LUPINUS ARBOREUS AND INORGANIC FERTILISER AS SOURCES OF NITROGEN FOR PINUS RADIATA ON A COASTAL SAND

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ABSTRACT

Soil sampling during early forest growth on coastal sand showed little indication of nitrogen accumulation in the mineral soil. In spite of 7 years' intermittent lupin (**Lupinus arboreus** Sims) growth and regular 6-monthly applications of fertiliser (a total of 900 kg N/ha, plus other nutrient elements) over a 10-year period, total-nitrogen levels remained below 0.03%.

A bioassay of soil samples using **Pinus radiata** D. Don seedlings showed that potentially-available-nitrogen was influenced by experimental treatment (fertiliser addition, lupin exclusion) to a greater extent than total-nitrogen. Potentially-available-nitrogen responses to the presence of lupins and to fertiliser were observed in the second year of the trial and from the fifth year onwards. The lupin effect was very similar to that of fertiliser treatment. Highest values resulted from the combined influence of lupins and fertiliser, but the effect was additive rather than interactive.

Foliar-nitrogen levels declined during the first 5 years of tree growth and showed no effect of lupins or fertiliser treatment. In the sixth year the onset of nitrogen stress in trees growing without fertiliser or lupins (foliar-nitrogen range 0.9–1.2%) was associated with significant and recurring treatment differences. The effect of fertiliser (foliar-nitrogen range 1.1–1.5%) was sometimes, but not always greater than that of lupins (foliar-nitrogen range 1.0–1.4%) and highest values (1.2–1.6%) were recorded where trees were influenced by both lupins and fertiliser. The lupin effect lasted for at least 3 years after lupins had died out of the understorey at tree age 4 years and the fertiliser effect for at least 4 years after the final application.

Evidence from foliar analysis indicated that tree nitrogen demand was not met by fertiliser treatment alone, and the efficiency of fertiliser-nitrogen utilisation appeared to be low. All improvements in tree nitrogen status attributable to lupins were achieved without additional management costs.

INTRODUCTION

In 1968 a long-term trial was set up at Woodhill State Forest to investigate the importance of soil moisture and soil fertility on the early growth of *Pinus radiata* planted on coastal sand dunes. Woodhill is one of the west coast areas in New Zealand where sand dune stabilisation, using the planting succession marram grass (*Ammophila arenaria* (L.) Link)/tree lupin/*P. radiata*, has resulted in a successful production-forestry operation. The only site factors known or suspected to limit tree growth were nitrogen availability and soil moisture. Because tree lupin, a nitrogen-fixing leguminous plant, was an integral part of the ecosystem, experimental treatments in the trial included lupin exclusion as well as inorganic fertiliser addition. A series of stocking reductions was superimposed on combinations of these two treatments.

Soil moisture data and tree growth measurements from this trial have already been presented (Jackson 1977; Jackson, Jackson & Gifford 1983; Jackson, Gifford & Graham 1983). Over the 11-year study period lupins and inorganic fertiliser addition were found to have positive independent and additive effects on tree growth. Jackson, Jackson & Gifford (1983) concluded that on this site tree productivity was influenced more by nutritional factors than by the occasional moisture deficits in the upper 3 m of soil. Jackson, Gifford & Graham (1983) were unable to relate growth differences to the supply of any one element because fertiliser treatment included six major nutrient elements.

In this paper we present the results of a 15-year monitoring programme designed to show whether the experimental treatments influenced the nitrogen status of either the soil or the *P. radiata* foliage.

Site Description and Experimental Treatment

Woodhill Forest is located 50 km north-west of Auckland, on yellow-brown coastal sands of the Pinaki suite (Cox 1977). The trial area was a west-facing dune slope in Cpt 138 which was being stabilised by the normal procedure (Restall 1964; Wendelken 1974). Marram grass had been planted in June 1965, topdressed with "Nitromoncal" (lime-coated ammonium nitrate) at 25 kg/ha in November 1965, and oversown with 3.4 kg lupin seed/ha in April 1966. In June 1968 the whole area was planted with *P. radiata* (2.4 × 1.8 m spacing) using Lowther machines which crushed, but did not kill the 2-year-old lupin cover.

Eight experimental treatment plots, each of 0.566 ha, were laid out in two blocks of four plots. Four treatments – designated 0 (lupins excluded, no fertiliser), L (lupins allowed to grow, no fertiliser), F (lupins excluded, fertiliser applied), and LF (lupins allowed to grow, fertiliser applied) – were allocated to the plots in a duplicated randomised block design.

In December 1968, lupins in the 0 and F plots were crushed and sprayed with herbicide. Further spraying and handpulling at regular intervals ensured that lupin regrowth in these plots never progressed beyond the seedling stage during the period over which tree measurements were made. Details of the lupin exclusion treatment have been given by Jackson, Gifford & Graham (1983).

Beginning in August 1969, fertiliser was applied to F and LF plots every 6 months. The aim was to supply an adequate and balanced dressing of macronutrients according to the following schedule:

Winter (August) in alternate (odd) years		(kg/ha)
	Magamp with potassium	336
	Diammonium phosphate	180
	Potassium sulphate	72
	Dolomite	207
Winter (August) in alternate (even) years		
	Urea	122
	Potassium sulphate	112
Summer (February) every year		
	Urea	122

Fertiliser treatment was discontinued after August 1978. Actual recorded applications of each nutrient element are listed in Table 1.

TABLE 1—Amounts and timing of nutrient element application

Method	Date	Tree age (yr)	Nutrients (kg/ha)					
			N	P	K	S	Mg	Ca
Per tree	Aug 1969	1	22	35	18	7	26	19
,,	Feb 1970		22					
,,	Aug*	2	22		18	7		
,,	Feb 1971		56					
Broadcast	Aug	3	56	93	47	12	67	46
Per tree	Feb 1972		56					
Broadcast	Aug	4	56		47	19		
,,	Feb 1973		56					
,,	Aug	5	56	93	47	12	67	46
,,	Feb 1974		56					
,,	Aug	6	56		47	19		
,,	Feb 1975		56					
,,	Aug	7	56	93	47	12	67	46
,,	Feb 1976		56					
,,	Aug	8	56		47	19		
,,	Feb 1977		56					
,,	Aug	9	56	93	47	12	67	46
,,	Feb 1978		56					
,,	Aug	10	56		47	19		
TOTAL			962	407	412	138	294	203

* No record of the August 1970 application exists and this may have been omitted.

Tree stocking reductions were superimposed on the main lupin and fertiliser treatments in a split plot design. Each main plot was divided into four subplots which were allocated at random to one of four thinning regimes (Table 2). The objectives of the schedule and details of general silvicultural management have been described by Jackson, Gifford & Graham (1983). Briefly, the aim was to investigate the effect of between-tree competition by a series of anticipatory thinnings based on the results of annual remeasurement. All trees were pruned to 2 m in January/February 1976. Mean tree heights (derived from the largest 15 trees in unthinned subplots) for 0, L, F, and LF treatments respectively were 9.50, 9.27, 9.54, and 9.66 m in 1975 and 15.84, 17.19, 18.48, and 19.46 m in 1981 (Jackson, Gifford & Graham 1983).

