AN EVALUATION OF LUPINS (*Lupinus* spp.) FOR SEED PROTEIN PRODUCTION

a thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy at Massey University, Palmerston North, New Zealand.

NEVILLE JOHN WITHERS

1979

ABSTRACT

Since 1972 there has been interest in the greater use of seed protein in grain-based meals for stock. Lupins were one of the crops proposed to fill this requirement. This study was initiated to provide information on the agronomic requirements of *Lupinus angustifolius*, *L. luteus* and *L. albus* for seed production with emphasis on the southern North Island of New Zealand. In addition, some more basic studies on carbon and nitrogen translocation and the response of lupins to water stress were also carried out to provide a better understanding of the lupin plant and its response to its environment.

Initially some field experiments were laid down to measure responses to sowing date, plant density, defoliation and cultivar. At wide spacing, *L. angustifolius* showed an approximately linear decrease in seed yield/plant as sowing date moved from April to October. At normal densities, however, sowing in late July gave the best seed yield. Autumn sowings were affected by disease. It was concluded that, in the absence of disease, seed yield was largely determined by the length of the period of favourable environmental conditions between the start of flowering and the finish of reproductive development. This period determined the number of lateral inflorescences produced which, in turn, determined the number of pods producing seed. Pod number was the main component influencing seed yield. Thus, early sowing and reliable summer rainfall or irrigation seem to be the factors determining high lupin seed yields.

Responses to density were variable. In one experiment there was no response in seed yield by four cultivars over these sowing times to densities ranging from 50-140 pl/m^2. In a further experiment, increases in seed yield were obtained as plant density increased from 25-100 pl/m^2.

Removal of the main stem growing point early in growth briefly stimulated lateral stem growth but the effect on lateral stem seed yield was insufficient to compensate for the loss of the main stem seeds.

There was little difference between the *L. angustifolius* cultivars Uniharvest, Uniwhite and Unicrop when sown early but, with late spring sowing, Unicrop flowered earlier which was an advantage under dry early summer conditions. In one experiment comparing a range of legume species, *L. albus* and *Pisum sativum* produced the highest seed yield but *L. albus* and *L. luteus* yielded the most protein per unit area. The peak rate of nitrogen accumulation in all species was similar and the main factor influencing protein yield appeared to be the duration of nitrogen accumulation. Provided each crop utilised similar durations of the growing period, the yield of seed protein/ha from various legume crops is likely to be similar; the main difference being the composition of the seed. It was suggested that, for maximum seed protein yield, indeterminate cultivars may have some advantage over more determinate cultivars provided appropriate management procedures are adopted.

Studies on water stress indicated that it plays an important role by influencing the distribution of assimilate between vegetative and reproductive growth. Mild water stress tended to stop vegetative growth and increase the rate of seed growth. When sufficiently severe, water stress appeared to initiate the senescence of the plant, the timing of which determined the potential seed yield for that situation. Water deficit had its main effect on seed yield by reducing pod number. Other yield components were relatively stable.

Day temperatures of 28^{o}C, when imposed early in growth, reduced vegetative and seed yield in *L. albus*. As the plant developed, however, the adverse effects of high temperature decreased until

growth was stimulated during first order lateral flowering. No direct effect of high temperature on pod abscission was apparent and it was suggested that pod loss under high temperatures which have been reported occurred largely because of an associated water stress.

A ^{14}C translocation study indicated that most movement of photosynthate in *L. albus* was into the branch on which the labelled leaf was inserted, or into lower branch orders directly connected to it. Results suggest that, in *L. albus* cv. Ultra, lower order stems are a more important competitor with the inflorescence for photosynthate than the new, rapidly developing, higher order lateral branches.

A possible strategy for growing lupin in a commercially viable situation in the Southern North Island is discussed.

TABLE OF CONTENTS

PAGE

ACKNOWLEDGEMENTS

Financial support from research contracts with Dalgety (N.Z.) Ltd, and DSIR and from grants by the Palmerston North City Corporation Economic Development and the Pork Industry Council made it possible to obtain more information in this, and other studies on lupins and this assistance is gratefully acknowledged.

To my supervisors, Prof. B.R. Watkin and Dr B.J. Forde who so willingly provided guidance and support, I would like to express my grateful thanks.

Technical assistance was provided at critical times by a number of people but in particular I wish to thank Lois Mather and Terry Lynch who provided reliable and valuable assistance over much of the experimental period and to Joan Hay for typing the thesis.

I am grateful for the use of controlled climate facilities at the Plant Physiology Division, DSIR and I would like to thank Mrs Liz Edge, Mr Ian Warrington and other members of the Climate Room Support Group for their help and interest.

Finally a big thank you to my wife, Marie, and my three boys for their patience and support. My heartfelt apologies also for neglecting them for so long.

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Annual grain legumes are an important world source of protein as they produce over 100 million tonnes of high protein food annually. However, they supply only 18% of the world's protein useage. In this context, lupins (*Lupinus* spp.) are not very important as they supply only about 0.75 million tonnes of seed annually (Sinha, 1977).

In New Zealand, because of our abundant supply of relatively cheap animal protein, plant protein, other than that from pastures, has not been very important. However, with a world-wide shortage of protein in 1971-72 the price of meat meals, the main source of protein in New Zealand stock feed meals, increased rapidly. This resulted in an awareness that seed protein may have a place in stock feed meals. A number of crops were considered but sweet lupins, which were known to be a good protein source (Gladstones, 1970), became one of the main crops considered.

Some of the advantages that have been noted for lupins as a seed crop are:

(a) High protein content in the seed (Gladstones, 1970; Hudson *et al.*, 1976) compared with most grain legumes which provides the opportunity to use lupins as a substitute for soybean (Williams, 1979).

(b) They can be grown throughout New Zealand, whereas soybean can only be grown in the warmer zones of the country.

(c) Ability to yield well on soils not normally suited for intensive cropping (Gladstones, 1970).

(d) Better able to utilise phosphate reserves in the soil compared with many plants (White, 1961; Gladstones *et al.*, 1964; Gladstones, 1970, 1972) possibly resulting in lower fertiliser inputs.

(e) Limited evidence that lupins are one of the better crops at fixing nitrogen (Nutman, 1976; Boundy, 1978).

Although lupins were not a new crop to New Zealand, they had been previously grown mainly as a forage or green manure crop (Allen, 1949). Seed production had been limited to supplying seed for resowing purposes and little consideration had been given to the potential as a stock food. In 1936-7, about 170 ha of lupin was grown for seed (Anon, 1938) and this increased to a peak of about 3000 ha in 1945 (White, 1961). Subsequently, the use of lupin for forage declined steadily as soil fertility improved until in the early 1970's it was a minor crop.

Information on lupin seed production in New Zealand was limited. Those references which are available (Anon, 1938; McPherson, 1940; Inch, 1947; van Steveninck, 1956; Whatman, 1959; White, 1961) provided only broad recommendations. Little basis for their recommendations was given and it is probable that they were largely based on farmer experience and designed for Canterbury conditions.

Since the main market for lupin seed destined as stock rations was likely to be in the North Island, this study investigated the potential for growing the crop in the southern North Island in order to minimise transport costs. Although lupin seed production had been investigated at Massey University previously (G.S. Robinson, pers. comm.), no records of that work exist. Bitter and sweet blue lupins have been grown for seed on the Manawatu/Rangitikei coastal sand country mainly as an autumn-sown crop often in association with wind erosion control (van Kraayenord, unpublished report).

Because of interest by farmers and feed manufacturers, it was decided to commence a research programme into lupin seed production and after an initial experiment in 1972 (Withers, 1973) the programme reported in this thesis commenced in 1973.

The overall objective of the programme was to provide data which would be useful in assessing the type of environment and management suitable for lupin seed production that could be used as a basis of recommendations to farmers; and to provide basic

information on the growth and development of lupins, including comparisons with other grain legumes, which would be of wider interest.

The programme was divided into two main sections:

(a) A series of simple field trials designed to provide basic agronomic information which would compliment work that was being conducted by other workers in Australia and New Zealand. These experiments aimed to:

(i) compare the characteristics of a range of lupin species and cultivars under Manawatu conditions. This work included comparative studies of the nitrogen and dry weight distribution of lupins and other grain legume species, so that the relative potential of lupins could be established.

(ii) determine the most suitable sowing time. Lupins have usually been sown in autumn but the southern North Island is traditionally an area where crops are spring-sown so it was important to determine whether lupins could yield well if spring-sown.

(iii) obtain information on plant density. Changes in sowing time may also require a change in recommended plant density.

(iv) indicate topics worthy of more detailed study.

(b) As a result of the field trials, three main topics were decided on for further study in more controlled environments:

(i) Water stress seemed to be an important factor determining the length of the growing season and hence yield. The Manawatu tends to have an erratic rainfall pattern and as brief periods of mild water stress can occur in late spring and through the summer, it was decided that the effects of such short periods of stress on growth and seed yield should be determined.

(ii) In conjunction with (i), further information on the nitrogen distribution pattern of adequately watered and water stressed plants was to be studied. Early observations indicated that massive translocation of nitrogen and possibly carbon was occurring during the life of the plant.

(iii) In dense canopies it was noted that lower leaves often senesced and lower pods developed in shade due to the dense upper canopy. This raised the question of whether the lower pods were

supplied from remobilised products or directly from the upper canopy. An experiment was therefore designed to indicate the translocation patterns in *L. albus* at a number of growth stages.

The Manawatu and other lowland areas of the Southern North Island has considerable potential for cropping. This programme was designed to evaluate whether lupins could be a suitable crop in this region and, if so, provide some of the basic agronomic information to enable farmers to successfully grow the crop.

SECTION A LITERATURE REVIEW

This review has two objectives. (1) To examine, in a general way, the major factors influencing seed production in grain legumes. As these crops have many features in common, such knowledge should help in the understanding of lupin seed production. (2) To review existing knowledge on lupin seed production and relate it as far as possible to the general principles of grain legume seed production.

Because of the wide range of topics covered in this project this review is extensive rather than intensive on selected topics.

A.1. SEED PRODUCTION IN ANNUAL LEGUMES

There are major problems with seed production from most legume crops. Compared with cereals, grain legumes are low yielding (Hardy *et al.*, 1977; Sinha, 1977) and their importance is declining relative to cereals as a source of food for humans and animals. For example, Sinha (1977) states that over the 20 years from 1952 to 1972, no improvements to the average yield from legumes occurred whereas rice and wheat had substantial yield increases. However, yield improvements did occur in some legume crops especially soybeans and peas.

Hardy *et al.*, (1977) suggests that the rate of net photosynthesis is a limitation to yield in grain legumes because CO_2 enrichment of the canopy results in substantial yield increases in crops such as soybeans, peas and peanuts. This hypothesis is supported by Shibles *et al.*,(1974) although Sprent *et al.*, (1977), on fairly slender evidence, suggested that assimilate was not a factor in *Vicia faba* yields.

Work is therefore urgently needed to break through what appears to be a yield barrier in grain legume crops. It is pleasing to note a considerable increase in the amount of research

work on the basic physiology of many legume species in recent years so that our understanding of the problems is greatly increased, although so far, no major solutions to the yield problem have been found.

A.2 BACKGROUND INFORMATION ON LUPIN

The history and development of lupins has been comprehensively reviewed by von Sengbusch (1938), Gladstones (1970; 1974; 1977) Hudson *et al.*, (1976)) so these aspects will be mentioned only briefly in this review.

The genus *Lupinus* is diverse and contains many species (Gladstones, 1970). There were two centres of lupin evolution. The more important was the Mediterranean-African region which has provided all the species presently used in modern agricultural systems. *L. albus* is the species which has been cultivated for the longest period. The second centre is South America. *L. mutabilis* is the oldest cultivated species from this area but only recently has it been receiving attention for development into a more sophisticated seed-producing crop plant. (Williams, 1979).

Despite its long history, lupin is not important today. Production is centred on the USSR (530,000 t), Europe (159,000 t) and Africa (56,000 t) (Sinha, 1977). These are assumed to be 1972 figures. At that time, Oceania produced only 2,000 tonnes but expanded production in Australia since then would have increased this amount.

Lupins are indigenous to a range of latitudes and tolerates a wide range of climatic conditions (Gladstones, 1970; Hudson *et al.*, 1976; Sinha, 1977), although adaptability within any one species is more limited. Lupins are grown as summer annuals in cool temperate climates and as winter annuals in sub-tropical climates (Gladstones, 1970). Best lupin growing areas have a season of at least five months free from serious moisture stress

and during that time, have mean monthly maximum temperatures between 15 and 25°C (Gladstones, 1970). Soils must be free draining and can vary between mildly acid to slightly alkaline with some differences in requirements between species (Gladstones, 1970; 1977).

A.2.1 LUPIN SEED QUALITY

Seed quality and feed value for a range of animals have been widely reported (e.g. Gladstones, 1970; 1972; 1977; Hove, 1974; Withers *et al.*, 1975; Hudson *et al.*, 1976, Hill, 1977; Hove *et al.*, 1978; Hudson, 1979; Williams 1979).

The main feature of the seed is its high protein content ranging between 28% and 43% crude protein depending on the species. The nitrogen-free extract is low (25-45%) compared with most legumes (55-75%) (Hill, 1977). The main disadvantage of lupin seed is a thick hull which makes up 15-25% of the seed dry weight. This hull contains much of the fibre but little of the protein so that its removal has the effect of considerably improving the feed value of the seed. Alkaloid is the significant toxic material and once this factor is removed by the use of sweet cultivars the seed is safer than most other legume seeds (Hill, 1977; Hudson, 1978) without the need for further processing (Hove *et al.*,1978).

Hudson (1979) and Williams (1979) both believe that lupin seed is suitable for human consumption and it has been shown to be suitable for this purpose (Herz, 1973; Gross *et al.*, 1976) but before it can be widely used in human diet further toxicological studies are probably required.

A.2.2 LUPIN SPECIES

Detailed descriptions of a number of lupin species has been published by Gladstones (1974). However only 3 species have been extensively developed and grown as seed crops. These are *L. angustifolius* L., *L. albus* L. and *L. luteus* L. which are also the species studied in this programme. Most attention will therefore be given to them in this review. *L. cosentinii* has received some attention in Western Australia and *L. mutabilis* is currently being selected in South America and a number of other centres for low alkaloid, non-shattering pods and higher seed yield.

A.2.2.1 Lupinus angustifolius

This species is often referred to as the narrow-leafed lupin or blue lupin, although there are a wide range of possible flower colours (Allen, 1949). This species was relatively late to be developed compared with the other species under consideration (Gladstones, 1970). Recently this species has been improved by selection for reduced shattering of pods, white flowers and seeds, reduced vernalisation requirement allowing earlier flowering, and more recently, disease resistance (Gladstones 1977). Initially three cultivars were released. Uniwhite (released 1967) was the first to have the combination of low alkaloid, white flowers and seed and reduced shattering (Gladstones, 1972). Uniharvest was released in 1971 and had increased shattering resistance but was otherwise similar to Uniwhite. Unicrop (released 1973) is isogenic to Uniharvest except for the gene *Ku* which removes most of the vernalisation requirement often resulting in early flowering relative to Uniwhite and Uniharvest (Rahman and Gladstones, 1972) .

In a series of 8 trials in Western Australia, Walton (1976) showed that Uniwhite was 4-62% lower in yield than Unicrop. Withers (1973) and Garside (1979) found that Unicrop had only a small advantage in wetter and cooler environments. Walton (1976) attributed differences between the cultivars in his trials to the greater susceptibility of Uniwhite to shattering in hot, dry summers.

The differences between Uniharvest and Unicrop were small except in warm, short season districts when Unicrop had earlier flowering (Gladstones, 1972).

More recently, two new cultivars have been developed which have resistance to grey leaf spot *(Stemphylium vesicarium)* and anthracnose *(Glomerella cingulata)* but otherwise they are similar to Uniharvest or Unicrop (Gladstones, 1977; Anon, 1979). *L. angustifolius* is the most cool tolerant of the three species considered in this thesis (Gladstones, 1970; 1972; 1977). It requires mildly acid to neutral soils (Gladstones, 1970) which are deep and friable (Gladstones, 1977). However, Corbin (1978b) suggests a wider range of soil types may be suitable. Although efficient at utilising phosphate reserves compared with other crops (Gladstones, 1977) *L. angustifolius* is more susceptible to phosphate and potassium deficiencies than *L. luteus* (Gladstones, 1970).

A.2.2.2 Lupinus albus (White Lupin)

This species has been a subsistence crop for over 3,000 years and its early forms had soft seeds and non-shattering pods (cf. *L. angustifolius*) (Gladstones, 1977). A number of cultivars have been released since 1950 that are better adapted to modern agriculture than previous ones. Ultra, the main cultivar used in this study, was originally released from a private German breeding programme (Pflugs) in 1950 but it was subsequently re-selected in Western Australia by Gladstones (Gladstones, 1977) and is being extensively grown in Eastern Australian States (J. Strang pers. comm.).

L. albus requires higher levels of fertility and rainfall than the other lupin species but has the highest yield potential (Gladstones, 1959; 1970). It is characterised by a long period from flowering to maturity (Gladstones, 1959) which can limit its usefulness in areas with short periods of weather suitable for

maturing the crop (Lucas *et al.*, 1976). *L. albus* was considered by Allen (1949) to be unsuitable for New Zealand conditions as it did not ripen regularly, presumably due to this later maturing characteristic. It grows well in slightly warmer conditions than the other species but there are variable reports on its tolerance to low temperatures possibly because of differing ecotypes (Gladstones, 1970).

A.2.2.3 Lupinus luteus (Yellow Lupin)

L. luteus has been used as a forage and green manure crop in the Mediterranean region for several hundred years and was once used extensively as a garden plant because of its yellow scented flower. After about 1850 it became widely cultivated on the acid soils of many parts of Europe (Gladstones, 1970).

As a seed crop it is highly desirable because its seed protein level (42%) is highest of the three lupin species considered here, with slightly better protein quality. (Gladstones, 1970; Withers *et al.*, 1975). Unfortunately the seed yield of this species is usually lower than for *L. angustifolius* and *L. albus* under Australian and New Zealand conditions (Gladstones, 1959; Stoker, 1975) although Palmer (1976) indicated that it may be better for the northern North Island.

L. luteus tolerates acid soils and brief periods of water-logging better than the other two species (Gladstones, 1972). It is also relatively better on poorer soils as it is slightly more tolerant of low phosphate and potassium levels than *L. angustifolius* (and presumably *L. albus*) (Gladstones *et al.*, 1964; Gladstones 1970; Rahman and Gladstones, 1974).

A.3. THE DEVELOPMENT OF LEGUME SEED YIELD

A.3.1 Plant Structure and Development

The development of seed yield in grain legumes is complex with many interacting factors influencing the final outcome, seed yield.

Meadley and Milbourn (1971) recognised two stages in the development of seed yield which are:-

(a) Vegetative growth which provides the structure on which seed yield is ultimately formed. They suggested that reproductive potential increases with vegetative growth largely because of its relationship with node number.

(b) Flowering and podfill (reproductive growth). Transfer of assimilate fixed in the previous period is limited so yield is determined largely by dry weight accumulated in this stage. Many workers (e.g. Herridge and Pate, 1977; Summerfield, 1977) sub-divide the second stage further into flowering and early fruit growth plus podfill and maturity.

An optimum balance of vegetative to reproductive growth is important to achieve high seed yield (Adams, 1975; Summerfield, 1977) but the specific balance has not been determined (Sinha, 1977). There is some evidence in *Vicia faba* for example that the amount of vegetative growth in normal plants is excessive (Chapman and Peat, 1978).

Adams (1975) described three types of plant development:

(a) where vegetative and reproductive phases do not overlap i.e. vegetative development ceases at the onset of flowering. Leaves are restricted in number but not size. Example of this type of growth can be found in some garden pea cultivars developed for processing and some early soybean cultivars. This is the type of growth generally referred to as determinate (Egli and Leggett, 1973). Sinha (1977) suggests that the short vegetative growth of these crops reduces their yield potential. Their small plant size however,

usually allows the smaller yield per plant to be offset by greater planting density. In areas of uncertain rainfall, determinate plants may be less reliable (Sinha, 1977).

(b) Where vegetative growth continues for about 20-30 days after the onset of flowering. Maturity of these plants is usually late and they are indeterminate. Examples given are many *P. vulgaris* and vining pea cultivars. Lupins usually fit this category but have the potential to continue vegetative growth beyond the 20-30 days after flowering. For example, Atkins *et al.*, (1978) noted a period of 44 days for flowering and early pod fill during which time vegetative parts grew vigorously.

(c) Where the vegetative phase is long, near the end of which a long period of flowering and podset commences but limited overlap of vegetative and reproductive growth occurs. e.g. North American soybeans. Some lupin cultivars have the characteristic of a long vegetative period (e.g. *L. albus*) but are more indeterminate than implied in this description.

A feature of type (b) and, to a smaller extent, (c) plants is the potential that exists for competition between vegetative and reproductive growth (Egli and Leggett, 1973; Shibles *et al.*, 1974; Greenwood *et al.*, 1975; Farrington, 1976) which may be a factor in reducing podset. The long vegetative period of type (c) may be a disadvantage as it reduces the chance of the sensitive flowering and podset occurring under favourable conditions (Adams, 1975; Sinha, 1977) which limits their ability to realise the high potential for seed yield which exists in their canopy structure (Adams, 1975).

Perry and Poole (1975) state that the indeterminate growth habit in lupin can fully exploit the environment because it can vary its growth period and that seed yield is not so dependent on early growth; a situation which contrasts with cereals. Garside (1979) however, suggests that the ability of lupins to utilise the available season is a cause of the large variation in yield.

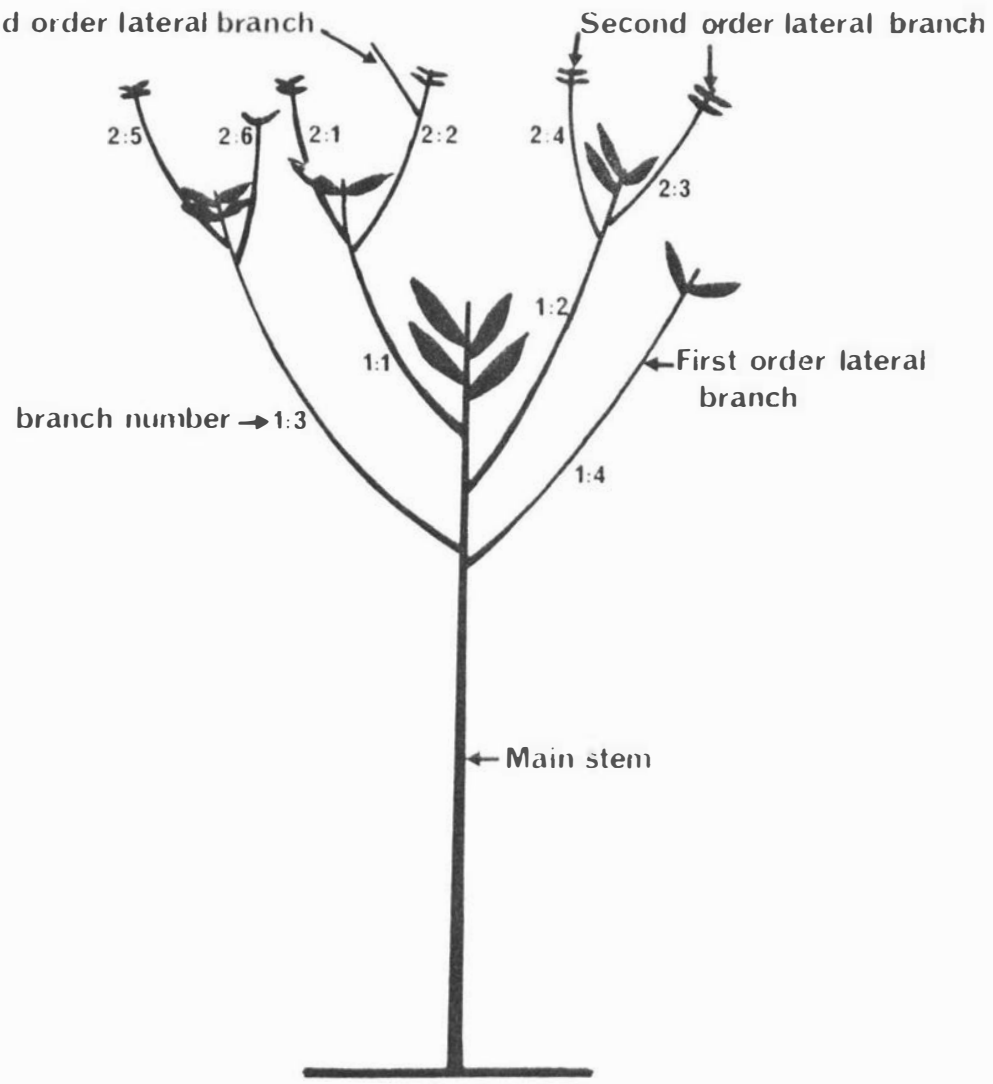

Fig. A.3.1 Schematic layout of a lupin plant showing the position and numbering of the branch orders.

Detailed descriptions of the structure of the annual lupin plant with emphasis on *L. angustifolius* are provided by Farrington and Greenwood (1975), Greenwood *et al.* (1975), Perry and Poole (1975), Farrington (1976) and Reeves *et al.* (1977). In brief, initial growth is by a single stem (main stem) with a terminal inflorescence. A varying number of lateral branches arise from the main stem, each of which can produce a terminal inflorescence and further lateral branches. In this way a series of branch orders are developed as illustrated in Fig. A.3.1.

Farrington and Greenwood (1975) and Perry and Poole (1975) use different systems for describing the various branch orders. The system proposed by Farrington and Greenwood (1975) is the more comprehensive but is more complex than required in the work reported here so a modification of the nomenclature used by Perry and Poole (1975) has been adopted (see Fig. A.3.1).

A.3.2 Components of Legume Seed Yield

Seed yield is built up by a series of yield components which in turn are determined by a combination of plant and environmental factors. Adams (1975) described the relationship of these components to plant structure (Fig. A.3.2). The development of lupin yield components have recently been discussed by some Australian workers with emphasis on *L. angustifolius* (e.g. Perry, 1975; Perry and Poole, 1975; Garside, 1979).

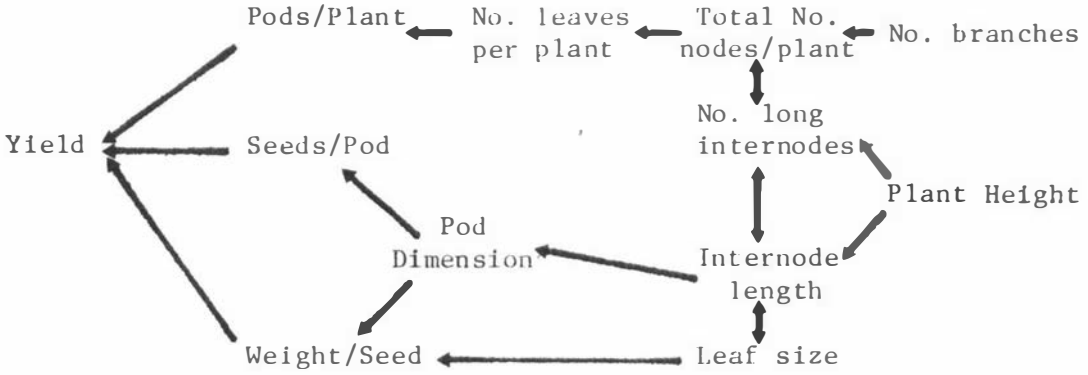

Fig A.3.2 Diagramatic representation of direct paths of influence of several structural components of the plant upon yield (Adams, 1975).

The number of pods per unit area or per plant is usually the main component to influence yield (Wallace and Munger, 1966; Ishag, 1973a,b Adams, 1975). The number of pods required for high yield is dependant on a satisfactory plant structure which influences the number of fruiting nodes. (Ishag, 1973a; Adams, 1975). In lupins the pod number is determined largely by the number of lateral branches which influences the number of inflorescences formed. (Withers, 1973; Garside, 1979). Once the number of floral units have been determined by the plant structure, the rate of abscission of flower and small pods is an important determinant of pod number (Gabelman and Williams, 1960). This aspect will be discussed further in Section A.3.3.

Pod number is usually the first seed yield component to be influenced by the environment and cultural practices (Bennett *et al.*, 1977) and is very sensitive to stress in the plant. Because of this ready adjustment, other components of yield, *viz* number of seeds per pod and seed weight, tend to be less variable (Ishag, 1973a; Seitzer and Evans, 1973). Seeds per pod and seed weight are, however, capable of considerable compensation depending on the number of pods set on the plant (Adams, 1967). Increases in the number of seeds per pod and/or seed weight can occur in response to low pod numbers on a plant (Chung and Goulden, 1971; Ishag, 1973a; Ndunguru *et al.*, 1978). Greenwood *et al.* (1975) noted in *L. angustifolius* that about 1/6 of the ovules did not produce mature seed indicating potential for flexibility in the number of seeds per pod.

Seed size is determined by genetic and environmental influences and is usually negatively correlated with seed number (Shibles *et al.*, 1974). Protein content of the seed does not vary greatly (Seitzer and Evans, 1973; Woodward and Begg, 1976) although Farrington (1976) noted lower nitrogen concentration in the latest developed seeds of lupins. These were, however, lighter in weight and not fully developed.

In lupins yield components on the main stem tend to be stable compared with those on lateral branches. Seed number per pod and seed weight usually reduce as lateral branch orders increase (Greenwood *et al.*, 1975; Perry, 1975; Farrington, 1976; Herbert and Hill, 1978b). The effect on seed weight may be a factor of the length of time between fertilisation and rapid seed fill which tends to be shorter for higher order lateral branches (Perry, 1975).

The development of yield components is sequential and the components are "to some extent interdependent in their development" (Adams, 1967). "Plasticity" in the development of yield components means size can take alternative pathways depending on environmental conditions. This helps to maintain a stable yield level. The tendency for components to compensate and to be negatively correlated, plus the tendency for potential sites not to be realised, indicates a limitation in assimilate (Adams, 1967; Shibles *et al.*, 1974; Dunphy and Hanway, 1976; Hardy *et al.*, 1977). Stimulating photosynthesis can increase yield components (Hardman and Brun, 1971; Schou *et al.*, 1978).

A.3.3 Flowering and Podset

Timing of floral initiation can be very complex depending on species and cultivar. Plants can be responsive to one or more factors - usually vernalisation, photoperiod and/or increasing temperatures. This topic has been reviewed by Leopold and Kriedemann (1976). Lupins usually have a high vernalisation requirement and a weak photoperiod response (See Section A.5.3).

Based on the number of flowers produced, legumes have a potential for high yields (Greenwood *et al.*, 1975; Sinha, 1977) but usually only a small proportion of flowers produced set mature pods although all flowers apparently have the ability to set pods (van Steveninck, 1957). For a range of sites in Western Australia, Francis *et al.* (1971) found that only 6-33% of lupin flowers set pods. McAlister and Kober (1958) and Adjei-Twum and Splittstoesser

(1976) regard the loss of flowers and pods as a mechanism for adjusting the reproductive load to the capacity of the plant to sustain it.

There appears to be many causes of flower and pod abscission which can act alone or in combination. Sinha (1977) lists the following:

1. Limited photosynthate
2. Limited nitrogen availability
3. Reduced light intensity in the canopy
4. Canopy temperature
5. Hormonal
6. Poor gas exchange in the canopy
7. Humidity in the canopy
8. Soil and water factors

Many of these factors are inter-related and can influence assimilate availability. Internal supply of carbohydrate and/or nitrogen seems to be the most widely favoured basic cause of abscission (Addicott and Lynch, 1955; Greenwood *et al.*, 1975; Cooper *et al.*, 1976; Egli and Legget, 1976; Ndgunguru *et al.*, 1978; Stewart *et al.*, 1978). Increasing light, temperature, air movement or CO_2 concentration at flowering and early pod development of soybeans can substantially increase pod numbers (Hardman and Brun, 1974; Schou *et al.*, 1978).

Intra-plant competition for assimilate between the inflorescence and rapidly growing lateral branches has often been mentioned as the cause of abscission in lupin (Greenwood *et al.*, 1975; Perry, 1975; Perry and Poole, 1975; Herbert, 1977c). Early work by van Steveninck (1957, 1958) indicate that a hormone may be involved in early abscission but that the supply of assimilate may be more important later. He differentiated between flower abscission (apparently caused by lateral stem growth) and pod abscission (related to leaf area).

Abscisic acid has been implicated as an important cause of abscission in water-stressed *L. luteus* (Porter, 1977). It is found in increasing quantities in abscising pods of this species and in pods, seed and leaves of *L. albus* plants subjected to water stress (Hoad, 1978). Zucconi (1975) and Porter (1977) believe that the presence of abscisic acid is an effect of stress rather than a cause of abscission. Subhadrabandhu *et al.* (1978) did not find a consistent relationship between abscisic acid and abscission in *P. vulgaris*. Ethylene has also been implicated in abscission (McMicheal *et al.*, 1973).

Addicott and Lynch (1955) suggests that insufficient carbohydrate can cause embryo abortion which reduces auxin supply to the abscission zone thus causing abscission. Water stress could cause abscission by reducing carbohydrate supply and/or by directly preventing embryo growth, thereby causing embryo death; or by slowing auxin production. Seeds are active producers of hormones which influences assimilate supply (Harvey, 1977) so that cessation of growth caused by water stress may also reduce hormone production which in turn, may reduce the carbohydrate supply to the pod, resulting in embryo abortion.

Adams (1967) suggested that, within each nutritional unit of *P. vulgaris* there is a priority order for abscission depending on the stage of growth of each flower/pod. This order is:

(1) Rapidly developing young pods
(2) Unopened flowers
(3) Opened flowers
(4) Young fertilised ovules in developing pods
(5) Freshly pollinated embryos and very young pods.

When competition for assimilates begins (if that is the cause), (5) is abscised first, followed by (4) etc, depending on the duration and extent of the shortage. Adams also suggested that each nutritional unit tended to be supplied equally with assimilate. However, because each unit was at a different stage of development, each would be affected differently.

Maximising seed yield may theoretically be achieved by minimising abscission of flowers and pods (Gabelman and Williams, 1960). This concept, however, overlooks the possibility that the plant may already be operating within environmental constraints and increased pod set may be offset by lower productivity of later yield components. It seems unlikely that yield improvement will be achieved by working on improving abscission alone if the rate of abscission is a result of the internal and external environment of the plant.

A.3.4 Pod and Seed Development

Sinha (1977) lists 2 types of fruit development:-

(a) where the fruit wall commences rapid growth first followed by seed - typified by peas or chickpeas. This type of development also occurs in lupin (Greenwood *et al.*, 1975; Farrington, 1976; Hocking and Pate, 1977).

(b) where pod and seed develop together. Examples are mung beans and cowpeas.

The growth of the pod and seed has been described in detail for a number of legume species (e.g. Flinn and Pate (1968) for *P. arvense*; Carr and Skene (1961) and Oliker *et al.* (1978) for *Phaseoulus vulgaris*). Generally, seed growth is initially slow coinciding with rapid pod growth and then grows rapidly. Often a short "lag phase" occurs with a short period (3-4 days) of slow growth followed by a further period of rapid growth. During the last period of rapid growth the pod usually loses dry weight and nitrogen and most of the protein reserves in the seed are accumulated.

Hocking and Pate (1977) compared the development of *P. sativum* *L. angustifolius* and *L. albus*. There were similar general patterns of pod, embryo and testa dry weight accumulation although relative timing of the rapid accumulation rate varied. *L. albus* had a considerable lag period before the pod or embryo commenced linear growth compared with the other species. *P. sativum* commenced pod growth and declined in dry matter earlier than *L. angustifolius*

although embryo growth commenced about the same time. Dry matter was lost by pod and testa during the last third of the embryo rapid growth phase in lupin but earlier in *P. sativum*. It was estimated that pod and testa could have contributed up to 13.5% of the seed weight for *P. sativum*, 17% for *L. angustifolius* and 26% for *L. albus*. Flinn and Pate (1968) estimated 19% of seed dry weight and 23% of nitrogen requirement of the embryo could have been made available from pod, testa and endosperm of *P. arvense*.

The linear phase of seed increase has a relatively constant rate within a species (Hanway and Weber, 1971b; Sinclair and de Wit, 1976) but differences in the timing of the commencement of this phase can vary between cultivars (Hanway and Weber, 1971b); variation can occur in the rate of the non-linear phase (Kaplan and Koller, 1974) or in the duration of the linear phase (Dunphy and Hanway, 1976; Sinclair and de Wit, 1976; Egli *et al.*, 1978) all of which can give rise to differences in seed size and/or yield between cultivars or environments. Hanway and Weber (1971a) and Egli and Legget (1973) have noted that the development of early formed pods of soybean may be delayed. Similar patterns occur in lupins. Seeds of the main stem inflorescence and those of the first order lateral branches however, tend to develop together (Greenwood *et al.*, 1975; Perry, 1975).

A.4 THE CARBON AND NITROGEN ECONOMY OF GRAIN LEGUMES

Carbon and nitrogen provide the basic 'building blocks' of yield so an understanding of their utilisation in the plant is important for the interpretation of the plant's reaction to internal and external factors. In attempting to maximise seed production we are trying to manipulate the carbon and nitrogen economy to achieve the maximum amount of seed possible within the environmental constraints. Two aspects need to be considered:-

(a) total assimilation of both nutrients as this will determine the maximum potential of seed production. This is largely a function of environment and management which will be considered mainly in Section A.5.

(b) distribution and redistribution of both nutrients to ensure the maximum proportion of the total nutrients assimilated become incorporated into the seed.

Each nutrient will initially be considered separately as their pathways are distinctly different although they are closely linked and interdependent.

A.4.1 The Carbon Economy

The important function of carbon assimilation (for seed production) prior to flowering is the building of a framework on which satisfactory flowering and seed development can take place.

Even before full expansion, leaves are exporting assimilates (Thaine *et al.*, 1959) most of which initially is transported upward to the meristem and newly developing leaves. However, as the leaf matures and it becomes lower in the canopy, the movement of exported assimilate becomes complex and less well defined. Usually, lower leaves are committed to supplying the lower stem and root system (Biddulph and Cory, 1965; Pate, 1966; Wardlaw, 1968).

Overall, patterns of movement are largely determined by the activity and position of the various organs requiring assimilates (sinks) in relation to the position of the supply organ (source) (Nelson, 1963). Within these patterns however, there are restrictions on the distance and direction of translocation as determined by the vascular links between particular sources and sinks (Nelson, 1963; Porter, 1966). Assimilate in excess of requirements can be stored in the stem (Carr and Pate, 1967, Wardlaw and Porter, 1967). In many grain legumes, most of the carbon is fixed by the plant after the commencement of flowering (Eaglesham *et al.*, 1978) and this is the main source of carbon for seed yield (Meadley and Milbourn, 1971). Atkins *et al.* (1978) noted that only 6% of the total net photosynthesis of *L. albus* was fixed before flowering. Much of this carbon was used in the leaflets (27-30%) and roots (54%) so that the productive potential of the plant was enhanced.

The change to the reproductive state involves major changes in the distribution of assimilate (Wardlaw, 1968). This change is due mainly to the increasing size of the seed as a sink until eventually the requirement of the seed dominates all other sinks so that activity of other important plant parts slows *viz.* roots (Leonard, 1962; Kursanov, 1963) vegetative meristems (Brouwer, 1962; Leonard, 1962) and nodules (Lawn and Brun, 1974; Hardy and Havelka, 1976; Sinha, 1977).

Thus, as the plant develops, the translocation stream becomes increasingly committed to supplying the seed with assimilate. Sources of assimilate are:

1. Current photosynthate from the leaf. Usually the photosynthetic area closest to the fruit provides the major part of this supply (Flinn and Pate, 1970; Lovell and Lovell, 1970; Hume and Criswell, 1973). Transfer of carbon assimilated by a fruiting plant can be transferred very efficiently to the seeds (Pate and Flinn, 1973). However, Dunphy and Hanway (1976) suggest that the translocation of sugars from leaves may be a limiting factor in soybean production.

2. Assimilate stored in the leaf and stem.

Carbon fixed early in growth seems to be inefficiently transferred to the seed (Hume and Criswell, 1973; Pate and Flinn, 1973). Probably most of the early-fixed assimilate which is remobilised was incorporated in proteins that were hydrolised during senescence and transfer as amino acids to the seeds (Simon, 1967; Wareing and Seth, 1967). Most of this remobilisation probably occurs in the leaves (Pitelka, 1977). The low efficiency of transfer is a consequence of carbon being important in the structural components of the plant and because easily mobilised early fixed carbon is dissipated in respiration before flowering (Pate and Flinn, 1973; 1977).

3. Supply from the pod.

Carr and Pate (1967) refer to the pod as "an organ of photosynthesis and transient storage". It is capable of photosynthesis (Sinha, 1977) including those of lupins (Greenwood *et al.*, 1975;

Pate *et al.*, 1977; Atkins and Flinn, 1978). Some of the CO_2 is derived from the external atmosphere but most is CO_2 respired by the seed into the pod cavity (Flinn and Pate, 1970; Crookston *et al.*, 1974; Pate *et al.*, 1977; Atkins and Flinn, 1978). During the final development of the seed, the pod contributes much of its assimilate reserves to the seed (Flinn and Pate, 1968; Sinha, 1977). The pod is therefore important for seed development (Lovell and Lovell, 1970). The fruit as an entity is efficient at utilising carbon for seed production. Flinn *et al.* (1977) estimated 69% conversion of translocated material to seed by peas and 52% by *L. albus*.

Pate *et al.* (1977) consider that photosynthesis by the pod and supply of pod reserves to the seed are important under water stress conditions when leaves are prematurely lost due to the stress.

A.4.2 The Nitrogen Economy

Excellent reviews of nitrogen assimilation have been given by Pate (1968; 1971; 1976).

Basically, metabolism of nitrogen involves several steps:-
(a) absorption and initial metabolism in the root and in the case of legumes, fixation in the nodule.
(b) transport to the upper parts of the plant, usually the leaf, via the xylem.
(c) utilisation in the leaf for a long or short period. Most is re-exported via the phloem at some time. Sometimes direct transfer from xylem to phloem occurs.
(d) secondary utilisation by a second meristematic region. If this region is not the seed further recycling may occur so that a high proportion of the absorbed nitrogen is finally metabolised in the seed.

Mobility and transport is therefore very important in nitrogen utilisation because of the distance between the various sites which metabolise nitrogen (Pate, 1971). This contrasts with the relative

immobility of carbon once it has become incorporated into plant structure. The type of nitrogenous compounds transported, the channel used, the characteristics of the transport process, source and sink are largely a function of species, stage of plant development and environmental influences (Pate, 1971).

A.4.2.1 Initial Assimilation

In nodulated legumes, a high proportion of the plant's nitrogen requirement is fixed from the atmosphere. The proportion of the total nitrogen which is fixed is determined by the level of inorganic nitrogen in the soil; the proportion reduces as soil nitrogen levels increase (Oghoghorie and Pate, 1972; Gibson, 1974; Summerfield *et al.*, 1978). Pate (1974) suggests that an ideal level of inorganic soil nitrogen for peas is 30-60 ppm which allows nitrogen fixation to occur at 60-80% of the rate of plants relying entirely on symbiotic fixation.

The rate of nitrogen fixation per plant as measured by acetylene reduction usually increases as the plant ages until a peak is reached at a specific growth stage when a decline in fixation is usually accompanied by degeneration of nodules. The pattern of fixation however, can vary depending on such factors as species and growth pattern of the cultivar (Summerfield *et al.*, 1978). For many legumes, the peak occurs when the seeds are beginning to fill. This pattern has been noted by Farrington *et al.* (1977) for *L. angustifolius*, Pate and Herridge (1978) for *L. albus* Trinick *et al.* (1976) for *L. cosentinii* Lawn and Brun (1974) for soybeans and Eaglesham *et al.* (1978) for cowpeas. However, rates of acetylene reduction for *L. angustifolius* reported by Trinick *et al.* (1976) reached a peak at 7 weeks and remained relatively constant until senescence. Atkins *et al.* (1978) noted that fixation in lupin carried on longer at a higher intensity than in cowpea.

The pattern of nitrogen fixation can be changed by external factors (Sinha, 1977) such as moisture deficit, density or waterlogging (Trinick *et al.*, 1976; Farrington *et al.*, 1977; Sprent and Bradford, 1977). Summerfield *et al.* (1978) suggested that the degree of sensitivity of nitrogen fixation to water stress and waterlogging may be related to nodule structure. Overall, the nitrogen fixation is more sensitive to environmental factors than the plant itself (Pate, 1977).

There is some evidence that fixed nitrogen is taken up preferentially by the shoot in the pea and field bean (Oghoghorie and Pate, 1971; Cooper *et al.*, 1976). On the other hand, Ryle *et al.* (1978) found that, for soybeans, fixed nitrogen was unable to supply sufficient nitrogen for full plant growth and that nodules imposed a high respiration load on the plant so plants fed with nitrate nitrogen grew and yielded best. Summerfield *et al.* (1978) stated that the efficiency of nitrogen uptake varied between soybean and cowpea largely in this case because soybean utilised 30% of the energy used in fixation for hydrogen evolution compared with 5% for cowpeas, which indicated that there may be important differences between species in nitrogen fixation efficiency. Westermann and Kolar (1978) noted differences in the quantity of nitrogen fixed between *P. vulgaris* cultivars. Rate of fixation per gram of nodule fresh weight was similar between cultivars so it was assumed that differences were due to variable nodule weight. Seed yield was related to nitrogen uptake.

Pate and Herridge (1978) found that, for *L. albus*, nodules used 4-6.5 g of carbon to fix 1 g nitrogen. As the plant aged, the ratio of total carbon fixed to nitrogen fixed increased as photosynthate was diverted away from the nodules. A similar trend was noted in cowpeas (Herridge and Pate, 1977). The amount of net photosynthate required to produce 1 g of seed dry weight and 1 g of seed protein was 9.9 and 31 g respectively for *L. albus* (Pate and Herridge, 1978). For a wider comparison between species see Atkins *et al.*, (1978).

