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THE NUTRITIONAL ROLE OF *LUPINUS*  
*ARBOREUS* IN COASTAL SAND  
DUNE FORESTRY

II. THE POTENTIAL INFLUENCE OF DAMAGED  
LUPIN PLANTS ON NITROGEN UPTAKE  
BY *PINUS RADIATA*  
by RUTH L. GADGIL \*

SUMMARY

Glasshouse experiments are described in which lupin plants growing in coastal sand were subjected to stress in the form of shading or defoliation. These treatments resulted in inhibition of root growth, nodulation and probably nitrogen fixation rate, and caused some degree of root decomposition. After defoliation there was some recovery of root growth and presumably nitrogen fixation rate. Decomposing root systems of dead lupin plants increased nitrogen availability to *P. radiata* seedlings either by nitrogen transfer or by stimulating nitrogen-fixing activity elsewhere in the system. It is suggested that damage to lupin plants could increase nitrogen availability to *P. radiata* in the field by causing decomposition of lupin root material. The results have potential significance in New Zealand coastal sand dune forestry where lupin, an intermediate species in the artificial vegetation succession, is frequently under stress from silvicultural operations and a natural pest, *Myzema maorialis*. Drying of surface sand in hot, dry weather could be responsible for some lupin root decomposition and is another factor to be considered.

INTRODUCTION

In the previous paper of this series <sup>7</sup> it was suggested that a study of the role of *Lupinus arboreus*, an intermediate species in the artificial vegetation succession used for forest establishment on sand dunes in New Zealand, might indicate a means of manipulating the supply of combined nitrogen to the *Pinus radiata* crop. A positive influence of lupin litter and lupin seedling exudate on nitrogen up-

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take by *P. radiata* seedlings was demonstrated in pot trials, using sand from Woodhill State Forest, and this was at least partly attributable either to direct nitrogen transfer or to the stimulation of non-symbiotic nitrogen fixation. In either case undamaged lupin plants were responsible for the effect.

Silvicultural practice associated with the sand dune stabilisation technique<sup>11</sup> involves the crushing of lupin stands by tractor as young trees are planted. The aim is to reduce competition from the lupin but at the same time to retain sufficient shelter for the trees during the first 6-12 months after planting. The crushing partly kills the lupin plants, but most of them recover and resprout. Numerous lupin seedlings also develop rapidly and it is usually necessary to release the trees from competition 6-9 months after planting. This is accomplished by aerial spraying with a mixture of 2,4-D and 2,4,5-T at a concentration which kills existing lupin plants but does not damage marram grass or *P. radiata*. Further lupin plants develop from seed but by this time the trees are capable of surviving competition and further releasing is unnecessary. As the *P. radiata* stand develops, lupin plants are gradually suppressed and once the tree canopy closes, the few lupin seedlings which do emerge become etiolated and die. Silvicultural operations thus suppress or damage the lupin in three ways:

- (i) by crushing at time of planting
- (ii) by spraying to release the trees
- (iii) by competition with the trees as the canopy closes. This competition is thought to be mainly for light because later thinning of *P. radiata* stands results in development of a dense lupin understory which is only suppressed as the canopy closes again.

More regular damage to lupin plants results from the activity of the kowhai moth, *Mycema maorialis*. Larvae of this moth feed on lupin leaves, and regular annual attacks of varying intensity can be expected. The population peak occurs in the summer, usually about January or February. Complete defoliation of plants can occur several times in one season and may result in death of whole branches and sometimes whole plants.

The literature contains many references to the demonstration of nitrogen transfer between legume and non-legume under conditions which involve damage to the legume, and some authors are reluctant to admit that significant transfer occurs unless the legume is under stress<sup>17</sup>. Certainly some of the highest figures for amounts of nitrogen transferred have come from systems where the vegetation was clipped or mown<sup>6,12</sup>. There are numerous reports of improved growth of associated plants when legumes are cut and used as green manure crops, and *Lupinus* spp. have proved particularly useful in this respect<sup>14</sup>. It seems reasonable to suppose that death and decay of whole lupin plants caused by crushing, spraying, and excessive defoliation and shading at Woodhill might cause similar improvement in the growth of *P. radiata*. Mineralisable nitrogen would be added to the soil in decaying roots and shoots, although there would be no incorporation of shoot material.

The effects of moderate (*i.e.* sub-lethal) defoliation and shading on nitrogen transfer are debatable. Strong and Trumble<sup>15</sup> noted 'apparent donation' of nitrogen from peas to oats only when the environment was modified, in this case by restricting daylight to two hours daily. J. K. Wilson<sup>16</sup> made a close observation of the effect of defoliation and shading on white clover plants and found that both treatments caused disintegration and disappearance of a proportion of the nodules. He believed that such disintegration, by liberating the high nitrogen content of the nodules into the soil, might account for nitrogen transfer to associated non-legumes. Butler and Bathurst<sup>3</sup> supported this theory, but Pate<sup>10</sup> held the view that nodule shedding was not a significant source of nitrogen for associated crops. P. W. Wilson<sup>17</sup> had earlier reviewed his own and Vitrano's work and maintained that the amount of nitrogen transferred was too large to be accounted for by sloughing of nodules. Butler *et al.*<sup>4</sup> revised their view of the importance of nodule shedding in nitrogen transfer when they found that defoliation and shading caused considerable root decay in three legumes. Working with mixed cultures, Simpson<sup>13</sup> came to the conclusion that different legumes might transfer nitrogen in different ways. He found that defoliation reduced competition for nitrogen in mixed cultures of white clover and cocksfoot, but also reduced positive nitrogen transfer between lucerne and cocksfoot. Butler *et al.*<sup>4</sup> had also reported a species difference, noting that patterns of nodule decay and root decomposition varied in different legumes.

