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The Effects of Height and Frequency of Previous Defoliation on Nodulation, Nitrogen Fixation and Regrowth of Phasey Bean

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Key words: Cumulative dry matter yield; recovery growth; nitrogen accumulation in new shoots.

ABSTRAK

Biji benih kacang phasey (Macroptilium lathyroides *cv. Murray) yang telah disuntik ditanam dengan kaedah kultur pasir dalam rumah kaca, dan disiram tiap-tiap hari dengan larutan nutrien tanpa nitrogen. Pada peringkat awal pembungaan, pokok-pokok ditinggal tanpa potong atau dipotong pada buku kelima (tinggi) atau buku pertama (rendah), meninggalkan daun tunggul seluas 74, 11 dan 0cm² per pokok. Selepas pemotongan asal ini, pucuk baru dipungut secara individu dari tunggul sebanyak satu, dua, tiga, empat atau lapan kali dalam jangka masa 56 hari dalam Fasa 1. Jumlah berat kering pucuk muda, hasil biji dan kepekatan nitrogen dalam hasil foraj ditentukan. Semua pokok dibiarkan tumbuh semula selama 21 hari berikut dalam jangka masa tumbuh pulih dalam Fasa 2. Kemudian sistem-sistem akar dan bahagian atasan pokok dipungut. Pembintilan, pengikatan nitrogen (jumlah N) dan analisis regresi terhadap beberapa parameter pokok dikira. Dalam Fasa 1, jumlah hasil pucuk baru yang dipungut selepas potongan tinggi atau rendah merosot dengan ketara dengan meningkatnya kekerapan pungutan, tetapi kekurangan hasil disebabkan oleh potongan rendah dapat dikesan cuma pada kekerapan pungutan yang tinggi sahaja. Di Fasa 2, tumbuh pulih sentiasa lebih baik selepas potongan tinggi daripada potongan rendah, tetapi di luar jangkaan, berbagai kekerapan pungutan tidak ada kesan terhadap tumbuh pulih selepas potongan tinggi. Selepas potongan rendah, kekerapan pungutan yang tinggi atau rendah menjejaskan tumbuh pulih berbanding dengan kekerapan sederhana (dua pungutan dalam masa 56 hari), yang berkebetulan dengan peringkat awal pembungaan di atas pucuk baru. Tumbuh pulih mempunyai korelasi linear yang positif (r = 0.98***) dengan pengikatan nitrogen, yang juga mempunyai korelasi linear dengan pembintilan. Keputusan hasil-hasil ini dibincangkan secara ringkas dengan merujukkan kepada konsep masa kini tentang tumbuh semula kekacang foraj berbintil bergantung kepada pengikatan nitrogen secara simbiotik.*

ABSTRACT

*Inoculated seeds of phasey bean (*Macroptilium lathyroides *cv. Murray) were sown in a sand culture in a naturally-lit glasshouse, and irrigated daily with nitrogen-free nutrient solution. At early flowering, the plants were either left uncut or cut at node 5 (high) or node 1 (low), retaining the corresponding residual leaf areas of 74, 11 and 0cm² plant⁻¹ respectively. Following this initial cutting, new shoots were individually harvested at the frequency of one, two, three, four or eight times over a period of 56 days in Phase 1. Total dry weight of new shoots, seed yields and nitrogen concentrations in the herbage were assessed. All plants were allowed to regrow during the next 21-day recovery period in Phase 2. Then, the root systems and plant tops were harvested. Nodulation,*

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*nitrogen fixation (total N) and regression analyses on some plant parameters were computed. In Phase 1, cumulative yields of new shoots harvested following high or low-level cutting declined significantly with increasing harvesting frequency, but yield reductions due to low-level cutting were detected only under high harvesting frequencies. In Phase 2, recovery growth was always better following high than low-level cutting, but unexpectedly, the various harvesting frequencies had no effect on recovery growth following high cutting. After low-level cutting, high or low harvesting frequency reduced recovery growth compared with moderately frequent defoliation (two harvests in 56 days), which coincided with early flowering on the new top growth. Recovery growth had a positive linear correlation (r = 0.98***) with nitrogen fixation, which was also linearly correlated with nodulation. These results are briefly discussed with reference to the current concept that regrowth of nodulated forage legumes is largely dependent on symbiotic nitrogen fixation.*

