

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

IV. NITROGEN DISTRIBUTION IN THE ECOSYSTEM
FOR THE FIRST 5 YEARS AFTER TREE PLANTING

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ABSTRACT

An age sequence of *Pinus radiata* D. Don stands was studied at Woodhill State Forest, where trees are planted at a nominal 1730 stems/ha into coastal sand which has been partly stabilised with marram grass and perennial tree lupin. During the first 5 years of tree growth the dynamics of dry matter and nitrogen accumulation in the ecosystem were dominated by changes which occurred in the herbaceous vegetation.

Crushing during tree planting and spray releasing of trees during the first year had a profound effect on both lupins and marram grass with the result that litter, rather than lupin plant tops, became the largest contributor to total dry matter and its nitrogen content for the remainder of the study period.

Lupins regenerated to 85% of their former productivity during the second year of tree growth but declined between years two and five. The marram component showed a much slower rate of decline during the same period.

There was no overall increase in dry matter or nitrogen content of the ecosystem between years two and five and it is inferred that the chief source of nitrogen for tree growth was the nitrogen fixed by the lupin and stored in the herbaceous plants and their litter.

INTRODUCTION

During the past decade it has become increasingly clear that *Pinus radiata* D. Don (radiata pine) forests established on coastal sand dunes in New Zealand are dependent on perennial tree lupin for much of their nitrogen supply. The standard stabilisation procedure for coastal dunes consists of building a continuous foredune barrier and then planting marram grass (*Ammophila arenaria* L.) followed by tree lupin (*Lupinus arboreus* Sims) and finally radiata pine. The timing of lupin and radiata pine plantings depends on the rate of development of the root systems and vegetation cover of the marram grass and lupins respectively. It is also governed by economic factors such as availability of labour.

Lupins growing with marram grass on the open dunes at Woodhill Forest can fix at least 160 kg N/ha annually and there is considerable evidence to show that this input is important in an ecosystem which contains little plant-available nitrogen before the lupins are introduced (Gadgil, 1971). Exclusion of lupin plants from the ecosystem results in lowered productivity and nitrogen content of marram grass (Gadgil, 1976), and a reduced growth rate, associated with symptoms of nitrogen deficiency, in radiata pine. Trials have shown that tree increment losses can be avoided in areas kept free of lupins if fertiliser nitrogen is applied (New Zealand Forest Service, 1976; Mead and Gadgil, 1978).

The study of nitrogen distribution in the ecosystem is an attempt to assess the influence of the lupin component at various stages of the artificial succession. Results from the pre-radiata pine phase have already been reported (Gadgil, 1971). The present report covers the tree establishment phase during which (i) the lupin is tractor-crushed as the trees are planted, (ii) lupin regrowth is killed with hormone spray to release the trees, and (iii) lupin plants regenerating from buried seed are suppressed by the developing tree stand.

METHODS

Selection of Sampling Sites

It was hoped that sampling for this phase of the study could be confined to one stand so that inconsistencies arising from differences in, for example, sand characteristics or stand history would be avoided. In the event this proved to be impossible. Details of the stages in the vegetation succession and the sites sampled are shown in Table 1. Each of the three sites sampled was approximately 1 km from the sea.

Sampling Techniques

Trees

In the 1-year-old tree stand (Stage C), 10 trees were selected at random. Each was dug carefully out of the sand and divided into foliage, stem, stump, and roots. The mean fresh weight, dry weight, and weight of nitrogen per tree were determined and the values obtained used to calculate stand biomass and nitrogen content on a kilogram per hectare basis.