The present investigation was undertaken in order to find out some of the ways in which *L. arboreus* could be expected to react to crushing, shading and defoliation, and to determine whether nitrogen uptake by *P. radiata* could be influenced by the presence of decaying lupin residues in Woodhill sand. As in the previous investigation this approach was considered essential to subsequent interpretation of field data. Three experiments are described, all of which were carried out in a lightly whitewashed glasshouse. Woodhill sand which had not previously supported any vegetation was

used throughout. The first experiment sought to examine the effect of shading and defoliation on the root system of *L. arboreus*. The second was designed to show whether distribution of nitrogen or rate of nitrogen fixation were influenced by defoliation of lupin plants. Finally the influence of decomposing lupin tops and roots on nitrogen uptake by *P. radiata* seedlings was investigated.

## EXPERIMENT 1. THE EFFECT OF SHADING AND DEFOLIATION ON THE ROOT SYSTEM OF *L. ARBOREUS*

### METHODS

The procedure was similar to that described by Butler *et al.*<sup>4</sup> Three wooden boxes (90 × 90 × 30 cm) were constructed so that one side (90 × 90 cm) formed a removable but lightproof door. A sheet of plate glass was fixed into each box in such a way that roots of plants growing in sand retained by the glass would be forced by gravity to grow against it. Interior wooden walls were coated with bituminastic paint. The boxes were placed in the glasshouse and filled with Woodhill sand which was packed evenly by watering successive layers. The sand was watered thoroughly with tap water once a week throughout the experiment; drainage holes had been provided but water loss by drainage was kept to a minimum.

Lupin seeds with chipped testas (to promote even germination) were sown, at a depth of 2 cm, in three groups of four against the glass in each box. On emergence, the seedlings were thinned to 3 evenly spaced plants per box. One seedling in Box 3 (subsequently the control) died after thinning and could not be replaced. Two weeks after sowing, and at weekly intervals throughout the experiment, the positions of all visible roots and nodules were located by means of a two-dimensional grid and recorded on squared paper. By means of careful tracing from a master diagram and a system of overlays it was possible to determine which roots and nodules had developed and which had disappeared during the previous week. In the absence of any other practical criterion, disappearance had to be accepted as the only evidence of root and nodule death. Root lengths were determined from the diagrams with a map measurer, and nodule numbers were noted.

Twelve weeks after sowing, plants in Box 1 were shaded with hessian which reduced the light intensity by about 70 per cent during dull weather and 35 per cent in sunshine. The plants in Box 2 were defoliated by removing all leaf laminae. From now on a special note was made of the appearance and fate of those nodules which were visible 12 weeks after sowing. At the end of a further 10 weeks plants in Box 3 had grown to such a size that recording of root

development became impossible. Observations were made on nodules in this box for a further two weeks but had to be discontinued when the glass plate cracked. Observations continued in the other boxes and further defoliation treatments were carried out on the plants in Box 2 when root and top growth indicated that good recovery from the previous defoliation had been made (weeks 24 and 33 respectively). Recording of root growth became impossible at week 33 but observations on nodules continued until week 36 when the experiment was terminated.

### RESULTS (EXP. 1)

The control plants in Box 3 developed large shoot systems, but defoliated plants were small and had short branches. Shading resulted in the development of tall, weak plants with only a few short branches.

#### 1. Gains and losses in root length

(a) Before treatment. Four days after sowing (before emergence), several seedlings had roots about 5 cm long. Two weeks after sowing the average tap root length was 29 cm and by the fifth week at least one root in each box had reached a depth of 80 cm. Rapid elongation of the tap roots was responsible for the initial increase in visible root length (Table 1, Fig. 1), and a peak between weeks 8 and 12 was recorded as the lateral system developed.

A weekly loss of about 2 per cent of the visible root system was fairly common, but for some reason larger losses of 4 to 8 per cent were recorded during two weeks in Box 1. Up to week 12, root loss invariably occurred in the top 20 cm of sand.