INTRODUCTION

Poor regrowth of temperate perennial pasture legumes following frequent cutting is often associated with low levels of root carbohydrate reserves (Graber *et al.*, 1927; Smith 1962; Reynolds 1971). Langer and Steinke (1965) showed that improved regrowth of lucerne *(Medicago sativa)* following high cutting was attributed to the retention of a larger foliage after defoliation and increased root weight which is often positively associated with root reserves. Ludlow and Charles-Edwards (1980) emphasized the importance of leaf area index and light interception in increasing the dry matter production of a tropical grass + legume pasture subjected to high cutting and long (five-weekly) interval of defoliation. *Crotalaria juncea,* an erect tropical forage legume, showed better nodulation and regrowth following high than low level defoliation (Kessler and Shelton, 1980). Other studies (Jones 1974; Lazier 1981) indicated that very long previous cutting intervals or repeated low level defoliation were detrimental to regrowth of some other tropical legumes. However, there is little experimental evidence in the literature on the influence of symbiotic nitrogen fixation in regrowth of forage legumes subjected to very long or very short harvesting intervals. This paper examines the effects of previous cutting heights and harvesting frequencies on nodulation, nitrogen fixation and subsequent regrowth of phasey bean, an erect annual or biennial tropical pasture legume.

MATERIALS AND METHODS

Cultural Techniques

Plastic pots of 17.5cm diameter were each lined on the inside with a plastic bag, the bottom of which was perforated for drainage, and filled with 3.43kg of thoroughly washed coarse (0.2 – 2.0mm diameter) and fine (0.02 – 0.2mm diameter) sand mixed in the ratio of 3:1. On 29th August, 1978 twelve phasey bean seeds were inoculated with *Bradyrhizobium* strain CB 756 (approximately 3000 cells per seed), and sown to a depth of 1.0cm in each pot. The pots were moistened daily with deionized water, and after seedling emergence, were irrigated on alternate days during the first month, and thereafter daily with 150ml pot^{-1} of nitrogen-free nutrient solution of the composition used in an earlier experiment (Wan Mohamad *et al.*, 1986).

The minimum and maximum air temperatures in the glasshouse throughout the experimental period were 22.2 and 29.5°C respectively. Two weeks after seedling emergence, the plants were thinned to six pot^{-1}.

Treatments and Experimental Design

When 10% of the plant population had one or more open flowers (10% flowering), approximately 10 weeks after sowing, the plants were defoliated according to the scheme described below:

In Phase 1 (treatment phase – 56 days), the plants were subjected to 11 treatment combinations including an uncut control. Plants were initially left uncut or cut at Node 5 (high) or Node 1 (low). The area of leaves remaining on the stubble was 74, 11 and 0cm^2 plant^{-1} respectively. The corresponding stubble height was 30cm for the uncut control and 11 and 5cm for the high and low stubble. Then, new shoots were carefully harvested from the stubble at five harvesting frequencies: one, two, three, four and eight times in 56 days. The approximate harvesting intervals were 56, 28, 18, 14 and 7 days respectively.

At the end of Phase 1, (the uncut plants were at seed-ripening stage), the control plants were cut at node 5, and then all plants were allowed to regrow concurrently for 21 days in the recovery period in Phase 2 (see *Fig. 1*)

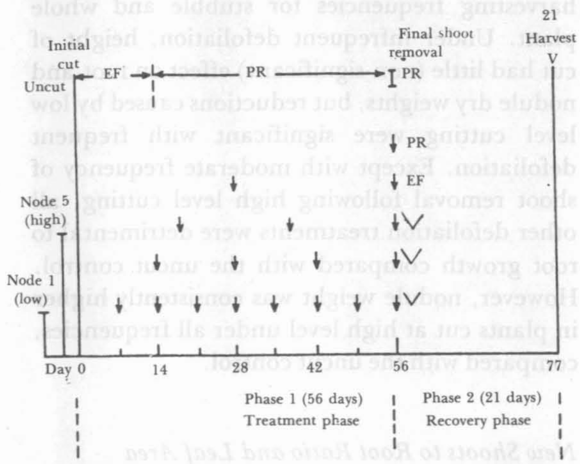

Fig. 1: Diagrammatic representation of defoliation scheme used in the present study. Each arrow indicates the approximate time of removal of shoots on the tall and short stubble. Stages of top growth at the end of Phase 1 are denoted by: V = vegetative; EF = early flowering; PR = pod-filling and ripening

The 11 factorial treatment combinations were arranged on a randomised block design with four replications. Pots within the same block were re-randomised once in three to four weeks to minimize any positional effect in the glasshouse.

