BIOLOGICAL NITROGEN FIXATION BY THREE LEGUMES IN A COASTAL SAND-DUNE FOREST, ESTIMATED BY AN ISOTOPE DILUTION TECHNIQUE

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ABSTRACT

Estimates of nitrogen input to chronically nitrogen-deficient sand-dunes were made at Woodhill Forest, near Auckland, using a site recently replanted with *Pinus radiata* D.Don. The study was aimed at screening three legumes—Maku lotus (*Lotus pedunculatus* Cav. "Grasslands Maku"), hairy canary clover (*Dorycnium hirsutum* (L.) Ser.), and everlasting pea (*Lathyrus latifolius* L.)—as possible nitrogen-fixing replacements for yellow tree lupin (*Lupinus arboreus* Sims). Seasonal biological nitrogen fixation (BNF) of the legumes was compared using the isotope dilution technique and above-ground dry matter productivity. Sampling was conducted in winter (July) and spring (November) of 1994, and summer (February) and winter (July) of 1995.

Dorycnium hirsutum plots contained the highest amount of legume dry matter and this did not differ significantly between seasons. When woody components were omitted, *La. latifolius* was the most productive species. *Dorycnium hirsutum* and *La. latifolius* derived, on average, 98% and 95% respectively of their annual nitrogen uptake from the atmosphere (%Ndfa). This was not significantly affected by season. *Lotus pedunculatus*, on the other hand, showed a lower %Ndfa in summer.

Lathyrus latifolius was found to contain more fixed nitrogen (214 kg/ha/year) above ground than *Lo. pedunculatus* or *D. hirsutum* (55 and 71 kg/ha/year respectively). In all legumes studied, high rates of nitrogen fixation were observed between winter and spring and BNF was highly correlated with dry matter production.

Overall, the results showed that *La. latifolius* may be considered as a replacement for lupin in the ecosystem studied because of its persistence, its capacity for high non-woody dry matter production, its dependence on nitrogen derived from the atmosphere, and its high nitrogen fixation rate.

Keywords: legumes; biological nitrogen fixation; ^{15}N isotope dilution technique; sand dunes; dry matter; *Lotus pedunculatus*; *Dorycnium hirsutum*; *Lathyrus latifolius*.

INTRODUCTION

Production of *Pinus radiata* timber in the coastal sand dune forests of New Zealand is limited mainly by nitrogen availability (Mead & Gadgil 1978). Recently-formed sand dunes contain very little nitrogen, and most of this is unavailable for plant growth (Gadgil 1983). In the past, trees depended on nitrogen fixed symbiotically by perennial yellow tree lupin for much of their nitrogen supply, and this reduced the need for artificial fertiliser application (Jackson *et al.* 1983). Sand dune stabilisation, using the artificial succession of marram grass (*Ammophila arenaria* (L.) Link) followed by tree lupin followed by *P. radiata*, resulted in a successful production forestry operation (Gadgil *et al.* 1984). Gadgil (1971) estimated that lupins could fix 160 kg N/ha/year in the lupin/marram stand. Exclusion of lupins from the ecosystem resulted in lowered productivity of the pines due to slow growth rates associated with symptoms of nitrogen deficiency (Gadgil *et al.* 1984; Beets & Madgwick 1988).

Lupin plants regenerated naturally from buried seeds after each thinning and harvesting operation and populations were, until recently, self-sustaining when established in an area. The sudden appearance of lupin blight, caused by the fungus *Colletotrichum gloeosporioides* (Penzig), was first recognised in sand dune forests in 1989 (Williams 1993). Its spread throughout New Zealand is of great concern, since stabilised sand dunes near the coast may once again be exposed to wind erosion due to declining vigour of the marram grass. It is also likely that older forest stands will stagnate and young ones will be less productive. There is thus an urgent need for introduction of alternative nitrogen-fixing legumes in order to maintain sand dune forest productivity and to protect inland properties from encroaching sand.

Ideally, any alternative legume species would be able to grow with marram grass on open dunes, and with *P. radiata* trees in thinned and replanted forest stands. If it interfered with tree growth it would, like lupin, be amenable to temporary chemical suppression during critical periods, but capable of regeneration (Mead & Gadgil 1978). It would be able to compete with other herbaceous plants, produce a continuous cover, and supply nitrogen for recycling in the ecosystem. In the present study, the biological nitrogen fixation of three promising legume species was measured in order to screen them as possible replacements for lupin. All three had performed well in a trial designed to assess relative persistence, growth, and nitrogenase activity of 14 nitrogen-fixing species in the sand-forest environment.