(b) After treatment. Following the commencement of shading and defoliation, patterns of root and nodule development and disappearance changed considerably. The roots of the control plants (Fig. 1) continued to grow, weekly increases ranging between 5 and 25 per cent of the existing visible root length. After week 12 root loss was almost negligible and only once reached 1 per cent of the total length in a week. Shading reduced root growth to 2 per cent or less between weeks 12 and 28, with two small peaks at weeks 18 and 23. Root loss dropped to nil after shading but showed a sharp rise to 4 per cent in weeks 16 to 17 followed by a reversion to a low level or nil. During these two weeks there was a net loss of visible root material. Defoliation reduced growth to 2 per cent or less for four to five weeks, after which recovery was observed. Loss of root material decreased to nil

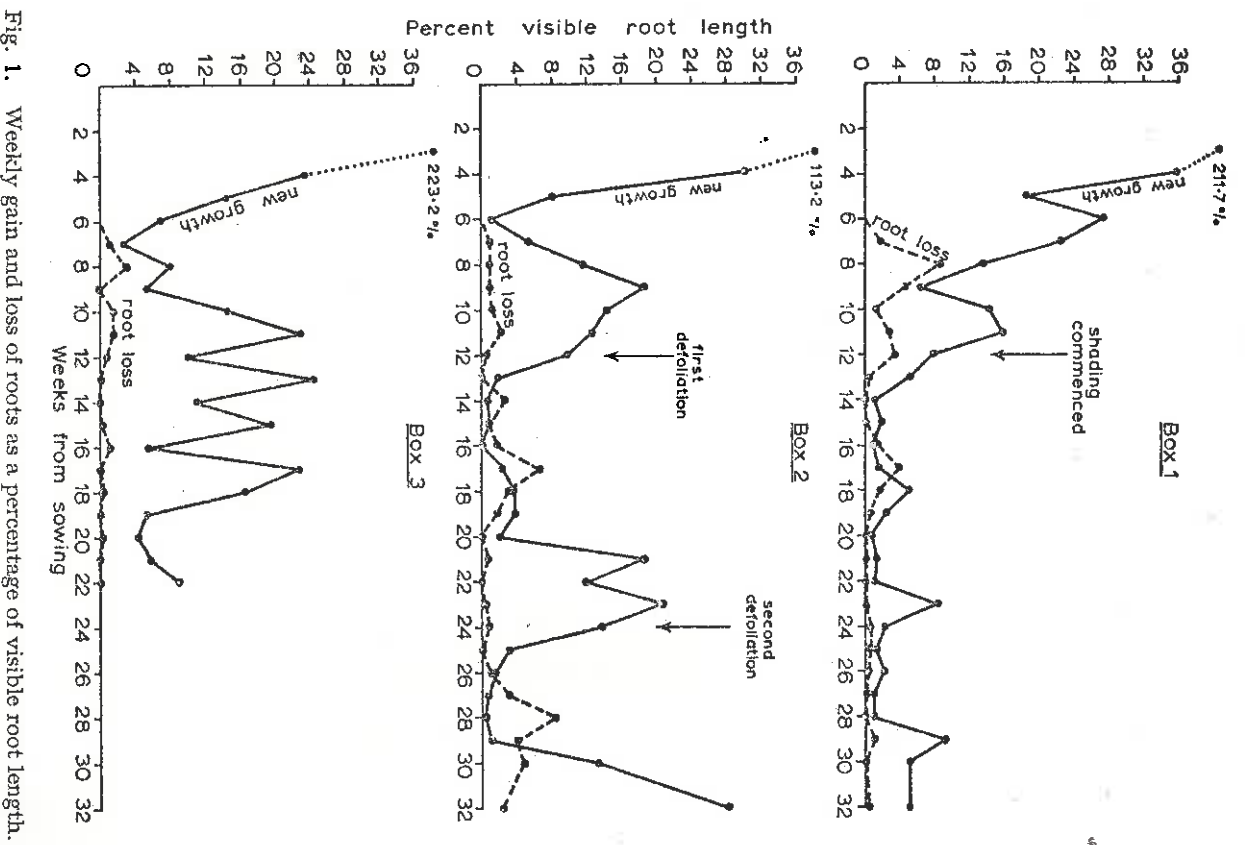


Fig. 1. Weekly gain and loss of roots as a percentage of visible root length.

TABLE 1

| Treatment | Gains and losses in root length of lupin plants |                          |       |       |           |       |       |
|-----------|---|--------------------------|-------|-------|-----------|-------|-------|
|           | Weeks from sowing                               | Visible root length (cm) |       |       | Root loss |       |       |
|           |   | Box 1                    | Box 2 | Box 3 | Box 1     | Box 2 | Box 3 |
| Nil       | 2   | 61                       | 76    | 56    | 0         | 0     | 0     |
|           | 3   | 129                      | 86    | 125   | 0         | 0     | 0     |
|           | 4   | 68                       | 49    | 43    | 0         | 0     | 0     |
|           | 5   | 47                       | 17    | 32    | 0         | 0     | 0     |
|           | 6   | 84                       | 24    | 18    | 1         | 4     | 3     |
|           | 7   | 87                       | 13    | 7     | 7         | 2     | 3     |
|           | 8   | 64                       | 30    | 22    | 40        | 2     | 8     |
|           | 9   | 31                       | 53    | 15    | 22        | 2     | 0     |
|           | 10  | 71                       | 48    | 44    | 6         | 4     | 5     |
|           | 11  | 89                       | 48    | 79    | 15        | 8     | 5     |
|           | 12  | 50                       | 42    | 43    | 22        | 2     | 3     |
|           | 13  | 34                       | 9     | 11    | 3         | 0     | 0     |
| 14        | 7   | 2                        | 62    | 0     | 12        | 0     |       |
| 15        | 14  | 4                        | 124   | 0     | 4         | 1     |       |
| 16        | 5   | 0                        | 41    | 12    | 8         | 8     |       |
| 17        | 11  | 10                       | 179   | 28    | 29        | 0     |       |
| 18        | 36  | 16                       | 160   | 12    | 13        | 2     |       |
| 19        | 17  | 16                       | 70    | 4     | 8         | 0     |       |
| 20        | 5   | 9                        | 50    | 0     | 0         | 2     |       |
| 21        | 9   | 83                       | 71    | 0     | 3         | 0     |       |
| 22        | 7   | 63                       | 144   | 0     | 0         | 0     |       |
| 23        | 63  | 121                      | —     | 0     | 2         | —     |       |
| 24        | 18  | 98                       | —     | 4     | 5         | —     |       |
| 25        | 10  | 22                       | —     | 3     | 0         | —     |       |
| 26        | 17  | 12                       | —     | 2     | 8         | —     |       |
| 27        | 8   | 5                        | —     | 0     | 23        | —     |       |
| 28        | 9   | 2                        | —     | 0     | .62       | —     |       |
| 29        | 80  | 6                        | —     | 9     | 28        | —     |       |
| 30        | 48  | 88                       | —     | 0     | 32        | —     |       |
| 31        | —   | —                        | —     | —     | —         | —     |       |
| 32        | 51  | 203                      | —     | 2     | 17        | —     |       |