Harvesting

In Phase 1 new shoots were individually removed from the leaf axils by cutting them at their bases, making sure that stubble leaves were left intact. Ripe pods on the uncut control or on the infrequently defoliated plants were harvested before they shattered, and seed yields recorded. Flowers and immature pods (of negligible weights) were included in vegetative yields.

At the end of Phase 2, plant tops (all at vegetative stage) were cut at the level of the sand surface and the sand washed off the root systems by placing them on a sieve under running water. The plants were later separated into roots, nodules, stubble, stubble leaves (if any) and new shoots. Area of new leaves was measured with an electronic leaf area meter. The plant parts were dried in a dehydrator at 80°C for 24 hours, weighed and ground in a hammer mill using a 0.25mm mesh screen.

Total Nitrogen Analysis

Subsamples of dried, ground plant material (approximately 0.25g) were subjected to Kjeldahl digestion and assayed for total nitrogen according to the methods described earlier (Wan Mohamad *et al.*, 1986).

RESULTS

Cumulative Yields and Recovery Growth

In Phase 1, the cumulative yields decreased with increasing frequency of shoot removal *(Fig. 2a)*. There was a tendency for yields to be lower following low (node 1) than high (node 5) level cutting, but differences were significant ($P < 0.01$) only with three and four harvesting frequencies during the 56 day period. Under infrequent harvesting (once in 56 days) new shoots on the 5-node and 1-node stubble started to flower approximately 20 and 28 days respectively after the initial cutting, followed by rapid pod-filling and ripening. Hence, in plants subjected to this frequency of defoliation, mature pods were the major component of regrowth, consisting of 43% (8.9g) and 53% (10.7g) of cumulative yields following low and high level cutting respectively. Although the yield of top growth in the uncut control was the highest among all treatments, approximately 62% (equivalent of 19.7g) of the total weight was ripe pods. Seed yields obtained in the infrequent defoliation were apparently unaffected by cutting height. However, compared with the control, cutting at node 1 or node 5 reduced seed yield by approximately 45 to 55%. This reduction was primarily due to the removal of existing racemes or the potential sites of pod development.

In Phase 2, recovery regrowth was little affected by various frequencies of previous defoliation when the initial cut was high. However, following low level cutting, infrequent or frequent harvesting significantly reduced ($P < 0.01$) regrowth compared with the moderately frequent defoliation of two harvests in 56 days.

Compared with high level cutting, low cutting reduced ($P < 0.01$) regrowth at all frequencies of defoliation, the reductions being particularly large with 3, 4 or 8 shoot removals in the previous phase (*Fig. 2b*). In this phase, the highest yields of regrowth were obtained with the control or with plants subjected to high level cutting and defoliation at a moderate frequency (i.e. at 28-day interval).