TABLE 2—Thinning sequence and nominal stocking (stems/ha) for the four subplots (i–iv) in each main treatment plot

Subplot	May 1968	July 1970	October 1972	February 1976
(i)	2224	2224	2224	2224
(ii)	2224	1483	1483	1483
(iii)	2224	2224	741	741
(iv)	2224	2224	1483	371
Tree age (yr)	0	2	4	7

Understorey Growth

(a) *Marram grass:* Effects of experimental treatment on marram grass have been documented by Gadgil (1977), Mead & Gadgil (1978), and Jackson, Gifford & Graham (1983). Marram was not killed by herbicide spray. Mean plant height response (an increase of about 30 cm) to fertiliser treatment recorded in 1972–73 was associated with increased foliar-nitrogen concentration. In 1974 almost total suppression was noted in unthinned subplots, and green, relatively even growth in subplots thinned to 741 stems/ha (Table 3). Denser growth was observed in L and LF plots than where lupin had been excluded. By 1976 marram growth was virtually confined to the 741 stems/ha subplots and at the last observation in 1981 it had not been totally suppressed in these stands.

TABLE 3—Marram grass assessment, November 1974

Stocking rate (stems/ha)	No. of subplots		
	Green marram absent	Green marram present	
		Continuous cover	Patchy distribution
2224	7	0	1
1483 (thinned July 1970)	5	1	2
1483 (thinned Oct 1972)	2	1	5
741 (thinned Oct 1972)	0	6	2

(b) *Lupin:* The course of lupin growth and development has not been presented fully elsewhere and is shown in Fig. 1. Alternate peaks and troughs in height growth reflected seasonal development, and growth in the unsprayed plots was particularly vigorous in the spring of 1969. A series of severe defoliations by kowhai moth larvae (*Uresiphita polygonalis maorialis* Felder) killed most of the plants during the summer of 1970. Recovery during the following year was poor, but in 1971 and 1972 spring growth showed progressive improvement with relatively little mortality during the intervening period. Between November 1972 and May 1973 lupin plants died throughout the experiment area. From this point until 1976 regeneration beyond the three- to four-leaf stage was observed only in the 0 plots, where handpulling at 3-month intervals was necessary to maintain effective control. Dense lupin regeneration followed the thinning to 371 stems/ha in 1976 but the large amounts of felled material made objective comparisons between L and LF plots impossible.

Lupin responses to fertiliser treatment was spasmodic and inconsistent. Significant ($p<0.05$) effects were recorded only in November 1969 (mean lupin height increase from 68 to 102 cm) and November 1971 (a reduction from 49 to 15 cm). Thinning alone did not influence lupin growth during the first 5 years of the trial, but a significant thinning × fertiliser interaction effect in November 1972 indicated that the suppressive effect of fertiliser was greater in thinned subplots.

In considering the results of the following studies it is important that the nature of the experimental treatments should be clearly understood:

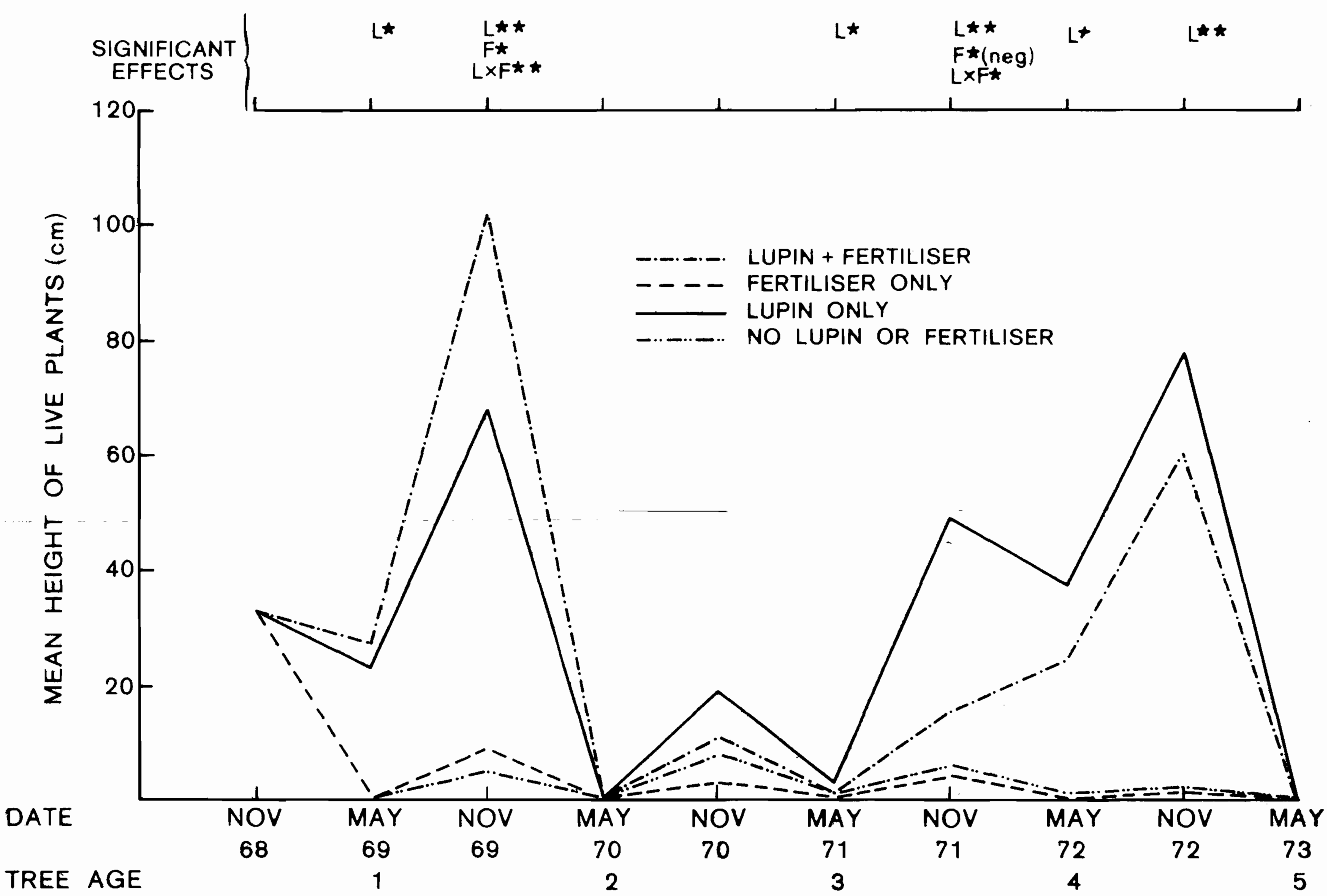


FIG. 1—Lupin height growth. Lupin height was measured at 1-m intervals along one 40-m transect in each subplot.