Box 2 defoliated→

Box 1 shaded }  
Box 2 defoliated }→

during the week after defoliation but then rose to a peak five weeks after treatment, with a resulting net loss of root material. Three weeks later the rate of loss had returned to a low level. The second defoliation at week 24 again resulted in a drastic reduction of active root loss 3-4 weeks later. This time the net loss of material was larger and although the growth rate recovered after week 29, losses continued until the observations ceased at week 32.

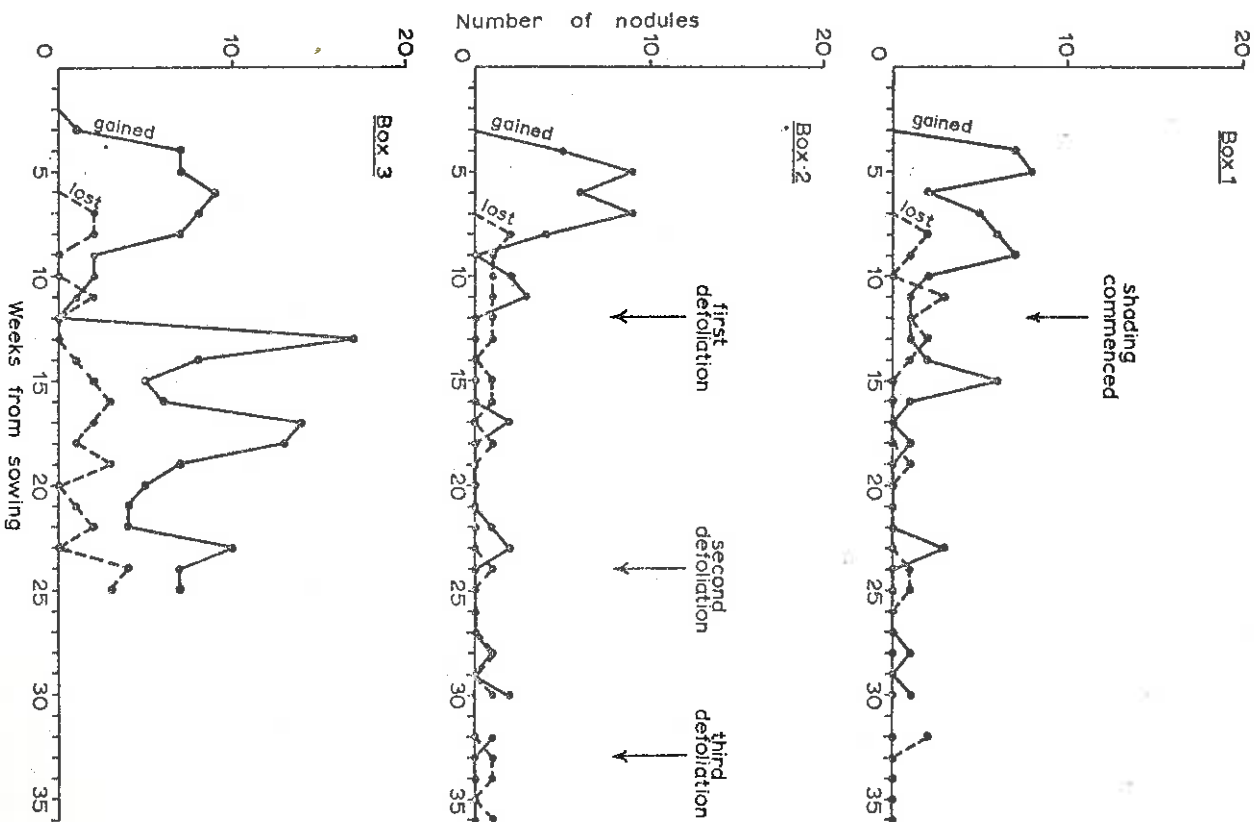


Fig. 2. Weekly gains and losses of nodules on the root systems of lupin plants subjected to shading or defoliation.