MATERIALS AND METHODS

Site Description

The study was conducted at Woodhill Forest, on the west coast of the North Island of New Zealand (latitude 36° 40' S). The forest is located 50 km north-west of Auckland on a yellow-brown coastal sand of the Pinaki suite. Nitrogen is the only element known to limit tree productivity in this forest (Beets & Madgwick 1988). Monthly temperature and rainfall data recorded at the nearest meteorological station during the period of the study are given in Table 1.

TABLE 1–Monthly rainfall and mean air temperature during the study period. Data recorded at River Park, Henderson (NIWA 1994,1995), which is the nearest meteorological station, 25 km south of the study site.

Year	Month	Temperature (°C)	Rainfall (mm)
1994	July	10.1	224
	August	10.7	96
	September	12.1	228
	October	13.7	154
	November	15.8	44
	December	18.7	18
1995	January	19.7	91
	February	20.6	55
	March	18.7	195
	April	18.1	89
	May	14.1	147
	June	11.6	193
	July	10.0	240

The field work was conducted in a young, second-rotation *P. radiata* stand, using a trial that had been established in 1991 in a recently-clearfelled area. Trees had been planted at approximately 1000 stems/ha in 1992.

Species Selection

The trial had been designed to compare the relative performance of 14 legumes in sand-forest conditions. Each plot (3.5 × 3.5 m) had been planted with 36 seedlings of a single species at 0.5 × 0.5 m spacing, and was replicated four times in a randomised complete block design. Seedlings had been raised at the New Zealand Forest Research Institute, Rotorua, using Woodhill sand and were treated with the appropriate *Rhizobium* sp. inoculum before being planted out in the field. The study described here concentrated on three species considered in 1994 to show best performance in terms of persistence, growth, and nitrogenase activity measured by the acetylene reduction assay. These were *Lotus pedunculatus*, *Dorycnium hirsutum*, and *Lathyrus latifolius*.

^{15}N Isotope Dilution Technique

A technique based on the atom ^{15}N difference between atmospheric nitrogen and soil nitrogen was used to monitor nitrogen fixation. Plants which are able to utilise atmospheric nitrogen contain a lower atom% ^{15}N than non-nitrogen-fixing plants because the latter derive their nitrogen from the soil which has a relatively higher atom% ^{15}N (Peoples & Herridge 1990). The difference in concentration of ^{15}N between nitrogen-fixing plants and non-nitrogen-fixing (reference) plants is used to determine the proportion of nitrogen derived from the atmosphere in the fixing plants. The method, described by Peoples & Herridge (1990), is based on three assumptions:

(a) All nitrogen in the reference plant is derived from the soil. The ratio of ^{15}N to ^{14}N in the plant tissue is thus identical to that in the soil mineral nitrogen pool.

(b) The nitrogen-fixer and the reference plant explore the same soil nitrogen pool.

(c) The isotope incorporated into the soil is equally available to the nitrogen-fixer and the reference plant.

The proportion of nitrogen derived from the atmosphere (%Ndfa) was calculated as follows :

$$\%\text{Ndfa} = (1 - a/b) \times 100 \quad (1)$$

where:

a = atom% ^{15}N excess in the legume
b = atom% ^{15}N excess in the reference plant
atom% ^{15}N excess = (atom% ^{15}N in sample) – (atom% ^{15}N in atmospheric nitrogen)
atom% ^{15}N in atmospheric nitrogen = 0.3663.

The amount of fixed nitrogen was calculated as :

$$\text{Wt of fixed nitrogen} = \frac{\%\text{Ndfa}}{100} \times \text{wt of nitrogen in legume} \quad (2)$$

In this study, Yorkshire fog (*Holcus lanatus* L.) was used as reference plant in November 1994 and July 1995. Sweet vernal grass (*Anthoxanthum odoratum* L.) was used in February 1995 as insufficient amounts of *H. lanatus* were present during this period. Initial analysis of the two grasses showed that there were no significant differences in their ^{15}N levels.

Plot Layout and ^{15}N Application

A 3 × 3-m experimental plot was laid out between trees in each of the selected legume plots (three per species) in July 1994. A 1-m^2 treatment plot was demarcated for ^{15}N application within this area and the rest (8 m^2) was regarded as the plot surround. The treatment plot received three equal applications of 30% ^{15}N-enriched ammonium sulphate fertiliser in July and November 1994 and February 1995. The total quantity applied was 5.547 kg/ha. The plot surround received the same rate of unlabelled ammonium sulphate fertiliser. The fertiliser was applied in solution and water was used to wash any residue adhering to the plants into the soil.