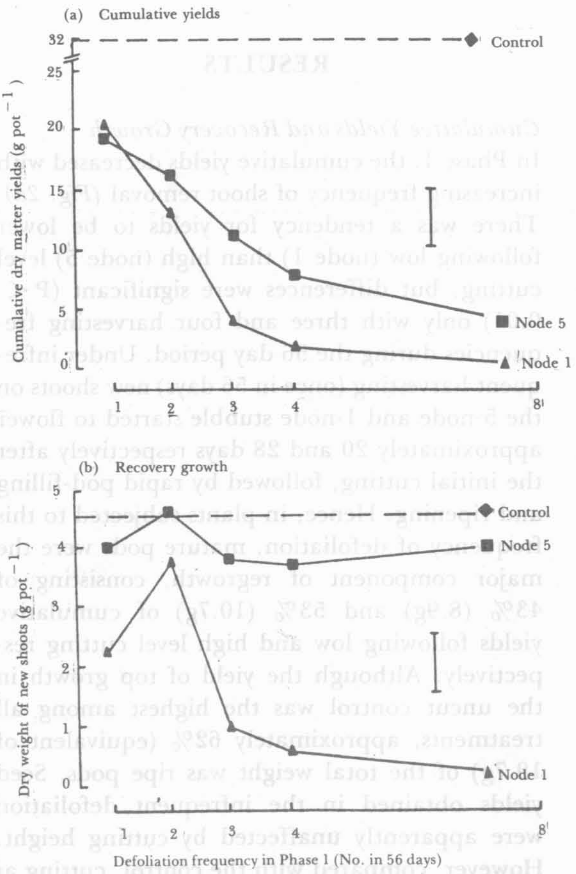

Fig. 2: Effects of high (node 5) and low (node 1) level cutting and frequency of defoliation on cumulative dry matter yields, in Phase 1, and on subsequent 21-day recovery growth in Phase 2. Vertical bars denote LSD's at P = 0.01.

Root, Nodule and Total Plant Dry Weights (Phase 2)

The dry weight of stubble, roots, nodules and hence the growth of whole plants were consistently greater following high than low level cutting (*Fig. 3*). Differences between these cutting heights were highly significant ($P < 0.01$) at all harvesting frequencies for stubble and whole plant. Under infrequent defoliation, height of cut had little (non-significant) effect on root and nodule dry weights, but reductions caused by low level cutting were significant with frequent defoliation. Except with moderate frequency of shoot removal following high level cutting, all other defoliation treatments were detrimental to root growth compared with the uncut control. However, nodule weight was consistently higher in plants cut at high level under all frequencies, compared with the uncut control.

New Shoots to Root Ratio and Leaf Area (Phase 2)

The dry weight ratios of new shoots to roots indicate the relative growth retardation caused by defoliation treatments. A high shoot to root ratio suggests that defoliation has a more depressing effect on root than shoot growth, and vice versa. Frequent defoliation following high level cutting increased ($P < 0.01$) new shoot to root ratio (1.34 or 1.64) compared with the control (0.71), but significantly reduced shoot to root ratio (0.30 or 0.65) in plants cut at low level (Table 1). Following high level cutting, new shoot to root ratio generally decreased with decreasing harvesting frequency, but it showed the reverse trend (up to 2 defoliations and again declined) when plants were cut at low level. New shoot to root ratio of plants cut at node 1 and defoliated at moderate frequency was significantly greater ($P < 0.01$) than that in the control (Table 1).

Following high or low cutting, area of new leaves increased with decreasing frequency of defoliation, reached maximum values at frequencies of 3 (node 5) or 2 (node 1) times shoot removal and then declined or remained unchanged after node 1 cutting. Under infrequent or moderately frequent defoliation, low level cutting increased ($P < 0.01$) area of new leaves

