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EDAPHIC ADAPTATION OF GORSE

(Ulex europaeus L.)

A thesis
submitted in partial fulfilment
of the requirements for the Degree
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Abstract of a thesis submitted in partial fulfilment
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by

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Aspects of the edaphic adaptation of gorse (*Ulex europaeus* L.) were investigated using field and glasshouse experiments. Variables compared included P and N supply, soil pH, frequency of cutting and stage of soil development. Particular emphasis was placed on soil chemical properties of most importance to legumes growing on low fertility soils in New Zealand (available P and acidity) and on the ability of gorse to fix nitrogen and thus thrive under conditions of low available soil N. Gorse was contrasted with the high soil fertility demanding pasture legume, white clover (*Trifolium repens* L.).

Under dryland conditions in Canterbury unfertilized gorse in its second growth season, grown on a soil with very low available P and cut frequently (twice yearly) had similar annual dry matter production (5053 kg ha^{-1}) to pasture (5870 kg ha^{-1}) fertilized with $250 \text{ kg ha}^{-1} \text{ year}^{-1}$ superphosphate. Infrequently cut, unfertilized gorse or gorse which was P-fertilized (and either frequently or infrequently cut) produced more than $18\,500 \text{ kg dry matter ha}^{-1}$. On a river terrace sequence in North Westland, established gorse grown on unfertilized soils with very low to low available P concentrations, and some of which had physical constraints to root growth, produced similar amounts of dry matter (7210 to $14\,600 \text{ kg ha}^{-1} \text{ year}^{-1}$) as pasture ($10\,920 \text{ kg ha}^{-1} \text{ year}^{-1}$) fertilized with $1000 \text{ kg ha}^{-1} \text{ year}^{-1}$ of 33% potassic, cobaltised, lime reverted superphosphate (giving about 42 kg P ha^{-1} , 165 kg K ha^{-1} and 56 kg S ha^{-1}).

Gorse gave dry matter responses to applied P, but was less responsive than white clover, both in the field (where the two species were grown together) and in pots (where the two species were grown separately). Gorse was able to take up more P than did white clover from soils with very low available P concentration both in pots and in the field.

The P response curves for gorse were quadratic in shape, suggesting a tendency for decline in yield at high rates of P, whereas those for white clover were exponential in shape with increases in dry matter yield diminishing at the greatest rates of P used but showing no tendency for decline.

Shoot P concentrations of field grown gorse were less than those of white clover at all rates of applied P (except for the nil rate at one sampling time) and the critical shoot P concentration for gorse (0.19%) appeared to be less than that for white clover (0.35%), indicating that gorse used P more efficiently in the processes of growth than white clover.

In the field infrequently cut gorse (at the end of 2 years growth) produced about twice as much dry matter as frequently cut gorse (cut twice yearly), but the total P contents of the two cutting treatments were similar, indicating similar capacities for P uptake. Critical P concentrations in young tissue were also similar for both cutting treatments. The ability of infrequently cut gorse to out-yield frequently cut gorse appeared to result from the greater potential for P transfer from old to young tissue in infrequently cut plants combined with their greater leaf area index. The P contained in harvested shoots was lost to the frequently cut plants, whereas infrequently cut plants appeared to make more efficient use of the P taken up by transferring it from old to new tissue.

Gorse grown in pots was less sensitive to soil acidity (0.02 mol l⁻¹ CaCl₂-extractable Al in particular) than was white clover and was also less responsive to applied lime. Nitrogen-fixing (acetylene reducing) activity did not appear to be any more sensitive to soil acidity than host plant growth, for either gorse or white clover.

Gorse did not have a noticeable soil acidifying effect when grown in pots, but white clover did.

Gorse grown in sand culture was responsive to increasing nutrient solution nitrate concentration within the range found in natural and agricultural soils (0-10 mmol l⁻¹). In terms of dry matter production, gorse was not significantly less responsive to increasing nitrate concentration than white clover, but was less responsive than white clover in terms of total N content. Gorse reached 90% maximum dry matter yield at a lower solution nitrate concentration (1.2 mmol l⁻¹) than white clover (2.9 mmol l⁻¹). Unlike white clover, gorse

growth and N accumulation were depressed at the greatest nutrient solution nitrate concentration used (20 mmol l^{-1}) which is about the top of the range which can temporarily occur in highly fertilized soils. Similarly to white clover, gorse was able to use available mineral N by increasing its nitrate reductase activity of its roots and shoots.

N concentration of gorse tissue was less than that of white clover tissue at all solution nitrate concentrations and the critical N concentration for gorse (2.79%) was less than that for white clover (4.62%), indicating that gorse used N more efficiently in dry matter production than white clover did.

The symbiotic nitrogen-fixing system of gorse appeared to be able to meet the needs of the plant in the field where the application of 200 kg N ha^{-1} gave no dry matter response. In sand culture the reduction in nodule weight and nitrogen-fixing activity with increasing nutrient solution nitrate concentration was less for gorse than white clover. This suggests that the N_2 -fixing system of gorse may be able to recover more readily than that of white clover following depression by applied N.

Dry matter yield of established gorse on a river terrace soil sequence in North Westland was not clearly linked with soil fertility but appeared to be more affected by physical factors affecting rooting volume and rooting depth.

It was confirmed that gorse is relatively tolerant of low soil fertility conditions, hence its significance as a pest in low input pastoral agriculture (low fertilizer inputs and low stocking rates).

Under conditions of high soil fertility, it should be possible to control gorse at the seedling stage when its growth is slow relative to high fertility-demanding pasture species. However, when it is mature, gorse has the potential to grow very rapidly and responds to applications of P and N within the range normally given to pastures.

High forage yields of gorse compared with pasture are possible under conditions of low soil fertility. However, yields were greatest from uncut plants. Therefore, if gorse is used as a forage it will be important to achieve an appropriate balance between browsing by animals and the maintenance of sufficient photosynthetic tissue to maintain rapid growth.

Key words: *Ulex europaeus*, *Trifolium repens*, edaphic adaptation, low fertility soils, interspecific competition, responses to N and P, critical N and P concentrations, Al toxicity, lime - P interactions, symbiotic N₂ fixation, nitrate reductase activity.

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CONTENTS

	PAGE
ABSTRACT	(i)
ACKNOWLEDGEMENTS	(v)
DECLARATION OF ORIGINALITY	(vii)
CERTIFICATE OF SUPERVISION	(viii)
TABLE OF CONTENTS	(ix)
LIST OF TABLES	(xx)
LIST OF FIGURES	(xxix)
LIST OF PLATES	(xxxv)
LIST OF APPENDICES	(xxxvi)
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: REVIEW OF LITERATURE	3
2.1	3
2.1.1	3
2.1.2	3
2.1.3	4
2.1.3.1	4
2.1.3.2	5
2.1.4	6
2.1.5	6
2.1.6	7
2.1.7	8
2.1.8	9
2.2	10
2.2.1	10
2.2.2	11
2.2.3	13
2.2.3.1	14

2.2.3.2	Dry matter production per unit of P absorbed	14
2.2.3.3	Critical plant P concentration	15
2.2.3.4	Summary - plant P uptake and use	15
2.2.4	Phosphorus and N ₂ fixation	15
2.3	SOIL ACIDITY AND PLANT GROWTH	17
2.3.1	The nature of soil acidity	17
2.3.2	Effects of Al toxicity and pH on plant growth	18
2.3.3	Methods of assessing soil Al status	20
2.3.4	Effect of soil acidity on plant P	20
2.3.4.1	Effect of lime on P availability	20
2.3.4.2	Interaction between P and Al	21
2.4	EFFECT OF COMBINED N ON LEGUME GROWTH	22
2.4.1	Effect of combined N on N ₂ fixation	22
2.4.2	Effect of combined N on nitrate reductase activity	23
2.5	SUMMARY	24

**CHAPTER 3: EFFECTS OF FERTILIZER PHOSPHORUS AND NITROGEN
AND FREQUENCY OF CUTTING ON GORSE AND
WHITE CLOVER GROWTH**

3.1	Introduction and aims	27
3.2	Experimental	28
3.2.1	Trial design	28
3.2.1.1	Statistical design	28
3.2.1.2	Treatments	30
3.2.1.2.1	Phosphorus	30
3.2.1.2.2	Nitrogen	31
3.2.1.2.3	Defoliation	31
3.2.2	Trial site	31
3.2.3	Establishment	33
3.2.3.1	Gorse seedling culture	33
3.2.3.2	Rhizobial inoculation	35

3.2.3.3	Transplanting	36
3.2.3.4	Watering - field site	37
3.2.4	Weed control	37
3.2.5	Basal nutrients	38
3.2.6	Measurement of gorse growth	39
3.2.6.1	Shoot elongation	39
3.2.6.2	Dry weight	39
3.2.7	Measurement of white clover growth	40
3.2.7.1	Visual assessment of dry matter production	40
3.2.8	Soil sampling	41
3.2.9	Plant sampling	41
3.2.9.1	Gorse	41
3.2.9.2	White clover	41
3.2.10	Nitrate reductase activity	42
3.2.10.1	Timing and plots sampled	42
3.2.10.2	Plant sampling procedure	43
3.2.11	Acetylene reduction	43
3.2.11.1	Preparation and sampling	43
3.2.11.2	Core sampling and incubation	44
3.2.11.3	Gas sampling and analysis	44
3.2.12	Chemical analysis of plant and soil samples	44
3.2.12.1	Plant analysis	44
3.2.12.2	Soil analysis	45
3.2.13	Rainfall and soil moisture measurement	45
3.2.13.1	Rainfall	45
3.2.13.2	Soil moisture	45
3.2.14	Statistical analysis	46
3.3	RESULTS	47
3.3.1	Effects of rate of P application on available soil P	47

3.3.2	Effects of rates of P and N application and cutting treatment on gorse dry weight and estimated white clover dry weight	48
3.3.2.1	Gorse and white clover dry weight at individual harvest times	48
3.3.2.2	Responsiveness of gorse and white clover to increasing rates of applied P and their capacity to acquire P from unfertilized soil	55
3.3.2.3	Annual and total gorse dry weights - F plots	57
3.3.2.4	Gorse dry weight - I plots	59
3.3.2.5	Gorse dry weight - comparison between F and I plots	61
3.3.3	P and N nutrition of gorse and white clover	63
3.3.3.1	P and N concentration in harvested gorse shoots - F plots	63
3.3.3.1.1	P concentration	63
3.3.3.1.2	N concentration	64
3.3.3.2	P and N concentration in gorse shoots from I plots - Dec 1990 and April 1991	68
3.3.3.2.1	P concentration	68
3.3.3.2.2	N concentration	70
3.3.3.3	P and N concentration in gorse shoots - comparison between F and I cutting treatments	72
3.3.3.4	Shoot P and N concentration - comparison between gorse and white clover	73
3.3.3.4.1	January 1990	74
3.3.3.4.2	December 1990	74

3.3.3.5	Critical P and N concentrations of gorse and white clover	78
3.3.3.6	P and N uptake of gorse	80
3.3.3.6.1	P and N content of gorse - F cutting treatment	80
3.3.3.6.2	P and N content of gorse - I cutting treatment	81
3.3.3.6.3	Effect of frequency of cutting on shoot P and N content	84
3.3.3.6.4	Comparative capacities of gorse and white clover to absorb P under conditions of low soil P	88
3.3.4	Effects of treatments, season and shoot type on elongation of gorse shoots	88
3.3.4.1	Effects of rate of P, rate of N and cutting treatment on total shoot length	88
3.3.4.2	Change in rate of shoot elongation over the growth season	90
3.3.4.3	Effect of shoot type on shoot length	94
3.3.5	Effect of rate of N application on nitrate reductase activity of shoot and root tissue of gorse	96
3.3.5.1	I cutting treatment, 22 Dec 1990	96
3.3.5.2	F cutting treatment, 28 Feb - 1 Mar 1991	96
3.3.6	Effect of N treatment on N ₂ -fixing (acetylene reducing) activity	98
3.4	DISCUSSION	99
3.4.1	Dry matter yield of gorse - responses to applied P and N	99

3.4.2	Contrasting responses of gorse and white clover to external P supply	101
3.4.2.1	Shape of response curves	101
3.4.2.2	Soil P requirement for maximum growth	102
3.4.2.3	Capacity to reach growth potential without applied P	102
3.4.3	Abilities of gorse and white clover to acquire P from unfertilized soil	104
3.4.4	P uptake and internal efficiency of P use	105
3.4.5	Critical P concentrations	106
3.4.6	N nutrition of gorse and white clover	108
3.4.6.1	Internal efficiency of N use	108
3.4.6.2	Effect of rates of P and N on N concentration and N content - gorse and white clover	109
3.4.6.3	Effect of N application on nitrate reductase activity (NRA)	110
3.4.6.4	Effect of N application on N ₂ -fixing activity	111
3.4.7	Effects of cutting frequency on yield P and N concentrations, and P and N contents	111
3.4.7.1	Effects of cutting frequency on yield	111
3.4.7.2	Effect of cutting frequency on P concentration and P content	112
3.4.7.3	Effect of cutting frequency on N concentration and N content	113
3.4.8	Effects of rate of P, rate of N and cutting frequency on shoot growth	113
3.4.9	Seasonal growth pattern of gorse	114

3.4.10	Likely ability of gorse to withstand browsing	115
3.5	CONCLUSIONS	116

**CHAPTER 4: EFFECTS OF AVAILABLE PHOSPHORUS AND SOIL
ACIDITY ON GORSE AND WHITE CLOVER GROWTH** 117

4.1	INTRODUCTION AND AIMS	117
4.2	EXPERIMENTAL	118
4.2.1	Soil	118
4.2.2	Trial design	118
4.2.2.1	Phosphorus treatments	118
4.2.2.2	Lime treatments	120
4.2.3	Plant culture	121
4.2.3.1	Planting	121
4.2.3.2	Watering	121
4.2.3.3	Rhizobial inoculation	122
4.2.3.4	Basal nutrient solutions	122
4.2.3.5	Glasshouse temperatures	123
4.2.4	Acetylene reduction assays	124
4.2.4.1	Incubation and gas sampling	124
4.2.4.2	Gas analysis	124
4.2.4.3	Calculation of ethylene production	125
4.2.5	Harvests	125
4.2.6	Chemical analysis of plant and soil samples	125
4.2.7	Statistical analysis	126
4.3	RESULTS	127
4.3.1	Effects of treatments on soil properties	127
4.3.1.1	pH	127
4.3.1.2	Soluble Al	130
4.3.1.3	Available P	133
4.3.2	Plant growth	135

4.3.2.1	Shoot growth	135
4.3.2.2	Root growth	138
4.3.2.3	Shoot:root ratio	140
4.3.2.4	Responsiveness of gorse and white clover to applied p and lime	143
4.3.3	Symbiotic N ₂ -fixing activity	144
4.3.4	Plant P and N concentration	147
4.3.4.1	Shoot P concentration	147
4.3.4.2	Root P concentration	150
4.3.4.3	Shoot N concentration	151
4.3.4.4	Root N concentration	154
4.3.4.5	Total P uptake under conditions of low P availability	156
4.3.5	Effect of lime rate on element concentration of gorse and white clover shoots at a high concentration of available P	157
4.4	DISCUSSION	160
4.4.1	Effects of rates of P and lime application on gorse and white clover growth	160
4.4.1.1	Shoot and root weight	160
4.4.1.2	Available P concentrations, soluble Al concentrations and pH values associated with near maximum growth and yield depression	162
4.4.1.3	Responsiveness of gorse and white clover to applied P and lime	163
4.4.1.4	Dry matter partitioning between shoot and root	165
4.4.2	P uptake and internal efficiency of use	166
4.4.2.1	P uptake	166

4.4.2.2	Maintenance of adequate shoot P concentration under conditions of low P availability	167
4.4.2.3	Internal efficiency of P use	168
4.4.3	N ₂ fixation and N use	168
4.4.3.1	N ₂ -fixing activity	168
4.4.3.2	Internal efficiency of N use	170
4.4.4	Soil acidifying effects of gorse and white clover	170
4.5	CONCLUSIONS	170

CHAPTER 5: EFFECTS OF NITRATE CONCENTRATION ON GORSE AND WHITE CLOVER GROWTH 172

5.1	Introduction and aims	172
5.2	Experimental	173
5.2.1	Trial design	173
5.2.2	Plant culture	175
5.2.2.1	Seed	175
5.2.2.2	Growth medium and pots	175
5.2.2.3	Planting	176
5.2.2.4	Watering	177
5.2.2.5	Glasshouse temperature	177
5.2.3	Nutrient solutions	177
5.2.4	Rhizobial inoculation	179
5.2.5	Acetylene reduction assay	180
5.2.5.1	Incubation, sampling and gas analysis	180
5.2.6	Final harvest	180
5.2.7	Nitrate reductase assay	180
5.2.7.1	Procedure	180
5.2.8	Statistical analysis	181
5.3	RESULTS	182
5.3.1	Growth and dry matter partitioning	182
5.3.2	Plant nitrogen	185

5.3.2.1	Shoot and root nitrogen concentration	185
5.3.2.2	Shoot, root and whole-plant nitrogen content	188
5.3.3	Nodulation and nitrogen fixing activity	191
5.3.3.1	Nodulation	191
5.3.3.2	Symbiotic N ₂ -fixing activity	193
5.3.4	Nitrate reductase activity	196
5.3.4.1	Specific nitrate reductase activity	196
5.3.4.2	Distribution of nitrate reductase activity between root and shoot	200
5.4	DISCUSSION	202
5.4.1	Effects of nutrient solution nitrate concentration on growth and N concentration	202
5.4.2	Effect of nutrient solution nitrate concentration on nodulation and N ₂ - fixing activity	206
5.4.3	Nitrate assimilation	208
5.5	CONCLUSIONS	209
 CHAPTER 6: GROWTH OF ESTABLISHED GORSE ON A SOIL CHRONOSEQUENCE IN NORTH WESTLAND		 211
6.1	INTRODUCTION AND AIMS	211
6.2	EXPERIMENTAL	212
6.2.1	Site and physiography	212
6.2.2	Fertilizer history	213
6.2.3	Estimation of bush age	213
6.2.4	Estimation of gorse growth	214
6.2.5	Plant sampling and chemical analysis	214
6.2.6	Soil sampling and analysis	215
6.2.7	Soil profile descriptions	215
6.2.8	Statistical analysis	215
6.3	RESULTS	216

6.3.1	Soil pattern	216
6.3.1.1	Profile descriptions	216
6.3.1.2	Soil chemical properties	226
6.3.2	Gorse growth	229
6.3.2.1	Height and diameter	230
6.3.2.2	Total bush weight	230
6.3.2.2.1	New shoots	230
6.3.2.2.2	Old wood	232
6.3.2.2.3	Total bush weight	232
6.3.2.3	0.1 m ² circles	232
6.3.2.4	Productivity on land area basis	233
6.3.3	Nutrient concentrations in shoots	233
6.3.3.1	Macronutrients	233
6.3.3.2	Micronutrients	234
6.3.3.3	Other elements	234
6.3.4	Distribution of gorse roots in soil profiles	236
6.4	DISCUSSION	239
6.4.1	Soil chemistry	239
6.4.2	Potential limitations to plant growth	241
6.4.3	Gorse growth and nutrient supply	242
6.4.4	Other edaphic factors influencing gorse growth on the Larry River soil chronosequence	247
6.4.5	Growth potential of gorse	250
6.5	CONCLUSIONS	251
CHAPTER 7: GENERAL CONCLUSIONS		252
REFERENCES		257
APPENDICES		291

LIST OF TABLES

TABLE		PAGE
3.1	Chemical properties of Wakanui silt loam	29
3.2	Rates of P application 1989 and 1990 - Springston trial	30
3.3	Composition of nutrient solution applied to Springston trial seedlings	35
3.4	Summary of gorse seedling development at inoculation - Springston trial	36
3.5	Rates of K, S and Ca application - Springston trial	38
3.6	Effect of rate of P application on Olsen P concentration in trial plots	47
3.7	Effects of P and N application rate on gorse dry weight - F plots, Springston trial	49
3.8	Effects of P and N application rate on estimated dry weight of white clover - Springston trial	50
3.9	Goodness of fit of different curve types when fitted to gorse and white clover mean dry weight data from individual harvest times - F plots	52

3.10	Responsiveness of gorse and white clover to applied P	55
3.11	Relative abilities of gorse and white clover to acquire P from unfertilized soil	57
3.12	Goodness of fit of different curve types when fitted to mean gorse dry weight data - I plots	59
3.13	Effects of rate of P, rate of N and cutting treatment on gorse dry weight	62
3.14	Effects of P and N rate on P concentration of harvested gorse shoots	63
3.15	Effects of P and N rate on N concentration of harvested gorse shoots - F plots	66
3.16	Effects of P and N rate on P concentration of harvested gorse shoots, I plots - summary of analysis of variance tables	68
3.17	Effects of P and N rate on N concentration of harvested gorse shoots - I plots	70
3.18	Effect of cutting treatment on P and N concentrations	72
3.19	Effects of P and N treatments on shoot P and N concentration of gorse and white clover, Springston trial January 1990 - summary of analysis of variance table	74

3.20	Effects of P and N treatments on shoot P and N concentration of gorse and white clover, Springston trial December 1990	76
3.21	Critical P and associated N concentrations of gorse and white clover	79
3.22	Effects of rate of P application on P content of gorse - F cutting treatment	80
3.23	Effects of rate of P on N content of gorse - F cutting treatment	81
3.24	Effects of rate of P, rate of N and cutting treatment on P and N content of gorse	87
3.25	P uptake of gorse and white clover from unfertilized soil - spring 1990	88
3.26	Effects of rate of P, rate of N and cutting treatment on gorse shoot length - Springston trial	89
3.27	Soil moisture characteristics of Wakanui soil	94
3.28	Effects of rate of P, rate of N and shoot type on gorse shoot length - I treatment 1989/90	95
3.29	Effect of rate of N application on rate of NRA in gorse - Springston trial	97
3.30	2 mol l ⁻¹ KCl-extractable N in soil (0-15 cm depth) (µg N g ⁻¹ soil)	98

3.31	Effect of N treatment on N ₂ -fixing (acetylene reducing) activity and 2 mol l ⁻¹ KCl-extractable N	99
3.32	Critical shoot P concentration - comparison of gorse with other temperate legumes	107
4.1	Chemical properties of soil - Katrine E. horizon	119
4.2	Phosphorus treatments - Lime/P experiment	120
4.3	Lime treatments - Lime/P experiment	120
4.4	Basal nutrient solutions Lime/P experiment	123
4.5	Effects of species, and rates of lime and P application on soil pH - lime/P experiment	128
4.6	Soil pH, all treatments lime/P experiment	130
4.7	Effects of species lime and P on soluble Al (CaCl ₂ -Al) - lime/P experiment	131
4.8	Effects of species, and rates of lime and P on available P (Olsen P) - Lime/P experiment	134
4.9	Effects of rates of lime and P application on total shoot dry weight of gorse and white clover, lime/P experiment - summary of analyses of variance for individual species	135

4.10	Effects of rates of P and lime application on total root dry weight of gorse and white clover, lime/P experiment - summary of analyses of variance for individual species	138
4.11	Effects of rates of lime and P application on shoot:root dry weight ratio of gorse and white clover, lime/P experiment - summary of analysis of variance tables for species together and individually	141
4.12	Responsiveness of gorse and white clover to applied P - lime/P experiment (based on treatments L1P0 and L1P1)	143
4.13	Responsiveness of gorse and white clover to applied lime - lime/P experiment (based on treatments L0P1 and L1P1)	144
4.14	Effects of rates of lime and P application on symbiotic N ₂ -fixing activity per unit whole-plant dry weight (N ₂ -fixing activity ratio), lime/P experiment - summary of analysis of variance tables	145
4.15	Effects of lime and P application rate on P concentration in gorse and white clover shoots, lime/P experiment, harvest 2 - summary of analysis of variance table	148
4.16	A comparison of the effects of soil P availability on shoot P concentration in gorse and white clover shoots - lime/P experiment	150

4.17	Effects of lime and P application rate on P concentration in gorse and white clover roots, lime/P experiment - summary of analysis of variance table	150
4.18	Effects of lime and P application rate on N concentration in gorse and white clover shoots, lime/P experiment, harvest 2 - summary of analysis of variance table	151
4.19	Effects of lime and P application rate on N concentration in gorse and white clover roots, lime/P experiment - summary of analysis of variance table	156
4.20	Comparative abilities of gorse and white clover to take up soil P under conditions of very low and relatively high availability - lime/P experiment	157
4.21	Effect of rate of lime application on element concentrations in gorse and white clover shoots under conditions of high available P	158
5.1	Nitrate treatments - rates of nitrate experiment	174
5.2	Physical properties of quartz sand used in rates of nitrogen experiment	176
5.3	Elemental composition of nil N nutrient solution	178

5.4	Timing of operations during establishment - Rates of nitrate experiment	178
5.5	Stage of development and nodule number of gorse and white clover plants at day 30 - rates of nitrate experiment	179
5.6	Effect of nutrient solution N concentration on shoot and root weight of gorse and white clover	182
5.7	Nitrate concentration at 90% maximum dry matter yield and responsiveness of gorse and white clover to increasing nitrate concentration	184
5.8	Effect of nutrient solution N concentration on shoot and root N concentration of gorse and white clover	185
5.9	Effect of nutrient solution N concentration on N content of gorse and white clover	188
5.10	Nitrate concentration at 80% maximum N content and responsiveness of gorse and white clover to increasing nitrate concentration	190
5.11	Effect of nutrient solution N concentration on nodule number and dry weight on a whole-plant dry weight basis (nodule number ratio and nodule weight ratio), and on individual nodule mass	191

5.12	Effect of nutrient solution N concentration on N ₂ -fixing activity of gorse and white clover	196
5.13	Effect of nutrient solution N concentration on specific nitrate reductase activity of gorse and white clover	198
5.14	Effect of nutrient solution N concentration on distribution of NRA between roots and shoots of gorse and white clover - summary of analyses of variance	200
5.15	Responsiveness to applied N in terms of whole-plant dry weight, shoot dry weight and whole-plant N content. Plants solely dependent on symbiotic N ₂ fixation are compared with plants supplied with abundant mineral N	204
6.1	Hokitika series - soil profile description	218
6.2	Ikamatua series - soil profile description	219
6.3	Ahaura series - soil profile description	222
6.4	Okarito series - soil profile description	223
6.5	Chemical properties of soils - Larry River chronosequence 1989	227

6.6	Chemical properties of soils - Larry River chronosequence 1990	228
6.7	Effect of soil series on the size and growth of gorse plants	229
6.8	Gorse productivity on land area basis	233
6.9	Element concentrations in gorse shoots - West Coast soil chronosequence	235
6.10	A comparison of annual P uptake in gorse and white clover - North Westland	251

LIST OF FIGURES

FIGURE		PAGE
3.1	Effect of rate of P application on dry matter yield of gorse - Springston trial	51
3.2	Effect of rate of P application on estimated white clover dry weight - Springston trial	53
3.3	Effect of rate of P application on annual and total dry matter yield of gorse - Springston trial, frequently cut (F) treatment	58
3.4	Effect of rate of P application on dry matter yield of gorse - Springston trial, infrequent (I) cutting treatment	60
3.5	Effect of rate of P application on P concentration in harvested gorse shoots - Springston trial	65
3.6	Effect of rate of P application on N concentration in harvested gorse shoots - Springston trial	67
3.7	Effect of rate of P application on P concentration in gorse shoots - Springston trial, infrequently cut (I) treatment	69
3.8	Effect of rates of P and N application on N concentration in gorse shoots - Springston trial, infrequently cut (I) treatment	71

3.9	Effect of rate of P application on P and N concentration in gorse and white clover - Springston trial January 1990	75
3.10	Effect of rate of P application on P and N concentration in gorse and white clover - Springston trial December 1990	77
3.11	Effect of rate of P application on shoot P content of gorse - Springston trial, frequently cut (F) treatment	82
3.12	Effect of rate of P application on shoot N content of gorse - Springston trial, frequently cut (F) treatment	83
3.13	Effect of rate of P application on shoot P content of gorse - Springston trial, infrequent (I) cutting treatment	85
3.14	Effect of rate of P application on shoot N content of gorse - Springston trial, infrequent (I) cutting treatment	86
3.15	Effect of rate of P application on shoot length of gorse - Springston trial, frequent (F) and infrequent (I) cutting treatments	91
3.16	Mean shoot elongation rate and soil water content - Springston trial, 1989/90 growth season	92

3.17	Mean shoot elongation rate and soil water content - Springston trial, 1990/91 growth season	93
4.1	Effects of rate of phosphorus and rate of lime application on total shoot dry weight of gorse and white clover (g per pot) grown in the E horizon from a Katrine soil	136
4.2	Effects of rate of phosphorus and rate of lime application on root dry weight of gorse and white clover (g per pot) grown in the E horizon from a Katrine soil	139
4.3	Effects of rate of phosphorus and rate of lime application on the shoot:root dry weight ratio of gorse and white clover grown in the E horizon from a Katrine soil	142
4.4	Effects of rate phosphorus and rate of lime application on nitrogen-fixing (acetylene-reducing) activity per unit whole-plant dry weight (N_2 -fixing activity ratio) of gorse and white clover (micromoles acetylene per g per hour) grown in the E horizon from a Katrine soil	146
4.5	Effects of rate of phosphorus and rate of lime application on shoot phosphorus concentration (harvest 2) of gorse and white clover grown in the E horizon from a Katrine soil	149

4.6	Effects of rate of phosphorus and rate of lime application on root phosphorus concentration of gorse and white clover grown in the E horizon from a Katrine soil	152
4.7	Effects of rate of phosphorus and rate of lime application on shoot nitrogen concentration (harvest 2) of gorse and white clover grown in the E horizon from a Katrine soil	153
4.8	Effects of rate of phosphorus and rate of lime application on root nitrogen concentration of gorse and white clover grown in the E horizon from a Katrine soil	155
5.1	Effect of nutrient solution nitrate concentration on shoot and root weight of gorse and white clover - rates of nitrate experiment	183
5.2	Effect of nutrient solution nitrate concentration on shoot:root ratio of gorse and white clover - rates of nitrate experiment	186
5.3	Effect of nutrient solution nitrate concentration on N concentration in shoots and roots of gorse and white clover - rates of nitrate experiment	187

5.4	Effect of nutrient solution nitrate concentration on total N content of gorse and white clover - rates of nitrate experiment	189
5.5	Effect of nutrient solution nitrate concentration on number of nodules per unit whole plant dry weight (nodule number ratio) - rates of nitrate experiment	192
5.6	Effect of nutrient solution nitrate concentration on nodule dry weight per unit whole plant dry weight (nodule weight ratio) - rates of nitrate experiment	192
5.7	Effect of nutrient solution nitrate concentration on individual nodule mass of gorse and white clover - rates of nitrate experiment	195
5.8	Effect of nutrient solution nitrate concentration on N_2 -fixing (C_2H_2 -reducing) activity per unit whole plant dry weight - rates of nitrate experiment	197
5.9	Effect of nutrient solution nitrate concentration on N_2 -fixing (C_2H_2 -reducing) activity per unit nodule dry weight - rates of nitrate experiment	197
5.10	Effect of nutrient solution nitrate concentration on shoot and root NRA of gorse and white clover - rates of nitrate experiment	199

5.11	Effect of nutrient solution nitrate concentration on the distribution of NRA between root and shoot of gorse and white clover - rates of nitrate experiment	201
6.1	Gorse growth - Larry River soil chronosequence, 1989	231
6.2	Gorse growth - Larry River soil chronosequence, 1990	231
6.3	Gorse root distribution - Hokitika soil	237
6.4	Gorse root distribution - Ikamatua soil	237
6.5	Gorse root distribution - Ahaura soil	238
6.6	Gorse root distribution - Okarito soil.	238
6.7	Monthly average rainfall (recorded at Reefton) for the 1988/89 and 1989/90 growth seasons and long term monthly average potential evapotranspiration rates for Westport	244

LIST OF PLATES

PLATE		PAGE
3.1	Springston field trial (24 Jan 1990)	32
3.2	Wakanui silt loam	32
5.1	Gorse root systems showing degree of nodulation	194
5.2	White clover root systems showing degree of nodulation	194
6.1	Hokitika loamy sand	221
6.2	Ikamatua sandy loam	221
6.3	Ahaura sandy loam	225
6.4	Okarito silt loam	225

LIST OF APPENDICES

APPENDIX	PAGE
3.1	Springston gorse trial layout 292
3.2	Determination of rate of P for the P3 treatment, Springston field trial, spring 1989 293
3.3	Determination of rates of P for the Springston field trial, spring 1990 294
3.4	Soil profile description - Wakanui silt loam 296
3.5	Effects of selected herbicides on growth and development of gorse seedlings 297
3.6	Monthly rainfall - Springston trial 306
4.1	P sorption isotherm for the E horizon from a Katrine soil - lime/P experiment 307
4.2	Lime/pH curve for the E horizon from a Katrine soil - lime/P experiment 308
5.1	Composition of zero N nutrient solution - rates of nitrate experiment 309
6.1	Estimation of gorse growth using cut 0.1 m ² circles and bush size measurements 310

CHAPTER 1

INTRODUCTION

Gorse (*Ulex europaeus* L.) is present on large areas of extensively managed land in New Zealand (over one million hectares) (Moss 1960; Blaschke *et al.* 1981). It grows very vigorously and produces large amounts of seed in the mild, moist climate of New Zealand and is consequently a major weed in both pastoral farming and forestry (Moss 1960; Ivens 1978; Bascand 1973; Zabkiewicz 1976). The control of gorse has very large direct costs to both of these industries (\$18 million and \$8 million respectively) and the indirect costs, such as land lost to productive pastoral or forestry use, are estimated to be much greater still (Sandrey 1985).

