost unbranched tap root. It is highly productive, with early growth, rapid post defoliation recovery and a variable degree of winter hardiness based on dormancy. Diseases are few so that little resistance has developed. Flowers are purple.

M. falcata is a plant of colder, more humid upland environments where it has been subjected to much more competition and diseases with resultant disease resistance. It has developed a prostrate growth habit, fine branched stems, small darker leaves, a much branched root system and a deep set crown giving good cold resistance. Productivity is low with late spring growth and slow recovery. Flowers are yellow.

M. media - Cultivated varieties tend to have stems which are fine numerous and branched, leaves small and numerous, and a high proportion of fasciculated roots; considerable resistance to disease and frost; flowers are a mixture of variegated, purple, green, white and yellow.

In the western world, M. sativa and M. media are the only species to be cultivated, while strains of M. falcata are used in Siberia and China. M. media varieties show considerable variation in growth form, its development probably being an interaction of natural selection and varying amounts of introgression with M. falcata (Palmer, 1967). Iversen and Meijer (1967, p.79), suggested a classification of lucerne varieties based on the dominance of M. falcata genes as indicated by agronomic and botanical characteristics. They considered this to be more complete than several previous classifications.

Studies of varietal growth form differences have supported the classification of Iversen and Meijer (1967).

#### 2.1.1. Shoot Growth.

Larson and Smith (1963) compared ten lucerne varieties and showed a strong correlation between increasing M. falcata content and decreasing autumn growth measured as height, increasingly prostrate growth habit, and a lack of winter injury. The prostrate growth was largely associated with the basal portions of the shoot stems. Using individual plants of Ranger lucerne, Kehr and Gardner (1960) showed that even within a single variety, such shoot growth variability can be quite extensive. They further noted the positive correlation between recovery growth rate and more erect growth.

Leach (1969a) using Totana, Hunter River and Rhizoma lucernes (erect, semi-erect and semi-prostrate respectively), demonstrated the differences of shoot numbers. After twenty-eight days regrowth from a 5cm stubble length, these varieties had 23, 34, and 44 stems respec-

tively per plant, while individual shoot sizes and growth rates showed the reverse sequence. Such differences of stem density persist with high plant population densities (Palmer, 1967). Leaf/stem ratios increase with M. falcata content (Davies, 1960b; Rogers 1961), although Zaleski and Dent (1960) found the reverse. Sheridan et al. (1968) observed that lucerne varieties expressing increasing amounts of M. sativa content were significantly associated with fewer but longer internodes. Between shoot types Keoghan (1970) observed with Wairau lucerne, that stubble shoots had greater leaf/stem ratios than basal shoots, the difference being due to differences of internode length rather than differences of leaf length. There does not appear to have been any study to determine whether the relative importance of each shoot type differs between varieties.

#### 2.1.2. Crown Growth.

From the study of the crown development of eight lucerne varieties, Smith (1955) demonstrated the positive correlation between the M. falcata content with 1. dry weight of rhizomes; 2. their average number; 3. average crown width. Associated shoot number differences (Leach, 1969a) are due in part, at least, to the increase of potential stem sites on the crown and/or stubble. Major varietal differences of crown positions relative to the soil surface are indicated in Iversen and Meijer's (1967) classification.

Lucerne rhizomes grow as short horizontal extensions of the crown below ground level. In some instances this growth property has been intensified by breeding to provide more persistent varieties under grazing (Heinrichs, 1963).

#### 2.1.3. Root Growth.

Four root systems for lucerne are described, (Bolton, 1962; Heinrichs, 1963).

a. Tap root system - characteristic of M. sativa lucernes, having a vertical tap root with side laterals. Lateral spread is by limited crown expansion.

b. Branched rooted system - characteristic of M. media lucernes,

having more than one primary root from the crown, with or without a tap root and able to develop adventitious shoots from the roots. Lateral spread is by more extensive crown expansion.

c. Rhizomatous system - as described (section 2.1.2.).

d. Creeping rooted system - characterised by the horizontal growth of lateral roots four to eight inches below the soil surface. Varieties have been isolated by breeding to provide persistence under grazing in dry land conditions (Heinrichs, 1963; Kilcher et al. 1966; Daday, 1968).

Smith (1951) demonstrated a large variation in root branching among the range of varieties studied, this being in accordance with the above classification. He postulated that these differences were likely to affect the adaptability and capacity of lucerne to survive drought, resist winter heaving and to absorb nutrients. Busch et al. (1968), related heaving resistance to greater root branching. The other aspects do not appear to have been investigated in detail. Carlson (1925) observed that soil structural differences could cause lucerne to adopt considerable variation in root form.

#### 2.1.4. Correlation of Growth Characteristics.

It appears that some of the associations of morphological and growth characteristics in lucerne which have been observed in the past, are probably based more on natural selection than genetic origin (Palmer, 1967). Supporting this statement are the demonstrations that the creeping rooted character can be combined with the earlier, quicker growing and higher yielding M. sativa varieties (Daday, 1962; Heinrichs, 1963). Similarly, Busbice and Wilsie (1969) and Davis and Baker (1966) have shown that it should be possible to combine these M. sativa growth characteristics with winter hardiness as their genetic linkage with poor winter hardiness is not strong. Although the types and morphological variations of lucerne varieties are quite extensive, very few studies have been made of the relationship of these growth form differences to yield. Further, growth form comparisons can only be made satisfactorily when similar management conditions exist. Recent work suggests good breeding potential exists for yield increase by combining some of the growth characteristics which until recently were thought to be genetically opposed.

## 2.2. The Seasonal Growth Pattern of Lucerne:

Lucerne is grown under a wide range of environments. These range from no winter growth due to excessively low temperatures in the higher latitudes through to continuous winter growth in the warmer lower latitudes, although this pattern may be modified by altitude. Summer temperatures are not "normally" excessively growth restrictive except for some regions where they are high - greater than 25 C (Feltner and Massengale, 1965), lack of moisture usually being more growth restrictive (Leach 1970)). The seasonal growth patterns are considerably controlled by the local environment. (Leach, 1968a).

### 2.2.1. Plant Growth

The seasonal pattern of lucerne growth has been described for cool temperate environments by Sonneveld (1962) in the Netherlands and by Nelson and Smith (1968a,b) in Wisconsin, U.S.A. In the Autumn, shoot growth rate steadily declines as temperatures and day length decrease; till the winter months during which there is little or no herbage growth. They and Grandfield (1943), and Feltner and Massengale (1965) found that crown buds enlarged and numbers increased in the late autumn and overwintered to provide the shoots for spring growth, which reached a maximum growth rate in late spring. In environments with milder winters, growth of lucerne continues through the winter (Stanhill, 1962; Leach, 1970c). Lower summer growth rates associated with limited moisture availability are often observed where irrigation is not used (Nelson and Smith, 1968b; Leach, 1970c). The latter author found summer growth was more restricted than winter growth in Adelaide, Australia.

The seasonal growth of lucerne underground organs has received limited attention. In a pot experiment (all roots) (Heipko, 1959), and field experiments sampling the top 9" of tap root (Baker and Garward, 1959) and the top 6" (Smith 1962; Nelson and Smith, 1968a), root dry weight showed a slow steady decline over the winter, becoming faster at the start of spring reaching an early spring weight minimum. Nelson and Smith (1968a) found root dry weight to have an increasing trend from this spring minimum through to relatively high values the following autumn if associated with an infrequent defoliation system.

They also observed that while root dry weight changed thus, crown dry weight was relatively constant throughout the season. These observations were made in cool temperate environments. The responses in warmer winter environments have not been specifically reported.

Floral initiation and development occurs throughout much of the growing season. The time for the appearance of floral primordia has been shown to be negatively related to the mean air temperature prevailing (Dobrenz et al. 1965; Dermine et al. 1967; Smith, 1969a), positively with shoot node number (Dobrenz et al. 1965), all leading to lower yields at maturity with higher temperatures (Smith, 1969a). The effect of moisture and/or its interaction with temperature on the time to floral appearance does not appear to have been investigated for lucerne.

The major environmental factor(s) controlling seasonal growth depends on the season and region considered. Lucerne growth has an approximate temperature optimum of 15 C for established plants, (Steinke, 1963; Feltner and Massengale, 1965; Robison, 1966; Smith, 1969a) while seedlings have a higher temperature optimum of 15 - 20 C (Gist and Mott, 1957). Mitchell (1955, 1956) observed the same optimal temperature occurrence for the growth of temperate and subtropical grass and clover species. Temperature is likely to be the major growth controlling factor during the winter and early spring when soil moisture is usually adequate. Feltner and Massengale (1965) observed reduced lucerne top growth and root dry weights during very high summer temperatures (greater than 25C) while using irrigated Moapa lucerne in Arizona. Soil temperatures also strongly influence top and root growth (Neilson et al. 1960; Levesque et al. 1963; Heinrichs, 1966). Early spring growth may thus be more limited by soil temperatures which tend to be slower rising than by air temperatures.

The light intensity at the canopy surface of a lucerne sward required for maximum photosynthesis was calculated by Thomas and Hill (1949) to be about 3,500 foot candles. Both Matches et al. (1962) and Cowett and Sprague (1962) found that a reduction from full sunlight to an approximately similar level had no measureable effect on top dry weight. Lower light levels tend to be associated with lower seasonal temperatures and so may not have an important effect on growth per se, while light temperature interactions may well be of greater

importance, especially for higher temperatures (Langar, 1967). Cowett and Sprague (1962) showed the beneficial effect on lucerne growth of increasing day length from 10 to 16 hours.

Soil moisture with dryland lucerne is generally a limiting factor for summer/autumn growth (Kilcher et al. 1966; Lobb, 1967; Leach, 1970c). This effect may be direct, or indirect due to lack of root growth and hence induced nutrient deficiency (Mitchell 1957).

These several environmental factors, individually or in combination are some major determinants of lucerne production during different seasons, those operating at any one season being dependant on the locality under consideration.

### 2.2.2. Chemical Composition of Roots

Seasonal changes and the chemical composition of lucerne roots and crowns are mainly of interest during the autumn, winter and early spring. At other times of the year, management, especially defoliation, modifies natural trends. Hodgkinson (1967) has reviewed the subject.

The carbohydrate reserves of plants represent the reserve energy stored in the vegetative organs of plants. The total of these carbohydrate reserves have been termed total available carbohydrates (TAC) and total non-structural carbohydrates (TNC). In accordance with the reasoning of Smith (1969b) the term (TNC) will be used in this thesis.

Several studies have shown that the percentage and/or weight of total non-structural carbohydrates (TNC), starch, and the weight of total nitrogen (TN) steadily increase in the autumn and early winter if growth is undisturbed (Graber et al., 1927; Grandfield, 1943; Bula and Smith, 1954; Jung and Smith, 1961); the combined effect is presumed to result from the hydrolysis of starch to sugars and the latter use as respiratory substrates. Except for any small early winter peak, reducing sugars represent only a minor component of the TNC over the Autumn/winter/early spring period (Bula and Smith, 1954; Jung and Smith, 1961). The concentration of the various fractions varies considerably between reports, this being determined by different extraction methods used and the growth conditions pertaining.