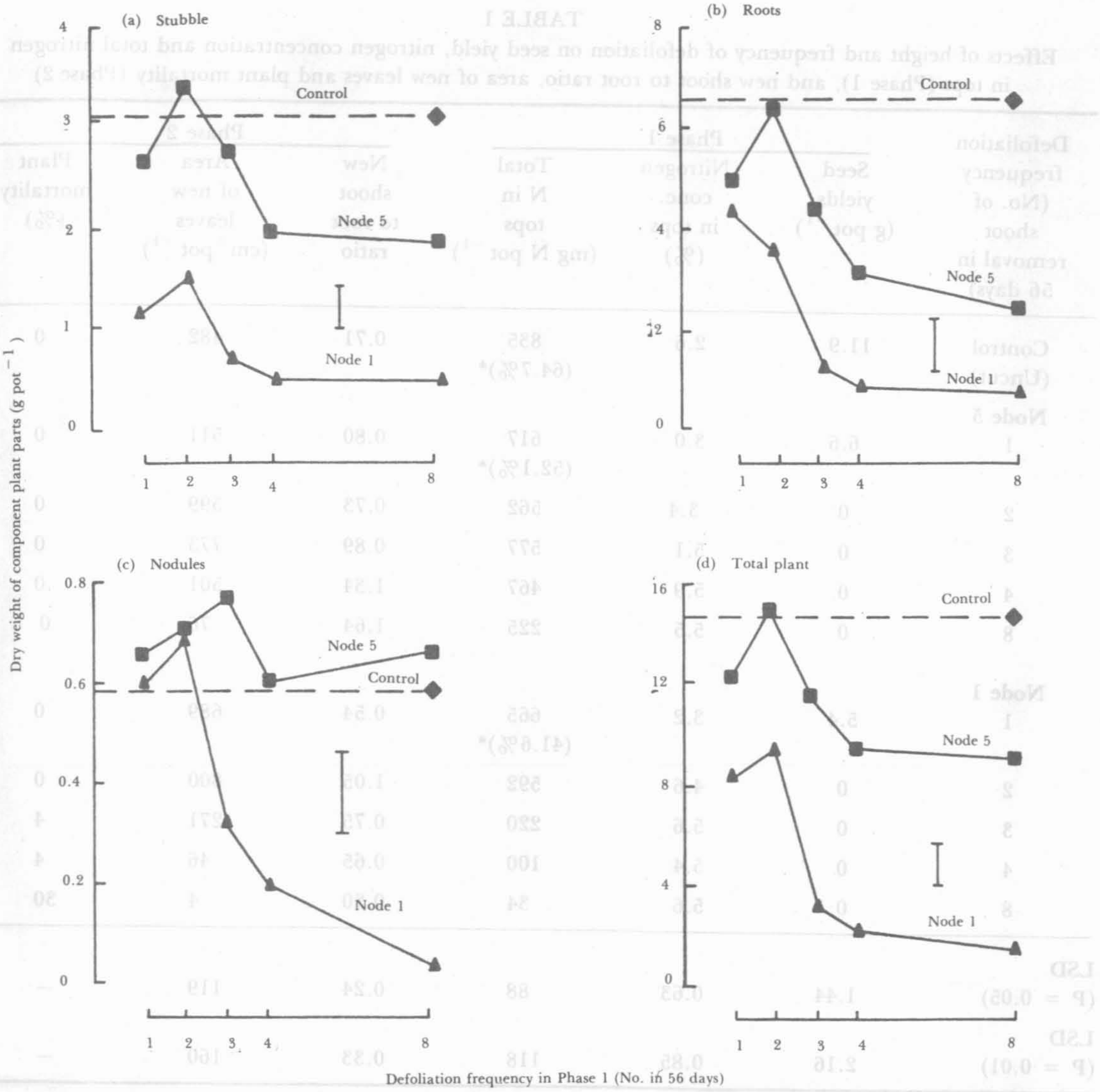

Fig. 3: Effects of high (node 5) and low (node 1) level cutting and frequency of defoliation on the dry weight of stubble, roots, nodules, and total plant, including new shoots, in Phase 2. Vertical bars denote LSD's at P = 0.01.

compared with high cutting or the control. However, height of cut had little effect on leaf area expansion when plants had been subjected to the most frequent defoliation treatment. In two frequent defoliation treatments (3 and 4 shoot removals in 56 days) area of new leaves was increased by raising the height of cut. Differences in leaf area between the control and infrequent defoliation after high level cutting were not significant.

Very frequent low level cutting caused a high proportion (30%) plant mortality, but this mortality could be reduced or avoided by harvesting less frequently or by raising the height of cut that retained some stubble leaves.

Nitrogen Concentration and Total N Recovered in Tops (Phase 1)

The nitrogen concentration in new shoots generally increased with increasing frequency of defoliation, but total nitrogen in herbage (and hence crude protein yields) followed a reverse trend (Table 1). Under infrequent defoliation, height of cut had no significant effect on nitro-

TABLE 1

Effects of height and frequency of defoliation on seed yield, nitrogen concentration and total nitrogen in tops (Phase 1), and new shoot to root ratio, area of new leaves and plant mortality (Phase 2)