For stages D-G, stand biomass and nitrogen content were determined by a logarithmic regression method, using diameter at breast height (d.b.h.) as the independent variable (Crow, 1971). Measurement of d.b.h. of all trees in a randomly selected 0.04-ha sample plot gave an estimate of the frequency distribution of d.b.h. in the population. Ten trees with d.b.h. reflecting the population distribution were selected for destructive sampling. For Stage E these were taken within the measured plot, but for Stages F and G the same plot was measured each time and sample trees were selected from areas just outside the plot boundary. Each stem was severed at ground level, and the fresh weight of needles, branches, stem wood, and stem bark was determined. A subsample from each category was sealed in a polythene bag and taken to the laboratory for dry weight determination and nitrogen analysis. A circular hole with a radius of 0.5 m from the centre of each tree stump was dug to a depth of 1 m and the tree roots were removed from the sand by sieving. After careful washing, the material from each hole

TABLE 1 - Details of stands sampled

Stage in succession	Compartment No.	Compartment history			Date of sampling
		Marram planted	Lupin sown	Radiata pine planted	
A. Lupin stand 2 years old in marram.	138	1965	1966	-	March 1968
B. Radiata pine planted in tractor-crushed lupin 1 month previously.	138	1965	1966	1968	June 1968
C. Radiata pine 1 year old. Lupin killed with 2,4,5-T spray 5 months previously.	138	1965	1966	1968	May 1969
D. Radiata pine 2 years old. Lupin regenerated.	202	1964	1965	1971	May 1973
E. Radiata pine 3 years old. Lupin present.	188	1964	1965	1971	May 1974
F. Radiata pine 4 years old. Lupin present.	188	1964	1965	1971	May 1975
G. Radiata pine 5 years old. Lupin present.	188	1964	1965	1971	May 1976

was divided into stump, roots > 3 cm diameter, roots 1-3 cm diameter, and roots < 1 cm diameter. The total dry weight and nitrogen content were determined for each sampling category of each tree, and estimates of the dry weight and nitrogen content of the stand were made from these data. Allowance was made for bias due to logarithmic regression (Mountford and Bunce, 1973).

Herbaceous vegetation and litter

In each stand, 3 quadrats (1 × 1 m) were laid in areas considered to be representative of the stand as a whole. Quadrats were never placed within 0.5 m of a tree stem and for Stages F and G they were located outside the tree measurement plot. The use of only three, small, selected, sampling areas to estimate dry weight and nitrogen content of the herbaceous vegetation was a compromise between a complete lack of information and an unacceptable workload. A vertical projection of each quadrat through the vegetation was delineated with stakes and string, and all plant tops within the defined volume were removed and placed in polythene bags after separation of lupin and non-lupin material. Litter, defined as dead fallen vegetation, and lupin seeds (which had all fallen) were collected separately. Animals such as snails and insect larvae were collected and weighed with the plant material.

The cubic metre of sand lying vertically below each marked square was excavated and root material was removed by sieving. After transport to the laboratory the roots were washed carefully and divided into radiata pine and non-radiata pine categories.

All material was oven-dried at 70°C. Each litter sample was hand sorted for lupin seed and separated with an 0.5-mm mesh sieve into a "litter" and "litter sand" fraction. The "litter sand" contained about 0.2% nitrogen.

Sand

During root excavation, three core samples of sand (3.3 cm long × 4.6 cm diam.) were taken at each of three levels — (1) before digging commenced, and when the floor of the pit was (2) 50 cm and (3) 100 cm below the sand surface. Each sample was sealed in a polythene bag and its dry weight and nitrogen content were determined in the laboratory. An estimate of the total nitrogen content of the sand to a depth of 1 m was derived, using the volume/weight data from the core samples.

Laboratory Analysis

All plant and litter material was dried at 70°C in forced-draught ovens, and ground in a Wiley mill. Subsamples were analysed for total nitrogen by a semi-micro Kjeldahl technique (Bremner, 1960). Sand was air-dried and root material was removed by sieving (0.5-mm mesh). Subsamples were used to obtain a factor for conversion to oven-dry weight. Total nitrogen content was determined by Bremner's method after pre-treatment to ensure quantitative assessment of nitrates and nitrites (Bremner and Shaw, 1958).

Amalgamation of Data

The eight components of the ecosystem selected for study were:

- (i) Sand to 1 m including "litter sand";
- (ii) Radiata pine roots;

- (iii) Roots other than radiata pine;
- (iv) Litter;
- (v) Lupin seed;
- (vi) Lupin tops;
- (vii) Tops other than radiata pine or lupin ("marram" tops);
- (viii) Radiata pine tops.