The amount of nitrogen fixed by nodules in the long term is closely related to the quantity and duration of effective nodule tissue which is, in turn, related to root development (Nutman,1976). Hardy *et al.* (1968) suggested nitrogen fixation matches demand but Lawn and Brun (1974), Hardy and Havelka (1976) and Herridge and Pate (1977) have shown that the supply of photosynthate to the nodule determines the rate of nitrogen fixed. Bethlenfalvay *et al.* (1978) noted that the capacity to fix nitrogen improved photosynthetic rate and efficiency compared with non-nodulated plants. All these factors are probably correct as they are linked to the net photosynthate supply of the plant.

Nodules may be more important to the plant than just a site for nitrogen fixation. For example they are a site for auxin, cytokinin, gibberelin and abscisic acid production although the interaction with the host plant is unknown. This may give rise to the situation where nodulated plants yield more than non-nodulated plants (Sinha, 1977; Summerfield *et al.*, 1978).

A.4.2.2 Utilisation of Nitrogen

Roots do not accumulate soluble nitrogen and products of assimilation are immediately released to the shoot. The xylem can account for 75-80% of the upward movement of nitrogen (Pate, 1971). The stem can intercept and absorb nitrogen from the xylem stream (Gates, 1968; Pate, 1971; Minchin and Pate, 1973) thus acting as a buffer, accumulating nitrogen in excess of requirements (Carr and Pate, 1967), which may be used when nitrogen is in short supply (Egli *et al.*, 1978).

Leaves are very important sites of synthesis and turnover of organic nitrogen solutes (Pate, 1971; 1974; Pate and Flinn, 1973). They can attract nitrogen and other metabolites in the xylem stream and reduce them, using simple organic compounds from photosynthesis to construct a large number of more complex products including protein and amino products (Pate, 1971; Lewis and Pate, 1973).

Once expanded, the leaf exports nitrogen compounds to younger tissue via the phloem, which, in *L. albus*, contains 12-16 times more nitrogen than xylem sap (Pate *et al.*, 1977). However, it has also been shown in *L. albus* that a high proportion of nitrogen in the phloem can result from a direct transfer of amino acids from the xylem. (Sharkey and Pate, 1976).

Older leaves senesce for a number of reasons; mainly shading, ageing or water stress. Nitrogen released from these leaves is made available to young tissue (Derman *et al.*, 1978) and nitrogen may be recycled through several tissues before being incorporated into the seed. (Cooper, *et al.*, 1976; Pate, 1976). Between 70 and 90% of leaf nitrogen may be mobilised from the leaf before senescence (Pate, 1971). Posipanov (1974) estimated that, in *L. angustifolius*, 75% of leaf nitrogen was transferred to the seed.

Young stems have initially high levels of nitrogen but these reduce with age; rapidly at senescence (Pate 1971). In lupins, Hocking and Pate (1978) found losses of 60-65% of the stem nitrogen in *L. albus* but only 30-55% in *L. angustifolius*. Farrington *et al.* (1977) found relatively stable levels in stems of *L. angustifolius*.

A.4.3 The Importance of Senescence in Legume Seed Production

A characteristic of annual plants is the often rapid senescence of non-seed organs which accompanies the final stages of seed development and maturation (the 'self destruction' characteristic). Senescence is particularly important in legumes as the direct supply of nitrogen from fixation and the soil is insufficient to meet the requirements of the high protein seed and so additional supplies from vegetative tissues are important (Sinclair and de Wit, 1975). Also, the timing of the senescence marks the end of carbon and nitrogen assimilation and governs to a large extent the amount of these nutrients that can be taken up and thus the level of seed production that can be obtained.

In an attempt to understand and simulate the relationship between seed growth and senescence, Sinclair and de Wit (1976) constructed a simple model (Fig. A.4.1) which suggests that seed protein supply from either assimilation or remobilisation is governed by the amount of carbohydrate (hexose) available for supporting seed production. The nitrogen supply from the root is converted immediately and the balance required for seed production is supplied at a rate determined by translocation of nitrogen from the vegetative tissues. The rate of utilisation of tissue nitrogen is largely governed by the size of the hexose pool and the proportion of it being utilised in the processing of root-supplied nitrogen. Thus, the utilisation of tissue nitrogen tends to be low when the supply of assimilated nitrogen is high relative to the amount that can be utilised by the available carbohydrate pool.

If supply of nitrogen from the root declines, then increasing amounts of shoot nitrogen would tend to be utilised. This however, can only occur to a limited extent before the physiological activity of the leaf starts to decline and the senescence cycle begins (Simon, 1967; Sinclair and de Wit, 1975; 1976). Posipanov (1974) has suggested a similar pattern for lupins.

Many workers have studied the decline in nitrogen fixation late in fruit development and attributed it to competition for photosynthate between fruit and nodule, with the fruit eventually dominating (Lawn & Brun, 1974; Ham *et al.*, 1976; Hardy and Havelka, 1976; Bethlenfalvay and Phillips, 1977; Sprent and Bradford, 1977). However, Pate (1976) points out that the decline in nodule activity is not always associated with fruit growth so competition may not be the only factor. Competition from fruit growth has also been implicated in reduced root and leaf growth. (Section A.4.1). Atkins *et al.* (1978) suggests that the root itself is a major competitor for photosynthate in *L. albus* during the later stages of growth.

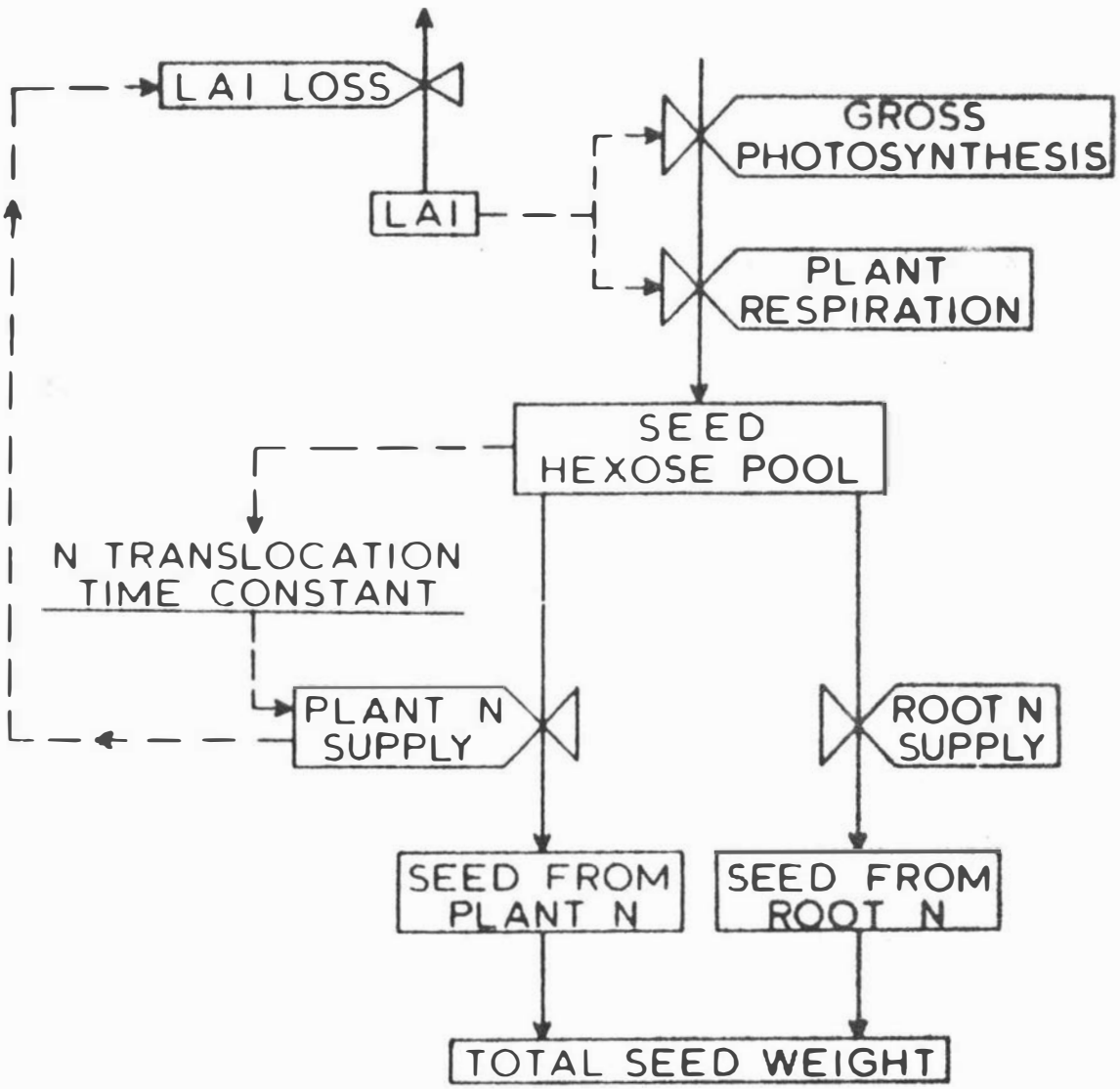

Fig. A.4.1 Outline of the model given by Sinclair and de Wit (1976).

Internal or external factors which increase the supply of nitrogen from fixation or increases the amount of tissue nitrogen should increase the total seed yield by delaying senescence and allow a longer duration of seed fill. (Carr and Pate, 1967; Sinclair and de Wit, 1976; Eaglesham *et al.*, 1977). The model indicates that if photosynthate is increased without also increasing nitrogen supply, senescence is hastened because of increased use of nitrogen reserves (Sinclair and de Wit, 1976). However, increased photosynthate supply would normally result in increased nitrogen fixation or assimilation (Carr and Pate, 1967; Ham *et al.*, 1976).

Some workers have stated that nitrogen supply is not limiting suggesting that net photosynthesis is the ultimate limiting factor (Shibles *et al.*, 1974, Sprent and Bradford, 1977; W.G. Duncan pers. comm.). The Sinclair and de Wit model essentially implies a limitation of carbohydrate and, because there is insufficient for both seed and nodules to produce at their maximum, the 'self destruction' cycle results.

External factors (such as water stress, high density, high or low temperatures) that may affect nitrogen fixation, absorption of nitrogen and/or net photosynthesis will also influence the timing of senescence and thereby affect seed yield. Leonard (1962) maintained that the restricting effect of fruit only occurred when some internal or external growth restriction was present. Ryle *et al.* (1978) found that supplying adequate nitrogen prevented loss of nitrogen from the leaves.

The hypothesis that senescence is a result of competition for assimilate is widely held. However, some workers (e.g. Leopold *et al.*, 1959; Wareing and Seth, 1967; Nooden *et al.*, 1978; Williams and Williams, 1978) suggest that senescence is under hormonal control. This does not necessarily preclude the competition theory as hormonal control may be a regulator in the competitive situation.

Whatever the physiological mechanisms are, it is apparent that legume seeds are very dependant on the supply of nitrogen from vegetative parts. The estimates of how important this remobilisation is varies widely. Egli *et al.* (1978) estimates 20-60% of the seed requirement is supplied by remobilisation in soybean. Estimates of between 50 and 62% have been made for *L. albus*, peas and cowpeas. (Minchin and Summerfield, 1978; Pate *et al.*, 1977; Pate and Herridge, 1978) and a high estimate of 89% has been made for *V. faba* by Sprent and Bradford (1977). Hocking and Pate (1978) found differences in the efficiency of remobilisation between lupin species and plant parts. *L. albus* was more efficient than *L. angustifolius;* leaves were more efficient than stems and the main stems were more efficient than lateral stems. Sprent and Bradford (1977) showed that the contribution from remobilisation varied with plant density.

It is possible that the tendency for an internal limitation to yield is the cause of the relatively poor yield performance of grain legumes relative to cereals (Sinclair and de Wit, 1975; Sinha 1977). Clearly an understanding of, and satisfactory manipulation of, this phenomenon is important in improving grain legume production, but the applications and implications need further study. For example, it is unclear whether breeders should select for the ability to build up large nitrogen reserves in vegetative structures (Carr and Pate, 1967; Atkins *et al.*, 1978) or to select for efficient direct transfer to the seed. (Pate, 1976; Sinha, 1977). Pate (1976) and Eaglesham *et al.* (1978) maintain that it is important to ensure that the nitrogen system is sufficiently active to delay senescence. Pulver *et al.* (1978) compared 10 cultivars of cowpea and found little correlation between seed yield and total plant nitrogen. Those cultivars most efficient at translocating nitrogen from vegetative tissue tended to have the highest yield. Westermann and Kolar (1978), working with *P. vulgaris* did find a positive correlation between nitrogen uptake and seed yield.

This section can be summarised by saying that the factors which mainly influence seed yield are duration of seed fill, rate of photosynthesis and the partitioning of assimilates (Egli and Leggett, 1973; Seligman *et al.*, 1975; Sinclair and de Wit 1976).

A.5 THE EFFECT OF ENVIRONMENT ON SEED YIELD

The previous section has largely considered the development of seed yield with little reference to the effect of environmental limitations which may greatly modify the situation apparent under ideal growing conditions. This section aims to consider the effect of selected environmental factors (including cultural practices) on legume seed production with emphasis on lupin seed production. This is a large topic and only those factors of relevance to the studies in this thesis are considered.

A.5.1 Water Deficit and Yield

A common and important limitation to seed yield in the field is water stress. An understanding of its effects is therefore important.

The water status of the plant is controlled by soil water availability and evaporative demand of the air surrounding the plant. Most work has concentrated on soil water supply but the evaporative demand is also important because, if it is high enough, plants can be stressed even if plants are well supplied with water (Salter and Goode, 1967; Forde and Thorne, 1974; Woodward and Begg, 1976).

Water deficit in individual plant tissues develops due to frictional resistances within the plant and when water loss exceeds supply from the soil (Begg and Turner, 1976). When there is adequate water, water potential in plant tissues, especially leaves, show diurnal fluctuations due to evaporative demand. At

night, tissue water potential reduces to a level determined by soil water potential. As the soil dries, the tissue water potential at night progressively lowers (Slatyer, 1967; Begg and Turner, 1976).

A.5.1.1 The Main Physiological Effects of Drought

There are many recent reviews of this topic (Hsiao, 1973; Hsiao and Acevedo, 1974; Boyer and McPherson 1975; Boyer, 1976; Hsiao *et al.*, 1976).

Cell growth is usually the first to be affected by water stress (Hsiao, 1973) and can be affected at very mild levels of stress (Wardlaw, 1969). This means vegetative growth is also very sensitive, the consequences of which can be long term (Boyer, 1976). Cell enlargement is more sensitive than cell division (Hsiao *et al.*, 1976). Photosynthesis and respiration are affected at stress levels greater than cell enlargement (Hsiao, 1973) so that short term growth may be affected without necessarily affecting long term potential. A sharp decline in photosynthesis occurred below 90% relative water content (RWC) in soybean although the rate of decline was slower as levels dropped below 80% RWC (Shaw and Laing, 1966; Chen *et al.*, 1971).

It has been shown in tomatoes by Gates (1955a, 1964) and in soybeans by Ludlow and Ng (1974) that after a mild water stress of short duration, recovery of growth is rapid and results in growth levels higher than control rates ("compensatory growth"). This does not always occur however (Boyer, 1976). A similar compensatory growth effect on leaf primordia of the apex of *L. albus* was noted by Gates (1968). It is usually the plant parts most actively growing that are most affected by water deficit (Williams and Shapter, 1955; Gates, 1955 a,b; Salter and Goode, 1967) but they retain the greatest potential for recovery on rewatering (Gates, 1964). Hsiao and Acevedo (1964) warns however, that claims for compensatory growth often do not take

into account the earlier maturation and senescence of non-stressed control tissue.

Water deficit encourages senescence of older tissues especially mature leaves. There appears to be a factor of water conservation in this response enabling the younger, more photosynthetically active tissue to function longer (Jordan *et al.*, 1975; Kassam, 1975). The mobilisation of reserves in senescing tissues could also be a valuable compensation for lowered primary assimilation caused by water deficit. However, Hocking and Pate (1978) found that leaflets of *L. albus* which senesced due to drought translocated nutrients less efficiently than normally senescing leaflets.

There is a close relationship between protein synthesis and plant moisture levels (Gates, 1968; Slatyer, 1973) with the reduction in protein synthesis commencing at low stress levels (Hsiao, 1976). In older leaves, hydrolytic breakdown of proteins increases (Gates, 1957; 1964). The effect of stress is thus a build-up of amino acids (Slatyer, 1973) which may be reversible if the stress is mild and not too prolonged (Gates, 1968) but the trend may become irreversible if stress continues for too long thus causing leaf death (Gates, 1964). During wilting, nitrogen can build up in the stem (Gates, 1955b and reduce again on rewatering.

The effect of water deficit on nodule activity has been reviewed by Pate (1976) and Sprent (1976). Pate made the following points:

(1) Water stress resulted in loss of nitrogen fixation activity (Sprent 1971, 1972).

(2) Effects are reversible provided loss of fresh weight of nodules does not exceed 20% of their maximum fresh weight (Sprent 1971).

(3) Irreversible structural damage can occur if dessication is severe (Sprent 1972).

Nodules with meristematic growth can recover better than those without (Sprent 1976). Sprent (1972) and Engin and Sprent (1973) concluded that the effect of water stress was a direct one, possibly because of reduced nodule respiration. They found nitrogen fixation more sensitive to water deficit than was photosynthesis. Huang *et al.* (1975) however, found differences between intact and detached nodules and suggested caution when interpreting Sprent's earlier work with detached nodules.

A.5.1.2 Effect of Water Stress on Legume Seed Production

All components of seed yield can be reduced by water deficit depending on the timing of the stress. Floral initiation and branch initiation are both sensitive to water stress but, as they usually occur early in growth, they tend not to be greatly affected in the field situation (Fischer and Hagan, 1965; Salter and Goode, 1967). Pod numbers are reduced by stress during flowering and early podset so yield is very sensitive at this stage (Salter and Goode, 1967; Sionit and Kramer, 1977). A major response to irrigation occurs at this stage due to reduced flower and pod abscission (Gabelman and Williams, 1960), although Fisher and Weaver (1974) and Biddiscombe (1975) showed that irrigation can increase flower number as well as reduce flower and pod fall. Salter and Drew (1965), Sprent *et al.* (1977) suggest that a reduction in root growth over flowering may play a part in the sensitivity of water stressed plants at this time.

If flower and pod abscission is caused by insufficient assimilates (See Section A.3.3), then reduction in photosynthate or nitrogen supply due to water stress, is likely to promote abscission. (Fischer and Hagan, 1965).

The number of seeds per pod can be reduced by water stress over flowering and early podfall (Robins and Domingo, 1965; Salter and Goode, 1967) presumably because water stress stimulates ovule abortion (Gabelman and Williams, 1960; Kato and Sakaguchi, 1954).

Herbert and Hill (1978b) however, found an overall increase in seeds per pod in non-irrigated compared with irrigated plants due to fewer lateral branches which tend to have lower numbers of seeds per pod. Stress late in development can reduce seed weight and/or prevent full development of seed (Robins and Domingo, 1956; Salter and Goode, 1967; Sionit and Kramer, 1977). However, seed weight may also be increased by water stress (Adjei-Twum and Splittstoesser, 1976; Herbert and Hill, 1978b). This effect seems to be associated with reductions in other yield components.

Seed development may be hastened by water stress (Robins and Domingo, 1956; Sinha, 1977; Herbert and Hill, 1978b), possibly because seed filling is less sensitive to water stress than vegetative growth (Gates, 1968; Hsiao and Acevedo, 1974; Begg and Turner, 1976). This would change the relative sink sizes causing changes in the direction of translocation (Weber, 1968; Wardlaw 1968). Water stress seems to have a small effect on translocation but interferes with the supply and utilisation of assimilate (Nelson, 1963; Wardlaw, 1967; 1968).

The period most sensitive to water deficit can vary between species and between cultivars within species. For example, the podfill period seemed to be a sensitive period in soybeans (Runge and Odell, 1960; Doss *et al.*, 1974) whereas in cowpea, stress during early growth, by reducing podset, was the most important (Summerfield *et al.*, 1976). Part of this effect could be due to differences between determinate and indeterminate plants. Because potential seed sites are initiated early in determinate crops, early stress is likely to reduce seed yield more than in indeterminate crops (Salter and Goode, 1967). Late stress will reduce the time for reproductive development in indeterminate crops.

Recovery from short water stress periods may be possible if later nodes can bear pods (Shibles *et al.*, 1974; Biddiscombe, 1975; Sinha, 1977) but this ability reduces as the plant ages (Shibles *et al.*, 1974).

Large increases in lupin seed yield have been obtained from irrigation on light soils (Stoker, 1975; 1977; 1978; Herbert and Hill, 1978a). An important effect of irrigation is to extend vegetative growth which results in more inflorescences, increased peak leaf area and longer leaf area duration (Herbert and Hill, 1978b). Thus lupin is very responsive to water supply during flowering (Stoker, 1977; 1978; Herbert and Hill, 1978b). However, under high densities the response to irrigation may be limited because inter-plant competition limits the growth of lateral branches. (Herbert and Hill, 1978 a,b). The extra vegetative growth promoted by irrigation may compete with main stem seed components causing a reduction in their number and/or size (Herbert, 1978; Herbert and Hill, 1978b) and may reduce the efficiency of seed production as measured by harvest index (Herbert and Hill, 1978a).

A.5.2 Relationship Between Temperature and Seed Yield

The reviews of Farrington (1974b) and Sinha (1977) include considerations of the effect of temperature on grain legume growth.

Most food legumes have an optimum temperature range between 20-30^{o}C (Sinha, 1977). An important limitation to yield can be long periods of sub-optimal rhizosphere temperature or short periods of high temperature (Gibson, 1974) as bacteroid tissue is sensitive to temperature although nitrogen fixation is unaffected between 12-32^{o}C (Sinha, 1977). For lupins, Rahman *et al.*, (1974) suggests root temperatures may be as important as air temperatures

Poor growth at low temperatures may cause slow development of nitrogen fixation capacity (Greenwood *et al.*, 1975; Trinick

et al., 1976; Farrington *et al.*, 1977). For peas, temperatures above about 25°C can reduce vegetative growth, pod number and seed size (Lambert and Linck, 1958; Ormrod *et al.*, 1970; Nonnecke *et al.*, 1971). Pumphrey *et al.*, (1979) estimated a 13 kg/ha drop in seed yield for every degree day above 25°C.

Gladstones (1970) suggests mean monthly maximum temperatures between 15 and 25°C as being optimal for lupins but Corbin (1978b), referring to *L. angustifolius*, suggests that 10-20°C is best for seed production. Corbin (1978a) recommends that flowering be completed before these temperatures reach 25°C to reduce the incidence of flower and pod abscission which can occur at higher temperatures. Gladstones (1970) and Perry (1975) also mentions that there is a strong tendency for lupins to lose flowers and/or small pods when temperatures are high. Garside (1979) found consistent podset over a range of sowing times when temperatures were between 15-20°C. He did note lower podset when maximum daily temperatures reached 27°C at the start of flowering. Pate (1977) stated that high temperatures markedly affects nitrogen fixation possibly by restricting carbohydrate supply to the nodules or by increasing root respiration. Nitrogenase activity seems to operate efficiently over a wide range of temperature.

Lupins can be damaged by severe frosts during flowering (McPherson, 1940; Inch, 1947; Corbin, 1978a; Hall, 1978). During the vegetative period however, lupins are tolerant of low temperatures. At this stage, *L. angustifolius* can tolerate temperatures as low as -6°C, with other species less tolerant (Gladstones 1970). MacGillivray (1934), however, mentions that lupins are susceptible to frost during early growth.

A.5.3 Time of Sowing

By determining water, temperature and insolation inputs at critical times, sowing time can have considerable influence on seed yield. The effect is most marked in non-uniform climates (Sinha, 1977). Also, sowing time influences the length of the vegetative period and the period of seed development (Sinha, 1977; Aitken, 1978). Ishag (1973b) considers it desirable to adjust sowing date so that maximum leaf area coincides with favourable light and temperature. Walton (1976) suggests that the reproductive phase of lupin should fall almost entirely within the period of adequate soil moisture.

Because of differences in plant size, planting date and optimum population may interact (Gladstones, 1977; Sinha, 1977; Corbin 1978a). Walton (1976) however generally found no interaction between time and density in *L. angustifolius* although one trial in his series indicated a higher optimum population at a later sowing.

Numerous studies on sowing date with lupins in Australia have been conducted in recent years almost all of which have concluded that sowing early in autumn is important to achieve high yields (Gladstones and Hill, 1969; Farrington, 1974a; Francis *et al.*, 1971 , Walton, 1976; Reeves *et al.*, 1977; Corbin, 1978b; Hall, 1978). Garside (1979), working in Tasmania, a similar climate to New Zealand, concluded that sowing between May to September gave similar yields. In fact, seasonal differences in this study meant that yields from sowings over this time were very variable between seasons depending on conditions later in the spring. After September sowing however, yields declined steadily with later sowings.

Most early New Zealand reports recommend March-April sowings although spring sowing may be successful (McPherson, 1940; Inch, 1947; van Steveninck, 1956; Whatman, 1959; White, 1961). The

basis for these recommendations however, was not stated but they were probably based on Canterbury farmer experience. More recently, Goulden (1976) found a substantial advantage in yield from May sowings of *L. angustifolius* compared with September sowings. In a preliminary study of spring sowings, Withers (1973) found a general reduction in yield with later sowings.

Early sowing allows greater development of lateral branching (Goulden 1976) which is an important determinant of seed yield (Withers, 1973; Farrington, 1974a; Walton, 1976; Reeves *et al.*, 1977) by influencing pod number. Pod number within each branch also tends to reduce with later sowings (Walton, 1976).

Sowing time influences start of flowering through a complex series of vernalisation, photoperiod and temperature requirements (Gladstones, 1970; Rahman and Gladstones, 1972; 1973; Reeves *et al.*, 1977). All lupin species respond to vernalisation to varying extents (Gladstones and Hill, 1969; Gladstones, 1970; Rahman and Gladstones, 1972). Some cultivars, however, have been developed to have a nil or small vernalisation requirement for adaptation to areas with shorter growing seasons (Gladstones and Hill, 1969; Rahman and Gladstones, 1972; Gladstones, 1977). Short photoperiods retard floral initiation especially in *L. luteus* but not significantly in *L. albus* (Rahman and Gladstones, 1972).

In field studies, Reeves *et al.* (1977) found the period from floral initiation to the end of flowering was shortened by late planting. Time to maturity after flowering varied. Garside (1979) also noted shorter duration of flowering with delayed sowings presumably because of less development of lateral branching.

Sowings in winter often result in problems of slow emergence and nodulation (Gladstones, 1970; Farrington, 1974a) waterlogging, disease, vermin and weeds (Walton, 1976; Garside, 1979). Thus location and season can greatly vary the response of lupin seed

yield to time of sowing as shown by the trial series of Walton (1976) and Garside (1979).

A.5.4 Plant Density Effects on Seed Yield

The relationship between seed yield and plant density is a very complex one because of the "plasticity" of yield components and the interaction with many other factors such as moisture supply (Lucas *et al.*, 1976; Herbert and Hill, 1978 a,b) genotype (Weber, 1968; Sinha, 1977) and sowing date (Sinha, 1977; Gladstones, 1977; Corbin, 1978b).

As density increases from low levels, seed yield usually increases (Ishag, 1973a; Tamaki *et al.*, 1973; Walton, 1976; Goulden, 1976; Herbert, 1977) until, eventually, constant or decreasing yields are reached with increasing density at high levels (Holliday, 1960; Lucas *et al.*, 1976; Herbert, 1978). These trends do not always occur however. For example, under irrigation Lucas *et al.*, (1976) and Herbert and Hill (1978b) found highest yields in lupin were obtained at low densities.

Early recommended lupin sowing rates for South Island conditions ranged between 1½ - 3 bu/ac (100-200 Kg/ha) (McPherson, 1940; Inch, 1947; White, 1961) although, again, the basis for these rates were not specified. More recent work by Goulden (1976) indicated an optimum density between 168 and 202 kg/ha with a linear response between 16-74 pl/m^2 (67-202 kg/ha) for both autumn and early spring-sown *L. angustifolius* and spring-sown *L. luteus*. Herbert (1978) found maximum yield of August-sown *L. angustifolius* at 130 pl/m^2 although 70 pl/m^2 produced 94% of the maximum yield. In an earlier experient however, there was little increase above 53 pl/m^2 (Herbert, 1977b) but *L. albus* continued to increase in yield up to 93 pl/m^2.

With the autumn sowings prevalent in Australia, recommended sowing rates for *L. angustifolius* are between 60-100 kg/ha with

higher rates for later sowings (Gladstones, 1977; Corbin, 1978a). In three of the experiments undertaken by Walton (1976), increasing density partially compensated for reduced yield from later sowings leading to the conclusion that greater density can compensate for the lower branch numbers which usually result from later sowing. Walton (1978) suggested that where plants were large through early sowing under favourable conditions, low densities (20-40pl/m^2) appeared sufficient and small changes in density had large competitive effects but smaller plants grown under less favourable conditions required higher densities to maximise yield.

Because of its larger seed, *L. albus* would be expected to require a higher sowing rate (Herbert, 1977b) and, because of a more stable branching pattern, Ultra *(L. albus)* has a lower variation in yield per plant with plant density changes compared with Unicrop *(L. angustifolius)* and perhaps is more responsive to high densities (Herbert, 1977 b,c).

However, it would appear that sowing rates are not a critical factor in lupin seed production from lupins as good yields can be obtained from a wide range of densities (Bauer, 1976; Goulden, 1976; Lucas *et al.*, 1976; Walton, 1976, Herbert, 1977c).

Seed yield components, leaf area and weight per plant declines with increasing density (Ishag, 1973a; Tamaki, 1973; Goulden, 1976; Herbert, 1977 a,b, 1978; Herbert and Hill, 1978 a,b) in a similar way to other stress factors. The effect of increasing density on the plant seems to arise from intra-plant competition for the reduced amount of assimilate produced by each plant as a result of the smaller quantity of environmental input available to each plant. This effect usually commences early in development (Adams, 1967; Bennett *et al.*, 1977; Herbert, 1978a; Herbert and Hill, 1978b). However, Sprent and Bradford (1977) suggests that at high densities, internal competition may be less important and external influences may be more important giving rise to greater seasonal variation in yield than at lower densities. Suppressed

plants at high densities may be more prone to lodging which may reduce seed yield (Weber, 1968).

As density increases, L.A.I. also increases (Meadley and Milbourn, 1971) although leaf area per plant is lower (Ishag, 1973a) due to shading (Tamaki *et al.*, 1973) or moisture stress (Sprent *et al.*, 1977). This may be partially compensated for by increased photosynthetic efficiency of the remaining leaves (McEwan, 1972), reduced competition for minerals or hormones within the plant or improved plant structure giving rise to better light utilisation (Ishag, 1973b; Herbert, 1978b). In some cases there may be excessive leaf area at high densities which, due to shading, may induce excessive abscission of flowers and pods resulting in reduced seed yields (Meadley and Milbourn, 1971). Gladstones (1977) suggests this can happen in lupins under good growing conditions.

Branch numbers are also reduced at higher densities (Tamaki *et al.*, 1973; Sinha, 1977; Herbert, 1977a; 1978a; Herbert and Hill, 1978a) which can have a large effect on lupin yields (Withers, 1973). Higher order branches are usually the most affected in terms of branch number and yield components (Sinha 1977, Herbert 1977a, 1978; Herbert and Hill 1978 a,b). Plants such as lupin which have a marked branching structure may be more structurally affected by density than plants with a lower tendance to branch (e.g. *V. faba*) (Bennett *et al.*, 1977). Branching plants can compensate more at lower densities, so seed yield per unit area may be less affected by density.

SECTION B FIELD TRIALS

B.1. INFLUENCE OF TIME OF SOWING ON SEED YIELD

B.1.1 INTRODUCTION

In a previous study (Withers, 1973), the two *L. angustifolius* cultivars Uniharvest and Unicrop were compared at six times of sowing during the spring. Generally, seed yield per plant and yield components declined as sowing was delayed. At that stage there seemed to be no other published study in New Zealand on sowing date although Gladstones and Hill (1969) had undertaken a similar study in Western Australia.

Although in the North Island emphasis was likely to be on spring sowing, data on autumn and winter sowings was thought to be valuable as sowing at this time may be possible and desirable on lighter soils. A time of sowing study was therefore started using the same two cultivars used in the previous study as differences in vernalisation requirement (Gladstones, 1970) were likely to give rise to different responses to sowing time (Gladstones and Hill, 1969).

B.1.2 MATERIALS AND METHODS

At ten sowing dates between 7 April and 5 October 1973 (Table B.1.1) two cultivars of *L. angustifolius* (Uniharvest and Unicrop) were sown in plots 20 m long which consisted of 3 rows of plants. Spacing of the plants was an equidistant 30 cm. This spacing was adopted to allow plants to develop fully and to minimise any interaction of plant size and sowing date. Experimental design was a randomised block with 4 replications. Soil type was Manawatu silt loam

The equivalent of 24 kg of P/ha and 112 kg K/ha as potassic superphosphate was broadcast prior to planting and raked in. Three seeds per position were sown by hand and thinned to one plant after emergence. Atrazine (1 kg/ha a.i.) was applied pre-emergence and provided excellent weed control. Fifteen plants were taken at maturity from the centre row of each plot. Seed yield and yield components were recorded. Date when 50% of plants commenced and finished flowering on each branch sequence for each sowing was also recorded.

TABLE B.1.1: Sowing and flowering dates, days to flowering and degree-days to flowering for Unicrop (UC) and Uniharvest (UH)

Sowing No.	Sowing Date	50% Flowering Date*		Sowing to Flowering			Degree days	
		UC	UH	UC	UH	Diff.	UC	UH
1	7 Apr	9 Aug	17 Sep	124	164	40	650	865
2	1 May	6 Sep	27 Sep	128	153	25	594	723
3	31 May	1 Oct	8 Oct	123	130	7	544	600
4	25 Jun	12 Oct	18 Oct	109	115	6	512	561
5	24 Jul	23 Oct	27 Oct	91	95	4	516	553
6	7 Aug	29 Oct	4 Nov	83	89	6	517	590
7	23 Aug	5 Nov	14 Nov	74	83	9	526	634
8	6 Sep	12 Nov	24 Nov	67	79	12	535	639
9	21 Sep	22 Nov	14 Dec	62	82	20	530	764
10	5 Oct	3 Dec	23 Dec	59	79	20	532	781

* Date when 50% of plants commenced flowering on main stem

B.1.3 RESULTS

Flowering dates, time from sowing to flowering and the degree days ($5^{o}C$ base temperature) are presented in Table B.1.1. Days from sowing to flowering tended to decrease for both cultivars as sowing became later. Unicrop was consistently earlier flowering although the difference between cultivars was small with sowings between 31 May and 6 September. After 23 August sowing, days from sowing to flowering in Unicrop continued to decline but for Uniharvest they tended to remain constant. Degree days for the period sowing to flowering declined until the June sowing. After this time, Unicrop had a relatively stable number of degree days whereas those for Uniharvest steadily increased which is consistent with the difference in vernalisation requirement between the two cultivars.

The spread of flowering for each inflorescence (Fig. B.1.1) was actually wider than indicated. The method of noting when 50% of the plants in the plot started and stopped flowering indicates the time of peak flowering. The general pattern was for there to be a shorter duration of peak flowering as sowing date become later especially for lower order inflorescences.

Despite the wide range of sowing dates, flowering stopped completely for most dates over a 4 week period after 1 December. It was about this time that water availability from rainfall was declining sharply (Fig. B.1.2) and air temperatures were rising. Thus it was probably increasing plant water deficit that caused flowering to stop. Earlier sown plants seemed to be more sensitive, possibly due to their greater leaf area and consequent larger water use.

Data for total seed yield was combined and subjected to linear regression analysis (Table B.1.2). There was a good relationship between seed weight and pod number per plant with time from the initial sowing. The high coefficient of determination (R^2) of the

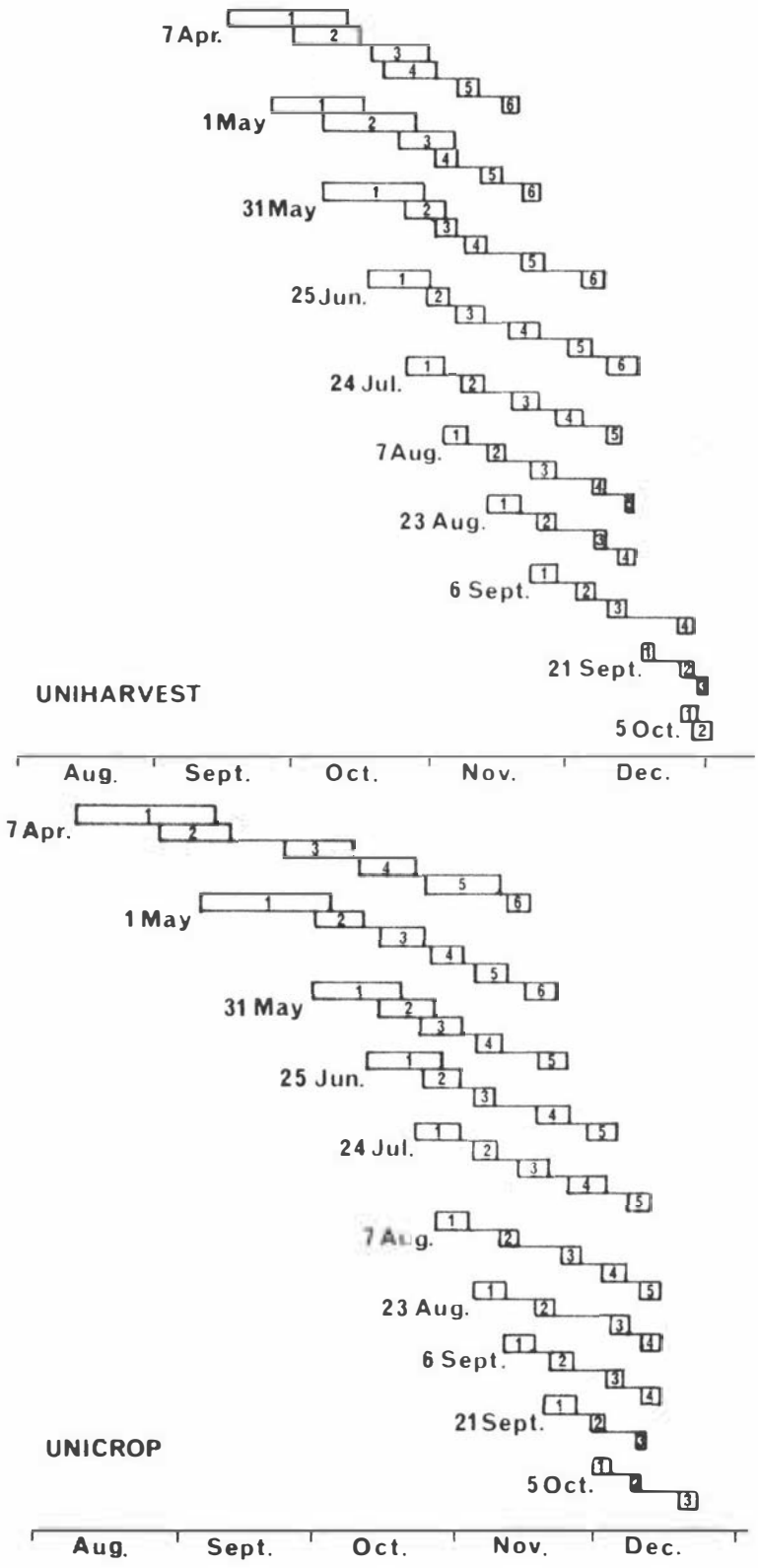

Fig. B.1.1: Period, for each inflorescence and sowing date, when 50% of plants were flowering. (1 = main stem, 2 = 1st order lateral, 3 = 2nd order lateral, etc)

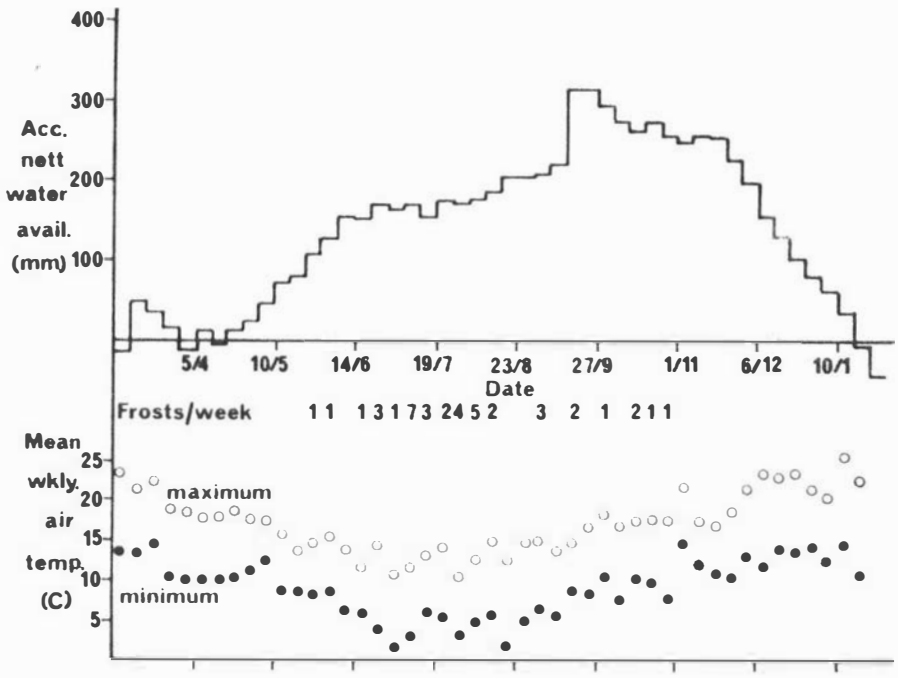

Fig B.1.2 Accumulated net water availability (rainfall - evaporation), number of frosts per week and mean weekly air temperatures for the 1973/4 season.

regression seed weight with pod number would indicate that pod number was the main component influencing seed yield in this study.

In Fig. B.1.3 it is apparent that, especially for Unicrop, the lower order sequences generally had a lower seed yield at the early sowings (7 April - 25 June) compared with later sowings. First order lateral branches were the most affected. For Unicrop, this means that total seed yield did not significantly change for these sowings and, for Uniharvest, the seed yield was not as high as would be expected from the linear regression.

TABLE B.1.2: Results of linear regression analysis of seed weight per plant, pod number per plant and time from sowing.

x	y	a	b	R^2	SE
Date *	Seed *	72.7	-0.282	0.78	8.7
Date	Pods *	122.1	-0.47	0.77	15.2
Pods	Seed	1.4	0.57	0.93	4.8

* Date - sowing time in number of days from 1 April
Pods - number of pods per plant
Seed - weight of dried seed/plant (g)

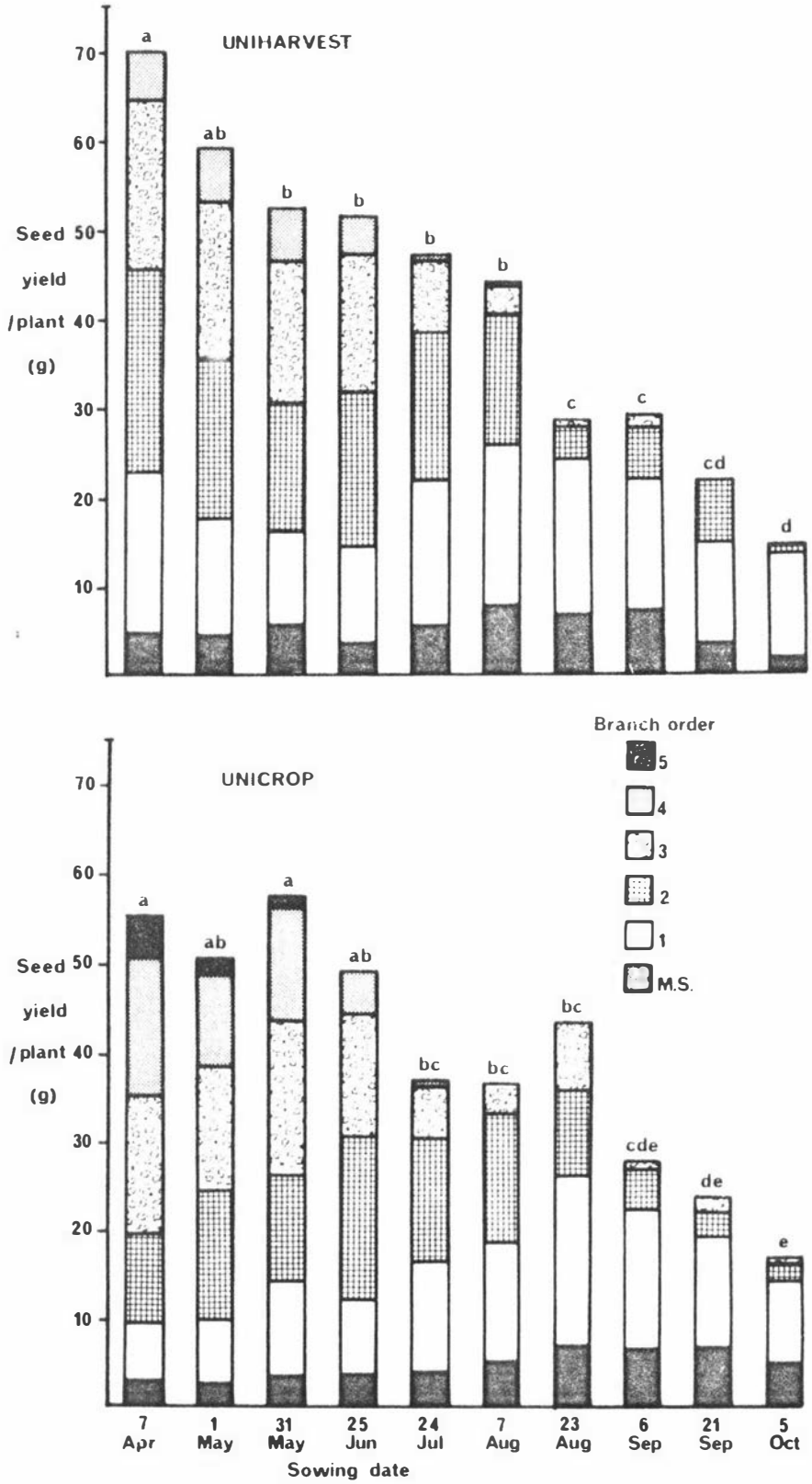

Fig. B.1.3 Seed yield per plant for each branch order (MS = main stem, 1 = 1st order lateral, 2 = 2nd order lateral, etc).