Harvesting and Analysis

Above-ground plant material was harvested from a 0.5 × 0.5-m area within each plot surround in July and November 1994, and February 1995. Different locations were used at each harvest. Plant cover across the plots was even and care was taken to sample representative areas so that errors associated with small sample size would be reduced. Samples were separated into legume and other plant species. *Dorycnium hirsutum* was further separated into woody and non-woody components. Plant material was oven-dried at 60°C to constant weight.

In November 1994 and February 1995, non-woody material was cut from four to five randomly-selected plants in each treatment plot and bulked. These samples were collected prior to application of ^{15}N-labelled fertiliser. In July 1995, above-ground plant material was harvested from a 0.5 × 0.5-m area demarcated in the treatment plot. Samples were separated into target legume, reference grass, and other plant species. Plant material was rinsed with water before being oven dried and ground using a Cyclotec 1092 sample mill. Total nitrogen and ^{15}N atom% were determined using a commercial continuous flow C-N analyser connected to an isotope ratio mass spectrometer (Goh *et al.* 1996). The amount of biological nitrogen fixation was estimated using the ^{15}N dilution technique (Cookson *et al.* 1990; Goh *et al.* 1996).

Statistical Analysis

Statistical analysis of data was performed using the Statistical Analysis System (SAS 1990). Comparisons among treatment means were made on the basis of least significant difference (LSD) at 5% probability ($p \leq 0.05$). For some variables log-transformation was conducted prior to data analysis in order to stabilise the variance, and for these back-transformed means are reported. Stepwise regression analysis was also used to examine relationships between the amount of nitrogen fixed, dry matter increment, and nitrogen concentration in above-ground plant material.

RESULTS

Legume Dry Matter

Dorycnium hirsutum plots contained the highest total amount of above-ground legume dry matter in summer (February) and winter (July) (Table 2). However, in spring (November) the amount of *D. hirsutum* present was not significantly different from that of *La. latifolius*, while in summer there was no significant difference between *Lo. pedunculatus* and *La. latifolius*.

TABLE 2–Weight of above-ground legume dry matter in spring (November 1994), summer (February 1995), and winter (July 1995).

Species	Legume dry matter (g/m^2)		
	Spring	Summer	Winter
Lotus pedunculatus	141.2bA	20.1bB	73.8cA
Dorycnium hirsutum	678.6aA	419.9aA	562.7aA
Lathyrus latifolius	432.7aA	66.7bB	201.4bA
CV(%)	8.2	16.6	6.5

Values followed by the same small letter in a column and capital letter in a row are not significantly different at LSD ($p \leq 0.05$) for differences between legumes and differences between seasons for each legume, respectively. Values are back-transformed means.

Dorycnium hirsutum showed no significant seasonal effects, but significantly lower amounts of *Lo. pedunculatus* and *La. latifolius* were present in summer (February). For both species the weight per unit area was approximately 15% of that recorded in spring (November).

The productivity of all legumes was highest during spring (July-November), decreased sharply during summer (November-February), and then increased gradually during autumn (February-July) (Fig. 1). Woody components of *D. hirsutum* showed little seasonal weight variation. They comprised 56%, 89%, and 76% of total *D. hirsutum* dry matter in spring, summer, and winter, respectively.

Legume Contribution to Total Above-ground Dry Matter

The proportion of the target legume in above-ground plant material ranged between 58% and 93% (Table 3). No seasonal differences were noted. Species differences were observed in winter (July), and in annual mean values, the proportion of legume being lowest in

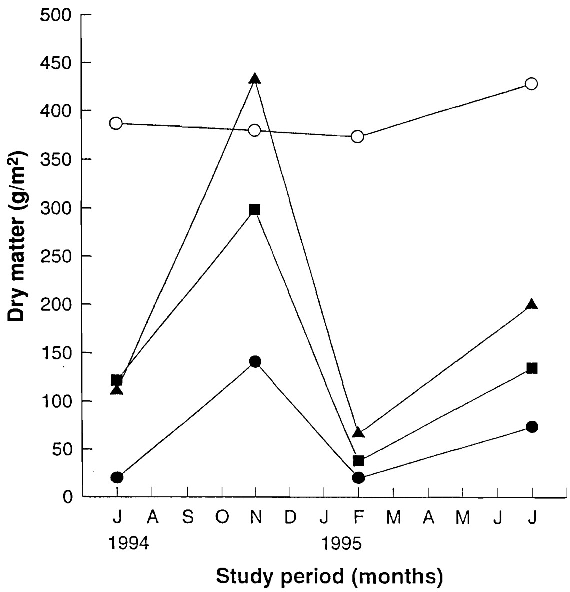

FIG. 1–Weight of above-ground legume dry matter: *Lotus pedunculatus* (●), *Dorycnium hirsutum* non-woody components (■), *D. hirsutum* woody components (○), and *Lathyrus latifolius* (▲).