(a) Fertiliser treatment included six major nutrients applied over a 10-year period.

(b) Lupin treatment, strictly speaking, was lupin exclusion, but all lupin effects have been attributed to the presence of lupins in the L and LF plots. Even here lupins were present only until the summer of 1973 (trees aged 5 years). There was a resurgence of growth after the 1976 thinning but only in the thinned subplots. This was effectively controlled in the 0 and F plots.

(c) Thinning treatments were irregular and progressive (Table 2). The prescription called for the felling of the smallest trees, and tree distribution in thinned subplots was therefore not necessarily even.

MATERIALS AND METHODS

Soil Nitrogen Determination

Sample collection and preparation

Two soil samples, each of about 10 kg, were collected from each experimental treatment subplot in November and May of each year from tree planting until 1978. These were composite samples of mineral soil taken at a depth of 0–10 cm and 60–70 cm from five sites in each of the duplicate subplots representing each treatment. Sites for the soil pits were selected at random in the area surrounding the central 0.04-ha tree-measurement area of the sub-plot. Soil samples were air-dried and passed through a 0.5-mm-mesh sieve to remove root material. No other organic fragments were present. By May 1972 it had become obvious that some reduction in work load was necessary and at this point sampling at 60–70 cm was abandoned. Six-monthly collection of 0–10 cm samples continued up to and including May 1978.

Total-nitrogen determination

After pre-treatment to ensure quantitative determination of nitrates and nitrites (Bremner & Shaw 1958), a portion of each soil sample was analysed for total-nitrogen using a semi-micro Kjeldahl digestion procedure followed by steam distillation (Bremner 1960).

Determination of potentially-available-nitrogen (PA-N)

A bioassay method was used to determine the proportion of the soil total-nitrogen which was potentially available to *P. radiata*. This took the form of a glasshouse assessment in which *P. radiata* seedlings were grown for 6 months in undrained plastic pots each containing 4 kg of soil. The seedlings were germinated in perlite and transplanted into the pots (four per pot) when 3 weeks old. Duplicate pots were prepared for each soil sample, and a randomised block layout was used. All the pots were watered to field capacity twice per week with demineralised water. At the end of the 6-month period, plant tops and roots from each pot were harvested separately and dried at 80°C in a forced-draught oven. The dried material was weighed and then ground finely before being analysed for nitrogen using Bremner's (1960) semi-micro Kjeldahl technique.

Determination of Foliar Nitrogen Levels

Foliage sampling commenced at the end of the second year after tree planting. In February and May 1970 a small handful of needles was taken from one branch of each of 10 trees selected at random in each experimental plot. Needles were amalgamated into one sample per plot. Composite samples collected at regular 3-monthly intervals from August 1970 consisted of current season's mature needles on second-order branches taken from two sides above the widest part of each selected tree crown. From May 1977 onwards the number of trees in each random sample was reduced from 10 to eight. Fertiliser treatment ceased in August 1978 and from this point onwards foliage collections were made annually in February (when nitrogen concentrations were lowest) until 1983.

Needle samples were dried in a forced-draught oven at 70°–80°C. The dried material was ground in a Wiley mill and subsamples were analysed for nitrogen using a modification of Bremner's (1960) method. In 1972 steam distillation and titration for determination of the ammonium content of the sample digest were replaced by an automated colorimetric determination using sodium phenate as the colour-producing agent.

In order to find out whether nutrient elements other than nitrogen were in short supply, dried and ground foliage collected in February 1979 was analysed for phosphorus, potassium, calcium, magnesium, manganese, zinc, iron, copper, and boron. Colorimetric methods using ammonium vanadomolybdate and curcumin respectively as colour-producing reagents were used for phosphorus and boron determination; the other elements were determined by atomic absorption spectrophotometry using strontium chloride to suppress ionisation interference during the measurement of potassium, calcium, and magnesium concentrations.

Statistical Analysis

Data for each sample collection were subjected to analysis of variance as indicated in Table 4. Only differences significant at the 5% probability level were acknowledged.

TABLE 4—Effects and degrees of freedom for analyses of variance

To May 1970		August 1970–Feb 1973		May 1973–August 1978	
Source	DF	Source	DF	Source	DF
Blocks	1	Blocks	1	Blocks	1
Lupins	1	Lupins	1	Lupins	1
Fertiliser	1	Fertiliser	1	Fertiliser	1
L×F	1	L×F	1	L×F	1
Error	3	Main plot error	3	Main plot error	3
Total	7	Thinning	1	Thinning	3
		T×L	1	T×L	3
		T×F	1	T×F	3
		T×L×F	1	T×L×F	3
		Subplot error	4	Subplot error	12
		Total	15	Total	31

RESULTS

Only the main plot treatment effects (L, F) will be considered here. Interactions involving thinning were small and inconsistent (Tables 5 and 6) and it is assumed that their influence on the main plot effects was negligible.

TABLE 5—Interaction effects of thinning with fertiliser treatment on soil- and foliage-nitrogen

Sampling date	Fertiliser				No fertiliser				Least significant difference (p=0.05)
	Stocking (stems/ha)				Stocking (stems/ha)				
	2224 throughout	2224 to 1483 (1970)	2224 to 741 (1972)	2224 to 1483 (1972) 371 (1976)	2224 throughout	2224 to 1483 (1970)	2224 to 741 (1972)	2224 to 1483 (1972) 371 (1976)	
Soil total-N, 0–10 cm (% o.d. wt)									
May '75	0.008	0.007	0.011	0.005	0.011	0.012	0.007	0.009	0.003
Nov. '75	0.009	0.007	0.007	0.005	0.004	0.008	0.006	0.006	0.003
Soil PA-N, 0–10 cm (mg/4000 g soil)									
Nov. '77	40	38	48	27	16	22	21	20	8
***P. radiata* foliar-N (% o.d. wt)**									
Feb. '72	1.31	1.36			1.53	1.23			0.20
Feb. '73	1.55	1.49			1.57	1.45			0.11
Aug. '74	1.53	1.54	1.45	1.50	1.24	1.26	1.35	1.09	0.15
Aug. '78	1.39	1.38	1.50	1.45	1.10	1.19	1.23	1.28	0.06

TABLE 6—Interaction effects of thinning with lupin treatment on soil- and foliage-nitrogen