B.1.4 DISCUSSION

Because of the longer duration of flowering from the early sowings, there would seem to be some potential for increased yields from autumn/winter sowings as indicated by other workers (see Section A.4.3). The seed yield however, did not realise this potential for reasons that were not clear except that it was early inflorescences which were mainly affected. Lack of response to sowing dates over the same period was also noted by Garside (1979).

Three possibilities for the low yield from the lower inflorescences are:

(1) Shading or competition by the higher order branches. In Fig. B.1.3, the yield of lower order branches increased when the yield (and number) of higher order branches decreased. However, it should be noted that the plants in this experiment were widely spaced and any shading effect should be less than at normal spacings. On the other hand, growth of lateral branches may have been greater than at normal spacings so any intra-plant competition may have been increased over normal spacing.

(2) Frosts at flowering may have been a factor as during the flowering of the lowest two sequences of the first four sowing dates a number of ground frosts occurred (Fig. B.1.1, B.1.2) so it is possible that low temperatures caused pod loss.

(3) Moderately severe infection of the fungal diseases *Pleiochaeta setosa* and *Stemphylium vesicarium* were noted especially on early-sown plants and these diseases have been shown to cause shrivelling and loss of pods and seed (Milne, 1964; Tate, 1968).

The reduction in yield with delayed sowings in the spring was very significant. This trend may have been accentuated by a dry December. In years or districts with higher rainfall in the critical late spring/summer period the drop in yield may not be so

severe. The main effect of moisture stress appeared to be on the production of new lateral inflorescences. Initiation of branches, leaves and flowers are all sensitive to water stress (Fischer and Hagan, 1965; Salter and Goode, 1967; Gates, 1968), Gates (1968) showed that leaf primordia production in *L. albus* can restart after short periods of stress are relieved so it is possible that inflorescence development could resume if sufficient moisture was supplied before irriversible changes occurred. Therefore, unless good summer water supply can be assured it would seem sowing early in spring would be desirable.

There would seem to be little difference between the two cultivars tested if they are sown before mid-September. After this time, Unicrop would seem to be preferred because of its earlier flowering which would probably be a particular advantage on free-draining soils and in summer-dry environments which was the initial reason for breeding Unicrop (Gladstones, 1977).

B.2 THE EFFECT OF SOWING TIME AND PLANT POPULATION ON FOUR CULTIVARS OF LUPINS

B.2.1 INTRODUCTION

This study was carried out concurrently with that previously reported (Section B.1) and was designed to complement the information expected from that experiment. Lupin plants sown at low densities differ greatly in size due to the greater development of lateral branches from early-sown plants. It would be expected therefore that there could be an interaction between sowing date and plant population (Sinha, 1977; Gladstones, 1977; Corbin, 1978a).

In addition it was thought valuable to repeat the cultivar comparison reported earlier by Withers (1973) in which there was little difference between the cultivars Uniwhite, Uniharvest and Unicrop in terms of seed yield. It was decided to include the *L. luteus* cultivar Weiko III in this trial for although it usually

has lower seed yield, its seed protein content (42%) is much higher than *L. angustifolius* cultivars and it has better protein quality (Gladstones, 1970). The higher seed protein level means a premium price should be warranted which could compensate for any lower yield.

B.2.2 MATERIALS AND METHODS

Four cultivars (Uniwhite, Uniharvest, Unicrop and Weiko III) were compared at three spacings which were 11, 8 and 4 cm spacings within constant 18 cm rows. These gave plant populations of approximately 50, 70 and 140 plants/m^2. These spacings were achieved by sowing at a slightly higher rate with a Stanhay spacing drill and thinning by hand to the required density. Plants were therefore not exactly equidistant but were thinned to produce as even a stand as possible at the required intrarow density when measured over a metre length.

This was repeated at three sowing dates (16 April, 20 July and 2 October 1973). The experimental design at each was a split-plot randomised block with four replicates. Replicates of each sowing date were however allocated at random to positions within the area to minimise the influence of soil differences on the time of sowing effects. Main plots were plant density with cultivars as the sub-plots. Each sub-plot was 7 m long by 8 rows wide. At maturity, 5 m of the centre 4 rows were harvested and measurements made of the number of productive plants and seed yield of each order of branches.

The soil type was Manawatu fine sandy loam which is free draining with poor moisture retention. Fertiliser application and weed control were the same as for the previous experiment (Section B.1.2).

B.2.3 RESULTS

Because of poor emergence, the plant numbers of the 70 plants/m^2 spacing of the April sowing and the Weiko III cultivar at the July sowing were too low or too variable so they were excluded from the experiment. The desired plant populations were attained in all other treatments. Some form of soil variation not visually apparent caused marked differences in plant growth within some plots. The resultant loss of replication and increased variation considerably reduced the sensitivity of the experiment.

There was no significant difference in seed yield between plant populations at all sowing times (Table B.2.1). An important factor at the high population was the large number of plants which did not produce seed. Plant survival was especially low in the autumn sowing. Both populations at this time were reduced to 17-18 pl/m^2 at harvest but for later sowings final populations were still approximately proportional to the initial populations. This may indicate that competition was much more important at the autumn sowing than at the spring sowings.

Seed yield of the cultivars was similar within the autumn and early spring sowings (Table B.2.2). At the late sowing however, significant differences between cultivars were apparent. The seed yield at this time was related to the start of flowering. Unicrop commenced on 29 November, Weiko III on 17 December and the other two on 22 December. As this was a time when the soil would have been drying rapidly (Fig. B.1.2), flowering a few days earlier would have been important in enabling pods to be set. Yield of Unicrop was also assisted by a slightly higher number of plants producing seed. Again this may have been due to its flowering under better environmental conditions.

TABLE B.2.1: Seed weight per m^2 and per plant; percentage of sown plants which produced seed for three sowing dates. Seed yield on oven-dried basis

Sowing Time	Density pl/m^2	Seed Weight g/m^2	Seed Weight g/plant	% productive plants
April	50	113 a	7.1 Aa	34 Aa
	140	92 a	4.2 Ab	13 Bb
July	50	187 a	4.3 Aa	94 Aa
	70	198 a	3.1 Bb	89 Bb
	140	175 a	2.4 Cc	74 Cc
October	50	112 a	2.7 Aa	93 Aa
	70	125 a	2.4 Aa	81 Bb
	140	93 a	1.2 Ab	55 Cc

Duncan lettering applies to within sowing dates only

TABLE B.2.2: Seed weight per m^2 and per plant; percentage of sown plants which produced seed for each cultivar at each sowing

Sowing Time	Cultivar	Seed weight g/m^2	Seed weight g/plant	% productive plants
April	Uniharvest	81 a	5.2 a	21 a
	Unicrop	99 a	5.9 a	22 a
	Uniwhite	117 a	6.0 a	24 a
	Weiko III	115 a	5.6 a	29 a
July	Uniharvest	191 a	3.1 a	88 A
	Unicrop	196 a	3.5 a	81 B
	Uniwhite	192 a	3.2 a	87 A
October	Uniharvest	88 C	1.5 C	73 B
	Unicrop	190 A	2.9 A	89 A
	Uniwhite	82 C	1.5 C	70 B
	Weiko III	129 B	2.4 B	75 B

Fig. B.2.1 shows the yield from the various branch orders for each cultivar at each sowing. The contribution from the lower branch orders is greatly different between the sowing dates. Some of this effect would be due to the different numbers of plants. However, the yield of main stems was 0.1g/plant from autumn sowing and 0.44g/plant from the July sowing so there was a direct effect on the plant itself. Within the autumn sowing, there seemed also to be compensation within each cultivar. For example, in Unicrop, low yields from the main stem and first order lateral stems was compensated for by higher yields from third and fourth order lateral stems compared with Uniharvest.

B.2.4 DISCUSSION

The results from the three sowing dates confirmed a trend that was apparent in the previous experiment *viz.* autumn sowing may not produce higher yields than early spring sowing. The inadvisability of delaying sowing until October was also confirmed.

Despite the higher yields per plant from autumn sowing this potential is not going to be realised in terms of yield per unit area if high plant losses are to be experienced. The plant death may arise from intense competition caused by extensive lateral branch production of early-sown plants. Another explanation may be the effect of the foliage diseases noted in the previous study. Withers (unpublished results) has shown that extensive death of autumn-sown plants can arise from these diseases and the effect can be more severe at high densities. It is possible that a large number of the non-productive plants were killed or stunted by disease and surviving plants expanded to produce the relatively high yield per plant. *Pleiochaeta setosa* and *Botrytis cinerea* can both infect plants seriously during cool wet weather (Gladstones, 1977).

The lack of response to plant population within each sowing date supports the conclusion of Herbert (1977c) that a wide range of

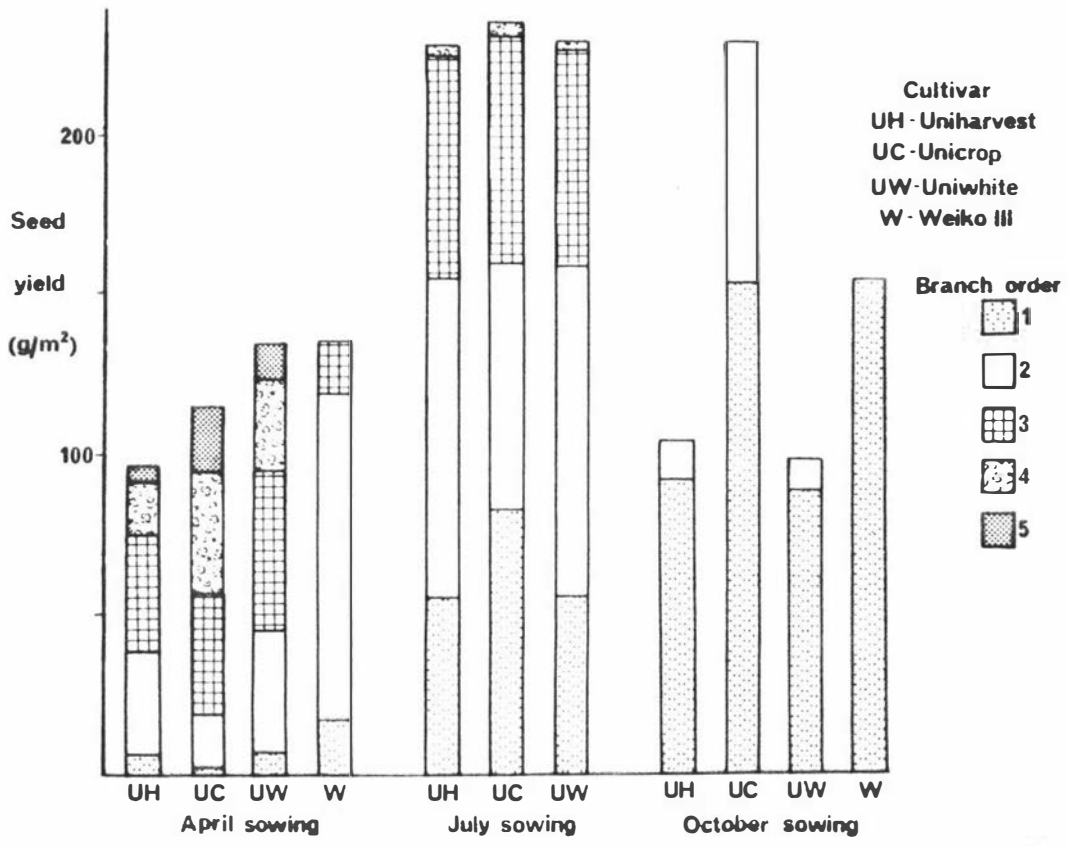

Fig. B.2.1 Total yield and yield of branch orders (1 = main stem, 2 = 1st order lateral, 3 = 2nd order lateral).

densities can give good seed yields. Sowing rate would thus seem to have a minimal effect on seed yield compared with the effect of sowing date. There was no interaction of sowing date and rate.

It should be noted that the yield level over the whole experiment was low possibly reflecting the poor water retention of the soil and the quite early onset of dry conditions in December (Fig. B.1.2). This low yield level may have interfered with any potential response to the treatments.

It is also apparent that there was no difference between the yields of Uniwhite, Uniharvest or Unicrop when sown early. This would be because the main difference between them is in their response to vernalisation (Section A.3.2.1) and once this is satisfied there should be little difference between them in flowering response and other important characteristics. Only at the latest sowing when Uniwhite and Uniharvest were incompletely vernalised were differences apparent. This effect was accentuated by the dry environmental conditions during early flowering of this sowing.

Weiko III had very satisfactory yields compared with the *L. angustifolius* cultivars considering the reports of poor yields from this cultivar (Gladstones, 1959; Stoker, 1976). Garside (1979), in Tasmania, found that Weiko III also yielded relatively well from late sowing. He attributed this to the lower vernalisation requirement and greater response to long days. In this case it flowered 3 weeks earlier than Uniwhite and Uniharvest and its main advantage seemed to be its ability to set a good seed yield on its main stem inflorescence under drying conditions. At the April sowing it was also able to produce similar yields to the other cultivars. It tended to produce a smaller number of lateral stem orders at this time but had higher yields on the main stem and first order lateral branch. Despite fewer lateral branch orders, the proportion of productive plants for Weiko III was similar to *L. angustifolius* cultivars. Most plots of Weiko III at the autumn

sowing lodged and this may have had some effect on plant survival. It also should be noted that in the two sowing times where comparison with *L. angustifolius* was possible, overall yields were relatively low. It was not shown that Weiko III could adjust to higher yield levels.

A comparison of Fig. B.1.3 and Fig. B.2.1. will show that the reduction in yield of the lower lateral branches is greater for Unicrop compared with Uniharvest which may indicate a greater susceptability of Unicrop to this cause of yield reduction.

B.3 A SPACING AND DEFOLIATION STUDY

B.3.1 INTRODUCTION

Data in previous sections indicated that seed yield in high yielding crops originated largely from lateral inflorescences. It was also observed that plants which had the main stem meristem removed at an early stage grew more large lateral branches than undefoliated plants. Should these extra branches produce sufficient seed to more than compensate for the loss of the main stem inflorescence, extra seed yield may be produced after early defoliation compared with undefoliated plants. An experiment was designed to test this hypothesis.

As plant population could markedly influence the response of lateral branching to the removal of apical dominance, it was decided to include plant density as a factor in this experiment. The previous experiment had not shown any marked response to plant density possibly due to adjustment in plant numbers. A wider range of densities was tried in this experiment as populations in the previous study may have been too high. More detailed information on the effect of spacing on plant growth than was obtained previously was also required.

B.3.2 MATERIALS AND METHODS

Two separate experiments with the same basic design were sown at Massey University on 25-26 April and 1-2 October 1974. Seeds of *L. angustifolius* cv. Unicrop were sown by hand in rows 20 cm apart and 5, 10, 20 and 30 cm apart within the row (equivalent to 100, 50, 25 and 17 pl/m^2). In order to contain the experiments within the time available for sowing and later defoliation treatments and the amount of land available, plots had equal plant numbers rather than equal plot size. Three seeds per position were sown and thinned to one per position after emergence. Three defoliation treatments were imposed; nil, early and late "topping". The early treatment was to remove the top of the plant with scissors when the plant had reached 7-8 expanded leaves so that 5 expanded leaves remained on the main stem. The late treatment was imposed when the main stem flower bud was just visible. Sixteen leaves remained on the main stem.

The design was a split plot randomised block with 5 replications. Populations were main plots and defoliation treatments were sub-plots. Prior to sowing, a dressing of 48 kg P/ha and 112 kg K/ha as potassic superphosphate was applied. Atrazine at 1.1 kg/ha was applied prior to emergence and provided good weed control.

Early harvests consisting of 2 plants per sub-plot were made on 14-15 August, 17-20 September and 18-20 October for autumn-sown treatments and on 5-7 December and 7-9 January for spring-sown crops. Harvested plants were dissected into vegetative and reproductive components of each stem order which were counted, dried at 80°C for 12 hours and weighed. A final harvest was made at seed maturity when 15 plants per sub-plot were sampled for seed yield and its components.

B.3.3 RESULTS

The Effects of Spacing

The dry weight of each branch order declined as plant density increased (Table B.3.1). This effect was apparent at the first harvest of the autumn sowing and was due to lower individual branch weight and fewer branch numbers (Table B.3.2). Higher order branches were more adversely affected. From the first harvest of the autumn sowing (Table B.3.2), it would appear that branch numbers were affected early in growth and before individual branch dry weight (Table B.3.1).

TABLE B.3.1: Effect of plant spacing on the dry weight of lateral stems per plant from early harvests

Autumn-Sown	Harvested 14-15 August (110 days from sowing)			
Plant spacing	D.W. of lateral branches		Mean D.W./lateral branch.	
	1st Order	2nd Order	1st Order	2nd Order
30	0.7 A	-	0.15 a	-
20	0.6 A	-	0.15 a	-
10	0.3 B	-	0.11 a	-
5	0.3 B	-	0.12 a	-
Autumn-Sown	Harvested 17-20 September (140 days from sowing)			
30	2.8 A	2.1 A	0.63 A	0.23 A
20	2.8 A	1.6 AB	0.59 AB	0.19 AB
10	1.6 B	1.0 BC	0.48 AB	0.17 AB
5	1.1 B	0.3 C	0.37 B	0.08 B
Spring-Sown	Harvested 5-7 December (63 days from sowing)			
30	6.3 A	1.4 A	0.56 Aa	0.06 A
20	4.8 B	0.8 B	0.46 ABb	0.05 A
10	3.2 C	0.5 C	0.35 BCc	0.03 B
5	2.3 C	0.3 C	0.28 Cc	0.02 B

TABLE B.3.2 Effect of spacing on the number of lateral stems per plant from early harvests

Autumn-Sown

	14-15 August	17-20 September	
	1st Order	1st Order	2nd Order
30	6.1 A	4.2 Aa	9.0 A
20	5.4 A	4.7 Aab	8.8 A
10	3.6 B	3.7 Abc	5.6 B
5	2.8 B	3.2 Bc	3.1 C

Autumn-Sown

	18-20 October			
	1st Order	2nd Order	3rd Order	4th Order
30	4.3 Aa	10.0 Aa	18.8 Aa	12.5 A
20	3.3 Bb	8.4 ABa	12.8 Bb	9.8 AB
10	2.8 Bb	6.3 BCb	8.1 BCb	3.7 BC
5	2.9 Bb	4.7 BCb	5.8 Cc	1.1 C

Spring-Sown

	5-7 December		7-9 January		
	1st Order	2nd Order	*2nd Order	3rd Order	4th Order
30	13.7 A	25.8 A	8.4 A	19.4 A	22.5 A
20	13.0 A	15.9 B	7.3 A	12.4 B	17.6 B
10	12.6 AB	10.6 B	4.2 B	7.2 C	9.3 C
5	10.8 B	5.6 C	3.5 B	5.6 C	4.9 D

* 1st order omitted to save space; similar trends to earlier harvest.

The trend of fewer branch numbers with increased plant density continued up to the final harvest (Table B.3.3) when the number of fertile inflorescences (those which produced at least one fully developed seed) were fewer within a branch order as density increased.

At the final harvest of the autumn sowing, there were no fertile inflorescences on first order lateral branches (or the main stem of undefoliated plants). The third order and higher lateral branches were the most responsive to spacing. Spring-sown plants were very responsive to spacing over both lateral branch orders.

TABLE B.3.3: Effect of spacing on the number of fertile inflorescences per plant for each branch order - final harvest

Autumn-Sown

Plant spacing	Branch Order Number				
	1st	2nd	3rd	4th	5th
30	0	2.5 a	3.3 Aa	4.0 Aa	1.2 Ab
20	0	2.2 a	3.1 Aa	2.4 ABb	1.6 Aa
10	0	2.1 a	2.4 ABb	2.1 BCc	0
5	0	1.1 a	1.6 Bc	1.3 Cc	0.5 Bc

Spring-Sown	1st	2nd
30	3.7 Aa	4.3 Aa
20	2.9 ABb	3.1 Ab
10	1.9 BCc	0.5 Bc
5	1.3 Cc	0.3 Bc

The overall number of inflorescences and pods per plant (Table B.3.4) reduced as density increased. The number of pods per plant was the main component contributing to the seed yield/ plant (r = 0.969) but pod number in turn was determined by the number of fertile inflorescences per plant (r= 0.884). All other components of yield were relatively stable. Thus the weight of seed per plant substantially reduced as plant density increased.

TABLE B.3.4: Effect of spacing on yield per plant and components of yield - final harvest

Autumn-Sown	Plant spacing			
	5cm	10cm	20cm	30cm
Seed yield/plant (g)	3.9 Cd	5.2 BC	7.1 B	11.0 A
Fertile inflorescences/ plant	3.4 C	5.5 B	6.7 B	8.7 A
No.pods/inflorescence	3.0 Aab	2.5 Ab	3.1 Aa	3.3 Aa
No.pods/plant	10.2 Cd	13.7 Cc	20.7 Bb	28.7 Aa
No.seeds/pod	3.7 a	3.9 a	3.8 a	4.0 a
Hundred seed weight (g)	11.4 a	11.2 a	10.9 a	11.1 a
Spring-Sown				
Seed yield/plant (g)	2.8 D	5.2 C	10.3 B	15.2 A
Fertile inflorescences/ plant	2.5 Cd	4.1 Cc	7.7 Bb	10.6 Aa
No.pods/inflorescence	2.1 B	2.3 B	2.6 A	2.9 A
No.pods/plant	5.2 D	9.33 C	19.3 B	27.7 A
No.seeds/pod	3.3 a	3.3 a	3.2 a	3.4 a
Hundred seed weight (g)	14.5 a	14.5 a	13.8 a	13.6 a

Duncan lettering applies within horizontal lines only

Seed yield (/m^2) over all defoliation treatments was unresponsive to spacing at the spring sowing but at the autumn sowing, yield increased as spacing decreased below 20 cm. (Table B.3.5). The lack of response to the spring sowing was due to opposing trends in the defoliation treatments. Undefoliated plants were more responsive to spacing than defoliated plants at both sowings. Analysis of variance of the undefoliated plots show that at both sowing times, the yields of the 5 and 10 cm spacings were significantly different and both were significantly different from the 20 and 30 cm spacings which were not significantly different.

TABLE B.3.5: Yield of oven dried seed (g/m^2) -final harvest

Autumn sown	Plant spacing				
Defoliation	5cm	10cm	20cm	30cm	Mean
Nil	542 A*	334 a	210 a	226 a	328 A
Early	272 B	235 b	152 a	159 a	204 B
Late	283 B	204 b	173 a	166 a	207 B
Mean	366 Aa	258 Bb	178 Bc	183 Bc	
Spring-sown					
Defoliation					
Nil	402 A*	330 A	288 a	272 a	323 A
Early	180 C	230 B	238 a	250 a	225 B
Late	265 B	228 B	247 a	235 a	245 B
Mean	283 a	263 a	258 a	253 a	

*Duncan lettering in body of table applies to within columns only

Autumn-sown plots were similar in yield to, or lower in yield, than, spring-sown plots except at the 5cm spacings. One reason for this is that no yield was obtained from the main stem and first order lateral stems (Table B.3.6), although pods were set earlier in growth. Despite this, autumn-sown plants produced seed from 4 lateral branch orders compared with the main stem and 2 lateral branch orders from spring-sown plants. Except for the 5cm spacing, spring-sown plants generally had a higher yield from each branch order. At the 5cm spacing, yields from the two highest yielding orders were similar. The superior yield of autumn-sown plants at this spacing arose mainly from the yield of the fourth order branch.

TABLE B.3.6: Seed yield (g) for each branch order at each spacing and sowing (total of 15 plants), and number of pods on main stem and first order laterals of the undefoliated autumn-sown plants on 18 October

Seed Yield		Branch Order					
Spacing	Sowing	MS*	1st	2nd	3rd	4th	5th
5	Autumn	-	-	28	30	19	5
	Spring	34	26	1			
10	Autumn	-	-	26	37	28	9
	Spring	45	49	5			
20	Autumn	-	-	25	50	39	12
	Spring	59	81	32			
30	Autumn	-	-	54	75	61	4
	Spring	73	101	71			

Pod Number

Branch Order	Spacing 5	10	20	30
MS*	4.4	5.7	3.7	9.2
1st	6.9	8.1	14.9	19.1

*MS = main stem

The Effects of Defoliation

Defoliation generally did not increase the number of lateral branches (Table B.3.7) except for second order lateral branches at the spring sowing as a result of the early defoliation. The significant interactions between spacing and defoliation for first order laterals were due to the early defoliation being less affected by density due presumably to the smaller number of branches of this treatment. The highly significant interaction for the second order laterals at the 17-20 September harvest was due to a very low branch number of the late defoliation at the 5cm spacing (0.3 branches/plant) compared with other treatments (4.8 and 4.3), whereas, at all other spacings, numbers were similar for each defoliation treatment.

TABLE B.3.7: Effect of the defoliation treatments on the number of lateral stems per plant - early harvests

Autumn-Sown

	14-15 August	17-20 September	
Defoliation	1st Order	1st Order	2nd Order
Nil	6.8 A	4.9 A	7.4 Aa
Early	2.8 B	3.3 B	6.5 Aab
Late	3.6 B	3.7 B	6.1 Ab
Spacing x defoliation	*	NS	**

	18-20 October		
	1st Order	2nd Order	3rd Order
Nil	4.2 Aa	8.3 A	12.2 a
Early	2.5 Bc	5.2 B	9.7 a
Late	3.3 ABb	7.9 A	12.2 a
Spacing x defoliation	NS	NS	NS

Spring-Sown

	5-7 December		7-9 January		
	1st Order	2nd Order	1st Order	2nd Order	3rd Order
Nil	19.1 A	12.6 B	6.6 A	10.7 AB	12.5 a
Early	5.5 C	22.2 A	4.5 B	8.9 B	13.4 a
Late	13.1 B	9.4 B	6.5 A	12.5 A	14.9 a
Spacing x defoliation	*	NS	***	*	NS

Duncan lettering applies within columns only

The mean dry weight of individual lateral branches was increased by the early defoliation during the early growth of first and second order lateral branches (Table B.3.8). There would appear to be an increase in total branch dry weight from the early defoliation during the early growth of each branch order but this effect was also transient. This effect is more apparent with leaf area (Table B.3.9) where, for example, leaf area of the first order lateral was highest within the early defoliation treatment at the 14-15 August harvest

but on the 17-20 September this superiority was lost. The early defoliated plants often had a greater leaf area per branch than other treatments. At no stage however did defoliated plants have higher total leaf area than undefoliated plants. The higher level interactions in Table B.3.9 were due largely to the early-defoliated plants having a wider range of values over the range of densities compared with other defoliation treatments. The lower order interactions were associated with a greater sensitivity of the late-defoliated plants to the highest density.

TABLE B.3.8: Effect of the defoliation treatments on the dry weight (g) of lateral stems per plant - early harvests

Defoliation	D.W. of lateral branches		Mean D.W. per lateral branch	
	1st Order	2nd Order	1st Order	2nd Order
Autumn-Sown				
Harvested 14-15 August (110 days from sowing)				
Nil	0.5 A	-	0.07 B	-
Early	0.7 A	-	0.24 A	-
Late	0.3 B	-	0.07 B	-
Spacing x defoliation	NS		NS	
Harvested 17-20 September (140 days from sowing)				
Nil	2.5 a	1.1 B	0.49 b	0.14 B
Early	1.9 b	1.7 A	0.61 a	0.24 A
Late	1.9 b	0.9 B	0.51 b	0.12 B
Spacing x defoliation	NS	**	NS	NS
Spring-Sown				
Harvested 5-7 December (63 days from sowing)				
Nil	4.5 a	0.6 Bb	0.23 B	0.04 B
Early	4.0 ab	1.2 Aa	0.73 A	0.06 A
Late	3.9 b	0.3 Bc	0.28 B	0.02 C
Spacing x defoliation	*	NS	NS	NS

TABLE B.3.9: Effect of the defoliation treatments on the total leaf area per plant (cm^2) and leaf area of lateral stems - early harvests

Autumn-Sown

Defoliation	L.A. of lateral branches		Total L.A.	Mean L.A. per lateral branch	
	1st Order	2nd Order		1st Order	2nd Order
Harvested 14-15 August					
Nil	44 A	-	191 A	6.3 B	-
Early	59 A	-	106 C	20.8 A	-
Late	23 B	-	134 B	6.2 B	-
Spacing x defoliation	NS		*	***	
Harvested 17-20 September					
Nil	231 Aa	172 ABb	476 a	46.7 A	16.1 B
Early	124 Bc	176 Aa	449 a	38.5 B	25.3 A
Late	160 Bb	108 Bb	367 a	42.9 AB	14.1 A
Spacing x defoliation	NS	**	*	*	NS

Spring-Sown

Harvested 5-7 December					
Nil	488 Aa	79 B	708 A	26.7 B	4.9 B
Early	333 Bc	178 A	532 B	59.4 A	7.8 A
Late	434 Ab	43 C	550 B	31.9 B	3.0 B
Spacing x defoliation	*	*	NS	NS	NS

At early harvests, the early defoliation resulted in greater numbers of flower sites and pods of the highest order of lateral branches (Table B.3.10) but lower order branches often had lower values than other treatments. However, defoliated plants usually had lower total flower and pod numbers than undefoliated plants, the difference being approximately equivalent to the number arising from the main stem of undefoliated plants.

TABLE B.3.10: Effect of the defoliation treatments on the number of flower sites and pods for each branch order - early harvests

Autumn-Sown (18-20 October)

Defoliation	Main stem	1st Order	2nd Order	3rd Order	Total
		Number of Sites			
Nil	17.2	20.7 a	22.8 a	6.6 b	67.4 a
Early	-	10.3 b	18.6 a	15.2 a	46.0 b
Late	-	12.5 b	28.8 a	4.3 b	45.5 b
		Number of pods			
Nil	4.8	12.6 a	9.7 a	-	27.1 a
Early	-	6.3 b	13.0 a	-	19.3 b
Late	-	8.3 b	7.1 b	-	15.1 b

Spring-Sown (7-9 January)

		Number of Sites			
Nil	25.5	17.0 a	11.5 b	1.2 b	55.2 a
Early	-	14.5 a	15.5 a	5.8 a	35.8 b
Late	-	15.7 a	12.4 b	1.3 b	29.4 b
		Number of pods			
Nil	5.9	8.5 ab	5.4 b	-	19.8 a
Early	-	8.2 b	8.1 a	-	16.3 a
Late	-	10.3 a	5.5 b	-	15.8 b

Unlike spacing effects, most components of yield at final harvest were reduced by defoliation (Table B.3.11) with the number of seeds per pod the only component not affected. Consequently seed yield per plant and per unit area was lower from defoliated plants than from undefoliated plants (Tables B.3.5 , B.3.11). However, the yield per unit area was significantly different only at the 5 and 10 cm spacings (Table B.3.5) resulting in a significant ($P < 0.01$) interaction between spacing and defoliation treatments.

TABLE B.3.11: Effect of defoliation on yield per plant and yield components

Autumn-Sown	Nil	Early	Late
Seed yield/plant (g)	8.5 a	5.8 b	6.1 b
Fertile inflorescences/ plant	7.3 A	5.5 B	5.4 B
No. pods/inflorescence	2.9 a	3.0 a	3.1 a
No. pods/plant	21.1 A	16.5 B	16.9 B
No. seeds/pod	3.5 a	3.1 a	3.3 a
Hundred seed weight (g)	11.6 a	10.9 b	10.9 b
Spring-Sown			
Seed yield/plant (g)	9.6 A	7.7 B	7.8 B
Fertile inflorescences/ plant	5.2 B	6.7 A	6.8 A
No. pods/inflorescence	3.4 A	2.1 B	2.0 B
No. pods/plant	17.7 A	14.9 B	13.6 B
No. seeds/pod	4.0 a	3.9 a	3.9 a
Hundred seed weight (g)	14.2 A	13.4 B	14.7 A

Duncan lettering applies within horizontal lines only

B.3.4 DISCUSSION

This experiment indicates that a response to plant density could be obtained over the range 50-100 pl/m^2. This contrasts with the lack of response to spacing in the previous experiment. However, the marked reduction in plant numbers producing seed which was apparent in the autumn-sown plants of the previous study did not occur and this allowed the higher plant numbers to influence yield. A disadvantage of the experimental design however, was that sample size of plants at the final harvest were the same for all spacings and plot size particularly for the high populations were quite small. This tends to inflate the yields from the high densities relative to the low densities which may account for some of the high yield especially of the undefoliated autumn-sown plants.

The highest spacing was approximately equivalent to 200 kg/ha of seed sown, assuming 80% survival. This is in the 150-200 kg/ha range Herbert (1977c) found to be optimum for Unicrop and close to the 168-202 kg/ha optimum of Goulden (1976).

Autumn-sown plots yielded more than spring-sown plots only at the highest density. This was largely due to no seed being produced by the lowest two inflorescence orders of autumn-sown plants and lower yield of each branch order although this was compensated for to some extent by having more productive branch orders. Possible causes for the lack of production from lower branch orders has been discussed previously.

Early harvests of the autumn-sown plants showed that a good podset occurred on the main stem and first order lateral which indicates that frosts and competition were not responsible for the lack of yield from these orders. At the harvest of autumn-sown plants on 18 October disease lesions were noted on many of the pods and it seems likely that the infection of *Stemphylium vesicarium* and/or *Pleiochaeta setosa* was the main cause of yield loss from lower order branches of this sowing.

Population density markedly influences the structure of the plant, even at an early stage, by reducing the number and weight of lateral branches as population increases. Higher order branches seem to be the most severely affected. The number of lateral branches influences the number of inflorescences which, in turn, affects the number of pods per plant as pod number per inflorescence is relatively constant. Pod number in turn directly influences seed yield as seed number per pod and seed weight are also relatively stable.

Comparison with other work (Withers, 1973; Farrington, 1974a Perry and Pool, 1975; Section B.2) would indicate that the response of lupin branch structure to sowing date and possibly other environmental influences such as moisture stress (Biddiscombe,1975)

is similar to the response to population. These factors apparently interact to determine the number of lateral branches which can be formed. Hence the aim when attempting to maximise seed yield would be to combine managerial and environmental factors to maximise the number of lateral branches and inflorescences per unit area.

Removing the main stem meristem would not seem to be a practical method of increasing seed yield. Early defoliation appeared to stimulate the highest order branches at any given time but the effect was short lived. This would indicate that this early removal of the main stem results in lateral branches slightly more advanced than branches of later defoliated or undefoliated plants. However, any advantage of this is small and does not compensate for the loss of the main stem pods.

The decline in seed yield due to the defoliation treatments at the high plant densities was probably because competition between plants prevented the development of lateral branching required to compensate for the loss of yield from the main stem.

B.4. A COMPARISON OF SEVERAL GRAIN LEGUMES AT TWO SOWING TIMES

B.4.1 SEED YIELD AND COMPONENTS*

B.4.1.1 INTRODUCTION

To this stage, the project had been concerned principally with *L. angustifolius* as this was the lupin species most widely cultivated in Australia and New Zealand. However, most legume seed production in New Zealand is produced from peas (*Pisum sativum*). In addition, cultivars of *L. albus* and *V. faba* were becoming available and seemed to have potential under the higher rainfall and more fertile soils of the North Island environment.

* Accepted for publication in N.Z. Journal of Experimental Agriculture 7 1979 (In Press).

Surprisingly, there has been little attempt to study these crops under comparable conditions. This information is needed if valid decisions are to be made on the place of each crop at a farm or national level. Hill *et al.*(1977) obtained similar yields from *L. albus* and *P. sativum* and slightly lower yields from *L. angustifolius* with October sowings in Canterbury. However, *L. albus* had a greater protein yield due to its superior protein content. Some limited comparisons (Stoker, 1975; 1978), found *L. luteus* to be inferior in seed yield to *L. angustifolius*. On pumice soils, Withers *et al.* (1976) found *L. angustifolius* superior in seed yield to both *L. luteus* and *L. albus* although this comparison was confounded to some extent by plant population differences. A comparison of the apparently most viable spring sown seed crops was therefore initiated.

In addition, it was decided to continue with some aspects of sowing time. In particular, the possible role of water deficit in influencing the yields of different sowing times and whether adequate water could compensate for late sowing was thought to be important as this would help determine the importance of adequate summer rainfall and irrigation.

The experiment by Withers (1973) and the results of previous sections have shown a marked reduction in yield per plant as sowing date became later. Much of this effect has been attributed to a reduction in pod number due to a shortened flowering period caused by the onset of moisture stress at approximately the same time for each sowing date. However, it was not clear if this was the only effect. Temperature could also be involved as it is important in the phenological development of lupins (Reeves *et al.*, 1977).

A trial was commenced in the 1974/5 season to study cultivars of a number of legume species at two sowing times with irrigation as a further treatment at the later sowing date. Measurements were made of seed yield and its components as well as dry matter and

nitrogen distribution patterns through the growing season. For simplicity, the results will be reported in two sections: -

1. Seed yield and its components which is reported in this section
2. Nitrogen distribution in the plant which is discussed in the following section.

B.4.1.2 MATERIALS AND METHODS

The trial was conducted at Massey University on Manawatu silt loam during the 1974/75 season. Two sowing dates and a range of grain legumes were involved. At the first sowing date (13 August 1974) *Lupinus angustifolius* cv. Unicrop, *L. luteus* cv. Weiko III, *L. albus* cvs. Ultra and Neuland, *Vicia faba* cvs. Maris Bead and Minor, and *Pisum sativum* cv. Pamaro were sown with a Stanhay precision seeder. Plot size was 12 m long and 10 rows at 20 cm spacing. Of this, 4 m length of plot was allocated to a final harvest and the balance was used for regular sampling for growth analysis. At the second sowing, (25 October 1974) similar sized plots of Weiko III, Ultra, Pamaro, Unicrop and Maris Bead were sown. Except for Pamaro, two plots of each cultivar were sown, one of which was irrigated by means of perforated polythene pipes laid permanently in place on the soil surface. Irrigation was applied to maintain the soil moisture tension below 500 mb at 10 cm depth as measured by a tensiometer buried at this depth in each irrigated plot. Each plot was irrigated individually as required. There was insufficient area for each cultivar to be irrigated so the irrigated treatment for peas was excluded as its response to irrigation is well documented. The experiment was a randomised block with 4 replicates for each sowing date. At maturity, a quadrat of 6 centre rows, 2m long was harvested by hand from the area allocated for this purpose. Plant, pod and seed number, seed weight and nitrogen content were measured.

Analysis of variance was performed on untransformed data. Error variances were not significantly different except for the protein yield at the late sowing. In this case, the data for Maris Bead was excluded from the analysis.

B.4.1.3 RESULTS

Establishment counts showed that both sowing dates had a mean population of 54 plants / m^2 ($\pm$ 3 and 4 for early and late sowings respectively).

Detailed climatic data are presented in Section 4.2. Generally the season favoured good growth. There was little rain during December. Irrigation was applied as required from November 26 and ceased after heavy rain on January 21.

August-sown plots were harvested from 5-18 January. Late-sown plots were harvested over a longer period. Pamaro and Unicrop were harvested on 27 January; Maris Bead on 10 February; unirrigated Weiko III and Ultra on 19 February and irrigated Weiko III and Ultra on 4 March.

Disease was an important factor in this experiment. The leaf disease caused by *Pleiochaeta setosa* and *Stemphylium vesicarium* were noted on early-sown Unicrop soon after flowering began but they did not significantly infect pods or seeds. On the late-sown Unicrop plots, infection occurred early in development and caused premature defoliation, pod lesions and shrivelled seed. A similar pattern occurred with rust (*Uromyces fabae* (Pers.) de Barry) on the beans so that the late-sowing was a failure as a seed crop. The remaining cultivars showed no significant levels of disease. Irrigation caused extensive vegetative growth in the late-sown Weiko III which ultimately resulted in the lodging of these plants.

As a result of these factors, Ultra was the only crop which responded to irrigation and had a significantly higher seed yield

than the unirrigated treatments despite relatively low plant numbers (Table B.4.1). In this case, yield from the irrigated late-sown treatment was similar to the earlier sowing indicating that moisture is an important factor in reduced yield from late sowing. Overall, Ultra was the highest yielding cultivar although, at the early sowing, Pamaro and Neuland were not significantly different from Ultra.

TABLE B.4.1: Total seed yield (g/m^2) and the number of plants contributing to yield (in parentheses)

	Early Sowing	Late Sowing	
		Irrigated	Not Irrigated
Unicrop	298 CD (52)	158 D (64)	204 CD (65)
Ultra	462 A (47)	444 A (38)	320 B (40)
Neuland	369 ABC (50)		
Weiko III	310 BCD (53)	208 CD (46)	164 D (52)
Minor	196 D (43)		
Maris Bead	281 CD (43)	35 E (59)	29 E (61)
Pamaro	423 AB (56)		253 C (46)

All lupin cultivars set similar numbers of pods per plant except under irrigation (Table B.4.2). The bean cultivars, Minor and Maris Bead had the lowest number of pods per plant and Pamaro was intermediate. Lupins had fewer pods per plant at the late sowing although, in Ultra, the number of seeds per pod partly compensated for this trend (Table B.4.3) as seed number per pod was higher for late sowing than for early sowing. This trend also occurred for peas. An important cause of the reduction in yield between irrigated and non-irrigated treatments for Ultra was therefore the drop in pod numbers.

TABLE B.4.2: Number of pods per plant

	Early Sowing	Late Sowing	
		Irrigated	Not Irrigated
Unicrop	11.6 ABC	6.7 B	6.4 B
Ultra	13.6 A	11.2 A	7.4 B
Neuland	9.8 ABCD		
Weiko III	12.6 AB	9.0 AB	6.8 B
Minor	7.1 D		
Maris Bead	7.0 D	0.9 C	0.7 C
Pamaro	9.6 BCD		6.3 B

TABLE B.4.3: Number of seeds per pod

	Early Sowing	Late Sowing	
		Irrigated	Not Irrigated
Unicrop	3.4 AB	3.6 B	3.6 B
Ultra	2.3 D	3.5 B	3.5 B
Neuland	2.6 CD		
Weiko III	4.0 A	4.0 AB	3.7 B
Minor	2.9 BC		
Maris Bead	3.2 BC	3.0 C	2.4 D
Pamaro	3.5 AB		4.3 A

Weiko III seemed to have a good potential for seed yield with pod number and seed number per pod comparable to, or superior to, Ultra but the low hundred seed weight (Table B.4.4) resulted in a relatively low seed yield. Unicrop, Maris Bead and Pamaro had lower seed weight from the late sowing although Weiko III and unirrigated Ultra had higher seed weight. At the late sowing, there tended to be a higher seed weight from irrigated treatments compared with treatments not irrigated.

TABLE B.4.4: Hundred seed weight (g)

	Early Sowing	Late Sowing	
		Irrigated	Not Irrigated
Unicrop	14.0 C	10.1 D	13.4 D
Ultra	31.1 A	31.7 A	33.1 A
Neuland	30.0 A		
Weiko III	11.6 C	12.4 D	12.6 D
Minor	23.6 B		
Maris Bead	30.3 A	23.1 BC	25.7 B
Pamaro	22.8 B		20.5 C

Nitrogen percentage of Weiko III seed (Table B.4.5) was consistently higher than for the other cultivars and Pamaro was the lowest. Irrigation did not significantly alter nitrogen percentage but nitrogen percentage of the seed from late sowing tended to be higher than that from early sowing.

TABLE B.4.5: Nitrogen percentage of seed

	Early Sowing	Late Sowing	
		Irrigated	Not Irrigated
Unicrop	4.8 C	5.2 C	5.0 C
Ultra	5.9 B	5.8 B	6.0 B
Neuland	6.1 AB		
Weiko III	6.6 A	6.8 A	7.0 A
Minor	4.6 C		
Maris Bead	4.5 C	5.2 C	5.4 C
Pamaro	4.0 D		4.2 D

Because of its medium nitrogen percentage and high yield, Ultra had the highest protein yield (Table B.4.6). Despite its low seed yield Weiko III had a relatively good protein yield from the early sowing and was second to *L. albus* cultivars overall.

TABLE B.4.6: Yield of protein (N x 6.25) (g/m^2)

	Early Sowing		Late Sowing
		Irrigated	Not Irrigated
Unicrop	88 DE	52 D	64 D
Ultra	169 A	162 A	119 B
Neuland	139 AB		
Weiko III	128 BC	88 C	72 CD
Minor	57 E		
Maris Bead	79 DE	12	10
Pamaro	107 CD		67 CD

Calculations of path coefficients between seed yield and yield components (Table B.4.7) confirmed the importance of pod number per plant in determining yield. Variation in seed weight was important in the overall comparison and for all cultivars except Ultra. For this latter cultivar, number of seeds per pod was more important. For other cultivars the number of seeds per pod was poorly related to yield.