Estimates of dry matter and nitrogen content were calculated for each of these categories at each of the seven sampling stages. It was assumed that all the organic material and all the combined nitrogen in the ecosystem was accounted for by summing the totals for categories (ii) to (viii) and (i) to (viii) respectively. The summed nitrogen contents of categories (ii) to (viii) will be referred to as "dry matter nitrogen" or DMN.

RESULTS

Data for dry matter and nitrogen accumulation in sand, litter, herbaceous plants, and trees are presented in Tables 2 and 3 and summarised in Table 4. An overall picture of dry matter and nitrogen accumulation in the various categories of the ecosystem at the seven stages sampled is given in Figs. 1-3.

Data for sand nitrogen content are based on small samples with a high dry weight/nitrogen ratio and the estimates may not be reliable in terms of absolute values. It seems clear from Fig. 1 that there was no continuous or massive build-up of sand total-N beneath the young radiata pine stands.

Total biomass and nitrogen values for plant material followed similar trends over most of the sampling stages (Table 4). An overall decline was caused by tree planting and spray releasing operations, but recovery occurred during the second year of tree growth and continued more slowly into the third year. Biomass accumulation in the fourth year (Stages E-F) fell slightly, but had increased again by Stage G. By contrast, nitrogen values continued to increase slowly during the fourth year but decreased during year five.

Throughout the study period the radiata pine component increased steadily. At age 5 the dry matter in tops and roots totalled 13.9 and 8.0 t/ha with a nitrogen content of 139.9 and 32.8 kg/ha respectively.

Damage to lupin plants caused by crushing and spraying reduced the dry weight of lupin tops from 9.9 to 0.2 t/ha and the nitrogen content from 85.8 to 3.5 kg/ha. Although another stand of lupins developed from seed its productivity never reached the original value. There was a continuous slight decline of the lupin component between Stages D and F and a sudden drop between Stages F and G to 1.5 t dry matter/ha containing less than 10 kg N/ha.

Marram plants were also damaged by crushing (Stage B). At Stage C the dry weight of the marram component was still slightly lower than that at Stage B, but the nitrogen content had increased. For the remainder of the study period marram dry matter and nitrogen content remained at levels higher than at Stages A, B, or C. A slight decline in nitrogen content, but not in dry weight, was detectable between Stages F and G.