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(ii) *Nodule gains and losses*

(a) Before treatment. Nodulation commenced between weeks 2 and 4 and was at first associated only with the tap roots; lateral roots developed nodules from about week 8. In all boxes nodules were eventually observed to occur to a depth of about 75 cm. Patterns of gain and loss were fairly similar in all boxes, with a large gain in numbers at first, followed by smaller gains from weeks 9 to 10 (Fig. 2). Nodule 'losses' occurred fairly regularly from weeks 6-7 onwards. A 'loss' was recorded when a nodule ceased to be visible but it is possible that invisibility was sometimes caused by shrinkage away from the glass and subsequent sand creep. 'Effective' and ineffective nodules could not be distinguished, the pink colour of the leghaemoglobin usually being obscured by the white outer layers of tissue.

(b) After treatment. Shading and defoliation both reduced the rate of nodule turnover, nodulation being reduced by shading and almost completely inhibited by defoliation. The number of nodules lost was consistently greater in the control box than in either of the others.

Study of the nodules already in existence at week 12 showed that although actual losses were reduced by treatment, a large number almost immediately changed from the normal opaque pinkish-white colour to a translucent yellow or brown (Fig. 3). Many were observed to shrink in size. Defoliation affected more of the original nodules more suddenly than did shading, but some recovery was noted about 8 weeks after defoliation when the translucent and yellow nodules resumed a healthy appearance. The second defoliation produced a similar effect to the first, as did a third defoliation carried out at week 33 after root measurements had been discontinued. Some discoloration was noted in a small number of nodules on the control plants but this affected only 10 per cent of the total under observation at week 24, compared with over 50 per cent in the shaded plants and about 40 per cent in the defoliated plants (here 80 per cent had been affected but about half of these had recovered).

In general the appearance of the nodules changed in one of three ways:

(i) Shrinking of white, healthy nodules to a concave shape. This was common in all three boxes and was observed mainly in the case of nodules formed on the tap roots.

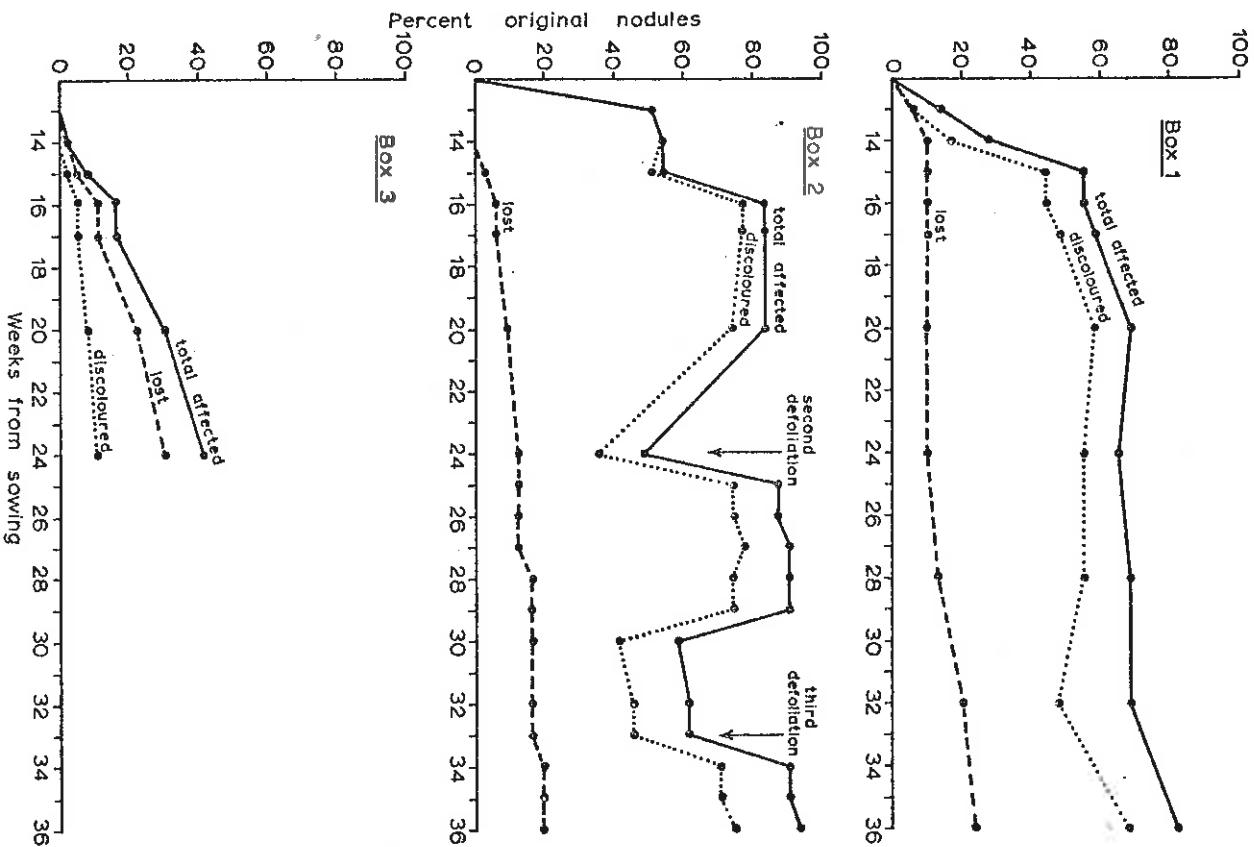


Fig. 3. Effect of shading and defoliation on subsequent changes in the number and appearance of nodules present at week 12.