TABLE B.4.7: Path coefficients of components on yield

	Hundred seed weight	Pod number per plant	Seeds per pod	Proportion of variance explained
All cultivars	0.630	0.815	-0.032	0.809
Pamaro	1.605	2.302	-0.139	0.884
Maris Bead	0.241	1.171	0.070	0.969
Ultra	-0.166	0.929	0.677	0.656
Weiko III	0.130	0.854	-0.178	0.899
Unicrop	0.428	1.158	0.295	0.972

B.4.1.4 DISCUSSION

This experiment indicates that *L. albus* cultivars have potential as seed crops under North Island conditions. The relatively high yield, good nitrogen content and disease resistance combine to make this species worthy of wider consideration. The results of the comparison by Hill *et al.*(1977) show that *L. albus* could also be suited to South Island conditions. The ranking in terms of seed and protein yield of the grain legume species in common between the two experiments is the same.

The good ranking of Weiko III in this experiment was not expected as in other experiments (Stoker, 1975: 1978) this cultivar was well below Unicrop in yield. The small seed size of this cultivar is its major limitation as all other components of yield were very satisfactory and certainly the high protein level makes it a very desirable crop. Provided seed protein is not sacrificed, selection of larger seeded cultivars within this species would be worth considering. However work by Hill (pers. comm.) indicates that increased seed size could lower seed nitrogen percentage thus giving less benefit in seed protein yield.

Pamaro and Ultra had similar yields at the early sowing but Ultra maintained yield better at the late sowing. Peas are the standard grain legume crop in the North Island. *L. albus* is unlikely to yield substantially more seed than peas and has a longer growing period. A premium price reflecting the higher protein content would have to be paid to enable it to be economically viable. Lupins do have the added advantage of having their pods well off the ground making harvesting easier especially under wet conditions. The potential for improvement of *L. albus* may be greater than peas as the breeding effort put into lupins is not great compared with peas. Improvement in protein content is probably limited (Jermyn, 1977) so selection pressure will have to be on yield.

The susceptibility of *L. angustifolius* and *V. faba* to disease when sown late in warm humid conditions is an important factor. To some extent, the early sowing escaped disease presumably because the cool conditions restricted the spread of the disease while the plant became established. The apparent resistance of *L. albus* and *L. luteus* cultivars is also important. In his review of *P. setosa*, Milne (1964) reported the presence of the disease on all three lupin species used in this experiment but noted that *L. luteus* and *L. albus* were reported to be more resistant. Gladstones (1972) reports that *L. albus* is highly susceptible although he more recently considers (pers. comm) that it may be resistant under favourable growing conditions. Tate (1968) found that reports of resistance of lupin species to *S. vesicarium* were very variable. Subsequent experiments have shown the relative resistance of Weiko III and Ultra to leaf disease is consistent over several seasons (Withers, unpublished data). The role of *L. angustifolius* cultivars in the warm humid areas of the North Island must therefore be limited and it is probable that *L. albus* cultivars will be more suited to these areas although Ultra did not yield well in preliminary trials at Wairakei (Withers *et al.* 1976).

The yield from unirrigated late sowings of all cultivars was lower than from early sowing. The incidence of disease confounded the effect on yield of irrigation at the late sowing. However, the results from Ultra indicate that adequate moisture during late spring and summer compensated for later sowing and that temperature and day length are probably not significant factors influencing yield in a single environment. Recommendations for early sowing dates (Withers 1973, Section B.2) may have to be modified for disease resistant cultivars where summer rainfall is reliable or if irrigation is available. However, as mentioned by Lucas *et al.* (1976), late sowing and irrigation can result in delayed maturity making it difficult to complete harvest before onset of autumn rain.

B.4.2 DISTRIBUTION OF NITROGEN WITHIN ABOVE-GROUND COMPONENTS

B.4.2.1 INTRODUCTION

There would seem to be important differences between legumes in the protein concentration of their seed and in their ability to produce high seed protein yields. Knowledge of the mechanisms of protein production would therefore be extremely useful in selecting, managing and breeding grain legume crops where protein yield rather than seed yield alone is important. Until recently however, detailed information in this area was limited. Short term studies of nitrogen translocation and uptake (e.g. Oghoghorie and Pate, 1972; Minchin and Pate, 1973; Pate and Flinn, 1973) were useful in providing some basic understanding of the mechanisms involved. Since 1975, several detailed studies on the whole plant over extended periods of a range of legume species have been made. Sinclair and de Wit (1975) after studying the chemical composition of seed from a wide range of plant species proposed that yields of legume seeds were limited by a "self-destruction mechanism". The significance of this has been discussed previously. (Section A.4.3).

Studies of other legumes such as peanuts (Duncan *et al.*, 1978) lupins, (Farrington *et al.*, 1977; Hocking and Pate, 1977), cowpeas (Eaglesham *et al.*, 1977) show that nitrogen is generally a mobile element and declines markedly in non-seed tissues as the seed develops.

B.4.2.2 MATERIALS AND METHODS

The plants sampled for this experiment were obtained from that reported in Section B.4.1. At approximately 10 day intervals, 3 plants were taken at random from each plot and were dissected into leaf, stem, pod and seed of each stem order as appropriate. Each component was counted, dried at $80^{o}C$ for 12 hours and weighed. Dried material was ground and analysed for total nitrogen using Kjeldahl digestion and steam distillation (Clements, 1970).

Towards the end of the experiment when dry conditions were becoming an important factor in growth, relative leaf water content measurements (Baars, 1968) were made on newly expanded leaves from the upper canopy. Ten leaf discs were taken at random from each plot using a punch with a screw-topped bottle attached. The discs were taken as quickly as possible and the bottle sealed. Once all samples were taken, the leaf discs were taken to the laboratory, weighed and floated on distilled water for one hour before weighing. The discs were then dried at $80^{o}C$ for 12 hours and the dry weight recorded.

The nitrogen data was subjected to regression analysis and curves fitted. A number of families of curves were tried. When nitrogen was accumulating, the logistic equation (Bliss, 1967; Gordon, 1975) was usually most appropriate. This is of the form

$$Y = yo \; / \; (1 + e^{-(a + b\,X)}) \qquad (1)$$

where yo is the upper asymptote and a and b are the regression coefficients. The linear form of the equation is

$$\ln (Y \; / \; (yo - Y)) = a + b\,X \qquad (2)$$

which is the equation used in the regression analysis. In some cases however the quadratic logistic equation fitted the data better. In its linear form this is:

$$\ln (Y \; / \; (yo - Y)) = a + b\,X + c\,X^2 \qquad (3)$$

In some cases this equation also adequately described the declining phase. In fitting logistic and quadratic logistic curves, the upper asymptote (yo) was estimated from plotted data. Subsequently, new estimates of yo depended on the value of the coefficient of determination (R^2) of the previous equation(s) and how well they fitted the data when plotted. The final equation selected had the highest R^2 provided it satisfactorily

fitted the data. In a few cases the final equation did not have the maximum R^2 but provided a better eye fit of the data. Where the data had no upper asymptote or where one could not be accurately estimated, exponential equations were used. The ones finally used were of two types (Bliss 1967, Gordon 1975):

(a) $Y = ab^X$ Its linear form is

$$\ln Y = a + bX \qquad (4)$$

(b) $Y = aX^b$, with its linear form

$$\ln Y = a + b(\ln X) \qquad (5)$$

The decline of leaf nitrogen sometimes did not seem to fit exponential curves very well and where possible, quadratic equations were fitted *viz.*

$$Y = a + bX + cX^2 \qquad (6)$$

B.4.2.3 RESULTS

As discussed earlier, foliage diseases affected Unicrop and the *V. faba* cultivars. These were particularly serious at the late sowing so that Maris Bead and irrigated Unicrop from this sowing have not been considered in this section. In addition, the full potential of Unicrop or Maris Bead were probably not expressed at the early sowing due to the effect of the diseases toward the end of the growth cycle. Because of the similarity of results between the *L. albus* and *V. faba* cultivars at the early sowing, Neuland and Minor were also omitted.

Data on air temperature over the experimental period are presented in Figure B.4.1. Also presented is the accumulated "net water availability" commencing at the 1st June. This was calculated by accumulating the difference between weekly rainfall and weekly pan evaporation taken at a meteorological station situated

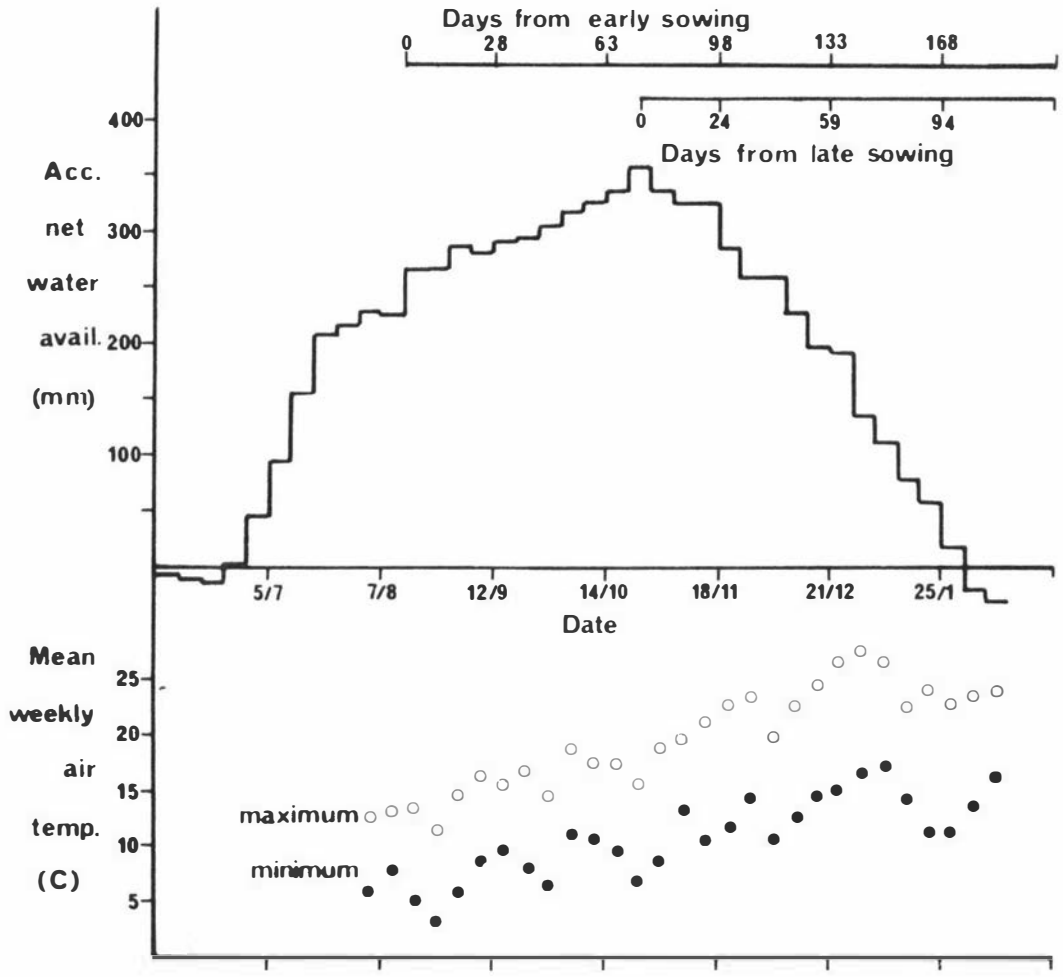

Fig. B.4.1 Accumulated net water availability and mean weekly air temperature for the 1974/5 season.

approximately 0.5 km from the site. No allowance was made for drainage or run-off so this method probably over-estimates actual availability. From this it can be seen that evaporation did not consistently exceed rainfall until about 100 days from early sowing and 25 days from late sowing after which there was a steady decline in net water availability. However, there were occasional periods of rain over this period (indicated by small changes in accumulated net water availability between weeks).

Relative leaf water content (RWC) data are presented in Table B.4.8. Other workers have shown that, when RWC falls below 90%, plants become increasingly water stressed (Shaw and Laing, 1966; Chen *et al.*, 1971; Sections C.2, C.3). Early-sown Unicrop became water stressed earlier than other lupin cultivars. Maris Bead had a low RWC at each sampling time and showed wilting symptoms earlier than other cultivars. Most cultivars appeared to be significantly stressed at about 57 days from late sowing (equivalent to 123 days from early sowing). Leaves of irrigated plants had similar levels to unirrigated plants when sampled during the day. All leaves probably returned to high levels at night (see day 67 from late sowing) until after 73 days from late sowing when non-irrigated plant leaves remained at stress levels.

Dry Weight

Although the main purpose of this paper is to report patterns of nitrogen accumulation, these are often related to dry weight changes so the mean dry weights of each component at each harvest are presented in Fig. B.4.2.

Each cultivar had similar total growth patterns arising from the sequential development of the various components. The early-sown cultivars had a 60-70 day establishment period before rapid growth commenced. Maximum dry weight occurred at 110-140 days for the early-sown cultivars. Duration of peak growth rate for late-sown cultivars was more variable than for the early-sown plants.

TABLE B.4.8: Relative water content of upper canopy leaves sampled 12-2 p.m. Results in parenthesis sampled 8-9 a.m.

Days from early sowing	106	113	114	118	122
Pamaro	85.7	90.4	85.8	90.7	90.2
Weiko III	87.4	86.2	83.0	87.5	88.0
Ultra	82.4	88.9	84.8	87.4	85.8
Unicrop	81.5	79.7	76.9	80.8	78.1
Maris Bead	75.7	68.9	71.1	78.3	76.1

Observations	hot dry light wind	cloudy warm humid	Hot, sunny Maris Bead wilting	Warm sunny, soil moist	Sunny, cool
Days from:-					
Early Sowing	123	127	137	143	149
Late Sowing	53	57	67	73	79
Pamaro	87.4	81.7	81.4 (90.1)	79.9 (86.4)	77.0 (85.5)
Weiko III					
Not Irrigated	88.7	83.6	85.9 (88.9)	81.7 (83.4)	73.6 (79.5)
Irrigated	90.3	85.6	87.2 (95.5)	84.0 (94.0)	88.8 (94.2)
Ultra					
Not Irrigated	87.0	79.3	84.3 (91.5)	80.0 (87.4)	77.5 (84.6)
Irrigated	88.6	81.8	86.6 (95.4)	85.7 (94.1)	88.6 (95.2)
Unicrop					
Not Irrigated	84.0	79.6	76.2 (84.6)	80.6 (85.4)	

Observations	Hot, dry, windy	Hot, sunny, wilting	Hot humid	Hot, dry	Cloudy not humid

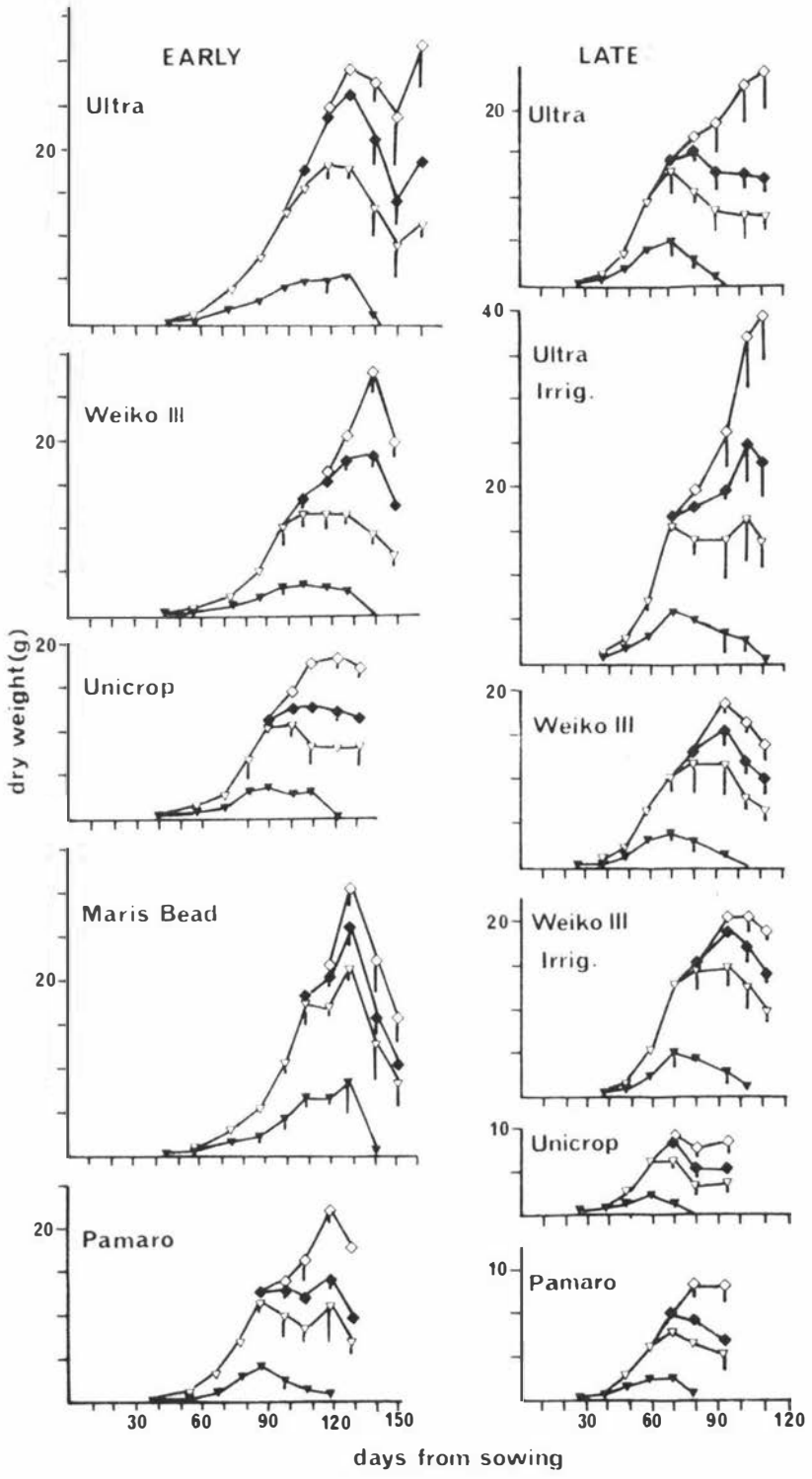

Fig. B.4.2 Dry weight per plant components for early and late sowings (▼ leaf, ▽ stem, ◆ pod, ◇ seed). Vertical bars are standard errors of the mean.

Late-sown Unicrop completed its growth earliest due probably to the premature defoliation caused by fungous disease. Irrigation increased the total growth rate mainly by increased stem growth.

Total Nitrogen

The term "total" in this paper refers to the combination of all above-ground parts.

Early Sowing

Logistic equations (Equation 2, see Materials and Methods) provided the best fit of the total nitrogen data during the accumulation phase (Fig. B.4.3). For Pamaro, a quadratic logistic equation (equation 3) provided a better fit towards the end of the phase (Line B). Although the pattern of accumulation was similar for all cultivars, the rate of accumulation varied. The rate coefficients (b coefficients) in Table B.4.9 show that Pamaro accumulated nitrogen significantly faster than Ultra or Weiko III. However, the duration of total nitrogen accumulation was also shorter for Pamaro (about 120 days) compared with Ultra and Weiko III (about 140 days) resulting in similar maximum total nitrogen for these three cultivars. Unicrop and Maris Bead had intermediate rates of nitrogen accumulation but had shorter periods of nitrogen accumulation so that maximum total nitrogen was lower than Ultra, Weiko III or Pamaro.

Towards the end of the growth period, nitrogen in non-seed components declined sharply (Fig. B.4.3). The difference between total nitrogen and non-seed nitrogen is accounted for by the accumulation of seed nitrogen and the loss of nitrogen in leaf fall. An exponential equation (equation 4) was fitted to the decline phase of non-seed nitrogen.

Fig. B.4.3 Total nitrogen per plant (●) and non-seed nitrogen per plant during the decline phase (○) for early and late sowing.

F = time of flowering

BS = beginning of seed growth - see Fig. B.4.4 and B.4.5

RS = beginning of rapid seed growth - See Fig. B.4.4 and B.4.5

Figures are coefficients of determination (R^2) for the adjacent curve.

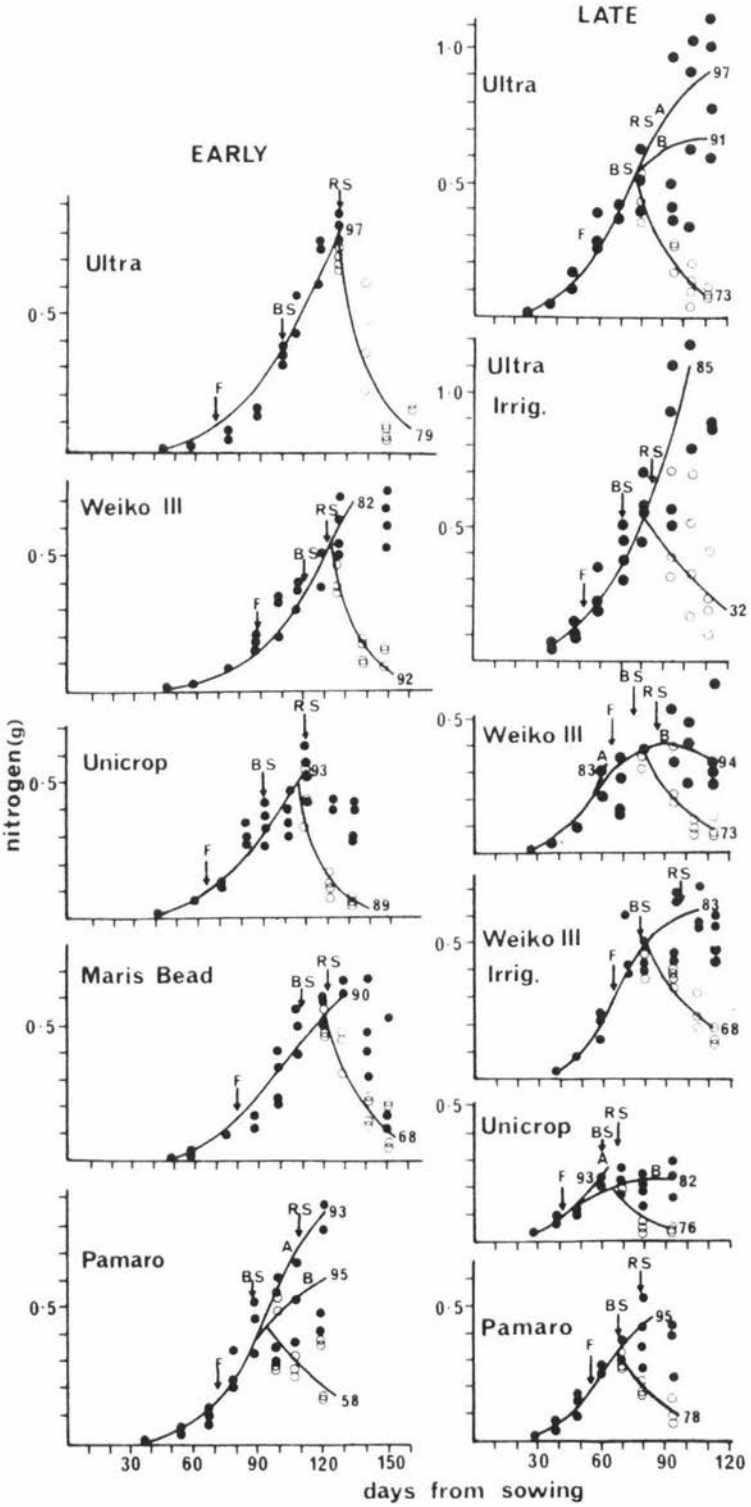
EARLY
LATE
Ultra
Weiko III
Unicrop
Maris Bead
Pamaro
Ultra Irrig.
Weiko III Irrig.
nitrogen (g)
days from sowing
F
BS
RS
A
B
0·5
1·0
30
60
90
120
150

TABLE B.4.9: Regression coefficient b for regression equations total nitrogen and non-seed nitrogen during the decline phase with days from sowing.

Logistic Equations

Cultivar		Total nitrogen	Non-seed Nitrogen
Early Sowing			
Pamaro		0.0720 a	-0.0272 b
Maris Bead		0.0675 ab	-0.0531 b
Unicrop		0.0617 ab	-0.0833 a
Ultra		0.0589 c	-0.0653 a
Weiko III		0.0578 bc	-0.0750 a
Late Sowing			
Pamaro		0.0920 bc	-0.0474 ab
Unicrop	NI*	0.0809 c	-0.0639 a
Ultra	I*	0.0542 e	-0.0257 c
	NI	0.0731 d	-0.0550 a
Weiko III	I	0.1120 ab	-0.0341 b
	NI	0.1209 a	-0.0510 a

Quadratic Logistic Equations

Early Sowing		
Pamaro		0.1396
Late Sowing		
Weiko III	NI	0.2143
Unicrop	NI	0.1944
Ultra	NI	0.1725

*I = irrigated NI = Non-irrigated

Coefficients with letters in common are not significantly different ($P < 0.05$) Comparisons may be made within columns and sowing times only. (Applies also to Tables B.4.11 and B.4.12.)

Non-seed components of early-sown Pamaro and Maris Bead lost nitrogen at significantly lower rates than the lupin cultivars (Table B.4.9). Except for Pamaro, the non-seed nitrogen decline commenced at about the time that the seed began to accumulate nitrogen rapidly (Arrow R.S. Fig. B.4.3), which also coincided with the beginning of the rapid senescence of leaf. The decline in non-seed nitrogen for Pamaro occurred at an earlier stage of growth *viz.* when seed growth commenced (Arrow B.S., Fig. B.4.3) Although RWC measurements were not being taken at that time, later measurements and accumulated net water availability would indicate that water stress was not a factor.

Pamaro did not utilise as much nitrogen from non-seed tissues as did the other cultivars (Fig. B.4.3). Dry weight differences can however confuse this trend so the ratio of nitrogen content and dry weight of non-seed components were calculated (Table B.4.10) Pamaro and Maris Bead had significantly more nitrogen per unit dry weight than the lupins at the early sowing.

Late Sowing

Logistic equations (curve A, Fig. B.4.3) fitted all total nitrogen data well for Ultra, irrigated Weiko III and Pamaro. These equations were applicable only to the early data of non-irrigated Weiko III and Unicrop for which quadratic logistic equations provide a better fit of all total nitrogen data. Weiko III had the highest rate of nitrogen accumulation at the late sowing, but Ultra again had the lowest rate. T-tests between the b coefficients of each cultivar at each sowing showed that late-sown plants accumulated nitrogen significantly faster ($P < 0.05$) than early-sown plants except for the comparison between early-sown and irrigated late-sown Ultra.

Late-sown plants started rapid nitrogen accumulation earlier than early-sown plants and had shorter duration. Unicrop had the shortest accumulation period (60 days). Although nitrogen accumulation of non-irrigated Ultra slowed after 90 days, it

continued for the whole period (110 days). Irrigation extended the nitrogen accumulation period of Weiko III and increased the rate of accumulation over the late growth period for Ultra.

TABLE B.4.10: Ratio of non-seed nitrogen to non-seed dry weight (mg/g) at the final sampling of each cultivar

	Early Sowing	Late Sowing	
Cultivar		Irrigated	Not Irrigated
Pamaro	40.6 a		14.0 a
Maris Bead	13.8 b		
Unicrop	6.0 c		8.0 ab
Ultra	6.0 c	10.0 ab	6.0 b
Weiko III	6.0 c	14.0 a	9.0 ab

The rate of decline in non-seed nitrogen was similar for all non-irrigated treatments (Table B.4.9) but was significantly slower for irrigated treatments. The decline in Pamaro again commenced relatively early and at a slightly slower rate than for other non-irrigated treatments. The ratio of non-seed nitrogen to non-seed dry weight (Table B.4.10) again tended to be higher for Pamaro particularly when compared with Ultra. Irrigated treatments also tended to have a higher ratio but this could be due to the final harvest being too close to the final leaf senescence (Fig. B.4.2) and complete redistribution of nitrogen had probably not taken place. Section C.3 shows that considerable redistribution of nitrogen takes place during the final maturation period in well-watered plants. Probably a further harvest should have been taken.

Decline in non-seed nitrogen started at about 80 days from sowing for irrigated and non-irrigated treatments of both Ultra and Weiko III. However, for Weiko III, irrigation enabled this decline to commence at a higher level of nitrogen than for non-irrigated plants but only small amount of additional total nitrogen was accumulated after this time. In the case of irrigated Ultra, the

decline occurred at the same level of total nitrogen as non-irrigated plants but considerable extra total nitrogen was later accumulated by the irrigated treatment and a lesser amount by the non-irrigated treatment. Variation between individual plants was however high.

Leaf and Stem Nitrogen

Early Sowing

Leaf nitrogen accumulation rates were similar (Table B.4.11) but, as for total nitrogen the duration of accumulation varied (Fig B.4.4) so the amount accumulated also varied. Once accumulation ceased there tended to be a period of relatively constant leaf nitrogen content ranging from approximatley 20 days for Maris Bead to about 40 days for Ultra. This period was not evident for Pamaro where the decline in leaf nitrogen occurred rapidly as soon as seed growth began (Arrow B.S. Fig. B.4.4).

Pamaro had the most rapid rate of stem nitrogen increase and Ultra the slowest (Table B.4.11). Duration of stem nitrogen accumulation and decline also varied considerably (Fig. B.4.4). Ultra and Unicrop had a long accumulation period but the decline in stem nitrogen was rapid, of short duration and began when rapid seed growth commenced (Arrow R.S. Fig. B.4.4). Other cultivars had a more rapid accumulation and a slower decline in stem nitrogen. The decline in stem nitrogen for these cultivars did not start until seed growth commenced (Arrow B.S.). Despite its marked stem growth (Fig. B.4.1), Ultra accumulated stem nitrogen more slowly than leaf nitrogen (Table B.4.11). Other cultivars accumulated stem nitrogen more rapidly than leaf nitrogen.

TABLE B.4.11: Regression coefficient b for regression equations leaf and stem nitrogen with days from sowing and coefficient c for quadratic logistic equations stem nitrogen with days from late sowing.

Cultivar	Leaf Nitrogen	Stem Nitrogen	
	Accumulation Phase (equation 2)	Accumulation Phase (equation 2)	Decline Phase (equation 4)
Early Sowing			
Pamaro	0.0766 a	0.0985 a	-0.0355 ab
Maris Bead	0.0638 a	0.0861 ab	-0.0192 b
Unicrop	0.0699 a	0.0823 ab	-0.0452 a
Ultra	0.06886 a	0.0598 c	-0.0485 a
Weiko III	0.0715 a	0.0748 b	-0.0224 b
Late Sowing		coefficient b (equation 3)	coefficient c (equation 3)
Pamaro	0.1074 a	0.2574 a	-0.0017 a
Unicrop NI	0.0760 b	0.2128 ab	-0.0016 a
Ultra I	0.0877 b	0.1618 b	-0.0009 b
NI	0.1002 ab	0.1799 b	-0.0011 ab
Weiko III I	0.0822 ab	0.2579 a	-0.0015 a
NI	0.1190 a	0.2338 a	-0.0014 a

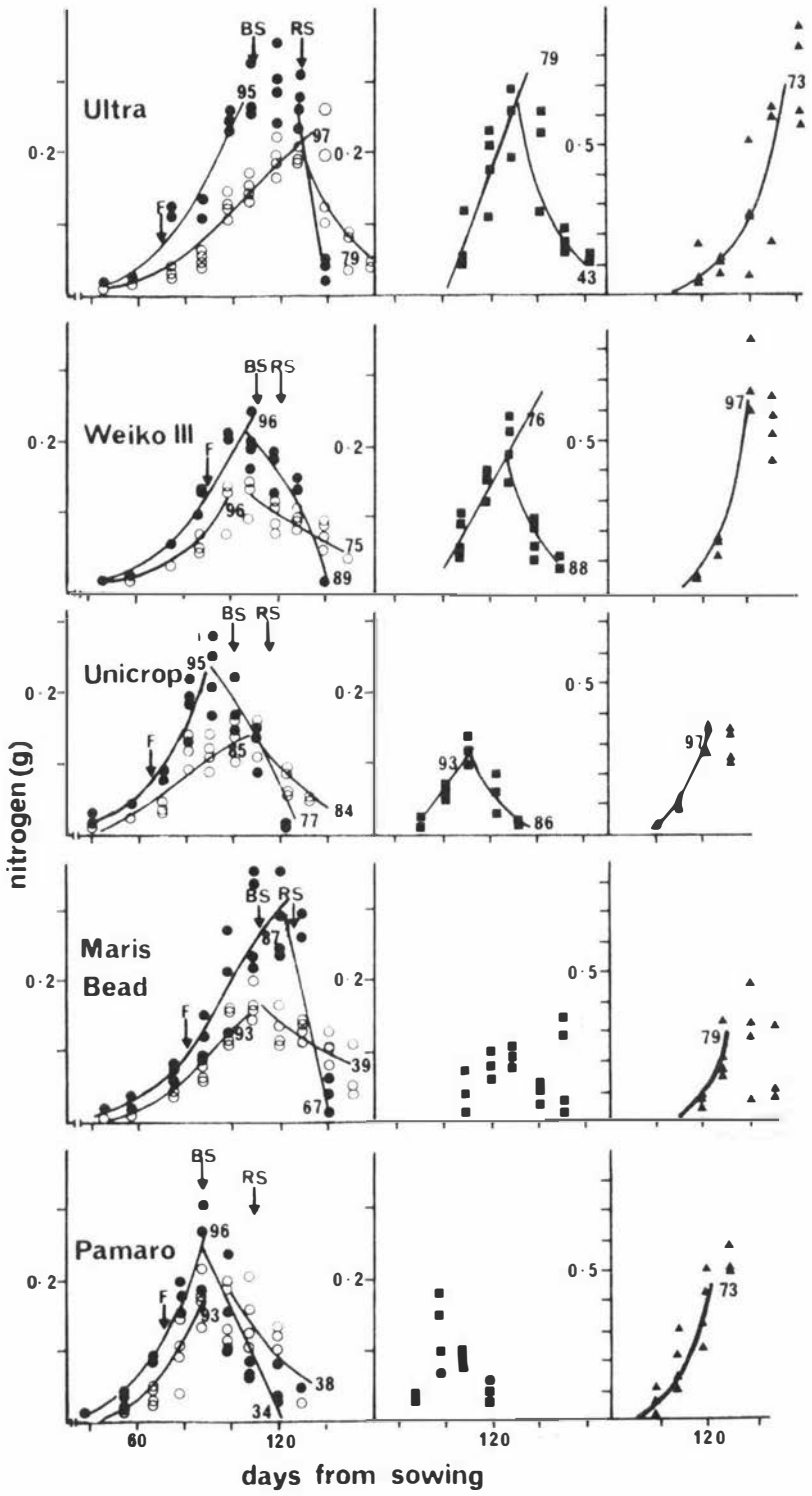

Fig. B.4.4 Nitrogen content of leaf (●), stem (○), pod (■) and seed (▲) per plant for early-sown plants. Figures and letters as for Fig. B.4.3.

Late Sowing

Differences between cultivars in the rate of accumulation of leaf nitrogen were greater at the late sowing compared with the earlier sowing (Table B.4.11). Irrigated plants tended to accumulate leaf nitrogen at a slower rate than non-irrigated plants so that they reached a peak of nitrogen content about 10 days later (Fig. B.4.5) at only a slightly higher level. The period of constant leaf nitrogen or slow decline previously noted was not present, presumably because of the more rapid onset of water stress. Ultra had slower accumulation of stem nitrogen than did other cultivars (Table B.4.11).

Pod Nitrogen

Early Sowing

Ultra increased pod nitrogen significantly faster than Unicrop with Weiko intermediate (Fig. B.4.4, Table B.4.12). There were insufficient data to compute curves for Pamaro and Maris Bead. Lupins had more nitrogen stored in pods than other cultivars and this seemed to be eventually available to the seed. Decline in pod nitrogen generally occurred at much the same time as the overall decline in non-seed nitrogen. The slower decline in pod nitrogen coincided with slower seed nitrogen accumulation rate.

Late Sowing

There were insufficient data to allow the fitting of curves. Weiko and Ultra again accumulated more nitrogen than Pamaro. Irrigation resulted in more nitrogen in pods at the peak of accumulation compared with non-irrigated plants of the same cultivar.

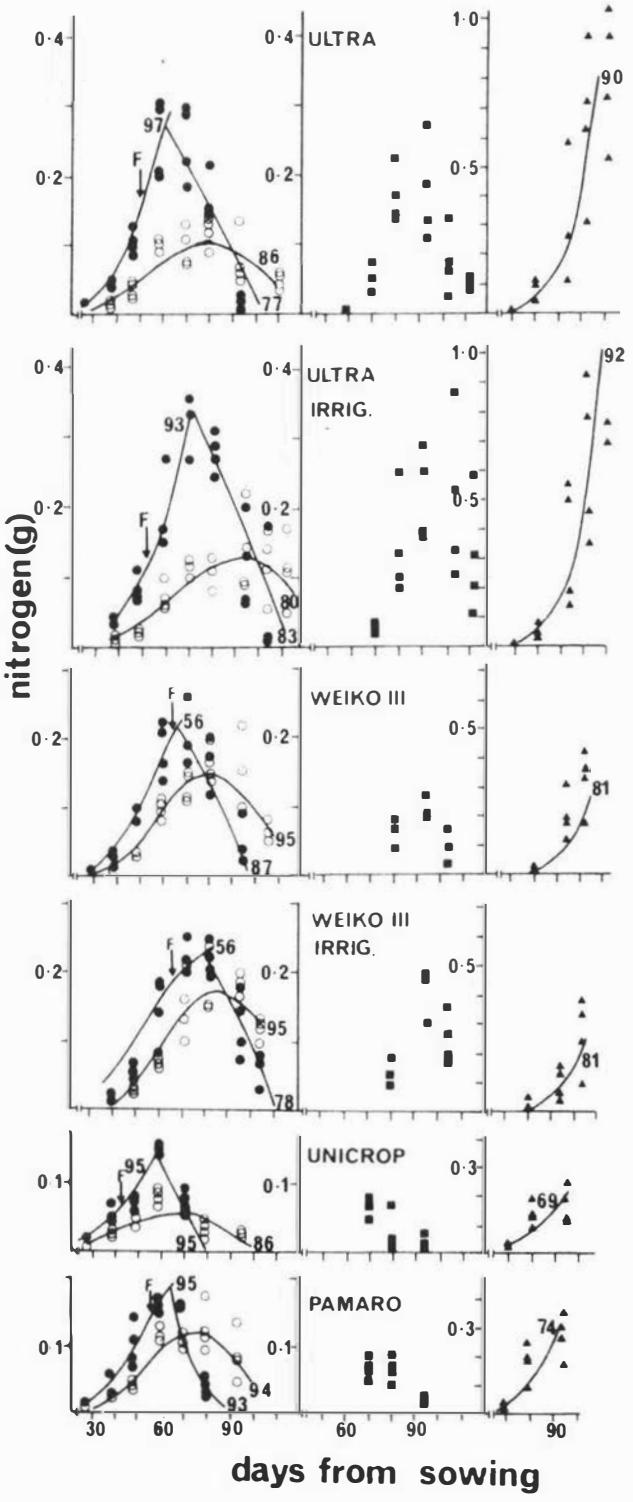

Fig. B.4.5 Nitrogen content of leaf (●), stem (○), pod (■) and seed (▲) per plant for late sowing. Figures and letters as for Fig. B.4.3.

TABLE B.4.12: Regression coefficient b for regression equations pod nitrogen and seed nitrogen with days from sowing

Cultivar	Pod Nitrogen		Seed Nitrogen
	Accumulation phase (linear equation)	Decline phase (equation 4)	(equation 5)
Early Sowing			
Pamaro	-		9.6296 b
Maris Bead	-		16.3283 a
Unicrop	0.0041 b	-0.0901 a	13.2518 ab
Ultra	0.0087 a	-0.0645 a	9.8070 b
Weiko III	0.0059 ab	-0.0739 a	15.0931 a
Late Sowing			
Pamaro			7.1740 a
Unicrop NI.			5.6170 b
Ultra I			10.2186 a
NI			9.5719 a
Weiko III I			9.4187 a
NI			8.7841 ab

Seed nitrogen

Maris Bead and Weiko III had the highest seed nitrogen increase at the early sowing (Table B.4.12). The early finish of seed nitrogen accumulation in Maris Bead and Unicrop (Fig. B.4.4) was probably due to the adverse influence of disease and again indicates that the potential of these cultivars was not indicated in this experiment. The rapid seed nitrogen increase in early-sown Weiko III compensated for a shorter duration of seed growth compared with Ultra so that both cultivars had a similar quantity of nitrogen in the seed.

The curves used did not fit the data well for some of the cultivars at the late sowing (Table B.4.12) and probably underestimated the rate of increase in seed nitrogen. However, apart from Weiko III, rates of seed nitrogen increase between sowing times were similar. Accumulation period (Fig. B.4.5) was shorter at the late sowing resulting in lower seed nitrogen yield except for Ultra.

The marked lag phase in early seed growth of Ultra noted by Hocking and Pate (1977) was also evident at the early sowing but was less pronounced at the late sowing.

To obtain a clearer picture of the contribution of various plant components to seed nitrogen, Table B.4.13 was constructed. Estimates of loss from plant parts were made by calculating the difference between maximum and minimum levels of stems and pods in Figs. B.4.4 and B.4.5. For leaves 60% of the maximum leaf nitrogen was used to allow for loss in senesced leaf. (Hocking and Pate (1978) found remobilisation of 60-75% for nitrogen from leaflets of *L. angustifolius* and *L. albus*).

The amount of nitrogen supplied by the leaf was relatively constant. The low contribution by Unicrop leaf at the late sowing was due again to the effect of disease. Remobilisation of nitrogen

TABLE B.4.13: Estimated contribution of nitrogen to seed from plant parts and that supplied direct from assimilation (mg).

		Leaf	Stem	Pod	Total Remobilised	Seed Content	*Direct
Early Sowing							
Pamaro		140	150	80	370	520	150
Maris Bead		170	90	50	310	450	140
Unicrop		130	90	90	310	280	30
Ultra		170	160	220	550	720	170
Weiko III		120	100	160	380	600	220
Late Sowing							
Pamaro		130	40	40	210	250	40
Unicrop	NI	80	30	40	150	160	10
Ultra	I	200	20	130	350	1000	650
	NI	160	50	120	330	750	420
Weiko III	I	130	40	80	250	250	0
	NI	130	80	70	280	300	20

* By difference

from pods and stem of Ultra and Weiko III was high. For Ultra, the amount of total remobilisation was lower at the late sowing but was compensated for by a greater supply of nitrogen "direct" to the seed. "Direct" supply at the late sowing was low for other cultivars.

B.4.2.4 DISCUSSION

The rates of accumulation of total nitrogen were remarkably similar considering the diverse genetic background and structure of the crops. Major differences between species were in the duration of accumulation and decline of nitrogen and the timing of these trends relative to days from sowing. Seed yield (Section B.4.1) was related to total nitrogen uptake, a trend also noted by Westermann and Kolar (1978).

The "self destruction" hypothesis of Sinclair and de Wit (1975) that considerable utilisation of non-seed nitrogen occurs at the time of rapid seed nitrogen accumulation is supported by the data from this experiment. The decline in non-seed component nitrogen at the early sowing occurred at the start of rapid seed accumulation (RS). The exception was Pamaro. Rapid seed development started approximately 110-120 days from the early sowing; about the same time that relative water content measurements were approaching 80%. Sections C.2 and C.3 show that, for Ultra, RWC at this level measured late in the photoperiod can cause cessation of vegetative growth and stimulate seed growth by remobilisation of assimilates. At the late sowing however, decline of nitrogen content in non-seed components commenced usually at the beginning of seed growth (BS). This was at day 60-80 when leaves of non-irrigated plants were approaching 80% RWC indicating again that water stress is the stimulus for the decline. However, irrigated plants also started their non-seed nitrogen decline at the same time as non-irrigated plants. RWC data indicated that on hot sunny days the RWC of irrigated plant leaves at 2 p.m. was not greatly different from those of non-irrigated plants and only at night, when non-irrigated

plants retained a low RWC, were the differences between irrigated and non-irrigated plants large. Hot days caused RWC of irrigated plant leaves to fall below 90% which could induce sufficient stress to affect photosynthesis (Shaw and Laing, 1966; Chen *et al.*, 1971) and to stimulate beginning of senescence. Irrigation allowed nitrogen uptake to continue for longer in Ultra and cause slower decline in the rate of remobilisation of nitrogen as would be expected from the "self-destruction" hypothesis of Sinclair and de Wit (1975, 1976). Water stress, by limiting leaf area expansion (Section C.2), photosynthesis (Boyer, 1976) and nitrogen fixation (Sprent, 1976) reduces the direct supply of nitrogen to the seed forcing a greater dependence on nitrogen reserves thus stimulating and/or aggravating the "self-destruction" cycle. If however the signal for senescence is hormonal (Nooden *et al.*, 1978; Williams and Williams, 1978), water deficit may stimulate production of the hormone. Nooden *et al.* (1978) suggest that the hormone travels only downward in the plant from the pod whereas in lupin much of the leaf is above the pods. However, if the lower leaves were induced to senesce by a hormone the upper leaves would probably start a "self-destruction" cycle because of the demand for assimilates by the plant as a whole on a reduced supply from the smaller leaf area.

This experiment supports trends apparent in controlled environment experiments (Sections C.2, C.3) where Ultra continued rapid vegetative growth when adequately watered. When water stressed, vegetative growth slowed with a concurrent increase in reproductive growth rate. The stimulus for cessation of vegetative growth, for rapid seed growth and for withdrawal of nitrogen from vegetative components seems to be due more to water stress than to the demand for photoassimilate inferred by Sinclair and de Wit (1975) and others. Possibly water stress caused reduction in photosynthesis (and thus nitrogen fixation) as well as increased seed growth both of which resulted in withdrawal of nitrogen from vegetative tissues. A similar hypothesis has been suggested by Eaglesham *et al.* (1978).