The above authors do not offer physiological explanation for the autumn increase of organic reserves. Sonneveld (1962) suggests that the

carbohydrate increase may result from the decreasing autumn temperatures reducing the growth processes, either directly on such functions as cell division or indirectly on functions such as ion uptake, while the photosynthetic process is less restricted. Brown and Blaser (1965, 1970) provide supporting evidence with grasses, demonstrating an increase of carbohydrate compounds under conditions of positive energy balance. Murata et al. (1965) showed that with lucerne, apparent photosynthesis was still relatively high between 0-10 C. With temperature decrease, respiration rate might be expected to decrease and contribute to the carbohydrate accumulation. In practise this may be of limited importance, as Marata et al. (1965) found little change in lucerne respiration rate over this lower temperature range. Day and Dart (1969) reported that the nitrogenase activity of lucerne root nodules was still substantial at temperatures of 3 and 5 C. This suggests that the autumn/early winter increase of TN concentration could result from a similar excess of supply over demand.

Unlike TNC, TN weight is relatively constant through the winter period (Jung and Smith, 1961). The slow fall of TAC weight indicates a slow use for maintenance respiration while the constancy of TN weight indicates little or no such use for nitrogenous compounds. These observations apply in circumstances of very little or no winter growth. In winter growing regions these fluctuations are more likely to resemble those of a normal growth period.

With the rise of spring temperatures, and associated increase or commencement of shoot growth, the concentration of TNC and its component fractions show a rapid decline (Graber, 1927; Willard, 1951; Bula and Smith, 1954; Jung and Smith, 1961; Smith, 1962; Nelson and Smith, 1968b), as does the TN concentration (Bula and Smith, 1954) and TN weight (Jung and Smith, 1961). As growth increases, organic reserves reach minimum levels and then start to increase as the supply of assimilates exceeds the growth and respiratory demands. It has been generally assumed that these spring concentration reductions result from the translocation of organic compounds from the roots and crown to the apices of newly growing shoots (Jung and Smith, 1961; Sonneveld, 1962). This is true in part, but of equal consideration is the use of these compounds in respiration and in new root growth during this period. Studies such as those of Hodkinson (1967), Smith and Silva (1969), Silva (1968),

and Smith and Marten (1970) who considered this same problem following defoliation, are needed to elucidate the situation during early spring growth.

Changes in the organic chemical composition of lucerne underground organs during the active growing season are generally dominated by those effects resulting from defoliation. Smith (1962) demonstrated a general increasing trend for TNC concentration in uncut lucerne during this period.

This may not be so apparent in regions where lucerne grows actively in the winter. Excessive summer temperatures (greater than 25 C) with associated high respiratory use of TNC can result in a decrease in their concentration (Feltner and Massengale, 1965). Small TNC decreases may be associated with floral and seed development (Dobrenz and Massengale, 1966). Moisture stress may cause TNC levels to increase (Brown and Blaser, 1970).

As Hodgkinson (1967) notes, all studies associated with the autumn/winter/spring seasons have been conducted with lucerne growing in cool temperate regions having milder winter climates. Further consideration of the subject of organic reserves will be made during the review of the effects of defoliation.

### 2.3. The Effects of Defoliation Frequency on Lucerne.

The following aspects are considered.

1. The effects of defoliation frequency on lucerne yield both on an area and plant basis.
2. The effects on botanical composition and persistence.
3. The growth form response and associated growth rates under different defoliation frequencies.
4. Where pertinent, the effects of defoliation height and its interaction with defoliation frequency.

#### 2.3.1. The Effects of Defoliation Frequency on the Yield and Chemical Composition of Lucerne.

##### 2.3.1.1. The Yield of Shoots.

Keoghan (1967) reviewed this subject fully and was freely referred to during the composition of this review. In "general terms",

from the earliest workers through to those of today, defoliation frequency has been shown to be an important determinant of lucerne yield, this increasing with decreased frequency. The end result is dependant on a number of factors such as the actual frequency in terms of time and/or stage of growth, associated climatic conditions and previous management. Keoghan (1967) has reviewed the early work, mostly in North America, which demonstrated the yield advantage of infrequent defoliation. Nelson (1925) found marked yield differences when defoliating lucerne at full bloom, early bud and a succulent growth stage. These were 3.8, 2.1, and 0.7 tons per year respectively - the average of three varieties and two years growth. Graber et al. (1927) at Wisconsin, observed an initial advantage in shoot yield with frequent defoliation, which in time was surpassed by the infrequent defoliation treatments. Dennis et al. (1959) and Tsuma (1968) observed a similar effect.

Keoghan (1967) observed that lucerne managements trials, many including the effects of defoliation frequency, have been conducted throughout the world in a wide range of climatic and edaphic conditions. He divides these climates into humid and dry regions. Although the effect of defoliation frequency is similar in each region, the quantitative response varies considerably between them. Weir et al. (1960) using irrigated Californian Common lucerne in the warm temperature, high light intensity and long growing season conditions of California, found shoot yield to increase from 14,700 lb/ac to 23,551 lb/ac between the extremes of frequent pre-bud through to infrequent half-bloom defoliation. In the fourth year, defoliation of all previous treatments at one tenth bloom showed no significant yield differences between them. In a similar environment, Jackobs (1950) and Jackobs and Oldmeyer (1955) demonstrated a similar yield response with defoliation frequencies ranging between 25 and 41 days. In each case, little reduction in plant vigour occurred with frequent defoliation under these conditions. Others have also shown similar results (see Willard, 1951; Keoghan, 1967). In these circumstances it is probable that inefficient light utilisation with frequent defoliation is a major determinant of the lower yields.

In the more rigorous conditions of Wisconsin, Kust and Smith (1961), using Vernal lucerne, obtained a yield of 1.14 tons/ac from 6 cuts/year increasing to 4.29 tons/ac from 3 cuts/year. Also at Wis-

consin, Smith and Nelson (1967) had similar results. The growing season in this region is considerably shorter and without the same extended high light intensities. Under English conditions, the results of Davies (1960b) using Du Puits and Grimm lucernes, indicated that while in most years three cuts will give best yields, in particularly wet and cloudy years, this frequency will be too severe. This is more apparent in the following years growth, which is restricted by low plant vigour and possibly death. Whitear (1959) made similar observations.

In the milder conditions of South Australia, using an irrigated three year stand of Hunter River lucerne, Judd and Radcliffe (1970) recorded 4,830, 9,890, 12,030, and 14,750 lb. D.M. for 3, 4, 5, and 6 week defoliation frequencies.

Keoghan (1967) discusses the reasons for the interactions of environmental conditions with defoliation frequency. The recorded yields are dependant on the vigour of the lucerne plant which in turn has been correlated with root reserve levels (Graber et al., 1927; Hildebrand and Harrison, 1939; Weinman, 1948; Neilsen et al., 1957; Weir et al., 1960; Kust and Smith, 1961; Sonneveld, 1962; Feltner and Massengale, 1965; Nelson and Smith, 1967; and others), and proportional to root weight (Dotzenko and Ahlgren, 1950; Nielsen et al., 1956; Weir et al., 1960; Langille et al., 1965; Langer and Steinke, 1965; Smith and Nelson, 1967; Caulsey, 1968; Ueno and Smith, 1970). Willard (1951) indicates that it is well known that plants in humid regions have higher shoot/root ratios than those growing in drier regions. Keoghan (1967) reasonably argues that the greater plant vigour in the drier climates is associated with the maintenance of a higher root reserve level and with time, a sustained root weight and growth. In these conditions, the evidence of Brown Blaser (1965, 1970) would indicate the positive energy balance existing, resulting in the higher organic reserve levels observed.

Iversen (1967) demonstrated the influence of edaphic factors. Using four lucerne varieties, he showed that lenient grazing was more productive per se, and more so on a heavier soil type, while severe grazing was more productive on a lighter soil. With severe grazing on the heavier soil, having a greater soil moisture content than lighter soil, there is more competition from other species. These take advantage of this soil moisture benefit to the weakened lucerne plants dis-

advantage. This defoliation frequency/soil moisture interaction is likely to be found between the range of soil types on which lucerne is grown.

Many other workers from similar and intermediary climatic regions have demonstrated the advantage of defoliating infrequently. Some of these defoliated at fixed time intervals or number of cuts per year (Hildebrand and Harrison, 1939; Nielsen et al., 1954; Davies and Davies, 1956; Dennis et al., 1959; Steinke, 1963; Bryant and Blaser, 1965; Langer and Steinke, 1965; Smith, 1965; Monson, 1966; Smith and Nelson, 1967; O'Connor, 1967; Tsuma, 1968), while many others have done so at different stages of growth (Burlison et al., 1930; Dent, 1955; Dexter, 1964; Feltner and Massengale, 1965; Langille et al., 1965; Keoghan, 1966; Lobb, 1967; Robison et al., 1968). Keoghan (1967) lists others in each group. Generally, with frequent defoliation, the reduction of plant vigour is cumulative over sequential years.

An important aspect of defoliation frequency is the cutting criterion selected. Those used have been, either set time intervals or dates and for stages of growth, height of shoots, presence of basal buds or shoots, height of basal shoots, presence of flower buds and stage of flowering. Keoghan (1967) points out that cutting according to stage of growth is superior, although practically a more difficult operation because of the difficulty of estimation. Growth rates vary with environmental conditions, so that set time intervals can result in variable yield quality as well as risking plant vigour and stand persistence by defoliation at too immature growth stages. Also, consistent hay quality requires harvesting to be at a relatively consistent stage of growth (Meyer and Jones, 1962). Crowder et al. (1960) obtained greatest yields and best quality when defoliating with 2" high crown shoots present, compared with a wide range of fixed time intervals. Tysdal and Kiesselbach (1939) observed the apparent benefits of such a criterion when comparing defoliation frequencies between different varieties. Crown shoot appearance can commence both before and during flowering (Willard, 1951; Keoghan, 1967), indicating their lack of correlation as defoliation criteria. Recently, Nelson and Smith (1968a) and Leach, (1969a) have suggested that this criterion takes advantage of the lucerne plants physiological readiness for defoliation (section 2.4.2.1.).

In practise, especially with mechanical harvesting, management and quality considerations may necessitate a combination of criteria be used.

In contrast to the effect of frequent defoliation, too infrequent defoliation can also result in reduced annual yields (Nelson, 1925; Willard, 1951; Crowder et al., 1960; Kust and Smith, 1961; Smith, 1962, 1965; O'Connor, 1967), or in little further yields increase (Davies, 1960a). Such results infer reduced growth rates at mature stages of growth. In favourable conditions however, lucerne crop growth rates may be sustained at maximum or near maximum levels for some time (Keoghan, 1966), as the lucerne shoot is not determanent in growth, producing floral and vegetative growth simultaneously. On the other hand plant growth is definately reduced with excessively infrequent defoliation. More usually crop growth rates will decrease, or, as Willard (1951) concluded, even become negative at mature growth stages due to death and loss of lower leaves, small branches and the attacks of forage feeding insects. Other factors such as lodging of heavy crops, and the associated death and decomposition of mature stems and also new basal shoots will reduce yields (Keoghan, 1966). Attacks by fungal diseases can cause serious leaf drop in mature lucerne (Keoghan, 1967). Fuess and Tesar (1968) studied the reasons for Kust and Smith (1968) and Smith (1965) obtaining greater yields from 3 (one-tenth bloom) compared to 2 (full bloom) defoliations each year in Wisconsin. Over 2 years, two-thirds of a 17% yield advantage for the 3 defoliations was due to net leaf loss, the remainder appearing to be due to higher net photosynthetic rates of the physiologically younger plants defoliated 3 times. The results of Brown et al. (1966a) and Pearce et al. (1968) demonstrating reduced lucerne leaf photosynthetic efficiency with age lends support to this latter conclusion.