Although gorse is a major problem in many situations, it can also be regarded positively. It is a highly productive plant which produces a forage which is nutritious for ruminants and which is palatable to goats (Radcliffe 1986; Lambert *et al.* 1989b & c). The information available suggests that gorse may be able to be used in combination with goats to form the basis of a low cost, sustainable farming system. Gorse can also be a nurse plant in the re-establishment of indigenous forest (Druce 1957; Healy 1961; Evans 1983), a source of pollen for bees, an erosion control agent and can provide shelter for livestock (Hill and Sandrey 1986).

Gorse is a legume (belonging to the family Fabaeae). The legumes include species with widely differing physical characteristics and edaphic requirements for growth. Gorse is commonly found on low fertility soils, particularly on hill country where the climate is moist and mild (Chater 1931; Egunjobi 1969; Thompson 1974). It is thought to have a competitive advantage under conditions of low soil fertility (Thompson 1974; Hartley and Phung 1982). In contrast, white clover which is the most important pasture legume in New Zealand (Williams 1987) is a high fertility demanding legume (Dunlop and Hart 1987) and therefore large inputs of P fertilizer are required to maintain it on low fertility soils (Scott 1973; Ball 1976). White clover is well adapted to developed agricultural soils whereas gorse appears to be well adapted to low fertility situations where P is likely to be the nutrient most limiting to legume growth (Scott 1973).

In 1984 there were radical changes in government agricultural policy including an end to

subsidies for fertilizers and weed control. This coincided with a time of poor farm product prices (Victoria University of Wellington 1991). The resulting decrease in farm profitability was followed by a sharp decline in fertilizer use, particularly by the sheep and beef industry (almost 50%). Sheep and beef production occupies most of the extensively managed pastoral land in New Zealand; land which is prone to infestation by gorse. Fertilizer use by the sheep and beef industry has remained at historically low levels from 1984 until the present time (N.Z. Meat and Wool Boards Economic Service 1992). The number of sheep and beef stock units carried has also declined steadily from 1984 until the present time (N.Z. Meat and Wool Boards Economic Service 1992).

This sequence of events means that extensively managed land has and will continue to become increasingly liable to infestation by gorse. If gorse is the only legume which will thrive on this low fertility land without large inputs of fertilizer or weed control, then consideration needs to be given to its potential value and management techniques for its use. Alternatively if gorse is very competitive with other species under conditions of low fertility, and it is perceived to be a weed, then management strategies need to be developed which will control it.

In order to develop management techniques to either use or control gorse, it is necessary to obtain a better understanding of the edaphic adaptation of the species. This includes knowledge of the adaptation of gorse to low soil fertility situations, its responses to improved fertility (P and lime application) and of the effectiveness of its symbiotic nitrogen-fixing system. A direct comparison between gorse and the high fertility demanding white clover would enable a better understanding of the potential role of gorse relative to white clover under a range of soil fertility conditions.

CHAPTER 2

REVIEW OF LITERATURE

2.1 GORSE

2.1.1 History of gorse in New Zealand

Gorse (*Ulex europaeus* L.) was introduced from England before 1835 as a hedge for livestock containment and shelter (Moss 1960). The practice of extensive agriculture, difficult terrain and the mild climate of New Zealand proved ideal for gorse growth and enabled it to spread rapidly throughout the country. It was declared a noxious weed in 1900 (Moss 1960). Gorse is the most important scrub weed in New Zealand agriculture and forestry (Bell 1961; Moffat 1965; Bascand 1973; Zabkiewicz 1976). It is present on 1 222 000 ha of land in New Zealand. On 112 000 ha it is recorded as the major element and on 1 110 000 ha as a minor element in the vegetation cover description (Hunter and Blaschke 1986). Areas of gorse according to vegetation cover category are as follows: Scrub containing gorse, 53 000 ha; exotic forest and fern or gorse dominated scrub, 99 000 ha; grassland and scrub containing gorse, 657 000 ha; pasture, gorse and crops, 127 000 ha (Blaschke *et al.* 1981). Total areas of land on which gorse is present in the North and South Islands respectively are 305 000 and 917 000 ha (Hunter and Blaschke 1986). Gorse is also a serious weed in Australia (Wilson 1968; Holst and Campbell 1987), Hawaii (Motooka *et al.* 1967), mainland U.S.A. (Warren and Youngberg 1968), Chile (Ramirez 1975) and Spain (Gaynor and MacCarter 1981).

2.1.2 Description

Ulex is a genus of woody legumes. Gorse (*Ulex europaeus*) is a much branched evergreen shrub (Grime *et al.* 1988). It commonly grows to a height of 2 m (Grime *et al.* 1988), but may grow up to 7.0 m with a stem diameter of 217 mm (Lee *et al.* 1986). Shoots produced during its current growth season are green, but turn brown approximately halfway through the next growth season (personal observation) resulting in bushes with a central volume of dry, brown vegetation (Warren and Youngberg 1968). Gorse has the ability to coppice, for example after burning (Egunjobi 1969; Radcliffe 1982 and 1985). Leaves are present during the seedling stage, but thereafter are found only in a reduced form as spines or scales

(Grime *et al.* 1988). The erect stems of young bushes provide a dense canopy and often have no vegetation beneath them. Gorse flowers mainly from January to March in the southern hemisphere (Grime *et al.* 1988). It is common however for some flowers to be present throughout the year (Zabkiewicz 1976). Seed set occurs about two months after flowering. Flowers are yellow, hermaphrodite, form in axillary clusters of 1-3, and are usually pollinated by insects (Grime *et al.* 1988) such as bees (Winter 1961; Walsh 1978). Seeds are approximately 2-3 mm in diameter and are explosively discharged from a 2-6 seeded pod. They have a hard seed coat, a low germination rate and can lie dormant yet viable for a period of 30 years or more (Moss 1959; Cornwell 1969; Rolston 1974; Zabkiewicz 1976). Physical scarification (this project) or other treatment such as soaking in boiling water (Millener 1961) is necessary to improve the germination rate. Gorse produces a large amount of seed (500-600 seeds m² year⁻¹) (Ivens 1978) and this combined with its ability to germinate at a low rate over a long period of time if left undisturbed in the ground, is largely responsible for its persistence (Zabkiewicz 1976; Ivens 1978).

Roots are infected with vesicular-arbuscular (VA) mycorrhizas and have long living N₂-fixing nodules (Pate 1961; Reid 1973; Grime *et al.* 1988). The rooting system of gorse is reported to have most of its fine roots within 10 cm of the surface (Grubb *et al.* 1969), extensive lateral roots within a few cm below the soil surface and a deep tap root (maximum depth observed = 76 cm) (Grubb *et al.* 1969; Heath and Luckwill 1938). The observations of Grubb *et al.* (1969) were made on chalk heath, where there was 10-25 cm of loam overlying chalk, therefore the distribution of fine roots described by this author may not be typical of that in the more acid New Zealand soils.

2.1.3 Favoured habitat

2.1.3.1 Temperature and water

Gorse prefers a mild climate where there are not extremes of temperature and tends to prefer habitats sheltered from cold winds (Zabkiewicz 1976; MacCarter and Gaynor 1980; Gaynor and MacCarter 1981). The optimum temperature for growth and N₂ fixation is about 22°C (Reid 1973). Lee *et al.* (1986) found that plant height and stem diameter decreased with increasing altitude, presumably reflecting decreasing temperature. Gorse can be killed by severe winter conditions (Burroughs 1982), although mature plants can survive severe frosts

(Zabkiewicz 1976). Seed germination reaches a maximum at 18°C, and viability is lost at 35°C (Ivens 1983). The distribution of gorse in Europe reflects its dependence on warm temperatures. It occurs in temperate lowland regions such as the western areas of Britain, France and Spain, and the coasts of Germany and Denmark (Zabkiewicz 1976). In New Zealand gorse is found from sea level to an altitude of 800 m (MacCarter and Gaynor 1980) and from the north to the south of the country (Healy 1961).

Gorse prefers moist environments (Meeklah 1979; Gaynor and MacCarter 1981) and tends not to occur in arid situations (MacCarter and Gaynor 1980). Optimum rainfall is 500-1500 mm (Healy 1961). Lee *et al.* (1986) found that height and stem diameter of gorse was greatest for plants growing on a southerly aspect which was presumably related to greater soil moisture. Gorse is generally absent from wetland (Grime *et al.* 1988).

2.1.3.2 Soils

Gorse is commonly found on low fertility soils (Chater 1931; Egunjobi 1969), especially on hill country where the climate is moist and mild (Thompson 1974). Gorse appears to have a competitive advantage under conditions of low fertility. Although gorse, when grown alone is responsive to applied P (Thompson 1974), the application of P and N are found to decrease seedling survival because of competition from other species as discussed in Section 2.1.6 (Thompson 1974; Hartley and Phung 1982).

Because it is a legume, gorse can thrive in nitrogen deficient situations, and it appears to be tolerant of low fertility generally. Thus gorse has a role as a pioneer species in low fertility situations (Egunjobi 1969; Dancer *et al.* 1977a; Roberts *et al.* 1981). It is found to grow successfully and fix nitrogen on low fertility New Zealand hill country soils (Egunjobi 1969), sand wastes from kaolin mining in Britain (Dancer *et al.* 1977a; Roberts *et al.* 1981) and gold dredge tailings (West coast, South Island, New Zealand, Fitzgerald 1980).

Gorse is reputed to be a calcifuge (Grubb and Suter 1970; Zabkiewicz 1976; MacCarter and Gaynor 1980). It is reported to favour soils with pH in the range 4.0 to 6.0 (Meeklah 1979; Grime *et al.* 1988). Lime application is found to reduce emergence, establishment, survival, and growth of gorse seedlings (Phung *et al.* 1984; Hartley and Popay 1982; Hartley and Phung 1979; Thompson 1974). Gorse does grow in calcareous soils, but on chalk heath

soils it avoids the chalk layer and acidifies the soil layer in the vicinity of its roots (Grubb *et al.* 1969). The mechanism for acidification appears to be removal of bases, particularly Ca, from the soil, rather than addition of acid (Grubb *et al.* 1969).

2.1.4 Nitrogen fixation

Gorse is a legume (member of the family Fabaceae) (Grime *et al.* 1988). As such it forms a symbiotic relationship with rhizobia (bacteria which operate within root nodules formed specifically for the purpose), enabling it to fix atmospheric nitrogen (Stewart 1966). Nodule development of gorse is similar to that of other legumes but mature nodules exhibit structural adaptations to longevity. They have meristematic activity, enabling them to elongate and become branched over time, and have a well developed vascular system (Reid 1973; Pate 1961). N₂-fixing activity has been measured in detached nodules of gorse (Reid 1973) and in intact plants removed from the field (Skeffington and Bradshaw 1980). In low fertility situations gorse is found to have a high capacity to accumulate N relative to other species (Egunjobi 1969; Dancer *et al.* 1977a). However, where nutrients other than N are supplied the higher fertility demanding legumes such as white clover (*Trifolium repens*) and red clover (*Trifolium pratense*) are found to accumulate more N than gorse (Dancer *et al.* 1977b).

2.1.5 Nutrient responses

A few studies have been done investigating nutrient responses of gorse in the absence of competition from other species, using low fertility soil. Thompson (1974) found that 6 month old container-grown gorse seedlings did not respond to applied N but after 1 year there was a significant response. Mature container grown gorse plants (18 months old, 0.5 m tall) did not respond to applied N. Applied N was found to completely inhibit the nodulation of seedling gorse, and greatly reduce the size and number of nodules on mature gorse (Thompson 1974). Ivens and Mlowe (1983) observed no response of 18 week old gorse plants to applied N. The N applied (50 kg ha⁻¹ equivalent) did not cause a decrease in nodule number. In small field plots, N application increased gorse seedling numbers in the absence of other species (Hartley and Popay 1982).

Thompson (1974) observed a small response to K for one year old container grown plants,

but no response for the one year old field grown plants or mature plants. Ivens and Mlowe (1983) observed no response to K with their 18 week old plants.

From the limited evidence available, gorse appears to be more responsive to P than either N or K. Thompson (1974) observed large increases in growth of 6 month, 1 year old and mature container grown plants with the application of P fertilizer. Likewise, Ivens and Mlowe (1983) observed increased shoot and root growth of 18 week old gorse plants with the application of P fertilizer. Applied P also resulted in increased shoot:root ratio and increased nodule number, which was correlated with shoot weight (Ivens and Mlowe 1983). Hartley and Popay (1982) observed increased numbers of germinating gorse seedlings with P fertilization (in the absence of other species).

Although gorse appears to be responsive to applied P there are also indications that it has the ability to successfully acquire it in low fertility situations. Gorse is able to grow well in materials such as sand and gravels without applied nutrients (Dancer 1977a; Roberts *et al.* 1981; Fitzgerald 1980).

It should be noted that much of the work of Thompson (1974) and Ivens and Mlowe (1983), cited above, was done with container grown plants. They would therefore have had a very restricted rooting volume and this may have resulted in a greater responsiveness to applied P than would occur in the field where roots would have access to a much greater volume of soil and therefore a larger amount of P.

2.1.6 Effects of competition on nutrient responses

The limited amount of work done investigating nutrient responses of gorse frequently involved competition with other species and in many instances the aim of the work was to develop fertilizer strategies which would suppress gorse establishment and growth.

In pastures the application of P and N reduced gorse seedling survival because of increased growth and therefore competition from other species such as white clover, perennial ryegrass (*Lolium perenne*), Yorkshire fog (*Holcus lanatus*) and browntop (*Agrostis capillaris*) and cocksfoot (*Dactylis glomerata*) (Thompson 1974; Hartley and Phung 1982; Popay *et al.* 1990). The application of P and N together enhanced the effect by further increasing

pasture yield and decreasing gorse seedling numbers (Thompson 1974). The application of N would tend to remove the competitive advantage that gorse has as a N-fixer. P application would tend to favour species which have potentially greater growth rates than gorse but also greater demand for P and species which compete more strongly for P than gorse. It has been found that pasture species which compete strongly for P do appear to compete most strongly with gorse seedlings. Hartley and Phung (1982) found that gorse seedling survival was more adversely affected by competition from browntop than from ryegrass, presumably because browntop competes more strongly for soil P (Mouat and Walker 1959). Competition from pasture species would be expected to be of most importance at the seedling stage of gorse while it is still dependent on obtaining P from the surface soil and before it develops the extensive and deep root system described by Grubb *et al.* (1969) and Heath and Luckwill (1938).

Thus, it appears that while gorse seedlings respond to applied P, and occasionally even to N (Section 2.1.5), the application of these nutrients benefits competing pasture species more than the gorse seedlings, resulting in decreased seedling survival. The application of lime, which by itself can have an adverse effect on gorse seedling survival (Section 2.1.3.2), is also found to enhance the adverse effect of applied P on gorse seedling survival by increasing the growth of and therefore competition from pasture species such as white clover (Hartley and Popay 1982).

2.1.7 Productivity

Gorse has the potential to be highly productive. Egunjobi (1969) reported dry matter (DM) production of 5869 kg ha⁻¹ year⁻¹ (fertilized) for one year regrowth on a low fertility hill country soil. Over the first four years of regrowth an average of at least 15 000 kg DM ha⁻¹ year⁻¹ was recorded. Over the period 7-10 years, mean annual DM accumulation was 10 000 kg ha⁻¹. The actual productivity would have been greater than this, however, as the annual litter fall for a 7-8 year old stand was approximately 9000 kg DM ha⁻¹ (Egunjobi 1967 and 1971)

Over two growth seasons (one wet and one dry) intensively browsed gorse produced an average of 19 500 kg DM ha⁻¹ (Radcliffe 1986). Productivity ranged from 11 600 kg DM ha⁻¹ year⁻¹ in a dry season to 27 300 kg DM ha⁻¹ year⁻¹ in a wet season. The browsed bushes

were cushion-shaped and generally <30 cm tall (Radcliffe 1986). The gorse was grown on a low fertility soil (Olsen P = 5-10 $\mu\text{g g}^{-1}$) which had received substantial applications of fertilizer P (Radcliffe 1985). Estimated dry matter productivity of unbrowsed gorse was more than twice that of browsed gorse (Radcliffe 1986). Lambert *et al.* (1989a) found that gorse cut once-yearly produced approximately twice as much dry matter as gorse cut 4 times-yearly. Regardless of cutting frequency gorse produced more dry matter annually on a low fertility hill country site than any of the other shrub species grown (including 5 other legumes) (Lambert *et al.* 1989a).

2.1.8 Economic importance

Direct costs of chemical control of gorse to New Zealand farming and forestry have been estimated at \$18 million and \$8 million respectively (Sandrey 1985). Indirect costs to the farming industry (opportunity cost of gorse covered land) have been estimated to be as high as \$150 million. No estimate of indirect costs to forestry have been made but these are thought to be great (Sandrey 1985).

While being considered a weed in many situations, gorse may have positive roles. Gorse can be a nurse plant in the re-establishment of indigenous forest (Druce 1957; Healy 1961; Evans 1983). It can be a source of pollen for bees, an erosion control agent and can provide shelter for livestock (Hill and Sandrey 1986). One of the more important potential uses for gorse is that it can provide forage for goats. It is well known that with appropriate management, goats or goats in combination with sheep will effectively control gorse (Rolston *et al.* 1983; Clark *et al.* 1982; Harradine and Jones 1985; Radcliffe 1986 and 1990). Lambert *et al.* (1989b) offered harvested forage from a range of shrubs, including 6 legumes, to goats and sheep. Gorse forage was preferred over that from the other shrubs by both goats and sheep. Gorse can be a year round maintenance feed for goats, which will eat green foliage, flowers and bark (Radcliffe 1986; Lambert *et al.* 1989c). When green foliage is sparse, they will also eat brown stems (Radcliffe 1986). Gorse digestibility tends to be low-moderate (less than that of pasture), and concentrations of P, S, K Cu and Mg tend to be low from the animal production viewpoint (Radcliffe 1986; Lambert *et al.* 1989c & d; Ulyatt *et al.* 1980). However, non-lactating goats with abundant gorse have been found to perform just as well as similar goats confined to pasture in terms of body weight and fleece growth rate (Radcliffe 1986).

Economic analysis has shown that the use of goats to control gorse is more profitable than chemical control, regardless of goat prices (Krause *et al.* 1984). However, if the financial return from goats becomes competitive with that from sheep, then gorse could be regarded as a resource and managed as such (Krause *et al.* 1984). It is thought that gorse country (generally low fertility hill country) may be suitable for cashgora type goats which produce a fibre between mohair and cashmere in fineness (Yerex 1986; Sandrey 1987). Thus gorse may have a useful role in any cashgora industry which develops.

White clover based pastures are expensive to maintain on hill country soils of low fertility because of the high costs of fertilization and weed control. It is therefore important that low cost alternative legumes be adopted in these situations. In this context, the gorse already present on much low fertility hill country may be able to be used in combination with goats as the basis for a low cost, sustainable form of agriculture for this type of land.

2.2 PHOSPHORUS NUTRITION

2.2.1 Phosphorus in plant nutrition

Phosphorus is essential to all forms of life because of its roles in genetics (formation of bonds in RNA and DNA) and energy transfer (formation of energy-rich bonds in ATP) (Ozanne 1980; Mengel and Kirkby 1987).

N and P are the two elements most commonly limiting to plant growth. Because legumes can fix atmospheric N_2 , P is generally the most important limiting factor for them (Fox 1978; Ozanne 1980). This situation is particularly true for New Zealand soils (Scott 1973; Ball 1976).

Plant species differ in their ability to grow vigorously under conditions of low available soil P. These differences are based on differing abilities to take up P from the growth medium and on differing abilities to efficiently use the P taken up to produce dry matter.

2.2.2 Plant P uptake

Factors affecting the ability of plants to take up P include P concentration in the external solution, the length, surface area, distribution and extent of their root systems, the rate of P absorption per unit quantity (weight or length) of roots and the ability of their roots to affect P solubility by chemically modifying the rhizosphere.

The concentration of P in soil solution is usually very low, commonly around 0.05 ppm (Barber *et al.* 1963) and seldom greater than 0.3 ppm (Fried and Shapiro 1961) where P fertilizer has not been applied. In addition to its low concentrations, the rate of diffusion of P through soil is very low (Barber *et al.* 1963). Plant roots are capable of absorbing P from solutions of very low P concentration (Loneragan and Asher 1967). Generally the P concentration of root cells and xylem sap is 100 to 1000 times greater than that of the soil solution, indicating that P is taken up by plants against a very steep concentration gradient (Mengel and Kirkby 1987). The external solution P concentration required for near maximum growth varies between species (Asher and Loneragan 1967; Parfitt *et al.* 1982; Fohse *et al.* 1988). Maximum yields for a range of 8 species grown in solution culture occurred at P concentrations ranging from 0.0062 to 0.77 $\mu\text{g ml}^{-1}$ (Asher and Loneragan 1967). Fohse *et al.* (1988) observed maximum yields for a range of 7 species at soil solution P concentrations ranging from 0.043 to 0.21 $\mu\text{g g}^{-1}$. Legumes appear to achieve near maximum yield at solution P concentrations in the medium to high range compared with other species (Asher and Loneragan 1967; Parfitt *et al.* 1982; Fohse *et al.* 1988).

Because P moves to the roots of plants by diffusion, the concentration of P in soil solutions is vital. Therefore the use of P sorption isotherms to determine rates of P application to give particular levels of P in soil solution are advocated as a means of predicting soil P requirements (Beckwith 1965; Fox and Kamprath 1970).

The ability of a plant to take up P can be regarded as a function of the size of its root system, the volume it occupies and the rate of absorption per unit quantity of roots (Loneragan and Asher 1967; McLachlan 1976; Fohse *et al.* 1988). Plants appear to regulate the amount of roots produced according to P supply, with shoot:root ratio tending to be less when P supply is limiting plant growth compared with the situation at maximum growth. P deficiency has been found to promote root elongation (Anuradha and Narayanan 1991).

Increase in P supply beyond that needed for maximum growth has no further effect on shoot:root ratio (Loneragan and Asher 1967; Fohse 1988).

The capacity of plants to absorb phosphate appears to be related to root surface area (Jeffrey 1967), rate of root growth and root length (Khasawneh and Copeland 1973), and the ability of roots to proliferate in the vicinity of available P (Strong and Soper 1973). The presence of root hairs is associated with enhanced P uptake under conditions of low available P, via their effect on root surface area (McLachlan 1976; Haynes and Ludecke 1981; Itoh and Barber 1983). Lewis and Quirk (1967) suggest that root hair length is important in determining the diameter of the zone of P depletion around roots. Root hairs appear to have particular importance when diffusion is the major means of movement of P to the root surface e.g. in soils compared with stirred nutrient solution (Barley and Rovira 1970). However, greater abundance of root hairs has not always been associated with increased absorption of P (Bole 1973). P uptake is enhanced by mycorrhizas. It is thought that mycorrhizal and non-mycorrhizal roots have access to the same sources of P (Sanders and Tinker 1971; Hayman and Mosse 1972; Powell 1975) but that mycorrhizas increase nutrient uptake by increasing the surface area for absorption and reducing the distance that nutrients must diffuse through the soil to reach the root (Hattingh *et al.* 1973; Abbott and Robson 1982). This is particularly important for P because of its very slow rate of diffusion through soil (Barber *et al.* 1963).

Another factor affecting P uptake is the rate of P absorption per unit quantity (weight or length) of roots. The P influx rate per unit quantity of roots varies widely between species (Loneragan and Asher 1967; Fohse *et al.* 1988). Rates of P absorption per unit quantity of roots increases rapidly with increasing solution P concentration at low P concentrations, before tending to level off when P concentration approaches that associated with near maximum yield (Loneragan and Asher 1967; Fohse *et al.* 1988).

Fohse *et al.* (1988) found that species which were inefficient at P uptake (required relatively high soil P concentration to reach near maximum yield) had low P absorption rates and high shoot:root ratio whereas species of medium to high efficiency (required low to medium soil P concentration to reach near maximum yield) had either high P absorption rates per unit length of root or low shoot:root ratios, but not both together in any of the species studied. The study of Loneragan and Asher (1967), however, did include species with both relatively

high P absorption per unit weight of root and low shoot:root ratio.

Plant species vary in their ability to absorb P from slowly soluble sources. Differences have been attributed to the cation exchange properties of roots (Drake and Steckel 1955) although it is more likely that species able to use slowly soluble P sources are those which absorb more cationic than anionic nutrients and develop acid conditions in their rhizospheres (Johnston and Olsen 1972; McLachlan 1976; van Ray and van Diest 1979). Aguilars and van Diest (1981) contrasted nitrate-fed legumes with legumes dependent on symbiotically fixed N with respect to their ability to obtain P from relatively unavailable forms. Legumes (soybean (*Glycine max*) and lucerne (*Medicago sativa*)) supplied with nitrate-N absorbed more anionic than cationic nutrients, resulting in increased pH of the growth medium and low P availability. In contrast, legumes dependent on symbiotically fixed N absorbed more cationic than anionic nutrients, which resulted in acidification of the growth medium and greater P availability.

It is likely that several of the factors discussed in this section are involved with the reputed ability of gorse to acquire nutrients from low fertility situations. Its root system is known to explore a large volume of soil (e.g. Heath and Luckwill 1938; Grubb *et al.* 1969) and to have vesicular-arbuscular mycorrhizas (Grime *et al.* 1988). It is a legume, and when dependent on symbiotically fixed N would be expected to acidify its growth medium and therefore render sparingly soluble form of P more soluble. A soil acidifying effect of gorse roots has been reported in association with high rates of Ca uptake (Grubb *et al.* 1969).