Early-sown Pamaro was an exception to this trend. Mobilisation of non-seed nitrogen occurred at the beginning of seed growth rather than at the beginning of the rapid seed growth phase as in the other species. RWC data indicated that peas were not severely water stressed until about 125 days from sowing; leaf senescence commenced early relative to stem nitrogen remobilisation and the leaf nitrogen did not have the constant period shown by other species; all indicating that some self-shading occurred resulting from its prostrate scrambling habit and faster development. This self-shading within the canopy may have produced a limitation to the development of maximum seed yield resulting in reduced demand for nitrogen reserves which may have given rise to the slower decline in non-seed nitrogen and the higher ratio of nitrogen to dry weight noted. However, these effects could also be due to the lower overall demand for nitrogen resulting from the lower nitrogen content of the seed. In Maris Bead the high ratio of nitrogen to dry weight could have been caused by the loss of pods due to the effects of disease.

Weiko III and Ultra tended to supply a greater proportion of the seed nitrogen from the pod a trend also noted in *L. albus* by Hocking and Pate (1977). Perhaps this is one reason for the higher seed nitrogen concentration of these cultivars. At the early sowing, the nitrogen supplied "directly" to the seed was approximately half of the amount supplied from plant reserves except for Unicrop. At both sowings Ultra was most efficient at remobilising nitrogen which was also noted by Hocking and Pate (1978).

The supply of "direct" nitrogen to the seed by late-sown plants was low except for Ultra. Water stress probably stopped fixation and started seed development earlier than was desirable. This may have caused most of the seed nitrogen to be supplied from remobilisation of reserves which were limited so seed development in most cultivars did not fully enter the rapid accumulation phase. This situation was however helped by a higher accumulation of nitrogen before flowering than for the early sowing. Rapid

nitrogen accumulation was sustained in Ultra for a longer period enabling greater contribution from the pod and the channelling of nitrogen directly to the seed which would have been helped by limited vegetative growth imposed by water stress that occurred during the day but which enabled seed growth to continue (Section C.3). Higher temperature at this time probably helped to stimulate growth in *L. albus* (Section C.4).

Although Ultra and Weiko III accumulated similar levels of seed nitrogen at the early sowing there appeared to be important differences in the pattern of this accumulation. Compared with Ultra, Weiko III had a very high rate of seed nitrogen accumulation. Ultra however had a marked "lag phase" where the accumulation rate was relatively slow before the rapid accumulation phase began. This trend has also been noted by Hocking and Pate (1977). The lag phase may be important to enable the preceeding growth period to continue for a longer period thus enabling a greater production of photosynthetic tissue and nitrogen reserves. This is achieved however at the expense of a longer growth period which, especially for spring sowing, can be undesirable.

An important determinant of seed nitrogen yield therefore seems to be the length of the total plant nitrogen accumulation phase and management of the crop must aim to allow it to be as long as possible. Relatively short extensions to the effective growth period can make significant increases in the amount of nitrogen assimilated, a high proportion of which can be available for seed production. For example, during the last 20 days of the linear phase of total nitrogen accumulation, Ultra was assimilating 0.017 g nitrogen per day. An extra 10 days of accumulation at that rate would increase the nitrogen available for seed production to allow for a 20% increase in seed nitrogen for Ultra. Thus early sowing is very important to maximise seed protein (nitrogen) yield especially for the more slowly developing cultivars. Even so, the slow development of cultivars such as Ultra and Weiko is a disadvantage as the growing season is always of limited

duration. Selection for cultivars with more rapid development in the early phase would be an advantage although a comparison between early and late sowings would indicate that the rate of early development is largely a function of the environment, mainly temperature (Reeves *et al.*, 1977). The faster nitrogen accumulation at the later sowing compared with the early sowing indicates that if adequate water can be provided during the summer by irrigation or by growing in an area with a good summer rainfall, late sowings could produce acceptable yields (Section C.2) or a very substantial improvement could be expected from early-sown crops provided disease or self-shading was not a problem.

These results would indicate that each of the species tested has similar potential to fix nitrogen and transfer this to seed protein. Other factors therefore must influence the choice of crop. For example, if high protein content is required in the seed, then lupins have some advantage. If the growing period is short, peas and *L. angustifolius* would seem to be most suitable, but for all species, early sowing would seem to be essential for maximising seed and protein yield.

SECTION C. WATER STRESS STUDIES ON LUPINUS ALBUS

C.1 GENERAL INTRODUCTION

Results from Section B.4 and Hill *et al.* indicated that *L. albus* was a grain legume with a potential for New Zealand despite poor earlier reports (Alan, 1949). For this reason and because relatively little work had been carried out in Australasia on this species compared with *L. angustifolius*, all further work was with *L. albus*.

The previous experiment showed that water supply is an important factor in seed yield. However, in New Zealand, moisture stress of various duration and intensity can affect the plant at almost any stage of growth from late spring. Study of the effect of short duration water stress on growth, nitrogen distribution and seed yield would thus seem to be important.

Salter and Goode (1967) state that most grain legumes are sensitive to moisture stress at most growth stages especially during flowering. However, lupins were not included in their review and the marked indeterminate nature of *L. albus* may make it different from most grain legumes. The range of development of pods over a sequence of stems may mean that lupin can recover from short duration moisture stress as previously noted by Biddiscombe (1975) for *L. angustifolius*.

In indeterminate plants such as lupins, knowledge of vegetative growth is important even for seed production as vegetative and reproductive growth occur concurrently and are probably in competition (Weber, 1968). Water deficits are known to adversely affect many aspects of growth and nitrogen metabolism (Salter and Goode, 1967; Hsiao, 1973; Hsiao and Acevedo, 1974). In a series of experiments, Gates (1955a,b; 1957) used tomato as the experimental plant. Water stress reduced total plant dry weight, particularly the laminae but, on rewatering, laminae recovered at

a higher rate than stems. Nitrogen was mobilised from the leaf to the stem during stress but moved mainly to younger leaves upon rewatering. Gates (1964) states that the younger leaves suffer the greatest depression in growth but retain the best capacity for regrowth upon rewatering.

There is limited information on the vegetative response of grain legumes to water stress as most studies concentrate on reproductive components. Some stress during early stages of growth which reduces plant size may increase seed yield (Salter, 1962; Salter and Drew, 1965; Salter and Goode, 1967) presumably because of less competition from the vegetative growth.

Results of experiments on timing of water stress with other grain legumes are confusing probably because of differing aims, methods and conditions. Pod fill has been found to be a sensitive stage in peas (Maurer *et al.*, 1968, Miller *et al.*, 1977) and soybeans (Doss *et al.*, 1974; Sionit and Kramer, 1977) resulting in lower seed weight. Adjei-Twum and Splittstoesser (1976) found water stress reduced seed numbers but increased seed weight and seed protein percentage of indeterminate soybeans. According to Salter and Goode (1967), irrigation before flowering often fails to increase seed yield. Runge and Odell (1960) and Sionit and Kramer (1977) found moisture stress at the vegetative stage reduced yields of soybeans but Stoker (1977) failed to obtain a response in lupin to irrigation before flowering although he stated that pre-flowering response probably depends on the degree of stress. Biddiscombe (1975) found stress during flowering most important in *L. angustifolius*, the main effect being a reduction in pod numbers. Plants watered after stress were able to recover and develop flowers and pods similar to non-stressed plants. Shaw and Laing (1966) also reported that, with soybean, water stress imposed early in growth reduced pod number on the lower stem but this was compensated for by additional pods set on the upper stem when stem growth resumed on rewatering. They found that water stress during seed fill reduced seed yield most.

Stress during flowering was less important, but significant. Stress at flowering reduced pod number and later stress reduced seed number per pod, increased the number of incompletely filled seed and increased seed protein content. Stoker (1977) reports a good response of *L. angustifolius* to irrigation over the flowering and pod-fill period. Improvement in pod number and seeds per pod were obtained.

In this section, three experiments are reported. The first examined the effect of water stress over a single defined growth period with emphasis on the early stages of growth under two levels of humidity. The second imposed water stress over two or three growth stages and examined more closely the effect over the period of seed growth. The interaction of temperature and water supply was considered in the third experiment.

In order to overcome the climatic uncertainties and other difficulties associated with field trials when investigating moisture stress (Gates, 1964; Salter and Goode, 1967), the experiments were conducted in controlled climate facilities.

C.2 EFFECT OF WATER STRESS IMPOSED DURING A SINGLE GROWTH STAGE AT TWO HUMIDITY LEVELS *

C.2.1. INTRODUCTION

This experiment examined the effect of short duration, mild water stress on *L. albus*. Emphasis was placed on early stages of growth and on the response of vegetative growth to water stress as well as the effect on final seed yield as it was believed the two aspects were closely related (Section B.4)

Because atmospheric humidity may influence the rate of water loss by the plant (Forde *et al.*, 1977), the effect of humidity may interact with the effect of water supply on the plant. Evidence of a direct effect of humidity on vegetative growth is

* Published in N.Z. Journal of Agricultural Research 22: pp 445-61 1979

limited. Forde and Thorne (1974) obtained a reduction of plant growth in sugar beet, kale and wheat under low humidity. Reduction in growth rate under low humidity was variable. No reduction was recorded for wheat in some experiments indicating that dicotyledon plants may be more sensitive to low humidity. Tops were more affected than roots, and leaf area more than dry weight so N.A.R. decreased under high humidity.

There is little information on the effect of humidity on grain yield of legumes. Fisher and Weaver (1974) found that high humidity during flowering tended to increase the number of pods of lima beans and suggested that this was caused by improved pollen germination. Woodward and Begg (1976) found that low humidity during flowering of soybean reduced seed yield. Low humidity after flowering had a smaller effect and before flowering it had no effect. The main effect was reduced pod numbers because of flower abortion, and this was attributed to poor supply of photosynthate to the flowers due to an estimated drop of 20% in photosynthesis.

In order to study the effect of humidity on lupin and as a means of imposing two stress levels on the plant identical watering treatments were carried out at two humidity levels.

C.2.2. MATERIALS AND METHODS

Lupinus albus cv. Ultra plants were grown in 1.9 l pots containing sterilised Manawatu silt loam. Pots were filled with 2.3 kg of air dried soil which was watered to run-off and allowed to drain for 24 hours before sowing. Three seeds per pot were sown on 11 May 1976 but were thinned to one per pot after emergence. *Rhizobium* strain 2076 was added at sowing and 6 days later the pots were transferred to two controlled environment rooms in the Climate Laboratory, Plant Physiology Division, D.S.I.R., Palmerston North. Except for humidity level, the environments in each room were the same.

Conditions in the controlled environment rooms were:

Photoperiod	-	14 hours
Av. irradiance	-	160 Wm^{-2} (400-700 nm)
Temperature	-	18^{o} day, 13^{o} night ($\pm$ 0.5^{o})
High humidity day	-	4 mb vpd*, 80% RH ($\pm$ 5%)
night	-	4 mb vpd, 73% RH ($\pm$ 5%)
Low humidity day	-	13 mb vpd, 35% RH ($\pm$ 5%)
night	-	10 mb vpd, 35% RH ($\pm$ 5%)
CO_2 level		340 ppm ($\pm$ 20)

* vpd = vapour pressure deficit

Initially, pots were weighed individually and watered by hand to reach 80% of the weight at field capacity. Once this was achieved, each pot was connected to a watering tube and watered automatically. Duration and timing of watering was adjusted during the experiment to maintain approximately 80% field capacity. Pots were checked regularly to ensure all were receiving adequate water. Modified nitrogen-free Hoaglands solution was added weekly except when water was being restricted.

Water stress was imposed at specific growth stages by removing the automatic watering tubes and watering daily by hand to specific weights. Pots were watered near the end of the photoperiod to a level which resulted in a leaf relative water content (RWC) after 24 hours of approximately 80% in plants grown under the high humidity regime (Baars,1968). Leaf RWC was determined immediately before watering from 2 leaflets of newly expanded leaves at the top of the canopy so that sample leaves were of similar physiological age. Treatment plants in the low humidity room were watered to the same pot weight as those in the high humidity room. The RWC method was used because the leaflets were too small to be used in the pressure bomb apparatus. The watering regime imposed is summarised in Table C.2.1. Timing of the start and end of the restricted watering regime was determined for each plant so that treatments were based on the physiological growth stage of individual plants rather than on an overall average growth stage.

TABLE C.2.1. Schedule of treatments

Growth Stage	Treatment					
	Control	S1	S2	S3	S4	S5
Floral initiation to appearance of main stem flower head	+	-	+	+	+	+
Emergence of main stem flower head to start of Main stem flowering	+	+	-	+	+	+
Duration of main stem flowering	+	+	+	-	+	+
Duration of 1st order lateral flowering	+	+	+	+	-	+
Duration of 2nd order lateral flowering	+	+	+	+	+	-

+ = adequate watering

- = restricted watering

Plants were harvested at the end of each treatment period. Because the number of plants were limited, the number of harvests for each treatment had to be restricted and the harvest schedule is summarised in Table C.2.2. Ten plants were scheduled for each harvest.

TABLE C.2.2. Schedule of harvests

Time of Harvest	Treatment					
	Control	S1	S2	S3	S4	S5
Emergence of main stem flower head (H1)	+	+				
Start of main stem flowering (H2)	+	+	+			
End of main stem flowering (H3)	+	+	+	+		
End of 1st order lateral flowering (H4)	+		+	+		
When seed at approximately 14% moisture content (final harvest)	+	+	+	+	+	+

The timing of harvests allowed observation of the immediate effects of, and the recovery from, water stress applied at early growth stages. A final harvest of all treatments measured the overall effect on seed yield and plant growth. Detailed study of the effect of stress on the later stages of growth was left for a subsequent experiment.

At each harvest, the plant was dissected into leaf lamina, stem, pod and seed of each stem order as appropriate. Soil was washed from the root system and nodules separated from the roots. Number and dry weight of each component was noted. Drying was carried out in a vacuum oven at 40^{o}C for 24 hours and equilibrated at 22^{o}C and 50% RH for several hours before weighing. Each component was retained and later analysed for total nitrogen using Kjeldahl digestion and steam distillation (Clements, 1970).

One-way analysis of variance and t-tests were performed on untransformed data.

C.2.3 RESULTS

C.2.3.1. Levels of Water Stress Imposed

Relative leaf water content (RWC) data measured before watering are presented in Figure C.2.1. RWC did not reach desired levels in S1 until about half way through the treatment. Because of a malfunction in the high humidity room the pots were accidentally overwatered just before water was to be withheld. This, combined with the low evapotranspiration at this stage, caused the delay in attaining the required stress level. To maintain comparability, the restriction of water under low humidity was delayed to a similar extent. Some difficulty in reaching the required level was also experienced with S2 but for other treatments a satisfactory stress regime was maintained. The difference in RWC between humidity levels was small except at the beginning of the late applied treatments (S4 and S5) when a marked drop occurred for the low humidity treatments. This drop was associated with severe wilting of all leaves but the lower leaves rapidly senesced and the upper leaves regained turgidity. For S5, little leaf remained after the initial stress and under low humidity, plants remained visibly wilted during most the photoperiod.

RWC of leaves on control plants declined slightly during the experiment and RWC in the low humidity room remained below that in the high humidity room at all times.

C.2.3.2. Duration of Growth Stages

There was little difference in the development of control and stress plants within each humidity although some small differences occurred between humidities. Mean duration for each treatment was:-

	High Humidity	Low Humidity
S1	19 days	19 days
S2	11 days	11 days
S3	21 days	21 days
S4	19 days	16 days
S5	17 days	13 days

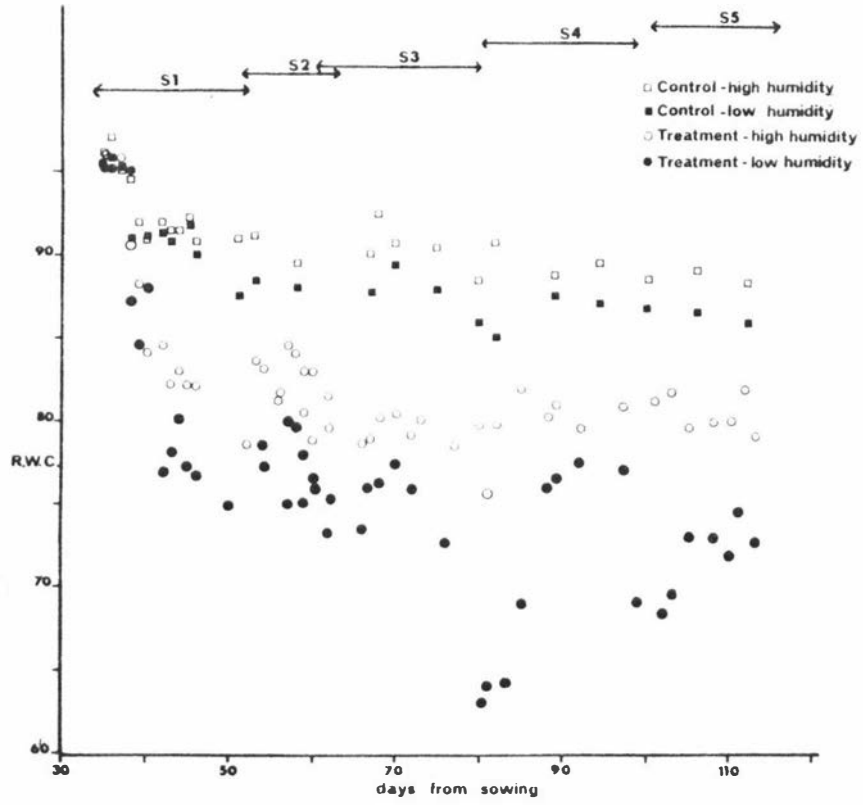

Fig. C.2.1 Results of relative leaf water content (RWC) measurements. Each point is a mean of 8 plants.

Durations of treatments were reasonably comparable except for S2 and S5 under low humidity.

C.2.3.3 Total Plant Growth

Water stress imposed after the start of flowering had the greatest effect on total plant dry weight (Fig. C.2.2). The results of pre-flowering treatments (S_1 and S_2) were greatly modified by humidity effects with plants from low humidity treatments significantly smaller than control plants. Differences between control and treatment plants were small at the end of each treatment period but the difference increased as growth progressed. Differences were greatest at final harvest although much of this could be due to the fact that leaf which was least affected by the stress, had senesced at this stage.

Water stress affected total plant nitrogen similarly (Fig. C.2.3). Differences between humidity levels in the yield of nitrogen were proportionally less than were observed for dry weight. There was a consistent trend for the nitrogen yield of control plants to be higher under low humidity.

Despite treatment differences in total dry weight and nitrogen yield, the proportion of seed remained relatively constant at about 33% of total dry weight and 74% of total nitrogen at final harvest, indicating that seed production efficiency was not altered by any treatment.

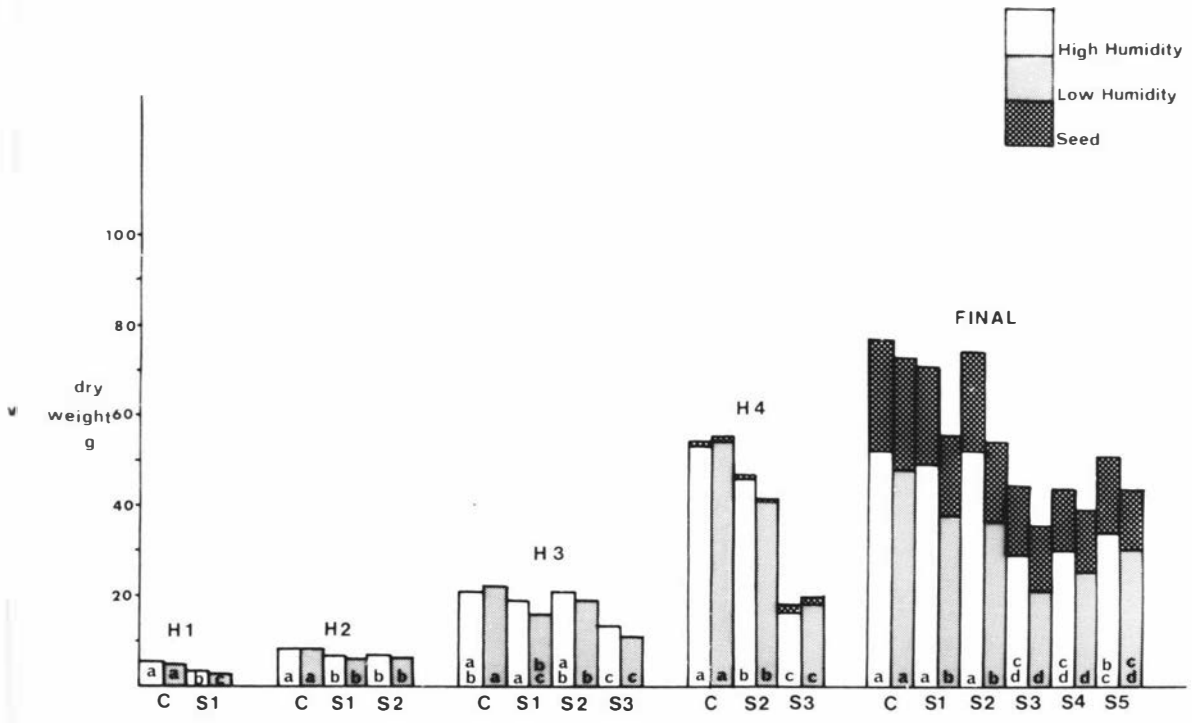

Fig. C.2.2 Total plant dry weight and proportion which was seed.

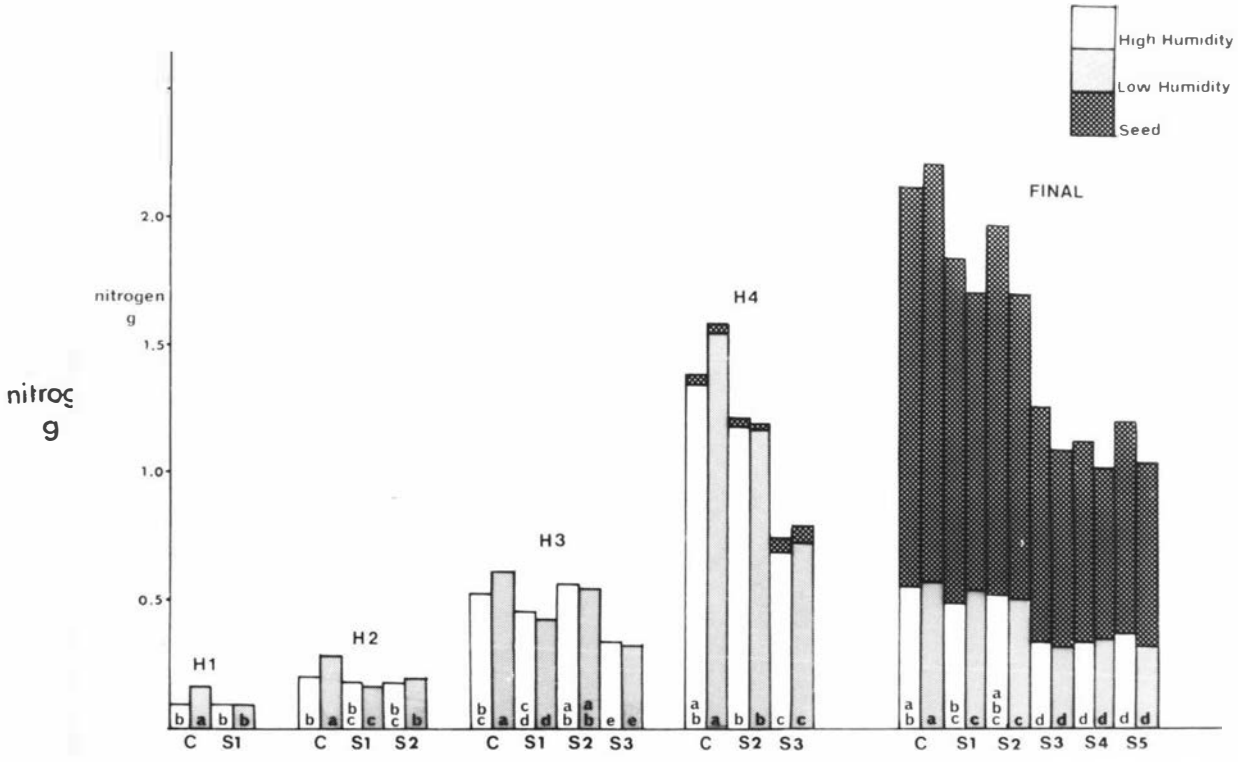

Fig. C.2.3. Total plant nitrogen and proportion which was seed.

C.2.3.4 Leaf Growth

Growth rate of main stem leaf in control plants was at a maximum up to the stage of main stem flower head emergence and thereafter fell to reach negative values at first order lateral flowering (Fig C.2.4). This effect tended to be more extreme at high than at low humidity. Nitrogen accumulation rate followed a similar trend to dry weight.

Little leaf growth or nitrogen accumulation occurred during stress but, on rewatering, both recovered to levels usually greater than control for S1 and S2 but not for S3 as growth of main stem leaf had already begun to decline.

First order lateral leaf growth commenced during main stem flowering and was rapid during first order lateral flowering coinciding with the decline in main stem leaf dry weight and nitrogen (Fig. C.2.4). Stress reduced dry weight and nitrogen accumulation.

The results of these trends at the end of first order lateral flowering (H4) was that plants from treatment S3 had lower total leaf weight than control plants because of lower first order lateral leaf weight (Table C.2.3) caused by smaller leaves as leaf number was similar.

T-tests of treatments combined within humidity levels showed that nitrogen percentage of main stem leaves grown under low humidity was significantly higher than that of those grown under high humidity (Table C.2.4), but generally leaf dry weight was not affected, so that leaf nitrogen yield was increased by low humidity.

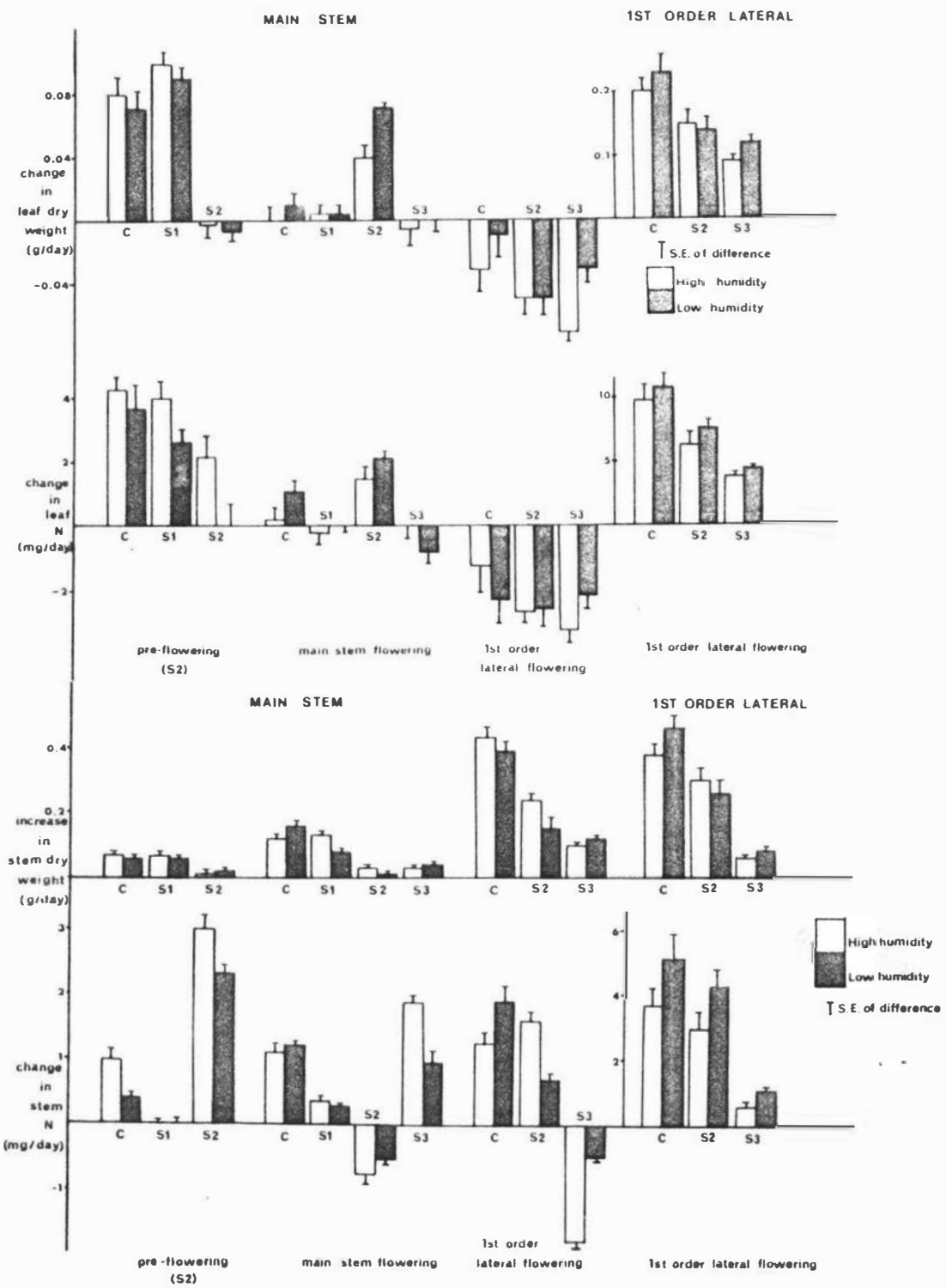

Fig. C.2.4 Rate of change in leaf and stem dry weight and nitrogen for the main stem over three growth stages and for the first order lateral stems over one growth stage.

TABLE C.2.3 Dry weight (g) of main stem and first order leaf and dry weight per leaf at the end of first order lateral flowering

	Main stem leaf		1st order lateral leaf			
	Total D.W.		Total D.W.		D.W. per leaf	
Humidity level	High	Low	High	Low	High	Low
Control	2.2 AB	2.9 A	7.1 A	7.2 A	0.14 A	0.14 A
S2	1.7 BC	2.4 AB	6.2 AB	5.4 B	0.12 A	0.12 A
S3	1.1 C	2.0 AB	2.5 C	2.6 C	0.06 B	0.05 B

Means with letters in common are not significantly different ($P < 0.01$). Comparisons apply between humidity levels and within columns).

TABLE C.2.4 Dry weight, nitrogen percentage and nitrogen yield of main stem leaf and stem at two humidity levels (treatments combined within humidity levels).

		Leaf			Stem		
Humidity		High	Low	Significance of Difference	High	Low	Significance of Difference
	Harvest						
Dry weight	1	1.4	1.5	NS	1.5	1.3	*
(g)	2	2.3	2.1	NS	2.4	2.1	**
	3	2.6	2.8	NS	4.8	4.2	*
	4	1.6	2.4	***	8.5	7.4	NS
	Final	-	-	-	9.6	7.4	***
% nitrogen	1	3.3	4.5	***	1.9	2.5	***
	2	3.7	4.4	***	1.6	2.0	**
	3	3.5	4.0	***	1.1	1.3	NS
	4	3.2	3.5	***	0.7	0.9	***
	Final	-	-	-	0.4	0.5	***
Nitrogen	1	43.2	65.6	**	28.8	32.0	NS
Weight	2	83.2	94.4	NS	40.0	41.6	NS
(mg)	3	92.8	113.6	**	52.8	51.2	NS
	4	52.8	86.4	***	62.4	65.6	NS
	Final	-	-	-	35.1	26.0	NS

C.2.3.5 Stem Growth

Main stem growth rate of control plants increased up to second order lateral flowering (Fig. C.2.4). Water stress reduced growth rate and, although growth rate recovered on rewatering, it did not regain control rates (except for S1 plants which were equal to control plants for their initial recovery). Thus stress imposed during the rapid growth phase of a stem order reduced the dry weight of that stem as shown in Fig. C.2.5. S3 and S4 reduced the growth of three stem orders and therefore had the most severe overall effect on total stem weight. However, the growth of second order lateral stems of S3 was showing signs of recovery.

During water stress, the rate of accumulation of nitrogen in the main stem usually continued at a rate greater than that of control (Fig. C.2.4), but during the period immediately after the stress, accumulation rate was zero or negative. As a result of the dry weight and nitrogen trends, the yield of nitrogen in the main stem of stressed plants tended to be equal to, or greater than that of control plants at the end of the stress period of each treatment, despite lower stem weight.

The nitrogen percentage of the main stem steadily fell with time (Table C.2.4) so that although stem weight continued to rise, nitrogen yield increased at a slower rate than dry weight. Between H4 and final harvest, dry weight remains relatively constant but the yield of nitrogen fell because of an approximately 50% reduction in nitrogen percentage.

Low humidity reduced dry weight of main stems (Table C.2.4) and increased nitrogen percentage, with the result that there was no significant difference between humidity levels for main stem nitrogen yield. Low humidity did not reduce the weight of first order lateral leaf or stem but significantly increased nitrogen percentage resulting in higher nitrogen yield than under high humidity.

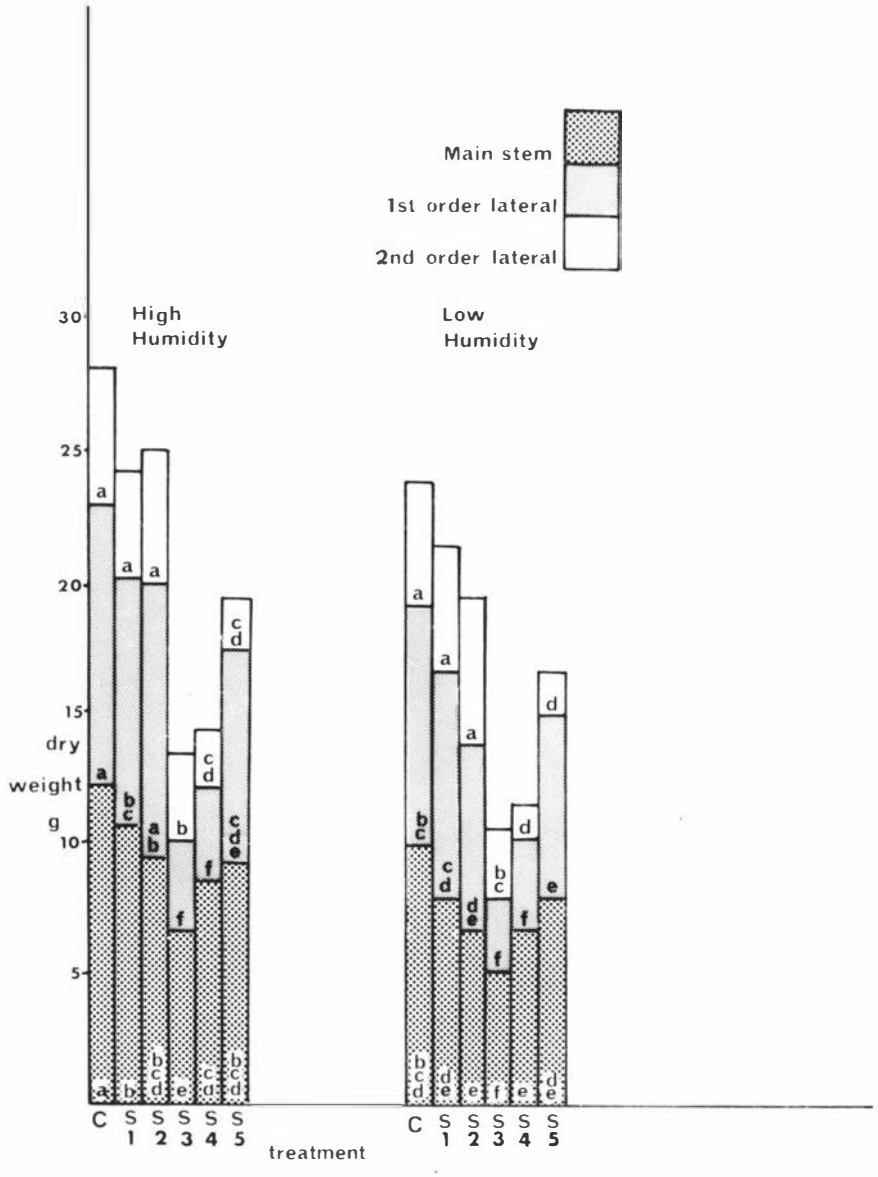

Fig. C.2.5 Dry weight of stems at final harvest.

C.2.3.6 Reproductive Growth

Seed yield of plants stressed before the start of main stem flowering (S1 and S2) were not significantly different from control plants when grown under high humidity (Fig. C.2.6). However, when grown under low humidity, plants from both treatments had significantly lower seed yield than control. All stress treatments imposed after flowering began had lower seed yield than control and were not significantly different from each other. Variation in total seed yield was due mainly to the seed yield of first order lateral stems (Fig. C.2.6) as seed yield from the main stem was relatively constant in stressed plants. This effect was apparently due to a difference in sensitivity to stress between pods of the main stem and first order lateral stems.

Pod numbers were related to seed yield except that plants stressed during second order lateral flowering (S5) had pod numbers higher than would be expected from seed yield (Fig C.2.6). S5 plants had fewest seeds per main stem pod (Table C.2.5). Number of seeds per first order lateral pod and hundred seed weight were not significantly different for all treatments (means 2.2 and 29.8g respectively). S3 and particularly S4 plants tended to have fewer productive first order lateral stems than plants of other treatments (Table C.2.6) although total stem numbers did not vary significantly from 5. Number of pods per productive first order lateral stem were low from all plants stressed during flowering.

Main stem seed grew most between H4 and final harvest (Table C.2.7) The results at H4 indicate that seed growth is stimulated by water stress although this was not apparent at final harvest. Many incompletely filled seed were found in the first order lateral pods of plants watered well over most of the development period

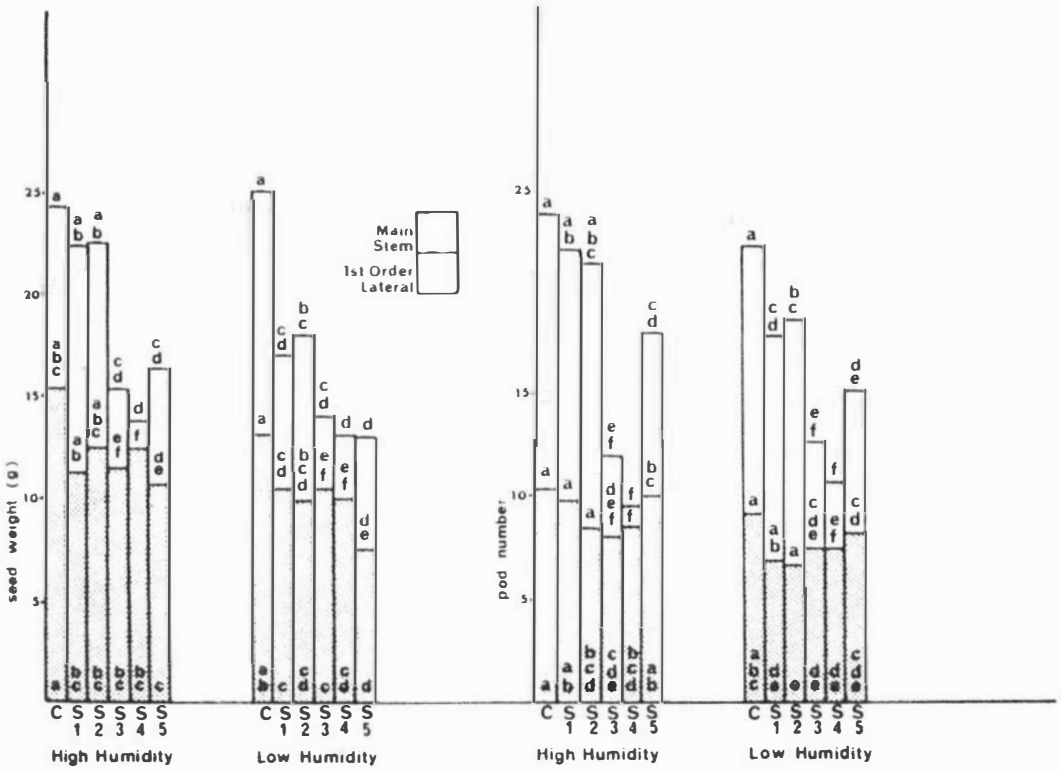

Fig. C.2.6 Weight of seed and number of pods per plant.

(Table C.2.8). Numbers were lower in plants stressed during main stem and first order lateral flowering (S3 and S4) and the late-stressed treatment (S5) had medium numbers. Very few were found in main stem pods.

Nitrogen percentage of seed tended to be reduced by later water stress especially for first order lateral seed (Table C.2.9). Main stem seed of S5 was affected less, possibly because of a smaller demand for reduced assimilate supply from the fewer seeds per pod. In an attempt to determine the cause of the variability in seed nitrogen percentage, seeds from control, S3, S4 and S5 plants were dissected into hull and kernal. The ratio at these components was not related to seed nitrogen so a change in the proportion of hull did not seem to be important in the above trends.

TABLE C.2.5: Number of seeds per main stem pod

Harvest	4		Final	
Humidity level	High	Low	High	Low
Control	4.6 A	4.4 AB	3.8 A	3.9 A
S1			3.0 B	3.6 A
S2	4.2 AB	3.8 B	3.8 A	3.4 AB
S3	4.1 AB	4.5 AB	4.1 A	3.9 A
S4			3.7 A	3.6 A
S5			2.9 B	2.3 C

TABLE C.2.6: Number of productive first order lateral stems and pods per productive * stem at final harvest

	Number of productive stems		Number of pods per productive stem *	
Humidity level	High	Low	High	Low
Control	3.9 AB	3.8 AB	3.5 A	3.5 A
S1	4.2 A	4.4 A	3.1 A	2.5 AB
S2	4.2 A	3.9 AB	3.1 A	3.1 A
S3	2.1 CD	2.8 BC	1.4 BC	1.7 B
S4	0.8 E	1.3 DE	0.6 C	2.3 B
S5	4.4 A	3.9 AB	1.8 B	1.8 B

* productive stem = a stem which had at least one pod containing a normally developed seed.

TABLE C.2.7: Weight of main stem seed per plant at harvest 4 (end of 1st order lateral flowering) and at final harvest

Harvest	4		Final	
Humidity level	High	Low	High	Low
Control	0.8 ABC	0.6 C	15.2 A	13.6 AB
S1			11.2 BC	10.4 BCD
S2	0.8 BC	0.3 C	12.5 ABC	9.8 CD
S3	1.5 AB	1.7 A	11.5 BC	10.5 BCD
S4			12.5 ABC	9.9 CD
S5			10.7 BCD	7.5 D

TABLE C.2.8: Number of incompletely filled seed in first order lateral pods - final harvest

	High humidity	Low humidity
Control	35.8 A	17.4 C
S1	20.0 C	23.7 BC
S2	31.7 A	21.9 C
S3	4.2 D	5.4 D
S4	0.5 D	1.8 D
S5	15.8 C	10.7 CD

TABLE C.2.9: Percentage of nitrogen in seed - final harvest

	Main stem		First order lateral	
Humidity level	High	Low	High	Low
Control	5.9 ABC	5.9 ABC	6.5 AB	6.7 A
S1	5.5 CDE	6.1 A	6.1 BC	6.5 AB
S2	5.8 ABCD	6.1 A	6.4 AB	6.4 AB
S3	5.6 CD	5.4 DE	6.1 BC	6.1 BC
S4	5.4 DE	5.2 E	5.5 CD	5.4 D
S5	5.5 CDE	5.7 BCD	5.3 D	5.4 D

Within humidity levels, main stem flower sites were not greatly affected by the stress treatments but first and second order lateral flower sites were substantially reduced, particularly in plants stressed at a later stage (Table C.2.10). T-tests comparing humidity levels over all treatments showed that plants grown under low humidity had significantly more main stem and first order lateral flowers.

Apart from the pre-flowering treatments, low humidity did not significantly affect total seed yield or pod number. Main stem seed yield and pod numbers tended to be lower under low humidity but this was significant for S5 plants only. This result is consistent with the long term effect on main stem vegetative components as already noted.

TABLE C.2.10: Number of flowers per plant

	Main stem (H3)		1st order lateral (H4)		2nd order lateral (final)	
Humidity level	High	Low	High	Low	High	Low
Control	36.3 BC	43.9 A	59.3 bc	79.6 a	40.5 ABC	54.6 A
S1	31.7 C	34.0 BC			37.1 BC	50.4 AB
S2	31.9 C	39.0 AB	50.4 bc	65.6 b	27.4 CD	40.6 ABC
S3	34.8 BC	35.9 BC	37.1 d	50.1 cd	17.0 DE	21.0 DE
S4					26.9 CD	11.9 E
S5					15.6 DE	13.7 DE

C.2.4 DISCUSSION

Water stress markedly changes plant structure, the specific effect at any growth stage depending on which plant parts are growing rapidly at that time. The effect of water stress on restricting vegetative growth can thus be reasonably predicted from a knowledge of the expected growth pattern of the plant during the period of stress. This effect on rapidly growing tissue has been noted in a number of plants (e.g., Gates, 1955b; Williams and Shapter, 1965).

Both stem and leaf growth were greatly reduced during the stress period but response to rewatering varied. Leaf growth rate recovers quickly to the rates similar to, or greater than, control. This effect has been noted in maize (Kleinendorst, 1975) and tomatoes (Gates, 1955a). Gates (1964) and Hsiao and Acevedo (1974) have attributed this effect to a delay in development of leaves during brief periods of stress. Stressed tissue is therefore physiologically younger and so is capable of faster growth rates on rewatering than physiologically older unstressed leaf. Loss of leaf in older stressed plants was rapid and severe. In all plants, lower leaves were lost while upper leaves visibly recovered. The plant therefore compensated for lower water availability by drastic reduction in leaf area to a level which could be sustained. Passioura (1976) maintains that leaf area adjustment is an important plant reaction to long term water stress as stomatal control is not satisfactory for extended periods of stress. A large loss of leaf area however, limits the ability of the plant to respond to later favourable conditions and this is likely to be an important factor in stress recovery. Presumably, leaf senescence during water stress would be complete when stress became so great no leaves could be retained or when residual leaf area ceased to function because of age.