The ultimate yield requirements for lucerne are in most cases a combination of dry weight yield and quality. The digestibility optimum for lucerne occurs at an earlier stage of growth than the maximum dry weight yield (Coop, 1967), while Griffith and Ramsay (1932) found little change in nutritive quality up to bud stage. Bailey et al. (1970) found a relatively steady decrease in feed quality during regrowth to early flower. Generally, some quality must be sacrificed with more infrequent defoliation so as to maintain sward productivity, vigour and

purity, except maybe, in drier regions using irrigation (Meyer and Jones, 1962). In Ontario, Canada, Winch et al. (1970) found that defoliation at the 50% visible bud stage of growth gave the best combination of all these requirements.

There is evidence to suggest that in many situations a single immature defoliation will not have particularly harmful residual effects. Yields will probably be reduced in the year of cutting, but the distribution of yield may have advantages for management (Keoghan, 1967). A very early spring defoliation generally results in decreased annual yield, but with little if any adverse residual effect (Jackobs, 1950; Jackobs and Oldemeyer, 1955; Dent, 1955; Langille et al., 1965). In a high light, low rainfall region, Jackobs (1950) defoliated with first spring growth at 4", 7", 12" and no defoliation, finding little yield difference and no residual treatment effect. In a less favourable climate, yield reduction was apparent (Langille et al., 1965). The timing of any late autumn defoliation is critical, especially in cooler temperate regions with overwintering problems. The last defoliation must be early enough before growth ceases to allow for the accumulation of sufficient organic reserves needed for the establishment of winter hardiness and to meet the requirements of early spring growth (Smith, 1964). In milder winter growing regions, the autumn accumulation of organic reserves is not likely to be of great concern, other than to maintain reserve levels in accordance with normally recommended defoliation practises.

#### 2.3.1.2. Root Growth.

There are three aspects involved: root dry weight differences between treatments, immediate post-defoliation root dry weight changes and new root growth. In most circumstances, under sward conditions, the cumulative effect of more frequent defoliation on the lucerne tap root is to reduce its dry weight (Graber et al., 1927; Dotzenko and Ahlgren, 1950; Baker and Garwood, 1959; Dennis et al., 1959; Langille et al., 1965; Bryant and Blaser, 1965; Smith and Nelson, 1967). This is in keeping with the loss of plant vigour generally observed with frequent defoliation. With pot experiments sampling the whole root system (Hildebrand and Harrison, 1939; Langer and Steinke, 1965; Leach, 1968a)

observed similar results at the end of their experiments.

Changes of root dry weight (mostly the top 6-8" of tap root and often including the crown) during the post-defoliation regrowth show initial decrease to a minimum at 2-4 weeks and then increase through to shoot growth maturity (Graber et al., 1927; Willard, 1951; Nielsen et al., 1957; Sonneveld, 1962; Smith and Silva, 1969). This decrease is expected to be considerably less when there is a substantial residual leaf area left. A large portion of the observed weight changes are due to similar changes in organic reserve levels (section 2.3.1.3).

With relatively infrequently defoliation, recent fine root growth can make a significant contribution to total root dry weight at the time of defoliation. Fine root growth (root tip extension) is markedly reduced or stops soon after relatively close defoliation; to start re-growing significantly some time later. Investigations show that this varies from 15 days (Hodgkinson, 1967; Ueno and Smith, 1970), to 10 days (Ginsburg, 1958) and 7 days (Smith and Silva, 1969). Hodgkinson (1967) observed that partial defoliation resulted in less restriction of root growth. Mitchell and Denne (1967) presents results which show a 50% loss of fine feeding roots 6 days after defoliation to 1 inch. Zykov (1969) reported that up to 55-60% of fine lucerne roots may die after each defoliation, being mineralised within 25-30 days. Further evidence is required to verify fine root death of such proportions. Mitchell and Denne (1967) stressed that the importance of this fine root growth reduction (and death) was in the associated reduction of the active nutrient absorbing capacity of the root system.

Decreasing defoliation frequencies of reasonable intensities will enable an increase of the rate and amount of fine root recovery between harvests. With more frequent defoliations the significance of this fine root loss is the probability of induced nutrient deficiency and the resultant loss of plant vigour (section 2.4.1.2). Although removing the supply of carbohydrates by defoliation is expected to limit the growth of lateral roots, Hodgkinson (1967) concluded from his own experimental results and the reports from others, that primarily "..... the growth of lateral roots following herbage removal is limited by the supply of essential growth substances which are synthesised by the leaves".

The depression of root dry weights following defoliation has been observed with other species; grasses (Jacques and Edmonds, 1952; Alberda, 1957), clover (Tesar and Ahlgren, 1950; Butler et al., 1959; Chu, 1971); and the reduction or cessation of root growth; grasses (Oswalt et al., 1959; Davidson and Milthorpe, 1966b).

In a cool winter region, Rather and Dorrance (1938) observed the drop in lucerne root dry weight after defoliating too late during the autumn growth period.

#### 2.3.1.3. Chemical Composition.

Compared to root growth, more attention has been given to the concentration changes of organic reserves following defoliation. Total non-structural carbohydrate (TNC) reserve changes are closely correlated with root dry weight changes, decreasing to a minimum at about 3 weeks and then increasing to a maximum at full bloom (Nielsen et al., 1956; Sonneveld, 1962 for others; Smith, 1962; Reynolds and Smith, 1962; Cooper and Watson, 1968; Smith and Silva, 1969; and others). Levels of starch in particular and sugars, change in a similar pattern to the TNC changes after defoliation (Nelson and Smith, 1968). As for root dry weight dry weight, partial defoliation reduces the fluctuations of these reserve levels. Nielsen et al., (1956) found the percentage of hemicelluloses in tap roots also declined after defoliation, while Hodgkinson (1967) observed that the levels of some polysaccharides declined following complete defoliation. With cocksfoot, (Milthorpe and Davidson, 1966b) observed that non-carbohydrate compounds declined after defoliation in circumstances of low initial reserve levels. With lucerne, it is possible that more complex compounds will be broken down and used for respiration and/or new growth following severe defoliation and/or with plants of low organic reserve levels.

Many reports show that increasing defoliation frequency results in reductions of the amount and often the concentrations of TNC reserves at the end of the experimental period (Nelson, 1925; Graber et al., 1927; Willard, 1930; Hildebrand and Harrison, 1939; Weinmann, 1948; Nielsen et al., 1956; Weir et al., 1960; Smith, 1962; Feltner and

Massengale, 1965; Langille et al., 1965; Smith and Nelson, 1967).

Concentrations and amounts of organic nitrogen reserves, usually recorded as total nitrogen (TN), are affected in a similar manner by defoliation frequency as are TNC reserves, except that immediately following defoliation a small concentration increase has sometimes been observed. This is considered to be due to the greater relative drop of the TNC concentration (Jansen, 1929; Graber et al., 1927; Grandfield, 1935; Nielsen et al., 1956; Smith and Silva, 1969). The levels of TN concentrations, amounts and associated fluctuations are considerably less than those for TNC reserves.

The TNC reserve fluctuations are in response to the net effect of new growth, respiration demands and assimilate supply (section 2.4.1.), which may be modified by the effect of environmental conditions on the net energy balance within the plant (Brown and Blaser, 1965, 1970). Lucerne is largely dependant on rhizobial activity in root nodules for its nitrogen supply. In sward conditions, defoliation and reduction of light intensity has been demonstrated to depress root nodule activity and numbers (Thornton and Nicol, 1934). Both treatments reduced photosynthetic activity and provide evidence suggesting that continued nodule activity is dependant on an adequate carbohydrate supply (Pritchett and Nelson, 1951). Butler et al. (1959) demonstrated similar responses with Trifolium and Lotus species. These studies demonstrated the need for plant nitrogen for regrowth following more severe defoliation and hence the observed TN fluctuations.

Nelson and Smith (1968a) showed that crown dry weight was considerably less than the top 6" of root, while Jung and Smith (1961) showed lower concentrations of carbohydrate reserves and less seasonal fluctuation for crowns. Ueno and Smith (1970) provide supporting evidence for the relative importance of roots, but showed further, that tap root wood stored more total non-structural carbohydrate (TNC) reserves than the tap root bark (separated by the cambium layer). TNC concentration and amount were both distributed in proportions of 25% (crown), 55% (tap root wood) and 20% (tap root bark). Following defoliation, the depletion and replenishment of TNC was in the same proportions, suggesting equal availability to storage sites for respiration and growth requirements.

Comparing changes in the level of TNC during regrowth between small, medium and large sized plants, Ueno and Smith (1.c.) showed minimal TNC weights per pot and TNC% on days 7, 14 and 14-21 respectively; the total amount of TNC utilised was proportional to initial plant size. The respective utilisation efficiencies were 1.50, 0.75 and 0.58 g of TNC used to produce 1g of shoot dry matter; it was not known why larger plants were more efficient. TN was not considered

Lukezic et al. (1969) using gnotobiotic greenhouse conditions showed that the carbohydrate reserve decrease with frequent defoliation is a true plant response and not influenced by micro-organisms.

The effects of defoliation on the levels of mineral reserves in lucerne has not been investigated, but from the effect on fine root growth, especially with more frequent defoliation, it would appear that mineral reserves may be of some importance (Mitchell and Denne, 1967; Hodgkinson, 1967; sections 2.4.1.1., 2.4.1.2.)

The actual role and significance of these reserves during regrowth is discussed later (section 2.4.1.1.)

#### 2.3.1.4. Defoliation Height.

Height of defoliation when infrequent tends to be unimportant, especially in practical circumstances, the wastage from residual stubble often being greater than new shoot growth gains. Higher cutting is only likely to be of importance with frequent defoliation when the residual leaf area may give a significant contribution to the plants assimilate supply. This interaction has been demonstrated by Kust and Smith, (1961), Langar and Steinke (1965), and Smith and Nelson (1967), and is likely to be most apparent in a low energy environment (Langar and Steinke, 1.c.).

#### 2.3.1.5. Defoliation by Cutting and Grazing.

There are several distinct differences between these two processes. Cutting is simple and direct. In comparison, grazing can be selective both for lucerne leaf (Arnold, 1960) and new shoots (Peart, 1968). Even when moderate, such grazing will depress lucerne's ability to compete with grasses and weeds (Iversen (1967)).

Animal treading reduces pasture yields (Edmonds, 1966), while nutrient recirculation via animal excreta boosts growth, having greater effect under conditions of adequate soil moisture and generally, giving non-legumes an increased competitive growth advantage due to an enhanced nitrogen availability (Watkin, 1954; Cuykendall and Marten, 1968). The determination of an optimum grazing frequency is dependant on yield, quality and persistency considerations, and further, on the growth stage effect on palatability and the associated utilisation efficiency. Residual mature stems are basically wasteful (Dann, 1968). In general, although absolute yields vary between cutting and grazing, relative yields are similar and Matches (1968) considers the latter parameter more important for evaluating swards.

#### 2.3.2. Effects of Defoliation Frequency on Lucerne Persistence.

The reduction of yields with frequent defoliation can be due to reduced plant numbers (stand reduction), reduced plant vigour or size and associated reduction of shoot numbers per plant. This latter is not loss of persistence per se, but rather an expression of it. Gross et al., (1958) observed that frequently cut lucerne plants were considerably smaller, but their numbers had not been decreased. Willard (1931) observed a similar situation in that he found a low correlation between shoot yield and stand density. Feltner and Massengale (1965) observed the same effect for several treatments. There have been many reports however, showing a decrease in plant numbers with frequent defoliation. For instance Nelson (1925) found 2, 3 and 4 cuts per year reduced plant numbers to 12, 3 and 0 plants per square foot over 2 years. Representing a milder environment, Judd and Radcliffe (1970) observed 4.1, 5.5, and 6.4 crowns per square foot after 3 years defoliating at 3, 4, 5 and 6 weekly intervals. Similar relationships between defoliation frequency and plant numbers were obtained by Jackobs and Oldmeyer (1955), Davies (1957), Dennis et al. (1959), Rixhon (1966), Cullen (1967), Smith and Nelson (1967), Peart (1968), Leach (1970).