2.2.3 Internal efficiency of plant P use

For the purpose of this review, internal efficiency of P use will be defined as the amount of dry matter produced per unit of P contained in the plant.

In addition to having a high capacity to take up P from the external growth medium, plants can perform efficiently under conditions of low available P by being able to translocate sufficient P from the root to the shoot to maintain vigorous growth, or by being able to maintain vigorous growth while having relatively low tissue P concentrations.

2.2.3.1 Partitioning between root and shoot

Under conditions of P deficiency more P tends to be retained in the roots than when P status is high because the shoot:root ratio tends to be lower (Loneragan and Asher 1967; Fohse *et al.*1988) and because tissues nearest the source of scarce nutrients tend to have their need satisfied before tissues further away (Brouwer 1962).

In short term experiments with no associated growth effects Russell and Martin (1953) observed retention of P in roots, caused by metabolic processes. This suggests low shoot:root ratios in P deficient plants result from P distribution (retention of P in roots) rather than P distribution resulting from dry matter distribution. At low external P concentrations, rates of P absorption may be insufficient to maintain tissue P at the concentrations needed for healthy growth and P concentration in the shoot will tend to suffer more than that in the root (Loneragan and Asher 1967). As external P concentrations increase the rate of P absorption will increase, more P will be translocated to the shoot and the plant will eventually reach a point where shoot tissue P concentration is sufficient for maximum or near maximum growth (Loneragan and Asher 1967). Legume species differ in the degree to which they translocate P from roots to shoots at low available P, and greater translocation is associated with better shoot growth (White 1972; Kee 1981; Paynter 1990).

2.2.3.2 Dry matter production per unit of P absorbed

Just as species vary in their ability to acquire P from the growth medium (especially under conditions of low fertility) so they also vary in the efficiency with which they use absorbed P in the processes of growth (Loneragan and Asher 1967). Internal efficiency of P use, along with efficiency of P acquisition from the growth medium, contributes to the overall efficiency of converting growth medium P into plant dry matter. McLachlan (1976) in a study with four species, including two legumes, considered that internal efficiency of P use was more important than P-acquiring ability in determining dry matter productivity.

2.2.3.3 Critical plant P concentration

The tissue P concentration at which plants approach maximum growth (with factors other than P non-limiting) is known as the critical P concentration (Macy 1936; Andrew 1960). Critical P concentrations vary widely between species (e.g. Andrew 1960; Andrew and Robins 1969a; McNaught 1970; Andrew and Robins 1971; Cornforth and Sinclair 1984). Legume species with relatively low critical P concentrations tend to be those having greatest P uptake per unit soil mass and which reach maximum yield at relatively low rates of applied P (Andrew and Robins 1969a).

2.2.3.4 Summary - plant P uptake and use

Three characteristics which may contribute to the ability of a plant to grow well under low P conditions are:

- a) An ability to absorb P from low external solution concentrations.
- b) An ability to translocate P from the root to the shoot, thus maintaining a shoot P concentration sufficient to enable rapid growth.
- c) Efficient use of P in the processes of growth i.e. low critical P concentration.

2.2.4 Phosphorus and N₂ fixation

Phosphorus deficiency is common in legumes (Munns 1977; Robson and Bottomley 1991). In P deficient soils applying fertiliser P to legumes increases plant growth, P and N concentration (Andrew and Robins 1969a & b; Israel 1987), number and weight of root nodules (Shaw *et al.* 1966; Gates 1974; Wagner *et al.* 1978; Zaroug and Munns 1979), nodule weight as a proportion of shoot weight (Graham and Rosas 1979; Robson *et al.* 1981) nodule P concentration and nodule activity (Zaroug and Munns 1979; Hart 1989). Inoculation with VA mycorrhizal fungi has also been found to increase nodulation and N₂ fixation by legumes grown in P deficient soils, by increasing plant P uptake (Crush 1974; Abbot and Robson 1977; Smith and Daft 1977; Crush 1982).

There is conflicting evidence on the mechanism by which P supply affects rhizobial N₂ fixation. There are some indications that P supply directly affects rhizobial N₂ fixation. Israel (1987) found that for soybean symbiotic N₂ fixation appeared to have a higher internal P requirement for optimum function than host plant growth or nitrate assimilation and P concentrations in nodules are found to be greater than those within leaves (Hart 1989). Smith and Daft (1977) state that mycorrhizal enhancement (by mycorrhizas) of P uptake and N₂ fixation precedes any effect on growth. If correct, this would indicate a direct effect of P supply on nodulation and N₂ fixation. However inspection of the data reported (Smith and Daft 1977) indicates that although the increases in nodule number and acetylene reduction appeared to be proportionally greater than that of plant dry weight, plant dry weight did increase. An increase in leaf area and photosynthate sufficient to account for the increases in nodule number and acetylene reducing activity cannot be ruled out on the basis of the evidence presented. Crush (1982) showed that endomycorrhizal fungi do not directly affect nodule activity in white clover but merely improve the P nutrition of the host plant when P availability is low. Zaroug and Munns (1979) reported no clear difference in P response between *Lablab purpureus* plants dependent on symbiotic N₂ fixation for their N supply and plants supplied with ammonium nitrate. Critical P concentration was the same for both sets of plants. Increases in N₂-fixing activity with increased P supply are associated with increased nodule P concentration, but the increases tend to be proportional to the increased P concentrations in young mature leaves (Hart 1989). Changes in concentrations of the different P fractions within the nodule were also similar to those within leaves, suggesting that the response of the nodules to increasing P supply is similar to that of the host plant. Robson and Bottomly (1991) express the view that P supply has its effect on the symbiotic N₂ fixing system primarily via effects on the host plant. In most cases where P responses of plants dependent on symbiotic N₂ fixation have been compared with plants supplied with mineral N, positive interactions have been observed indicating that correcting P deficiency does not directly increase nitrogen supply to legumes (Robson and Bottomly 1991). Also, for nutrients where the requirement for symbiotic N₂ fixation is greater than that for host plant growth, correction of deficiencies may not necessarily lead to increased nodule weight or number (Robson 1983).

The evidence discussed above suggests that P affects symbiotic N₂ fixation in legumes via effects on host plant growth. The close relationship frequently observed between shoot growth and nodule weight (Graham and Rosas 1979; Cassman *et al.* 1981; Robson *et al.*

1981; Israel 1987) is probably related to energy supply. N_2 fixation is closely linked with energy use (e.g. Mahon 1977) photosynthate supply (Bethlenfalvay *et al.* 1978; Atkins *et al.* 1978; Sheehy *et al.* 1980) and leaf area (Streeter 1973).

2.3 SOIL ACIDITY AND PLANT GROWTH

2.3.1 The nature of soil acidity

Soil acidity is largely controlled by ion exchange and other adsorptive reactions (Coleman and Thomas 1967). Important adsorbents in soils are the inorganic layer silicates and oxide minerals, and organic matter. The quantitative measure of a soil's ability to hold exchangeable cations (via the negative charges on its colloid surfaces) is known as its cation exchange capacity (CEC) (McLaren and Cameron 1990). Soils become acid when considerable proportions of their CECs are occupied by H^+ and various forms of hydrated aluminium (Al).

Most acid soils develop because of leaching of bases. As water containing hydrogen cations from weak acids (such as carbonic and organic acids) moves through the soil some of the H^+ ions, along with hydrolysed Al^{3+} released during weathering of aluminosilicate minerals, replace adsorbed exchangeable cations (bases) such as Ca^{2+} , Mg^{2+} , K^+ and Na^+ , which are then removed deep into the soil profile or ground water (Tisdale and Nelson 1975; Donahue *et al.* 1983; McLaren and Cameron 1990; van Breemen 1991). Acidification of the Katrine soil used in this research programme (Chapter 4) is thought to have occurred largely via this process (T.H. Webb pers. comm.) Soluble acids formed through biological activity within the soil may also influence soil acidity (Coleman and Thomas 1967; van Breemen 1991). The uptake of more basic components than acidic components by plants may also acidify the soil and removal of biomass will lead to permanent acidification (van Breeman 1991). Soil acidification tends to be more pronounced under N_2 -fixing legumes because they tend to absorb more cations than anions (because they have less need for NO_3^- uptake than non-legumes) (Aguilars and van Diest 1981). Within the pH range normally found in acid soils (4.0 - 5.5), Al is the predominant cation and there is little exchangeable H^+ . However the hydrolysis of Al^{3+} results in the presence of H^+ in the soil solution (Coleman and Thomas 1967; Thomas and Hargrove 1984).

In New Zealand soils low pH has been associated with a high degree of leaching, low percentage base saturation, low acid-extractable P, and high titratable acidity values (Widdowson and Wells 1968; McIntosh *et al.* 1983). Decreasing white clover growth was associated with increasing degree of leaching (Widdowson and Wells 1968).

2.3.2 Effects of Al toxicity and pH on plant growth

The chemical factors associated with poor plant growth in highly leached acid soils are toxicities of H⁺, Al and Mn ions, and deficiencies of Ca, Mo and P (Jackson 1967; Adams 1981). While P availability is often reduced under very acid conditions, P deficiency may also result from immobilisation of P within the plant (Jackson 1967). Solubilities of the soil minerals that determine soil solution concentrations of Al, Mn and Mo are highly pH dependent. However soil pH is a poor predictor of toxicity or deficiency of these elements because soils vary widely in the solid phase components (soil minerals and organic matter) that control solution ion concentrations (Adams 1981).

Al toxicity has been identified as the major factor resulting in reduced plant growth in many acid soils (Adams and Pearson 1967; Foy 1974). The solubility of Al in soils increases sharply below pH 5.5 (Coleman *et al.* 1958; McCart and Kamprath 1965) and is therefore a potential problem for plant growth in soils below this pH. The Al species of importance is monomeric Al. The activity of monomeric Al in solution was closely linked to reduced root growth of soybean, subterranean clover (*Trifolium subterraneum*), lucerne and sunflower (*Helianthus annuus*) (Munns 1965b; Blamey *et al.* 1983; Alva *et al.* 1986). Toxic Al concentrations have been found to reduce growth of a range of legume species in solution or sand culture (e.g. Andrew *et al.* 1973; de Carvalho *et al.* 1981; Edmeades *et al.* 1991b), in pots containing soil (e.g. McLeod and Jackson 1965; Munns 1965c; Evans and Kamprath 1970) and in the field (Mahoney *et al.* 1983). Depression of yield by Al toxicity is sometimes closely associated with high leaf Al concentration (e.g. Bouton *et al.* 1981). The effect of Al concentration in the root medium on Al concentration in leaves varies between species depending on their sensitivity to Al (Andrew *et al.* 1973).

High aluminium concentrations in the growth medium appear to have their initial effect on the root system (Clarkson and Sanderson 1969). Al toxicity appears to disrupt cell division (Rios and Pearson 1964) and results in reduced root elongation (Munns 1965b), reduced

lateral root weight and root length per unit weight (Sartain and Kamprath 1975). The ratio of fine root length per unit shoot weight (Pinkerton and Simpson 1981) and root hair formation (Wood *et al.* 1984) are also both reduced by toxic Al concentrations.

Most evidence suggests that Al toxicity directly affects symbiotic N₂ fixation. Al toxicity can affect rhizobial multiplication in the rhizosphere and nodulation (Wood *et al.* 1984). Al toxicity is found to depress growth in legumes more severely when they are dependent on symbiotic N₂ fixation than when they are provided with mineral N (Munns 1965a; de Carvalho *et al.* 1981). Decreases in growth are associated with strong reductions in nodule number and weight which are, in turn, associated with decreased lateral root density and therefore decreased number of potential infection sites (de Carvalho *et al.* 1981). It is suggested (de Carvalho *et al.* 1981) that the tolerance of legumes to Al toxicity is associated with their ability to form a successful N₂-fixing symbiosis. For some more tolerant species (e.g. subterranean clover and soybean) Al toxicity has not affected symbiotic N₂ fixation any more than its effect on the host plant (Munns 1965a; Munns *et al.* 1981).

Legume species vary in their sensitivity to Al toxicity, with tolerant species such as *Stylosanthes humilis*, subterranean clover and lotus (*Lotus pedunculatus*) showing relatively less decline in yield with increasing Al concentration in the growth medium than sensitive species such as lucerne, red clover and birdsfoot trefoil (*Lotus corniculatus*). Species such as white clover have intermediate sensitivity to increasing Al concentrations (Munns 1965b; Andrew *et al.* 1973; Bouma *et al.* 1981; Edmeades *et al.* 1991a & b). Pinkerton and Simpson (1981) associated the ability to grow fine roots with tolerance of soil acidity. In acidic soil the tolerant species *Stylosanthes humilis* produced a greater length of fine roots relative to shoot weight than the acid sensitive lucerne. The symbiotic N₂-fixing systems of different legumes also appear to differ in their abilities to tolerate acidity. For example, Munns (1965a) found the N₂-fixing system of subterranean clover to be more tolerant of soil acidity than that of lucerne.

Although Al appears to be the major factor limiting plant growth in acid soils, pH can also affect growth. A decrease in pH from 6.0 to 5.5, in the absence of Al, was associated with substantial decreases in dry matter yield of white clover, red clover and one variety of subterranean clover. The effect was apparently due to an effect on symbiotic N₂ fixation. Two *Lotus* species and a second variety of subterranean clover were unaffected (Edmeades

et al. 1991a & b).

2.3.3 Methods of assessing soil Al status

Various methods of measuring soil acidity have been used and successfully correlated with plant growth. Al saturation of the effective cation exchange capacity (ECEC) of soils is found to provide a good indication of Al concentration in the soil solution (Evans and Kamprath 1970) and has been found to be well correlated with plant growth under conditions of Al toxicity (Adams and Pearson 1967; Kamprath 1970; Evans and Kamprath 1970; Abruna *et al.* 1975; Sartain and Kamprath 1975).

For many acid soils CaCl₂-extractable Al has been found to be at least as closely correlated with plant growth as exchangeable Al or Al saturation of ECEC (Hoyt and Nyborg 1971); Hoyt and Nyborg 1972; Hoyt and Webber 1974; Webber *et al.* 1977; Webber *et al.* 1982). Extraction of soils with 0.02 mol l⁻¹ CaCl₂ was recommended as a simple reliable indicator of Al toxicity (Hoyt and Nyborg 1972; Webber *et al.* 1977). Edmeades *et al.* (1983) suggested that 1 mol l⁻¹ KCl-extractable Al and 0.02 mol l⁻¹ CaCl₂-extractable Al had advantages over some other methods (namely pH (H₂O) and soil solution Al) for the assessment of Al toxicity in soils because they are less sensitive to ionic strength of the soil solution. Shoot and root growth of white clover was more closely correlated with 0.02 mol l⁻¹ CaCl₂-Al than exchangeable Al or pH for a range of acid New Zealand soils (Hume *et al.* 1988).

2.3.4 Effect of soil acidity on plant P

2.3.4.1 Effect of lime on P availability

Lime has been found to increase, decrease or have no effect on available soil P (Haynes 1982). Liming may result in the formation of new P adsorbing surfaces as Al³⁺ ions precipitate as insoluble polymeric hydroxy-Al cation species (Haynes 1983). However if air drying occurs between lime application and the application of P, P adsorption is decreased because an increase in net negative surface charge (Haynes 1983). Lime can also increase phosphate availability by stimulating mineralisation of soil organic P. However at high soil pH (≥7.0) values, the precipitation of insoluble calcium phosphates may decrease

P availability (Haynes 1982).

2.3.4.2 Interaction between P and Al

Al toxicity in plants often manifests itself as an apparent P deficiency (e.g. Munns 1965a). Phosphate and monomeric Al ions interact in solution to form polymers or precipitates (Blamey *et al.* 1983). Thus, the addition of P tends to reduce Al toxicity and the presence of monomeric Al in solution tends to reduce the availability of P for uptake by roots (Munns 1965b; Clarkson 1966; Dodd *et al.* 1992). The effects of Al toxicity on root elongation, root hair formation, rhizobial multiplication in the rhizosphere and nodulation can be overcome by increased P concentration and consequently reduced concentration of monomeric Al in solution (Blamey *et al.* 1983; Wood *et al.* 1984). Raising P concentration sufficiently to cause Al to precipitate was sufficient to overcome the effects of Al toxicity in lucerne, and enable normal use of P in the processes of growth (Munns 1965b). The effect of P in reducing Al toxicity is observed for both soils and solution culture (Munns 1965a & b).

In a study of lime \times P interactions on pasture growth in field trial data from the North Island of New Zealand there were negative lime \times P interactions in 19 out of 25 trials (Mansell *et al.* 1984), suggesting that, as well as supplying P, P was also having a liming effect, possibly by reducing concentrations of Al in the soil solution.

Toxic concentrations of Al in the growth medium may decrease P concentrations in both shoots and roots (Andrew *et al.* 1973), immobilise P, leading to its accumulation in roots (McLeod and Jackson 1965; Bouma *et al.* 1981) and inhibiting the translocation of P from roots to shoots, especially in species sensitive to Al toxicity, inducing P deficiency in the leaves (Munns 1965b; Andrew and Vanden Berg 1973; Bouma *et al.* 1981). Al toxicity may diminish the efficiency with which P is used in the processes of root and shoot growth (Clarkson 1966; Munns 1965b). This may result in apparent P deficiency at tissue P concentrations normally regarded as adequate for growth (Munns 1965b).

2.4 EFFECT OF COMBINED N ON LEGUME GROWTH

2.4.1 Effect of combined N on N₂ fixation

While generally resulting in increased growth, combined N is found to depress nodulation of a wide range of legumes including lucerne (Munns 1968; Heichel and Vance 1979) *Vicia faba*, *Phaseolus vulgaris*, *Pisum sativum* (Dean and Clark 1980; Saito *et al.* 1984), *Lens esculenta* (Wong 1980), soybean (Streeter 1982) and lupins (*Lupinus angustifolius* and *L. albus*; Cowie *et al.* 1990). Observations of young seedlings suggest that the stages of root hair curling and infection thread formation are more susceptible to disruption than the later stages of nodulation, and that nitrate and nitrite are more potent suppressors of nodulation than ammoniacal forms of N (Munns 1968; Pate 1977). It has been proposed that nitrate acts externally through the catalytic action of its reduction product, nitrite, in the destruction of indole acetic acid (which is thought to be the agent of root hair curling) (Tanner and Anderson 1964). Effects of combined N on infection and nodulation depend on the amount and frequency of application, and tolerance of combined N varies between species and between varieties within species (Allos and Bartholomew 1959; Pate 1976).

Combined N may also substantially reduce N₂-fixing activity in legumes where the N₂-fixing symbiosis has been previously established (Allos and Bartholomew 1955; Allos and Bartholomew 1959; Oghoghorie and Pate 1971; Hojjati *et al.* 1978; Barta 1979; Dean and Clark 1980; Wong 1980; Silsbury 1987). The degree to which nitrogen-fixing activity is depressed by combined N varies widely between species (Harper and Gibson 1984; Dakora *et al.* 1992). Low rates or concentrations of combined N, however, are frequently found to stimulate N₂ fixation (e.g. Allos and Bartholomew 1959; Copeland and Pate 1969; Bethlenfalvay *et al.* 1978). When applied N exceeds needs for plant growth it tends to replace N₂ fixation (Allos and Bartholomew 1955 and 1959).

Species and varieties within species vary widely in their capacity to provide the N required to meet their growth potential from symbiotic fixation. Allos and Bartholomew (1959) found that the range of legumes in their study were able to supply from 33 to 79% (approx) of their N requirements from fixation. Soybeans and *Vicia faba* were found to fix about 33% (Ryle *et al.* 1979a) and 70-80% (Richards and Soper 1979; Hill-Cottingham and Lloyd-Jones 1980) of their own N needs respectively. The N requirements of cowpea (*Vigna*

unguiculata) were almost fully met by symbiotic fixation.

As available N increases, its rate of uptake by legumes (and nitrate reductase activity (NRA)) increases and the rate of symbiotic fixation (via nitrogenase activity) decreases proportionately (Silsbury 1987). In the field situation a major factor in determining the rate of legume N₂ fixation is the mineral N content of the soil (Hoglund and Brock 1987).

Two main mechanisms are suggested by which nitrate may reduce symbiotic N₂ fixation in legumes. The first is that the reduction of nitrate to nitrite in the roots causes a substantial drain on the C reserves of the root (Pate 1976) resulting in decreased carbohydrate accumulation in root nodules (Small and Leonard 1969; Latimore *et al* 1977). Secondly a direct effect of nitrate within the nodules is also possible, and an inhibitory effect of nitrite on nitrogenase has been demonstrated (Trinchant and Rigaud 1980).

Symbiotic N₂ fixation has been linked with energy use (Allison 1935; Brun 1972; Streeter 1974; Mahon 1977) and its energy requirement has been found to be greater than that for nitrate reduction (Finke *et al.* 1982). Therefore it is presumably advantageous for plants to absorb nitrate rather than fix N₂.

2.4.2 Effect of combined N on nitrate reductase activity

Nitrate reductase is a substrate induced enzyme in higher plants (Campbell 1988). In most species, including most legumes, nitrate reductase activity (NRA) is low or undetectable in the absence of external nitrate (Andrews 1986; Rajasekhar and Oelmuller 1987; Andrews *et al.* 1990). Induction of nitrate reductase in plant tissue appears to be inevitable in a nodulated legume when nitrate is available for assimilation (Beever and Hageman 1983).

The level and activity of nitrate reductase appears to be closely regulated by the flux of nitrate ions to the root (Pate and Atkins 1983).

Legume species differ in the distribution of NRA between roots and shoots. For example, cowpea roots appeared to have a lesser capacity for nitrate reduction than those of white lupin (*Lupinus albus*). At any given external nitrate concentration the proportion of total NRA contained in the root was less for cowpea than white lupin (Atkins *et al.* 1979; Atkins

et al. 1980). For both species the proportion of NRA contained in the root declined with increasing external nitrate concentration and increasing total NRA (Atkins *et al.* 1979; Atkins *et al.* 1980).

The way in which distribution of NRA between root and shoot changes with external N concentration also varies between species. A range of temperate legumes showed an increased proportion of total plant NRA in their shoots as external nitrate concentration was increased (Andrews *et al.* 1984; Sutherland *et al.* 1985). In contrast several legumes of tropical origin maintained the proportions of NRA in root and shoot relatively constant, regardless of nitrate concentration (Andrews *et al.* 1984).

The following patterns of NRA distribution between root and shoot were suggested (Andrews 1986):

- a) Temperate, annual legume species growing in low external nitrate concentrations do most of their nitrate assimilation in the root. Shoot nitrate assimilation increases in importance as external nitrate concentration is increased.
- b) For tropical and subtropical species the partitioning of nitrate assimilation between root and shoot remains constant with changing external nitrate concentration.

From an energy viewpoint it is thought to be advantageous for nitrate reduction to occur via photo-reduction in leaves or stems rather than via respiratory-driven reduction in roots (Schrader and Thomas 1981; Smirnoff and Stewart 1985). It is thought that the greater reliance on root nitrate assimilation in temperate species may be due to possible disadvantages associated with shoot assimilation at low temperatures (Andrews 1986).

2.5 SUMMARY

Gorse is present on large areas of land in New Zealand. It has been traditionally regarded as a major weed in both pastoral agriculture and forestry. Its control is a major cost to these industries. However, gorse does potentially have value. It could be used in combination with goats to form the basis of a low cost sustainable farming system, and can also have value as a nurse plant in the regeneration of indigenous forest, as an erosion control plant, as a source of pollen for bees and as shelter for livestock.

Edaphic conditions which appear to favour gorse are low soil fertility (particularly low available P and N) and strong to moderate soil acidity (pH 4.0 - 5.5).

While there is a certain amount of information on the growth requirements of gorse, there are few detailed studies on its adaptation to low fertility and on its responses to applied P, N and lime. Of particular importance is the lack of comparative studies between gorse and high fertility requiring legumes such as white clover. Comparison with white clover is particularly relevant because white clover is the most important legume in New Zealand pastoral farming systems, and is the main species which gorse replaces as the dominant legume when previously high soil fertility and stocking rates decline due to decreasing fertilizer inputs.

In order to develop management techniques to either use or control gorse it is necessary to gain a better understanding of the edaphic adaptation of the species particularly with regard to its nutrient requirements, tolerance to soil acidity and its ability to supply its own N needs via symbiotic fixation. Comparative studies with white clover would enable a better understanding of the relative competitiveness and potential role of gorse relative to white clover under a range of soil fertility conditions.

Specific topics requiring further study include:

- 1) Productivity of gorse under conditions of low available soil P.
- 2) The ability of gorse to take up P, its responsiveness to applied P and its internal efficiency of P use, compared with white clover.
- 3) The effects of combined N supply on growth, symbiotic N₂-fixing activity and NRA of gorse compared with white clover.
- 4) The ability of the symbiotic N₂-fixing system of gorse to meet the plant's needs for N, compared with white clover.
- 5) The internal efficiency of N use in gorse compared with white clover.

- 6) The effects of soil acidity, particularly Al toxicity, on the growth and N₂-fixing activity of gorse compared with those on white clover.
- 7) The comparative effects of lime and P application and their interaction on gorse and white clover.
- 8) The effects of varying soil chemical fertility and soil physical conditions on the growth of gorse under similar climatic conditions in a field study in North Westland.

CHAPTER 3

EFFECTS OF FERTILIZER PHOSPHORUS AND NITROGEN AND FREQUENCY OF CUTTING ON GORSE AND WHITE CLOVER GROWTH

3.1 INTRODUCTION AND AIMS

Gorse is reported to have low nutrient requirements (Meeklah 1979) and is found to be more responsive to P fertilisation than to N or K fertilisation (Thompson 1974; Ivens and Mlowe 1983). Nitrogen fertilizer was found to inhibit nodulation, but increase the growth of mature gorse (Thompson 1974). The effect of P and N application on gorse seedling survival appears to be influenced by the other species present. Where white clover (*Trifolium repens* L.) was scarce, applied P was found to increase gorse seedling numbers, but where clover was abundant, applied P depressed gorse because of competition from the clover (Hartley and Popay 1982). Likewise, where grass establishment was poor, applied N was associated with increased numbers of gorse seedlings but where grass cover was good applied N depressed gorse (Hartley and Popay 1982). The findings of Thompson (1974) also indicate a decline in gorse seedling numbers when pasture growth is stimulated by the application of P or N fertilizer.

Gorse is reputed to prefer low pH (Meeklah 1979), to be a calcifuge, and to have a possible soil acidifying effect (Chater 1931; MacCarter and Gaynor 1980). Phung *et al.* (1984) found that lime application (sufficient to raise soil pH above 7.0) reduced the number of gorse seedlings emerging, but that seedling growth and nodulation were increased by applying sufficient lime to raise soil pH from 4.8 to 6.5. Thompson (1974) found that lime (3000 kg ha⁻¹ retarded gorse seedling growth (when applied to soil with an initial pH of 5.0), but that established plants were unaffected (when lime was applied to soils with an initial pH values of 5.0 and 5.5).

In order to further investigate the tolerance of gorse to low soil phosphate concentrations and responsiveness to applied phosphorus and nitrogen, a field trial was established with the following aims:

- 1) To assess the performance of young gorse plants under conditions of low available phosphate in comparison with white clover.
- 2) To estimate the responsiveness of gorse to increasing rates of applied phosphate, compared with white clover.
- 3) To assess the efficiency of the N₂-fixing system of gorse.
- 4) To investigate the effect of cutting frequency on the growth of gorse and on its responses to applied nutrients.

3.2 EXPERIMENTAL

3.2.1 Trial Design

3.2.1.1 Statistical Design

The trial was of randomised block design with 5 rates of P application, 2 rates of N application, 2 cutting treatments (20 treatment combinations) and four replicates or blocks. The trial was conducted on a site having very low available P concentrations (Section 3.2.2). The blocks were arranged to span any soil variability which might have been associated with the slight slope that there was across the trial site. Topsoil chemical properties were generally very uniform between blocks (Table 3.1) and auger holes made across the trial site indicated little variation in soil depth. Different size categories of seedlings were allocated to different blocks as described in section 3.2.3.3. The 20 different treatment combinations were allocated randomly to the plots within each block. The layout of the trial is illustrated in Appendix 3.1.

Table 3.1 Chemical properties of Wakanui silt loam

Sample Depth (cm)	pH (H ₂ O)	C (%)	N(%)	C/N ratio	P retention (%)			Phosphate-ext. SO ₄ (µg S g ⁻¹)		
0 - 7.5	5.4	4.9	0.32	16	24			5		
s.e.	0.05	0.08	0.010	0.6	2.1			2.0		
7.5 - 15	5.5	3.6	0.25	14	24			3		
s.e.	0.05	0.10	0.017	1.2	7.1			1.2		
Cation exchange properties (NH ₄ OAc at pH 7, me.%)										
Sample depth (cm)	CEC	Sum bases	%BS	Ca	Mg	K	Na	KCl-ext. Al (me.%)	Reserve (me.%)	
									Mg _r	K _c
0 - 7.5	17.7	11.0	62	8.15	2.05	0.43	0.34	0.2	2.0	0.40
s.e.	0.21	0.21	1.8	0.131	0.067	0.103	0.092	0.10	0.53	0.006
7.5 - 15	15.7	9.32	60	7.20	1.51	0.24	0.37	0.4	2.2	0.39
s.e.	0.43	0.194	1.9	0.277	0.057	0.080	0.076	0.10	0.61	0.033

Samples were taken from individual plots (section 3.2.8). Subsamples from the plot samples were bulked to form a composite sample for each block. The values presented are means of the 4 blocks.