Stems however, did not fully recover their growth, and growth rates of main stems were reduced for the rest of the growth period. The overall effect is similar to that found by Gates (1955a) in tomatoes viz. leaf weight values of stressed and control plants tended to converge whereas stem values tended to diverge upon rewatering.

The main stem appears to act as a temporary storage organ for nitrogen which accumulates in the stem when vegetative growth is reduced by stress. As nitrogen uptake seems usually to match dry weight this increase in stem nitrogen probably results from transfer from older leaves as a response to stress. (Gates, 1955b; 1957; 1964). Nitrogen probably accumulates in the stem due to little growth in potential sink sites. Pate (1973) has shown that lupins and peas can store excess nitrogen in the shoot system. Upon rewatering, the accumulated stem nitrogen was rapidly mobilised, presumably to help sustain the rapid growth of new leaves, a trend also noted by Gates (1955b).

Although results presented here concentrate on main stems and leaves, it is expected that other stem sequences follow similar trends and measurements of the higher order sequences support this.

Sinclair and de Wit (1975) propose that, for seeds high in nitrogen, supply of nitrogen from plant reserves is essential as contribution of nitrogen from nodules and soil is insufficient to supply all the seed requirements during seed protein accumulation. This hypothesis is confirmed in *L. albus* by other workers (Hocking and Pate, 1978; Pate and Herridge, 1978) and by a later experiment (Section C.3). The marked reduction in vegetative growth caused by water stress with the smaller reserve of nitrogen that would result must therefore have important implications for later seed growth. Results from Section C.3 show that leaf is the most important source of nitrogen mobilised to the seed. Therefore the tendency of leaf to recover more rapidly than stem is important for the recovery of nitrogen

reserves as well as the more usually considered reason for increasing the plant's capacity to assimilate carbon. The relatively constant proportion of nitrogen and dry weight in the seed and non-seed components (approximately 66% of the dry weight and 26% of the nitrogen was in the non-seed components) indicates that the treatments did not greatly affect the efficiency of mobilisation of nutrients to the seed and that stressed plants could supply sufficient assimilate for the seed sites available.

Moderate water stress for 11-21 days can adversely affect seed yield in *L. albus*. The effect of water stress prior to flowering was detrimental to seed yield only at low humidity. This lack of effect at high humidity may have been due to the accidental flooding before S1 under high humidity and the subsequent difficulty of attaining the required levels of stress quickly enough. A similar problem was encountered with S2 plants under high humidity because of the short duration of this treatment and the low water use by the small plants at this stage. Under low humidity this problem was less marked and seed yield was significantly reduced for S1 and S2 plants to the extent that they were not much different from other stress treatments and were lower yielding than control. Thus, if moisture deficit is severe enough during the pre-flowering stage, it can cause a reduction in seed yield. In New Zealand, soil moisture during early growth is usually adequate and as water use at this stage is low, water stress probably occurs only with some late spring plantings.

Once main stem flowering starts, which coincides with the onset of rapid vegetative growth, sensitivity of seed yield to water stress seems to increase, largely through a direct effect on pod abscission. It is the loss of pods which most influences seed yield. Other components of yield are affected less, presumably because the plant is capable of filling the remaining seeds. The large number of unfilled seed in well-watered plants indicates that shortage of assimilate can occur when pod abscission is low.

L. albus therefore reacts to water stress by ready loss of pods which means that changes in other seed yield components need to be minimal. This type of response seems to be associated with indeterminate plants and has been reported by Gabelman and Williams (1960), Fisher and Weaver (1974) and Adjei-Twum and Splittstoesser (1976). Another reaction to water stress is the disruption of seed filling and resultant reduction in seed size. (Maurer *et al.*, 1968; Doss *et al.*, 1974; Miller *et al.*, 1977; Sionit and Kramer, 1977) but this reaction usually occurs when pod numbers are not greatly affected.

Adjustment to water shortage by flower or pod abscission results in a limited ability to respond to a later improvement in moisture supply. In this experiment, seed yield from first order lateral pods did not recover in plants stressed during main stem flowering. In fact there is strong evidence that the effects of stress carried over into later periods of growth as illustrated by S3 plants which had markedly reduced first order lateral pod numbers and by the lower main stem pod numbers of S1 and S2 plants. Part of this effect may have been due to the design of the experiment which ended the stress immediately before the start of flowering of the next sequence so that flowering of that sequence would occur during early recovery and readjustment. There was insufficient time for stems of higher order than first order lateral to contribute to yield. Biddiscombe (1975) noted recovery from stress in *L. angustifolius* but this species develops lateral stems at a faster rate than *L. albus* (Withers, unpublished data).

The late stressed treatment (S5) had an intermediate number of pods probably because pods (especially main stem pods) were developed sufficiently to resist the effect of water deficit. The reduction in the number of seeds per main stem pod of S5 plants is interesting as it indicates that when water stress affects a plant with a good pod set, reduction in seed number by abortion of seeds may be the second mechanism of adjustment after pod abscission.

Few seeds per pod have been noted in field-grown *L. albus* plants affected by drought late in growth (Withers unpublished data, D.B. Bishop, pers. comm.) and in soybeans (Shaw and Laing, 1966).

The last two treatments to be imposed (S4 and S5) markedly reduced the nitrogen percentage of the seed from first order lateral stems, indicating some interference with nitrogen transfer by these two treatments. Possibly leaves senesced rapidly before nitrogen could be fully mobilised from them. Hocking and Pate (1978) noted that mobilisation of nitrogen from leaves of water-stressed plants was reduced compared with those that senesce normally. Shortage of water can therefore lower seed quality. In soybean, Sionit and Kramer (1977) did not find a similar effect and Adjei-Twum and Splittstoesser (1976) noted an increase in seed protein.

There is some evidence that seed growth rate is stimulated by water stress. Also, pod growth was not reduced at a time when stem and leaf growth was severely restricted by water deficit. This aspect will be discussed later in more detail.

The high proportion of total nitrogen in the seed must raise the question of whether production of lupin seed is suitable as a fertility building step in a rotation. The amount of nitrogen supplied to the soil is likely to be limited. The main advantage would be that demand for nitrogen from soil sources would be low as most of the lupin's nitrogen could be supplied by the nodules.

The relatively constant proportion of nitrogen and dry weight in the seed however, indicates that the treatments did not greatly affect the efficiency of mobilisation of nutrients to the seed and that stressed plants generally could supply sufficient assimilate for the sites available.

Humidity did not have a major effect on vegetative growth in the short term or on seed yield. However, the effects of humidity on main stem leaf and stem growth and on nitrogen percentage indicate that low humidity had a slight depressing effect which was more readily measured on older tissues. The preferential effect on stem growth noted by Woodward and Begg (1976) was apparent in this experiment. The results from this experiment indicate that low humidity would increase the detrimental effect of low soil moisture on the growth of the lupin plant but should cause little reduction in the growth of well-watered plants and may have a slightly beneficial effect on the nitrogen status of the plant.

C.3. EFFECT OF WATER STRESS IMPOSED DURING TWO OR THREE GROWTH STAGES*

C.3.1 INTRODUCTION

Earlier work examined the effect of water stress during a single growth stage and at 2 intensities imposed by 2 humidity levels. Results indicated that seed yield of *Lupinus albus* L. was sensitive to water stress at all growth stages although the preflowering treatment yields were rather variable. Duration of water stress is an important factor determining its effect on growth (Hsiao and Acevedo, 1974) and therefore on seed yield. This experiment was designed to study longer durations of stress, again at a number of growth stages. Greater emphasis was placed on measurements during the later phases of growth in contrast to the previous experiment which concentrated on early growth.

The shorter stress periods in the previous experiment resulted in high levels of pod and flower abscission which appeared to reduce pod and seed development to a level which could be sustained by the reduced leaf area, an effect also noted by Adjei-Twum and Splittstoesser (1976). Longer stress periods are likely to increase abscission or reduce other components of yield because of the extended reduction in photosynthesis (Hsiao, 1973; Boyer, 1976) and nitrogen

*Published in N.Z. Journal of Agricultural Research 22:463-74. 1979

fixation (Sprent, 1976). These effects could also be caused by reduced sink strength (Sionit and Kramer, 1977) although the previous experiment showed that seed growth rate increased in stressed plants.

C.3.2 MATERIALS AND METHODS

Plants of *Lupinus albus* cv. Ultra were established and maintained as in the previous experiment. Seeds were sown on 30 September 1976 and plants were moved to the controlled environment room on 11 October. Environmental conditions in the room were similar to the high humidity treatment in the previous experiment. Temperatures were 18°C day and 13°C night with a 14 hour photoperiod and 153 Wm^{-2} (400-700 nm) average irradiance. A constant vapour pressure deficit of 4 mb was maintained by relative humidities of 80% during the day and 73% during the night.

Restricted watering treatments were imposed by weighing pots daily near the end of the photoperiod and applying water to maintain a mean relative water content (Baars, 1968) of approximately 80% in newly expanded leaflets sampled prior to watering. The range of treatments imposed aimed to reach the intensity of water stress achieved in the high humidity room in the previous experiment but to continue the stress for longer durations. The schedule of treatments is shown in Table C.3.1.

TABLE C.3.1: Schedule of Treatments

Growth Stage	Treatments					
	Control	P	PF1	F123	F23	F13
From floral initiation to beginning of main stem flowering	+	-	-	+	+	+
Duration of main stem flowering	+	+	-	-	+	-
Duration of first order lateral flowering	+	+	+	-	-	+
Duration of second order lateral flowering	+	+	+	-	-	-

+ = adequate water

- = restricted water

Treatment P (water withheld before main stem flowering) was added after the experiment was designed because of the problems attaining early stress levels experienced in the previous experiment.

Plants were harvested and measured as described for the previous experiment according to the schedule in Table C.3.2.

TABLE C.3.2: Schedule of harvests

Time of Harvest	Treatment					
	Control	P	PF1	F123	F23	F13
Beginning of main stem flowering (H1)	+	+				
Beginning of first order lateral flowering (H2)	+		+	+		
Beginning of second order lateral flowering (H3)	+	+	+	+	+	+
Beginning of third order lateral flowering (H4)	+		+	+	+	+
Seed at approximately 14% moisture content (final harvest)	+	+	+	+	+	+

No harvests were made at H2 for treatment F13 as plants at this stage were equivalent to plants in treatment F123. All treatments were designed to cease at the commencement of third order lateral flowering when harvest 4 was carried out. Plants allocated to the final harvest were not watered after this stage. Differences between H4 and the final harvest should indicate the extent of final translocation to the seed under dry soil conditions.

An infestation of thrips was noticed late in the experiment and the 1 g/l of menazon used to control them damaged some plants which had to be discarded. Treatment F123 was most affected which meant no plants of this treatment were available at H4 and only six for the final harvest.

C.3.3 RESULTS

The watering regimes were maintained as scheduled and the planned water stress levels were satisfactorily achieved. Generally, the length of each growth period was not affected by water stress although stress imposed late in growth did stop development. Total growth period (sowing to H4) varied from 100 to 128 days which is a normal duration in the field with spring sowings.

C.3.3.1 Vegetative Growth

All water stress treatments severely depressed final total plant dry weight (Table C.3.3) and nitrogen yield (Table C.3.4). Plants never recovered from the severe check to growth caused by early stress despite high relative growth rates (RGR) during later growth (Table C.3.5). Most of this was vegetative growth of upper stem sequences so that second and third order branches were a similar size to control.

Stress applied during first order lateral flowering resulted in lower RGR of vegetative components (leaf and stem) compared with non-stressed plants (See F123, F23 in Table C.3.5).

TABLE C.3.3: Total plant weight (g)

Harvest	1	2	3	4	Final †
Control	10.3 A	29.7 A	51.4 A	101 A	118 A
P	4.3 B		33.3 B		45 BC
PFI		6.1 C	18.0 C	37 C	31 CD
F123		13.5 B	29.4 BC		28 D
F23			56.2 A	64 B	57 B
F13			28.7 BC	47 BC	46 BC

† Does not include senesced leaf

Means with letters in common (within columns only) are not significantly ($P<0.01$).

TABLE C.3.4: Total plant nitrogen content (mg)

Harvest	1	2	3	4	Final †
Control	168 A	631 A	1021 AB	2140 A	2497 A
P	143 B		815 BC		942 BCD
PF1		159 B	413 D	793 C	550 D
F123		255 B	554 CD		681 CD
F23			1158 A	1313 B	1171 B
F13			661 CD	1040 BC	1092 BC

† Does not include senesced leaf

TABLE C.3.5: Relative growth rates (g/100 g/day) during 3 flowering periods for total plant weight and for vegetative parts only.

Flowering Period	Main Stem	1st order lateral		2nd order lateral	
	Total	Vegetative	Total	Vegetative	Total
Control	5.6	2.5	2.9	2.6	4.2
PF1	1.5	4.2	5.4	3.2	3.4
F123	1.4	1.3	4.0		
F23		1.5	3.3	-0.3	0.5
F13		2.7	3.9	0.4	1.4

TABLE C.3.6: Number of flower sites per plant

	Main Stem	1st order lateral	2nd order lateral
Control	44.0 A	56 A	41.0 A
P	28.0 C	43 ABC	
PF1	20.0 D	27 BC	20.3 B
F123	34.3 B	25 C	
F23	49.2 A	33 BC	0
F13	36.0 B	44 AB	18.9 B

Total RGR of these stressed treatments were similar to, or higher than, control indicating a greater RGR of reproductive components (pod and seed) in stressed plants. F13 which was not stressed over this period had similar vegetative RGR to control but the higher total RGR of F13 would suggest that there was a carry-over of the previous stress on reproductive growth rates.

Stress during second order lateral flowering reduced vegetative and total RGR more severely, largely because of extensive senescence of leaf which occurred at this time. The high RGR of reproductive growth compared with vegetative growth of late stress treatments (F123, F23, F13) resulted in high harvest indexes (0.52, 0.41, 0.54 respectively). In contrast, the early stress treatments had lower harvest indexes (0.28 for P, 0.26 for PF1) because the vegetative RGR was high after stress. Control had an intermediate harvest index (0.33).

C.3.3.2 Flower Number

Water stress applied before flowering significantly reduced the number of main stem flower sites (Table C.3.6). When stress continued during main stem flowering (PF1) the effect was more severe and also significantly depressed first and second order lateral flower sites. Another effect of stress duration is shown by treatment F13. Main stem and second order lateral flower sites were reduced as these inflorescences were stressed but flower site numbers of the first order lateral inflorescence were not significantly different from control. Therefore, water stress reduced the number of flower sites of those inflorescences directly affected. The extent of the reduction and the carry-over effect into subsequent inflorescences appears to depend on the duration of stress. A comparison of main stem flower numbers from treatments stressed pre-flowering (P and PF1) with treatments which were stressed during main stem flowering (F123, F13) indicates stress during floral development is more important than stress during flowering, but as illustrated by the first order lateral

flower sites of F13, this effect is again a function of duration. The pre-flowering water stress period lasted longer than stress during flowering.

C.3.3.3 Seed Yield and Components

The difference in final seed yield was large between control and all treatments (Fig C.3.1). Plants stressed during pre-flowering (P and PF1) were significantly lower in yield than plants stressed for a similar period at a later stage (F23 and F13). Stress during the full flowering period (F123) resulted in a seed yield similar to that of the pre-flowering stressed treatments. Unlike the previous experiment, main stem seed yield varied significantly. Main stem seed yield was related to the time water stress was imposed. Pre-flowering stress resulted in the lowest main stem seed yield and stress applied after main stem flowering had the least effect. First order lateral seed yield was severely reduced by all treatments.

Effects of duration of water stress on seed yield are apparent only in the comparison between F123 and other flowering stress treatments (F13 and F23). The difference between P and PF1 was not significant for seed yield but it was for main stem pod number which was the main component to influence yield (Table C.3.7). Apart from control, first order lateral pod numbers at final harvest were not significantly different between treatments.

The difference in first order lateral pod numbers for PF1 between harvest 4 and final harvest was due largely to a relatively high number of pods which shrivelled during this period and did not produce seed and were thus not counted as pods in the final harvest. Plants of the pre-flowering treatment (P) also had a high number of these pods (2.7 per plant) but in no other treatment were they present in significant numbers. Water stress during first and second order lateral flowering (F23) resulted in significant differences in first order lateral pod numbers between harvest 4

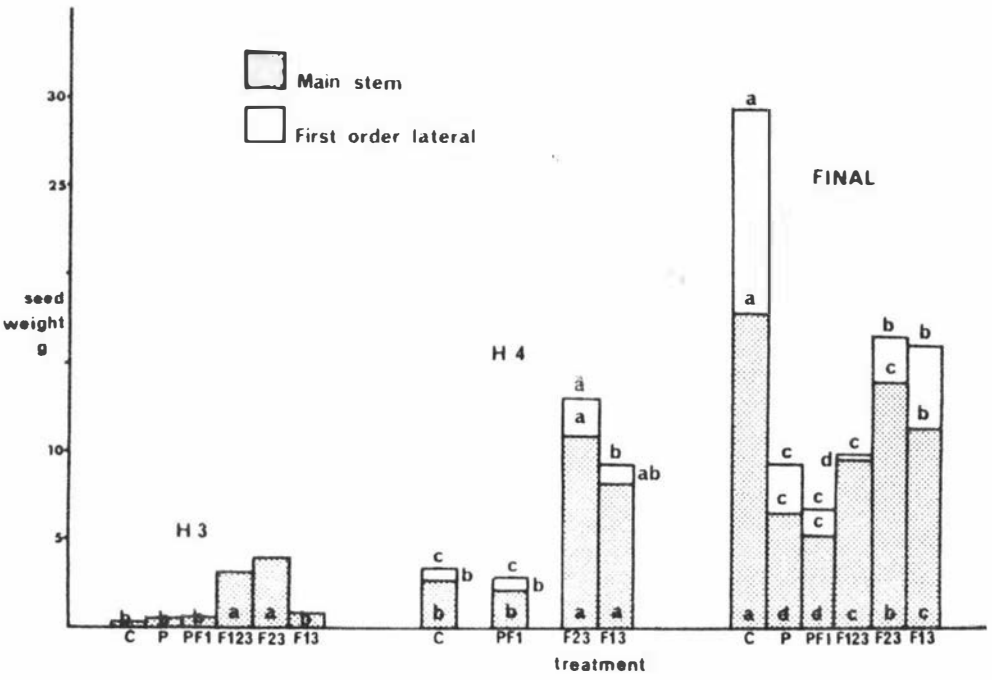

Figure C.3.1 Seed weight per plant at H3 (beginning 2nd order lateral flowering), H4 (beginning 3rd order lateral flowering) and at the final harvest. Bottom row of letters refers to main stem seed weight, middle figures refer to lst order lateral seed weight and the letter at the top of the histogram refers to total seed yield. For each component and within each harvest weights without letters in common are significantly different ($P < 0.05$).

and final harvest which must have been due to pod loss as very few shrivelled pods were noted at final harvest.

Generally, components of yield other than pod number did not greatly influence seed yield (Table C.3.8). The long duration stress treatment (F123) significantly reduced all first order lateral seed components. Both pre-flowering treatments reduced the weight of main stem seed. Late applied water stress (F23, F13) resulted in heavier first order lateral seed than control or early applied stress.

TABLE C.3.7: Number of main stem pods at final harvest and first order lateral pods at harvest 4 and final harvest

	Main stem pods	First order lateral pods	
Harvest	Final	4	Final
Control	11.4 A	15.2 A	14.4 A
P	7.4 B		5.4 B
PF1	4.4 C	6.2 B	3.6 B
F123	6.3 BC		1.7 B
F23	8.6 B	7.4 B	4.3 B
F13	7.1 B	7.7 B	6.5 B

TABLE C.3.8: Number of seeds per pod and hundred seed weight at final harvest (g)

	Seeds per pod		Hundred seed weight	
	Main stem	1st order lateral	Main stem	1st order lateral
Control	3.7 A	2.7 A	41.7 A	28.8 BC
P	2.6 B	2.0 A	32.7 B	24.9 BC
PF1	3.2 AB	1.9 AB	30.9 B	22.9 C
F123	3.2 AB	0.7 C	44.2 A	10.6 D
F23	3.4 AB	1.8 B	48.2 A	33.9 AB
F13	3.6 AB	1.9 AB	44.3 A	39.1 A

C.3.3.4 Effect of Water Stress on Reproductive Growth

An interesting feature of Fig C.3.1 is that treatments which have undergone water stress immediately before a harvest (F123, F23 at H_3; F23, F13 at H_4) had higher seed yield than treatments which were well watered before harvest. This effect was evident at harvest 3 and 4 and was also reflected in seed size at the final harvest (Table C.3.8). However, there was a very large increase in seed yield of control plants between harvest 4 and final harvest. This accumulation of seed weight is remarkable in that no water was applied to the pods during this stage.

Figures C.3.2 - C.3.5 show the changes in dry weight between harvests of the various plant components. (It should be noted that each histogram in these figures represents the differences between harvests made before and after each growth stage). They show clearly the dominance of stem growth in control plants until the rapid growth of seed at the final stages (Fig C.3.2). The situation changes however in stressed plants. The growth of reproductive structures increases relative to vegetative growth of the same plant and relative to the reproductive growth of well watered plants. Treatment F23 (Fig C.3.5) shows however, that stimulation of pod growth is short so that the overall effect is not great. This additional reproductive growth occurs at the same time as increased leaf senescence and reduced stem growth compared with watered plants. Stressed plants lost more pod dry weight than control plants. Treatment PF1 (Fig C.3.3) clearly illustrates the long term effect of a long period of stress early in growth on the growth of all components at later stages.

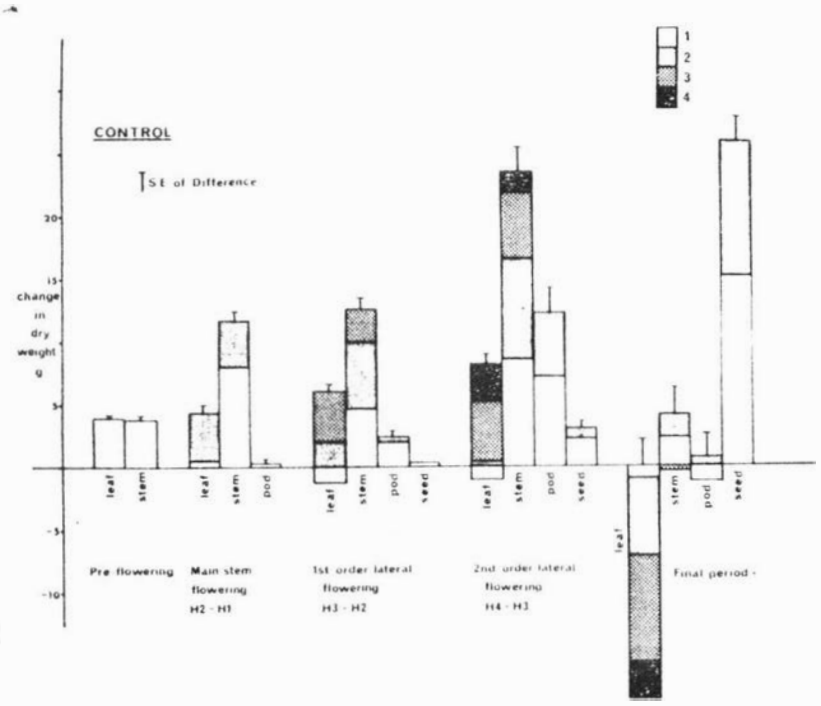

Fig. C.3.2 Changes in dry weight of components between harvests for control plants. Key for Figs. C.3.2 - C.3.5: 1-main stem; 2-1st order lateral; 3-2nd order lateral; 4-3rd order lateral.

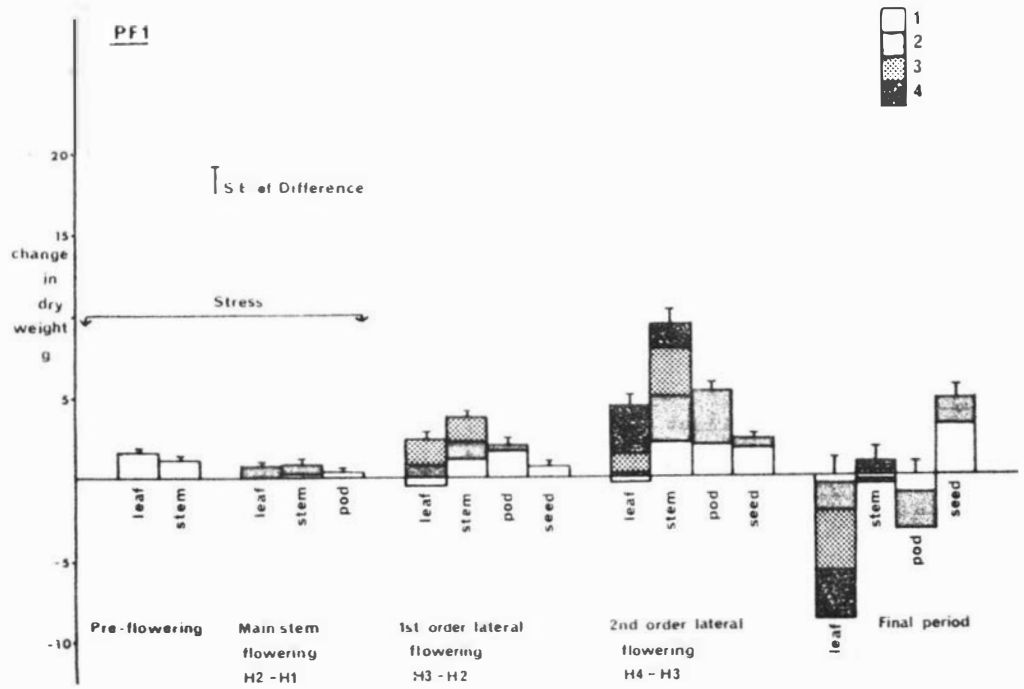

Fig. C.3.3 Changes in dry weight of components between harvests for treatment PF1 (water stress imposed from floral initiation until end of main stem flowering).

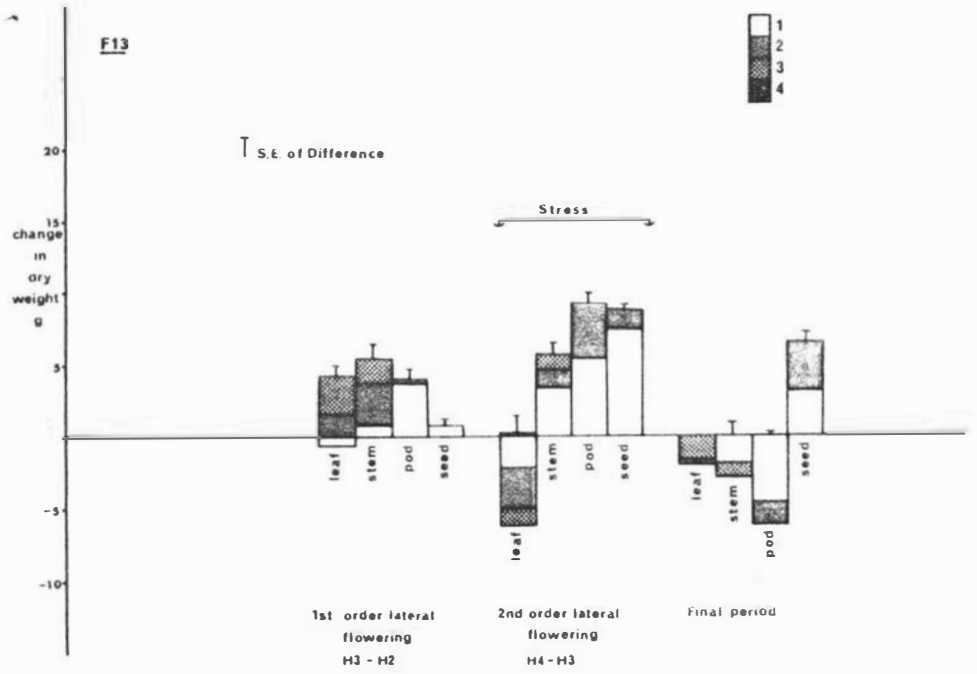

Fig. C.3.4 Changes in dry weight of components between harvests for treatment F13 (water stress imposed during main stem and second order lateral flowering.

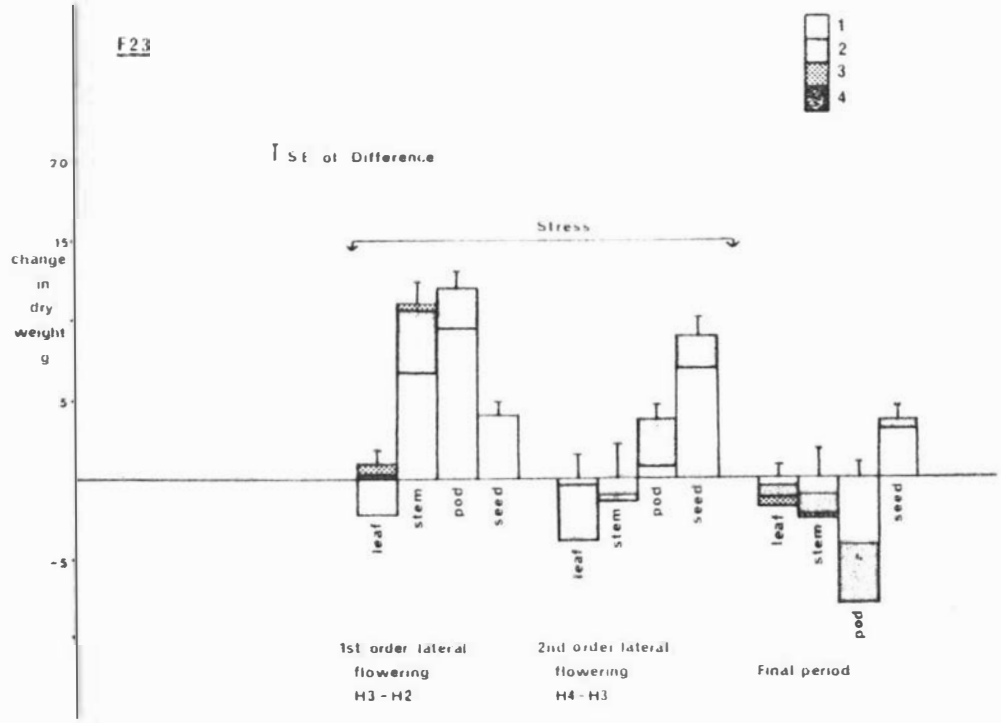

Fig C.3.5 Changes in dry weight of components between harvests for treatment F23 (water stress imposed during first and second order lateral flowering).

C.3.3.5 Source of Nitrogen for Seed Growth

To obtain information on the source of nitrogen accumulated rapidly by the seed, nitrogen budgets were constructed for the final growth period between harvests 3 and 4 (Table C.3.9) and for the maturity period between harvest 4 and final harvest when no water was applied to any of the pots but when seed growth was rapid in control plants (Table C.3.10). As senesced leaf could not be collected from individual plants, loss of nitrogen in fallen leaf was estimated. The concentration of nitrogen in the leaf litter was 1.8% (± 0.3%). To estimate the weight of senesced leaf, leaf weight at harvest 4 less a 50% loss in dry weight was used (Hocking and Pate 1978 measured a loss of 40% in dry weight of senescing *L. albus* leaves).

Plants subject to water stress during second order lateral flowering (F23, F13) accumulated more seed nitrogen (Table C.3.9) than did well watered plants. Non-seed accumulation in stressed plants was low and most of this accumulation was in pods as most vegetative parts were losing nitrogen. Plants stressed just before F23 were utilising more nitrogen from stems and pods than F13 plants which had previously been watered. Presumably this was because F23 plants had little leaf nitrogen to draw on due to earlier senescence and lack of leaf growth (Fig. C.3.4). In contrast, nitrogen accumulation in vegetative growth for control was high especially in upper order lateral leaves and lower order lateral stems. Accumulation of seed nitrogen in PF1 plants was similar to control but, due to low accumulation in non-seed components, net total accumulation was relatively low. The third order lateral leaf and stem were the only non-seed parts to accumulate a similar amount of nitrogen to control.

During the final stage (Table C.3.10), seed nitrogen accumulated rapidly in control with less accumulated in other plants. Pods supplied some of the nitrogen for seed growth, although, for control and PF1, leaves were the main source. More nitrogen accumulated

in the seed of control than could be accounted for by translocation. As control plants were actively fixing nitrogen at the beginning of the final stage (Table C.3.9) most of this extra nitrogen would probably have been fixed before pots completely dried out. At the mean rate of nitrogen estimated in Table C.3.9 the required amount of nitrogen could have been fixed in 7 days.

TABLE C.3.9: Estimated increase or decrease of nitrogen in plant parts, loss of nitrogen in senescing leaf and total net nitrogen accumulation rate during second order lateral flowering (mg). Levels of significance from t-tests on the means at each harvest (where applicable).

	Control	PF1	F23	F13
Roots and nodules	96**	88**	0	-18 NS
Main stems	41**	2 NS	-56 ***	2 NS
1st order lateral stems	109***	9 NS	-75 **	-6 NS
2nd order lateral stems	103***	32 NS	0	22 NS
3rd order lateral stems	59	35	0	1
Main stem leaves	-26	-9	0	-38
1st order lateral leaves	-4	-5	-132	-88
2nd order lateral leaves	237	44	19	-78
3rd order lateral leaves	182	142	0	12
Main stem pods	177***	13 NS	-40 NS	144***
1st order lateral pods	134***	53 ***	83 **	96***
Main stem seed	86***	65 **	371 ***	377***
1st order lateral seed	41	26	91	48
Estimated loss in senesced leaf	-18	-7	-63	-122
Increase in seed nitrogen	127	91	462	425
Increase in non-seed nitrogen	1138	418	102	277
Decrease in non-seed nitrogen	-48	-21	-366	-264
Net accumulation	1217	488	198	438
Net accumulation rate (mg/day)	76	23	9	13

TABLE C.3.10: Estimated translocation of nitrogen between plant parts for the period between harvest 4 and final harvest (mg). Levels of significance from t-tests on the absolute values at each harvest (where applicable).

	Control	PF1	F23	F13
Estimated increases				
Main stem seed	978 **	110 NS	252 *	268 ***
1st order lateral seed	721 ***	103 **	81 *	240 **
Total increase	1699	213	333	508
Estimated decreases				
Main stem leaves	48	14	8	39
1st order lateral leaves	213	41	11	0
2nd order lateral leaves	409	108	14	47
3rd order lateral leaves	152	90	0	9
Main stem	0	0	35*	29**
1st order lateral stem	45 NS	18 NS	45*	14*
2nd order lateral stems	17 NS	7 NS	4 NS	42**
3rd order lateral stems	8	0	0	1
Main stem pods	189***	46***	202***	203***
1st order lateral pods	80*	43**	151***	92***
Roots and nodules	0	11	0	13
Total decrease	1161	378	470	489
Balance	538	-165	-137	-19

C.3.4 DISCUSSION

C.3.4.1 Seed Yield

All stress treatments severely reduced seed yield. In contrast to the previous experiment, early stress had a more severe effect than late stress of similar duration. This is probably because of the longer duration of early stress in this experiment. Other reports (e.g. Salter and Drew,1965; Stoker, 1975) record little effect from preflowering irrigation in grain legumes. These were mainly field trials however, in which an adequate stress early in growth is often difficult to obtain. Runge and Odell (1960) and Sionit and Kramer (1977) both report loss of yield after pre-flowering water stress in soybeans. The effect of the long duration of pre-flowering water stress could be due to the prevention of development of floral primordia as described by Gates (1968) and would explain why early stressed plants had few flowers.

Despite the longer duration of stress during flowering, seed yield was not greatly different than that found in the previous experiment. Also, the differences in the number of pods between stress treatments were not significant in this experiment. The main reason for both effects would be the overall effect of flower and pod abscission which is non-reversible and occurs early in the water stress period so that it is not greatly affected by duration of stress. Abscission regulates the number of pods to a level that can be sustained under existing conditions (Adjei-Twum and Splittstoesser, 1976).

The reason for this abscission is not clear. Addicott and Lynch (1955) have suggested that shortage of carbohydrate or nitrogen could be important. Greenwood *et al.* (1975) working with *L. angustifolius* suggested that pod abscission was caused by the growth of lateral branches competing with the developing flowers

and pods for assimilate. However, results from this experiment show that lateral branches do not grow rapidly during water stress. Adequate assimilate would then be available for reproductive development, as shown by the relatively high rate of seed growth during water stress. Abscisic acid (Porter, 1977) or ethylene (McMichael *et al.*, 1973) have been implicated in the abscission of *L. luteus* pods and cotton leaves respectively and may be involved directly or indirectly in this situation. (See Section A.3.3).

The effect of the large loss of pods was that other components of seed yield did not alter greatly. However, changes in first order lateral seeds per pod and first order lateral seed weight contributed significantly to the seed yield of F123 being lower than that of F13 and F23.

Because the lupin plant is indeterminate, it should have the capacity to recover from initial stress when later growth periods are favourable by producing pods on higher order laterals as noted for *L. angustifolius* by Biddiscombe (1975) and for soybeans by Shaw and Laing (1966). Second order lateral branches fully recovered the capacity in vegetative growth, but pod development seemed to be very sensitive to previous stress so that seed yield did not recover. This effect can be a long term one as illustrated by the severe reduction in first order lateral pods of the pre-flowering treatment (P) between harvest 3 and 4, so readjustment from an early stress could cause instability in pod number. A similar effect was noted in the previous experiment.

The treatments well watered during late growth lost a significant number of seeds per first order lateral pod during the period between H4 and final harvest but the late stressed treatments did not, as their number of seeds per pod was already low. The degree of adjustment was greater for first order lateral pods than for main stem pods. Greenwood *et al.* (1975) found similar patterns of aborted seed sites in field-grown *L. angustifolius*.

This is consistent with the adjustment of first order lateral pod numbers already noted with well-watered plants in this and the previous experiment and indicates a limitation of some plants to fill all potential seed sites when high pod numbers are retained, even under favourable conditions.

C.3.4.2 Effect of Water Stress on Assimilate Distribution

The data support the hypothesis that reproductive growth is in some way protected from the effects of water stress compared with vegetative meristems which Gates (1968) states are sensitive to water deficit. The rapid reduction in leaf area caused by leaf senescence would reduce the total demand for water, enabling some available water to be conserved for limited growth. Within this constraint, the reproductive tissues seem to compete effectively for available assimilate. As seeds are actively excluding water from their tissues during their development (Leopold and Kriedemann, 1975), they should be able to resist the effects of drought water deficits in the plant. Hsiao and Acevedo (1974) also suggest that yield is less sensitive to water stress during the filling of a storage organ than during the vegetative phase. Seed development is more dependant on photosynthesis and translocation than on cell division which is highly sensitive to water stress so seed growth should be less sensitive to water stress than vegetative growth (Boyer and McPherson, 1975). Weber (1968) suggests, that under mild water stress, vegetative growth ceases but photosynthesis can continue so that an apparent diversion of assimilate to reproductive tissues can occur. Because pod as well as seed growth was stimulated in this experiment diversion probably occurred. Although current photosynthesis and nitrogen fixation will fall during water deficits, the pool of available assimilate will be supplemented by mobilisation from senescing leaves (Hocking and Pate, 1978). The increased harvest index of water stressed plants and the growth data presented, all indicate a major diversion of assimilate from vegetative to reproductive structures.

Most of the remobilised nitrogen for seed growth seems to come from the leaf, pods being a second, but important source. In control plants over the main seed growth phase, leaves supplied 47% and pods 15% of the seed requirement for nitrogen, approximately 33% of the seed nitrogen coming directly from fixation. Pate *et al.* (1977) estimated that *L. albus* pods supplied 16% of the seed requirements Pate and Herridge (1978) however found that 28% of seed nitrogen came from pods and a similar amount from current fixation.

In the late stressed treatments, F23 and F13, leaves supplied less nitrogen to the seed over the same period (21% and 32% respectively) than in control plants but pods (44% and 32%) and stems (16% and 9%) were relatively more important. However, nitrogen in pods and stems decreased significantly only after a period of stress had already been applied. Therefore they probably supply, in part, nitrogen already transferred to them from the accelerated senescence of leaf during the earlier stress. Thus, even in stressed plants, leaves are probably the main suppliers of reserve nitrogen to the seed. Current fixation of nitrogen used directly for seed growth was probably low in stressed plants although, for F13, the proportion of seed nitrogen requirements (27%) is similar to that estimated for control seed. In early stressed plants (PF1), mobilisation of nitrogen from leaf and pod was sufficient to supply all seed nitrogen. Thus the early stress, by reducing seed number but allowing regrowth of upper order leaf and stem resulted in an imbalance of nitrogen supply and demand. The apparent nitrogen surplus however, was not reflected in increased seed size or nitrogen percentage. Adequate water supply after a drought stress has been applied early in growth may therefore not be beneficial due to reduced seed yield potential and the diversion of growth into vegetative structures. Nitrogen reserves thus formed may not be able to be utilised in a normal growing season.

However, yield potential and nitrogen reserves to supply seed requirements usually seem to develop in reasonable balance. The main effect of water stress is to reduce yield potential by affecting pod numbers and the nitrogen reserves required to ensure high protein levels in the seed (Sinclair and de Wit 1975). Thus the ideal environment would appear to be one which supplies adequate moisture for as long as possible but with a late period of dry weather to enable seed maturity to be completed before the land is required for other purposes. The indeterminate growth habit is useful to ensure that the whole period of favourable weather can be efficiently utilised but, at least in the slowly developing *L. albus* cultivars such as Ultra, the potential for recovery in seed yield after periods of stress is unlikely to be important in the time period usually available in a normal season.

Maintenance of a good moisture supply for as long as possible would seem to be essential for maximum seed yield. This can be done by irrigation which is not always possible or economic. Early spring sowing or, on free draining soils, autumn sowing, would therefore seem to be required to ensure a reasonable period of reliable moisture conditions.

C.4. EFFECT OF HIGH TEMPERATURE UNDER CONDITIONS OF ADEQUATE AND RESTRICTED WATER SUPPLY*

C.4.1. INTRODUCTION

Response of *Lupinus albus* to restricted water supply over several developmental phases and two humidity levels had been studied previously. These experiments were conducted under a temperature regime of 18°C day and 13°C night which generally represents the temperature in many parts of New Zealand during late spring. In some districts however, especially eastern districts such as Canterbury, periods of high temperatures, often associated with dry soil conditions, are experienced for periods of varying lengths of time. Some workers have reported lower seed yield of lupin at high temperatures (Perry, 1975; Corbin, 1978) caused mainly by excessive flower or pod abscission. Usually this effect occurred when soils were dry but it was not clear whether water stress was a factor. These reports however have referred to *L. angustifolius*. Rahman and Gladstones (1973) suggest that *L. albus* has adaptability to a wider temperature range.

It is also important to know when deciding on suitable areas for lupins if hot or cool summer conditions are desirable. Some areas such as the Manawatu have wide fluctuations in temperatures within and between seasons and it is desirable to know the possible effect of this.

For all these reasons, an experiment was designed to gain some information on the response of *L. albus* to short periods of high temperatures with either adequate or restricted water supply.

* Accepted for publication in N.Z. Journal of Agricultural Research 22. 1979 (In Press)

C.4.2 MATERIALS AND METHODS

Plants of *Lupinus albus* L. cv. Ultra were grown as previously described (Section C.2.2). Seeds were sown on 30 September 1976 and emerged seedlings were transferred to a controlled environment room at the Plant Physiology Division, DSIR, 11 days later. Plants were grown at 18°C day and 13°C night with a 14 hour photoperiod at an average of 153 Wm^{-2} PAR at plant container height. A constant 4 mb vapour pressure deficit (vpd) was maintained. Conditions therefore were comparable with those in previous experiments. High temperature treatments were applied by moving the required plants to another room which was run at 28°C day and 20°C night. Other conditions were maintained at the same level as in the cooler room except that, to maintain a constant 4 mb vpd, the relative humidity was changed to 89% day and 82% night.

The treatments were: high temperatures from main stem floral initiation to beginning of main stem flowering (PF), duration of main stem flowering (F1) and duration of first order lateral flowering (F2). Within each of these, plants were either given adequate water (W) or restricted watering (D). The restricted watering regime was to be the same as in previous experiments i.e. maintenance of 80% leaf relative water content (RWC) (Baars, 1968) near the end of the photoperiod with a watering immediately after measurements were taken. However, when plants were experiencing high temperature, additional water had to be provided early in the photoperiod in order to maintain the required level of stress. Control plants were adequately watered and remained in the 18/13°C temperature regime. Plants were harvested at the end of main stem and first order lateral flowering with a final harvest at seed maturity. Harvesting methods were the same as previously described (Section C.2.2).

C.4.3 RESULTS

Growth of vegetative organs (including roots and nodules) was depressed by water stress compared with control plants (Table C.4.1) but reproductive parts (including pods) were heavier when water stress was applied after flowering. With adequate water, reproductive growth was stimulated compared to control by high temperature treatments imposed after flowering began. The effect of high temperature on vegetative growth was variable. Compared with control plants, the weight of PFW plants was depressed; F1W plants were not significantly affected; and there was a tendency for F2W plants to have a higher weight of vegetative tissue. If the shorter growth periods under high temperatures (Table C.4.2) are taken into account, F1W plants and F2W plants had higher growth rates than control plants. (e.g. Table C.4.3). Growth returned to control levels on return to the cool treatment conditions (see F1W Table C.4.3) and there was some compensation in vegetative growth for previous water stress as shown by PFD treatment values.

Flower numbers were reduced mainly by water stress in the preflowering period (PFD) (Table C.4.4). Water stress during flowering (F1D) reduced flower numbers slightly as did high temperatures in the preflowering period (PFW).