Reduced plant vigour, virtually a basic component of reduced persistence, results largely from the effects of environmental conditions and the individual or the combined effect of frequency and seasonal timing of defoliation (sections 2.3.1.1.; 2.3.1.2.; 2.3.1.3.). Further,

reduced plant vigour is often aggravated by a concomitant increase of weeds and grasses which provide direct environmental competition (Nelson 1925; Petersen et al., 1953; Nielsen et al., 1954; Dennis et al., 1959; Weir et al., 1960; Iversen 1967; Judd and Radcliffe, 1970; Leach, 1970c). With moderate defoliation frequencies, it has been suggested that an initial reduction of plant numbers will decrease plant competition, enabling remaining plants to grow larger and thus maintain yield (Grandfield, 1934; Kust and Smith, 1961). It is possible that after the initial defoliations, a more infrequent treatment may be needed to establish this effect.

Some more specific aspects depressing lucerne persistence have been demonstrated. In cool winter regions, considerable winter death of plants can result from an ill-timed autumn defoliation (Smith, 1965). In drier regions or seasons, lucerne is more persistent with more frequent defoliation if not irrigated. Ward et al. (1966) demonstrated this with a lucerne cocksfoot sward; the deeper lucerne root system giving it a competitive advantage for soil moisture, in spite of reduced vigour. With infrequent defoliation, the lucerne plant's vigour is such that it can successfully compete with grasses and weeds, even under irrigation. Van Riper and Owen (1964), Iversen (1967), and Lobb (1967) also noted better dry land persistence. Feltner and Massengale (1965) found that the reduction of lucerne stands under frequent defoliation was aggravated by excessively high summer temperatures of greater than 25 C. It has been observed that lucerne is more persistent in conditions of high fertility, especially for potassium (Graber and Sprague, 1938; Markus, 1966; Smith, 1969a). Lobb (1967) found that on the soils used, selective withholding of phosphorous fertilisation gave lucerne a competitive advantage over grasses and weeds which have a greater phosphorus requirement, and hence, for lucerne, improved persistence. It should be noted, that this management may be at the expense of maximum potential lucerne yields on phosphate deficient soils (Stephen, 1970). Differences in lucerne persistence associated with varietal growth form differences have been demonstrated by Kehr et al., (1962) Leach (1969b). Smith and Graber, (1941) suggested that management techniques detrimental to lucerne production and survival, may also increase susceptibility to diseases

and amplify differences in disease tolerance between varieties. Thus, lucerne persistence is very dependant on the defoliation frequency used, but may well be further modified by any of the other considered aspects.

### 2.3.3. The Growth Form Response of Lucerne to Different Defoliation Frequencies.

The effect of increased defoliation frequency reducing plant size, as evidenced by smaller roots has often been demonstrated (section 2.3.1.2). This has been shown to be associated with the death or size reduction of crown stems (Nielsen et al., 1954; Gross et al., 1927; Peltier and Tysdale, 1935; Grandfield, 1945) and stems per plant (Peltier and Tysdale, l.c.; Cowett and Sprague, 1962; Rumbaugh, 1963; Leach, 1968a, 1970c) are also reduced. This would be expected with the fewer crown and stubble sites present on the smaller plants. The combined effect of these factors is expressed in the lower yields obtained.

At the single shoot level, the results of Leach, (1968a, 1969a) indicated that the individual shoot length at harvest depends on when it resumes extension growth and is largely independant of stage of maturity at defoliation or the intensity of cutting. With defoliation at an earlier growth stage, Leach (1968a) observed fewer shoots, while Keoghan (1970) found little difference in shoot numbers, but both observed reduced initial shoot growth due to the delayed commencement of shoot elongation. Keoghan (l.c.) suggests that shoot numbers will only be reduced with prolonged immature defoliation when the crown size is reduced. This is supported by another of his observations that lucerne has "a tremendous reserve of buds for future regrowth". Thus with more frequent defoliation average shoot length is likely to be less, (e.g. Tsuma, 1968) and more immature at a given harvest time. Comparing his results with those of Leach (l.c.), Keoghan (l.c.) suggests that inter-plant competition within his simulated sward compared to Leach's (l.c.) spaced plants, may well explain their differences of shoot numbers.

The later stage of growth at defoliation, the higher the stem/leaf ratio is likely to be. This is because of increasing lower leaf loss (Fuess and Tesar, 1968) and increasing dry matter accumulation in

the stems (Meyer and Jones, 1962). The residual growth results of Tsuma (1968), showed a lower stem/leaf ratio for previously more frequently defoliated treatments. This correlates with the slower initial shoot growth and longer time to maturity of more frequently defoliated lucerne. Hodgkinson (1967) found that population density did not affect the stem/leaf dry weight ratio of shoots at the same stage of growth.

Both Leach (1968a, 1970 a,b). and Keoghan (1970) consider the relative importance of stubble and basal shoots as components of yield. Keoghan's (l.c.) classification defined stubble shoots as arising on upper stubble nodes with inter-node length greater than 0.6 - 0.7 cm, while basal shoots arise from the crown and lower nodes not exceeding 0.5 cm in length. For discussion, Leach's (1970a) classification for shoots arising on the 0-2 cm and 2-10 cm stubble segments are similar. Both authors found that the contribution of basal shoots to yield was much more important at all stages of defoliation. This was represented in terms of numbers and earlier extension growth. Stubble shoots probably only approach important proportions with high level, very immature defoliation (Keoghan, l.c.). Under field conditions, Keoghan (l.c.) noted even greater basal shoot dominance with all stages of defoliation. Both authors also observed indications of intershoot competition. With very intensive defoliation resulting in smaller shoot numbers (all basal shoots), individual shoot size was slightly larger than with less intensive defoliation when some stubble shoots were present as well (more shoots). Hodgkinson (1967) demonstrated a similar result in an experiment in which shoot numbers were experimentally controlled (section 2. 4. 2. 3.).

As the height of defoliation is raised, with immature stubble, a greater residual leaf area is left. However, there is negligible residual leaf area with mature stubble regardless of defoliation height, although this latter can be increased by a significant leaf area contribution of newly elongating basal shoots (Keoghan, 1967). Such leaf area is capable of significantly contributing to the lucerne plant's initial post defoliation carbohydrate assimilation, particularly with immature stubble (Hodgkinson, 1967; Keoghan, 1970; section

2. 4. 1. 3. ).The interaction of defoliation frequency with defoliation height is implicit.

2.3.4. The Effect of Defoliation Frequency on Lucerne Growth Rates.

The lower yields with more frequent defoliation represents an overall lower crop growth rate (CGR). For given growth periods, comparisons of lucerne growth rates between treatments of different defoliation frequencies, appear to have been confined to studies at Lincoln, Canterbury (Steinke 1963; Langer and Steinke, 1965; Keoghan, 1966, 1970). The majority of studies have considered only total annual yields. Steinke (1963) showed that frequent defoliation, reducing plant weight, was associated with lower relative growth rates (RGR), indicating less efficient growth from the smaller plants. He also obtained initially negative root RGR for closely defoliated plants. In some cases this could also apply to whole plant growth, when this below-ground weight loss is faster than the rate of new growth. Implicit in the lower yields at each harvest of more frequently defoliated lucerne are lower CGR's.

Most of the work on lucerne growth analysis has been concerned with the relationship between CGR or rate of photosynthesis and leaf area index (LAI) (Steinke, 1963; Keoghan, 1966, 1970; King and Evans, 1967; Wifong Brown and Blaser, 1967). This work, as in other crops (Watson, 1958; Ludwig et al., 1965 - cotton; Shibles and Weber, 1965 - soy beans; Williams et al., 1965 - maize; and others) was aimed at determining whether an optimum LAI would be attained and if so, the nature of it; i.e. narrow, broad, or plateau. Keoghan (1970) considers the subject and its explanations fully. Steinke (1963), with a lucerne field experiment, demonstrated a narrow LAI optimum, thought to be due to soil moisture limiting the more mature growth. King and Evans (1967), Wilfong et al., (1967) and Keoghan (1970) obtained broad optimum LAI, while in 1966 and in other experiments in 1970, Keoghan obtained plateau LAI relationships. These varied results indicate the complexity of factors controlling this relationship. Among these factors are the efficiency of light inter-

ception related to changes of the light extinction coefficient (Keoghan, 1970); differences of leaf photosynthetic capacity between species (Brown, Blaser and Duntun, 1966) and possibly varieties (Dornhoff and Shibles, 1970); reduced leaf respiration rate of older and more shaded leaves in the canopy, probably explained by an associated increase of specific leaf area (Wilfong et al., 1967; Williams et al., 1965; Shibles and Weber, 1965); and the effects of other environmental variables, especially moisture (Keoghan, 1970).

The influence of different defoliation frequencies has not been reported. With more prolonged treatments resulting in differences of sward morphology (e.g. stem density), light interception will be varied which may well influence the form of the CGR/LAI relationship. Postulated changes for the more physiological factors are less obvious, although Keoghan (1970) found a denser lucerne sward had a greater average specific leaf area than a less dense sward.

#### 2.4. Factors Controlling the Yield and Regrowth Rate of Lucerne.

These factors are grouped as a physiological, morphological and environmental classification, and are considered as they contribute to the explanation of the various aspects of yield and regrowth discussed in the previous sections. Of necessity, the control of regrowth per se, will tend to precede the situation in respect to different defoliation frequencies.

##### 2.4.1. Physiological Factors.

###### 2.4.1.1. The Role of Reserves.

There are three types of reserves to consider: non-structural carbohydrates, nitrogen and mineral reserves. The effect of different defoliation frequencies on subsequent shoot growth and root weight, organic reserves and plant vigour has been discussed. The carbohydrate reserves have received far more attention in the past, in particular, for their contribution to new shoot growth. A relatively consistent line of thought has developed over the last forty-five years in respect to this role of carbohydrate reserves, but in the last decade its

validity has been questioned, and during the last few years the question has been elucidated considerably.

In 1927, Graber et al. postulated that "..... New top growths especially in the earlier stages, are initiated and developed largely at the expense of previously accumulated organic reserves." This postulation was generally accepted over subsequent years, supported by repeated demonstrations of good correlations between plant yield and/or vigour with carbohydrate reserve levels (Harrison, 1939; Sprague and Graber, 1938; Weinman, 1948; Weir et al., 1960; Feltner and Massengale, 1965; Langille et al., 1965; Smith and Nelson, 1967; and others) and that growth after defoliation is generally associated with a decrease in the level of carbohydrate reserves (Graber et al., 1927; Grandfield, 1935; Brown and Munsell, 1942; Reynolds and Smith, 1962; Smith, 1962; Nelson and Smith, 1968b) which follows the general cyclic pattern described (section 2.3.1.3.). Doubt as to the soundness of this postulation was expressed notably from two sources. May and Davidson (1958) suggested that the post-defoliation use of carbohydrate reserves for respiration could be of greater importance. Soon after, May (1960) questioned the acceptance of the hypothesis of accumulated carbohydrate reserves having a specific role in initiating regrowth since "..... the paucity of knowledge of mobilising hormones, mechanisms of translocation and utilisation of carbohydrate reserves at meristems precluded a critical evaluation of the part played by reserves in determining regrowth." Smith (1962) still contended that carbohydrate reserves in part contribute to new foliar regrowth of lucerne after defoliation, and recent work has supported this view.