Defoliation frequency (No. of shoot removal in 56 days)	Phase 1			Phase 2		
	Seed yields (g pot $^{-1}$)	Nitrogen conc. in tops (%)	Total N in tops (mg N pot $^{-1}$)	New shoot to root ratio	Area of new leaves (cm ^{2} pot $^{-1}$)	Plant mortality (%)
Control (Uncut)	11.9	2.6	835 (64.7%)*	0.71	482	0
Node 5						
1	6.6	3.0	617 (52.1%)*	0.80	511	0
2	0	3.4	562	0.73	599	0
3	0	5.1	577	0.89	773	0
4	0	5.9	467	1.34	501	0
8	0	5.5	225	1.64	76	0
Node 1						
1	5.4	3.2	665 (41.6%)*	0.54	689	0
2	0	4.6	592	1.05	800	0
3	0	5.6	220	0.75	271	4
4	0	5.4	100	0.65	46	4
8	0	5.6	34	0.30	4	30
LSD ($P = 0.05$)	1.44	0.63	88	0.24	119	—
LSD ($P = 0.01$)	2.16	0.85	118	0.33	160	—

*Figures in parenthesis refer to the proportion of nitrogen accumulated by ripe pods. Top growth of plants in other treatment was in vegetative or pre-flowering stages.

gen concentration and nitrogen recovered in tops. With frequent defoliation, total nitrogen in herbage was higher ($P < 0.01$) following high than low level cutting. The trends of total nitrogen in tops were closely related to those of cumulative yields in *Fig. 2a.* Although nitrogen accumulation in tops of uncut control and in new shoots removed infrequently was significantly high ($P < 0.01$) compared with that of other treatments, a major proportion (42 to 65%) of the nitrogen was gained by ripe pods (Table 1)

Nitrogen Accumulation in New Shoots and Nitrogen Fixation (Phase 2)

Nitrogen accumulation in new shoots and total plant nitrogen recovered in Phase 2 were generally greater ($P < 0.01$) following high than low cutting especially when harvesting frequency had been high *(Fig. 4a).* In plants cut at low level, nitrogen accumulated by new shoots reached a maximum level (228mg N pot $^{-1}$) when previous harvesting frequency was moderate, but nitrogen gained by these shoots was significantly reduced ($P < 0.01$) when harvesting frequency had been low or high. In plants cut at high level nitrogen accumulated by new shoots showed a tendency to increase with increasing frequency of defoliation, but these increases were generally not significant. Only when plants were subjected to a moderate frequency of defoliation in Phase 1, height of cutting had no significant effect on nitrogen accumulation in new shoots, and on total plant nitrogen recovered in Phase 2.

Since nitrogen from seed source was very small (approximately 0.5mg N seed^{-1}), no supplementary nitrogen was applied to these plants, and the recovery period was the same for all treatments, total nitrogen in the whole plant was considered a reliable estimate of rates (or amounts) of symbiotic nitrogen fixation, the major source of nitrogen for regrowth in these cultural environments. Nitrogen fixation followed the general trend of reaching a peak amount at moderate frequency of defoliation when plants were cut at either high or low level in the previous phase *(Fig. 4b)*. Under moderate harvesting frequency, height of cut had little (non-significant) effect on nitrogen fixation, but reductions due to low cutting were particularly large (significant at $P < 0.01$) under infrequent or frequent defoliation. Nitrogen fixation was virtually unaffected by various harvesting frequencies when plants were cut at high level. However, in plants cut at low level, nitrogen fixation was significantly reduced by frequent or infrequent defoliation. Of the nitrogen fixed by plants at the end of the second phase, a large proportion (45 to 65%) accumulated in the new top growth *(Fig. 4a)*.