3.2.1.2 Treatments

3.2.1.2.1 Phosphorus

Five rates of P were applied, including a nil rate (P0, P1, P2, P3 and P4). It was intended that the P3 rate of P would be sufficient to raise the concentration of P in soil solution to 0.20-0.25 ppm, a concentration thought to be sufficient for near maximum growth of most plants (Beckwith 1964) including white clover (Parfitt *et al.* 1982). The rate of applied P necessary to achieve this was determined on the basis of a P sorption isotherm (Appendix 3.2; Fox and Kamprath 1970). The estimated quantity of applied P needed to raise the concentration of P in soil solution to 0.20-0.25 ppm, in the top 7.5 cm, was 20 g per plot or 6 g per m². Based on this rate of application for the P3 treatment, rates of P were increased from zero, in a geometric progression, as shown in Table 3.2.

Table 3.2 Rates of P application 1989 and 1990 - Springston trial

P treatment	Rates of applied P			
	1989		1990	
	g m ⁻²	kg ha ⁻¹	g m ⁻²	kg ha ⁻¹
P0	0	0	0	0
P1	1.5	15	0.3	3
P2	3.0	30	2.7	27
P3	6.0	60	4.0	40
P4	12.0	120	6.8	68

P was applied in the form of monocalcium dihydrogen orthophosphate ($\text{Ca}(\text{H}_2\text{PO}_4)_2$) to the soil surface.

Because the fertilizer was not mixed uniformly throughout the top 7.5 cm, the concentration of P in soil solution would be expected to be greatest near the soil surface, rather than uniform to a depth of 7.5 cm. This would simulate normal topdressing practice.

At the beginning of the 1990/1991 growth season, an attempt was made to duplicate the soil

solution P concentrations which existed at the beginning of the 1989/1990 season (Appendix 3.3). The rates of P applied at the beginning of the 1990/1991 growth season are given in Table 3.2.

3.2.1.2.2 Nitrogen

Two rates of N were applied as follows:

- 1) Nil
- 2) 200 kg N ha⁻¹ year⁻¹ (20 g m⁻²), divided into 4 applications of 50 kg ha⁻¹ (5 g m⁻²).

The nitrogen was applied in the form of ammonium nitrate (NH₄NO₃) at approximately 6 week intervals, starting at the beginning of the growth season (early October). Application dates for 1989/1990 were 2 Oct 1989, 24 Nov 1989, 15 Jan 1990, 11 Mar 1990; and for 1990/1991 were 4 Oct 1990, 14 Nov 1990, 5 Jan 1991 and 17 Feb 1991.

3.2.1.2.3 Defoliation

There were 2 defoliation treatments as follows:

- 1) Frequent (F):
Cut twice yearly at 20 cm from ground level. Cutting times were the middle and end of the growth season.
- 2) Infrequent (I):
Cut once, at the end of the second growth season. Plants were cut at 20 cm height and the cut material was separated into first and second year's growth.

3.2.2 Trial site

The trial (Plate 3.1) was situated at Springston, Canterbury on Wakanui silt loam (Aquic Ustochrept) (Profile description, Appendix 3.4; profile photograph, Plate 3.2).

Some soil chemical properties of the site are shown in Table 3.1. It was chosen primarily because of its low available P levels. 0-7.5 cm samples taken in a 5 m × 5 m grid pattern over the proposed trial site had a mean Olsen P concentration of 5.9 µg g⁻¹. (Olsen P



Plate 3.1 Springston field trial (24 Jan 1990)



Plate 3.2 Wakanui silt loam

concentrations in the P0 plots are given in Table 3.6). P retention (Saunders 1965) was in the low range of Blakemore *et al.*(1987). Exchangeable (exch.) K concentrations (0-7.5 cm) were low to medium, exch. Mg and Ca concentrations were in the medium range and phosphate extractable sulphate levels were very low to low (Blakemore *et al.* 1987). EDTA-extractable Cu and Zn concentrations (7.93 and 5.15 $\mu\text{g g}^{-1}$ respectively) and CaCl_2 -extractable B concentration (1.48 $\mu\text{g g}^{-1}$) in the 0-7.5 cm soil layer all appeared to be adequate for good plant growth (McLaren *et al.* 1984; Wolf 1971).

The trial was securely fenced to exclude farm livestock, rabbits and hares.

3.2.3 Establishment

3.2.3.1 Gorse seedling culture

Over 7000 seedlings were raised in order to enable the selection of 2400 healthy, uniform seedlings for the trial plots. A further 600 seedlings were needed for a double border row around the perimeter of the trial.

During July 1988 a supply of gorse (*Ulex europaeus* L.) seed was collected from gorse bushes at a single location at Hororata (inland mid-Canterbury.) The seeds were air dried then removed from their pods using a mechanical thresher. Before germination, seeds were scarified, using a compressed air device lined with P80 sand paper. This was done in order to increase germination percentage after two weeks from about 4% to 50-60% (data not shown). Because of their relatively low germination percentage, and because they tended to germinate progressively over a period of weeks, the gorse seed was pre-germinated. Seeds were placed on moist blotting paper which had been laid on trays and sprayed with Thiram (3 g per litre) to minimise fungal growth. The trays were placed inside plastic bags to prevent moisture loss. Additional water was added as necessary to prevent drying and additional Thiram was sprayed onto areas affected by fungal growth. Room temperature during germination was 20-25°C. Seeds germinated after about 10 days and were planted out into biodegradable paper pots (FS 315, distributed by Lannen Tehtaat Oy, Finland) which were 7.5 cm deep and 3.5 cm in diameter. They came in sets of 238 and were clipped into purpose built trays. The bottoms of the trays were lined with fibreglass insect screen (mesh size 1.2 × 1.8 mm) to prevent loss of the growth medium. Each pot contained

pproximately 8.0 g dry weight of 1:1 perlite/vermiculite growth medium.

The growth medium in a single pot had a water holding capacity (amount of water held against gravity after saturation) of 36 ml (gravimetric water content = 452%). At the limit of readily available water (-100 kPa), gravimetric water content was 63% (measured using a tension plate apparatus). Therefore the amount of water retained in the medium at -100 kPa was 5.0 ml, and that available between saturation and -100 kPa (readily available water) was 31 ml.

Gorse seeds were planted into the paper pots over the period 13 Nov 1988 to 5 Dec 1988 as they germinated. After planting the paper pots were watered to saturation using tap water (unchlorinated and unfluoridated). After emergence the seedlings were transferred to a glasshouse where mean daily max/min temperatures were 29.5/16.5°C. Seedlings were provided with water only, until day 22.

On days 23 and 42 after the mean planting date 8 litres per tray (sufficient to completely flush the pots) of complete nutrient solution (modified from that of Andrews et al. (1989), Table 3.3) was applied. The seedlings were inoculated with rhizobia on day 44 (Section 3.2.3.2), after which nutrient solution was added in small amounts so as not to flush rhizobia from the growth medium. Weekly nutrient solution application (8 litres per tray) began on day 59.

Between nutrient applications, trays were watered as necessary, taking care not to displace nutrients.

On day 85 (14 Feb 1989) the seedlings were moved from the glasshouse to a shadehouse, where mean daily max/min temperatures were 22.5/10.0°C. On day 102 (3 Mar 1989) they were moved outdoors.

Table 3.3 Composition of nutrient solution applied to Springston trial seedlings

Compound	Stock solution concentration	Stock solution litre ⁻¹ nutrient solution (ml)	Nutrient solution concentration
Macronutrient	(mol l ⁻¹)		(mmol l ⁻¹)
KH ₂ PO ₄	1.00	1	1.1
K ₂ HPO ₄	0.10	1	0.1
MgSO ₄	0.50	2	1.0
CaCl ₂	1.00	1	1.0
KNO ₃	1.00	1	1.0
Micronutrients†	(mmol l ⁻¹)		(µmol l ⁻¹)
MnSO ₄ ·4H ₂ O	1.00	1	1.0
CuSO ₄ ·5H ₂ O	0.10	1	0.1
ZnSO ₄ ·7H ₂ O	0.10	1	0.1
NaMoO ₄ ·2H ₂ O	0.50	1	0.5
H ₃ BO ₃	5.00	1	5.0
CoSO ₄ ·7H ₂ O	0.02	1	0.02
NaCl	10.00	1	10.00
Ferric citrate	5.00	1	5.0

† A combined stock solution was made up containing all micronutrients except Fe.

3.2.3.2 Rhizobial Inoculation

On day 44 (4 Jan 1989) the seedlings were inoculated with *Bradyrhizobium* sp. (*Ulex*) - ICMP 6303 (Plant Diseases Division, DSIR 1988). The inoculum was cultured in yeast-mannitol broth. Two ml of the broth containing approximately 2.9×10^8 rhizobia per ml, was applied to each pot. Rhizobial numbers were estimated by dilution plate counts done according to the method of Sirockin and Cullimore (1969). Following inoculation pots were gently sprinkled with water to wash in the rhizobia, and care was taken to avoid flushing rhizobia through the pots when watering or applying nutrients (Section 3.2.3.1). A simple

indication of stage of seedling development at the time of first inoculation is given in Table 3.4.

Table 3.4 Summary of gorse seedling development at inoculation - Springston trial

	Total shoot length (cm)	Leaf no.	Root length (cm)	Nodule no.†
No. of observations	32	31	32	32
mean	6.0	17	10.9	0.1
s.e.	1.28	2.5	1.19	0.6

† Only two plants were nodulated. One had 3 pink nodules, one had 1 nodule with no pink colouration.

Ten days following transplantation into the field, seedlings were again inoculated with the same *Bradyrhizobium* strain. The rhizobia were grown in peat culture by ICI Cropcare. The peat culture contained 3.2×10^9 rhizobia per gram. This was mixed with water to give a suspension containing 7.5×10^7 bacteria per ml, 20 ml of which was applied to the base of each seedling (using a livestock drenching gun). The inoculum was washed into the soil with 500-1000 ml of water per plant.

3.2.3.3 Transplanting

Before transplanting the seedlings into the field, the trays were flushed twice with tap water (12 litres per tray) to minimise transfer of nutrients onto the field site.

Immediately before transplanting the seedlings were grouped into 5 size categories on the basis of shoot length: <10 cm, 10-15 cm, 15-20 cm, 20-25 cm and >25 cm. 20-25 cm seedlings were transplanted into block 1, 15-20 cm seedlings into blocks 2 and 4 and 10-15 cm seedlings into block 3 (Appendix 3.1).

The trial plots measured 2.00×1.67 m. Thirty seedlings per plot were planted at 33 cm spacings. A 33 cm \times 33 cm grid was laid on the plots, and cores the same size as the

seedling pots were removed from the centre of each square. The seedlings, still in their paper pots were placed in the holes. Transplanting was done on 20-23 March 1989 (seedling age about 120 days). To avoid edge effects the trial was surrounded by a double row of seedlings which were the same distance from plots on the edge of the trial as neighbouring plots were within the trial.

3.2.3.4 Watering - field site

Five days before the seedlings were transplanted into the field, the field trial site was watered (via a sprinkler line) with approx 35 mm of water. Immediately following the planting of individual replicates, 1 litre of water was applied to the base of each plant.

The day following completion of planting a further 35 mm (approx.) of water was applied using the sprinkler line. After this watering the soil was wet to a depth of only 1-1.5 cm, but the holes in which plants were located were quite wet.

Throughout April 1989 1.5 litres of water was applied to the base of each plant at approximately 4 day intervals. This was necessary because of the very dry conditions over the summer of 1988/1989.

3.2.4 Weed control

Ten days before transplanting the seedlings onto the trial site, the area was sprayed with 6 litre ha⁻¹ of the herbicide glyphosate (Roundup). This treatment successfully removed plant competition from the gorse seedlings during the autumn/winter of 1989, but because the weather was very dry at the time of application, the other vegetation, predominantly browntop (*Agrostis capillaris*) began to grow again in early spring.

On 17 September 1989 the whole trial site was sprayed with 8 litres ha⁻¹ of Gallant (haloxyfop) (see Appendix 3.5) using a hand-held boom sprayer. An excellent kill of grass species was achieved, with no apparent damage to the gorse seedlings. White clover and broadleaf weeds were not killed.

During the first growth season of the trial all plots were hand weeded at approximately

monthly intervals to minimise competition for light with the young gorse seedlings from other vegetation in the plots. In the P0 plots the other vegetation was more than 50% broadleaf weeds, and the level of competition for light was low. In the high P plots (from P2 upwards) the other vegetation was mainly white clover, and the level of competition necessitated weeding.

All plots were weeded at the beginning of the second growth season. Thereafter only the frequently defoliated (F) plots were weeded, because in the undefoliated (I) plots the gorse shaded out the white clover. The defoliated plots were weeded once more, immediately before the first cut of the 1990/91 growth season (12-13 Dec 1990). From this point the gorse plants grew sufficiently rapidly not to suffer substantial competition for light from the white clover. (Although the gorse shoots rapidly grew taller than the white clover, they did not smother the clover. Clover growth was still vigorous between gorse plants in the F plots.)

3.2.5 Basal Nutrients

Based on chemical analysis of composite soil samples from the trial site (Table 3.1), a basal dressing of K, S and Mo was applied to the whole trial. The rates of S and Mo were based on Cornforth & Sinclair (1984). Although exch. K was in the low range, reserve K (K_c) levels were high (Table 3.1, Blakemore *et al.* 1987). Although this implied that soil K status was adequate, K was applied to ensure that supply did not limit growth. The rates of K, S and Ca application, given in Table 3.5, were applied at the beginning of the growth season in 1989 and 1990.

Table 3.5 Rates of K, S and Ca application - Springston trial

Compound	Rate of K application		Rate of S application		Rate of Ca application	
	g m ⁻²	kg ha ⁻¹	g m ⁻²	kg ha ⁻¹	g m ⁻²	kg ha ⁻¹
K ₂ SO ₄	5.00	50.0	2.02	20.2		
CaSO ₄			2.98	29.8	3.72	37.2
Total	5.00	50.0	5.00	50.0	3.72	37.2

Mo was sprayed onto the trial site in solution at a rate of 50 g sodium molybdate ($\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$) per ha (5 mg m^{-2}). This rate applied at the beginning of the 1989 season was thought to be sufficient for 4 years (Cornforth and Sinclair 1984).

Lime was not applied because:

- 1) Soil pH was above the range normally associated with Al toxicity (Coleman et al. 1958; McCart and Kamprath 1965; Section 2.3.2).
- 2) pH appeared to be suitable for good gorse growth (Thompson 1974; Phung *et al.* 1984) and was close to the range thought to be optimum for pastures on mineral soils (5.5 - 6.2, Edmeades et al. 1984).

3.2.6 Measurement of gorse growth

3.2.6.1 Shoot elongation

In the first growth season four plants were randomly chosen from the 12 central plants in each plot. For each of these plants one shoot arising from each of the terminal, mid-stem and basal positions on the original seedling were tagged. The lengths of these shoots were measured at approximately one month intervals throughout the growing season. After plots receiving the frequent defoliation treatment were cut, one new terminal shoot from each of the chosen plants was tagged and subsequently measured.

In the second growth season one terminal shoot per plant was tagged (from the same plants as for the previous year). Occasionally, on the infrequently cut plants, a shoot arising from further down the stem was tagged if there were no actively growing shoots at the terminal. As for the previous season, tagged shoot lengths were measured at approximately one month intervals.

3.2.6.2 Dry weight

Plants in the frequently cut (F) plots were cut at 20 cm height twice during each growth season. In these plots the cut material was entirely current seasons growth.

The material from the central 12 plants was cut and weighed separately from the material from the 18 perimeter plants in each plot. For the first 3 harvests all of the cut material was dried and weighed. At the fourth harvest there was too much material to enable this to be done, so it was weighed fresh in the field and a weighed sub-sample (approx. 1000 g) was taken for percentage dry matter determination.

The central 12 plants in the infrequently cut (I) plots were cut at 20 cm height at the end of the second growth season. The cut material was then divided into current and previous season's growth. Total fresh weight of each seasons growth was measured in the field, and weighed sub-samples (approx. 1000 g) were taken for dry matter determination.

Plant material was dried to constant weight at 70°C.

Harvest dates for the F plots were 31 Jan 1990, 31 May 1990, 12-13 Dec 1990, and 16-17 April 1991. The I plots were harvested on 15-16 April 1991.

Although the plot size used was 3.33 m², dry weights were expressed as kg ha⁻¹ for ease of comparison with other published dry matter production data.

3.2.7 Measurement of white clover growth

3.2.7.1 Visual assessment of dry matter production

White clover (*Trifolium repens* L.) dry weight was estimated on two occasions during each growth season; on 11 Dec 1989 (representing regrowth from 1 Oct to 11 Dec), 24 May 1990 (regrowth from 15 Jan to 24 May), 30 Nov 1990 (regrowth from 28 Sept to 30 Nov) and 27 Mar 1991

(regrowth from 10 Dec 1990 to 27 Mar 1991). Each plot was given a visual score from 1-10 based on the height and density of white clover present. 0.05 m² quadrats were then cut at ground level in at least 25% of the plots scored. Sub-samples of the plant material from the quadrats were sorted into white clover, other species and dead material. The plant material was then dried to constant weight at 70°C. A relationship was then established between plot score and dry weight of cut clover using regression analysis. This relationship was applied to all plots to convert the scores into estimated clover dry weights.

3.2.8 Soil Sampling

Soil samples were taken during the winter of 1989 (3-4 July 1989) before treatment application, during late spring 1989 (21-22 Dec 1989), during the winter of 1990 (1 Aug 1990) during late spring 1990 (13-14 Dec 1990) and during the winter of 1991 (22, 26 Aug 1991).

At each sampling time, five 0-7.5 cm and five 7.5-15 cm cores were taken from random locations in each plot using a 2.3 cm diameter stainless steel coring device.

3.2.9 Plant sampling

3.2.9.1 Gorse

Shoots were sampled for chemical analysis as follows:

31 Jan 1990: A representative sample of shoots was taken from the harvested material from the frequently cut (F) plots.

31 May 1990: A representative sample of shoots was taken from the harvested material from the F plots.

9 Dec 1990: One actively growing shoot was taken from each of the 12 central plants of all plots 3 days before the F plots were cut.

13 April 1990: One typical shoot was taken from each of 9-10 central plants per plot, for all 80 plots, two days before commencement of the final harvest of both the F and I plots.

3.2.9.2 White Clover

White clover foliage (petioles and leaflets) was sampled during periods of active growth, on 11 Jan 1990 and 8-9 Dec 1990, from all 80 plots.

Each plot was considered to be divided into quarters. A sample of white clover was cut

from a central position in each quarter. Samples from each quarter were bulked for each plot.

Samples were cut 2-3 cm above ground level to avoid soil contamination.

3.2.10 Nitrate reductase activity

3.2.10.1 Timing and plots sampled

Nitrate reductase activity was measured in gorse tissue from the field trial plots on two occasions during the second growth season. The aim was to compare the rate of nitrate reductase activity (NRA) in plants provided with a high rate of fertilizer N with that in plants dependent on N_2 fixation.

The first assay was done on 22 Dec 1990, 38 days after the most recent application of N to the high N plots. Plant material was sampled from the I (uncut) P3 high N and nil N plots from each block. It was decided to sample from the P3 plots because maximum growth appeared to be occurring in this treatment, and from the I plots because these plants had not been cut and were therefore more representative of naturally occurring gorse. Samples were taken from one typical guard row plant in each plot. Guard plants were sampled in order to minimise disturbance to the central 12 plants during the period of rapid spring - early summer growth. Guard plants received the same fertilizer treatments as the central plants; therefore their NRA should have been similarly affected by the application of N fertilizer.

The second assay was done on 28 Feb 1991-1 Mar 1991, 11 days after the most recent application of N to the high N plots. Plant material was sampled from the F, P3 high N and nil N plots from each block. Samples were taken from one of the outer of the central 12 plants in each plot. It was decided to sample from the F plots on this occasion because their plants appeared to be more actively growing (having been cut about 11 weeks previously) than those in the I plots.

Concentrations of 2 mol l^{-1} KCl-extractable nitrate and ammonia were measured in fresh field-moist soil samples less than 5 days from the time of assay. Two 0-15 cm depth, 2.3

cm diameter soil cores were taken 5-10 cm from the base of each plant sampled. The extraction and analytical procedures were those of Blakemore *et al.* (1987).

3.2.10.2 Plant sampling procedure

A shoot sample containing both current and previous seasons growth was removed from each chosen plant. A large soil core (15 cm deep and 8.5 cm in diameter) was taken 3-4 cm from the base of each chosen plant. The shoot samples and soil cores were stored on ice until reaching the laboratory, when they were placed in a refrigerator. Nitrate reductase assays were done on new shoots, previous season's shoots, and roots (from the soil core). The procedure for the assay was as described in Section 5.2.7.

3.2.11 Acetylene Reduction

3.2.11.1 Preparation and sampling

Acetylene reduction assays were done on soil cores removed from the field trial plots on 17 March 1991, 28 days after application of 50 kg N ha⁻¹ to the high N plots. The five pairs of plots assayed were the uncut (I), P3 high N and nil N plots in each block and the uncut, P4, high and nil N plots in block 1. Time allowed five pairs of plots to be sampled, so one pair of P4 plots was included. Plots with high rates of P were chosen because rates of N₂ fixation would be expected to be higher where growth was not limited by low available P concentrations. The uncut plots were chosen because they had little white clover growth (it was being severely shaded by the gorse). The little clover which was present was removed by hand 8 days before the assays were done, so that it would not contribute to the acetylene reducing activity of the soil cores. Clover regrowth was regularly removed until the assays were completed. An area of vigorously growing white clover adjacent to the trial plots was also defoliated, and soil cores from this area were assayed to check the effectiveness of defoliation in stopping acetylene reducing activity. Acetylene reducing activity was negligible in cores from the area of defoliated clover.

Concentrations of 2 mol l⁻¹ KCl-extractable nitrate and ammonia were measured in fresh 0-15 cm soil samples collected 3 days before measurement of acetylene reduction, using the methods of Blakemore *et al.* (1987).

3.2.11.2 Core sampling and incubation

Ten 15 cm deep 2.3 cm diameter cores were removed from among the central 12 plants of each plot. The cores were removed from close to the base (10-15 cm) of each of 10 different plants. The cores were placed together in a 1 litre glass preserving jar which was immediately sealed with a lid fitted with a rubber septum. Sixty five ml of air was removed, and replaced with 65 ml of acetylene to give a pC_2H_2 of approximately 0.1 atmospheres. The soil cores were incubated for 1 hour, commencing between 2 and 3 pm. Incubations were done in the field, shaded from the sun and at an ambient temperature of approximately 19°C. Temperature within the incubation jars was within 2°C of external air temperature. Soil temperature at 10 cm depth at the same time was approximately 17°C.

3.2.11.3 Gas sampling and analysis

Gas sampling and analysis was done as described in Sections 4.2.4.1 and 4.2.4.2.

3.2.12 Chemical analysis of plant and soil samples

3.2.12.1 Plant analysis

Analysis of plant samples for P and N were done using a semi-micro Kjeldahl method (Blakemore *et al.* 1987). Initially Kjeldahl catalyst tablets were used in the digestion process, but because new batches of tablets had been found to contain small amounts of P these were replaced by a powdered catalyst mixture containing the same quantities of sodium sulphate and copper sulphate as the tablets. Very similar results were obtained for samples digested with the tablets and again with the powdered catalyst, indicating that results using different forms of catalyst were comparable.

P and N concentrations in the digests were determined using auto analysis. The P determination differed from that of Blakemore *et al.* (1987) in that a vanadomolybdate (yellow) colour reagent was used instead of Murphy and Riley (blue) reagent, because the less sensitive vanadomolybdate reagent was better able to cope with the wide range of plant P concentrations encountered.

3.2.12.2 Soil analysis

Soil analyses were done according to the methods of Blakemore *et al.* (1987) unless otherwise specified.

Measurement of Olsen P (Olsen *et al.* 1954) involved extraction of air-dried soil by 0.5 mol l⁻¹ NaHCO₃ (Blakemore *et al.* 1987). The extracts were centrifuged at 10 000 rpm for 6 minutes. 5 ml of supernatant was then transferred to a second centrifuge tube and acidified to precipitate organic materials (Tiessen *et al.* 1983). The supernatant was then transferred to a 50 ml volumetric flask, neutralised (P-nitrophenol) using 1.8 mol l⁻¹ NaOH and 0.5 mol l⁻¹ H₂SO₄, and allowed to stand overnight. 5 ml of Murphy and Riley B reagent (Blakemore *et al.* 1987) was added to each flask which was then made up to 50 ml with deionised water and shaken. The solutions were then allowed to stand for 30 minutes before absorbances were read at 880 nm along with a suitable range of standards (Blakemore *et al.* 1987).

EDTA-extractable Cu and Zn were measured according to the method of McLaren *et al.* (1984) and CaCl₂-extractable B according to the method of Wolf (1971).

3.2.13. Rainfall and soil moisture measurement

3.2.13.1 Rainfall

Rainfall at the trial site was recorded at weekly intervals and immediately following major rainfall events. Monthly totals for the duration of the trial are recorded in Appendix 3.6.

3.2.13.2 Soil moisture

Soil moisture contents at 1-20, 0-40 and 0-60 cm depths were monitored using time domain reflectometry (TDR) (Topp and Davis 1982). The frequency of measurement varied depending on the rate of change of soil water status (Figs 3.16 and 3.17).

3.2.14 Statistical Analysis

Statistical analysis was done using Genstat 5, Release 2 (Genstat 5 Committee 1987, 1990). When doing analyses of variance, care was taken to ensure that the underlying assumptions for analyses of variance were not violated. In particular, checks were done to ensure that the residuals were approximately normally distributed and had approximately common variance. When the magnitude of residuals did not remain approximately constant over the range of measurements recorded, the data was log-transformed in the following way:

$$\text{transformed value} = \ln (\text{value} + 0.325)$$

(0.325 was generally added to the data values to avoid the problems encountered when data including zeros or very low numbers are log-transformed.) Unless otherwise stated, data were untransformed.

Analysis of variance for P treatments was divided into low order polynomial components; and both quadratic and exponential curves were fitted, in order to model the P response functions. Where curves are presented these were fitted (using least squares methods) to the P treatment means, so that the tests of adequacy of fit would be independent of the underlying population variability (Elias and Causton 1976).

Responsiveness and P acquisition capacity are useful parameters in biological terms (Section 3.3.2.2). Responsiveness is defined as maximum dry matter yield (Y_m) minus the dry matter yield without applied fertilizer (Y_0) (P0 treatment) expressed as a proportion of maximum dry matter yield i.e. responsiveness = $(Y_m - Y_0) / Y_m$ (Ozanne 1980). Y_m was taken to be the maximum point of the fitted quadratic or the asymptote of the fitted exponential curve. The capacity of plants to acquire P from the soil (P acquisition capacity) was taken to be the rate of P where the fitted P response curve cuts the x-axis i.e. the (negative) rate of P at the point of no growth (Ozanne 1980). P acquisition capacity was expressed as a positive value (Table 3.11).

To estimate responsiveness (Table 3.10) and P acquisition capacity (Table 3.11) they were expressed as a function of the parameters of the appropriate regression model. Their precision was estimated from the variance covariance matrices of the appropriate regression parameters using Genstat. For this estimation, regressions were fitted using all of the data points rather than just the P treatment means, in order to get satisfactory estimates of the

residual variance of the plot data and hence of the parameters. *t*-tests were used to determine the significance of differences between gorse and white clover for each of the parameters.

Critical P concentration is defined as the P concentration associated with 90% of maximum yield where maximum yield was estimated from the fitted P response curves as above.

Response curves involving 1989/90 growth season data were plotted against the spring 1989 rates of applied P (Table 3.2). Response curves involving 1990/91 growth season data or totals for both growth seasons were plotted against the total rates of P applied for both seasons (1989 plus 1990, Table 3.2).

3.3 RESULTS

3.3.1 Effects of rate of P application on available soil P

The effects of rate of applied P on Olsen P concentrations in soil samples taken from the trial plots are summarised in Table 3.6.

Table 3.6 Effect of rate of P application on Olsen P concentration in trial plots. Phosphorus treatments are shown in Table 3.2.

P treatment	Olsen P ($\mu\text{g g}^{-1}$)			
	Dec 1989		Dec 1990	
	0-7.5 cm	7.5-15 cm	0-7.5 cm	7.5-15 cm
P0	9.0 a	5.8 a	7.3 a	4.9 a
P1	12.1 b	6.3 a	9.0 b	5.8 b
P2	16.1 c	6.4 ab	14.2 c	6.7 c
P3	23.1 d	7.0 b	20.5 d	7.8 d
P4	42.7 e	8.7 c	38.7 e	12.2 e

Note: Values within columns followed by different letters differ at the 5% level of significance according to Fishers least significant difference (LSD).

The samples were collected approximately 8-10 weeks after application of the fertilizer and

therefore should be representative of available P concentrations at the time of rapid spring growth (Section 3.3.4.2).

Analysis of variance of the Olsen P data was done using log-transformed data.

In addition to raising Olsen P concentrations in 0-7.5 cm soil, increasing rates of P application also resulted in slight increases in Olsen P concentration at a depth of 7.5-15 cm (Table 3.6). This was slightly more obvious in the second growth season of the trial.