In response to these reconsiderations, much work has been done to elucidate this aspect of regrowth, this being particularly successful with lucerne (Hodgkinson, 1967, 1968, 1969; Silva, 1968; Smith and Silva, 1969; Smith and Marten, 1970), and other species (Davidson and Milthorpe, 1965, 1966a, 1966b; Carlson, 1966a 1966b; Alberda, 1966; Mitchell and Denne, 1967). Earlier work was done with grasses showing grass shoot stubble to be the main source of carbohydrate reserve, rather than the roots, and that these reserves were used

for both respiration and new growth (Davidson and Milthorpe, 1966a; Alberda, 1966). Marshall and Sagar (1965), using  $^{14}\text{C}$  tracer, showed a grass inter-tiller photosynthate interdependence following partial defoliation, while Ehara et al. (1967), using Paspalum notatum demonstrated that new leaf tissue used in part at least,  $^{14}\text{C}$  labelled compounds from the stubble and roots. With severe defoliation and low initial reserve levels, Davidson and Milthorpe (1966b) and Alberda (1966) found that substances other than non-structural carbohydrates were used to supplement their reserve supply. Nitrogenous compounds were suggested, but also plant parts may be sacrificed to provide a source of substance for regrowth and/or respiration (Alberda, 1966), and Hodgkinson (1968) stated that even structural compounds could be broken down and retranslocated.

Particularly good progress has been made in resolving the role of organic reserves in lucerne regrowth by studying their re-distribution after being  $^{14}\text{C}$  labelled. By this method, Hodgkinson (1967), Silva (1968) and Smith and Marten (1970) have all conclusively demonstrated that organic reserves are used in part, for the formation of new lucerne shoot growth. In more intensive studies, Hodgkinson (l.c.) followed this redistribution over 30 days regrowth, while Smith and Marten (l.c.) did so by harvesting at 5 regrowth stages - 15 and 30cm height, bud, first bloom and 50% bloom. Their results showed several similarities. Notably, the greater proportion of  $^{14}\text{C}$ -labelled compounds was used as respiratory substrates, although during the early regrowth period, respiratory and new shoot growth use was approximately equal. Also, the percentage content of  $^{14}\text{C}$ -labelled compounds in the total new shoot growth was initially high, decreasing with time as current photosynthate increasingly contributed. Thus the intensity of shoot labelling was inversely proportional to the length of the post-defoliation period.

In marked contrast, Smith and Silva (1969) in a quantitative study and Silva (1968) using  $^{14}\text{C}$ -labelling, found at 21 and 26 days respectively, that much greater proportions of the originally stored organic compounds in the roots and crowns were used in new shoot and root growth; that used as a respiratory substrate being relatively small.

In agreement however, was the high initial use of organic compounds stored in the roots and crowns for new shoot growth, followed by the rapidly increasing contribution from current photosynthate. Both groups observed the continued use of labelled organic compounds throughout the vegetative growth stage. All except Hodgkinson (1967), found that they had a high utilisation of labelled compounds (70-80%). Hodgkinson (l.c.) observed a 50% utilisation by 20 days regrowth, after which there was little change.

Smith and Marten (1970) found that much of the initially labelled non-structural carbohydrates later located in new shoot growth occurred as translocated non-structural carbohydrates; that incorporated in shoot structural tissue being relatively low, fluctuating between 4 and 9% of the initial reserve level. Hodgkinson (1967) did not distinguish between these fractions.

More complex organic compounds may be depleted during regrowth (section 2.3.1.3.). Nielsen et al. (1956)

reported hemi-cellulose mobilisation during lucerne regrowth. Hodgkinson (1967) had evidence suggesting this may occur, but also quoted Whistler and Young (1960), and Porter (1962) as providing evidence suggesting that hemicellulose and cellulose are stable end products of metabolism. Nitrogenous compounds located in storage organs are necessarily translocated for new shoot growth, but if necessary, as Steward et al., (1958) have shown, they can be utilised as respiratory substrates. This evidence supports other reports that other non-structural carbohydrate reserves can be utilised during pasture regrowth, as respiratory substrates at least (Davidson and Milthorpe, 1965, 1966b, Alberda, 1966; Humphreys and Robinson, 1966), particularly if defoliation is reasonably severe and reserve levels are low. More detailed investigation to determine the relative importance and use of these compounds during regrowth, and under what conditions are required.

This has been done to some extent with quantitative studies of the importance of nitrogenous compounds in plant regrowth. Such studies are few, even though Graber et al., (1967) included organic nitrogen compounds in his definitions of reserves. Using grass species, Bommer (1966) obtained considerably greater yields from plots reciev-

ing heavier applications of nitrogen fertiliser, with an associated greater reduction of carbohydrate reserves, suggesting greater use of the latter. More directly, both Dilz (1966) and Sheard (1968b, 1970) found a high correlation between plant nitrogen content at defoliation and weight of regrowth, while that between regrowth and turf carbohydrate content was low, (Dilz, 1966) and negative with fructose concentration in the tertiary shoot of timothy (Sheard, 1968b, 1970), the vegetative organ most influencing the spring growth of timothy (Sheard, 1968a). Dilz (1966) demonstrated a considerably greater shoot yield per a unit weight of protein compared to a unit weight of carbohydrate. This efficiency of proteinaceous compounds suggested that they were at least as important for herbage regrowth as non-structural carbohydrates. Sheard (1968b, 1970) found that a high internal N supply provided a ready supply of organic N for new shoot growth. If in low supply, though, it may well be growth limiting, even though the carbohydrate reserve level is adequate to meet the energy demands of growth and respiration from these non-nitrogenous substrates. He concludes ".....a balance of carbohydrate for energy and a readily available source of protein for the synthesis of new protoplasm within the plant is superior to a high carbohydrate-low protein relationship."

This work with grasses has not been extended to legumes and in particular, to lucerne. The effect of severe defoliation restricting lucerne root nodule nitrogen fixation (section 2.3.1.3.) and restricting root growth (section 2.3.1.2.), means that initially, protein precursors required for new shoot growth, must largely be provided from reserve sources. Using the nodulated legume, Pisum sativum during vegetative growth, Pate (1956) showed the direct export of fixed nitrogen from the root nodules to the shoots as amides (observed in other symbiotic associations; see Pate et al., 1965). Sugars translocated from the leaves provide essential carbon skeletons for amide synthesis in the roots (Pate et al., l.c.). It is reasonable to expect a similar occurrence in lucerne, and as such, it is most probable that some of the  $^{14}\text{C}$  labelled organic compounds in the lucerne roots in the experiments of Hodgkinson (1967) and Smith and Marten (1970)

were amides or other nitrogenous compounds. In lucerne this is yet to be experimentally verified. In turn, a proportion of the translocated material used in new lucerne shoot growth was most probably these  $^{14}\text{C}$ -labelled nitrogenous compounds. With a number of species it has been shown that these translocated amides and amino acids are transaminated in the leaves to form different amino acids and proteins (Pate, 1966; Joy, 1967).

Hodgkinson (1967) found that  $^{14}\text{C}$ -activity was located throughout the shoot after 20 days regrowth, although more intense in the earlier formed tissue. This indicates a continued acropetal movement of  $^{14}\text{C}$ -labelled material into the shoot during this period. At the same time he found new shoots started to export assimilates to the roots by the 6th day after complete defoliation. Although a bi-directional movement of carbohydrate has been questioned (Hodgkinson, 1967), a continued acropetal movement of  $^{14}\text{C}$ -labelled amides and amino acids to be incorporated in the growing leaves and apical region tissue of the shoot could well explain the continued labelling of the shoot over this period. Normally, this process would be expected to last until such time as root nodule activity and/or soil nitrogen absorption return to a level satisfying shoot growth requirements. Pate and Wallace (1964) showed that the field pea shoot receives much nitrogen in organic form through the xylem, as well as some in the phloem. Lucerne may have a similar method of acropetal nitrogen distribution. Recent work suggests the possibility of bidirectional movement in the phloem should not be ruled out (Crafts, 1967; Trip and Gorham, 1968; Ho and Peel, 1969). More probable is a bidirectional movement of photosynthate basipetally and nitrogenous compounds acropetally. The directional distribution of these compounds is probably largely controlled by the influence of the various plant parts as sites of demand (sinks), their relative importance varying in relation to their individual intensities of demand for each compound. Wardlaw (1965) demonstrated this principal with wheat, and Hale and Weaver (1962) with Vicia.

It is suggested that the role of nitrogenous reserves in lucerne and other species regrowth probably warrants study of a similar nature to that already performed with carbohydrate reserves. Their

importance in shoot regrowth may well be relative to the level of carbohydrate reserves, as concluded by Sheard (1968b). The greater role of lucerne organic reserves as respiratory substrates has been reasonably established, although at the same time as Hodgkinson (1970) concluded, the hypothesis of Graber et al., (1927) has been confirmed, but "..... it still remains to be shown that the availability and quality of these compounds (nitrogenous and carbohydrate) regulate the rate of shoot regeneration." Environmental factors aside, it may be that the relative levels of nitrogenous and carbohydrate from residual leaf area and/or new shoot leaf will soon confound the relationship.

The influence of defoliation frequency on the role of organic reserves is through its control over the levels and amounts of reserves available in the storage organs at defoliation; possibly the relative levels of available nitrogenous and carbohydrate reserves; its influence on root nodule activity; the extent of residual leaf area left, and its activity; and whether or not more complex compounds are broken down. Further work, is needed to elucidate the relationship of these aspects with different frequencies of defoliation.

The role of mineral reserves does not appear to have been investigated, except that Hodgkinson (1967) regrew lucerne in both phosphorous containing and phosphorous-free media, and obtained no yield differences for the single regrowth period studied. This indicated a high level of surplus phosphorous within the root and crown, and that with reasonable nutrient availability mineral reserves may not be a problem in the short term. In the longer term, with repeated frequent defoliation, they may be growth limiting (see section 2.4.1.2.).

In the preceding discussions and some of those to follow, the use of work on grasses to provide support or indicators for the same situation in lucerne, should be considered with some reservation. Being monocotyledons and dicotyledons respectively, their leaf morphology and development is very different. Davidson and Milthorpe (1966a) concluded from their studies with Dactylis glomerata, that photosynthate export from the leaves did not occur until they were close to full expansion. In contrast Hodgkinson (1967) observed export from new lucerne shoots on the 6th day of growth, and with the field pea, individual leaves commence significant assimilate

export when only one quarter their final area (Pate, 1968). These differences result from their differences of leaf anatomical development (Esau, 1960; Fahn, 1967). The other major consideration is their different modes of nitrogen nutrition. However, providing these differences are recognised and kept in mind, hypothetical extrapolations may be useful.