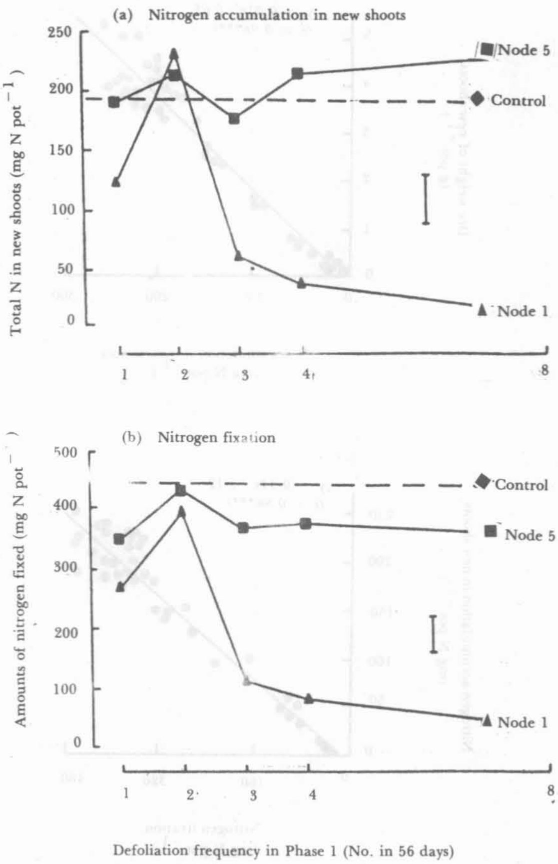

Fig. 4: Effects of high (node 5) and low (node 1) level cutting and frequency of defoliation on nitrogen accumulation in new shoots during Phase 2, and the amounts of nitrogen fixed. Vertical bars denote LSD's at P = 0.01.

Relationships Between Nodule Dry Weight, Nitrogen Fixation and Regrowth

There was a highly significant ($P < 0.01$) positive linear correlation between the dry weight of new shoots and the amount of nitrogen gained by these shoots *(Fig. 5a)*. Similarly, regrowth, nitrogen accumulation in new shoots and nitrogen fixation were linearly related *(Figs. 5b, 5c)*. The slopes in *Figs. 5c* and *5b* indicated respectively that for every 100mg N fixed by the plant, 53mg N was gained by the new shoots which consequently resulted in 1g increase in regrowth. The amount of nitrogen fixed was in turn dependent on the growth of nodules *(Fig. 5d)*. The relationship between nodule dry weight and nitrogen fixation was also linear, and positively correlated.

DISCUSSION

Effects of Pod Development and Nitrogen Fixation on Regrowth

The results *(Fig. 2* and Table 1) indicated that repeated low-level defoliation was detrimental to dry matter production, subsequent regrowth and plant survival. However, this detrimental effect was markedly reduced by high level cutting that