TABLE 2 - Dry matter and nitrogen data from unit area sampling

Stage	Lupin tops		Tops other than lupin and radiata pine		Litter		Lupin seed		Roots other than radiata pine		Sand to 1 m	
	Dry matter (t/ha)	Nitrogen (kg/ha)	DM (t/ha)	N (kg/ha)	DM (t/ha)	N (kg/ha)	DM (t/ha)	N (kg/ha)	DM (t/ha)	N (kg/ha)	DM (t/ha)	N (kg/ha)
A	9.74	73.16	4.45	30.55	3.42	60.92	0.08	5.14	4.49	27.61	4.49	1475.90
	10.39	83.76	2.03	19.37	2.69	34.38	0.15	10.11	3.15	21.84	3.15	1298.83
	9.45	100.51	3.24	22.61	4.18	89.13	0.34	22.42	3.90	22.86	3.90	1004.01
B	9.43	69.65	3.91	4.65	7.98	62.14	0.37	24.97	4.60	24.34	4.60	1485.42
	5.53	40.33	3.32	26.51	4.51	39.72	0.33	21.47	2.72	13.75	2.72	1543.88
	12.09	88.50	1.24	12.88	11.98	84.31	0.14	9.85	1.37	8.09	1.37	1259.95
C	0.13	5.06	1.76	25.22	12.34	120.12	0.04	2.50	4.57	37.99	4.57	1006.35
	0.01	0.12	3.90	18.00	9.76	3.71	-	-	7.78	18.27	7.78	1064.11
	0.35	5.43	0.61	7.12	4.87	42.02	0.02	1.17	2.45	16.79	2.45	1243.89
D	9.91	62.00	12.23	70.20	45.71	607.50	0.05	0.30	11.57	50.00	11.57	1549.04
	-	-	6.18	29.20	33.74	323.60	0.01	1.00	9.41	41.10	9.41	1291.37
	15.47	101.80	7.70	44.80	16.75	251.60	0.08	4.90	10.33	76.60	10.33	1557.11
E	0.60	2.66	20.48	101.18	11.41	139.87	0.14	8.66	10.61	53.04	10.61	1400.24
	-	-	10.23	42.45	35.69	364.43	0.07	4.24	14.30	78.48	14.30	1706.86
	20.65	131.53	5.21	33.21	20.99	262.85	0.02	1.38	15.39	128.02	15.39	1902.38
F	3.83	23.21	8.56	53.27	19.78	263.12	0.23	14.71	10.00	56.41	10.00	2495.36
	0.78	5.58	11.78	77.19	11.17	186.15	0.35	20.87	12.74	69.41	12.74	1255.42
	11.95	85.09	3.83	27.62	17.03	237.19	0.09	5.77	12.38	80.46	12.38	1298.32
G	0.01	0.30	11.77	59.77	17.90	229.95	0.04	3.11	11.97	37.74	11.97	1261.55
	3.50	23.07	13.58	63.28	18.28	239.45	0.02	1.09	7.24	29.96	7.24	1149.81
	1.03	12.81	6.76	36.16	18.41	185.21	0.02	1.01	10.37	31.69	10.37	1772.61

TABLE 3 - Radiata pine biomass and nitrogen data

Sampling stage	Tree age	Foliage		Branches		Stem wood		Stem bark		Stump		Roots >3 cm		Roots 1-3 cm		Roots <1 cm (tree samples)		Roots <1 cm (Unit area samples)	
----- Dry weight (t/ha) -----																			
C	1	0.02	0.03*	-	-	0.01	0.02*	-	-	0.006	0.006*	-	-	0.009	0.012*	-	-	-	-
		0.01	0.01			0.01	0.01			0.004	0.004			0.006	0.006				
D	2	0.19	0.24	0.06	0.06*	0.16	0.20	-	-	0.05	0.06	-	0.006	0.007*	0.04	0.05	0.11	0.05†	0.19
		0.14	0.14	0.06	0.06	0.11	0.11			0.04	0.04		0.005	0.005	0.03	0.03	0.08	0.08	0.08
E	3	0.45	0.59	0.16	0.22	0.33	0.43	0.08	0.10*	0.10	0.13	0.02	0.02*	0.05	0.06	0.10	0.14	0.20	0.08
		0.31	0.31	0.11	0.11	0.23	0.23	0.05	0.05	0.07	0.07	0.01	0.01	0.03	0.03	0.07	0.07	0.39	0.12
F	4	1.68	2.26	1.05	1.42	1.45	1.96	0.24	0.32	0.64	0.86	0.10	0.13	0.23	0.32	0.14	0.19	1.13	0.97
		1.16	1.16	0.71	0.71	0.95	0.95	0.16	0.16	0.42	0.42	0.08	0.08	0.16	0.16	0.10	0.10	1.21	1.21
G	5	4.66	6.37	3.50	4.61	5.11	7.01	0.65	0.89	1.81	2.43	0.72	1.00	0.42	0.57	0.32	0.41	4.77	4.80
		3.01	3.01	2.58	2.58	3.27	3.27	0.42	0.42	1.22	1.22	0.50	0.50	0.29	0.29	0.23	0.23	2.85	6.66
----- Nitrogen (kg/ha) -----																			
C	1	0.35	0.45	-	-	0.07	0.09	-	-	0.01	0.02	-	-	0.06	0.08	-	-	-	-
		0.24	0.24			0.05	0.05			0.01	0.01			0.04	0.04				
D	2	3.23	4.12	0.43	0.43	0.50	0.65	-	-	0.15	0.19	-	0.02	0.02	0.17	0.21	0.30	0.40	0.20
		2.37	2.37	0.43	0.43	0.37	0.37			0.11	0.11		0.01	0.01	0.13	0.13	0.50	0.50	0.50
E	3	6.74	8.85	0.79	1.05	0.51	0.67	0.51	0.67	0.26	0.35	0.04	0.06	0.14	0.18	0.49	0.63	1.27	0.69
		4.72	4.72	0.55	0.55	0.36	0.36	0.36	0.36	0.19	0.19	0.03	0.03	0.10	0.10	0.36	0.36	2.53	0.61
F	4	24.80	33.30	7.58	10.27	2.46	3.32	1.58	2.13	1.53	2.07	0.21	0.27	0.70	0.95	0.63	0.84	7.52	7.07
		17.05	17.05	5.37	5.37	1.62	1.62	1.07	1.07	1.02	1.02	0.15	0.15	0.47	0.47	0.43	0.43	7.77	7.74
G	5	64.47	88.10	13.15	17.67	6.40	8.69	3.68	4.98	3.11	4.15	1.23	1.69	0.87	1.16	1.56	2.02	25.95	27.45
		41.59	41.59	8.86	8.86	4.14	4.14	2.42	2.42	2.15	2.15	0.83	0.83	0.60	0.60	1.17	1.17	20.59	29.82