3.3.2 Effects of rates of P and N application and cutting treatment, on gorse dry weight and estimated white clover dry weight

3.3.2.1 Gorse and white clover dry weight at individual harvest times - F plots

The rate of P application had significant effects on dry matter production of both gorse and white clover.

At all harvest times for gorse and for all times at which white clover yield estimates were made, there were significant rate of P effects on dry matter yield (Tables 3.7 and 3.8). Only for gorse at the April 1991 harvest was there a significant effect of N rate on dry weight (Table 3.7). There were no significant P \times N interactions (Tables 3.7 and 3.8).

Table 3.7 Effects of P and N application rate on gorse dry weight - F plots, Springston trial

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance			
	Date			
	31 Jan 90	31 May 90	12-13 Dec 90	15-17 April 91
P	***	***	**	***
N	ns	ns	ns	*
P × N	ns	ns	ns	ns

Note: Significance levels are shown by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) and ns (nonsignificant).

(b) N treatment mean dry weights (kg ha^{-1})

Date	Rate of N		LSD ($p < 0.05$)
	nil N	high N	
Jan 1990	1088	1057	232
May 1990	451	482	141
Dec 1990	3227	3054	429
April 1991	4615	3900	645

At the first harvest in January 1990, dry matter production of gorse (cut at 20 cm height) increased with increasing P application rate up to 60 kg ha^{-1} (Fig 3.1 (a)). The slight decline in mean dry weight at 120 kg P ha^{-1} was not statistically significant. However the quadratic curve fitted to the treatment means gave a better fit (percentage variance accounted for = 97.8), than the exponential which was also fitted (percentage variance accounted for = 85.7) (Table 3.9(a)) suggesting a decline in dry matter yield at the P4 rate of P. Similarly to gorse, growth of white clover, (estimated in Spring 1989), showed no significant change beyond the 60 kg ha^{-1} rate of applied P, but tended to increase rather than decline at the highest P rate (Fig 3.2(a)). This is supported by the very good fit of the exponential curve to the estimated white clover weights (Fig 3.2(a), Table 3.9(b)).

Table 3.8 Effects of P and N application rate on estimated dry weight of white clover - Springston trial

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance			
	Date			
	11 Dec 89†	24 May 90	30 Nov 90	27 Mar 91
P	***	***	***	***
N	ns	ns	ns	ns
P × N	ns	ns	ns	ns

† Before the first gorse harvest (31 Jan 1990) estimated white clover weights from both cutting treatments were analysed together.

See Table 3.7 for description of significance levels.

(b) N treatment mean dry weights (kg ha⁻¹)

Date	Rate of N		LSD (p<0.05)
	nil	high	
11 Dec 1989	1916	1871	246
24 May 1990	992	1071	96
30 Nov 1990	1746	1734	177
27 Mar 1991	679	623	163

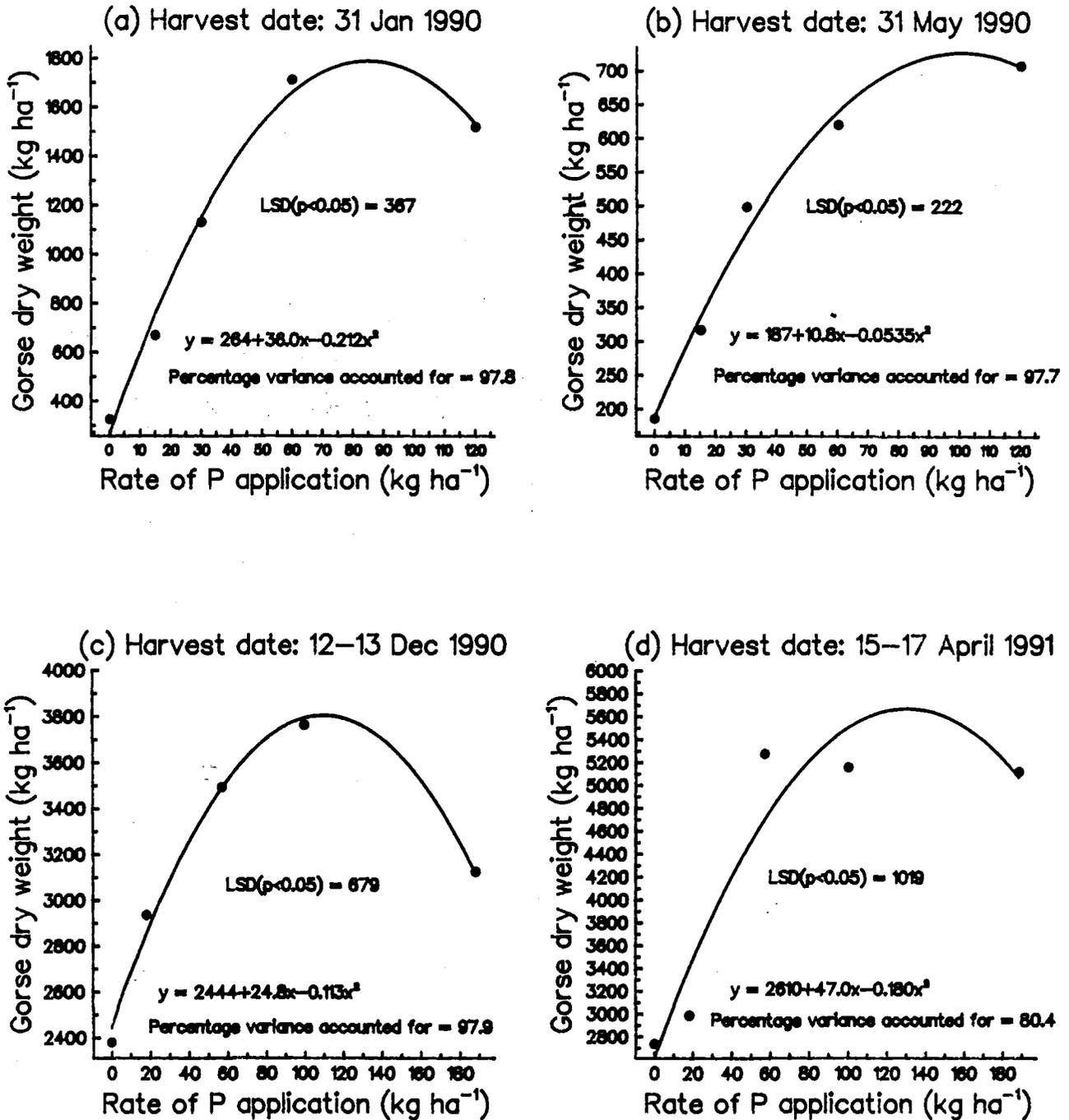


Fig. 3.1 Effect of rate of P application on dry matter yield of gorse – Springston trial.

Table 3.9 Goodness of fit of different curve types when fitted to gorse and white clover mean dry weight data from individual harvest times - F plots

(a) Gorse

Harvest Date	Percentage variance accounted for	
	Quadratic ($y=a+bx+cx^2$)	Exponential ($y=a+br^x$)
31 Jan 1990	97.8	85.7
31 May 1990	97.7	97.8
12-13 Dec 1990	97.9	60.4
15-17 April 1991	80.4	76.6

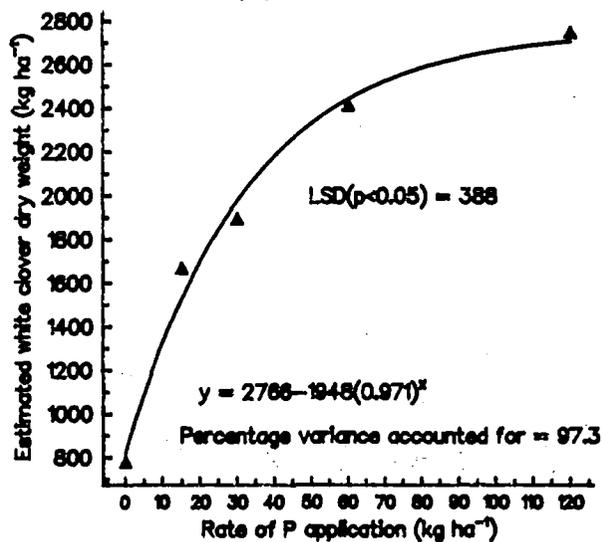
(b) White clover

Harvest Date	Percentage variance accounted for	
	Quadratic ($y=a+bx+cx^2$)	Exponential ($y=a+br^x$)
11 Dec 1989†	93.2	97.3
24 May 1990	94.7	99.6
30 Nov 1990	99.1	98.6
27 Mar 1991	98.1	98.1

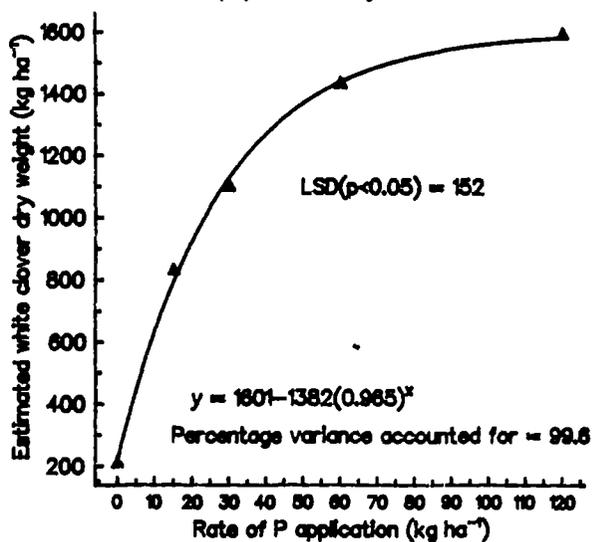
†Based on data from all plots before the first gorse cut.

At the second gorse harvest in May 1990, there was no significant increase in gorse yield beyond the P2 treatment (30 kg P ha^{-1}) but there was no tendency for decline in yield at the highest rate of P (Fig 3.1(b)). In contrast, white clover yields increased progressively with increasing rates of P up to the highest rate (Fig 3.2(b)). For gorse, the quadratic and exponential curve types gave equally good fits to the mean dry weights, but the exponential curve type appeared to give a better fit to the estimated white clover yields (Table 3.9).

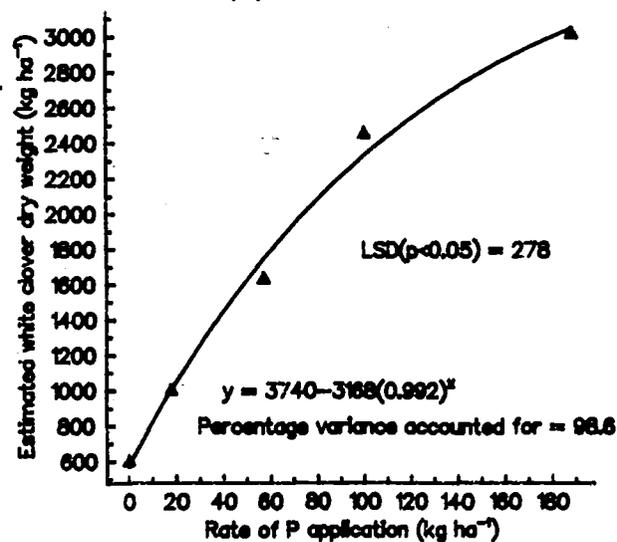
(a) 11 Dec 1989



(b) 24 May 1990



(c) 30 Nov 1990



(d) 27 Mar 1991

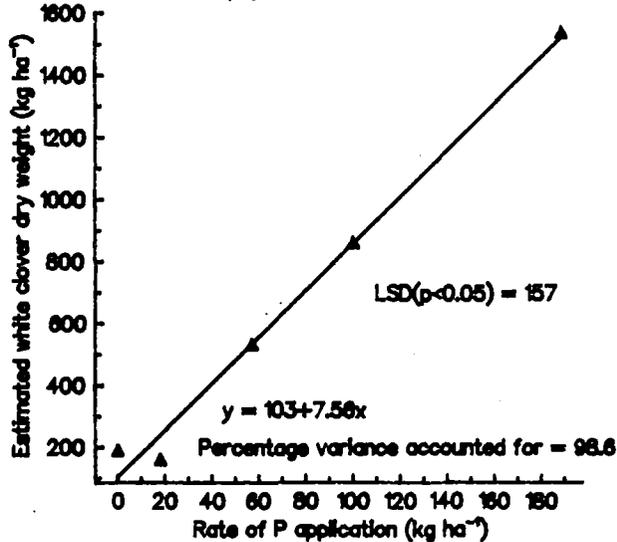


Fig. 3.2 Effect of rate of P application on estimated white clover dry weight – Springston trial.

Dry weight of gorse in spring 1990 (as measured at the Dec 1990 harvest) increased significantly with increasing rate of P up to the P2 rate of P (total of 57 kg P ha⁻¹ over the 2 seasons), beyond which there was no further significant increase in yield (Fig 3.1(c)). However, consistently with the earlier harvests, the curve type which best fitted the treatment means was the quadratic (Table 3.9(a)), suggesting a decline in dry matter yield at the P4 rate of P. In contrast, estimated white clover yields again increased significantly up to the P4 rate of P (total of 188 kg P ha⁻¹ over the 2 seasons, Fig 3.2(c)). Also in contrast to the gorse data, the exponential curve was a good fit to the means of the clover dry weight estimates (percentage variance accounted for = 98.6, Table 3.9(b)).

At the final harvest (April 1991) there were significant rate of P effects on gorse dry weight and also, for the first time, a significant N treatment effect (Table 3.7). Gorse dry weight increased significantly with increasing rate of P up to the P2 rate with no significant change in yield at the two higher rates (Fig 3.1(d)). In contrast estimated white clover growth continued to increase significantly with increasing rate of P up to the highest (P4) rate. (Fig 3.2 (d)). Again a quadratic curve best fitted the mean gorse dry weights, whereas for white clover means a straight line gave best fit (Fig 3.2(d); Table 3.9(b)). It should be noted that where quadratic curves are good fits for mean clover dry weights (Table 3.9(b)), they have their maxima at a point on the x-axis beyond the highest (P4) rate of P applied (Fig 3.2), unlike the quadratics fitted to the gorse dry weights, which had maxima within the range of P rates applied (Fig 3.1). The quadratic curves, depicting a declining rate of increase in dry weight with increasing rate of P, followed by a decline, gave consistently the best fits to the gorse mean dry weights (Table 3.9). These curves were therefore plotted in Fig 3.1.

In contrast the exponential curves, depicting a declining rate of increase in dry weight with increasing rate of P, before reaching a plateau, gave consistently good fits to the mean estimated yields of white clover (Table 3.9). Because there was no evidence from the data to support a decline in white clover yields at high rates of P, the exponential curves, and in one case a straight line, were favoured over the quadratics and were therefore plotted in Fig 3.2.

3.3.2.2 Responsiveness of gorse and white clover to increasing rates of applied P and their capacity to acquire P from unfertilized soil

The responsiveness of gorse to applied P is compared with that of white clover in Table 3.10. Responsiveness is defined in section 3.2.14.

Table 3.10 Responsiveness of gorse and white clover to applied P

Time period	Responsiveness to applied P (($Y_m - Y_0$)/ Y_m Section 3.2.14)		Significance of between species differences
	Gorse	White Clover	
F cutting treatment			
Spring 1989 s.e.	0.85 0.059	0.74 0.070	ns
Autumn 1990 s.e.	0.74 0.089	0.86 0.031	ns
Spring 1990 s.e.	0.36 0.063	0.85 0.021	***
Autumn 1991 s.e.	0.54 0.066	0.87† 0.080	**
I cutting treatment			
1990/91 (new shoots) s.e.	0.41 0.047		
1989/91 (total) s.e.	0.53 0.050		

Degrees of freedom = 34

See Table 3.7 for description of significance levels.

† In autumn 1991 white clover dry weight increased linearly with increasing rate of P over the range of rates applied (Fig. 3.2 (d)). Therefore it was not possible to estimate Y_m from the fitted curve. Responsiveness was estimated using dry matter yields from the 8 pairs of P4 and P0 plots (Section 3.3.2.2). Degrees of freedom = 7.

Relatively low responsiveness indicates that plants have reached a relatively high proportion of their yield potential without applied P. Low responsiveness could result from good

growth without applied P or poor growth with applied P or a combination of both. Conversely, high responsiveness could result from poor growth without applied P, good growth with applied P or a combination of both. Responsiveness values were estimated from fitted P response curves (Section 3.2.14). For white clover in autumn 1991 a straight line best fitted the data and this did not provide an estimate of Y_m (Fig 3.2(d)). Therefore responsiveness was estimated using data from the 8 individual pairs of P0 and P4 plots i.e. responsiveness = $(Y_{P4} - Y_{P0}) / Y_{P4}$. This estimate of responsiveness would probably have been less than the true value. Gorse and white clover were similarly responsive to applied P in the first year of the trial, but gorse was significantly less responsive in the second year (Table 3.10) i.e. in the second year gorse showed a greater capacity than white clover to reach its growth potential with no applied P.

P acquisition capacity was estimated (Section 3.2.14) by extrapolating the P response curves (Figs 3.1 and 3.2) back to zero growth. The intercept with the x-axis was then an estimate of the P-supplying power of the soil for the particular species. In doing this extrapolation, an assumption is made that the growth curve is valid outside the range of the points to which it is fitted. Given the very good fits of the growth curves to the P treatment means for all except the final harvest of the frequently cut (F) gorse, this assumption seems to be reasonable. However, the results should be treated with caution. The estimated P acquisition capacities of gorse and white clover are presented in Table 3.11. Except for spring 1989 gorse appears to have the greater capacity to acquire P from the unfertilized soil. The apparently greater ability of gorse to take up soil P is consistent with the smaller response of gorse to applied P compared with white clover (Table 3.10).

Table 3.11 Relative abilities of gorse and white clover to acquire P from unfertilized soil

Time period	Capacity to acquire P (kg P ha ⁻¹ equivalent)		Significance of between species differences
	Gorse	White clover	
Frequent cutting treatment			
Spring 1989	7.0	7.0	ns
s.e.	3.3	3.3	
Autumn 1990	16	4.1	ns
s.e.	8	1.3	
Spring 1990	74	20	**
s.e.	16	5	
Autumn 1991	47	14	*
s.e.	12	9	
Cutting treatment			
1990/91 (new shoots)	69		
s.e.	12		
1989/91 (total)	49		
s.e.	9		

Degrees of freedom = 34 for all estimates, except that for white clover in autumn 1991 where a straight line was fitted and degrees of freedom = 35.

3.3.2.3 Annual and total gorse dry weights - F plots

In order to make comparisons with data from the uncut (I) plots, analyses of variance were done on annual dry matter production and the total for both growth seasons.

In 1989/90, 1990/91 and 1989/91 there were significant ($p < 0.001$) effects of rate of P on gorse dry weight, but the effects of N treatment and the P \times N interactions were nonsignificant for all of those growth periods.

As for the individual harvest times, quadratic curves, with maxima within the range of P rates applied, gave good fits to the P response data from each growth season and to the total over both seasons (Fig. 3.3).

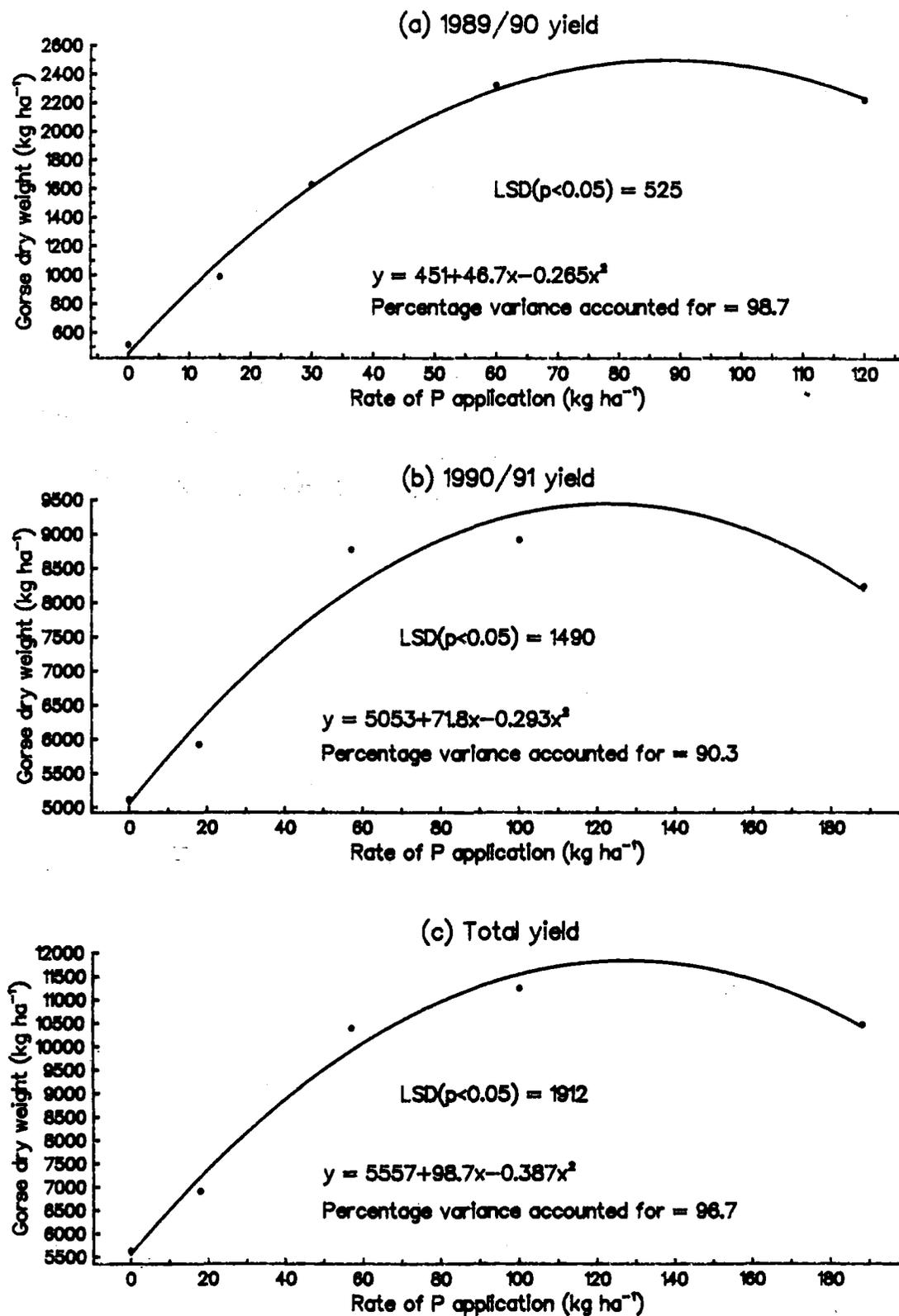


Fig. 3.3 Effect of rate of P application on annual and total dry matter yield of gorse – Springston trial, frequently cut (F) treatment.

3.3.2.4 Gorse dry weight - I plots

There were significant ($p < 0.001$) rate of P effects on new (1990/91) shoot, old (1989/90) wood and on total (1989/91) dry weight of the uncut plots, but no significant effect of N treatment or P \times N interaction on any of the above.

New shoot, old wood and total dry matter yield all increased progressively with increasing rate of P up to the P3 rate of applied P (100 kg P ha⁻¹ over 2 years, Fig. 3.4). The declines in yield at the P4 rate of applied P were not statistically significant (Fig. 3.4). However, quadratic curves with maxima within the range of P rates applied gave better fits to the mean dry weight data than exponential curves (Fig. 3.4; Table 3.12), suggesting that gorse yields were tending to decline at the P4 rate of P.

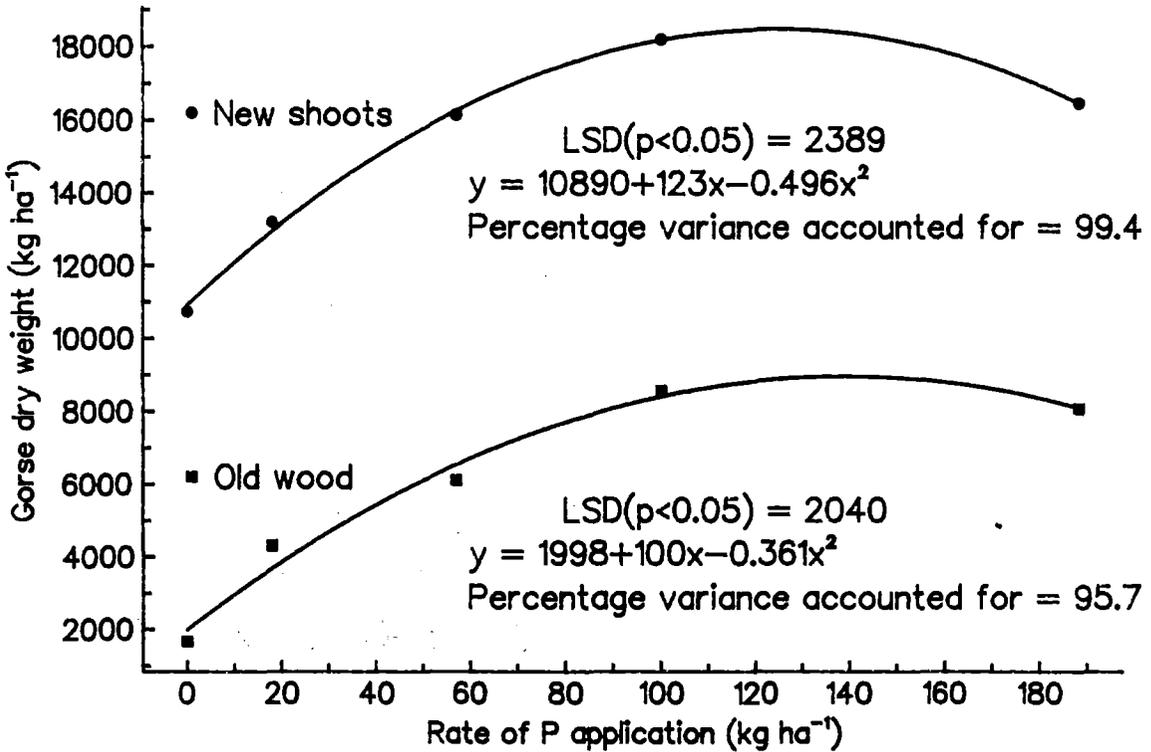
Table 3.12 Goodness of fit of different curve types when fitted to mean gorse dry weight data - I plots

Tissue age	Percentage variance accounted for	
	Quadratic ($y=a+bx+cx^2$)	Exponential ($y=a+br^x$)
1990/91 shoots	99.4	87.5
1989/90 wood	95.7	93.5
Total (1989/91)	98.0	92.1

In terms of responsiveness to applied P (defined in Section 3.2.14), values for the new shoots and total dry weight were similar to those from the second year frequently cut plants and less than those of white clover (Table 3.10).

Gorse in the infrequently cut (I) treatment had a capacity to acquire P from unfertilised soil which was similar to that for gorse from the frequently cut (F) treatment in the second year of the trial, but greater than that of white clover (Table 3.11).

(a) New shoots and old wood



(b) Total dry matter yield

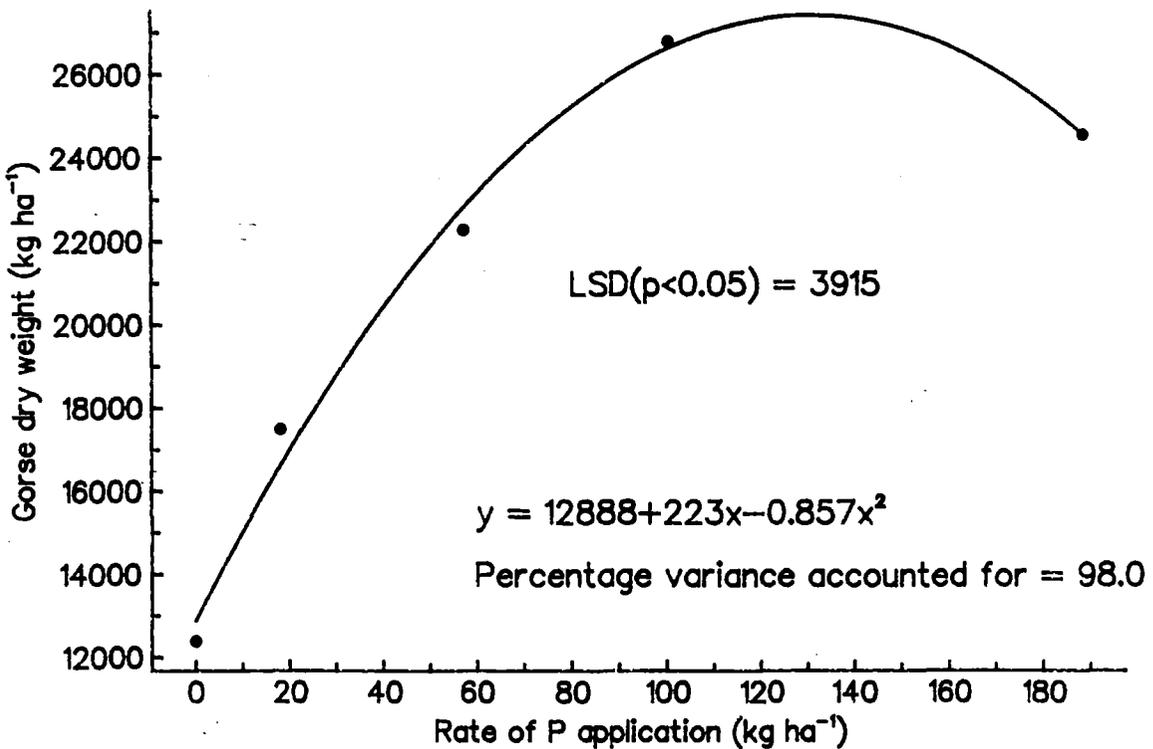


Fig. 3.4 Effect of rate of P application on dry matter yield of gorse – Springston trial, infrequent (I) cutting treatment.