Sampling date	Lupins				No lupins				Least significant difference (p=0.05)
	Stocking (stems/ha)				Stocking (stems/ha)				
	2224 throughout	2224 to 1483 (1970)	2224 to 741 (1972)	2224 to 1483 (1972) 371 (1976)	2224 throughout	2224 to 1483 (1970)	2224 to 741 (1972)	2224 to 1483 (1972) 371 (1976)	
Soil total-N, 0–10 cm (% o.d. wt)									
May '75	0.009	0.012	0.012	0.008	0.010	0.008	0.007	0.006	0.003
Nov. '76	0.021	0.013	0.021	0.015	0.012	0.014	0.014	0.013	0.004
May '77	0.017	0.017	0.013	0.019	0.011	0.013	0.014	0.014	0.004
Soil PA-N, 0–10 cm (mg/4000 g soil)									
May '78	34	29	26	27	19	20	26	19	7
P. radiata foliar-N (% o.d. wt)									
Feb. '75	1.19	1.14	1.20	1.32	0.92	1.11	1.01	1.15	0.11
Nov. '75	1.15	1.08	1.21	1.18	1.07	1.15	1.09	1.18	0.07
Feb. '82	1.14	1.10	1.17	1.08	0.93	0.98	1.02	1.00	0.05

Soil Nitrogen

Total-nitrogen

No significant differences due to fertiliser or lupin treatment were observed in the nitrogen concentrations of soil samples collected at 60–70 cm (Fig. 2). Although a general increase in nitrogen levels was recorded in November 1969 and May 1970, this was not sustained and values never exceeded 0.015%.

Concentration of nitrogen in 0–10 cm samples was generally greater than in 60–70 cm samples, but even the highest values did not exceed 0.031%. There were no obvious seasonal trends. Although the highest total-nitrogen values were usually recorded for LF plots, statistically significant treatment effects were noted only in May 1972 (a positive fertiliser effect), May 1975 (a positive lupin effect), and November 1977 (fertiliser and lupin both independently positive). In absolute terms the differences were not large, and November 1977 samples reflected a low value for 0 plots rather than elevated levels in L and F plots. The marked fluctuations in nitrogen values recorded between November 1968 and May 1971 were not repeated later. After May 1973 there was a decline in nitrogen levels until November 1975. An increase during the following year established concentration levels that remained fairly constant for L, F, and LF plots until sampling was discontinued.

Potentially-available-nitrogen

For the 60–70 cm samples, PA-N values were low and virtually indistinguishable on the basis of experimental treatment (Fig. 3). The single exception was a significant positive lupin effect in May 1970 when a high value was recorded from LF plots.

Values for 0–10 cm samples were higher but showed great fluctuation and inconsistency during the first 3 years. Significant fertiliser and lupin effects were observed in samples taken in November 1969 (lupin effect negative; L×F interaction effect significant due to a larger fertiliser effect in sprayed plots) and May 1970. No significant differences were recorded during the following 2 years. From November 1972 a positive lupin effect was sustained for 18 months, and a concurrent positive fertiliser effect was observed in May and November 1973. During the next 2½ years differences attributable to lupin and fertiliser were noted only in November 1975. From November 1976 fertiliser, and from May 1977 lupin and fertiliser treatments exerted a positive effect until sampling was discontinued. From November 1971 values for samples from LF plots were nearly always higher and those from 0 plots were always lower than those from L or F plots. On two occasions during this period F plot values were considerably greater than those for L plots, but otherwise there was little difference between them.

Foliar Nutrient Levels

General

In 0 plots sampled in 1979, concentrations of all nutrients except nitrogen and copper were in the range considered by Will (1978) to be satisfactory for *P. radiata* growth (Table 7). Copper levels were just below the 4 ppm regarded as adequate, but nitrogen concentrations indicated severe deficiency. Samples from L plots had higher concentrations of nitrogen and magnesium than those from 0 plots. Fertiliser

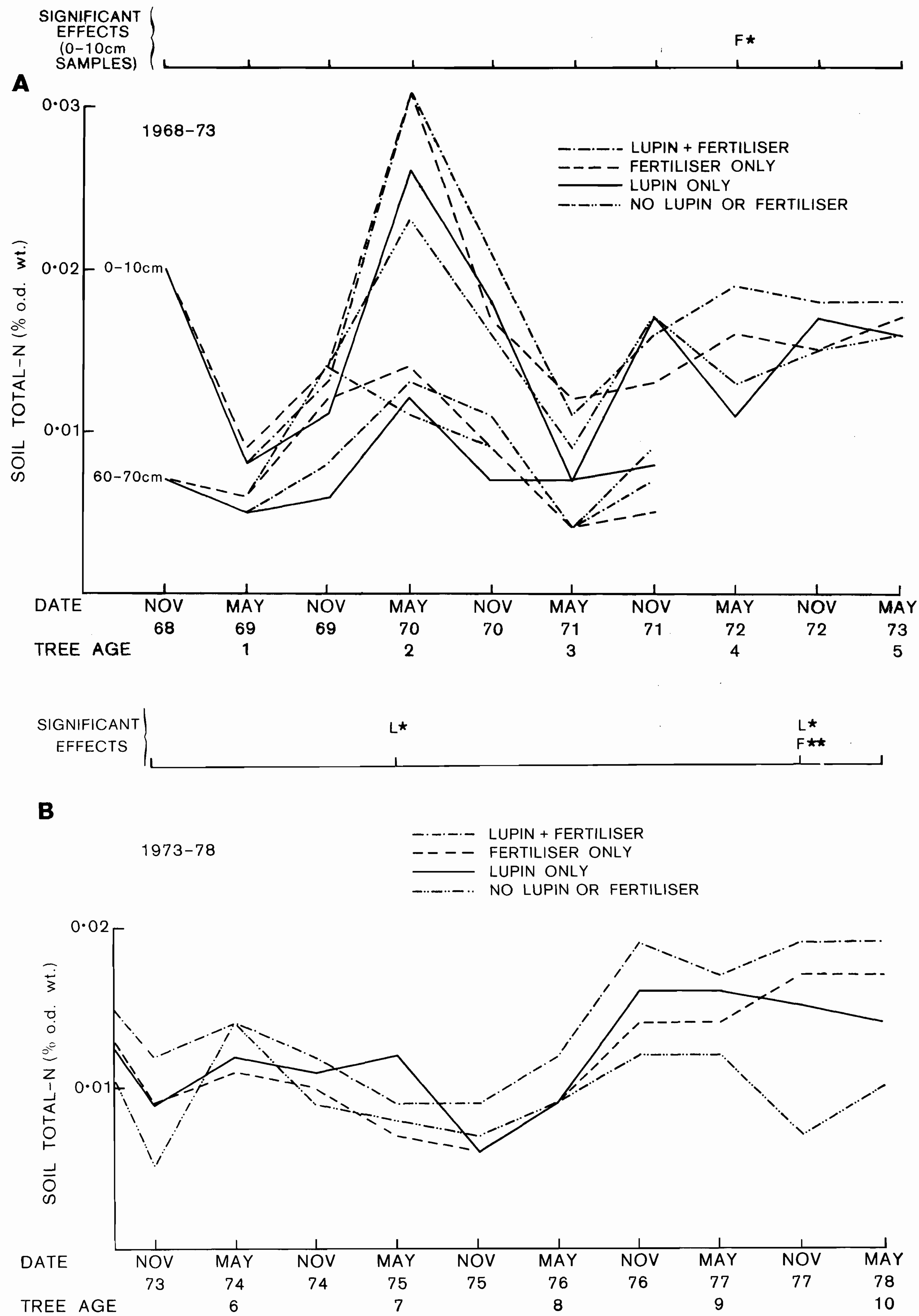


FIG. 2—Total-nitrogen values
(a) Seasonal values 1968–73.
(b) Seasonal values 1973–78.