* Figures in this column represent 95% confidence limits.

† Figures in this column are actual values for the three sample areas.

TABLE 4 - Dry matter and nitrogen distribution in the ecosystem

	Stage A 2-yr-old lupin and marram	Stage B Lupin crushed	Stage C 1-yr-old radiata pine	Stage D 2-yr-old radiata pine	Stage E 3-yr-old radiata pine	Stage F 4-yr-old radiata pine	Stage G* 5-yr-old radiata pine
	----- t/ha -----						
Total dry matter	20.6	23.2	16.3	60.3	56.8	48.2	54.5
Litter	3.4	8.2	9.0	32.1	22.7	16.0	14.6
Biomass	17.1	15.0	7.3	28.3	34.1	28.3	39.9
Total tops	13.1	11.8	2.3	17.6	20.1	14.2	24.0
Tree tops	-	+	+	0.4	1.0	4.4	13.9
Herbaceous tops	13.1	11.8	2.3	17.2	19.1	13.6	10.1
Lupin tops	9.9	9.0	0.2	8.5	7.1	5.5	1.5
Marram, etc., tops	3.2	2.8	2.1	8.7	12.0	8.1	8.6
Total roots	3.9	2.9	5.0	10.7	13.9	14.0	15.9
Tree roots	-	+	+	0.2	0.5	2.3	8.0
Herbaceous roots	3.9	2.9	5.0	10.4	13.4	11.7	7.9
Lupin seed	0.2	0.3	+	0.1	0.1	0.2	+
	----- kg/ha -----						
Total N in ecosystem							
Sand to 1 m	1259.6	1429.7	1104.8	1465.8	1669.8	1683.0	1394.7
Litter †	61.5	62.1	55.3	394.2	255.7	228.8	174.6
Biomass	146.7	115.1	46.4	165.6	205.7	220.2	200.6
Total tops	110.0	80.9	20.7	106.9	112.2	127.1	139.9
Tree tops	-	+	0.4	4.2	8.5	36.4	87.7
Herbaceous tops	110.0	80.9	20.3	102.7	103.7	90.7	52.2
Lupin tops	85.8	66.2	3.5	54.6	44.7	38.0	9.7
Marram, etc., tops	24.2	14.7	16.8	48.1	59.0	52.7	42.5
Total roots	24.1	15.4	24.5	56.6	88.7	79.3	59.3
Tree roots	-	+	0.1	0.7	2.2	10.5	32.8
Herbaceous roots	24.1	15.4	24.4	55.9	86.5	68.8	26.5
Lupin seed	12.6	18.8	1.2	2.1	4.8	13.8	1.4

* Unit area estimates at Stage G were corrected for an estimated 20% site occupancy by radiata pine.