3.3.2.5 Gorse dry weight - comparison between F and I plots

F and I plots were statistically analysed together for both the 1990/91 growth season yield and for total yield over both growth seasons (1989/91). A summary of the analysis of variance table is presented in Table 3.13, along with rate of N and cutting treatment means. Rate of P treatment means were omitted because rate of P effects have been discussed for the separate cutting treatments in Sections 3.3.2.3 and 3.3.2.4.

In the 1990/91 yield data, some of the dry matter accumulation in the I plots would have been secondary thickening of the old (1989/90) wood (previous seasons stems). Therefore the dry matter production from the I plots for 1990/91, which was estimated by the weight of new shoots only, will almost certainly be an underestimate. Total production of dry matter from the I plots may also be underestimated because of shedding of foliage from the 1989/90 stems.

Even though 1990/91 dry weights in the I plots were probably underestimated, cutting treatment had a significant effect on dry weight (Table 3.13), with mean dry matter accumulation being much greater for the I plots (14 967 kg ha⁻¹) than for the F plots (7398 kg ha⁻¹).

A similar trend was observed for total dry weight over both growth seasons (Table 3.13) with mean total dry matter from the I plots (20 712 kg ha⁻¹) again being much greater than that from the F plots (8936 kg ha⁻¹) (Table 3.13).

For 1990/91 dry weight, the effect of N treatment was statistically significant at the 5% level (Table 3.13), as was the case for the F plots at the final harvest (15-17 April 1991, Table 3.7). Mean dry weight from the nil N plots (11 552 kg ha⁻¹) was greater than from the high N plots (10 812 kg ha⁻¹).

There were significant effects of rate of P on gorse dry weight for both the 1990/91 and 1989/91 growth periods (Table 3.13) with responses following patterns similar to those discussed previously for the F and I treatments separately (Sections 3.3.2.3 and 3.3.2.4, Figs 3.3 and 3.4).

Table 3.13 Effects of rate of P, rate of N and cutting treatment on gorse dry weight (F and I plots analysed together)

(a) Summary of analysis of variance table (log-transformed data, Section 3.2.14)

Treatment or interaction (source of variation)	Significance of effect Growth period	
	1990/91	1989/91
P	***	***
N	*	ns
Cut	***	***
P × N	ns	ns
P × cut	ns	ns
N × cut	ns	ns
P × N × cut	ns	ns

See Table 3.7 for description of significance levels

(b) Rate of N and cutting treatment means, untransformed data (kg ha⁻¹)

Treatment	Treatment mean Growth period	
	1990/91	1989/91
Nil N	11552	15323
High N	10812	14325
F	7398	8936
I	14967	20712

3.3.3 P and N nutrition of gorse and white clover

3.3.3.1 P and N concentration in harvested gorse shoots - F plots

3.3.3.1.1 P concentration

At the first three harvest times (Jan 1990, May 1990 and Dec 1990) P concentration increased significantly with increasing rate of P up to the P4 rate (Table 3.14, Fig 3.5).

Table 3.14 Effects of P and N rate on P concentration of harvested gorse shoots

(a) Summary of analysis of variance tables

Source of variation (Treatment or interaction)	Level of significance			
	Harvest date			
	Jan 1990	May 1990	Dec 1990	April 1991
P	***	***	***	**
N	*	ns	*	*
P × N	ns	ns	ns	ns

See Table 3.7 for description of significance levels

(b) P concentration (%) - date × N treatment means

Date	Rate of N		L.S.D. (p<0.05)
	nil N	high N	
Jan 1990	0.14	0.13	0.012
May 1990	0.14	0.14	0.006
Dec 1990	0.20	0.19	0.012
April 1991	0.09	0.10	0.010

At these three harvest times, the changes in mean P concentration with increasing rate of P application were well defined by exponential curves showing diminishing rates of increase in P concentration with increase in rate of applied P (Fig. 3.5). However at the April 1991 harvest a straight line gave the best fit (Fig 3.5(d)).

There was a significant rate of N effect at three of the four harvest times, but never a significant P \times N interaction (Table 3.14). At the Jan 1990 and Dec 1990 harvests, P concentration was greater in the nil N than the high N treatment, while at the April 1991 harvest P concentration was greater in the high N treatment. There was no N treatment effect on P concentration at the May 1990 harvest.

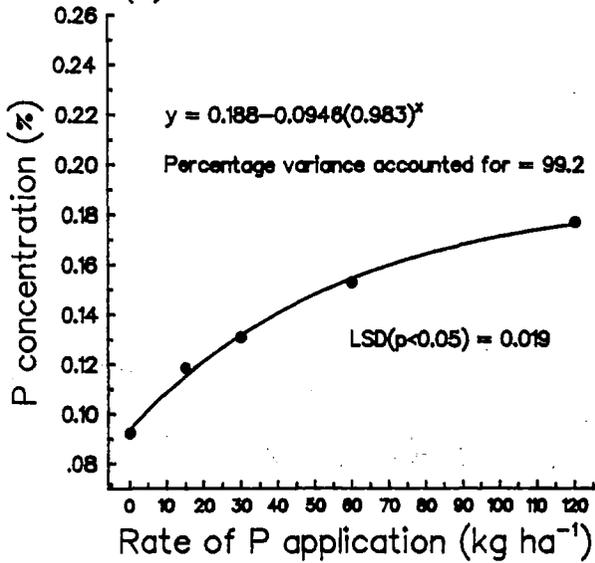
3.3.3.1.2 N concentration

Shoot N concentration was significantly affected by rate of P in all but the final harvest (Table 3.15(a)). There were significant rate of N effects at all except the first harvest, and a significant N \times P interaction at the May 1990 harvest. In May 1990 fertilizer N did not increase plant N concentration unless fertilizer P was also applied (Table 3.15 (c)). The most important features of the data appear to be the main effects of P and N: the increasing N concentrations with increasing rate of P application and the greater N concentration at the high rate of N compared with the low rate (Table 3.15).

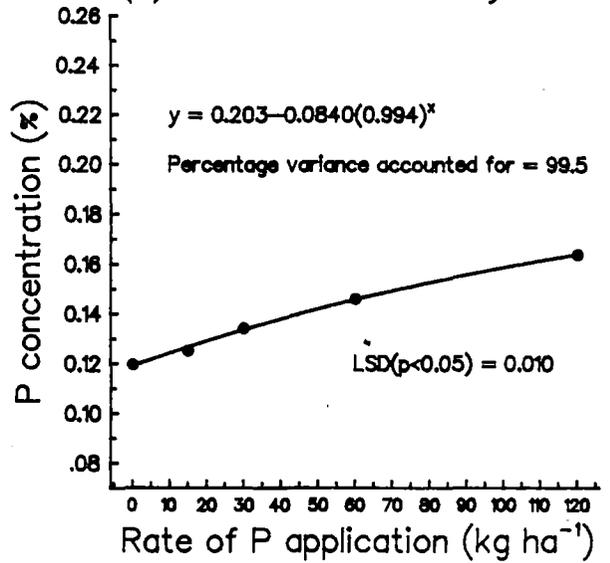
At the Jan and May 1990 harvests, increases in N concentration with increasing rates of P application were well defined by the exponential curves fitted (Fig. 3.6).

At the third harvest, N concentration followed a different pattern with increasing rate of P; increasing up to the P2 rate, then declining to the P4 rate (Fig 3.6(c)). Neither the quadratic or exponential curves were a particularly good fit to the P treatment means, so a fitted curve was not plotted. At the final harvest the effect of rate of P on N concentration was nonsignificant (Table 3.15(a)). At the May and Dec 1990 and the April 1991 harvests N application resulted in increased plant N concentrations (Table 3.15(b)).

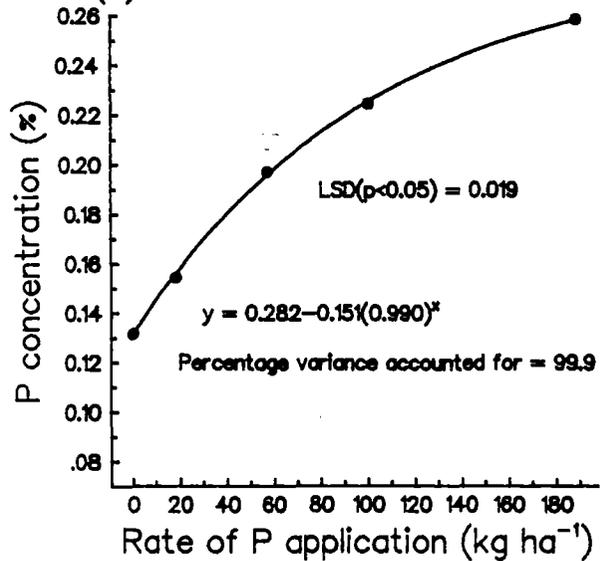
(a) Harvest date: 31 Jan 1990



(b) Harvest date: 31 May 1990



(c) Harvest date: 12–13 Dec 1990



(d) Harvest date: 15–17 April 1991

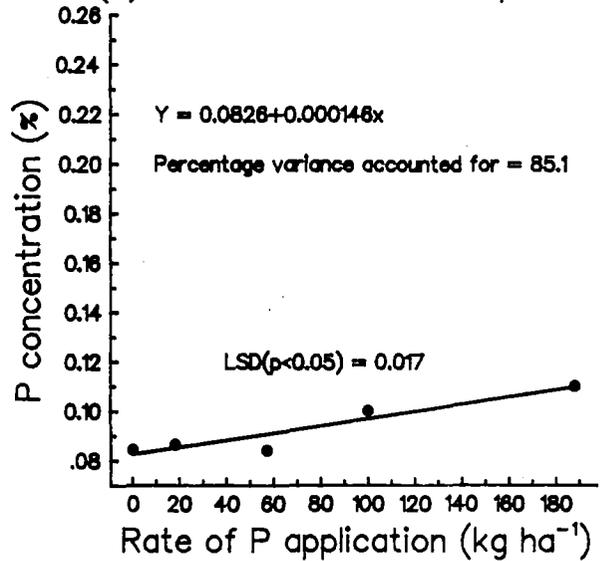


Fig. 3.5 Effect of rate of P application on P concentration in harvested gorse shoots – Springston trial.

Table 3.15 Effects of P and N rate on N concentration of harvested gorse shoots - F plots

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance			
	Harvest date			
	Jan 1990	May 1990	Dec 1990	April 1991
P	***	***	***	ns (p=0.056)
N	ns	**	*	**
P × N	ns	*	ns	ns

See Table 3.7 for description of significance levels

(b) N concentration (%) - date × N treatment means

Date	Rate of N		L.S.D. (p<0.05)
	nil N	high N	
Jan 1990	2.01	2.04	0.06
May 1990	2.07	2.16	0.05
Dec 1990	2.63	2.74	0.10
April 1991	1.83	1.90	0.04

(c) N concentration - P × N treatment means, May 1990

Rate of N	Rate of P					L.S.D. (p<0.05)
	P0	P1	P2	P3	P4	
nil N	2.02	1.97	2.00	2.19	2.19	0.12
high N	1.99	2.13	2.23	2.20	2.25	

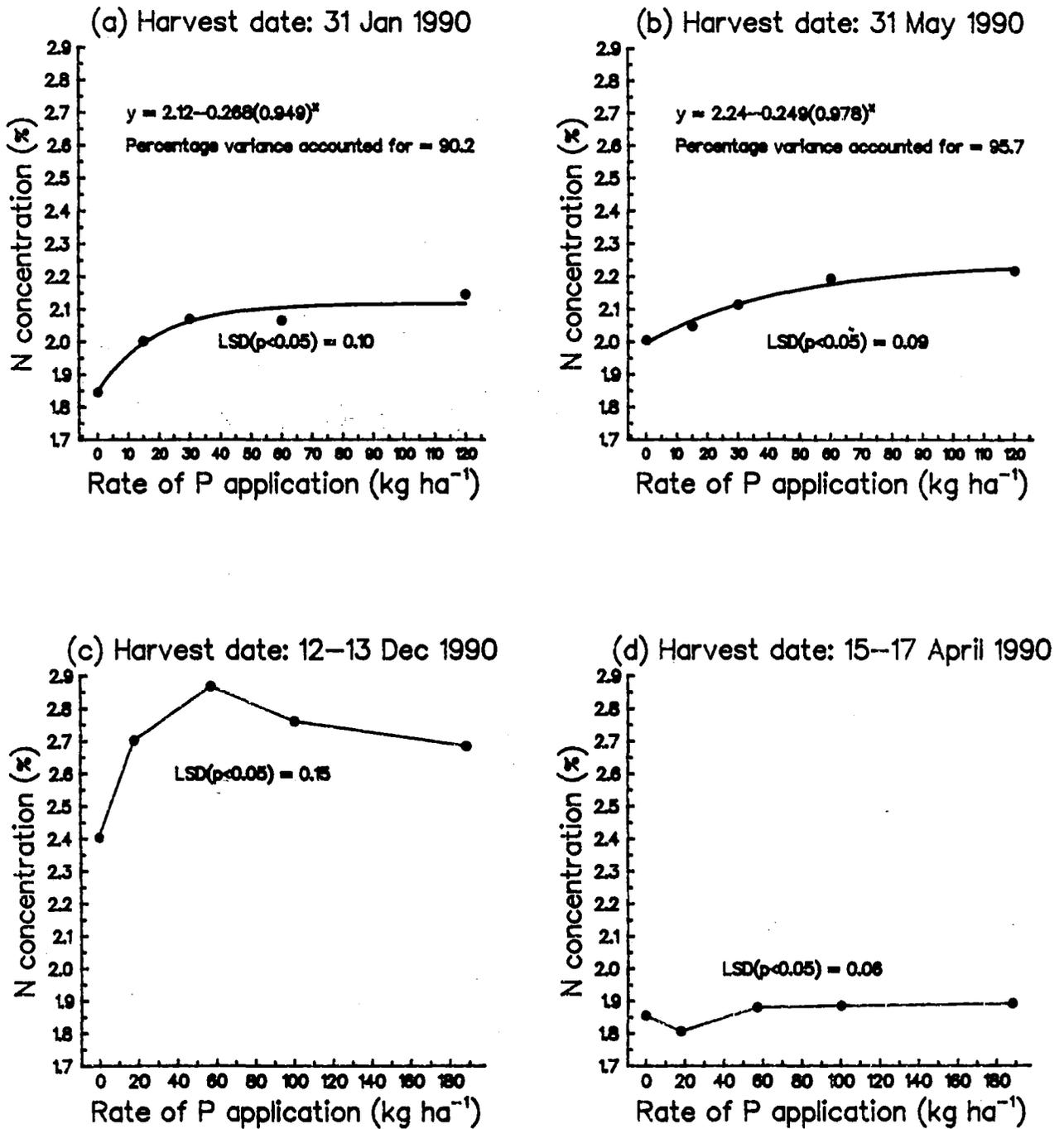


Fig. 3.6 Effect of rate of P application on N concentration in harvested gorse shoots – Springston trial.

3.3.3.2 P and N concentration in gorse shoots from I plots - Dec 1990 and April 1991

3.3.3.2.1 P concentration

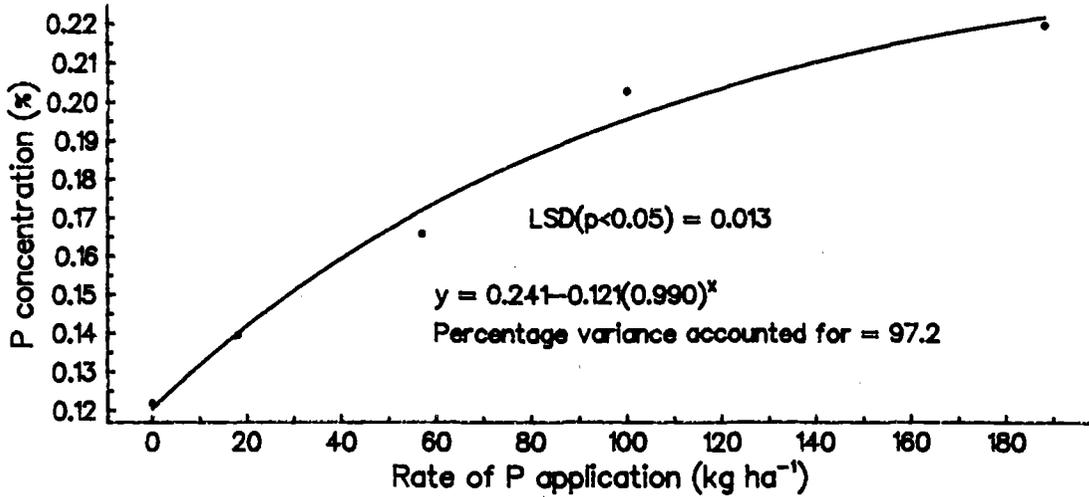
In Dec 1990, shoot P concentration increased significantly with increasing rate of P application, up to the highest rate of P (Fig 3.7(a), Table 3.16) in much the same way as for the F plots harvested at this time (Fig 3.5(c)). An exponential curve fitted the data well. At the final harvest (April 1991), P concentration in new shoots was greater at the P4 rate of P than at the lower rates. The increase in P concentration did not follow the pattern of the previous spring, or that of the F plots at the first three harvests (Figs 3.7(b) and 3.5). The effect of rate of P on P concentration in the old wood appeared to follow a similar pattern to that for the new shoots but was barely significant (Fig 3.7(b) and (c), Table 3.16). There were no significant effects of rate of N or N \times P interactions (Table 3.16).

Table 3.16 Effects of P and N rate on P concentration of harvested gorse shoots, I plots - summary of analysis of variance tables

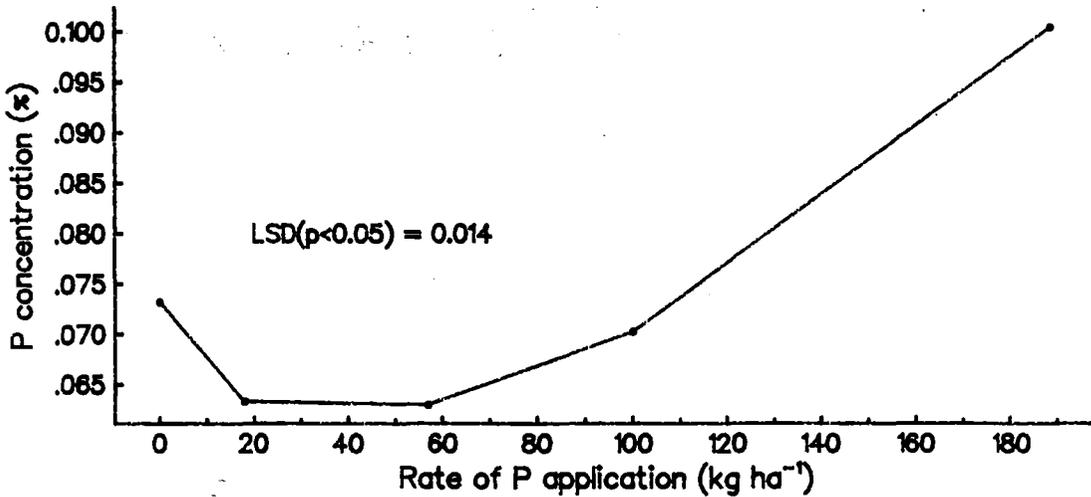
Source of variation (treatment or interaction)	Level of significance Tissue type		
	Spring shoots (9 Dec 1990)	New shoots (15-17 April 1991)	Old wood (15-17 April 1991)
P	***	***	ns (p=0.052)
N	ns	ns	ns
P \times N	ns	ns	ns

See Table 3.7 for description of significance levels.

(a) New shoots — 9 Dec 1990



(b) New shoots — 15–17 April 1991



(c) Old wood — 15–17 April 1991

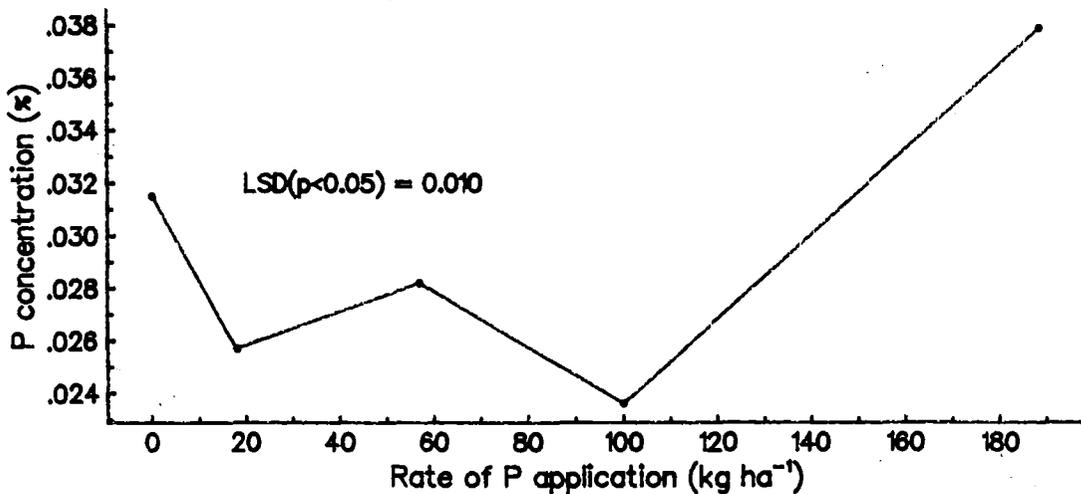


Fig. 3.7 Effect of rate of P application on P concentration in gorse shoots — Springston trial, infrequently cut (I) treatment.

3.3.3.2.2 N concentration

There was no significant $P \times N$ interaction and there were no significant effects of P or N on N concentration in shoots from the I plots at 9 Dec 1990 (Table 3.17(a)). In April 1991 there were significant effects of both P and N rates on N concentration, and a significant $P \times N$ interaction (Table 3.17(a)). N concentration in new shoots appeared to increase slightly with N application when P was also applied (Fig. 3.8(b)), resulting in a greater mean N concentration with applied N (Table 3.17(b)).

Table 3.17 Effects of P and N rate on N concentration of harvested gorse shoots - I plots

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance Tissue type		
	New shoots Dec 1990	New shoots April 1991	Old wood April 1991
P	ns	**	*
N	ns	**	ns
$P \times N$	ns	*	ns

See Table 3.7 for description of significance levels.

(b) N concentration (%) - N treatment means

Tissue Type	Rate of N		L.S.D. ($p < 0.05$)
	nil N	high N	
New shoots Dec 1990	2.65	2.74	0.12
New shoots April 1991	1.68	1.73	0.04
Old wood April 1991	0.97	0.97	0.04

N concentration in old wood tended to be greater at the low rates of P and decline at the intermediate rates before increasing slightly, but nonsignificantly, at the P4 rate (Fig 3.8(b)).

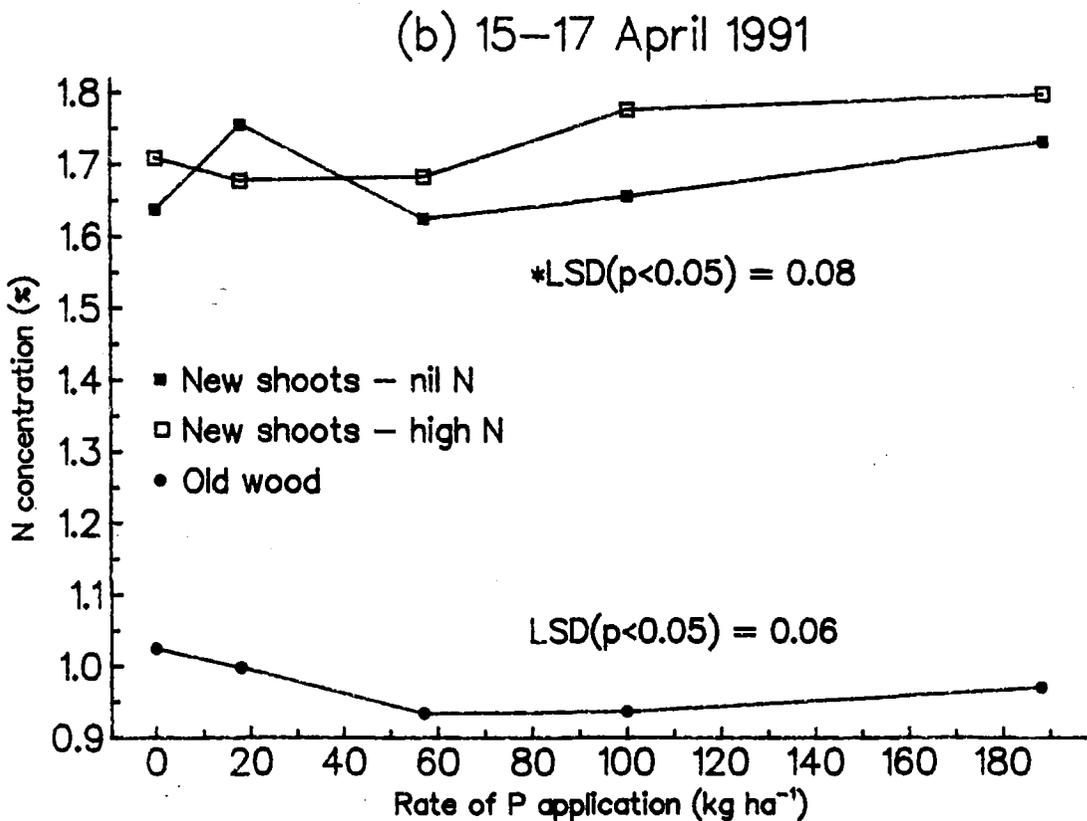
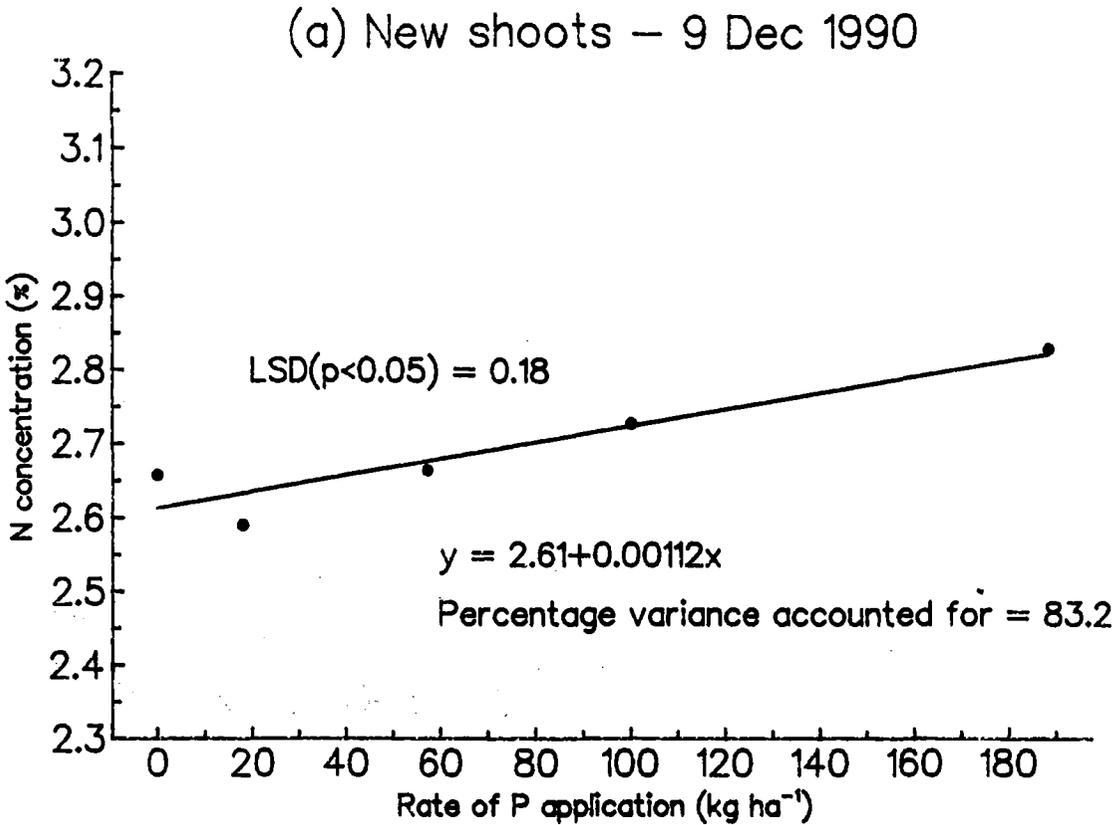


Fig. 3.8 Effect of rates of P and N application on N concentration in gorse shoots – Springston trial, infrequently cut (I) treatment.
* For rate of P x rate of N comparisons.

3.3.3.3 P and N concentration in gorse shoots - comparison between F and I cutting treatments

New shoots from the F and I cutting treatments were sampled at the time of the spring 1990 harvest of the F treatment (12-13 Dec 1990) and at the time of the final harvest (15-17 April 1991). Because of their common sampling times during the second year of the trial, data from the F and I treatments were analysed together to determine the effect of cutting treatments on P and N concentration. Because the effects of P and N and the P \times N interaction have been discussed previously (Sections 3.3.3.1 and 3.3.3.2) for the individual cutting treatments, these were not presented here (although they were included in the analysis) (Table 3.18). At both dates, cutting treatment had a significant effect on P concentration, with shoot %P being greater in the F cutting treatment than in shoots from the I cutting treatment (Table 3.18(a) and (b)).