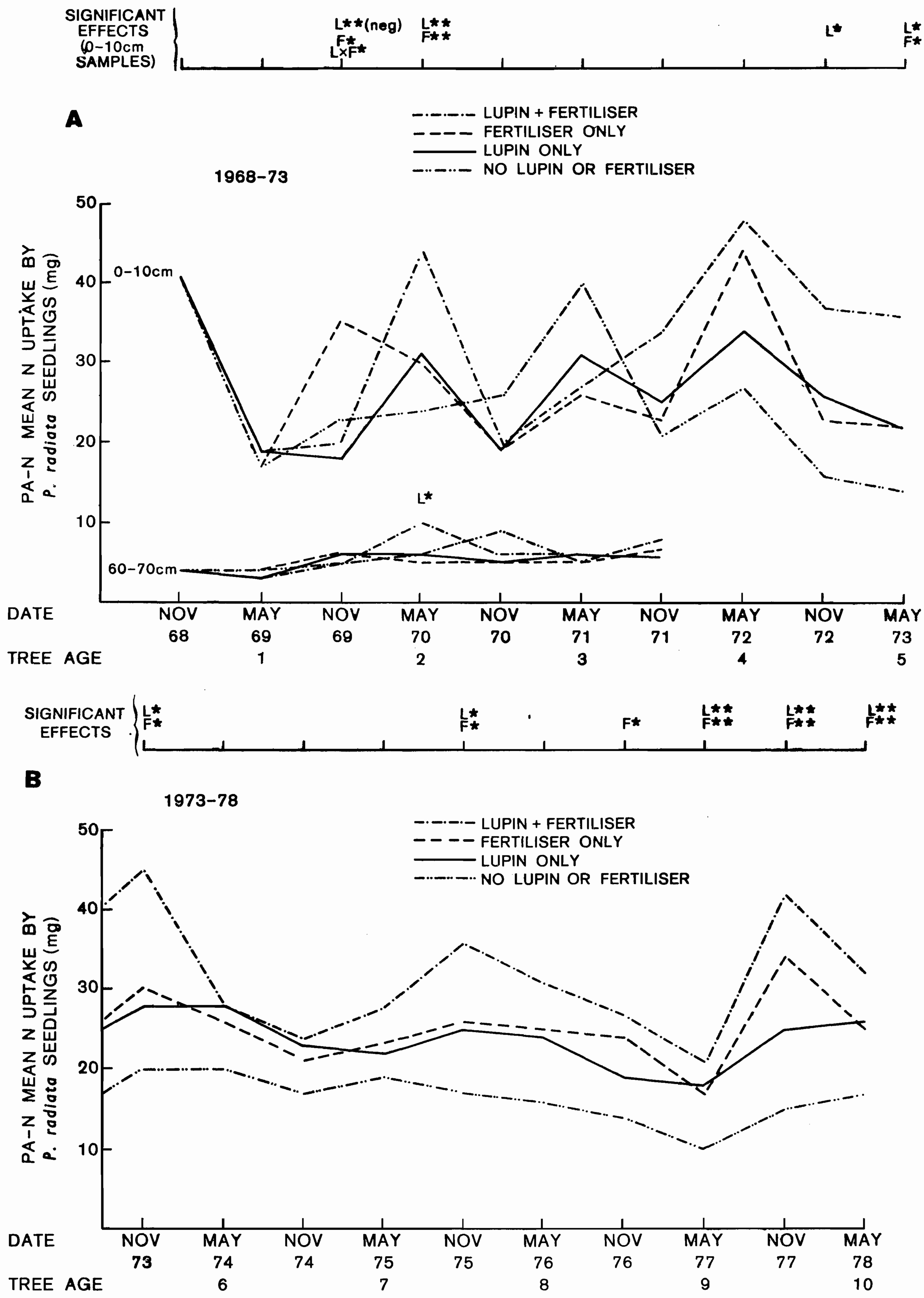


FIG. 3—Potentially-available-nitrogen values. Values represent nitrogen uptake by four seedlings from 4 kg sand over a 6-month period.
(a) Seasonal values 1968–73.
(b) Seasonal values 1973–78.