† Includes "litter sand"

+ Present, but value less than 0.1.

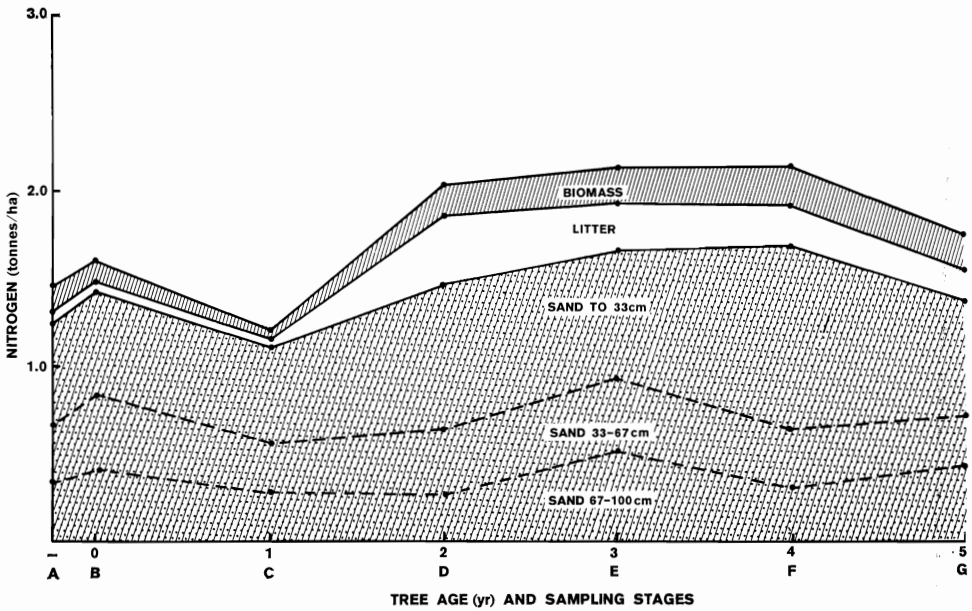


FIG. 1—Nitrogen in the ecosystem.

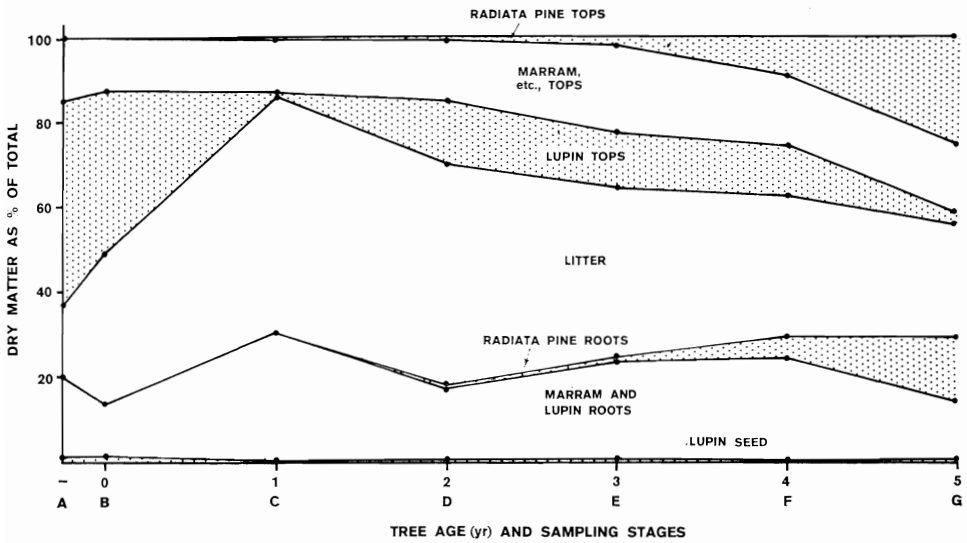


FIG. 2—Relative contribution of individual components to dry matter accumulation.