TABLE 3–Proportion of legume in total (non-tree) above-ground dry matter in spring (November 1994), summer (February 1995), and winter (July 1995).

Species	Legume (%)			
	Spring	Summer	Winter	Mean
Lotus pedunculatus	58aA	62aA	60bA	60b
Dorycnium hirsutum	83aA	86aA	93aA	87a
Lathyrus latifolius	77aA	73aA	88abA	80ab
CV (%)	25.3	23.0	19.0	16.0

Values followed by the same small letter in a column and capital letter in a row are not significantly different at LSD ($p \leq 0.05$) for differences between legumes and differences between seasons for each legume, respectively.

Lo. pedunculatus, intermediate in *La. latifolius*, and highest in *D. hirsutum* plots. The mean contribution of legumes to annual dry matter production ranged between 60% and 87%.

Biological Nitrogen Fixation

Proportion of nitrogen derived from the atmosphere (%Ndfa)

Significant differences in %Ndfa among legume species were observed in summer and winter, when *Lo. pedunculatus* derived less nitrogen from the atmosphere than the other two species (Table 4). Seasonal differences in %Ndfa for each legume were observed only in *Lo. pedunculatus* which derived a significantly higher amount of nitrogen from the atmosphere during spring than in summer. On average, the annual mean %Ndfa in *D. hirsutum* and

TABLE 4—Seasonal and annual proportion of nitrogen derived from the atmosphere (%Ndfa) in above-ground legume dry matter in spring (November 1994), summer (February 1995), and winter (July 1995).

Species	%Ndfa			
	Spring	Summer	Winter	Mean
Lotus pedunculatus	96.8aA	67.1bB	78.1bAB	80.7b
Dorycnium hirsutum	98.5aA	98.1aA	96.7aA	97.8a
Lathyrus latifolius	97.3aA	95.2aA	92.8aA	95.1a
CV%	2.1	15.8	7.0	9.6

Values followed by the same small letter in a column and capital letter in a row are not significantly different at LSD ($p \leq 0.05$) for differences between legumes and differences between seasons for each legume, respectively.

La. latifolius was 98 and 95, respectively; that of *Lo. pedunculatus* was significantly lower at 81% (Table 4).

Amount of fixed nitrogen in above-ground legume material

In spring (July-November), *La. latifolius* fixed the highest amount of nitrogen (Table 5). However, in the other seasons, the amount of nitrogen fixed by *La. latifolius* did not differ significantly from that fixed by *D. hirsutum*. The amount of nitrogen fixed by *Lo. pedunculatus*, *D. hirsutum*, and *La. latifolius* in spring (July-November) constituted 62%, 55%, and 64% of their annual fixation, respectively, but in summer (November-February), only 10%, 17%, and 17% of the total annual amount was fixed.

Annually, *La. latifolius* fixed the highest amount of nitrogen (21.4 g N/m^2), which was three and four times that fixed by *D. hirsutum* and *Lo. pedunculatus*, respectively.

TABLE 5—Seasonal and annual amounts of nitrogen fixed in above-ground non-woody legume dry matter between July 1994 and July 1995.

Species	Nitrogen fixed (g/m^2)			
	Winter/Spring	Spring/Summer	Summer/Winter	Per year
Lotus pedunculatus	3.4bA	0.53bB	1.3bAB	5.5b
Dorycnium hirsutum	3.9bA	1.2abB	1.9abAB	7.1b
Lathyrus latifolius	13.6aA	3.7aB	4.0aB	21.4a
CV%	22.3	41.8	31.1	20.5

Values followed by the same small letter in a column and capital letter in a row are not significantly different at LSD ($p \leq 0.05$) for differences between legumes and differences between seasons for each legume, respectively. Values are back-transformed means.