#### 2.4.1.2. The Role of Lateral Roots.

Finer lateral root growth slows considerably or even ceases after defoliation, dependant on its severity (section 2.3.1.2.). Evidence from grasses (Mitchell and Denne, 1967), indicates that this reduction of root (tip) growth, if prolonged, may soon be followed by root hair death, and hence a reduction of the active nutrient absorbing area. This will recover only by renewed root tip growth as Hodgkinson (1967) observed with lucerne lateral roots, which became brown along their length, and suberised in the exodermal cells. There is little absorption of ions through the walls of suberised roots (Kramer, 1956), and ion uptake is an active process (Brouwer, 1965) requiring a supply of assimilates. Thus severe defoliation will sharply or completely reduce the assimilate supply to the lateral roots, reduce root growth, and also reduce ion uptake. With grasses Oswalt et al., (1959), and Davidson and Milthorpe (1966b) have demonstrated a marked reduction of  $^{32}\text{P}$  uptake following defoliation. It is probable that the same occurs with lucerne, for a time period largely dependant on the potential energy supply of the plant. In this latter context Hodgkinson (1967) found that  $^{14}\text{C}$ -labelled assimilates were translocated equally into the tap root and lateral roots for the first 20 days' regrowth but there-after a higher proportion was translocated into the lateral roots, this being coincident with the renewed lateral root growth and activity after 15 days, these providing a stronger sink.

In the short term, with plants of reasonable vigour, this root growth reduction may not be excessively important in restricting the plants' nutrient supply as shown by Hodgkinson (1967; section 2.4.1.1.). With less vigorous plants, lower internal available nutrient levels may exist, resulting in the root growth reduction being more significant. This potential deficiency will be countered in part

by the nutrient remobilisation (including nitrogen) that occurs within the plant, from older, and especially senescing organs to active growing regions (Hopkinson, 1964; Leopold, 1964). With other non-nodulated species, a resultant induced nitrogen shortage may be significant at an earlier regrowth stage. With lucerne, reduced nodule activity may create a similar nitrogen effect.

In the longer term, a continuation of frequent defoliation will aggravate the situation in that nutrient and nitrogen levels in the roots will not be adequately replenished, because of the limited root growth. These deficiencies will certainly start to limit shoot growth. In these circumstances, Mitchell and Denne (1967) suggested that these factors may be the major determinants of the yield reductions generally recorded. They emphasise that where there is a decrease of the effective nutrient absorbing surface and nodule activity, the decreased root efficiency will probably be considerably greater than a reduction in the weight of the total root system would indicate. Ueno and Tsuchiya (1968) observed this with lucerne, top growth, having a greater dependence on lateral root growth, compared with tap root growth.

A further root factor limiting shoot growth, may be a reduced root production of growth substances. Waring et al., (1968) performed experiments which suggested that root-synthesised cytokinins may be needed for protein synthesis in shoots. These are likely to be produced in the lateral root tips, and consequently production would be curtailed in association with reduced root activity following defoliation. Although initial root supplies may result in a temporary excess above demand following defoliation (section 2.4.1.3.), they may be limiting to shoot growth a few days later, when defoliation is severe. In complete contrast, Hodgkinson (1967) concluded from his own results, and the work of others, that following defoliation, shoot produced growth substances (auxins-Torrey (1950) and Pilet (1965); vitamin B compounds-Robins (1951)) are more restrictive than the supply of carbohydrates to the growth of lateral roots. The most important conclusion from this, is that growth substances are probably an important controlling factor during the regrowth of shoots and associated root growth.

### 2.4.1.3. The Role of Residual Leaves.

In the past, the area of residual leaf following defoliation has largely been considered as it is affected by the defoliation height. At a given height, though, the stage of maturity at defoliation (frequency) can also influence the area and efficiency of residual leaf. Thus the inter-relation of its photosynthetic contribution with organic reserve levels in promoting shoot regrowth must be considered. Further, the several reports showing that a leafy stubble can alleviate the adverse effects of frequent defoliation on yield (section 2.3.1.4.) are directly pertinent.

Both Hodgkinson (1967) and Keoghan (1970) studied the physiology of the subject.

The primary requirement is that any yield advantage must outweigh the disadvantage of incomplete herbage utilisation. Further, more mature defoliation is usually associated with a low residual leaf area giving little if any regrowth benefit (Ridgman, 1960; Van Riper and Owen, 1964; Keoghan, 1966; Hodgkinson, 1967). A further problem in field conditions is the high rate of stubble death observed by Ridgman (1960), and Keoghan (1966, 1970), especially if the stubble is relatively mature.

Keoghan (1970), lists several factors that will determine the effectiveness of residual leaves:

1. The area of leaves on the stubble and their light intercepting properties.
2. The photosynthetic efficiency of these leaves including their adaptation to the marked change in environment caused by defoliation.
3. The longevity of these leaves during regrowth.

The basal leaf area of reasonably dense lucerne swards decreases as shoot growth ages (Keoghan, 1966; Fuess and Tesar, 1968), to very low levels with maturity; e.g. 0.14 LAI for 34 days growth (Keoghan, l.c.). Pearce et al. (1968) and Keoghan (1970) showed that this residual basal leaf life is of limited duration relative to natural leaf longevity. This is still shorter in the field. This suggests that a leafy stubble can be attained only by relatively immature defoliation. There is the exception, in that with mature swards, new basal shoot leaf area can be significant, providing defoliation

is high enough to retain these shoots. Keoghan (1966) measured a basal shoot LAI of 0.41. In the only reported case, Keoghan (1970) found a 10cm leafy stubble to have a considerable light interception capacity.

Several workers have demonstrated that the photosynthetic efficiency of lucerne leaves decreases with age (Pearce et al., 1965; Brown et al., 1966a,b; Hodgkinson, 1967; Fuess and Tesar, 1968; Keoghan, 1970; and others with other species). From this evidence Brown et al. (1966b) thought that stubble residual leaves, the older leaves, were probably not very efficient. However Hodgkinson (l.c.) found that the apparent photosynthetic rates of residual leaves increased considerably following defoliation, irrespective of age. Keoghan (l.c.) showed a similar response, this adaptation to the increased light environment being complete within 24 hours, causing him to conclude that in good light conditions a leafy stubble could provide a significant assimilate contribution, reducing the stress of frequent defoliation on the root system. There is some uncertainty as to how comparable the residual leaf improved photosynthetic rate and that of newly produced leaves are. Hodgkinson (l.c.) found little difference at 10 days in a glasshouse study. In contrast Keoghan (l.c.) found new leaves appeared to be more active in an out-door experiment, which is possibly the more likely situation in the field in view of the greater leaf senescence rate observed in field conditions (Keoghan, l.c.). In turn though, there must be a leaf age limit to this adaptation. Any improvements of basal leaf photosynthetic efficiency will be more beneficial following immature defoliation, as Brown et al. (1966b) showed that younger residual leaves survived longer.

Both Hodgkinson (1967) and Keoghan (1970) demonstrated the beneficial effects on shoot growth of residual leaves, using 15cm and 10cm high stubble respectively. Total plant weight decreased to a minimum for the first 7-10 days with no residual leaf, but showed no decrease with residual leaf area. After this minimum weight point, Keoghan (l.c.) observed that the whole plant and shoot growth rates were very similar. The yield results of Hodgkinson's (l.c.) experiment show a similar effect. The commencement growth stages of this common growth rate, appears to correlate with the stage of a critical leaf area observed by Silva (1968). He considered that the attainment of this growth stage during regrowth is associated with shoot growth becoming largely independent for (presumably) carbohydrate supply, this coming from photosynthesis. Yields of shoots were greater,

the sooner this point was attained. Leach (1970a) also observed that retaining residual leaf area increased total yield by enabling the earlier resumption of shoot growth, the effect being independent of stage of maturity at defoliation. Davidson and Milthorpe (1966a) after examining the results of Ward and Blaser (1961) demonstrated that they had obtained the same effect with cocksfoot. This correlates with the conclusions of Leach (1969a) for each of three lucerne varieties, that regrowth yield depends on the number of shoots and particularly, the time when each shoot resumes growth. Keoghan (1970), also found that the shoots elongating earliest contributed most to the final yield.

#### 2.4.1.4. The Inter-relationship of the Physiological Factors.

The evidence indicates that carbohydrate reserves largely influence lucerne regrowth indirectly. They are used to a greater extent as a respiratory substrate in the roots and crowns; to a lesser extent as carbon skeletons for the formation of amides and amino acids in the roots, and for translocation as carbohydrates into the new shoots. This latter occurs for each shoot until the attainment of a critical leaf area enabling the new shoot growth to be relatively self sufficient for respiratory and growth carbohydrate requirements. Continued root to shoot organic translocation occurs (Hodgkinson, 1967) probably largely as nitrogenous compounds needed for leaf and apical growth in particular. The pattern of translocation and the importance of nitrogenous compounds in regrowth and respiration requires further study. It is feasible that an organic reserve combination of low nitrogen and high carbohydrate levels may limit growth, although this may be more likely in non-leguminous species which generally have a lower nitrogen content. For lucerne to attain a high carbohydrate reserve level, the growth conditions will be such that nitrogen fixation activity is likely to increase giving a higher nitrogen reserve level unless there are specific factors limiting fixation. In most instances, high carbohydrate reserves will be associated with improved nitrogen levels, and probably enhanced top growth.

Residual leaf area makes an important positive contribution of assimilate in regrowth conditions of low carbohydrate reserves. This

is directed to new growth and for respiration, but also in an indirect manner by easing the withdrawal on root and crown carbohydrate reserves by the shoots, leaving more for root respiration and potentially for root growth; this, providing that defoliation is high enough and at an early enough growth stage to ensure there is sufficient residual leaf area obtained. The benefit from residual leaf area is particularly apparent in these latter circumstances, in view of the increased photosynthetic activity of residual leaves after defoliation (section 2.4.1.3.) and that these conditions are typical of frequent defoliation. In practice, in the field, residual leaf area is probably of limited importance, as the density of a reasonable stand coupled with the more usual defoliation at later stages of growth, will result in considerable senescence of basal leaf (section 2.4.2.2.). Hence very little residual leaf will be left even with higher defoliation.

These regrowth aspects, largely related to the plant's carbohydrate balance, tend to be of more importance in the short term after each defoliation.

With prolonged sequential frequent defoliation, it is suggested that depletion of nutrient and nitrogen levels in the plant may be more influential in causing the reduced plant vigor and size so often observed.

In this context, there is the importance of the reduced lateral root growth and the associated reduction of nutrient uptake. For Hodgkinson (1967) this probably lasted for 15-20 days, as new root growth was not significant till the 15th day. During the latter stages of this period of reduced root activity, a nutrient shortage may develop, even though shoots are probably relatively independent for assimilates. The availability of carbohydrates at the root tips is possibly an important factor restricting this root growth. However, Hodgkinson (l.c.) presented evidence which indicated that a supply of essential growth substances which are synthesised in the leaves may be the primary restricting factor (section 2.4.1.2.). With lucerne, many of these aspects of root growth, activity, and their control are likely to be equally applicable to the reduced root nodule activity and hence nitrogen availability, following defoliation.

From these responses, it may be postulated that with continued close and frequent defoliation, the short regrowth interval will initially result in the depletion of carbohydrate, nitrogen and nutrient root reserves with only a limited replenishment by the next harvest. Root growth is

restricted for longer periods than shoot growth, which would result in nutrient reserves (probably including nitrogen) staying relatively depleted, in turn resulting in more restricted shoot growth, so further restricting the supply of carbohydrates and possibly necessary growth substances for root growth. The plant would become progressively weaker, with root death and overall reduction in weight and size as has been frequently demonstrated. These various growth restrictive factors will be more marked in plants of low vigour and probably more so if small. Also, competition with larger lucerne plants and/or other species will be increasingly evident accentuating the defoliation effect. Needless to say, the above discussion assumes that the various environmental factors necessary for growth are not limiting.