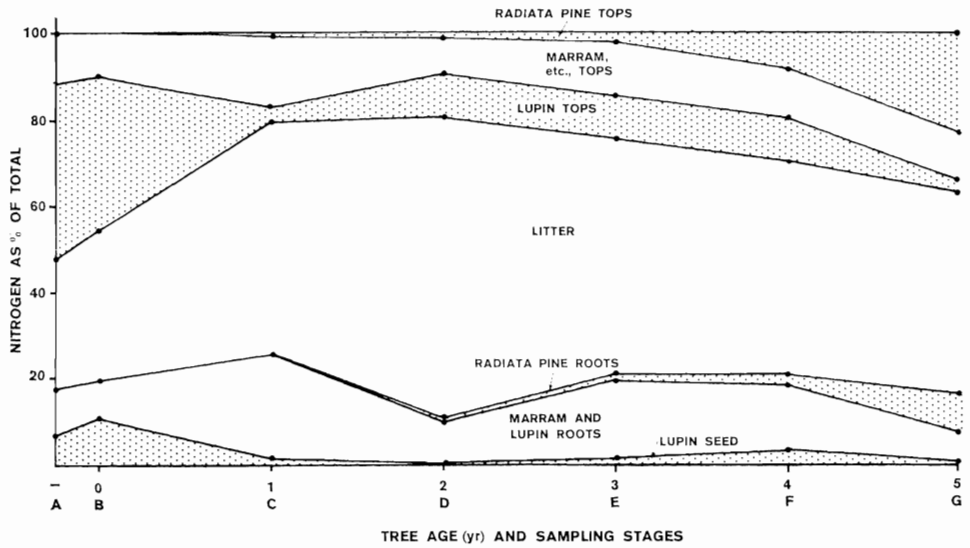


FIG. 3—Relative contribution of individual components to dry matter nitrogen (DMN).

Weight and nitrogen content of the non-radiata pine root fraction reflected to some extent the fluctuations of the combined lupin + marram tops category. A decrease between Stages A and B was followed by a steady increase to Stage E after which a slight decline in dry weight and a sharper drop in nitrogen content were observed.

The average weight of lupin seed at each stage varied between 20 and 300 kg/ha. The largest accumulations occurred at Stages A, B, and F, and the seed contained between 10 and 20 kg N/ha at each of these three stages.

The litter component was responsible for much of the between-year variation in total dry matter and DMN. Crushing the vegetation increased dry matter accumulation at Stage B but had little effect on nitrogen accumulation which remained at about 60 kg/ha at Stages A, B, and C. The large increase in the litter component observed between Stages C and D coincided with a change of sampling site. Litter dry weight at Stages E and F was double the amount recorded at Stages B and C and the nitrogen content was 4 times higher. By Stage G there was a slight decline in the litter contribution but nitrogen values were still 3 times as great as they had been at Stages A, B, and C.

DISCUSSION

In this study, errors due to (i) low numbers of sampling sites and (ii) seasonal variation were intentionally ignored. The main object was to follow the relative distribution of dry weight and nitrogen among the various ecosystem components rather than to make a statement about absolute amounts. Thus total dry matter accumulation in the 2-year-old lupin stand (Stage A) was lower than might be expected from Gadgil's (1971) data, probably because sampling was carried out at a different time of year (May rather than November). The relative proportions of plant tops, roots, and litter were, however, similar.

The increase in litter with low nitrogen content 1 month after the vegetation was crushed during tree planting, suggests that the marram may have been more severely affected than the lupin although recovery was rapid. Much of the damaged lupin material was sprouting and could not be classified as litter. Crushed marram leaves, on the other hand, were not capable of regeneration and contributed to the litter fraction.

Although the total dry matter content of the stand was reduced, the impact of 2,4,5-T on the lupin component resulted in an increase in nitrogen content, rather than growth, of the marram at Stage C. Root biomass and nitrogen content were increased by 72% and 59% respectively. Probably the most important change brought about by spray treatment was the increase in status of the litter component as a "reservoir" of nitrogen. Before spraying, lupin tops made the largest contribution to DMN. Although the lupin component regenerated, it never regained dominance in terms of relative nitrogen content. Litter nitrogen continued to exceed biomass nitrogen until Stage G and even then it contained more nitrogen than any other single dry matter category.