Relationship between growth and nitrogen fixation

In order to explore the relationships between the amount of nitrogen fixed, legume dry matter increment, and nitrogen concentration in the above-ground legume material, stepwise regressions were conducted using logarithmically transformed data. The equations obtained were:

Step 1

$$\text{Log } a = -4.0 + 1.1 (\text{Log } b) \qquad r^2 = 0.92 \qquad (3)$$

Step 2

$$\text{Log } a = -4.97 + 1.1 (\text{Log } b) + 0.29c \qquad r^2 = 0.98 \qquad (4)$$

where: a = amount of nitrogen fixed (g/m^2)
b = legume dry matter increment (g/m^2)
c = nitrogen concentration in the above-ground material (%)
r^2 = coefficient of determination

DISCUSSION

The three species investigated in this study were selected on the basis of persistence, growth, and an estimate of nitrogen-fixing potential after 3 years in the sand-forest environment. These "best performers" differed from each other in many respects, including their growth habit.

Lotus pedunculatus is a procumbent herb which spreads by means of both stolons and rhizomes, but also has erect leafy stems (Armstrong 1974). Its root system is shallow (Lambrechtsen 1986). *Dorycnium hirsutum* is a low woody perennial with a branching upright habit and a deep tap root (Douglas & Foote 1994). *Lathyrus latifolius* has long scrambling stems and large compound leaves with some leaflets modified to form tendrils. Roots are large and fleshy and rhizome development is common (Lambrechtsen & Douglas 1986).

Legume Productivity

The small size of the sampling area used in this study (50 × 50 cm) was dictated by the need for repeated destructive harvesting. Sample sites were not related to original plant positions (50 × 50-cm spacing), but uncontrolled within-species error associated with plant form was expected to be low in plots with continuous cover after 3 years' growth.

Of the three legumes studied, *Lo. pedunculatus* showed the lowest overall above-ground dry matter accumulation. Maximum third-year productivity of this species (141.2 g/m^2) did not compare favourably with the 226.7 g/m^2 recorded after 2 years in a mid-rotation *P. radiata* stand growing on pumice soil (Gadgil *et al.* 1986). *Lotus pedunculatus* does not withstand drought on sandy soils (Clarkson *et al.* 1991), and this is likely to be the reason for lower dry matter accumulation in the young, open, tree stand at Woodhill Forest. Dieback observed during the summer and regrowth in autumn and winter support this theory. Sheath (1981) observed that the extensive underground rhizome system of *Lo. pedunculatus* expands in autumn and fragments in winter. West *et al.* (1988) reported that many new plants appearing in spring originate from rhizomes developing in the late summer and autumn.

The woody components of *D. hirsutum* certainly contributed to its higher relative productivity. Moderate-to-high tolerance of soil moisture deficit (Chapman *et al.* 1989) is likely to have been a further contributory factor. Although some decrease in the non-woody component was observed in summer, no overall seasonal differences were apparent.

Above-ground parts of *La. latifolius* died back in summer but new growth occurred in autumn and spring. This species is known to survive summer drought when the fleshy root system is sufficiently well-developed (Lambrechtsen & Douglas 1986).

The legumes constituted between 60% and 87% of the total non-tree above-ground dry matter, indicating that at least to the fourth year of growth they were capable of competing with other herbaceous plant species in the sand-forest ecosystem. The ability of legumes to survive and grow with companion plants is an important characteristic in sand-dune forestry, although interference with tree growth should be controllable. In this trial some *La. latifolius* stems had scrambled on to the lower parts of the 3-year-old trees, but were not considered to be a threat to tree growth. All three species provided low ground cover which displaced resident weeds and may have had a moderating effect on diurnal temperature and moisture fluctuation at the sand surface. It is likely that any deleterious effect on tree growth, if demonstrated, would be temporary and manageable by a single aerial application of herbicide designed to suppress but not to kill the legume.

Biological Nitrogen Fixation

Values for %Ndfa did not vary significantly across seasons in *D. hirsutum* and *La. latifolius*, but *Lo. pedunculatus* derived more nitrogen from the atmosphere in spring than in summer. This implies greater dependence by *Lo. pedunculatus* on soil nitrogen during summer. Ledgard & Steel (1992) working in a grazed pasture, and Mansur (1994) and Goh *et al.* (1996) in a tree understorey, found significantly lower %Ndfa values for the legume component of grass/legume mixtures during summer and winter than in spring and autumn. This was attributed to high and low temperatures, both of which reduce biological nitrogen fixation. Sprent's (1976) observations on the effect of moisture stress on root nodule function suggest that temporary drought may also have been involved. Maku *Lotus pedunculatus*, a shallow-rooting cultivar bred especially for winter growth on cool moist sites (Armstrong 1974), is likely to have been less tolerant than *D. hirsutum* and *La. latifolius* to diurnal temperature extremes and drought, but capable of rapid increase in nitrogen-fixing activity when conditions became favourable. The suggestion of Nesheim & Boller (1991) that legumes fix more atmospheric nitrogen in a warm spring due to competition for soil nitrogen from companion grasses, is not supported by the present study.