If appears as though shoot regrowth may basically be restricted firstly, by the time taken to attain a leaf area permitting the shoots to be self-sufficient for carbohydrate, and secondly, through a limited availability of nitrogenous compounds and nutrients restricting the rate of the subsequent regrowth, or even the first regrowth.

#### 2.4.2. Morphological Factors.

##### 2.4.2.1. Basal shoot status in mature lucerne.

It has been established that greatest annual yields are often obtained if the presence of new basal shoots is used as a defoliation criterion (section 2.3.1.1.). Mitchell and Denne (1967) suggested that defoliation before either flowering or the start of new basal shoot growth would mean the lucerne plant has to re-establish active meristems from the crown at a time when the plant is not physiologically ready for this. This re-establishment period will involve an initial growth delay, even in conditions of large residual leaf area as can be the case with immature defoliation. Nelson and Smith (1968a) concluded similarly from their studies of lucerne morphological development.

The advantage of the basal shoot presence criterion, presupposes that defoliation height is such as to leave any developed basal shoots intact. If cut, Meyer and Jones (1962) found that there was a time delay while new shoots developed. Keoghan (1970) demonstrated a significant yield advantage when these shoots are left intact. The photo-

synthetic capacity of basal shoot leaves has not been investigated. It is probable that they have lower light saturating intensities typical of leaves that have developed in the shade (Leopold, 1964). It is not known if these leaves photosynthetically adapt to the higher light intensities following defoliation, as observed for mature residual leaves (Hodgkinson, 1967; Keoghan, 1970). If they do not adapt, growth delay may occur while the shoots develop their first sun leaves. Keoghan (l.c.), presents evidence suggesting that even if these leaves do adapt, they are less photosynthetically active than newly produced leaves.

#### 2.4.2.2. Senescence.

Keoghan (1970) stated; "...The extent to which a measure of viable plant material underestimates productivity depends on the rate of loss of dry matter produced during regrowth." Fuess and Tesar (1968) demonstrated the large loss of leaf and hence yield if lucerne is allowed to become fully mature. With time, this loss is progressive from the bottom of the shoot following the leaf age gradient. From the studies on leaf longevity in outdoor grown lucerne, Keoghan (l.c.) found little leaf loss up to 30 days regrowth, but progressive older leaf death after this. Pearce et al. (1968) found significantly less leaf senescence in thinned plots. It is probable that improved light conditions in the thinned sward largely contributed to this extra longevity. This has been demonstrated for other species (Brougham 1962, Hopkinson 1966). It is probable that as lower lucerne leaves become excessively shaded, photosynthesis of these leaves will be very low and senescence initiated or accelerated, resulting in the lifting of the leaf canopy as shoot growth approaches maturity. Leaf canopy depth and leaf area may be increased during growth because of a decrease of the mean light extinction coefficient due to changes of leaf arrangement, permitting better light penetration (Keoghan 1970) The rate of lower leaf senescence would probably be reduced.

Defoliation frequencies may affect leaf senescence by the rate of leaf area production and hence the time before basal leaves are in excessive shade and thus encouraged to senesce. Differences in stem density under different defoliations frequencies (section 2.3.3.) may alter the light environment of the sward although changes of leaf angle and arrangement may also influence this result.

On a larger scale, Keoghan (1970) observed that whole shoots sen-

esced and died; this probably being more applicable for the last shoots elongating as they would be subjected to strong light competition from the earlier elongating and hence larger shoots.

These losses from senescence have been discussed in the productive agronomic sense. It should be remembered that the physiological loss is smaller as a large proportion of the nutrient content (including nitrogen) of the senescent organs are retranslocated to actively growing organs. This is important in helping to maintain growth when the source of these nutrients may be limited (Benson et al., 1961; Leopold, 1964; Greenway et al., 1968).

Other environmental factors influence leaf longevity; moisture stress and high temperatures generally accelerate the onset and rate of senescence (Leopold, 1964). Disease attacks can also reduce leaf life (Keoghan, 1966).

A further requirement is the maintenance of adequate root growth to provide new centres for cytokinin synthesis, adequate levels of which are required for the normal leaf longevity in the conditions prevailing. (Leopold, 1964; Waring, et al., 1968).

#### 2.4.2.3. Shoot Numbers and Plant Intershoot Competition.

Leach (1968a, 1969a) concluded that regrowth yield is dependant primarily on the number of shoots and time each starts elongating. This latter factor is largely controlled by the physiological factors discussed. The number of shoots are partly controlled by crown and stubble morphology and modified by varietal differences. Leach (1969a) obtained significantly greater shoot numbers and a resultant yield from a lenient defoliation compared to a severe defoliation, but with varietal differences evident only with the lenient defoliation. These results "tended" to reflect differences in the number of potential shoot sites, although some of the varietal influence was obviously genetic. Keoghan (1970) did not find this yield advantage of greater shoot numbers, considering this was explained by intra-plant competition, but was also likely to be in part due to inter-plant aerial competition as he used potted plants arranged in a simulated sward. Leach (1968a, 1969a) used spaced plants as did Cowett and Sprague (1962) who obtained a similar yield advantage for shoot numbers per plant. Rumbaugh (1963) demon-

strated that increased lucerne plant density reduced stem number and size due to interplant competition. As Keoghan (1970) concluded, and Leach (1968a) recognised, extrapolation from spaced plants to sward conditions may lead to variances such as this.

The evidence for, or suggestion of, plant intershoot competition has been presented severally (Hodgkinson, 1967; Leach, 1968a, 1970a; Keoghan, 1970). Leach (1970a) noted a competitive advantage for shoots elongating earliest which Keoghan (1970) confirmed from his experiments. Keoghan (l.c.) considered from his observations that this arose from the very heterogeneous nature of the lucerne shoot population which varied widely in time of elongation and thus size and stage of maturity. The competitive effect was such in one experiment, that some complete shoots senesced.

Hodgkinson (1967) using single plants on which only 4, 8 or 12 shoots were permitted to grow, observed an extreme plasticity of shoot growth. Weight per shoot changed inversely with shoot numbers per plant, thus retaining a relatively constant yield. He suggested the evidence indicated, that providing the environment was non-limiting for growth it was not the number of shoots per plant that limited regrowth yield, but the rate of supply of organic and inorganic compounds from the roots to the new shoots. Leach (1968a) also observed evidence for inter-shoot competition; shoot size and number present showing an inverse relationship.

This would suggest that the time of shoot elongation is more important as a determinant of yield, than the number of shoots. Further Keoghan (1970) noted that lucerne has a tremendous reserve of buds for future regrowth, of which only a small proportion elongate after each defoliation. These buds are largely located on the crowns and stem bases. This is in accordance with the greater relative importance of basal shoots compared to stubble shoots (Cowett and Sprague 1962; Hodgkinson, 1967; Leach, 1970a; Keoghan, 1970). This dominance of basal shoots is accentuated in the field (Keoghan, l.c.).

### 2.4.3. Environmental Factors.

#### 2.4.3.1. Light transmission and interception in the lucerne canopy.

This is considered in association with the lucerne's physiol-

ogy. Langer (1967) and more recently Keoghan (1970) reviewed this subject. Lucerne is a potentially high yielding species, this being partly due to the good light interception properties of its canopy.

The amount of light intercepted is dependant on the stage of growth and stem density as major variables. Cowett and Sprague (1963) demonstrated a decrease in the amount of light intercepted as plant density was decreased, this effect possibly being initially countered in sward conditions by increases of stem numbers per plant due to the reduced interplant competition (Smith, 1962). Stanhill (1962) demonstrated that a decrease of defoliation frequency from 31 to 48 days resulted in an increase of the proportion of light intercepted during the season with an associated yield increase. This is expected with lucerne, where the induction of a more prostrate growth form due to frequent defoliation is not generally apparent as compared to such induction for some other species (Brougham, 1959). Normally a more prostrate growth form has a greater residual light interception capacity.

For several species, a range of light transmission patterns have been recorded; from an abrupt light decrease for white clover (Mitchell and Calder, 1958; Stern and Donald, 1962), Less so for red clover (Mitchell and Calder, l.c.), to a relatively uniform decrease for grasses and grass/clover mixtures (Mitchel and Calder, l.c., Stern and Donald, l.c.). Of the several studies for lucerne (Steinke, 1963; Warren Wilson, 1965; Keoghan, 1966, 1970; Tsuma, 1968) it has been shown that the percentage light decrease is relatively sharp in the top third of the canopy, below which there is a more gradual decrease. The transmission curves tend to be similar to that of red clover. Keoghan (1966, 1970) observed that previous management (different defoliation heights) can modify the transmission pattern, presumably resulting from changes of sward structure. He also demonstrated differences between establishing and established stands, these differing in the pattern of stem arrangement and stem density. Tsuma (1968) used previous defoliation frequencies of 2,3,4 and 6 weeks, and found, a little unexpectedly, that there was little difference between the transmission patterns in the upper canopy layers of the first common residual regrowth. Heights of regrowth were significantly different. Stem densities were different, especially between the 6 weeks treatment and

and each of the other treatments collectively, thus implying that leaf arrangement must vary to account for the lack of transmission differences. Further, LAI was significantly different between all treatments. His results imply that the sward's leaf arrangement and presentation adapted in each case to give a relatively similar light extinction coefficient in the in the leaf layers of the canopy.

Stratified leaf sampling has been performed with lucerne (Steinke, 1963; Keoghan, 1966, 1970) and with point quadrat (Warren Wilson, 1965) for comparison with light transmission values. These reports have shown a larger proportion of leaf in the top 20-30 cm of the canopy. The combination of basal leaf senescence and stem growth, results in the leaf canopy lifting off the ground in the later stages of growth. At the same time, there is an increasing stem weight distribution with depth in the canopy. This basic similarity occurred both for spaced plants (Steink, 1963) and swards (Keoghan, 1966, 1970). Keoghan (1970) observed that the canopy light transmission pattern was not closely related to the leaf distribution pattern. This was in part due to the light extinction coefficient values differing between canopy levels and in turn not correlating well with the associated leaf area values. This indicated differences of leaf orientation and distribution with canopy height, which may also change with maturity. Warren Wilson (1965) and Scott and Wells (1969) have both shown changes of leaf angle with canopy height.

Lucerne light interception varies with stage of growth, between canopy layers and between different canopies resulting from different agronomic management treatments, and probably between varieties. This variance largely originates from associated differences of canopy structure, evidenced by the variation of the light extinction coefficient (Keoghan, 1970). It seems to be increasingly evident, that lucerne canopy structure is quite plastic. Possibly, this has an important indirect compensatory role in maintaining good light interception. A main effect of frequent defoliation is the greater post-defoliation light wastage, hence the need for management to provide for rapid recovery growth to reduce this. A further requirement is to keep the canopy at maximal light interception as long as possible, consistent with continued near maximal crop growth rates, plant quality requirements and other pertinent management considerations.

#### 2.4.3.2. The effect of temperature on lucerne growth.

In general, the work reported for air temperatures indicates that 15C is an approximate optimum for the shoot growth of established lucerne (Steinke, 1963; Langer, 1967; Iversen and Meijer, 1967; Smith, 1969a; Nelson and Smith, 1969; Stock, 1969). Seedlings favour higher temperatures (Gist and Mott, 1957; Garza et al., 1965; Trevine, 1966). With temperature increase above the apparent optimum, yields of both tops and roots decrease, as also do the levels of carbohydrate reserves (Smith, 1969a; Nelson and Smith, 1969). Also noted was an advanced maturity, first flowering occurring considerably sooner in warmer temperatures. Temperatures used were warm (32/24C day/night) and cool (18/10C). Nelson and Smith (l.c.) found that the advantage of the cool regime was partly due to the longer growth period to maturity, development of a larger leaf area, and a higher net assimilation rate. With somewhat higher summer temperatures of 37.5 to 42.5C, Feltner and Massengale (1965) and Robison (1966) also showed yield decreases, but more particularly, large decreases of carbohydrate reserves.