TABLE 7—Mean nutrient levels in **Pinus radiata** foliage in February 1979

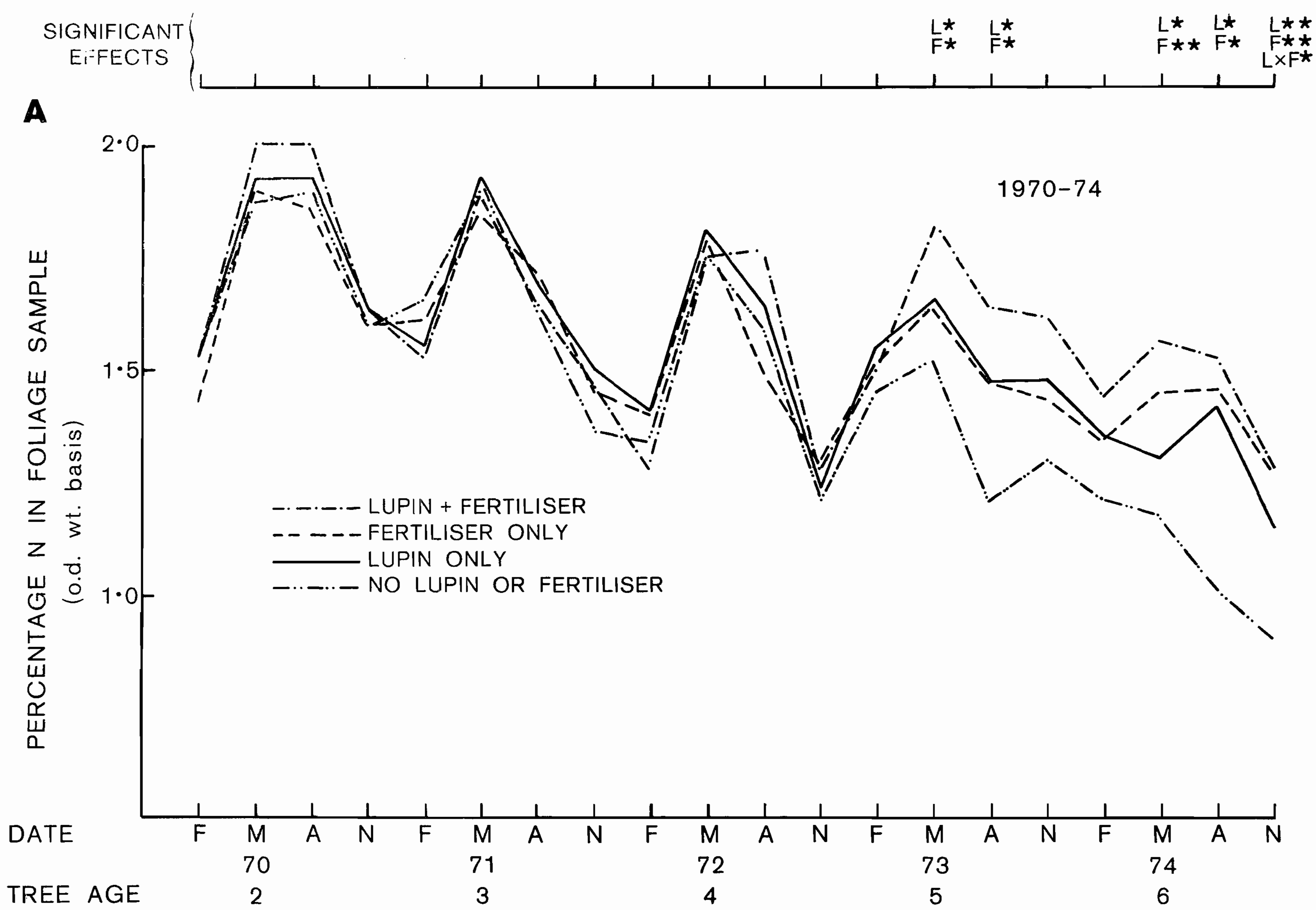
Treatment	N	P	K	Ca	Mg	Mn	Zn	Fe	Cu	B
	%					ppm				
0	0.90	0.16	0.94	0.14	0.150	117	43	62	3	16
L	1.09	0.16	0.91	0.12	0.169	98	40	54	3	14
F	1.21	0.19	0.90	0.14	0.177	84	36	57	3	12
LF	1.24	0.18	0.93	0.14	0.171	69	32	53	3	12
Least significant difference ($p = 0.05$)	0.18	0.03	0.15	0.03	0.015	70	7	19	1	4
Level considered satisfactory for growth of **P. radiata** (Will 1978)	1.5	0.14	0.50	0.10	0.10	20?	20	—	4	12

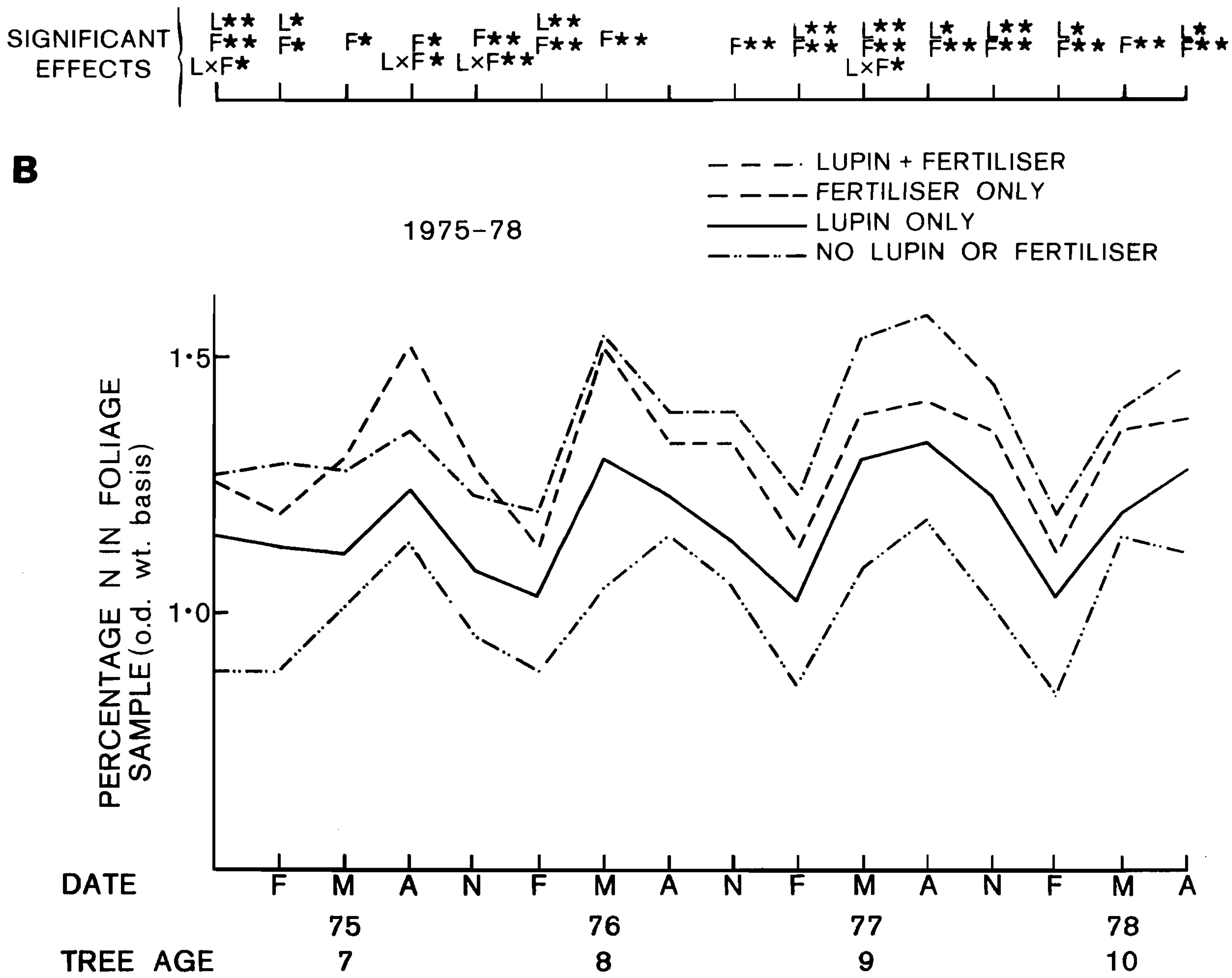
treatment had increased the concentrations of nitrogen and magnesium. Concentrations of all nutrients other than nitrogen and copper were satisfactory in both L and F plots. The copper levels were not significantly different from those in 0 plots.

Nitrogen concentration

Neither lupin nor fertiliser treatment had a significant effect on foliar-nitrogen concentration during the period February 1970 to February 1973 (i.e., before the trees were 5 years old). Nitrogen concentrations were always highest in May or August and lowest in February (Fig. 4A). The peaks and troughs were quite sharply defined, but after May 1970 there was an over-all decline in nitrogen level. In February 1973 a change occurred. Seasonal peaks and troughs became much less accentuated (Fig. 4A). A further general decline in nitrogen level was apparent between May 1973 and February 1974 and treatment differences which were apparent for the first time in May 1973 established a hierarchy which was maintained over this period. In May and August 1973 fertiliser and lupins each had a significant and equal effect on foliar-nitrogen concentration. Their combined effect was additive rather than interactive.