The amount (in grams per square metre) of nitrogen fixed by *Lo. pedunculatus* and *D. hirsutum* was greatest during the winter/spring (July to November) and summer/winter (February to July) periods. *Lathyrus latifolius* fixed more nitrogen between July and November (winter/spring) than at other times of the year. Spring is a period when low moisture stress and moderate temperatures would be expected to favour nitrogen fixation and growth. It is not clear why *Lo. pedunculatus* and *D. hirsutum* , but not *La. latifolius*, were able to recover their nitrogen-fixing capacity during the autumn. The estimates made here were based on above-ground material only and it is possible that autumn data for *La. latifolius* reflected preferential allocation of metabolic resources to the large fleshy root system as conditions became more favourable.

In spite of differences related to season, the total amount of nitrogen fixed by *La. latifolius* during the year was three times as great as that fixed by the other two species. The amount of nitrogen fixed by legumes has been reported to be closely related to dry matter production (Mansur 1994; Goh *et al.* 1995). In the present study, these two variables were highly correlated (r^2 = 0.92). In the nitrogen-limited Woodhill Forest ecosystem, high legume productivity in spring was probably dependent on the amount of nitrogen fixed during this period.

Jorgensen (1980) suggested that legumes in nitrogen-limited forests should provide at least 50–100 kg N/ha/year for the first 3–5 years to provide an economic return in terms of timber production. In this study *Lo. pedunculatus*, *D. hirsutum*, and *La. latifolius* fixed minimum (above-ground only) amounts of 55, 71, and 214 kg N/ha/year respectively during the third year of the second rotation. Nothing is known about the absolute amounts that would have been fixed during Years 1 and 2. Some nitrogen-fixing activity had been demonstrated by acetylene reduction assay in all three species during the spring of each year since planting (R. Gadgil unpubl. data). Even if no nitrogen had been fixed before 1994, the 214 kg/ha fixed by *La. latifolius* during the third year exceeded the minimum 4-year total (200 kg) considered by Jorgensen to be economically desirable. Natural senescence and decomposition of *La. latifolius* plant parts, accelerated by *P. radiata* canopy closure, would eventually be expected to add at least 214 kg/ha, plus the fixed nitrogen in the root system, to the soil nitrogen pool.

The amount of nitrogen fixed by *La. latifolius* during the fourth year of growth exceeded the highest estimate of nitrogen fixed by *Lupinus arboreus* (160 kg/ha/year—Gadgil 1971). From a nitrogen accumulation study, Gadgil reported a decrease in the nitrogen-fixing activity of lupin after the first growing season to a rate of 85 kg/ha/year during the third and fourth seasons. Comparison of these data suggests that *La. latifolius* may have more potential than lupin as a source of fixed nitrogen in sand dune forests.

CONCLUSIONS

Dorycnium hirsutum and *La. latifolius* had an annual mean %Ndfa of 98 and 95, respectively, and values did not differ significantly with season. *Lotus pedunculatus* showed a significantly lower %Ndfa in summer, due probably to unfavourable temperature and moisture conditions.

Nitrogen fixation varied greatly with legume and season. *Lathyrus latifolius* fixed a minimum of 214 kg N/ha/year, an amount significantly higher than that fixed by *Lo. pedunculatus* (55 kg/ha/year) or *D. hirsutum* (71 kg/ha/year). The higher rate of nitrogen fixation by *La. latifolius* was associated with higher non-woody dry matter increment. All three species showed highest productivity in spring. Favourable moisture and weather conditions were considered to be responsible for the higher amounts of nitrogen fixed during this period.

On the basis of a 1-year study, *La. latifolius* appears to be the most suitable of the three legume species for use in young second-rotation *P. radiata* stands growing on coastal sand. Provided that the scrambling habit is acceptable, its persistence for 4 years after planting, high non-woody dry-matter production, and relatively high nitrogen fixation rate in all seasons suggest that it would be a suitable replacement for *Lupinus arboreus* on these inherently nitrogen-deficient sandy soils.

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