The early, well-watered treatments, PFW and F1W, significantly reduced total seed yield below that of control although F2W did not (Table C.4.5), indicating that high temperatures alone early in growth can affect seed yield. As expected, water stress reduced total seed yield levels although not significantly for F2D. First order lateral seed yield was significantly reduced by all treatments except F2W. Main stem seed yield was lower in the preflowering treatments and when water stress was applied during flowering (F1D).

TABLE C.4.1: Dry weight (g) of the total plant, vegetative and reproductive tissues at the end of main stem flowering (Harvest 1) and end of 1st order lateral flowering (Harvest 2).

	Harvest 1			Harvest 2		
	Vegeta - tive	Reprod- uctive	Total	Vegeta- tive	Reprod- uctive	Total
Control	29.4 A	0.3 B	29.7 A	48.3 AB	3.1 C	51.4 B
PFD	10.3 D	0.2 B	10.5 D	22.9 D	2.1 C	25.0 C
PFW	20.1 BC	0.2 B	20.3 BC	27.4 D	1.5 C	28.9 C
F1D	15.5 CD	1.2 A	16.7 CD	24.9 D	9.0 A	33.9 C
F1W	24.5 AB	0.8 A	25.3 AB	41.7 BC	8.4 A	50.1 BC
F2D				31.6 CD	5.2 B	36.8 CD
F2W				56.9 A	10.7 A	67.7 A

Means with letters in common are not significantly ($P<0.01$) different.
Comparisons can be made within columns only.

TABLE C.4.2: Mean duration of growth periods (days)

	Preflowering	Main stem flowering	1st order lateral flowering
Control	56	19	19
PFD	49	23	22
PFW	42	16	22
F1D		14	22
F1W		11	20
F2D			10
F2W			10

TABLE C.4.3: Relative growth rates (g/100g/day) during 1st order lateral flowering (between harvests 1 and 2)

	Vegetative	Reproductive	Total
Control	2.6	12.2	2.8
PFD	3.6	10.6	3.9
PFW	1.4	9.1	1.6
F1D	2.1	9.1	3.2
F1W	2.6	11.7	3.4
F2D	0.7	28.5	2.1
F2W	6.6	35.7	8.3

TABLE C.4.4: Number of flowers

	Main stem	1st order lateral
Control	44 A	56 A
PFD	22 C	23 BC
PFW	35 B	45 A
F1D	35 B	13 C
F1W	42 AB	43 AB
F2D	42 AB	37 AB
F2W	41 AB	45 A

TABLE C.4.5: Weight of seed per plant (g)

Harvest	Main stem		1st order lateral	Total
	End 1st lateral flowering	Final	Final	Final
Control	0.4 B	17.7 A	11.6 AB	29.3 A
PFD	0.3 B	4.3 C	4.7 C	9.0 D
PFW	0.2 B	9.6 BC	5.3 C	14.9 CD
F1D	1.6 A	9.8 BC	2.0 D	11.8 D
F1W	1.4 A	14.2 AB	6.2 BC	20.4 BC
F2D	0.5 B	14.6 AB	9.7 BC	24.0 AB
F2W	1.4 A	16.9 A	17.0 A	33.9 A

TABLE C.4.6: Number of pods per plant at final harvest

	Main stem	1st order lateral
Control	11.4 AB	14.4 A
PFD	5.4 D	7.1 CD
PFW	8.3 BCD	9.6 ABC
F1D	8.0 CD	2.6 D
F1W	10.6 ABC	8.8 ABC
F2D	9.3 BC	8.1 BCD
F2W	14.1 A	13.9 AB

As in previous experiments, pod number was the main determinant of yield. No significant reduction in pod numbers could be attributed to high temperatures alone (Table C.4.6), although there was a tendency for fewer pods for some treatments (PFW and F1W). Water stress significantly reduced pod number compared with the control treatment except for main stem pods of F2D plants. Generally, the pod number of water stressed treatments were not significantly lower than that of well watered treatments although there was a consistent trend for them to be lower. Number of seeds per pod was affected more than was noted in previous experiments (Table C.4.7). Preflowering treatments reduced numbers of seeds in main stem and first order lateral pods with the latter also being affected by main stem flowering treatments (F1D and F1W). Hundred seed weight was variable and no clear patterns emerged.

TABLE C.4.7: Number of seeds per pod at final harvest

	Main stem	1st order lateral
Harvest		
Control	3.7 A	2.7 AB
PFD	2.0 C	2.0 BC
PFW	2.7 BC	1.8 BC
F1D	3.6 A	1.3 C
F1W	3.2 AB	1.7 BC
F2D	3.9 A	3.3 A
F2W	3.8 A	3.5 A

C.4.4 DISCUSSION

This experiment indicates that *L. albus* is sensitive to the level of temperature imposed at various times throughout the growth period. Trends in the well watered treatments would indicate that the plant growth is adversely affected by high temperature during the preflowering period but as the plant develops, it is less affected and at later stages, growth rate may be stimulated. The plants were visibly affected at the preflowering stage with smaller, distorted leaves and smaller stems at the start of main stem flowering. The more rapid development of the plant at higher temperatures is important for spring-sown crops where the onset of dry conditions limits growth soon after sowing.

The expected reduction in pod number and consequent loss of yield due to high temperatures alone did not occur. The general trend for lower pod numbers in earlier treatments seemed to be related more to the overall effect on plant growth than a direct effect on abscission. This may have been because of the temperatures used in this study were not high enough, although Corbin (1978) states that above 25^{o}C maximum daily temperature, seed set will be reduced. In the field, high temperatures are often associated with an increase in vapour pressur deficit and even if vapour pressure deficit is held constant, water use by well watered plants increases as temperature increases (Forde *et al.*, 1977). Also, where high temperatures have been reported to cause pod loss, soil moisture was probably also low. The effect of high temperatures may be to aggravate any soil moisture deficit situation which may exist i.e. high temperatures act through an increase in plant water stress due to increased water use by plants.

The lack of significance between well watered and water stressed treatment plants could have resulted from the difficulty of maintaining the required stress levels at the high temperatures. The additional water supplied to the stress treatments possibly resulted in a shorter period under stress. Most water stressed treatments had significantly lower pod numbers and seed yield than control.

The most interesting feature of the seed weight data is that plants at high temperature and with adequate water had higher seed weights than control plants. A similar trend in seeds of water stressed plants was noted in this and previous experiments. This effect has been noted in peas by Williams and Marinos (1977) who showed that an increase in pod temperature increased the transfer of ^{14}C to pods so the effect of increased growth rate of seeds is probably due to greater assimilate availability to the seed. In the case of well watered plants at high temperature, the increased assimilate could be the result of greater photosynthetic activity perhaps combined with greater sink activity by the seed. Under water stress, increased assimilate supply could result from remobilisation of reserve assimilate and reduced competition from vegetative meristems (Section C.3). Unlike water stressed plants however, vegetative growth rate of well watered plants at high temperature is not reduced and the long term growth potential is maintained or even increased.

In previous experiments, water stress treatments had an adverse effect on pod numbers of subsequent stem sequences. This effect is apparent in this experiment but in addition, a consistent effect on the number of seeds per pod has been noted. For example, F1D and control plants had main stem pod seed numbers similar to control plants but F1D had fewer first order lateral pod seeds. Preflowering water stress significantly reduced main stem seeds per pod compared with control plants. A similar, although less significant effect of temperature was shown by the well watered treatments. This could indicate an adverse effect

of high temperature on seed primordia (Ormrod *et al.*, 1970). Stanfield *et al.*, (1966) found similar effects to these with peas grown under high temperatures. Pod number, seed number per pod and vine growth were affected by day temperatures of 29°C and 32°C.

Karr *et al.*, (1959) and Lambert and Linck (1958) found that the thermal sensitive period of peas was 6-10 days after full bloom. In this experiment however, the most sensitive period appeared to be the preflowering phase and interference with development at this stage may have reduced yield. However, Karr *et al.*, (1959) also found that night temperatures were more important in determining yield than day temperatures. The 20°C night temperatures in this experiment may have been too low to have a significant effect. In New Zealand it would be unusual to have night temperatures consistently above 20°C.

As the duration of the growing season is limited, especially with spring sowings, the faster plant development at high temperatures and the stimulation of both vegetative and reproductive growth is highly desirable. Thus, air temperatures of about 28°C provided they occur after the commencement of flowering and in the presence of adequate moisture, should benefit seed production from *L. albus*.

SECTION D. TRANSLOCATION STUDY

D.1 TRANSLOCATION OF ^{14}C IN *LUPINUS ALBUS**

D.1.1 INTRODUCTION

Many workers have shown that the distribution of the products of photosynthesis within a grain legume is complex. Blomquist and Kust (1971) working with an indeterminate soybean cultivar showed that before pod fill, photosynthate moved to growing regions above the labelled leaf but once pods began to fill, translocation was mainly to pods below the labelled leaf. Stephenson and Wilson (1977) found the opposite direction of carbon movement in a determinate cultivar during pod fill and suggested that determinate and indeterminate plants may have different translocation patterns. The above authors and others (e.g., Nelson, 1963; Porter, 1966; Pate and Flinn 1973; Hume and Criswell, 1973; Wareing and Patrick, 1975) found direct vascular links between source and sink organs. However, the direction and distance of movement is dependent on the activity and position of the various sinks relative to the source leaf (Nelson, 1963). Stems can act as temporary storage organs for carbon (Hume and Criswell, 1973; Stephenson and Wilson, 1977) and nitrogen (Minchin and Pate, 1973; Section C.2) which can be used later to supply the seed. The efficiency of remobilisation of early-fixed carbon to supply the seed in legumes can be low (Flinn and Pate, 1968; Pate and Flinn, 1973; Hume and Criswell, 1973) but in cereals it can be over 50% (Cock and Yoshida, 1972). However, as the seed develops it is increasingly fed directly by its subtending leaf so that the recovery of labelled carbon in seed increases as seed development proceeds (Hume and Criswell, 1973).

* Accepted for publication in N.Z. Journal of Agricultural Research 22 (In Press).

Pate *et al.*, (1974) showed that main stem pods of *L. albus* were supplied by both main stem leaves and those from the first order lateral branch with a definite relationship between specific pods and leaves. The study reported here aimed to investigate the pattern of translocation in *L. albus* including the contribution of higher order lateral branches to the photosynthate requirement of main stem components. Movement of early fixed carbon and its contribution to seed dry weight was also measured.

D.1.2 MATERIALS AND METHODS

Inoculated seeds of *Lupinus albus* L. cv. Ultra were sown on 20 November 1975 in planter bags (1.35 l volume) containing sterilised Manawatu fine sandy loam. The soil contained 20 g per bag of 30% potassic superphosphate (0-6-14 NPK). After establishment, plants were transferred to a glasshouse and watered as required. The glasshouse temperature was controlled within the range 15°C to 28°C. The glass was whitewashed to help maintain these conditions and the plants received natural photoperiods.

Individual, attached leaves were labelled by enclosing them within a small perspex leaf chamber (approximate volume 500 ml) and injecting a known quantity of $^{14}CO_2$ through a rubber diaphram. The chamber had a hinged lid with foam rubber around its edge to ensure the connecting petiole was undamaged. A small internal fan ensured rapid circulation of the gas inside the chamber. The leaf was exposed to $^{14}CO_2$ for 2 minutes after which time the chamber was flushed with air for 3 minutes. The extracted air was passed through a solution of sodium hydroxide and vented outside the glasshouse. Labelling took place in indirect sunlight between 10 a.m. and 4 p.m. In seven experiments, various groups of leaves on a number of positions on the plant were individually labelled at various stages during the growth of the plant. One to three subsequent harvests were made to determin sites of initial accumulation of label or to allow estimates of the remobilisation of tracer. Details of labelling sites and times to harvest are included in the results section.

In experiments 1-5 inclusive, each labelled leaf was exposed to $^{14}CO_2$ with an activity of 20μCi. A total of 80μCi of $^{14}CO_2$ was used to label the whole branch in experiments 6 and 7. For experiments 1-6, ten labelled plants were taken for each harvest. Unfortunately only three plants were available for labelling and harvest in experiment 7. Unlabelled plants were placed among labelled plants in the glasshouse and they were harvested and assayed for activity in the same manner as labelled plants. No significant levels of activity were detected in these unlabelled plants.

At each harvest, plants were dissected into leaf, stem, head (unexpanded leaves or flower head), pod and seed of each branch order as appropriate. Components were also separated depending on whether they were labelled, part of a labelled branch, part of a branch inserted directly or indirectly on to a labelled branch. For example, if three leaves on branch 1:1 in Fig A.3.1 were labelled, these leaves were separated from other leaves of that branch. All other components of branch 1:1 were kept apart from components of first order lateral stems 1:2 to 1:4 all of which were bulked together. Components of second order lateral branches 2:1 and 2:2 were bulked together but kept separate from other second order lateral branches which were bulked together.

Plant parts thus separated were dried at 80°C for 12 hours, weighed and stored for later analysis of ^{14}C activity. The assay used to measure ^{14}C was modified from that described by Shimshi (1969). A 50 mg ground sample was placed in the bottom of a 100 ml screw-topped jar. A vial containing 5 cc of a CO_2 absorbent containing 10% ethanolamine and 10% ethanol in water was also placed in the jar. Chromic acid (25 cc) was added to the sample and the lid firmly screwed on. The jars were placed in an oven at 45°C for approximately 3½ hours. After allowing to cool, the vial of CO_2 absorbent was removed from the jar and 0.5 ml of the absorbent was pipetted into 10 ml of scintillation cocktail (a mixture of toluene containing 0.05% w/v p-terphenyl, triton and

water in the ratio 20:10:3 (Laing and Christeller, 1976). The activity of the sample was determined using a Beckman L1700 liquid scintillation counter.

Comparisons between harvests for relevant components in experiments 1-3 were made using one-way analysis of variance.

D.1.3 RESULTS

Plants were similar to those grown under field conditions. Mean dry weight at labelling ranged from 3.7 to 50.1 g for shoots and 5.3 g to 60.3 g for whole plants.

In experiment 1, leaves 4, 9 and 14 from the base of the main stem were labelled during 4-8 January 1976. Plants were harvested 2 or 50 days after labelling or when they were approaching seed maturity as indicated by the senescence of most leaves (approximately 110 days from labelling).

The major sink for ^{14}C from labelled leaves in Experiment 1 was the main stem on which the leaves were inserted (Table D.1.1). It was also apparent that the younger, rapidly growing leaves above the upper labelled leaf were attracting more activity than the lower, older leaves which were presumably in the assimilate export phase of growth.

At later harvests, activity in first order lateral leaf and stem showed that assimilate was transferred from the main stem. At harvest 2, 5.9% of the original activity in the plant was in first order lateral tissues. Early fixed carbon contributed to the growth of pod and seed and this continued between the last two harvests. At the final harvest, 4.4% and 2.9% of the total activity at that harvest was found in the pod and seed respectively. However, the total counts at the final harvest were lower than at the early harvests and the percentage of the total counts at harvest 1 recovered in pods and seed at final harvest was 2.7% and 1.8% respectively.

TABLE D.1.1 Total activity in plant components from Experiment 1 (when leaves 4,9 and 14 from the base of the main stem labelled).
S.E. of the mean in parenthesis

	Activity in component (d.p.m. x 10^{-4})			Significance of difference between harvests		
	H_1 (2 days)	H_2 (50 days)	Final	H_1-H_2	H_2-F	H_1-F
Main Stem (MS)						
Labelled (L) leaves	3140 (606)	2310 (266)	609(147)	NS	**	**
Leaves inserted below L leaves	77 (25)	9 (2)		**		
Leaves inserted between L leaves	318 (52)	179 (29)	872 (242)	*	**	**
Leaves inserted above L leaves	1069 (150)	1428 (166)		NS		
Stem	6862 (629)	8969 (864)	5251 (478)	*	**	NS
Head	925 (198)					
Pod		128 (27)	358 (138)		NS	
Seed		32 (7)	215 (35)		***	
First Order Lateral						
Leaf		670 (70)	175 (29)		***	
Stem		249 (22)	185 (25)		NS	
Pod			67 (6)			
Seed			67 (6)			
Upper Foliage			59 (10)			
Roots	3103 (414)	2940 (313)		NS	NS	**
			1779 (197)			
Nodules	158 (60)	220 (48)				
TOTAL	15652	17144	9570			

Counts in the main stem increased between harvest 1 and 2 accompanied by a decline in labelled and lower unlabelled leaves. Also, first order lateral components not present at labelling were labelled at the second harvest. This indicates senescence of the lower main stem leaves and a transfer of assimilate from these leaves to main stem and first order lateral leaf and stem. Loss of total activity between harvest 2 and final harvest was high and was lost mainly from main stem leaf and stem. Of this loss, only 7.3% was recovered in seed and pods, mostly in main stem components.

Experiment 2 was carried out on 8-10 February, one month later than experiment 1. The main stem leaves subtending the three uppermost first order lateral branches (number 1:1, 1:2 and 1:3 in Fig. A.3.1) were labelled. Plants were harvested 2 days after labelling or when the plants approached maturity (approximately 75 days after labelling).

Results (Table D.1.2) show that labelled leaves were supplying assimilate to main stem components rather than the lateral branches they subtended. The main stem received most of the activity although main stem pods and seed were also important recipients (19% and 8% of the total activity at final harvest). Only 5% of the activity was found in first order lateral branches at the first harvest, most of which was in the stem.

Loss of total activity between harvests in experiment 2 was low. Final recovery of ^{14}C in seed was higher than in experiment 1 (Tables D.1.1 and D.1.2) probably because seed growth had commenced when labelling occurred in experiment 2 and the seed received ^{14}C directly from the fed leaves.

TABLE D.1.2: Total activity in plant components from Experiment 2 (leaves subtending the three uppermost 1st order lateral branches labelled). S.E. of the mean in parenthesis.

	Activity in organ (d.p.m. x 10^{-4})		Significance of difference between harvests
Harvest	Early (2 days)	Final	
Main Stem (MS)			
Labelled leaves	5163 (623)	517 (164)	**
Non-labelled leaves	165 (55)	82 (27)	NS
Stem	4162 (477)	7648 (917)	**
Pod	3433 (517)	2936 (320)	NS
Seed	863 (80)	1270 (318)	*
1st Order Lateral			
Labelled † Branches			
leaves	185 (25)	117 (21)	*
stem	501 (67)	1022 (220)	*
pod		70 (12)	
seed		78 (24)	
Non-labelled † Branches			
leaves	58 (6)	70 (21)	NS
stem	132 (58)	229 (75)	NS
pod		20 (5)	
seed		24 (9)	
2nd Order Lateral			
Labelled † Branches			
leaves		139 (51)	
stem		47 (5)	
Non-labelled † Branches			
leaf		22 (6)	
stem		7 (2)	
Roots	1836 (270)	1366 (67)	**
Nodules	55 (57)		
TOTAL	16906	15664	

† Labelled branches are those arising from the axils of labelled main stem leaves. Non-labelled branches are those arising from lower, non-labelled main stem leaf axils.

Experiment 3 commenced immediately after experiment 2. The top, middle and basal expanded leaves of the uppermost first order lateral branch (number 1:1, Fig. A.3.1) were labelled during 10-13 February and plants were harvested two days after labelling or near maturity (approximately 70 days after labelling).

The level of activity in main stem pods and seeds was again high (Table D.1.3) *viz.* 19% for pods and 10% for seeds at final harvest. This represented a percentage of the total activity similar to that in experiment 2. At the early harvests the percentage of activity in main stem pods plus seeds was also similar in experiments 2 and 3 (25% and 21% of total activity) so first order lateral leaves were supplying similar percentages to these main stem components and to upper main stem leaves. Between the two harvests in experiment 3, no significant change in the level of activity occurred in main stem components. First order lateral leaf did, however, lose ^{14}C. First order lateral pods and seed at final harvest contained the equivalent of only 13% of this loss.

Experiment 3 studied the distribution of ^{14}C from the whole first order lateral branch. Experiments 4 and 5 examined the distribution from the 4 lowest and uppermost leaves respectively of the top first order lateral branch. Labelling dates were 5-9 March for experiment 4 and 10-13 March for experiment 5. All plants were harvested two days after labelling.

Experiments 4 and 5 showed that upper and lower leaves tended to have different distribution patterns (Table D.1.4). Lower leaves of the first order lateral branch contributed proportionately more activity to main stem pods and seeds while upper leaves were more active in supplying ^{14}C to the stem, pods and seed of the same branch. Little upward movement occurred into second order lateral branches.

TABLE D.1.3: Total activity in plant components from Experiment 3 (top, middle and basal expanded leaves of the uppermost first order lateral branch labelled). S.E. of the mean in parenthesis

	Activity in organ (d.p.m. x 10^{-4})		Significance of difference between harvests
Harvest	Early (2 days)	Final	
Main Stem (MS)			
Leaf	54 (11)	44 (14)	NS
Stem	1534 (179)	1738 (335)	NS
Pod	1812 (322)	1256 (241)	NS
Seed	453 (137)	652 (150)	NS
1st Order Lateral			
Labelled† Branches			
Labelled† leaves	2932 (455)	400 (83)	***
Non-labelled† leaves	58 (9)	9 (3)	*
Stem	2065 (300)	1226 (480)	NS
Head	502 (143)		
Pod		213 (49)	
Seed		111 (34)	
Non-labelled Branches	236 (30)	115 (20)	
2nd Order Lateral			
Total foliage	240 (82)		
Labelled† Branches			
Leaf		189 (68)	
Stem		219 (45)	
Pod and seed		25 (10)	
Non-labelled Branches		34 (7)	
Roots	770 (154)	367 (73)	
Nodules	108 (20)		
TOTAL	10708	6645	

† Labelled first order lateral branches were those on which leaves were labelled. Within these branches leaves were divided into those which received the label (labelled) and those which did not (non-labelled). Labelled second order lateral branches were those that arose from the labelled first order lateral branch (see Fig. A.3.1.).

TABLE D.1.4 Total activity in plant components 2 days after labelling for Experiments 4-6 and the proportion of total activity in each component for Experiments 4-7. Upper and lower first order lateral leaves were labelled in Experiments 4 and 5 respectively. All leaves on second and third order lateral branches were labelled in Experiments 6 and 7 respectively. Due to the low number of plants (3) in Experiment 7, proportions only are presented for comparison with other treatments.

	Activity in component (d.p.m. x 10^{-4})			Proportion of total activity in each component (%)			
Experiment	4	5	6	4	5	6	7
Main Stem							
leaf	62 (13)	44 (11)	36 (7)	0.3	0.2	0.2	0.1
stem	2772 (364)	2386 (322)	2552 (294)	14.7	9.3	9.4	5.5
pod	2790 (792)	1170 (269)	506 (122)	14.8	4.4	1.7	0.9
seed	4838 (1123)	4593 (746)	949 (201)	25.7	17.9	3.3	1.4
1st Order Lateral							
Labelled Branches							
Labelled leaf	2962 (441)	2742 (319)		15.7	10.8	0.2	0.1
Non-labelled							
leaf	71 (12)	55 (11)	59 (11)	0.4	0.2		
stem	3119 (657)	5724 (998)	4266 (715)	16.5	22.4	15.7	12.3
pod	340 (100)	4539 (945)	5959 (686)	1.8	17.7	21.8	7.5
seed	127 (57)	2649 (722)	3930 (745)	0.8	10.3	14.4	6.7
Non-labelled Branches							
leaf	75 (14)	66 (17)	63 (13)	0.4	0.3	0.2	0.1
stem	203 (33)	183 (35)	153 (46)	1.1	0.8	0.6	0.5
pod	38 (10)	34 (8)	102 (18)	0.2	0.1	0.4	0.1
seed	13 (3)	11 (4)	32 (11)	0.07	0.04	0.1	0.05

continued over....

Table D.1.4 continued

	Activity in component (d.p.m. x 10^{-4})			Porportion of total activity in each component (%)			
Experiment	4	5	6	4	5	6	7
2nd Order Lateral							
Labelled Branches *							
leaf	98 (49)	73 (14)	4046 (470)	0.5	0.3	14.8	0.2
stem	120 (50)	117 (17)	2592 (573)	0.6	0.5	9.3	13.1
pod			857 (351)			3.0	16.9
seed			127 (86)			0.2	
Non-labelled Branches			166 (47)			0.4	0.2
Roots	801 (123)	861 (169)	550 (114)	4.3	3.5	2.1	2.0
Nodules	369 (58)	334 (74)	238 (63)	2.1	1.4	1.0	0.8
TOTAL	18798	25598	27250				

* For Experiments 4 and 5, labelled second order lateral branches arose from the labelled first order lateral branches. In Experiment 6 labelled second order lateral branches had leaves exposed to $^{14}CO_2$ and in Experiment 7 they subtended branches with exposed leaves.

Experiment 6 labelled all leaves on a second order lateral branch (number 2:1, Fig. A.3.1) during 13-18 March. All plants were harvested two days after labelling. The results (Table D.1.4) showed that this branch supplied more ^{14}C to first order lateral tissue than it retained. Only 16% of the activity which was translocated from the labelled leaf during the first 48 hours was retained in the tissues of its own branch. The equivalent figures for experiments 1-5 were 74, 73, 37, 25 and 57% respectively, indicating significant translocation from lateral branches into lower order branches. Of the activity translocated from the labelled leaf, 17% was recovered in main stem tissues and 3% in underground tissues so that the distribution was widespread.

Experiment 7 labelled all leaves on a third order lateral branch during 13-18 March and the plants were harvested two days later. No specific branch was taken as development of branches of this order was uneven and the most developed branch was selected. As only 3 plants were available no emphasis can be placed on the results of this experiment. However, trends apparent in earlier experiments are present in the results of this experiment. Percentages of activity in all components except third order lateral components are included in Table D.1.4 for comparative purposes. Of the total ^{14}C in the plant, 68% was present in the second and lower order components. Main stem components and underground organs were still receiving significant quantities of label. (7.9% and 2.8% of the total label in the plant).

Comparing experiments 4-7, main stem tissues received a lower proportion of the total activity as labelling progressed higher up the canopy. (Table D.1.4). Adjacent lower order branches were the main recipients of translocated activity. Pods and seed of the first order lateral branch received similar percentages of the total activity from upper leaves of its own order (experiment 5) and from leaves of the next highest order (experiment 6) a situation similar to that observed for main stem pods and seeds (experiments 2 and 3).

D.1.4 DISCUSSION

Generally, pods and seeds of an inflorescence are supplied with carbon from leaves within the same branch, especially the upper leaves, and from leaves of branches of the next higher order inserted on it. Thus, as reported for other species (e.g. soybeans - Stephenson and Wilson, 1977) pods and seed receive assimilate from leaves in close proximity to them. This trend was reported in *L. albus* by Pate *et al.* (1974) for main stem pods and this study shows a similar pattern of assimilate movement in first order lateral pods. This pattern might well occur because the pods are structurally close to both sets of leaves and linked to them by vascular tissue (Pate *et al.*, 1974). However, appreciable quantities of ^{14}C reach roots and main stem tissues from second and third order lateral branches so that transport can occur in significant quantities over relatively large distances past strong sinks. This is important because relatively large numbers of higher order branches can be present on lupin plants (Farrington and Greenwood, 1975).

The strong growth of main stem pods, seeds, stem and roots observed during the late phases of growth would be an important factor in attracting assimilate as growth rate is related to sink strength (Nelson, 1963). Measurement of ^{14}C in roots and main stem organs at this time may be underestimating the total carbon which would have reached the lower parts of the plant at this stage. These organs would have a high respiration rate and much of the carbon reaching them may be respired and not incorporated into dry matter. For example, Pate and Herridge (1978) have shown that root respiration can use about 40% of the carbon fixed by net photosynthesis during later growth and the percentage of carbon included in dry matter declines as a branch ages. The steady decline in the ^{14}C recovered in roots as experiments progressed could be due as much to increased respiration losses as increasing distance from the source leaf. The combined sink strength of rapid growth of pods and seeds and high root and stem respiration may be the

cause of the movement of carbon from the relatively distant upper canopy. This movement enables reproductive development to occur even if lower canopy leaves are shaded, diseased or senesced.

As reported by many workers (e.g. Nelson, 1963; Pate *et al.*, 1974; Wareing and Patrick, 1975), distribution of ^{14}C from a specific source leaf is dictated by position and strength of sink organs and by phyllotactic restrictions of connecting tissues. With lupin it appears that movement is generally downward towards the older, larger organs and is confined to branches connected directly to the source stem. Early in growth, stems are the main sinks but as reproductive structures increase in size they become more important sites of activity from labelled leaves but stems remain significant sites throughout growth.

Experiment 1 indicates that carbon fixed early in development does make some contribution to the dry matter of pods and seeds and much of this may be contributed early in the development of these organs. A low percentage of carbon is however incorporated into seed and pod dry matter as has also been reported for soybeans by Hume and Criswell (1973) and Stephenson and Wilson (1977) and for peas by Pate and Flinn (1973) and Minchin and Pate (1973). Of the carbon lost by leaf and stem in experiment 1, only an amount equivalent to 8% was recovered in the seed. However, recovery in seed of the original carbon assimilated (1.8%) is similar to recovery of carbon assimilated by field peas in mid vegetative growth reported by Pate and Flinn (1973) and lower than the 4-8% reported in soybeans by Hume and Criswell (1973). If this early fixed carbon is used for respiration, more current assimilate which would otherwise be used for this purpose can be directly utilised in seed production. Other indirect benefits may also accrue. For example, the use of remobilised carbon in root respiration would be important in maintaining root growth thus ensuring maximum drought resistance (Pate and Herridge, 1978) and high rates of nitrogen fixation up to final senescence (Section C.3). All remobilised carbon could therefore be useful in contributing to

seed production. Assimilate is mobilised from leaves more readily than stems, although some can be stored temporarily in the stem before being utilised (Minchin and Pate 1973, Sections C.2 and C.3).

Experiment 1 showed that lower main stem leaves lost ^{14}C earlier than upper leaves which resulted in increased activity in the stem; but by final harvest, all leaves had lost considerable ^{14}C and activity in the stem had returned to the level at harvest 1. This increase in activity in the main stem could be associated with translocation of amino acids which would account for the rise and subsequent fall of activity in the main stems of experiment 1 and for the apparent good mobility from the leaves. In experiment 2, activity in the main stem remained high at the final harvest. As the leaves labelled in this experiment were the upper main stem leaves which would have senesced later than those in experiment 1, there may have been insufficient time for the stored assimilate to be utilised before the harvest.

Farrington (1976) expressed concern at the possible competition between vegetative and reproductive growth. Section C.3 showed there was competition for nitrogen between reproductive and vegetative growth in *L. albus* , the balance of which depends on previous and present environmental conditions. Competition for carbon is apparent in this experiment. For example, in experiments 6 and 7, the main stem contained more label than either the seed or pod. Stems were major sites for activity in all experiments. Greenwood *et al.* (1975) were concerned that the lateral branches of *L. angustifolius* were competing with the inflorescence for carbon. This study would indicate that, at least in *L. albus*, the main competition is from stems on the same or lower order branches. The major diversion of carbon to stems instead of reproductive structures, even when the latter are rapidly growing, must be of concern when considering the efficiency of *L. albus* for seed production. It has been shown (Hocking and Pate, 1978; Section C.3) that nitrogen reserves are valuable contributors to

seed growth but it is unlikely that the same is true for carbon (Pate and Flinn, 1973).

Because of the competition between upper canopy branches and the lower parts of the plant, development of the upper canopy is likely to be easily affected by adverse conditions which limit the supply of photosynthate. Even mild water stress would therefore be expected to severely restrict or stop continued growth. This trend is apparent in the results of experiments in Section C and was commented on by Farrington (1976) for *L. angustifolius* . Provided the plant is well developed, this trend is useful in checking the indeterminate growth of lupin when it is required to mature seed for harvest. At early stages of growth however, it may limit seed yield potential by preventing the plant developing sufficiently to produce the required number of pods. The further developed the plant, however, the more sensitive will its development be to adverse conditions due to the increasing commitment to supplying assimilate to lower plant parts.

SECTION E. CONCLUDING DISCUSSION

E.1 Basic Considerations

It is important to bear in mind that the lupin seed crop is primarily concerned with protein production whereas for many other crops, including many legumes, other criteria are important and it may be total yield (process peas) oil yield (soybeans) or a balance of nutrients (food grains) which is required. Thus our concern in assessing lupin for stock feed must be to maximise the seed protein yield rather than merely aim for maximum seed yield, although obviously this is important. To achieve this, it may also be necessary to reconsider the crop ideotype and management normally associated with cropping in the North Island of New Zealand.

Knowledge of nitrogen utilisation in the plant is obviously desirable in a crop where protein is such an important component of yield. It was shown that most seed nitrogen was accumulated when nitrogen fixation was allowed to continue at its maximum rate for as long as possible and when this nitrogen was transferred efficiently to the seed. Experiments in this study indicate that the indeterminate growth habit, which allows for nitrogen fixation to occur over most of the available growing season, can have an advantage for nitrogen accumulation over more determinate crops which may not be able to fully utilise the environmental resources available. That is, the initiation of the normal "self destruction" mechanism changes from largely "plant control" to "environmental control".

The nitrogen initially fixed becomes involved in vegetative growth which influences the supply of nitrogen to the seed in a number of ways. (1) The priority was for nitrogen to be used for leaf and stem growth which provided photosynthate for increasing rates of growth and nitrogen fixation thus ensuring an extended and rapid nitrogen accumulation period if the environment permitted it. The high rate of nitrogen fixation thus achieved should delay the onset of the

"self destruction" phase by supplying sufficient nitrogen for the relatively slow reproductive growth which seems to be a feature of rapidly growing lupins (Sinclair and de Wit, 1976; Eaglesham *et al.*, 1978). (2) Extended vegetative growth provided the framework for a high seed yield. There were strong indications that the number of potential seed sites exceeded the amount of assimilate available to fill them, supporting the hypothesis that assimilate is the basic limiting factor in legume seed production. (3) Most of the nitrogen involved in the vegetative structure became available for seed production so that the total nitrogen fixed in the season influenced yield and not just that fixed and translocated directly to the seed.

Lupins, besides having an indeterminate growth habit seemed to have two other valuable characteristics. First, the upright growth habit with its spreading branch pattern is well suited to efficiently displaying a large leaf area which would be important if a large vegetative structure is desirable. Prostrate legumes such as peas, may be less efficient and a suggestion that self-shading was a factor was recorded in Section B.4.3. Second, lupins may also be able to utilise their large nitrogen reserves a little more efficiently than some crops (Section B.4.3). The relatively high protein yield and seed protein concentration of lupin thus may be related to its growth habit and efficient utilisation of the nitrogen reserves created.

If the available growing season is being fully exploited by the plant and the nitrogen produced during the season is being efficiently used for seed, the problem of further increasing yield will be difficult to solve. Increasing seed yield on the same structure would not be advantageous if the total nitrogen pool of the plant is not increased. One solution would be to increase the rate of nitrogen fixation. However, in Section B.4.3 there did not appear to be any important difference between species in the peak rate of nitrogen uptake. Nitrogen fixation is probably largely determined by assimilate availability which is likely to be limited more by environmental constraints than plant factors. Some improvement may be obtained by selecting for *Rhizobium* strains or

nodule systems which can utilise available assimilate more efficiently but any signficant progress is likely to be slow.

Plants which divert more available assimilate to the nodules may be able to increase protein yield if the assimilate is not divered away from other important areas. In *L. albus*, it may be preferable to divert some assimilate away from lower order stem production which is not very important as a nitrogen reserve (Section C.3) but which (at least in Ultra) continues growing for an extended time and which seemes to be excessive. Cultivars which appear to do this are being tested at present.

In *L. albus* and *L. luteus*, early development is slightly slower than *L. angustifolius* and selection for more rapid early growth may be advantageous to allow a longer peiod of peak growth and nitrogen fixation within a set growth period. *L. albus* in particular is slow to develop lateral branches and selection for earlier branching may be advantageous. Although, in Section B.3, early defoliation did not increase seed yield due to the loss of main stem yield, it showed that early diversion of assimilate to lateral branches can speed up development, especially leaf area, which may increase total assimilate (and thus nitrogen) produced in a season.

However, none of these possibilities are likely to greatly increase the nitrogen fixation rate which probably can only be boosted to a large extent by relatively expensive methods such as by increasing CO_2 concentration (Gibson, 1974).

It was shown in the controlled climate studies that water stress tended to control the balance between vegetative and reproductive growth. Relatively mild stress levels caused vegetative growth to stop, apparently releasing assimilate for an increased rate of reproductive growth. This was largely reversible, especially if the duration of stress was short. Leaf growth in particular was able to resume when the stress was removed and "compensatory growth" enabled leaf not produced during the stress to be grown. This trend is important to ensure continuation of assimilate

supply, including the pool of nitrogen, for later seed growth. Stem growth however, recovered less rapidly which is perhaps desirable if stem growth is an important competing sink with reproductive growth (Section D.). As the plant ages however, loss of leaf by senescence when water stress is applied can be large and rapid, making it very difficult to completely recover vegetative growth. At this stage, even mild water stress, which may occur under high temperatures and low humidity even with adequate soil moisture, may be sufficient to ensure reproductive growth dominates assimilate demand.

Although vegetative growth has the capacity to recover quite quickly from water stress, reproductive growth potential recovers more slowly due to the great sensitivity of flowers and young pods to the effects of water stress which may last even after water has been reapplied. As the loss of pods is irreversible, several new stem orders may have to be produced before reproductive potential is restored. In species such as *L. albus* and *L. luteus*, where lateral branch development is slow, recovery in a normal growth period is unlikely and full potential would never be realised anyway due to the irreversible pod loss. *L. angustifolius* has more rapid lateral branch order development and more rapid recovery is possible (Biddiscombe, 1975). Thus, water stress during growth must be slight and of short duration if seed yield potential is not to be impaired. Lupins are already adapted to minimise the effect of short term drought by having a deeply penetrating taproot system which enables water at depth in the soil to be utilised provided the soil structure enables root penetration to occur (Gladstones, 1970). Herridge and Pate (1978) point out however, that this advantage may have a significant cost in terms of the photosynthate requirement by the root.

Thus the greatest practical potential for ensuring maximum seed protein production seems to lie in minimising the environmental constraints so that the longest period of active growth is possible within the constraints of a particular environment and farming

system. The important concept for farmers to grasp is that lupins are a "full season" crop (cf. maize) and not a "short term" crop such as barley or process peas.

The various management aspects studied in this thesis will be discussed in the following sections in relation to these basic considerations.

E.2 Sowing Time

It became apparent that the time of sowing is a critical factor determining the final seed yield in lupins especially for spring sowing. One of the major causes for crop failures during the early 1970's was due to sowing the crop too late (Withers *et al.*, 1974).

It seems likely that, in the presence of the foliage diseases *Pleiochaeta setosa* and *Stemphylium vesicarium* there is little advantage in sowing *L. angustifolius* cultivars susceptible to these diseases before July in the North Island. Unfortunately the more resistant species were not autumn-sown in this study but trials with *L. albus* (Withers, unpublished data) showed an advantage of autumn-sown plants over spring-sown ones and further work is being conducted at present with *L. albus* and with *L. angustifolius* cultivars resistant to *S. vesicarium*.

Time of sowing is important to allow the plant to develop as many sequential branch orders and fix as much nitrogen as possible in the time available. This is largely a function of time and temperature between first flowering and the time when water stress prevents further development of vegetative growth. The lighter the soil and rainfall, the more important it would be to sow the crop early.

In the Manawatu and many other North Island areas which have high winter/early spring rainfall and limitations in soil drainage, early sowing can be difficult to achieve in practice, especially as lupins

are sensitive to waterlogged soil conditions (Gladstones 1970). Thus autumn and early spring sowing would be restricted to areas of free draining soils. The most suitable ones probably are sandy loams and volcanic soils.

Although not satisfactorily tested in this study, it is likely that, on free draining soils and in the absence of disease, late autumn sowing would produce maximum yields. The relatively non-productive establishment period would occur during the winter so that flowering and the rapid growth phase would occur during the whole of the available spring/summer growing period. The actual sowing date would have to be adjusted to ensure that flowering did not occur before the risk of severe frost was over.

Sowing date is an important mangement tool to enable a particular farmer to maximise his available growing period but this is really adjusting the relatively insensitive part of the season. Because of the slow growth in the early part of the season, relatively large adjustments in sowing date are required for small differences in flowering date. For example, early-sown crops in Section B.4.3 had a long establishment period relative to late-sown crops. (See also Fig. B.1.1 and Table B.1.1). A few days additional growth in the warm summer period, when growth is rapid, can be equivalent to several weeks earlier sowing at the cool time of the year (Section B.4.3, C.3, C.4). Therefore consideration must also be given to the moisture supply during the summer months. Response of seed and protein yield to irrigation in disease resistant cultivars is likely to be good (Stoker, 1975; 1978; Lucas *et al.*, 1976; Herbert and Hill, 1978 a,b; Section B.4.3) when temperatures and leaf area are high (Section C.4). Where irrigation is not available and/or not economic, selection of soils with good moisture retention or districts with reliable summer rainfall would be important. Unfortunately soils with good moisture retention are often unsuitable for early sowing and a combination of both attributes would be valuable.

E.3 Lupin Species

Most of the field work in this study was conducted on *L. angustifolius* because it was the species attracting most interest at that time; largely due to the influence of Australian experience and to unfavourable early reports of alternative species (Allen, 1949). This species seemed to be well adapted to the Manawatu environment. Its major weakness in the warmer and wetter North Island conditions is its susceptibility to foliage diseases which appear to be especially serious on autumn-sown crops. This problem has not been reported as being serious on South Island crops but a number of unpublished reports of complete losses of crops in the Northland, Waikato and Bay of Plenty regions have been made. This aspect must seriously limit the potential of this species in the North Island.

Provided the crop is sown early, there seems to be little difference between the "Uni" cultivars of *L. angustifolius*. With late sowings, especially in warm districts, Unicrop may have an advantage because of earlier flowering resulting from its lack of vernalisation requirement.

Most of the detailed work was conducted on *L. albus* because it showed promise in the comparative field trial reported in this thesis and in a number of smaller unpublished trials. Overseas reports (e.g. Gladstones, 1970) indicated that it would be suited to the moderately high fertility and rainfall of the Manawatu. The apparent disease resistance and higher seed protein content compared with *L. angustifolius* combined with satisfactory seed yield make it a species worth wider investigation in the Manawatu and other areas of the North Island. Some disadvantages of the species would appear to be slow initial development; a long period for pods to dry out and seed mature once leaves drop; and a tendency to have too high an alkaloid level for safe pig and human use. The cultivar (Ultra) used in this study suffers from the problems of slow development, excessive vegetative growth and large seeds which are often difficult to handle mechanically at sowing and

harvest. Other cultivars such as Kali and Kievskij Mutant at present being tested may overcome some of these limitations (Withers, unpublished data, Gladstones, pers. comm.). However, it should be noted that the large seed size of Ultra may be an important factor in the good yield of Ultra in comparison with other species (Section B.4.2.3) and that a large vegetative structure and extended maturity period may have some advantage in achieving high protein yields (Sections B.4.3, C1 and C2).

Although having a reputation for low yields, *L. luteus* yielded well in comparison with *L. angustifolius* and certainly was consistently better in terms of protein yield. This, combined with its resistance to foliage diseases and high protein content of the seed make it a species worthy of further development. Its chief limitation to higher seed yield seems to be its small seed size and limited ability to develop lateral branching. Slow branch development may not be a major limitation provided the yield potential on those branches produced is high. Weiko III has the ability to produce relatively high numbers of seed on the main stem but yield is limited by the small seed size. The logical approach would be to select for increased seed size but Section B.4.3 would indicate that this may not increase protein yield unless vegetative nitrogen reserves are also increased. Hill (pers. comm.) has shown that selection for increased seed size can result in lower protein percentage in the seed.

E.4 Plant Density

The structure of the lupin plant is very sensitive to plant density with branch number being readily reduced by increasing density; the effect being apparent early in growth (Section B.3). High order lateral branches are most affected which may limit the ability of dense stands to respond to long growing seasons. Branch number, pod number and seed yield are all closely related as other yield components seem to be relatively stable. The plant is thus very "plastic" in its response to density so a low variation in seed yield with density changes is to be expected. For this reason, plant density was not a major component in the field trials.

Unfortunately the two experiments studying density produced conflicting trends in seed yield. The first experiment (Section B.2) represented a final population range of 47-103 pl/m^2 for the July sowing and 46-77 pl/m^2 for the October sowing and showed no response to plant density but it was at a relatively low yield level (92-198 g/m^2). The second experiment (Section B.3) represented a range of 17-100 pl/m^2 and showed a response to plant density for undefoliated plants but at a higher yield level (210-542 g/m^2). How much the difference in response was due to environmental effects between the two sites is not clear. It is likely that, in the second experiment, the small plot and sample size were at least partly responsible for the high response at the highest density due to edge effects and multiplication factors.

Thus these experiments were unable to contribute significantly to the determination of optimum densities for lupin seed but useful information on the reaction of the lupin plant to competition was obtained.

E.5 Potential for Lupin in the North Island

Provided a market can be established, there would seem to be a potential for the growing of lupin in some areas of the North Island. A range of seed yield from a low of about 100 g/m^2 to over 500 g/m^2 was obtained from the field trials with most yields falling in the range 300-400 g/m^2. Limited land area meant that plots had to be small so that the conversion of these plot yields to t/ha must be done with caution. However, these yields are similar to the yields obtained by many farmers. Thus although 3 t/ha could be regarded as a reasonable expectation in yield, these trials indicate that higher yields than this may be obtained under suitable conditions. Withers (1978) has shown that, to be competitive with high return crops such as wheat on good soils in the Manawatu, yields of over 4 t/ha would be required consistently. However, it was pointed out that, on lower fertility free draining soils, the high return crops cannot be grown whereas lupin may not have a significant reduction in yield because of its adaptability to lower fertility soils. Returns from livestock

are also not high on these soils. However, to ensure satisfactory and reasonably consistent yields, farmers would have to adjust to the longer term nature of the crop by accepting late-autumn or winter sowings rather than the normal mid-spring sowings. The readiness with which farmers will do this will, of course, depend on the expected returns. The other aspect which farmers will probably have to adjust to is a larger than normal variation in yield between seasons as the crop adjusts to varying lengths of the growing period.