(ii) Irreversible browning, wrinkling and shrinking which occurred to some extent in the nodules of all plants.

(iii) Yellowing, browning and translucence followed by shrinking. This was associated with shading and defoliation and was sometimes reversible.

#### DISCUSSION (EXPT. 1)

Under the culture conditions used, small losses of root and nodule material occurred even in untreated plants. Since roots disappeared only in the upper sand layers it is possible that intermittent drying of the sand could have been at least partly responsible. The irreversible browning and shrinking of nodules observed in all boxes may have been an expression of natural nodule senescence. Shrinking of healthy nodules to a concave shape could have been caused by distortion due to physical stretching, since it occurred mainly in the case of nodules on the fleshy tap roots. Laterally elongated nodules have been observed on lupin tap roots in the field.

The effect of shading in permanently retarding root growth and nodulation was similar to that observed for three other legumes by Butler *et al.*<sup>4</sup> Also similar was the cyclic pattern of decay and renewal of roots caused by successive defoliations. The reaction of lupin plants was more like that of the red clover and lotus of their experiments than the white clover, since nitrogen fixation was quite clearly impaired rather than stimulated by defoliation.

This can be assumed from the changes which are observed in a proportion of the existing nodules and from the inhibition of nodulation after the treatment was imposed. Plant growth generally was retarded by defoliation which must have caused temporary reduction in carbohydrate supply as well as a more permanent reduction in nitrogen fixation rate.

Nodule 'shedding' or 'sloughing' was not associated with the treatments imposed in this experiment. It is doubtful whether the observed shrinking of the nodules was due to decomposition, in the sense of disintegration of outer layers of tissue, since nodule outlines remained well-defined even when the surface was wrinkled. Shrinking may have been due to internal disintegration of the kind described by Chen and Thornton<sup>5</sup>.

## EXPERIMENT 2. THE EFFECT OF DEFOILIATION ON THE AMOUNT AND DISTRIBUTION OF NITROGEN IN LUPIN PLANTS

### METHODS

Lupin seeds were germinated in Woodhill sand and seedlings were transplanted after 7 days into 8 undrained pots, each containing 11.8 kg of Woodhill sand, at the rate of 2 per pot. The pots were watered regularly and uniformly with demineralised water. When the plants were 12 weeks old, those in four of the pots were completely defoliated. The leaf laminae were dried at 80°C in a forced draught oven, weighed and ground in a small Wiley mill. Ten days later all the plants were harvested and divided into leaf, stem, root and nodule fractions for each pot. A core sample of sand was taken from the base of every pot, roots and nodules being dissected out carefully and placed with the appropriate plant samples. The sand was dried at room temperature.

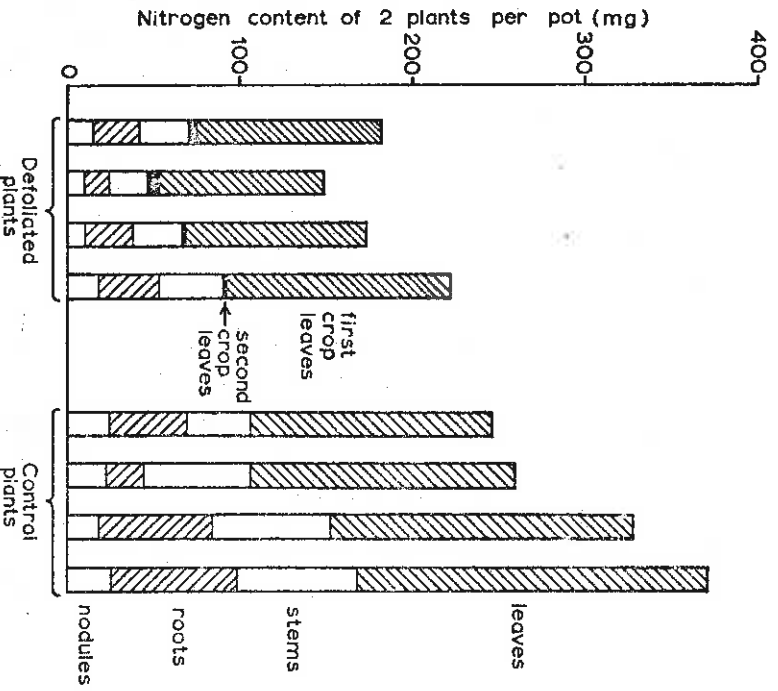


Fig. 4. Distribution of nitrogen in defoliated and control lupin plants.

Plant material was oven-dried, weighed, ground and analysed for nitrogen using a semi-micro Kjeldahl technique<sup>1</sup>. Sand samples received pretreatment<sup>2</sup> to ensure quantitative determination of nitrites and nitrates by Kjeldahl analysis.