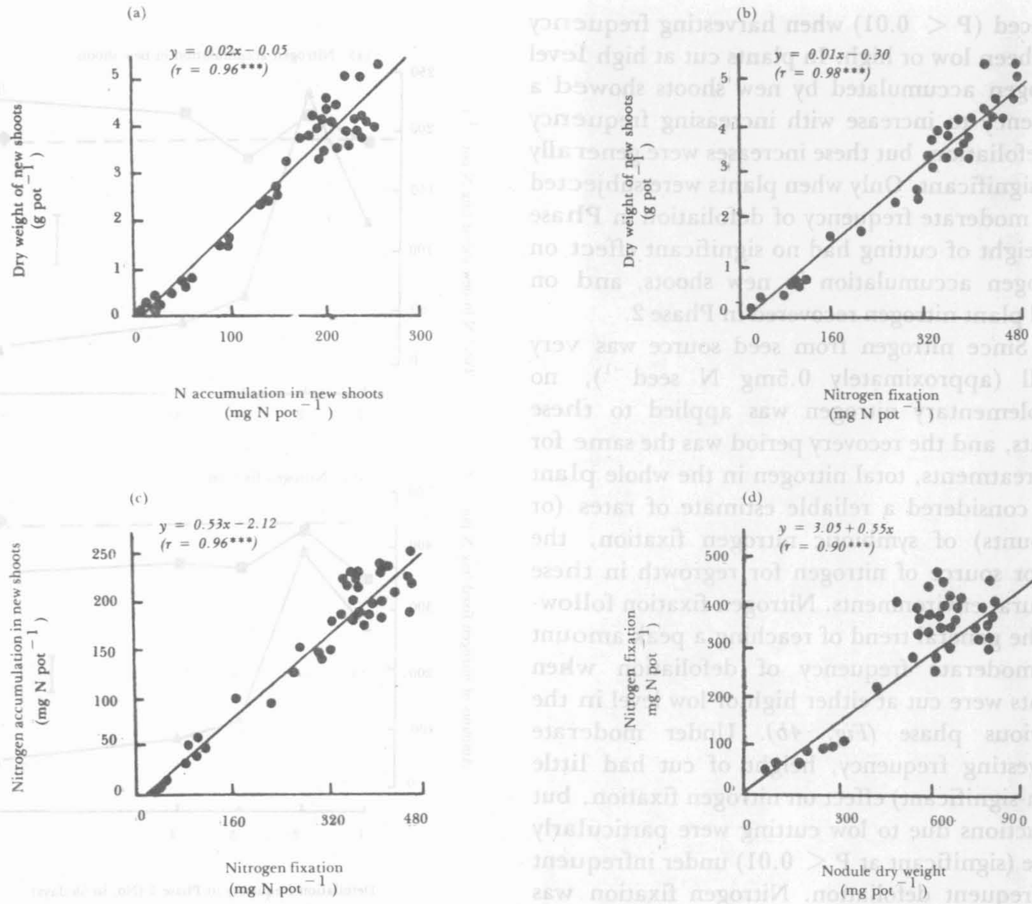

*Fig. 5: Regression lines, regression equations and correlation coefficients (r) of nitrogen fixation by cut phasey bean plants, on a number of related parameters: (a) nitrogen accumulation in new shoots and regrowth, (b) nitrogen fixation and regrowth, (c) nitrogen fixation and nitrogen accumulation in new shoots, and (d) nodule dry weight and nitrogen fixation. Highly significant level (P = 0.001) is denoted by***.*

retained some green leaves. These findings generally agreed with studies with other pasture legumes (Langer and Steinke 1965; Kessler and Shelton 1980). The poor recovery growth following this severe (frequent low-level) defoliation was apparently associated with low rates of nitrogen fixation and consequently reduced nitrogen supply to the new shoots *(Figs. 2b and 4)*. This severe defoliation practice also retarded root growth, nodule development and general plant growth, compared with the frequency of defoliation that coincided with early flowering and with peak period of nitrogen fixation *(Figs. 2, 3, 4)*. Since nodule dry weight, nitrogen fixation, nitrogen accumulation in new shoots and regrowth showed similar responses to defoliation, the highly significant correlation between these parameters *(Fig. 5)* emphasized the interdependence of recovery growth on symbiotically fixed nitrogen. The strong sink effect of pods for nitrogen, especially in the uncut control (Table 1) was consistent with the results reported earlier (Wan Mohamad *et al.* 1986). The marked reduction in seed yield following cutting supports the results of another study with Townsville stylo (Loch and Humphreys, 1970).

An excessively long harvesting interval that allowed plants to produce pods and set seeds markedly impaired subsequent nitrogen fixation and regrowth, although nodule and root development were seemingly unaffected by this treatment *(Figs. 2b, 3b, 3c, 4b)*. The deleterious effect of pod development on nitrogen fixation was considerably reduced by high level cutting, suggesting that organic reserves in the tall stubble or the physiological functions of stubble leaves might be important in relieving this stress. Although other erect tropical pasture legumes reportedly responded to height or frequency of defoliation (Akinola and Whiteman 1975; Anning 1980; Kessler and Shelton 1980) the importance of nitrogen fixation and the effect of pod development on regrowth were not elucidated.

The data strongly imply that there is a substantial residual effect of severe defoliation from one regrowth cycle to the next, and that cutting heights and frequencies have interacted. Under a moderate harvesting frequency (twice in 56 days), few advantages accrue from leaving a tall leafy stubble. The benefit of high level cutting is distinctly prominent when defoliation is or has previously been frequent. In these respects, phasey bean behaves like perennial temperate legumes such as lucerne (Keoghan 1970; Langer and Keoghan 1970). However, in some other aspects, phasey bean behaves differently. Unlike results obtained in lucerne (Langer and Steinke 1965), with phasey bean repeated low level defoliation had a much more depressing effect on new shoots than the roots, as indicated by the extremely low shoot to root ratio (Table 1). Changes in soluble carbohydrates in the roots were not examined in the present study. The effects of intensity of defoliation on the level of organic reserves in stubble and roots need further investigation.

CONCLUSIONS

Comparable high dry matter yields can be obtained by high or low level cutting provided that harvesting commences at early flowering stage. The data emphasize the correct timing of defoliation to coincide with the period of active nodulation and rapid increase in the rate of nitrogen fixation. Repeated low level cutting is detrimental to nitrogen fixation and regrowth, causing 30% plant mortality. Since vegetative yields, nitrogen concentration in herbage, and subsequent nitrogen fixation and regrowth decrease when phasey bean plants are harvested at pod-ripening stage, this defoliation practice is not normally recommended.

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