Cutting treatment had a significant effect on shoot N concentration at the April 1991 sampling, with shoot %N being greater in the F than in the I treatment (Table 3.18(a) and (b)). The effect of cutting treatment on shoot N concentration at the Dec 1990 sampling date was non-significant (Table 3.18(a)).

Table 3.18 Effect of cutting treatment on P and N concentrations

(a) Effects of cutting treatments on P and N concentration - summary of analysis of variance table

Source of variation (treatment or interaction)	Level of significance Date			
	Dec 1990		April 1991	
	%P	%N	%P	%N
Cut	***	ns	***	***
P \times cut	ns	***	ns	*
N \times cut	ns	ns	ns	ns
P \times N \times cut	ns	ns	ns	ns

See Table 3.7 for description of significance levels.

Table 3.18 continued

(b) Effects of cutting treatment on P and N concentrations

Cutting treatment	Cutting treatment means			
	Date			
	Dec 1990		April 1991	
	%P	%N	%P	%N
F	0.19	2.68	0.09	1.86
I	0.17	2.69	0.07	1.70
L.S.D.(p<0.05)	0.008	0.07	0.006	0.03

(c) Effect of cutting treatment and rate of P on N concentration.

Rate of P application	N concentration (%)			
	Dec 1990		April 1991	
	F	I	F	I
P0	2.40	2.66	1.85	1.67
P1	2.70	2.59	1.81	1.72
P2	2.87	2.66	1.88	1.65
P3	2.76	2.73	1.89	1.72
P4	2.68	2.83	1.89	1.77
L.S.D. (p<0.05)	0.17		0.06	

There were significant rate of P \times cutting treatment (P \times cut) interactions on N concentration at both sampling times (Table 3.18(a)) indicating differing patterns of change in N concentration with increase in rate of applied P (Table 3.18 (c)).

3.3.3.4 Shoot P and N concentration - comparison between gorse and white clover

Comparisons of P and N concentrations between species were done using data from the F plots only in order to match up with the gorse yield data from these plots, and because white clover growth in the I plots was restricted by shading from gorse in the second growth season.

3.3.3.4.1 January 1990

Shoot P and N concentration of gorse and white clover (in the F plots) both increased significantly with increase in rate of applied P, and the increases were well defined by exponential curves showing diminishing rates of increase of P and N concentration with increase in P application rate (Table 3.19, Fig 3.9). N application had no effect on shoot P or N concentration of either species (Table 3.19).

Table 3.19 Effects of P and N treatments on shoot P and N concentration of gorse and white clover, Springston Trial January 1990 - summary of analysis of variance table

Source of variation (treatment or interaction)	Level of significance	
	%P	%N
P	***	***
N	ns	ns
Species	***	***
Species × P	***	***

See Table 3.7 for description of significance levels.

Note: Interactions not significant at the 5% level were omitted.

Shoot P and N concentrations in gorse were less than those of white clover over the entire range of P rates applied (Fig 3.9).

The increase in P and N concentrations with increase in rate of applied P tended to be proportionately less for gorse than white clover (Fig 3.9) leading to significant species × P interactions (Table 3.19).

3.3.3.4.2 December 1990

Shoot P concentration of both gorse and white clover increased significantly with increase in rate of P and the rates of response diminished with increasing rate of applied P as shown by the fitted curves (Table 3.20, Fig 3.10).

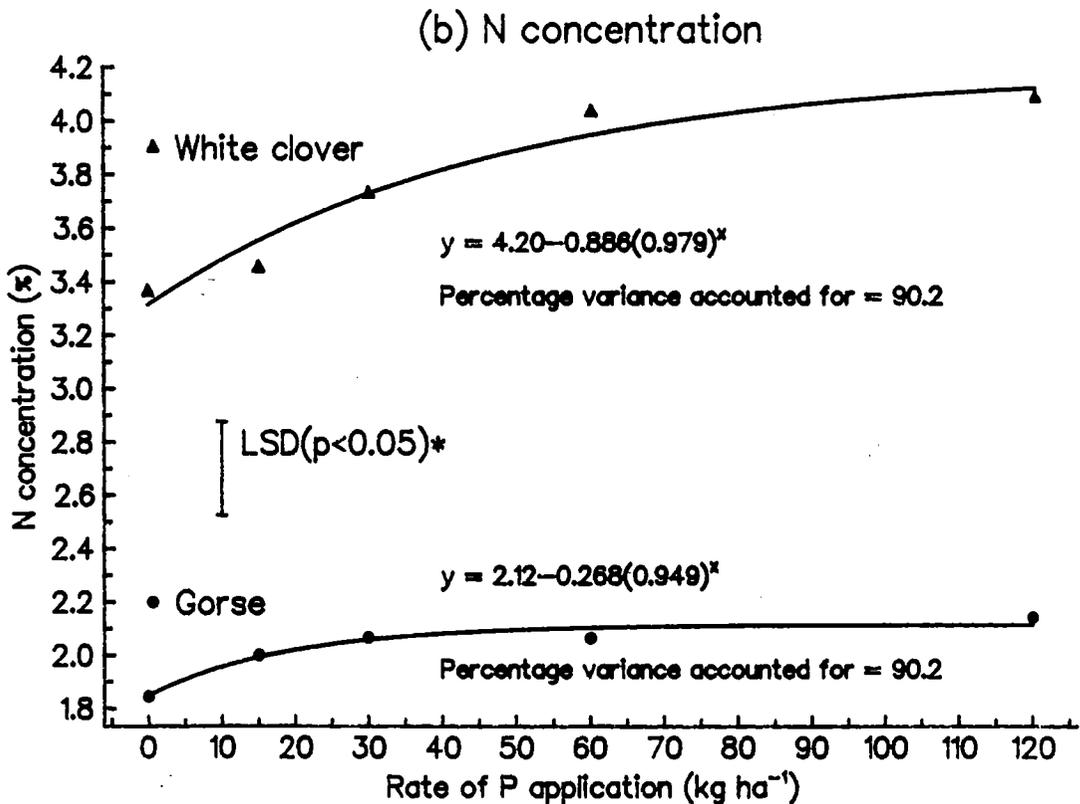
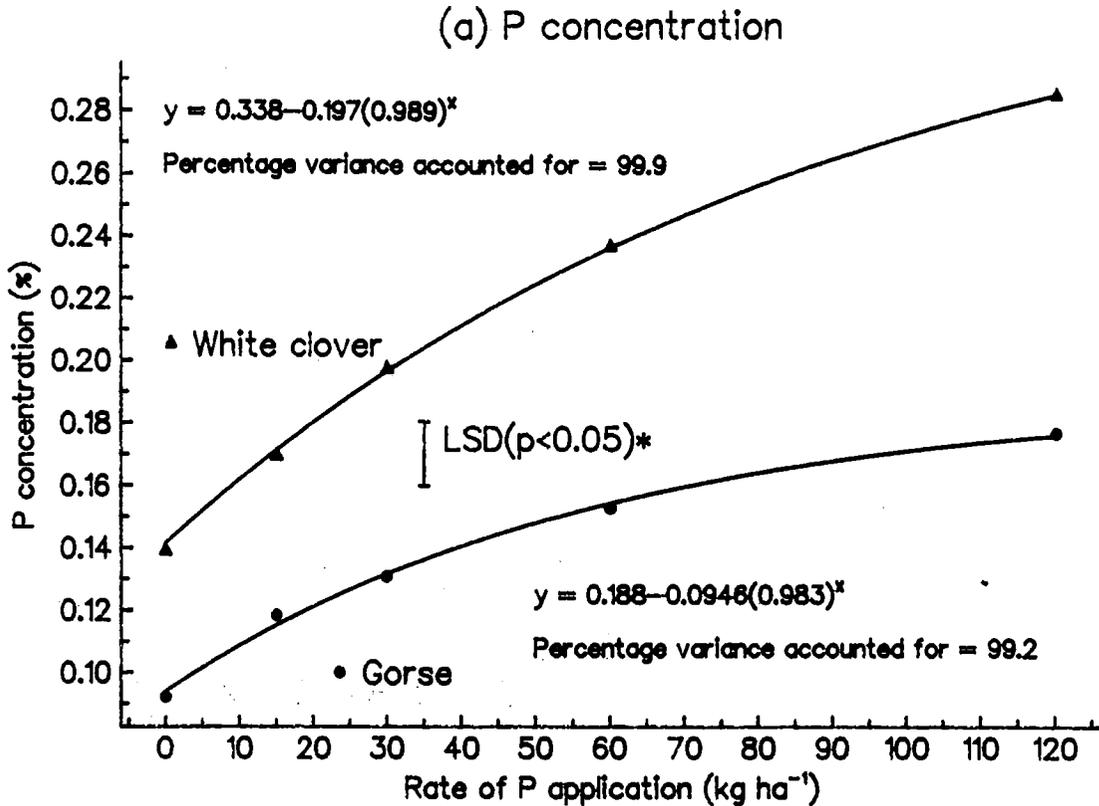


Fig. 3.9 Effect of rate of P application on P and N concentration in gorse and white clover – Springston trial January 1990.
* For species \times rate of P comparisons.

Table 3.20 Effects of P and N treatments on shoot P and N concentration of gorse and white clover, Springston trial December 1990.

(a) Summary of analysis of variance table

Source of variation (treatment or interaction)	Level of significance	
	%P	%N
P	***	***
N	ns	***
Species	***	***
Species × P	**	ns
Species × N	*	*

See Table 3.7 for description of significance levels.

Note: Interactions not significant at the 5% level were omitted.

(b) P concentration (%) - species × rate of N means

Species	Rate of N application		LSD (p<0.05)
	Nil	High	
Gorse	0.20	0.19	0.015
White clover	0.23	0.24	

(c) N concentration (%) - species × rate of N means

Species	Rate of N application		LSD (p<0.05)
	Nil	High	
Gorse	2.63	2.74	0.16
White clover	3.53	3.91	

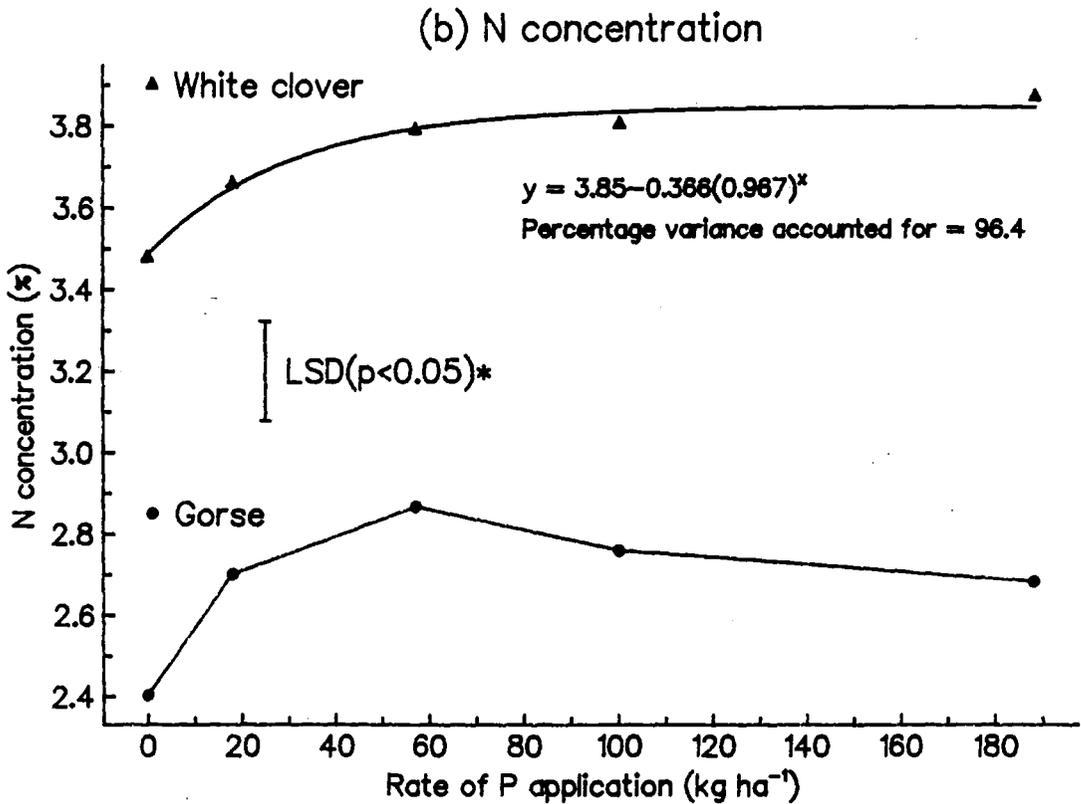
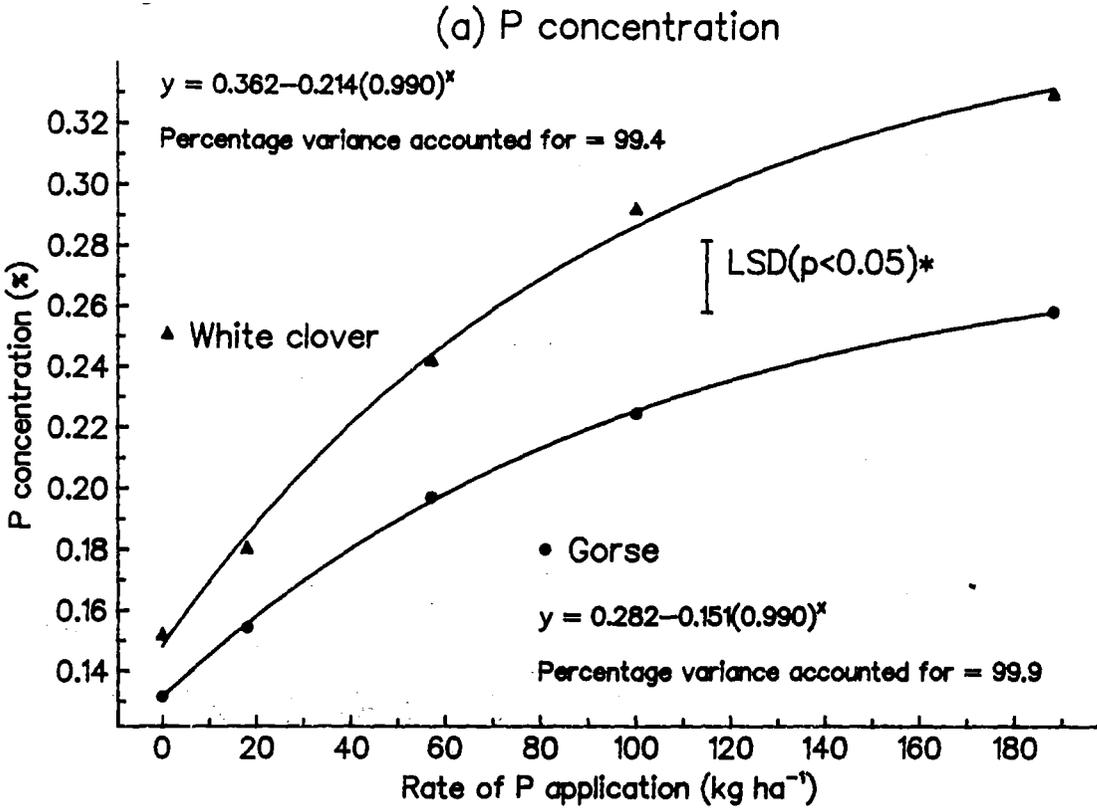


Fig. 3.10 Effect of rate of P application on P and N concentration in gorse and white clover – Springston trial December 1990.
* For species x rate of P comparisons.

Shoot P concentration was significantly less in gorse than white clover at all but the nil rate of applied P (Fig 3.10).

The increase in shoot P concentration with increase in rate of applied P appeared to be proportionately less for gorse than white clover (Fig. 3.10(a)) leading to the significant species \times P interaction.

The species \times rate of N means (Table 3.20(b)) show a slight decrease in gorse shoot P concentration and a slight increase in white clover shoot P concentration with N application (non-significant in both cases).

Shoot N concentration increased significantly with increase in rate of P application for both gorse and white clover (Table 3.20(a), Fig. 3.10(b)).

N concentration in gorse shoots was less than that in white clover throughout the range of P rates applied (Fig. 3.10(b)).

N application resulted in a significant increase in shoot N concentration for white clover but not for gorse (Table 3.20 (c)).

3.3.3.5 Critical P and N concentrations of gorse and white clover

Critical shoot P concentrations are defined here as those concentrations associated with 90% of maximum yield. The N concentrations associated with 90% maximum yield were also calculated but were not true critical values according to the concept developed by Macy (1936), Andrew (1960) and Andrew and Robins (1969a), because of the limited number of N application rates and because the plants were largely independent of soil N supply because of their ability to fix atmospheric N_2 . The values for critical P concentration and N concentration associated with 90% maximum yield were derived from the fitted dry matter response curves presented in Figs 3.1, 3.2 and 3.4, the P concentration curves presented in Figs 3.5, 3.7, 3.9 and 3.10, and the N concentration curves presented in Figs 3.6, 3.8, 3.9 and 3.10.

Estimated critical shoot P concentrations for gorse appeared to be less than those for white

clover, as were the associated shoot N concentrations (Table 3.21). The autumn 1991 critical P values for gorse appeared to be less than those for previous sampling times for both the I and F cutting treatments (Table 3.21). For the I cutting treatment critical P values were calculated using 1990/91 shoot growth and concentrations of shoots sampled in either Dec 1990 or April 1991. It was thought that the value calculated using the Dec 1990 P concentrations was most valid, because this was a time of rapid growth whereas April 1991 was a time of very slow growth (Fig. 3.17).

Table 3.21 Critical P and associated N concentrations of gorse and white clover

Time period	P and N concentrations in gorse and white clover shoots at 90% maximum yield			
	%P		%N	
	gorse	clover	gorse	clover
F cutting treatment				
Spring 1989	0.15	0.24	2.10	4.00
Autumn 1990	0.15		2.18	
Spring 1990	0.19	0.35	-	3.85
Autumn 1991	0.09		-	
I cutting treatment				
Spring 1990	0.18			
Autumn 1991	0.06			

It should be noted that in spring 1990, white clover yield was still increasing with increasing rate of P, up to the P4 rate of P. Therefore the estimates of critical shoot P and associated shoot N concentration were obtained by extrapolation of the yield and P and N concentration curves. The estimates (0.35% P and 3.85%N, Table 3.21) were similar to the P and N concentrations at the P4 rate of applied P (0.33% P and 3.87% N), suggesting that they were reasonable.

3.3.3.6 P and N uptake of gorse

P and N uptakes of gorse were estimated by its shoot P and N contents.

3.3.3.6.1 P and N content of gorse - F cutting treatment

(a) P content

Rate of P application had a significant effect on total shoot P content of gorse at every harvest time on total P uptake for the two growth seasons, (1989/90 and 1990/91) both individually and for the whole period of the trial (1989/91) ($P < 0.001$). There were no significant rate of N effects or $P \times N$ interactions. At the Jan 1990, May 1990 and Dec 1990 harvest dates P content increased with increasing rate of P, but there were no significant changes in P content above the P3 rate of P (Table 3.22). At the final harvest (April 1991), there were no significant increases in P content beyond the P2 rate of applied P.

Table 3.22 Effects of rate of P application on P content of gorse - F cutting treatment

Date or growth period	Shoot P content (kg ha ⁻¹)					L.S.D. (p<0.05)
	Rate of P application					
	P0	P1	P2	P3	P4	
31 Jan 1990	0.27	0.77	1.49	2.62	2.61	0.62
31 May 1990	0.22	0.40	0.67	0.91	1.19	0.37
12-13 Dec 1990	3.10	4.51	6.88	8.35	7.86	1.36
15-17 Apr 1991	2.24	2.57	4.42	5.13	5.67	1.39

Quadratic curves fitted the P content data very well (better than the diminishing response exponential curves) and these are presented to show the responses to applied P for the individual growth seasons and for both seasons combined (Fig. 3.11).

(b) N content

Rates of P application had significant effects on total shoot N content at each harvest time for both growth seasons individually, and for both seasons combined ($P < 0.001$). There were no significant rate of N effects or $P \times N$ interactions. On 31 Jan 1990 shoot N content increased with increasing rate of P application up to the P3 rate of P (Table 3.23).

Table 3.23 Effects of rate of P on N content of gorse - F cutting treatment

Date or growth period	Shoot N content (kg ha ⁻¹) Rate of P application					L.S.D. ($p < 0.05$)
	P0	P1	P2	P3	P4	
31 Jan 1990	6.0	13.4	23.4	35.1	32.5	7.9
31 May 1990	3.8	6.5	10.6	13.8	15.7	5.0
12-13 Dec 1990	57.7	79.8	100.6	103.8	83.5	19.1
15-17 April 1991	50.8	53.8	98.8	96.6	96.5	17.9

At the following three harvests, however there was no significant increase in shoot N content beyond the P2 rate of P (Table 3.23).

Quadratic curves fitted the plant N content data well and these are presented in Fig 3.12 to indicate the nature of responses to increasing rates of P for the individual growth seasons and for both growth seasons combined.

3.3.3.6.2 P and N content of gorse - I cutting treatment

Rate of P application significantly affected the P content of new shoots, old wood and the total material harvested ($p < 0.001$). There were no significant rate of N effects or $P \times N$ interactions.

P content increased linearly with increasing rate of P up to the P4 rate (Fig 3.13), in contrast to the F cutting treatment, where P content tended to level off beyond the P3 rate of P (Table 3.22, Fig 3.11).

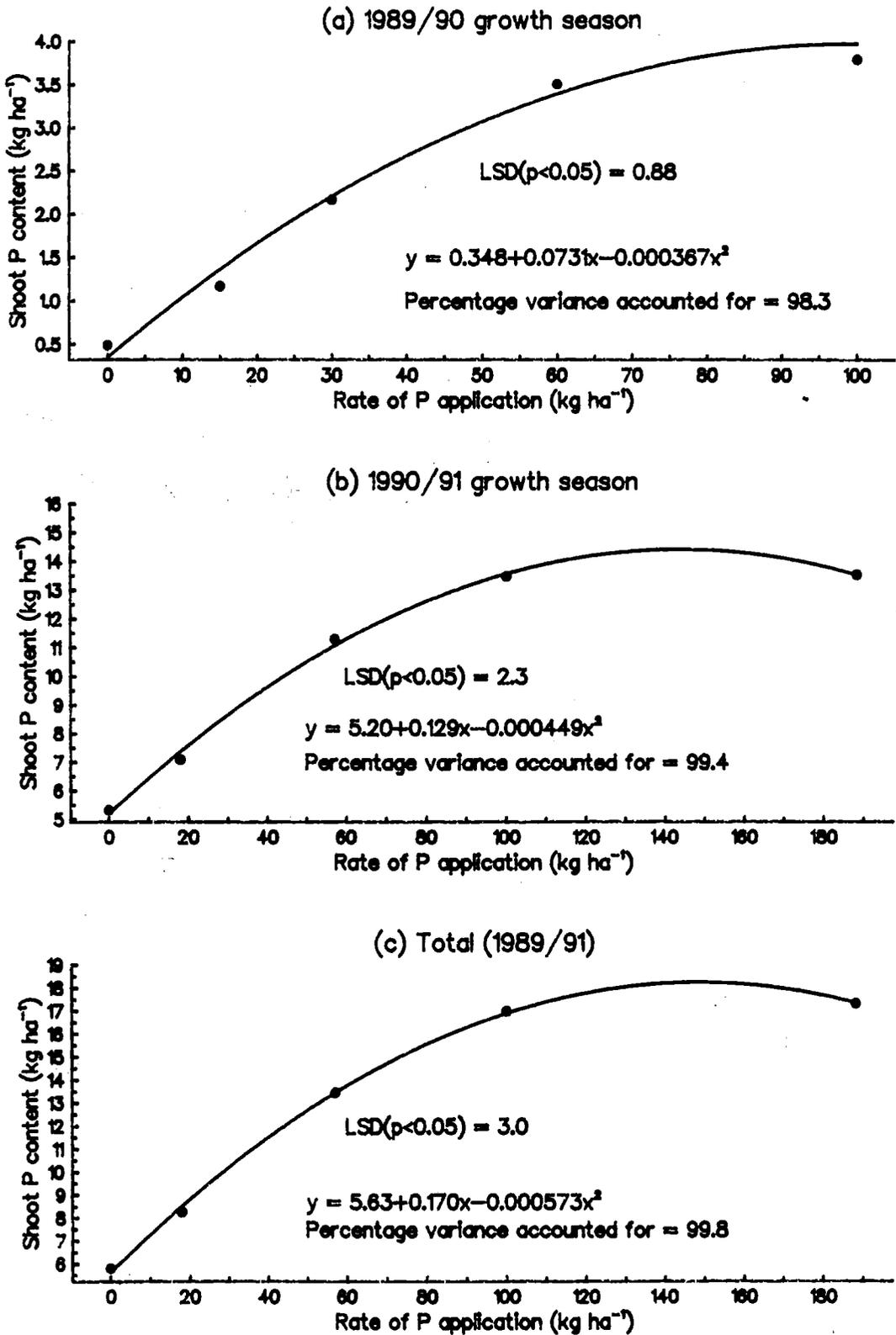


Fig. 3.11 Effect of rate of P application on shoot P content of gorse – Springston trial, frequently cut (F) treatment.

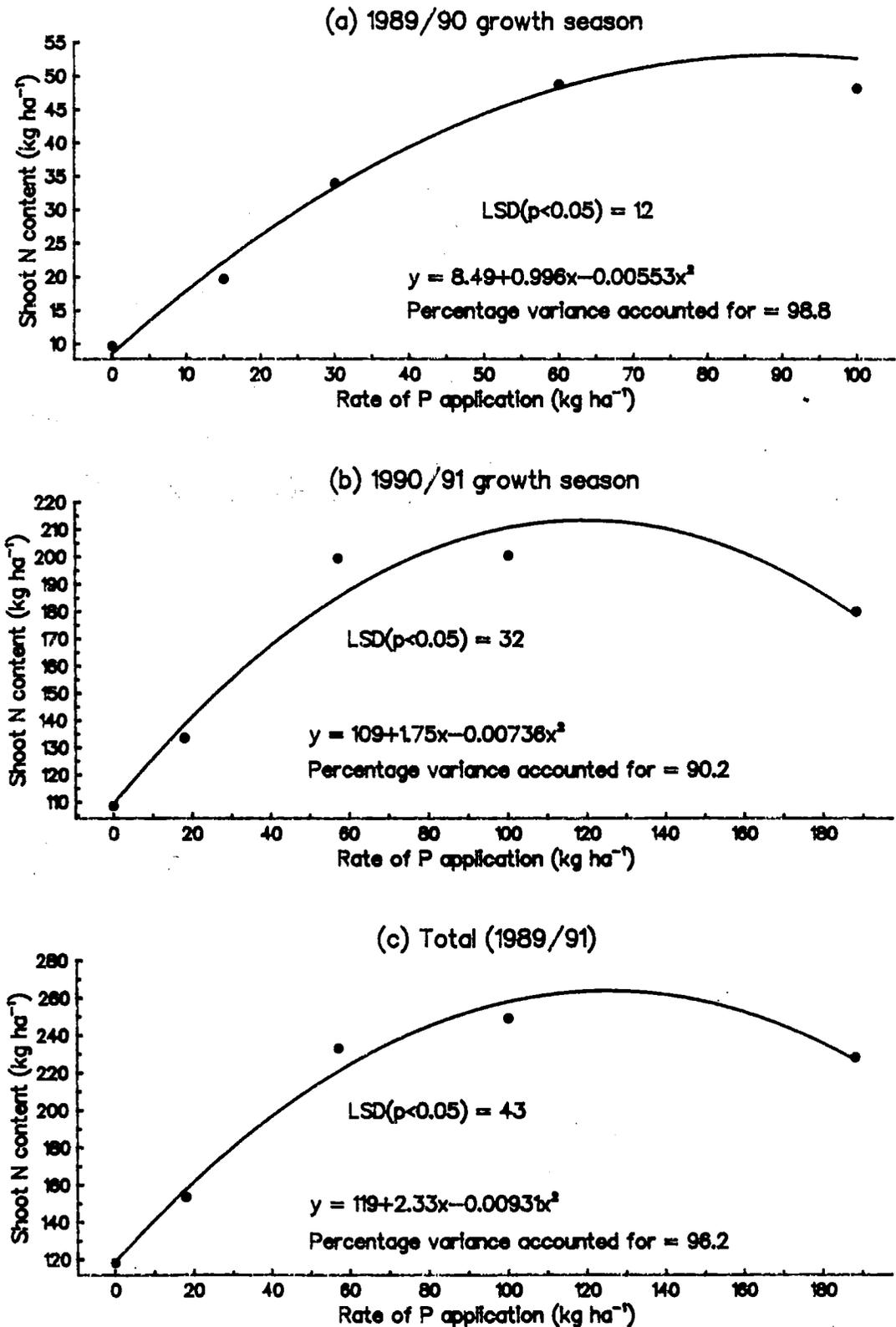


Fig. 3.12 Effect of rate of P application on shoot N content of gorse – Springston trial, frequently cut (F) treatment.