If the disease resistant but less frost tolerant species such as *L. albus* are to be grown, high altitude inland areas may not be suitable for autumn-sown crops because of the risk of frost and the growing season may not be long enough for satisfactory yields from spring sowing (Withers *et al.*, 1976). An area with apparent potential is the area of sand country present along the South-West coast of the North Island. Considerable areas of flat to undulating land exists within this complex system. Land value and production is relatively low and it is generally unsuitable for intensive cropping because of its low nitrogen levels and tendency to summer drought and wind erosion. The soil has poor moisture retention however, but in many cases the early summer water table should be accessible to the lupin taproot. Autumn sowing of disease resistant cultivars would allow reproductive development over the available spring-summer growing period and would make the best use of the potential productive period of this class of land. Yield would be dependant on the amount of early summer rainfall so yields are likely to be variable, but given a reasonable price range ($160-180/tonne), returns should be competitive with most alternative enterprises. A series of trials and small commercial areas are being established during 1979-81 to test this hypothesis.

This study has been able to establish that lupin species other than the standard *L. angustifolius* have a potential for seed protein production in some areas of the North Island of New

Zealand. It has shown some of the strengths and weaknesses of these crops and has highlighted that the approach of farmers to the crop may have to be different from that required for crops at present extensively grown if yields are to be maximised.

REFERENCES

Adams, M.W. 1967: Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Science 7* : 505-10.

Adams, M.W. 1975: Plant architecture and yield in the grain legumes. Report of the T.A.C. Working Group on the Biology of Yield of Grain Legumes. F.A.O., Rome. 16 p.

Addicott, F.T.; Lynch, R.S. 1955: Physiology of abscission. *Annual Review of Plant Physiology 6* : 211-38.

Adjei-Twum, D.C.; Splittstoesser, W.E. 1976: The effect of soil water regimes on leaf water potential, growth and development of soybeans. *Physiologia Plantarum 38* : 131-7.

Aitken, Y: Flower initiation in relation to maturity in crop plants. IV. Sowing time and maturity type in pea (*Pisum sativum* L.) in Australia. *Australian Journal of Agricultural Research 29* : 983-1001.

Allen, F.C. 1949: Lupins. *Agronomy Review 2* : 1-6.

Anon, 1938: Blue lupins *Canterbury Chamber of Commerce Agricultural Bulletin*. No. 110. 4p.

Anon, 1979: Another variety for northern areas - Illyarrie lupin, *Journal of Agriculture, Western Australia 20* : 55.

Atkins, C.A.; Flinn, A.M. 1978: Carbon dioxide fixation in the carbon economy of developing seeds of *Lupinus albus* (L.). *Plant Physiology 62* : 486-90.

Atkins, C.A.; Herridge, D.F.; Pate, J.S. 1978: The economy of carbon and nitrogen in nitrogen-fixing annual legumes: Experimental observations and theoretical considerations. *In* "Isotopes in Biological Dinitrogen Fixation" pp 211-42. International Atomic Energy Agency, Vienna.

Baars, H.D. 1968: Determination of water deficits in plant tissues. *In* "Water Deficits and Plant Growth" Vol. 1 pp 336-68. Ed. T.T. Kozlowski, Academic Press, New York.

Bauer, P.J. 1976: Lupins in East Africa - A review. Technical Report No. 12, Ministry of Agriculture, Kenya. 20 p.

Begg, J.E.; Turner, N.C. 1976: Crop Water deficits. *Advances in Agronomy 28* : 161-217.

Bennett, J.P.; Adams, M.W.; Burge, C. 1977: Pod yield component variation and intercorrelation in *Phaseolus vulgaris* L. as affected by planting density. *Crop Science 17* : 73-5.

Bethlenfalvay, G.J.; Phillips, D.A. 1977: Ontogenetic interactions between photosynthesis and symbiotic nitrogen fixation in legumes. *Plant Physiology 60* : 419-21.

Bethlenfalvay, G.J.; Abu-Shakra, S.S.; Phillips, D. 1978. Interdependence of nitrogen nutrition and photosynthesis in *Pisum sativum* L. *Plant Physiology 62* : 127-30.

Biddiscombe, E.F. 1975; Effect of moisture stress on flower drop and seed yield of narrow-leafed lupin (*Lupinus angustifolius* L. cv. Unicrop). *Journal of the Australian Institute of Agricultural Science 41* : 70-2.

Biddulph, O.; Cory, R. 1965: Translocation of C^{14} metabolites in the phloem of the bean plant. *Plant Physiology 40* : 119-29.

Bliss, C.I. 1967: "Statistics in Biology; Statistical Methods for Research in the Natural Sciences". Vol. 2. McGraw-Hill, New York.

Blomquist, R.V.; Kust, C.A. 1971: Translocation pattern of soybean as affected by growth substances and maturity. *Crop Science 11* : 390-3.

Boundy, K. 1978: The exciting promise of lupins in crop rotations. *Journal of Agriculture, Victoria 76* : 8-9.

Boyer, J.S. 1976: Photosynthesis at low water potentials. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences 273* : 501-12.

Boyer, J.S.; McPherson, H.G. 1975: Physiology of water deficits in cereal crops. *Advances in Agronomy 27* : 1-23.

Brouwer, R. 1962: Distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science 10* : 361-76.

Carr, D.J.; Pate, J.S. 1967: Ageing in the whole Plant. *In* "Aspects of the Biology of Ageing". Symposium of the Society for Experimental Biology No. 21. pp 559-99.

Carr, D.J.; Skene, K.G.M. 1961: Diauxic growth curve of seeds with special reference to french beans (*Phaseolus vulgaris* L.) *Australian Journal of Biological Sciences 14* : 1-12.

Chapman, G.P.; Peat, W.E. 1978: Procurement of yield in field and broad beans. *Span 9*: 267-72.

Chen, L.H ; Mederski, H.J.; Curry, R.B. 1971: Water stress effects on photosynthesis and stem diameter in soybean plants. *Crop Science 11* : 428-31.

Chung, J.H.; Goulden, D.S. 1971: Yield components of haricot beans (*Phaseolus vulgaris* L.) grown at different plant densities. *N.Z. Journal of Agricultural Research 14* : 227-34.

Clements, R.S.J. 1970: Breeding for improved value of *Phalaris tuberosa* herbage. Ph.D. thesis, Massey University, Palmerston North: 171 p.

Cock, J.H,; Yoshida, S. 1972: Accumulation of ^{14}C-labelled carbohydrate before flowering and its subsequent redistribution and respiration in the rice plant. *Crop Science Society of Japan Proceedings 41* : 226-34.

Cooper, D.R.; Hill-Cottingham, D.G.; Lloyd-Jones, C.P. 1976: Absorption and redistribution of nitrogen during growth and development of field bean, *Vicia faba*. *Physiologia Plantarum 38* : 313-8.

Corbin, E. 1978a: Lupin growing increasing in Southern N.S.W. *Agricultural Gazette of N.S.W. 89* : 1-3.

Corbin, E.J. 1978b: Lupin production in 1978. In "Lupin Production in 1978" pp 6-25. New South Wales Department of Agriculture.

Crookston, R.K.; O'Toole, J.O.; Ozbun, J.O. 1974: Characterisation of the bean pod as a photosynthetic organ. *Crop Science 14* 708-12.

Derman, B.D.; Rupp, D.C.; Nooden, L.D. 1978: Mineral distribution in relation to fruit development and monocarpic senescence in Anoka soybeans. *American Journal of Botany 65* : 205-13.

Doss, B.D.; Pearson, R.W.; Rogers, H.T. 1974: Effect of soil water stress at various growth stages on soybean yield. *Agronomy Journal 66* : 297-9.

Duncan, W.G.; McCloud, D.E.; McGraw, R.L.; Boote, K.J. 1978: Physiological aspects of peanut yield improvement. *Crop Science 18* : 1015-20.

Dunphy, E.J.; Hanway, J.J. 1976: Water soluble carbohydrate accumulation in soybean plants. *Agronomy Journal 68* : 697-700.

Eaglesham, A.R.J.; Minchin, F.R.; Summerfield, R.J.; Dart, P.J.; Huxley, P.A.; Day, J.M. 1978: Nitrogen nutrition of cowpea (*Vigna unguiculata*). III. Distribution of nitrogen within effectively nodulated plants. *Experimental Agriculture 13* : 369-80.

Egli, D.B.; Leggett, J.E. 1973: Dry matter accumulation patterns in determinate and indeterminate soybeans. *Crop Science 13:* 220-2.

Egli, D.B.; Leggett, J.E. 1976: Rate of dry matter accumulation in soybean seeds with varying source-sink ratios. *Agronomy Journal 68* : 371-4.

Egli, D.B.; Leggett, J.E.; Wood, J.M. 1978: Influence of soybean seed size and position on the rate and duration of filling. *Agronomy Journal 70* : 127-30.

Engin, M.; Sprent, J.I. 1973: Effects of water stress on growth and nitrogen-fixing activity of *Trifolium repens*. *New Phytologist 72* : 117-26.

Farrington, P. 1974a: Effect of planting time on growth and seed yield of lupins, peas and vetches on the Swan Coastal Plain, Western Australia. *Australian Journal of Experimental Agriculture and Animal Husbandry 14* : 539-46.

Farrington, P. 1974b: Grain legume crops: Their role on the world scene and in Australian agriculture. *Journal of the Australian Institute of Agricultural Science 40* : 99-108.

Farrington, P. 1976: Fruit development and associated changes in the distribution of dry weight and nitrogen in *Lupinus angustifolius* cv. Uniharvest and *L. cosentinii* selection CB 12. *Australian Journal of Experimental Agriculture and Animal Husbandry 16* : 387-93.

Farrington, P.; Greenwood, E.A.N. 1975: Description and specification of the branching structure of lupins. *Australian Journal of Agricultural Research 26* : 507-10.

Farrington, P.; Greenwood, E.A.N.; Titmanis, Z.V.; Trinick, M.J.; Smith, D.W. 1977: Fixation, accumulation, and distribution of nitrogen in a crop of *Lupinus angustifolius* cv. Unicrop. *Australian Journal of Agricultural Research 28 :* 237-48.

Fischer, R.A.; Hagan, R.M. 1965: Plant water relations, irrigation management and crop yield. *Experimental Agriculture 1 :* 161-77.

Flinn, A.M.; Atkins, C.A.; Pate, J.S. 1977: Significance of photosynthetic and respiratory exchanges in the carbon economy of the developing pea fruit. *Plant Physiology 60 :* 412-8.

Flinn, A.M.; Pate, J.S. 1968: Biochemical and physiological changes during maturation of fruit of the field pea (*Pisum arvense* L.). *Annals of Botany 32 :* 479-95.

Flinn, A.M.; Pate, J.S. 1970: A quantitative study of carbon transfer from pod and subtending leaf to the ripening seeds of the field pea (*Pisum arvense* L.). *Journal of Experimental Botany 21 :* 71-82.

Forde, B.J.; Mitchell, K.J.; Edge, E.A. 1977: Effect of temperature, vapour-pressure deficit, and irradiance on transpiration rates of maize, paspalum, westerwolds and perennial ryegrass, peas, white clover and lucerne. *Australian Journal of Plant Physiology 4 :* 889-99.

Forde, M.A.; Thorne, G.N. 1974: Effects of atmospheric humidity on plant growth. *Annals of Botany 38 :* 441-52.

Francis, C.M.; Poole, M.L.; Chopping, M.H. 1971: A new look at sweet lupins in Western Australia. *Journal of Agriculture, Western Australia 11 :* 85-8.

Gabelman W.H.; Williams, D.D.F. 1960: Development studies with irrigated snap beans. University of Wisconsin Agricultural Experiment Station, Research Bulletin No. 221, 56 p.

Garside, A.L. 1979: Effect of sowing time on the development, yield and yield components of some cultivars of *Lupinus angustifolius* and *Lupins luteus* in Northern Tasmania. *Australian Journal of Experimental Agriculture and Animal Husbandry 19 :* 64-71.

Gates, C.T. 1955a : The response of the young tomato plant to a brief period of water shortage. I. The whole plant and its principal parts. *Australian Journal of Biological Sciences 8 :* 196-214.

Gates, C.T. 1955b : *Ibid* II. The individual leaves *Ibid 8 :* 215-30.

Gates, C.T. 1957: *Ibid* III. Drifts in nitrogen and phosphorous. *Ibid 10 :* 125-46.

Gates, C.T. 1964: The effect of water stress on plant growth. *Journal of the Australian Institute of Agricultural Science 30 :* 3-22.

Gates, C.T. 1968: Water deficits and growth of herbaceous plants. *In* "Water Deficits and Plant Growth". Vol II. pp 135-90 Ed. T.T. Kozlowski. Academic Press, New York.

Gibson, A.H. 1974: Consideration of the growing legume as a symbiotic association. *Indian National Science Academy Proceedings 40 B :* 741-67.

Gladstones, J.S. 1959: The potential of lupins as crop and forage plants in Western Australia. *Empire Journal of Experimental Agriculture 27 :* 333-42.

Gladstones, J.S. 1970: Lupins as crop plants. *Field Crop Abstracts 23 :* 123-48.

Gladstones, J.S. 1972: Lupins in Western Australia. Department of Agriculture, Western Australia, Bulletin No. 3834. 37 p.

Gladstones, J.S. 1974: Lupins of the Mediterranean region and Africa. Department of Agriculture, Western Australia, Technical Bulletin No. 26.

Gladstones, J.S. 1977: The narrow-leafed lupin in Western Australia. Department of Agriculture, Western Australia, Bulletin No 3990 39 p.

Gladstones, J.S.; Hill, G.D. 1969: Selection for economic characters in *Lupinus angustifolius* and *L. digitatus*. 2. Time of Flowering. *Australian Journal of Experimental Agriculture and Animal Husbandry 9 :* 213-20.

Gladstones, J.S.; Leach, B.J.; Drover, D.P.; Asher, C.J. 1964: Field studies on the potassium and phosphorus nutrition of lupins. *Ibid 4 :* 158-64.

Gordon, I.L. 1975: Sprouting damage in wheat (*Triticum aestivum* L.) Ph.D. Thesis, University of Sydney.

Goulden, D.S. 1976: Effect of sowing rate and sowing date on lupin seed yield. *N.Z. Journal of Experimental Agriculture 4 :* 181-4.

Greenwood, E.A.N.; Farrington, P.; Beresford, J.D. 1975: Characteristics of the canopy, root system and grain yield of a crop of *Lupinus angustifolius* cv. Unicrop *Australian Journal of Agricultural Research 26 :* 497-510.

Gross, R.; Morales, E.; Gross, U.; von Baer, E. 1976; Die lupine, ein beitrag zur nahrungsversorgung in den Anden. 3. Ernahrungsphysiologische untersuchung mit dem mehl der suslupine *(Lupinus albus)*. *Z. Ernährungswiss 15 :* 391-5.

Hall, B.D. 1978: Grain lupin research on the eastern Darling Downs. *Queensland Agricultural Journal 104 :* 380-3.

Ham, G.E.; Lawn, R.J.; Brun, W.A. 1976: Influence of inoculation, nitrogen fertilisers and photosynthetic source-sink manipulations on field-grown soybeans. *In* "Symbiotic Nitrogen Fixation in Plants" pp 239-53. Ed. P.S. Nutman, Cambridge University Press, Cambridge.

Hanway, J.J.; Weber, C.R. 1971a: Dry matter accumulation in soybean (*Glycine max* (L.) (Merrill) plants as influenced by N.P. and K. fertilisation. *Agronomy Journal 63 :* 263-6.

Hanway, J.J.; Weber, C.R. 1971b: Dry matter accumulation in eight soybean (*Glycine max* (L.) (Merrill) varieties. *Ibid 63 :* 227-30.

Hardman, L.L.; Brun, W.A. 1971: Effect of atmospheric carbon dioxide enrichment at different developmental stages on growth and yield components of soybeans. *Crop Science 11 :* 886-8.

Hardy, R.W.F.; Criswell, J.G.; Havelka, U.D. 1977: Investigations of possible limitations of nitrogen fixation by legumes. *In* "Recent Developments in Nitrogen Fixation" pp 451-67. Eds. W. Newton, J.R. Postgate, C. Rodriguez-Barrueco. Academic Press, London.

Hardy, R.W.F.; Havelka, U.D. 1976: Photosynthate as a major factor limiting nitrogen fixation by field-grown legumes with emphasis on soybeans. *In* "Symbiotic Nitrogen Fixation in Plants". pp 421-39. Ed. P.S. Nutman, Cambridge University Press, Cambridge.

Hardy, R.W.F.; Holston, R.D.; Jackson, E.K.; Burns, R.C. 1968: The acetylene-ethylene assay of N_2 fixation: Laboratory and field evaluation. *Plant Physiology 43 :* 1185-1207.

Harvey, D.M. 1977: Photosynthesis and translocation, *In* "The Physiology of the Garden Pea". pp. 315-48. Eds. J.F. Sutcliffe and J.S. Pate. Academic Press, London,

Herbert, S.J. 1977a: Growth and grain yield of *Lupinus albus* at different plant populations. *N.Z. Journal of Agricultural Research 20 :* 459-65.

Herbert, S.J. 1977b: Influence of branch removal, plant density and species on pod set and seed yield of lupins. *Proceedings Agronomy Society of N.Z. 7 :* 69-74.

Herbert, S.J. 1977c: Density and irrigation studies in *Lupinus albus* and *L. angustifolius*. Ph.D. Thesis, Lincoln University College of Agriculture, Canterbury.

Herbert S.J. 1978: Plant density and irrigation studies on lupins,III. Seed yield relationships of *Lupinus angustifolius* cv. Unicrop *N.Z. Journal of Agricultural Research 21 :* 483-9.

Herbert, S.J.; Hill, G.D. 1978a: Plant density and irrigation studies on lupins, I. Growth analysis of *Lupinus angustifolius* cv. WAUIIB. *Ibid 21 :* 467-74.

Herbert, S.J.; Hill, G.D. 1978b: Plant density and irrigation studies on lupins. II. Components of seed yield of *Lupinus angustifolius* cv. WAUIIB *Ibid 21 :* 475-81.

Herridge, D.F.; Pate, J.S. 1977: Utilization of net photosynthate for nitrogen fixation and protein production in an annual legume. *Plant Physiology 60 :* 759-64.

Herz, K.O. 1973; Report on a mission (March-April 1973) to evaluate and assist a project on flours and products from lupins and quinoa at the University of Concepcion, Chile. Report ESN:MISC/73/6, F.A.O. Rome. 15 p.

Hill, G.D. 1977: The composition and nutritive value of lupin seed. *Nutrition Abstracts and Reviews, B : Livestock Feeds and Feeding 47 :* 511-29.

Hoad, G.V. 1978: Effect of water stress on abscisic acid levels in white lupin (*L. albus* L.) fruit, leaves and phloem exudate *Planta 142 :* 287-90.

Hocking, P.J.; Pate, J.S. 1977: Mobilization of minerals to developing seeds of legumes. *Annals of Botany 41 :* 1259-78.

Hocking P.J.; Pate, J.S. 1978: Accumulation and distribution of mineral elements in the annual lupins *L. albus* L. and *L. angustifolius* L. *Australian Journal of Agricultural Research 29 :* 267-80.

Holliday, R. 1960: Plant population and crop yield. Part 1. *Field Crop Abstracts 13 :* 159-67.

Hove, E.L. 1974: Composition and protein quality of sweet lupin seed. *Journal of the Science of Food and Agriculture 25 :* 851-9.

Hove, E.L.; King , S.; Hill, G.D. 1978: Composition, protein, quality and toxins of seeds of the grain legumes *Glycine max, Lupinus* spp., *Phaseolus* spp., *Pisum sativum,* and *Vicia faba. N.Z. Journal of Agricultural Research 21 :* 457-62.

Hsiao, T.C. 1973: Plant responses to water stress. *Annual Review of Plant Physiology 24 :* 519-70.

Hsiao, T.C.; Acevedo, E. 1974: Plant responses to water deficits, water use efficiency, and drought resistance. *Agricultural Meteorology 14 :* 59-84.

Hsiao, T.C.; Acevedo, E.; Feveres, E.; Henderson, D.W. 1976: Water stress, growth and osmotic adjustment. *Philosophical Transactions of the Royal Society of London B. Biological Sciences 273 :* 473-500.

Huang, C-Y.; Boyer, J.S.; Vanderhoef, L.N. 1975; Acetylene reduction (nitrogen fixation) and metabolic activites of soybean having various leaf and nodule water potentials. *Plant Physiology 56 :* 222-7.

Hudson, B.J.F. 1979; The nutritional quality of lupinseed *Qualitas Plantarum 29 :* 245-51.

Hudson, B.J.F.; Fleetwood, J.G.; Zand-Moghaddam, A. 1976; Lupin : an arable food crop for temperate climates. *Plant Foods for Man 2 :* 81-90.

Hume, D.J.; Criswell, J.G. 1973: Distribution and utilization of ^{14}C-labelled assimilates in soybeans. *Agronomy Journal 13 :* 519-24.

Inch, R. 1947: Blue lupins. *N.Z. Journal of Agriculture 74 :* 369-74.

Ishag, H.M. 1973a: Physiology of seed yield in field beans (*Vicia faba* L.). I. Yield and yield components. *Journal of Agricultural Science, Cambridge 80 :* 181-9.

Ishag, H.M. 1973b: Physiology of seed yield in field beans (*Vicia faba* L.). II. Dry matter production *Ibid 80:* 191-9.

Jermyn, W.A. 1977: Limitations on breeding high-protein field peas. *Proceedings Agronomy Society of N.Z. 7:* 89-91.

Jordan, W.R.; Brown, K.W.; Thomas, J.C. 1975: Leaf age as a determinant in stomatal control of water loss from cotton during water stress. *Plant Physiology 56 :* 595-9.

Kaplan S.L.; Koller, H.R. 1974: Variation among soybean cultivars in seed growth rate during the linear phase of seed growth *Crop Science 14 :* 613-4.

Karr, E.J.; Linck, A.J.; Swanson, C.A. 1959: The effect of short periods of high temperatures during day and night periods on pea yields. *American Journal of Botany 46 :* 91-3.

Kassam, A.H. 1975: Wilting of leaves in *Vicia faba* L. *Annals of Botany 39 :* 265-71.

Kato, I.; Sakaguchi, S. 1954: Studies on the mechanism of occurrence of abortive grains and their prevention in soybeans *Glycine max* M. Tokai - Kinki National Agricultural Experimental Station Bulletin No. 1. 115-32 (Cited by Shibles *et al.*, 1974).

Kleinendorst, A. 1975: An explosion of leaf growth after stress conditions. *Netherlands Journal of Agricultural Science 23 :* 139-44.

Kursanov, A.L. 1963: Metabolism and the transport of organic substances in the phloem. *Advances in Botanical Research 1 :* 209-76.

Laing, W.A.; Christeller, J.T. 1976: A model for the kinetics of activation and catalysis of ribulose 1,5-bisphosphate carboxylase. *Biochemical Journal 159 :* 563-70.

Lambert, R.G.; Linck, A.J. 1958: Effects of high temperature on yield of peas. *Plant Physiology 33 :* 347-50.

Lawn, R.J.; Brun, W.A. 1974: Symbiotic nitrogen fixation in soybeans. I. Effect of photosynthetic source-sink manipulation. *Crop Science 14 :* 11-16.

Leonard, E.R. 1962: Inter-relations of vegetative and reproductive growth with special reference to indeterminate plants. *The Botanical Review 28 :* 354-400.

Leopold, A.C.; Kriedemann, P.E. 1976: "Plant Growth and Development" 2nd Edition. pp 426-7. McGraw-Hill, New York.

Leopold, A.C.; Niedergang - Kamien, E.; Janick, J. 1959: Experimental modification of plant senescence. *Plant Physiology 34 :* 570-3.

Lewis, O.A.M.; Pate, J.S. 1973: The significance of transpirationally derived nitrogen in protein synthesis in fruiting plants of pea (*Pisum sativum* L.) *Journal of Experimental Botany 24 :* 596-606.

Lovell, P.H.; Lovell, P.J. 1970: Fixation of CO_2 and export of photosynthate by the carpel in *P. sativum*. *Physiologia Plantarum 23 :* 316-22.

Lucas, R.J.; Pownall, D.B.; Herbert, S.J. 1976: October-sown *Lupinus angustifolius* in Canterbury. *Proceedings Agronomy Society of N.Z. 6 :* 75-8.

Ludlow, M.M.; Ng, T.T. 1974: Water stress suspends leaf ageing. *Plant Science Letters 3 :* 235-40.

McAlister, D.F.; Kober, O.A. 1958: Response of soybeans to leaf and pod removal. *Agronomy Journal 50 :* 674-7.

McEwan, J. 1972: Effects of defoliating different zones on the plant in field beans (*Vicia faba* L.) *Journal of Agricultural Science, Cambridge 78 :* 487-90.

MacGillivray, G. 1934: Blue lupins in Canterbury. *N.Z. Journal of Agriculture 49 :* 41-3.

McMicheal, B.L.; Jordon, W.R.; Powell, R.D. 1973: Abscission processes in cotton: Induction by plant water deficit. *Agronomy Journal 65 :* 202-4.

McPherson G.K. 1940: Blue Lupins as a sheep feed. *N.Z. Journal of Agriculture 60 :* 95-9.

Maurer, A.R.; Ormrod, D.P.; Fletcher, H.F. 1968: Response of peas to environment. IV. Effect of five soil water regimes on growth and development of peas. *Canadian Journal of Plant Science 48 :* 129-37.

Meadley, J.T.; Milbourn G.M. 1971: The growth of vining peas. III. The effect of shading on abscission of flowers and pods. *Journal of Agricultural Science, Cambridge 77 :* 103-8.

Miller D.G.; Manning, C.E.; Teare, I.D. 1977: Effects of soil water levels on components of growth and yield in peas. *Journal of the American Society of Horticultural Science 102 :* 349-51.

Minchin, F.R.; Pate, J.S. 1973: The carbon balance of a legume and the functional economy of its root nodules. *Journal of Experimental Botany 24 :* 259-71.

Minchin, F.R.; Summerfield, R.J. 1978: Potential yield improvement in cowpea (*Vigna unguiculata*): The role of nitrogen nutrition *Annals of Applied Biology 88 :* 468-73.

Ndunguru, B.J.: Summerfield, R.J.; Stewart, K.A. 1978: Effects of source-sink manipulation on seed yield of cowpea (*Vigna unguiculata* (L) Walp.). II. Depodding. *Tropical Agriculture 55 :* 297-305.

Nelson, C.D. 1963: Effect of climate on the distribution and translocation of assimilates. *In* "Environmental Control of Plant Growth" pp 149-74. Ed. L.T. Evans. Academic Press, New York.

Nonnecke, I.L.; Adedipe, N.O.; Ormrod, D.P. 1971: Temperature and humidity effects on the growth and yield of pea cultivars. *Canadian Journal of Plant Science 51 :* 479-84.

Nooden, L.D.; Rupp, D.C.; Derman, B.D. 1978: Separation of seed development from monocarpic senescence in soybean *Nature 271 :* 354-6.

Nutman, P.S., 1976: Alternative sources of nitrogen for crops. *Journal of the Royal Agricultural Society of England 137 :* 86-94.

Oghoghorie, C.G.O.; Pate, J.S. 1972: Exploration of the nitrogen transport system of a nodulated legume using ^{15}N. *Planta 104 :* 35-49.

Oliker, M.; Poljakoff-Mayber, A.; Mayer A.M. 1978: Changes in weight, nitrogen accumulation, respiration, and photosynthesis during growth and development of seeds and pods of *Phaseolus vulgaris*. *American Journal of Botany 65 :* 366-71.

Ormrod, D.P.; Maurer, A.R.; Mitchell, G.; Eaton, G.W. 1970: Shoot apex development in *Pisum sativum* L. as affected by temperature. *Canadian Journal of Plant Science 50 :* 201-2.

Palmer, J. 1976 : Lupins for the North. *N.Z. Journal of Agriculture 137 :* 53.

Passioura, J.B. 1976: The control of water movement through plants *In* "Transport and Transfer Processes in Plants". pp 373-80. Eds. I.F. Wardlaw and J.B. Passioura. Academic Press, New York.

Pate, J.S. 1966: Photosynthesising leaves and nodulated roots as donors of carbon to protein of the shoot of the field pea (*Pisum arvense* L.) *Annals of Botany 30 :* 93-109.

Pate, J.S. 1968: Physiological aspects of inorganic and intermediate nitrogen metabolism (with special reference to the legume *Pisum arvense* L.) *In* "Recent Aspects of Nitrogen Metabolism in Plants". pp 219-40. Eds. E.J. Hewitt and C.J. Cutting. Academic Press, London,

Pate, J.S. 1971: Movement of nitrogenous solutes in plants. *In* "Nitrogen - 15 in Soil/Plant Studies". pp 165-87. International Atomic Energy Agency, Vienna.

Pate, J.S. 1973: Uptake, assimilation and transport of nitrogen compounds by plants. *Soil Biology and Biochemistry 5 :* 109-19.

Pate, J.S. 1974: Pea. *In* "Crop Physiology. Some Case Histories" pp 191-224. Ed. L.T. Evans. Cambridge University Press, Cambridge.

Pate, J.S. 1976: Physiology of the reaction of nodulated legumes to environment. *In* 'Symbiotic Nitrogen Fixation in Plants". pp 239-53. Ed. P.S. Nutman, Cambridge University Press, Cambridge.

Pate, J.S., 1977: Nodulation and nitrogen metabolism. *In* "The Physiology of the Garden Pea". pp 349-84. Eds. J.F. Sutcliffe and J.S. Pate. Academic Press, London.

Pate, J.S.; Flinn, A.M. 1973: Carbon and nitrogen transfer from vegetative organs to ripening seeds of field pea (*Pisum arvense* L.). *Journal of Experimental Botany 24 :* 1090-9.

Pate, J.S.; Flinn, A.M. 1977: Fruit and seed development. *In* "The Physiology of the Garden Pea". pp 315-48. Eds. J.F. Sutcliffe and J.S. Pate, Academic Press, London.

Pate, J.S.; Herridge, D.F. 1978: Partitioning and utilisation of net photosynthate in a nodulated annual legume. *Journal of Experimental Botany 29 :* 401-12.

Pate, J.S.; Sharkey, P.J.; Atkins, C.A. 1977: Nutrition of a developing legume fruit. Functional economy in terms of carbon, nitrogen, and water *Plant Physiology 59 :* 509-10

Pate, J.S.; Sharkey, P.J.; Lewis O.A.M., 1974: Phloem bleeding from legume fruits - a technique for study of fruit nutrition. *Planta 120 :* 229-43.

Perry M.W. 1975: Field environment studies on lupins. II. The effects of time of planting on dry matter partition and yield components of *Lupinus angustifolius* L. *Australian Journal of Agricultural Research 26 :* 809-18.

Perry, M.W.; Poole, M.L. 1975: Field environment studies on lupins. 1. Development patterns in *Lupinus angustifolius* L., the effects of cultivar, site and planting time. *Ibid 26 :* 81-91.

Pitelka, L.F. 1977: Energy allocation in annual and perennial lupines (*Lupinus* : Leguminosae). *Ecology 58* : 1055-65.

Porter, H.K. 1966: Leaves as collecting and distributing agents of carbon. *Australian Journal of Science 29 :* 31-40.

Porter, N.G. 1977: The role of abscisic acid in flower abscission of *Lupinus luteus*. *Physiologia Plantarum 40 :* 50-4.

Porter, N.G.; van Steveninck, R.F.M. 1966: An abscission - promoting factor in *Lupinus luteus* (L.). *Life Sciences 5 :* 2301-8.

Posipanov, G.S. 1974: The role of various vegetative and soil organs in the formation of seeds of the blue lupin (*Lupinus angustifolius*) *Timiryazev Agricultural Academy News Issue 4 :* 29-33. (Cited by Herbert, 1977c).

Pulver, E.L.; Brockman, F.; Nangju, D.; Wien, H. 1978: IITA's programme on N_2 fixation. *In* "Isotopes in Biological Dinitrogen Fixation". pp 269-84. International Atomic Energy Agency, Vienna.

Pumphrey, F.V.; Ramig, R.E.; Allmarus, R. 1979: Field responses of peas (*Pisum sativum* L.) to precipitation and excess heat. *Journal of the American Society for Horticultural Science 104 :* 548-50.

Rahman, M.S.; Gladstones, J.S. 1972: Control of lupin flower initiation by vernalisation, photoperiod and temperature under controlled environment. *Australian Journal of Experimental Agriculture and Animal Husbandry 12* : 638-45.

Rahman, M.S.; Gladstones, J.S. 1973: Temperature responses of lupin species during germination and flowering development. *The Journal of the Australian Institute of Agricultural Science 39* : 259-62.

Rahman, M.S.; Gladstones, J.S. 1974: Differences among *Lupinus* species in field response to superphosphate. *Australian Journal of Experimental Agriculture and Animal Husbandry 14* : 214-23.

Rahman, M.S.; Gladstones, J.S.; Thurling N. 1974: Effects of soil temperature and phosphorus supply on growth and composition of *Lupinus angustifolius* L. and *L. cosentinii* Guss. *Australian Journal of Agricultural Research 25* : 885-92.

Reeves, T.G.; Boundy, K.A.; Brooke, H.D. 1977: Phenological development studies with *Lupinus angustifolius* and *L. albus* in Victoria. *Australian Journal of Experimental Agriculture and Animal Husbandry 17* : 637-44.

Robins, J.S.; Domingo, C.E. 1956: Moisture deficits in relation to the growth and development of dry beans. *Agronomy Journal 48* : 67-70.

Runge, E.C.A.; Odell, R.T. 1960: The relationship between precipitation, temperature and the yield of soybeans on the Agronomy South Farm, Urbana, Illinois. *Agronomy Journal 52* : 245-7.

Ryle, G.J.A.; Powell, C.E.; Gordon, A.J. 1978: Effect of source of nitrogen on the growth of Fiskeby soya bean: The carbon economy of whole plants. *Annals of Botany 42* : 637-48.

Salter, P.J. 1962: Some responses of peas to irrigation at different growth stages. *Journal of Horticultural Science 37* : 141-9.

Salter, P.J.; Drew, D.H. 1965: Root growth as a factor in the response of *Pisum sativum* L. to irrigation. *Nature 206* : 1063-4.

Salter, P.J.; Goode, J.E. 1967: "Crop responses to water at different stages of growth". Research Review No. 2. Commonwealth Bureau of Horticulture and Plantation Crops. Commonwealth Agricultural Bureaux. Bucks, England: 49-60.

Schou, J.B.; Jeffers, D.L.; Streeter, J.G. 1978: Effects of reflectors, black boards or shades applied at different stages of plant development on yield of soybeans. *Crop Science 18 :* 29-34.

Seitzer, J.F.; Evans, L.E. 1973: Response of small faba beans to seed rate and spacing. *Canadian Journal of Plant Science 53 :* 279-83.

Seligman, N.G.; van Keulen, H; Goudriaan, J. 1975: An elementary model of nitrogen uptake and redistribution by annual plant species. *Oecologia 21 :* 243-61.

Sengbusch, von R. 1938: The breeding of sweet lupins. *Herbage Reviews 6 :* 64-71.

Sharkey, P.J.; Pate, J.S. 1976: Translocation from leaves to fruits of a legume, studied by a phloem bleeding technique: Diurnal changes and effects of continuous darkness. *Planta 128 :* 63-72.

Shaw, R.H.; Laing, D.R. 1966: Moisture stress and plant response. *In* "Plant Environment and Efficient Water Use". pp 73-94. Eds. W.H. Pierre, D. Kirkham, J. Pesek, R. Shaw. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin.

Shibles, R.; Anderson, I.C.; Gibson, A.H. 1974: Soybeans. *In* "Crop Physiology. Some Case Histories". pp 151-89. Ed. L.T. Evans. Cambridge University Press, Cambridge.

Shimshi, D. 1969: A rapid field method for measuring photosynthesis with labelled carbon dioxide. *Journal of Experimental Botany 20 :* 381-401.

Simon, E.W. 1967: Types of leaf senescence. *In* "Aspects of the Biology of Ageing". pp 215-30. Symposium of the Society for Experimental Biology No. 21.

Sinclair, T.R.; de Wit, C.T. 1975: Photosynthate and nitrogen requirements for seed production by various crops. *Science 189 :* 565-7.

Sinclair, T.R.; de Wit, C.T. 1976: Analysis of the carbon and nitrogen limitations to soybean yield. *Agronomy Journal 68 :* 319-24.

Sinha, S.K. 1977: Food legumes: distribution, adaptability and biology of yield. F.A.O. Plant Production and Protection Paper No. 3. F.A.O., Rome 124 p.

Sionit, N.; Kramer, P.J. 1977: Effect of water stress during different stages of growth of soybean. *Agronomy Journal 69 :* 274-8.

Slatyer, R.O. 1967: "Plant-water Relationships" Academic Press New York,

Slatyer, R.O. 1973: The effect of internal water status on plant growth, development and yield. *In* "Plant Response to Climatic Factors". Proceedings of the Uppsala Symposium. pp 177-91. Ed. R.O. Slatyer. UNESCO, Paris.

Sprent, J.I. 1971: The effects of water stress on nitrogen-fixing root nodules. I. Effects on the physiology of detached soybean nodules. *New Phytologist 70 :* 9-17.

Sprent, J.I. 1972: The effects of water stress on nitrogen-fixing root nodules. IV. Effects on whole plants of *Vicia faba* and *Glycine max. Ibid 71 :* 603-11.

Sprent, J.I. 1976: Nitrogen fixation by legumes subjected to water and light stress. *In* "Symbiotic Nitrogen Fixation in Plants". pp 405-20. Ed. P.S. Nutman. Cambridge University Press, Cambridge.

Sprent, J.I.; Bradford, A.M. 1977: Nitrogen fixation in field beans (*Vicia faba*) as affected by population density, shading and its relationship with soil moisture. *Journal of Agricultural Science, Cambridge 88 :* 303-10.

Sprent, J.I.; Bradford, A.M.; Norton, C. 1977: Seasonal growth patterns in field beans (*Vicia faba*) as affected by population density, shading and its relationship with soil moisture. *Ibid 88 :* 293-301.

Stanfield, B.; Ormrod, D.P.; Fletcher, H.F. 1966: Response of peas to environment. II. Effects of temperature in controlled environment cabinets. *Canadian Journal of Plant Science 46 :* 195-203.

Stephenson, R.A.; Wilson, G.L. 1977: Patterns of assimilate distribution in soybeans at maturity. II. The time course of changes in ^{14}C distribution in pods and stem sections. *Australian Journal of Agricultural Research 28* : 395-400.

Steveninck, van, R.F.M. 1956: Borre, a new sweet blue lupin variety. *N.Z. Journal of Agriculture 93* : 215-6.

Steveninck, van R.F.M. 1957: Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteus* L.). I. The effect of different patterns of flower removal. *Journal of Experimental Botany 8* : 373-81.

Steveninck, van R.F.M. 1958: Factors affecting the abscission of reproductive organs in yellow lupins (*Lupinus luteus* L.). II. The effects of growth substances, defoliation and removal of lateral growth. *Journal of Experimental Botany 9* : 372-83.

Stewart, K.A.; Summerfield, R.J.; Ndunguru, B.J. 1978: Effects of source-sink manipulations on seed yield of cowpea (*Vigna unguiculata* (L.) Walp.). I. Defoliation. *Tropical Agriculture 55* : 117-26.

Stoker, R. 1975: Effect of irrigation on yield and yield components of sweet lupins. *Proceedings Agronomy Society of N.Z. 5* : 9-12.

Stoker, R. 1977: Irrigation of annual legumes. Proceedings Soil and Plant Water Symposium. DSIR Information Series No. 126 : 84-9.

Stoker, R. 1978: Yield and water use of sweet lupins. *Proceedings Agronomy Society of N.Z. 8* : 23-6.

Subhadrabandhu, S.; Dennis, F.G. Jnr.; Adams, M.W. 1978: Abscission of flowers and fruits in *Phaseolus vulgaris* L. II. The relationship between pod abscission and endogenous abscisic phaseic and dihydrophaseic acids in pedicels and pods. *Journal of American Horticultural Science 103* : 565-7.

Summerfield, R.J. 1977: Vegetative growth, reproductive ontogeny and seed yield of selected tropical grain legumes. *In* "Crop Protection Agents : Their Biological Evaluation". pp 251-71. Ed. N.R. Macfarlene. Academic Press, London.

Summerfield R.K.; Huxley, P.A.; Dart, P.J.; Hughes, A.P. 1976: Some effects of environmental stress on seed yield of Cowpea (*Vigna unguiculata* (L.). (Walp). cv. Prima. *Plant and Soil 44* : 527-46.

Summerfield, R.J.; Minchin, F.R.; Roberts, E.H. 1978: Realisation of yield potential in soybean (*Glycine max* (L.) Merr.) and cowpea (*Vigna unguiculata* (L.). Walp.). Proceedings BCPC/BPGRG Symposium - "Opportunities for Chemical Plant Growth Regulation". pp 125-134.

Tamaki, K.; Asanuma, K.; Naka, J. 1973: Physiological studies of the growing process of broad bean plants. VII. Effects of plant density on the growth and the seed production. *Technical Bulletin of the Faculty of Agriculture, Kagawa University 25 :* 1-11.

Thaine R.; Ovenden, S.L.; Turner, J.S. 1959: Translocation of labelled assimilates in the soybean. *Australian Journal of Biological Sciences 12 :* 349-72.

Trinick M.J.; Dilworth, M.J.; Grounds, M. 1976: Factors affecting the reduction of acetylene by root nodules of *Lupinus* species. *New Phytologist 77 :* 359-70.

Wallace, D.H.; Munger, H.M. 1966: Studies of the physiological basis for yield differences. II. Variations in dry matter distribution among aerial organs for several dry bean varieties *Crop Science 6 :* 503-7.

Walton, G.H. 1976: Agronomic studies on *Lupinus angustifolius* in Western Australia : effect of cultivar, time of sowing and plant density on seed yield. *Australian Journal of Experimental Agriculture and Animal Husbandry 16 :* 893-904.

Walton, G.H. 1978: Trials indicate best lupin seeding rates. *Journal of Agriculture, Western Australia 19 :* 59.

Wardlaw, I.F. 1967: The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. *Australian Journal of Biological Science 20 :* 25-39.

Wardlaw, I.F. 1968: The control and pattern of movement of carbohydrates in plants. *Botanical Review 34 :* 79-104.

Wardlaw, I.F. 1969: The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. *Australian Journal of Biological Science 22 :* 1-16.

Wardlaw, I.F.; Porter, H.K. 1967: The redistribution of stem sugars in wheat during grain development. *Australian Journal of Biological Sciences 20* : 309-18.

Wareing, P.F.; Patrick, J. 1975: Source-sink relations and the partition of assimilates in the plant. *In* "Photosynthesis and Productivity in Different Environments". pp 481-99. Ed. J.P. Cooper. Cambridge University Press, Cambridge.

Wareing, P.F.; Seth, A.K. 1967: Ageing and senescence in the whole plant. *In* "Aspects of the Biology of Ageing" pp 543-58. Symposium of the Society for Experimental Biology No. 21.

Weber, C.R. 1968: Physiological concepts for high soybean yields. *Field Crop Abstracts 21* : 313-7.

Westermann, D.T.; Kolar, J.J. 1978: Symbiotic N_2 (C_2H_2) fixation by bean. *Crop Science 18* : 986-90.

Whatman, C.P. 1959: Blue lupins *N.Z. Journal of Agriculture 99* : 147-51.

White, J.G. 1961: Lupins. *Canterbury Chamber of Commerce Agricultural Bulletin* No. 386 4 p.

Williams, A.A.; Williams, R.R. 1978: Regulation of movement of assimilate into ovules of *Pisum sativum* cv. Greenfeast. A 'remote' effect of the pod. *Australian Journal of Plant Physiology 5* : 295-300.

Williams A.M.; Marinos, N.G. 1977: Regulation of the movement of assimilate into ovules of *Pisum sativum* cv. Greenfeast. Effect of pod temperature. *Australian Journal of Plant Physiology 4* : 515-21.

Williams R.F.; Shapter, R.E. 1955: A comparative study of growth and nutrition in barley and rye as affected by low water treatment. *Australian Journal of Biological Sciences 8* : 435-66.

Williams, W. 1979: Studies on the development of lupins for oil and protein. *Euphytica 28* : 481-8.

Withers, N.J. 1973: Sweet lupins for seed production. *Proceedings Agronomy Society of N.Z. 3* : 63-8.

Withers, N.J. 1978: Seed protein crops: what are their future? *Proceedings Agronomy Society of N.Z. 8* : 1-4.

Withers, N.J.; Baker, C.J.; Lynch, T.J. 1974 : Some effects of date, rate, and method of sowing on lupin seed yield. *Proceedings Agronomy Society of N.Z. 4 :* 4-8.

Withers, N.J.; King, S.; Hove, E.L. 1975: Seed weight, proportion of seed coat and nitrogen content of several species of sweet lupin : a note. *N.Z. Journal of Experimental Agriculture 3 :* 331-2.

Withers, N.J.; McQueen, I.P.M.; Clark, K.W. 1976: A preliminary study of lupins on pumice soils. *Proceedings Agronomy Society of N.Z. 6 :* 71-4.

Woodward, R.G.; Begg, J.E. 1976: The effect of atmospheric humidity on the yield and quality of soybean. *Australian Journal of Agricultural Research 27 :* 501-8.

Zucconi, F. 1975: Reassessment of the relationship between hormonal and developmental changes during abscission with particular reference to peach (*Prunus persica* L. Batsch) fruit. Ph.D. Thesis, Michigan State University, East Lansing. (Cited by Subhadrabandhu *et al.*, 1978).