TABLE 2

Distribution of nitrogen among the various parts of lupin plants (Figures expressed as a percentage of the total weight of plant nitrogen in each culture)

| Plant parts | Defoliated plants | Control plants |
|-------------|-------------------|----------------|
| Leaves      | 62.2              | 56.9           |
|             | 69.2              | 59.3           |
|             | 61.8              | 53.7           |
|             | 60.2              | 54.9           |
|             |                   |                |
| Stems       | 15.2              | 14.9           |
|             | 14.7              | 23.7           |
|             | 16.1              | 20.8           |
|             | 16.4              | 18.9           |
|             |                   |                |
| Roots       | 14.6              | 18.4           |
|             | 9.3               | 8.5            |
|             | 16.2              | 20.1           |
|             | 15.5              | 19.5           |
|             |                   |                |
| Nodules     | 7.9               | 9.7            |
|             | 6.8               | 8.5            |
|             | 5.8               | 5.3            |
|             | 7.9               | 6.7            |

### RESULTS AND DISCUSSION (EXPT. 2)

Defoliation caused a decrease in total plant nitrogen content per pot (Fig. 4) and appeared to be responsible for certain changes in the proportion of nitrogen found in the various plant parts. Leaf nitrogen, totalled where appropriate for both harvests, and expressed as a percentage of the total plant nitrogen for each pot (Table 2) apparently increased slightly as a result of defoliation while stem and root nitrogen decreased. The nitrogen content of the nodule material was not affected. No consistent differences were observed between the nitrogen content of sand from the pots which had contained defoliated plants and that of sand from pots which had contained the control plants (Table 3).

TABLE 3

| Nitrogen content (% oven-dry weight basis)<br>of sand from Experiment 2 cultures |                  |
|--|------------------|
| Defoliated cultures  | Control cultures |
| 0.004  | 0.008            |
| 0.008  | 0.008            |
| 0.012  | 0.008            |
| 0.012  | 0.007            |

There was no evidence in this experiment that the decreased nitrogen content of the defoliated plants was associated with release of nitrogen into the sand. A more probable explanation is that the capacity for nitrogen fixation was impaired as a result of damage to the plant, possibly through temporary curtailment of carbohydrate supply. When harvested, the newly developing leaves contained the same percentage of nitrogen as the leaves already removed. This could have been accumulated at the expense of stem and root nitrogen.

### EXPERIMENT 3. EFFECT OF DECAYING LUPIN RESIDUES ON NITROGEN UPTAKE BY *P. RADIALTA* SEEDLINGS

#### METHOD

Sixteen 10-l undrained plastic pots containing Woodhill sand were used in this experiment. Each pot was watered to field capacity twice weekly. Two lupin plants per pot were raised from seed in each of 8 pots, and allowed to grow for 12 weeks, when the tops of each pair of plants were severed at sand level, cut into several pieces and crushed between two layers of plastic sheeting. Four pairs of crushed tops were returned to the surface of sand in four unplanted pots. The remaining pots acted as controls. *P. radiata* seedlings which had been germinated in perlite were transplanted when three weeks old into all pots at the rate of 2 per pot. Shoots developing on the lupin 'stumps' in cultures containing lupin roots were removed periodically until the plants were killed. *P. radiata* seedlings were allowed to develop for 12 weeks, when those from two pots in each of the four treatments were

harvested. The remaining plants were harvested 12 weeks later. Tops and roots were dried, weighed, ground and analysed for nitrogen using the same methods as in Experiment 2.

#### RESULTS AND DISCUSSION (EXPT. 3)

*P. radiata* seedlings which grew in the pots containing decomposing lupin roots absorbed more nitrogen than either the control seedlings or those grown in the presence of lupin tops only (Fig. 5). There was little or no difference in terms of nitrogen uptake between *P. radiata* seedlings grown with lupin roots plus tops and those grown only with lupin roots. The effect produced by decomposing lupin roots was apparent after three months. The lupin roots had almost completely decomposed by the time of the second *P. radiata* harvest, but the lupin tops were still recognisable. Whether the additional nitrogen absorbed by the *P. radiata* seedlings has been fixed by the lupin-*Rhizobium* symbiosis is open to question: the lupin residues may have stimulated the activity of other nitrogen-fixing systems in some way.