The root yield decrease at higher temperatures also applies to higher night temperatures alone, particularly if associated with lower light conditions (Steinke, 1963). These results are consistent with an increasing depletion of available substrates for night respiration. Support comes from Murata et al. (1965), who showed that lucerne had a broad optimum temperature range for photosynthesis (10-25C), while respiration rate increased steadily with temperature increase, particularly beyond 30C.

Iversen and Meijer (1967) clearly demonstrated shoot growth increase over the lower temperature range to an optimum of 65/50 F (an approximate mean of 15C). At the lower temperatures, root growth (probably weight increase more than root extension) and carbohydrate reserve levels appear to benefit, as evidenced by their increase in the autumn and their importance for overwintering in cool winter environments (Smith, 1964). Murata et al. (1965) also showed that lucerne photosynthesis was maintained at quite high levels with temperatures approaching 0C. Actual shoot growth limitations at these lower temperatures does not appear to have been investigated.

Langer (1967) reviewed the strong interaction between light and temperature levels which can occur with lucerne. The adverse effects

of higher temperatures on growth are particularly evident with low light conditions e.g. 1000 f.c. Strong light can reduce and in some cases reverse the effect of higher temperatures (Gist and Mott, 1957; Steinke, 1963; Garza et al., 1965), since the assimilation rate increases while respiration rate is little changed (Murata et al., 1965; Nelson and Smith, 1969). Seedlings are likely to be more responsive with their higher optimum growth temperature. Further, longer photoperiods will tend to compensate for lower light intensities (Rhykerd et al., 1960).

A defoliation interaction exists with temperature, lucerne growth having a higher temperature optimum when not cut (Steinke, 1963). This probably results from higher temperatures causing greater respiratory use of organic reserves in defoliated plants, so aggravating an already depleted reserve level (section 2.3.1.3.). This would suggest that the lucerne growth temperature optimum may tend to decrease with more frequent defoliation.

There is much less information on the effect of soil temperatures on lucerne growth, and what there is has been confined to seedlings and very young plants. Lucerne root growth has an optimum soil temperature but with reports ranging from 12C (Heinrich et al., 1966) to 19.4C (Neilsen et al., 1960), while shoot growth showed a linear response up to the highest reported soil temperature of 26C (Levesque et al., 1963). Further work is needed to clarify the situation. Ueno et al. (1968) found a significantly higher correlation between lateral root growth and shoot growth, than that with tap root growth, over a soil temperature range of 10-25 C. This is logical, since both active root tip growth, and nutrient uptake - an active process (Brouwer, 1965), probably respond positively to soil temperature increase over this range. In support, Neilsen et al. (1960), Levesque et al. (1963) and Heinrich et al. (1966) found that shoot nitrogen and phosphorus content increased with temperature increase and the same in the roots (Neilsen et al., l.c.). The nitrogen increase indicates the active response of the root nodules, although this is probably in part an indirect benefit due to an enhanced carbohydrate supply to the nodule systems, as lucerne nodule nitrogenase activity is still substantial at 3 and 5C (Day and Dart, 1970).

In the whole plant, these temperature effects will be operating on any one organ in two ways. Firstly, the direct effect of temperature on the growth of that organ, and secondly, an indirect effect of temperature on the activity of other organs which supply compounds required else where in the plant. A notable example, is not only temperature reducing root growth directly, but also indirectly, through a reduced supply of growth factors from the shoots.

The adverse effect of freezing or near freezing temperatures during the winter on lucerne overwintering is important in the relevant regions, having dependance on adequate energy reserves, with varietal differences involved (Smith 1964; Langer, 1967). A problem of persistence also exists in climates of very high summer temperatures (Feltner and Massengale, 1965).

Although temperature has definite influences on lucerne growth, between temperature extremes, in field conditions, it's effect is likely to be dominated by its interaction with light intensities. Its main influence on lucerne yield during seasons of active-growth may be in modifying the time to flowering, although in good growth conditions this may be countered to some extent by the non-determinant nature of lucerne growth (Keoghan, 1967).

#### 2.5. Lucerne Varietal Comparisions for defoliation and Growth.

Early reports concluded that different cutting schedules resulted in little difference between adapted varieties (Willard, 1951). On the other hand, the large morphological variation that exists between lucerne varieties (section 2.1.), suggests that varietal response differences to defoliation are likely to exist, probably in interaction with various other management and environmental factors. Keoghan (1967) concluded similarly.

With relatively infrequent defoliations the M. sativa type lucernes are more productive than the M. falcata types. Davies (1970) compared eight varieties of differing falcata content, using 2,3 and 4 defoliations per year. Early varieties (sativa type) yielded well over this defoliation range, while late varieties (falcata type) only yielded well with infrequent defoliation. It was thought this result was associated with a slower growth rate and later spring growth

for the falcata types. Using three reasonably genetically diverse varieties as spaced plants, Leach (1969a) observed this growth rate advantage for the sativa variety (Totana), but also its earlier maturity, expressed by an earlier commencement of active shoot elongation following defoliation. For optimum yields, this maturity difference may mean that sativa types can be defoliated more frequently by comparison with falcata types, within an overall system of relatively infrequent defoliation. With 4 varieties, Tysdal and Kiesselbach (1939) found a similar growth maturity response related to falcata content. With a large range of varieties, Kehr et al., (1963) confirmed the greater productivity of sativa lucernes with defoliation at one tenth bloom, while in a milder climate using the same defoliation frequency, Leach (1970b) confirmed this. With frequent defoliation of 5 varieties, Gross et al., (1958) found the yield of all varieties was depressed, but found that of sativa type lucernes, was more severely affected. Both Feltner and Massengale (1965) in warm temperature summer conditions and Iversen (1967) observed the same effect with frequent defoliation.

The effect of frequent defoliation between varieties, is also expressed in differences of persistence. With frequent defoliation it is generally accepted that sativa type lucernes are less persistent than falcata types. This has been demonstrated severally (Iversen, 1967; Daday, 1968; Bray, 1967; Leach 1970c.). Daday's (1968) study included a comparison with creeping lucernes, these being the most persistent. With the same varieties, Leach (1969b) found the order of persistence to be reversed. He concluded that the creeping habit alone, does not necessarily confer better persistence under grazing. This possibly has to be combined with active growth (Leach l.c.) and lighter textured soils permitting the development of the creeping habit (Heinrich, 1963; Rogers 1967; Leach, l.c.). The effect of regional climatic conditions on lucerne persistence has been stressed (section 3.2.). With the more extreme environmental conditions and a common defoliation treatment, there seems to be little difference between the response of the sativa and falcata lucernes. Jackobs and Oldmeyer (1955) in a dry high light climate, with 4 genetically varied varieties, found no loss of persistence with 4 to 7 week defoliation frequency treatments. In contrast, in a humid, very low light year in Ireland, Farragher (1968), found all of 8 varieties had a high mortality rate with early bud defoliation, although an earlier than recommended stage of defoliation for this climate

(Dent, 1955). In more intermediary climatic conditions, the varietal interaction between defoliation frequency and persistence will tend to be dominant. Kehr et al. (1963), confirmed this to some extent, finding that broad crowned varieties (falcata type) had greater persistence than narrow crowned varieties (sativa type) over a wide range of management conditions.

The reasons for better falcata persistence and production with frequent defoliation are not clear. With relatively infrequent defoliation in the field, residual leaf area is, probably of limited importance for lucerne regrowth (section 2.4.1.3.). This may not be so with frequent defoliation or continuous grazing. With this management falcata persistence has been associated with their more prostrate growth form (Keoghan, 1967) which later may be intensified by the effect of frequent defoliation (Brougham, 1959). Leach (1970c) observed the extreme of some slow growing very prostrate Spanish varieties having excellent persistence under continuous grazing. It is generally thought that this response is associated with a greater residual leaf area. With lucerne, this situation has yet to be verified.

Another aspect relates to some earlier work indicating that rapidly growing sativa varieties reduced their root reserves at a greater rate and to lower levels following immature defoliation and were consequently more harmed (Keoghan, 1967). Leach (1969a) demonstrated this, as indicated by root weight changes, between Totana, Hunter River and Rhizoma lucernes, these having increasing falcata content respectively. Whether the growth and activity of fine lateral roots are similarly affected between types is not known. In turn, the influence of the associated differences of root form is another unknown, although it may be that the more fasciculated root system of the falcata types (Iversen and Meijer 1967, section 2.1.3.) provides them with a more lasting potentially active root absorption system. With these lucerne types under frequent defoliation, this may in part be achieved by the assimilate and possibly growth substance contribution of the residual leaf area (section 2.3.1.2.), providing this is significant.

The nature of lucerne shoot growth shows considerable variation between varieties of different types (Leach, 1969a; section 2.1.1.), but with this variation there are compensatory morphological differences operating. Differences of shoot numbers being countered by reciprocal leaf size and shoot weight differences, leading to a "relative" equality of plant leaf area and yield; actual values for each variety being dependant to a considerable extent on how soon shoots commence elongating after defoliation (Leach, l.c.). A similar canopy compensatory effect was suggested in respect to light transmission (section, 2.4.3.1.). The observations of Leach (l.c.) were with spaced plants. In sward conditions competition influences modify plant morphology (section 2.4.2.3.), although the extent to which varietal differences are maintained with different plant densities and management treatment is again largely unknown. Palmer (1967) did observe that stem densities typical of each lucerne type tended to persist over a range of plant densities. The complexity of the situation is indicated by the observations of Chisci (1968), that due to interplant competitiveness, the relative yields of the same varieties differed when grown as spaced plants and in swards. One shoot growth factor which appears to be common to most varieties is the dominance of basal shoots in contributing to yield, although with higher defoliation stubble shoots may be of more importance, albeit still smaller, with the more falcata type varieties.

Iversen and Meijer (1967) studied the response of a genetically representative range of lucerne varieties to photoperiod and temperature. With 8 and 12 hour photoperiods, African (sativa type) was more productive, while with 16 hours both sativa and falcata hybrids had similar production. With 20 hours all had reduced production. A common temperature of 65/50 F (day/night) was used. They suggested, that in regions with milder winters and earlier springs temperature rises, sativa types may be more productive. Using a 12 hour day they found a sativa type to be more responsive at lower temperatures of 60/40 F, enhancing the early spring photoperiod advantage. Schonhurst et al. (1975) also obtained a significant divergence of response to photoperiod and temperature between 10 varieties, the varietal response was similar.

Over the range of lucerne types being used, there are some significantly different responses to defoliation and environment. There is

also a considerable paucity and future need for information to explain these varietal differences, particularly defoliation responses. The shoot growth study of Leach (1969a) has been a start. In practise, the choice of variety for a given environment is obviously important for best yield and persistence under the subsequent anticipated management. For the future, it may be that this choice can be significantly aided by the availability of improved varieties bred for each region. This breeding potential appears to be available (Heinrich, 1963; Davis and Baker, 1963; section 2.1.4.). Further, Leach (1970a) noted the inverse relationship between shoot number and shoot size in the range of cultivars he used and suggested; "..... genetic recombination may be necessary to produce plants with large numbers of rapidly growing shoots."