The apparent increase in dry matter accumulation which occurred between Stages C and D coincided with a change in sampling site. The fact that the marram/lupin association at time of sampling was 5 years older in Cpt 202 (Stage D) than in Cpt 138 (Stages A-C) means that the data for Stage D relate more directly to those for Stages E, F, and G than to those for Stages A-C. It would be unwise to place any emphasis on actual magnitude of results at Stage D but it is interesting to note the roughly equal dry matter and nitrogen contributions of lupin and marram tops and the very large proportion of total nitrogen present in the litter.

The gradual decline of the lupin component which began at Stage E continued until it represented only 3% of total dry matter and DMN at Stage G. This decline coincided with a steady increase in the contribution from radiata pine but there was no corresponding reduction in the contribution from marram tops. The inference is that in these relatively open tree stands the lupin and litter material were the chief source of nitrogen for radiata pine up to age 5.

Although there were some fluctuations, the proportion of dry matter contributed by each ecosystem component was broadly similar to its nitrogen contribution. Lupin seed was an exception to this generalisation because of its high nitrogen content. A remarkable 10% of total DMN was found in lupin seed at Stage B.

The data indicate a general loss in total nitrogen between Stages D and G even though total dry matter increased between Stages F and G. This reflected an increase in the proportion of tree components with a low nitrogen content, particularly stems and branches. Overall, increased nitrogen uptake by radiata pine and biological nitrogen fixation evidently did not compensate for nitrogen losses from the ecosystem.

From Gadgil's (1976) data for a radiata pine stand at Woodhill it would appear that a heavier stocking rate (1900 stems/ha compared with 900 stems/ha in the present study) would not have greatly increased nitrogen uptake by 4-year-old trees. Tree tops at Stage F contained 36.4 kg N/ha compared with 44.8 kg N/ha in the denser stand. The pattern of dry matter and nitrogen distribution in above-ground biomass in the present study resembled that of the stand with lupin more closely than that of the stand in which lupin had failed to regenerate after spray-releasing (Table 5). In the

TABLE 5 - Comparison of stage F data with those from an earlier study

Stand	Dry matter (t/ha)					Nitrogen (kg/ha)				
	Litter	Lupin seed	Lupin tops	Marram tops	Radiata pine tops	Litter	Lupin seed	Lupin tops	Marram tops	Radiata pine tops
Compt 134. Radiata pine 4 years old; 1900 stems/ha. Lupin present (Gadgil, 1976).	10.0	0.1	9.2	7.1	6.0	107.9	5.8	83.1	50.0	44.8
Compt 139. Radiata pine 4 years old; 2325 stems/ha. Lupin absent (Gadgil, 1976).	13.0	0.0	0.0	6.6	12.2	113.4	0.0	0.0	26.1	61.1
Compt 188. Radiata pine 4 years old; 900 stems/ha. Lupin present (This study).	16.0	0.2	5.5	8.1	4.4	228.8	13.8	38.0	52.7	36.4

absence of lupin, tree tops contained twice as much dry matter and nitrogen as herbaceous plant tops. Where lupin was present the relative distribution was reversed, the herbaceous plants accounting for more than twice as much dry matter and three times as much nitrogen as the trees. This undoubtedly reflects some degree of suppression of 4-year-old trees by the herbaceous plants when lupin was present. Data from Stage G in the present study indicate that during the fifth year the tree top component is capable of assuming a greater dry weight and nitrogen content than the combined lupin and marram top component.

The absence of any overall increase in nitrogen accumulation after the decline in lupin growth had begun, underlines the importance in this particular ecosystem of (i) symbiotic nitrogen fixation and (ii) the retention of the fixed nitrogen in organic form. The suggestion that nitrogen accumulation in herbaceous plants and their litter constitutes the main source of nitrogen supply for trees at Woodhill (Gadgil, 1971) is amply supported by this study.

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