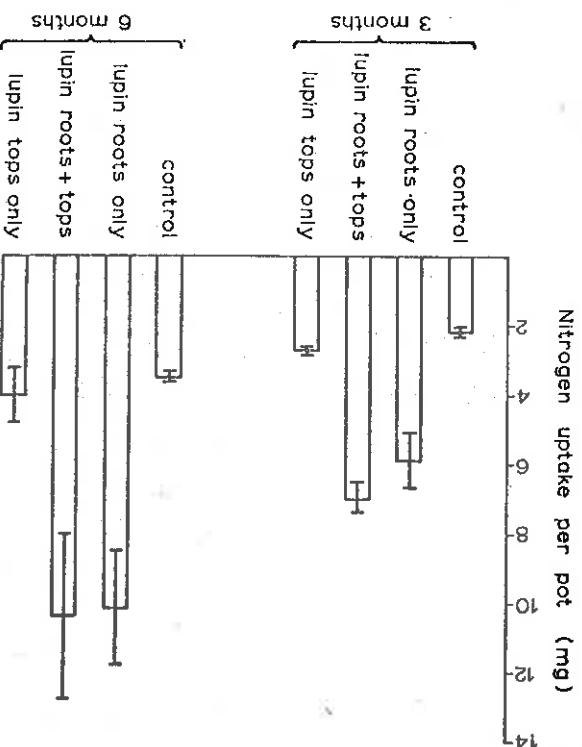


Fig. 5. Effect of lupin residues on nitrogen uptake by *Pinus radiata* seedlings



## GENERAL DISCUSSION

These investigations have established that all three forms of stress imposed on lupin plants (sudden shading, defoliation, slashing and crushing) caused changes in the root system leading to a certain amount of abnormal decomposition. Although there is no evidence that nodule sloughing or shedding was associated with the treatments, changes certainly occurred within the nodules. These were apparently reversible in the case of defoliation. Root growth and nodulation were both inhibited by the treatments although after defoliation root growth recovered. It is not known whether inhibition of nodulation or the internal nodule changes were responsible for decreased nitrogen content of defoliated plants in Experiment 2. The harvesting of these plants was probably carried out too early for the full effects of the treatment to be observed: at 10 days after defoliation in Experiment 1 root decomposition resulting from the treatment had only just begun, and maximum root loss was usually observed 4 to 5 weeks after treatment.

Experiment 3 showed that the presence of decomposing lupin root material increased nitrogen availability to *P. radiata* in some way. Considering the fact that lupin tops contain more nitrogen than the root system (Experiment 2) it is surprising that no noticeable effect on *P. radiata* could be attributed to the tops. Rapid decomposition was unlikely to have been encouraged by laying the lupin plant material on the sand surface in the rather dry atmosphere of the glasshouse, and a period of time longer than six months may have been required for effective decomposition to occur. The material dried out rapidly even though it was carefully moistened each time the pots were watered. Günther and Morgeneyer<sup>8</sup> compared the effect of dry lupin tops with that of roots (both ploughed into the soil) on growth of poplar cuttings and came to the conclusion that the tops produced a stimulatory effect, but at a much later stage than that produced by the roots. In their work, and also in Experiment 3 above, the effect of the lupin tops might have occurred sooner if they had been incorporated into the soil without drying. Kobus and Pacewiczowa<sup>9</sup> have shown that lupin residues decompose rapidly in sandy soil, with consequent rapid mineralisation of nitrogen. It would be surprising if none of the nitrogen absorbed by *P. radiata* in Experiment 3 was derived from the lupin material. While

it is clear that in this experiment the killing of the lupin plants ensured that all the lupin-nitrogen (mineralisable or not) was returned to the sand, it cannot be assumed that equivalent amounts of decomposing root material from plants subjected to sub-lethal treatment would liberate equivalent amounts of nitrogen into the environment. The results of Experiment 2 indicate that rather rapid changes in the proportion of nitrogen found in various plant parts can occur after defoliation and it is possible that maintenance of a supply of nitrogen to newly developing leaves may involve net export from the root tissue before fixation by root nodules has resumed its normal rate.

The significance of these results in future evaluation of the nutritional role of lupin in the field can now be discussed. Dead lupin plants and to a lesser extent those subjected to stress in the form of shading or defoliation are potentially capable of releasing decomposable material into the environment and this material is potentially capable of increasing nitrogen availability to *P. radiata*. Therefore under certain conditions, which may well exist in the field but have not yet been defined, a positive effect on the nitrogen nutrition of *P. radiata* additional to that of undamaged plants might be expected when lupin is:

- (i) defoliated by kowhai moth larvae
- (ii) crushed when *P. radiata* is planted
- (iii) killed by hormone spray
- (iv) suppressed by shading as the tree canopy closes

In the case of hormone spraying, shading, and to a certain extent crushing, the ultimate death of individual lupin plants would terminate their influence. Some recovery from crushing and kowhai moth attack is observed in the field and it might be expected that the influence of individual plants on the nitrogen nutrition of *P. radiata* could continue at a rate dependent on the extent to which their nitrogen fixation rate and growth rate had been affected.

A small amount of lupin root loss was observed in all the cultures in Experiment 1 even before shading or defoliation commenced and this could have been the result of drying out of the surface layers of sand. The possibility of this type of damage occurring in hot, dry weather and its potential significance in the release of nitrogen from lupin plant material to the soil should not be overlooked.

Finally it must not be forgotten that kowhai moth attacks could have a very important secondary effect on transfer of lupin nitrogen in the field. Faecal material and dead larval bodies falling to the ground undoubtedly result in the release of nitrogenous compounds into the soil when they decompose. This nitrogen must originate from the lupin leaves on which the larvae feed. Should it eventually become available for plant growth the mechanism would have to be regarded as a component in the overall effect of kowhai moth defoliation of lupin plants on nitrogen uptake by *P. radiata*.

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## SEED QUANTITIES

|        |      |      |   |   |     |
|--------|------|------|---|---|-----|
| Yellow | culm | 3600 | : | 1 | lb. |
| Blue   | "    | 3200 | : | 1 | lb. |
| White  | "    | 3200 | : | 1 | lb. |