After May 1974 a significant effect of fertiliser treatment was recorded for every sample collection except that of August 1976. A significant lupin effect was observed only once during the period May 1975 to November 1976, but was present at all other collection times with the exception of May 1978. A lupin × fertiliser interaction effect was noted in four separate collections but there was no obvious pattern of incidence. From 1974 foliar-nitrogen values for 0 plots dropped to less than 1.0%





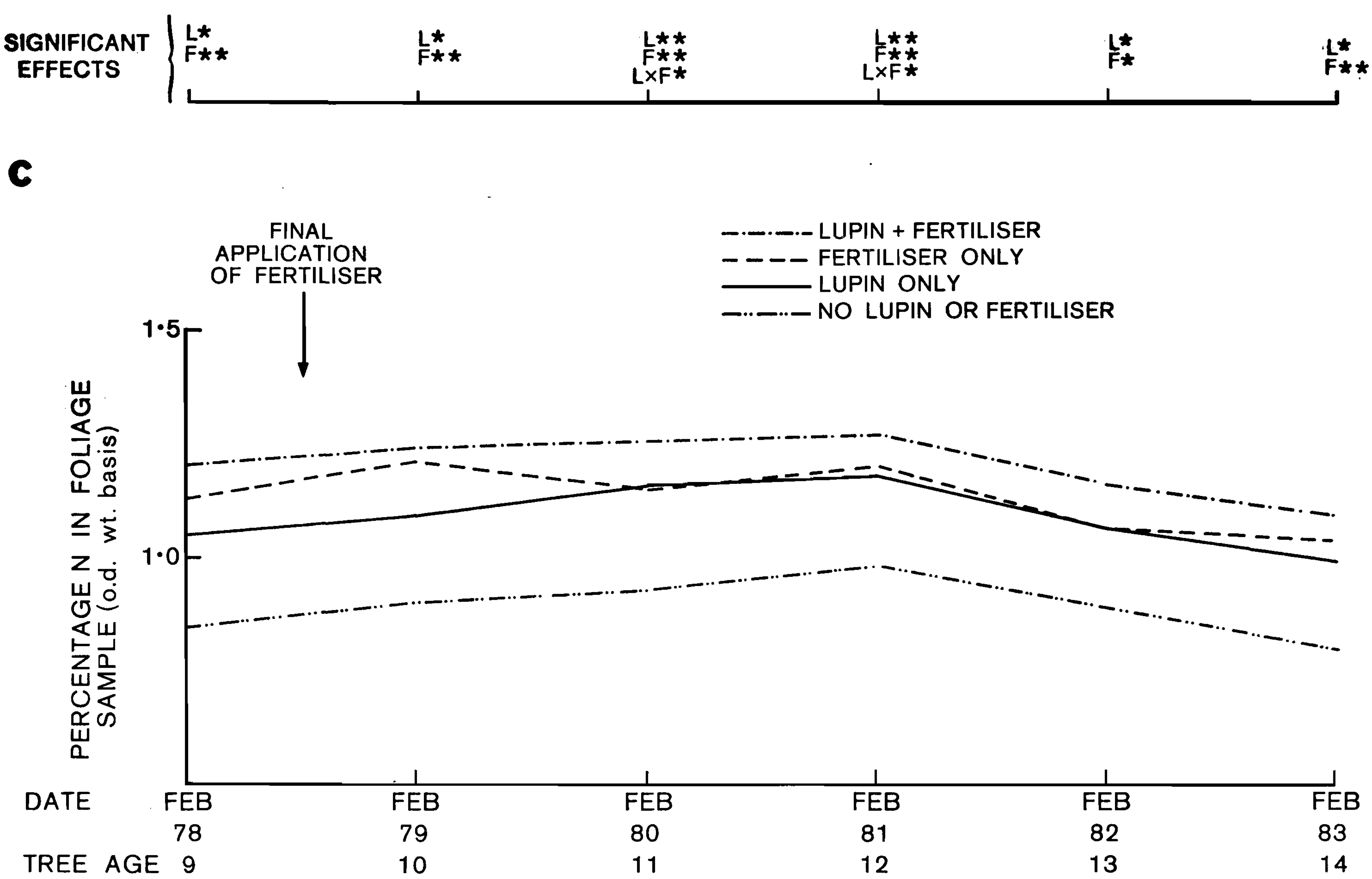


FIG. 4—Foliar-nitrogen concentration in **Pinus radiata**

(a) Seasonal values 1970–74 (facing page).

(b) Seasonal values 1975–78.

(c) Annual values 1978–83.

during the summer of each year and never rose above 1.2% (Fig. 1B). Between August 1974 and August 1978 ranges for L, F, and LF plots were 1.0–1.4, 1.1–1.5, and 1.2–1.6% N respectively. Nitrogen concentrations in February 1976 ascended in the order 0, L, F, LF and this hierarchy was maintained until August 1978 with no over-all increase or decrease in nitrogen level.

Annual monitoring (after fertiliser treatment ceased in August 1978) showed that fertiliser and lupin effects were significant until the final sampling in February 1983. Significant interaction effects were noted but only in 1980 and 1981. In these collections and during the remainder of the study foliar-nitrogen values for L and F plots were very similar, while differences between L, F, and LF were smaller than those between 0 and L plots (Fig. 1C). In 1982 values for LF plots fell below 1.2% for the first time, and in 1983 values for all plots were at their lowest recorded levels.

DISCUSSION

Soil Nitrogen

In view of the "low" rating given by Cox (1977) to a total-nitrogen concentration of 0.13% in a Pinaki sand sample (0–9 cm), the levels detected in this study must be regarded as very low indeed. A value of 0.008% has been reported for unstabilised sand (Gadgil 1971) and although concentrations twice as high were recorded in the top 10 cm in 1978, they were still an order of magnitude lower than that considered marginal for pasture establishment.

The bioassay showed that although total-nitrogen levels were very low, some of the nitrogen was available for uptake by *P. radiata* if moisture and temperature conditions were suitable. Because glasshouse conditions were not rigidly controlled, differences between sampling times were less pertinent to results for potentially-available-nitrogen than for total-nitrogen levels. Treatment comparisons within each set of samples were considered to be more meaningful for potentially-available-nitrogen than for total-nitrogen because the 6-month bioassay added a time dimension.

There is no doubt that potentially-available-nitrogen levels were more sensitive to the effects of lupin and fertiliser treatments than total-nitrogen. The negative lupin and positive fertiliser influence in November 1969, coupled with the greater increase in values for 0 and F plots, suggests either that growing lupins were removing soil-nitrogen or that lupin residues in sprayed plots were decomposing and contributing to the soil-nitrogen pool. The second alternative seems more probable in view of the fact that, although lupin growth in the LF plots was significantly greater than in the L plots at this point (Fig. 1), the potentially-available-nitrogen value was slightly lower in the L plots.

There is a possibility that nitrogen detected in the soil samples was actually a component of live root material at time of sampling: a 0.5-mm-mesh sieve could be expected to screen out most, but not necessarily all of the fine root material, which would tend to contract and become brittle with drying. This type of sampling error is present in nearly all soil analytical procedures and is usually ignored, but in studies where root material has a relatively high nitrogen content (e.g., leguminous plants) or where soil-nitrogen is monitored over a period of active vegetation growth, the error could influence interpretation. In the present study the absence of any large build-up in total-nitrogen with time suggests that root fragments were not a major source of detectable nitrogen.

Chemical tests for nitrogen availability are not widely accepted for agronomic ecosystems and Keeney (1980) has shown that forest ecosystems present even more problems in this respect. Biological methods based on anaerobic incubation under carefully controlled conditions probably offer the best predictive tool at present. The bioassay described in this paper was basically an aerobic incubation study carried out under partially controlled conditions but it did measure actual plant uptake. A hierarchical order of treatment effects was established from November 1971 which agreed with that described for tree growth response from June 1971 (Jackson, Gifford & Graham 1983).

Foliar Nutrient Levels

The effect of adding nitrogenous fertiliser alone was not tested in this trial. The F and LF plots received regular dressings with five nutrient elements in addition to nitrogen. Although the full analysis (February 1979) suggests that individual effects were negligible compared with that of nitrogen, their combination may have had a different effect on *P. radiata* nitrogen concentration from that of nitrogen alone. Similarly, although the major effect of lupins in a nitrogen-deficient ecosystem might be expected to result from biological nitrogen fixation (Gadgil 1971), other factors could also have exerted an influence. Dyke (1973) has shown that legume residues can increase crop yield in a way that is not matched by fertiliser-nitrogen additions. On the other hand, soil sampling and analysis in the present trial did show differences in soil-nitrogen content which were attributable to lupins and to fertiliser treatment. There can be little doubt that, in this ecosystem, the major effects of the L and F treatments were attributable to biologically fixed nitrogen and nitrogenous fertilisers respectively.

Waring (1981) concluded from a literature review that "foliar analysis for total N is not useful for the precise monitoring of N status . . .". We would agree with this statement to the extent that the absence of treatment differences in the present study cannot be interpreted as absence of influence on nitrogen availability. The well-known "dilution effect" whereby additional growth tends to decrease the over-all foliar-nitrogen concentration, was certainly operating in this ecosystem (Gadgil 1979). Demonstrable differences associated with experimental treatment can be taken to indicate differences in nitrogen status when one set of data (for 0 plots) clearly represented foliar-nitrogen concentrations associated with nitrogen stress (the onset of chlorosis and reduction in growth rate observed in 0 plot trees during 1974 – *see* Jackson, Gifford & Graham 1983). The fact that consistent differences in nitrogen concentration attributable to treatment were observed only from 1973 onwards, when nitrogen values were generally lower than at the beginning of the trial, may reflect the absence of nitrogen stress in any of the trees before this point. Stress was most probably associated with the very high nitrogen demand in 5- to 6-year-old trees (Madgwick *et al.* 1977). Chlorosis was observed in all subplots of the 0 treatment and inter-tree competition cannot have been the major contributing factor at this point. It is clear that the nitrogen effect of lupin residues from exclusion spraying was negligible by 1973.

Relative Nitrogen Contributions from Lupins and Fertiliser

The actual amounts of nitrogen contributed by lupins and fertiliser to the *P. radiata* trees cannot be estimated from foliar analysis and mensurational data. It is hoped that results of biomass sampling carried out in 1975 and, 1978–79 (H. Madgwick and P .Beets, pers. comm.) and the associated analytical data will provide valuable information on this subject.

Soil-nitrogen levels were increased by both L and F treatments. There is little evidence to suggest that fertiliser had a greater effect than lupins on either total-nitrogen or potentially-available-nitrogen values. In fact the over-all effect of lupin influence and regular nitrogen applications was surprisingly small in absolute terms. No significant interaction effects were recorded after 1969. This indicates that the consistently higher values for LF plots were the result of independent additive effects of the treatment components. The absence of any marked signs of nitrogen accumulation in the soil after 12 years of vegetation influence suggests either that plant uptake was extremely efficient or that leaching/volatilisation losses were large. The results confirm and extend earlier observations that in this sand/pine forest ecosystem, nitrogen is retained in the vegetation and litter layers rather than in the mineral soil (Gadgil 1979).

The effect of fertiliser on *P. radiata* foliar-nitrogen levels was greater than the lupin effect between May 1974 and February 1979. At other times nitrogen concentrations for these treatments were indistinguishable. In winter 1970 and from May 1973 onwards (with the exception of the May–November 1975 period) samples from LF plots had the highest foliar-nitrogen levels, due mainly to additive effects, although some interaction was noted. Lupin regeneration after the 1976 stocking reduction was confined to the 371 stems/ha subplots. During 1976, lupin effects on *P. radiata* foliar-nitrogen levels were seldom significant, but from February 1977 to February 1983 the lupin effect was observed in 11 out of 12 sample collections. Although responses to lupin and to (discontinued) fertiliser treatment were indistinguishable from February 1980 to February 1983, foliar-nitrogen levels were consistently higher in plots which had received both fertiliser and the lupin influence. It would have been surprising if a total of more than 900 kg N/ha in 56-kg/ha 6-monthly doses had not had an effect on tree nutrition. However, the additional response, in terms of foliar-nitrogen concentration, to the presence of lupins indicates that tree nitrogen requirement was not satisfied by fertiliser treatment alone. There is also evidence that continued, regular fertiliser application was necessary for maintenance of foliar-nitrogen above the 1.1% level.

The lupin effect is interesting because the nitrogen input from biological fixation was not continuous. No significant lupin growth was present in any of the L or LF plots between November 1972 and February 1976 and yet responses to the presence of lupins were noted during this period in five of the nine 3-monthly sample collections. The role played by marram grass at the time of canopy closure has already been discussed by Mead & Gadgil (1978) and it would have made a contribution to the delayed effect. Recycling of nitrogen through *P. radiata* (uptake and litter decomposition) would also have been a contributing factor.

The results point to a low level of retention of fertiliser-nitrogen in the mineral soil and a low efficiency of nitrogenous fertiliser in terms of tree nitrogen uptake. The evidence that tree growth was limited by nitrogen supply even when 56 kg N/ha had been applied at 6-monthly intervals for 10 years, underlines the importance of lupins in this ecosystem. Their effect on soil and tree nitrogen status was at times indistinguishable from that of fertiliser, yet under these particular circumstances it was achieved with zero management cost. There is reason to believe that careful management of the understorey to improve lupin-nitrogen input might be economically justifiable and would repay further investigation.

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