As for the F cutting treatment, rate of P significantly affected N content for new shoots, old wood and total shoot growth ($p < 0.001$) but there were no significant rate of N effects or $P \times N$ interactions. The response curves showing change in N content with increases in rate of applied P are shown in Fig. 3.14. N contents showed quadratic responses to increasing rates of P, reaching peaks at about the P3 rate of P before tending to decline slightly (Fig 3.14).

3.3.3.6.3 Effect of frequency of cutting on shoot P and N content

The purpose of this section is to illustrate the effect of cutting treatment on P and N uptake. Total P and N contents from the 1990/91 growth season and the totals from both growth seasons for the F (frequent) cutting treatment were statistically analysed with the equivalent data from the I (infrequent) cutting treatment.

As for the individual cutting treatments (Sections 3.3.3.6.1 and 3.3.3.6.2) rate of P had significant effects on both the P and N content of gorse shoots (Table 3.24). There was no significant effect of rate of N (Table 3.24) and no significant interactions.

Because data illustrating changes in P and N content with increasing rate of P application for the two cutting treatments have been presented separately in Sections 3.3.3.6.1 and 3.3.3.6.2, mean data for the cutting treatments will not be presented here.

The effect of cutting treatment on P content was nonsignificant and mean P contents were very similar for both treatments, especially for total P content over both growing seasons (12.38 and 12.81 kg ha⁻¹ for the F and I treatments respectively, Table 3.24). Hence, in terms of P uptake, the lesser dry weight produced in the F treatment compared with the I treatment (Table 3.13(b)), was almost exactly compensated for by greater P concentration in harvested material from the F treatment compared with that from the I treatment (Figs 3.5 and 3.7, Table 3.18(b)). Differences in total P content between cutting treatments for individual rates of P were nonsignificant. Note that P content for the F treatment was calculated using dry weights and P concentrations for individual harvests and for the I treatment using dry weight and P concentrations for the final (April 1991) harvest only.

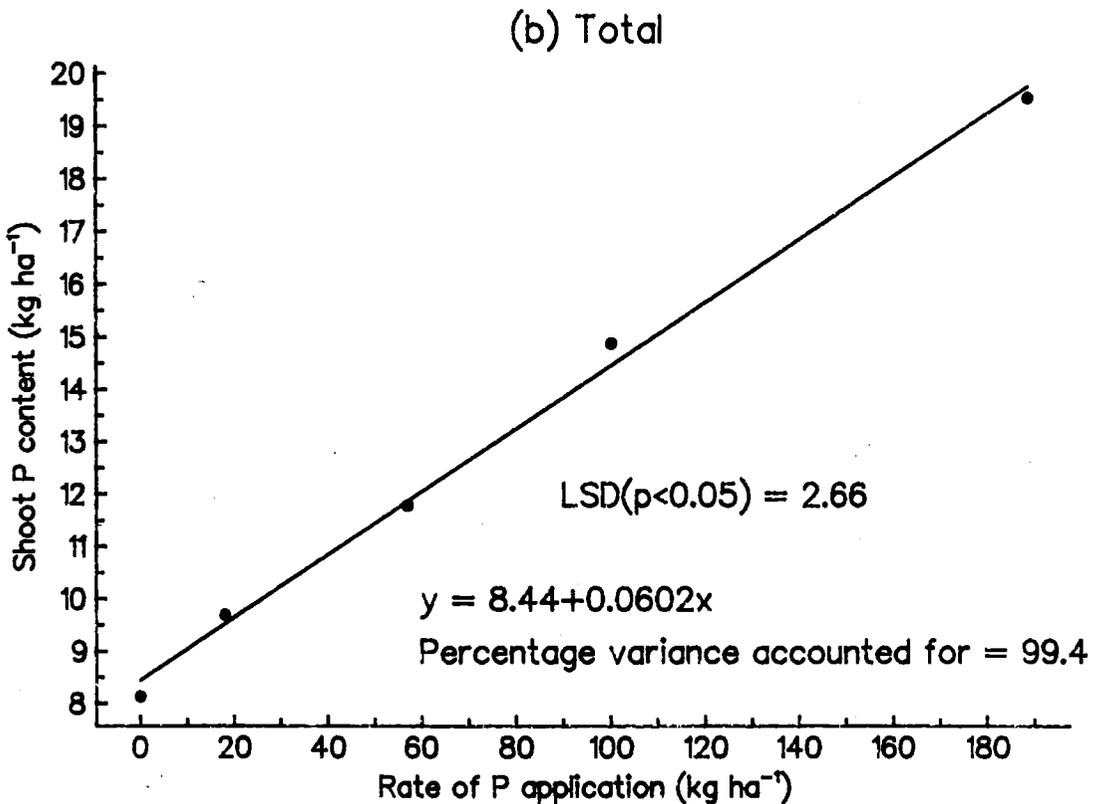
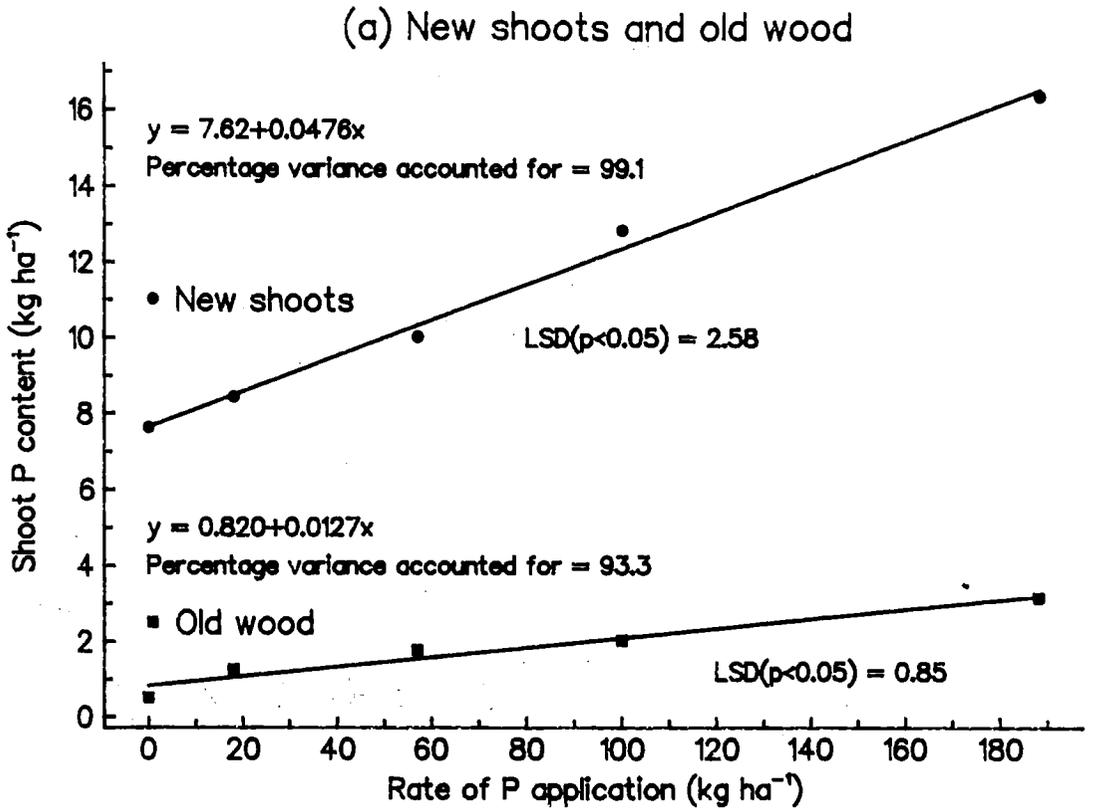


Fig. 3.13 Effect of rate of P application on shoot P content of gorse – Springston trial, infrequent (I) cutting treatment.

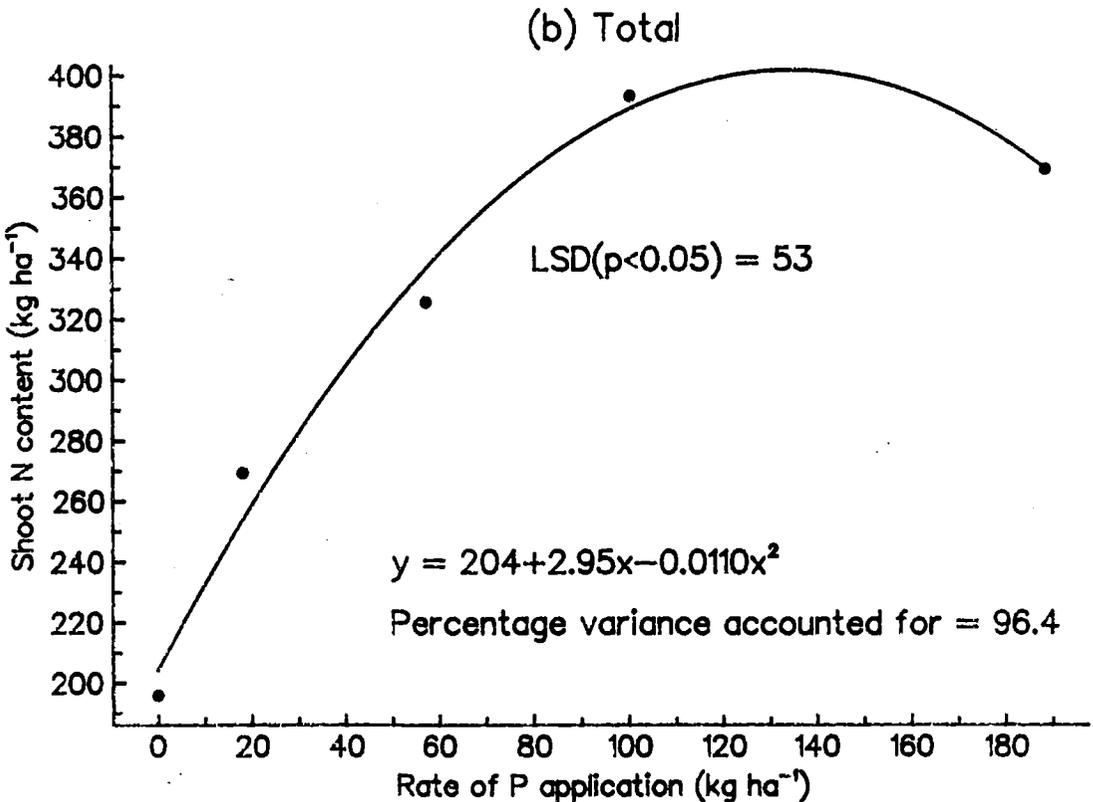
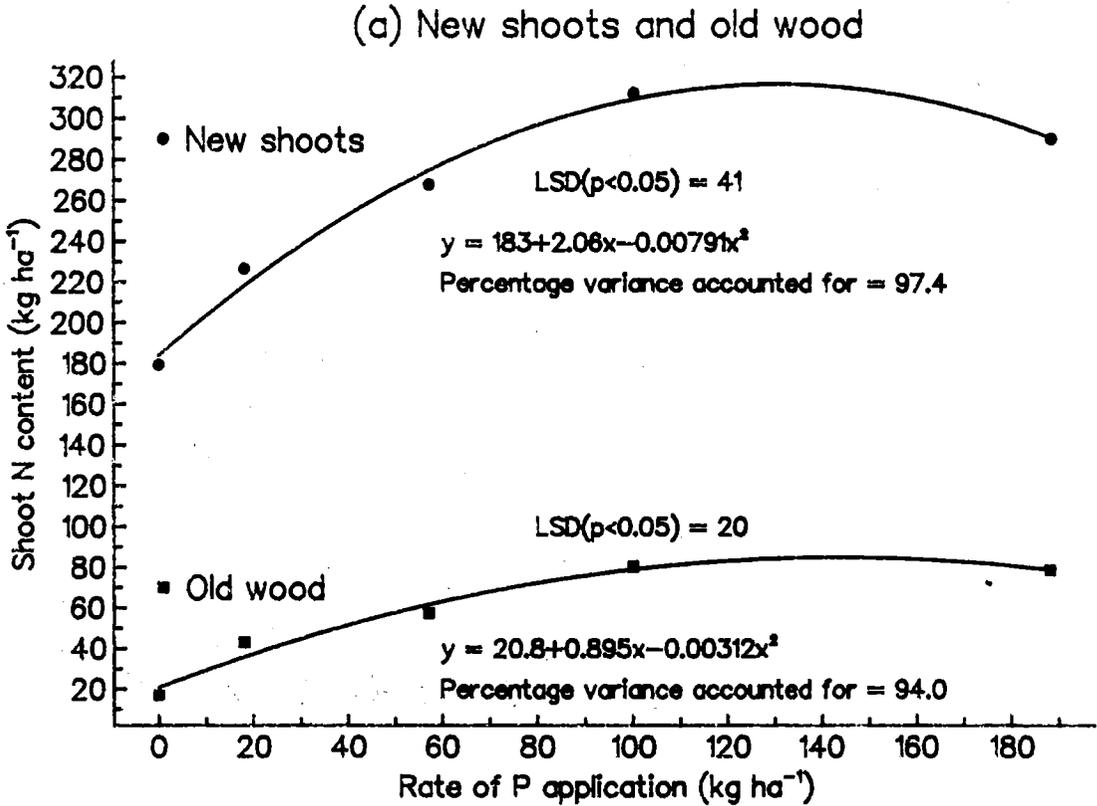


Fig. 3.14 Effect of rate of P application on shoot N content of gorse – Springston trial, infrequent (I) cutting treatment.

Table 3.24 Effects of rate of P, rate of N and cutting treatment on P and N content of gorse

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Levels of significance			
	P content		N content	
	1990/91	1989/91	1990/91	1989/91
P	***	***	***	***
N	ns	ns	ns	ns
Cut	ns	ns	***	***

See Table 3.7 for description of significance levels.

(b) Effect of cutting treatment on P and N content of gorse

Cutting treatment	P content (kg ha ⁻¹)		N content (kg ha ⁻¹)	
	1990/91	1989/91	1990/91	1989/91
F	10.15	12.38	164.4	196.6
I	11.07	12.81	255.5	310.7
L.S.D. (p<0.05)	1.08	1.25	16.5	21.5

Note: See final sentence page 84.

Cutting treatment had significant effects on N content, with total N contents being substantially greater for the I treatment compared with the F treatment (Table 3.24) indicating that the substantially greater dry weight from the I compared to that from the F cutting treatment (Table 3.13(b)) outweighed the effect of lower N concentrations in the I compared to the F cutting treatment (Figs 3.6 and 3.8, Table 3.18(b)).

3.3.3.6.4 Comparative capacities of gorse and white clover to absorb P under conditions of low soil P

Total P uptake by gorse and white clover in the P0 treatment was compared for similar growth periods in spring 1990 (1 Oct - 12 Dec 1990 and 1 Oct - 30 Nov 1990 for gorse and white clover respectively). The rates of P uptake presented in Table 3.25 are means for the F cutting treatment, including both N treatments (i.e. means from 8 plots).

The rate of P uptake by gorse from the unfertilized plots was approximately three times greater than that by white clover (Table 3.25).

Table 3.25 P uptake of gorse and white clover from unfertilized soil - spring 1990

Species	Mean P uptake (kg P ha ⁻¹ day ⁻¹)	Standard error of mean
Gorse	0.0424	0.0072
White clover	0.0149	0.0046

3.3.4 Effects of treatments, season and shoot type on elongation of gorse shoots

3.3.4.1 Effects of rate of P, rate of N and cutting treatment on total shoot length

For the purpose of investigating the effects of rate of P, rate of N and cutting treatment on shoot length, terminal shoot length only was included in the statistical analysis. The reason for this is that after the first harvest, the length of terminal shoots only were measured for the F cutting treatment (Section 3.2.6.1). In the second growth season, only terminal shoots were measured for both cutting treatments. A summary of the analyses of variance of total shoot length for both growth seasons is given in Table 3.26(a).

Table 3.26 Effects of rate of P, rate of N and cutting treatment on gorse shoot length - Springston trial

(a) Summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance Growth season	
	1989/90	1990/91
P	***	***
N	ns	ns
Cut	ns	***
P × N	ns	ns
P × cut	ns	***
N × cut	ns	ns
P × N × cut	ns	ns

See Table 3.7 for description of significance levels.

(b) Total shoot length - cutting treatment means 1990/91

	Cutting treatment		L.S.D. ($p < 0.05$)
	F	I	
Total shoot length (cm)	56.1	40.3	3.1

In the 1989/90 growth season there was a significant rate of P effect on shoot length (Table 3.26(a)), but the effects of rate of N and cutting treatment were nonsignificant as were all interactions. Shoot length increased with increasing rate of P, before tending towards a plateau at the high rates (Fig 3.15(a)).

In the 1990/91 growth season, total shoot length again increased with increasing rate of applied P, but, unlike the previous season, there was a significant effect of cutting treatment and a significant rate of P × cutting treatment interaction (Table 3.26(a)). Total shoot length in the 1990/91 growth season was significantly greater in the frequent (F) cutting treatment than in the infrequent (I) cutting treatment (Table 3.26(b), Fig. 3.15(b)). The shape of the

P response curve appeared to differ for the two cutting treatments. For the F cutting treatment, shoot length increased significantly with increasing rate of P up to the highest rate, whereas for the I cutting treatment, shoot length showed little increase with increasing rate of P (Fig 3.15(b)).

3.3.4.2 Change in rate of shoot elongation over the growth season

Rates of terminal shoot growth (mm day^{-1}) over the 1989/90 and 1990/91 growth seasons are presented in Figs 3.16 and 3.17, along with soil volumetric water contents for the corresponding periods. Monthly rainfall data for the trial site are presented in Appendix 3.6. In both growth seasons, shoot growth began in early October and had ceased by the end of April.

In both growth seasons, rates of shoot elongation were greatest during the spring/early summer (October-December) period (Figs 3.16(a) and 3.17(a)). Declines in rates of shoot elongation approximately coincided with the onset of flowering and declines in soil water contents to levels which would be expected to result in decreased plant growth (Figs 3.16(b) and 3.17(b)).

In both growth seasons plants began to flower in January, with greatest intensity of flowering in February and March (based on counts of flowering and non flowering plants in 1989/90 and visual observation in 1990/91). The onset of flowering may have been a cause of the decline in shoot growth rate in the summer/autumn period of both growth seasons, with emphasis being transferred from vegetative growth to reproductive development. However, the rate of growth of plants in the F cutting treatment declined in a similar way to those in the I treatment, even though flowering was much reduced by the F cutting treatment.

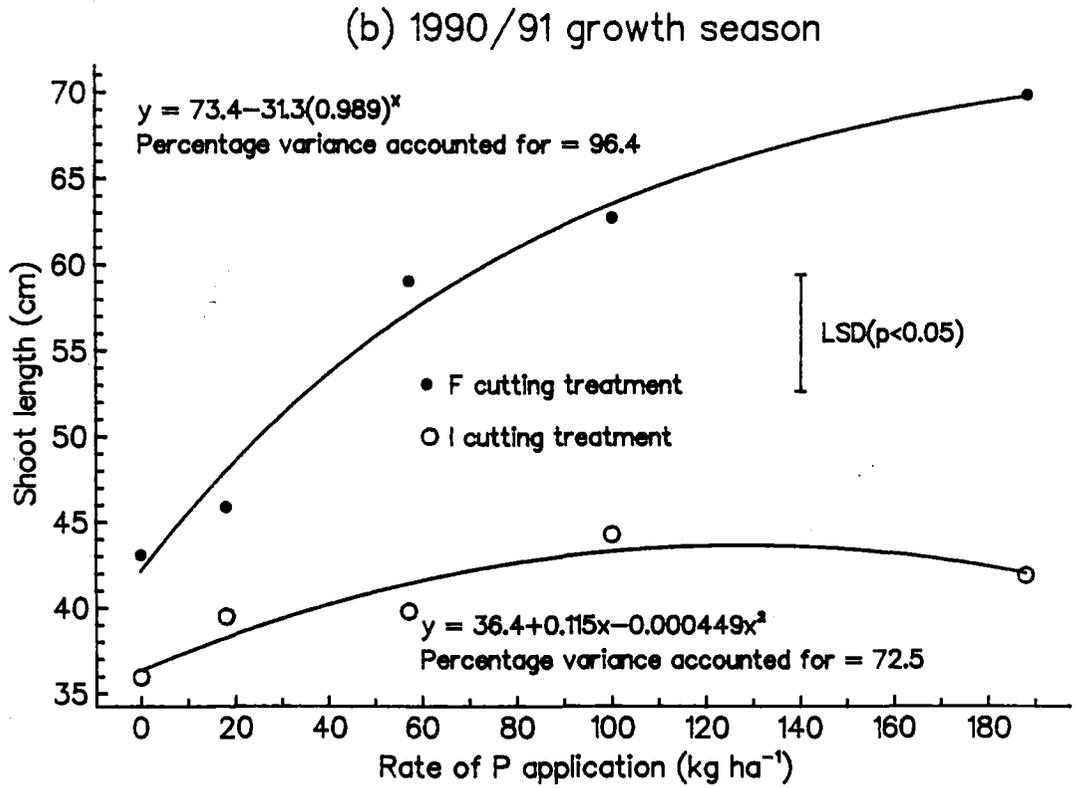
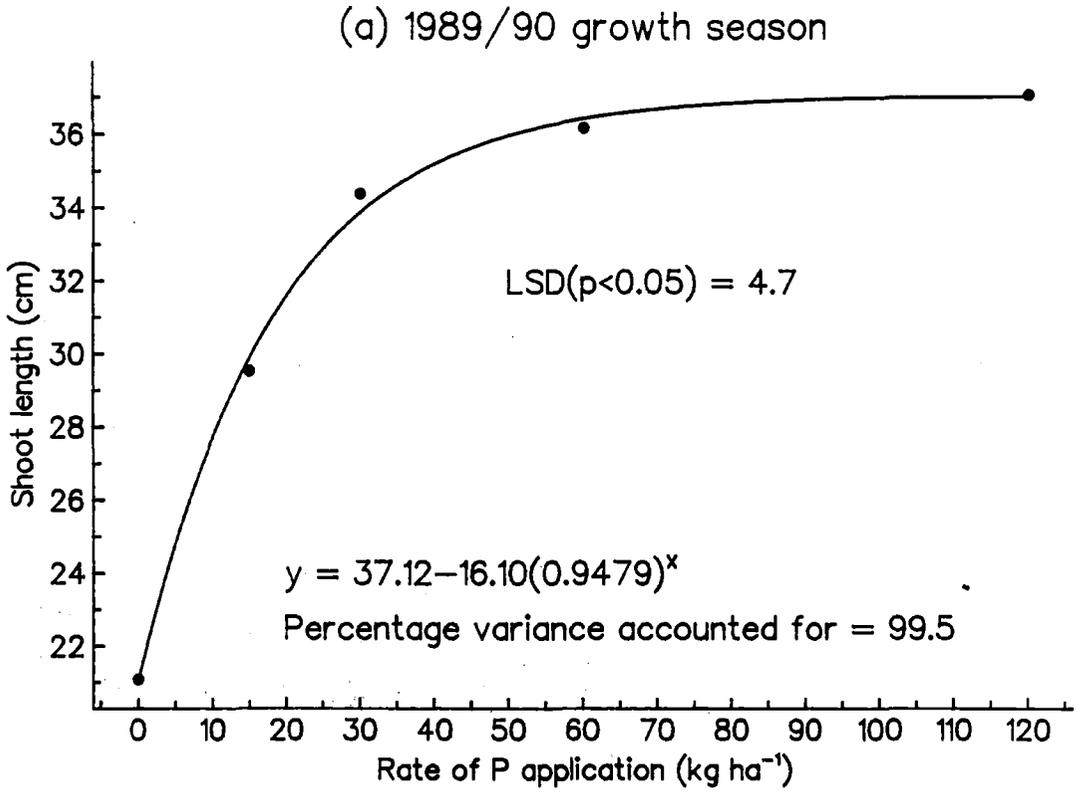
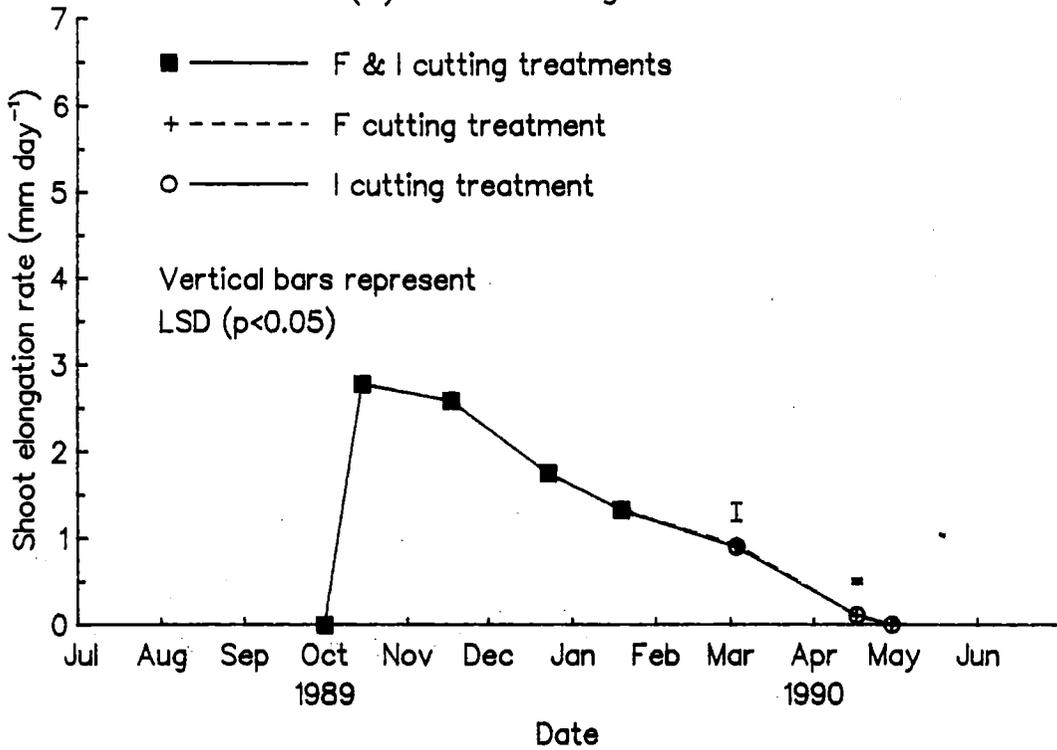


Fig. 3.15 Effect of rate of P application on shoot length of gorse – Springston trial, frequent (F) and infrequent (I) cutting treatments.

(a) Shoot elongation rate



(b) Volumetric water content of soil

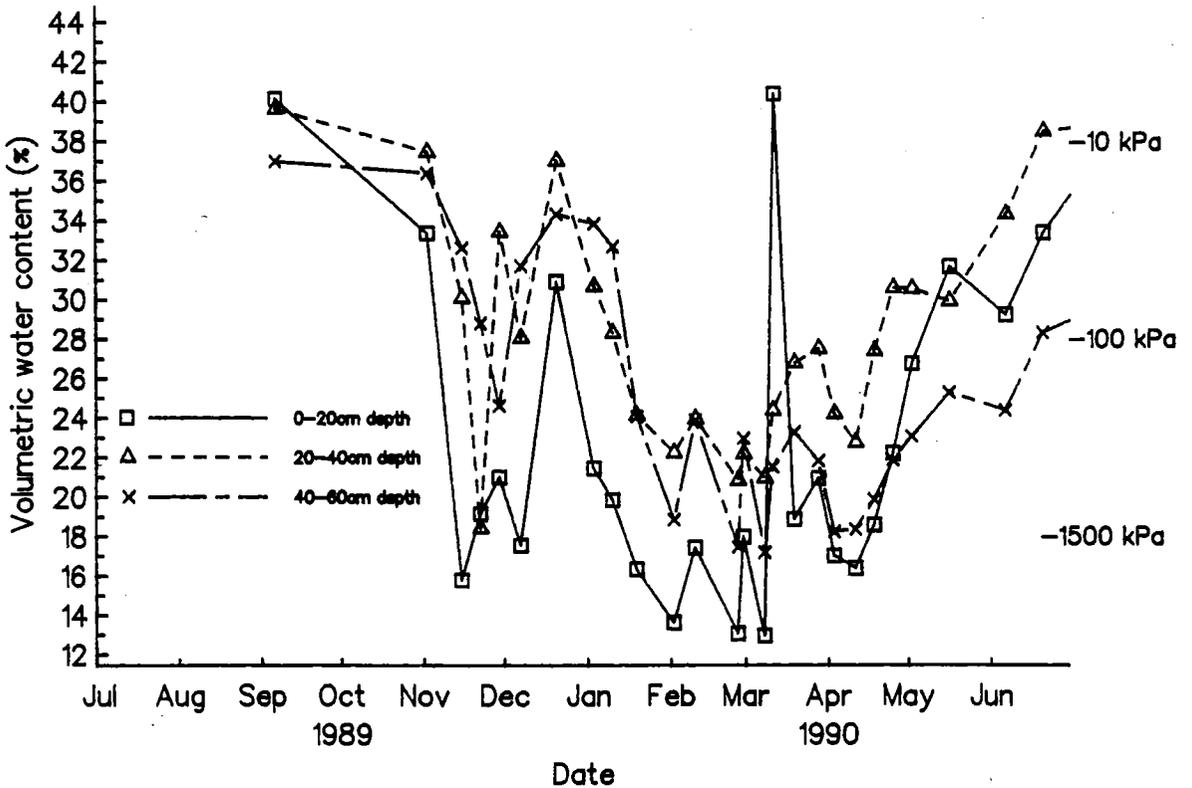
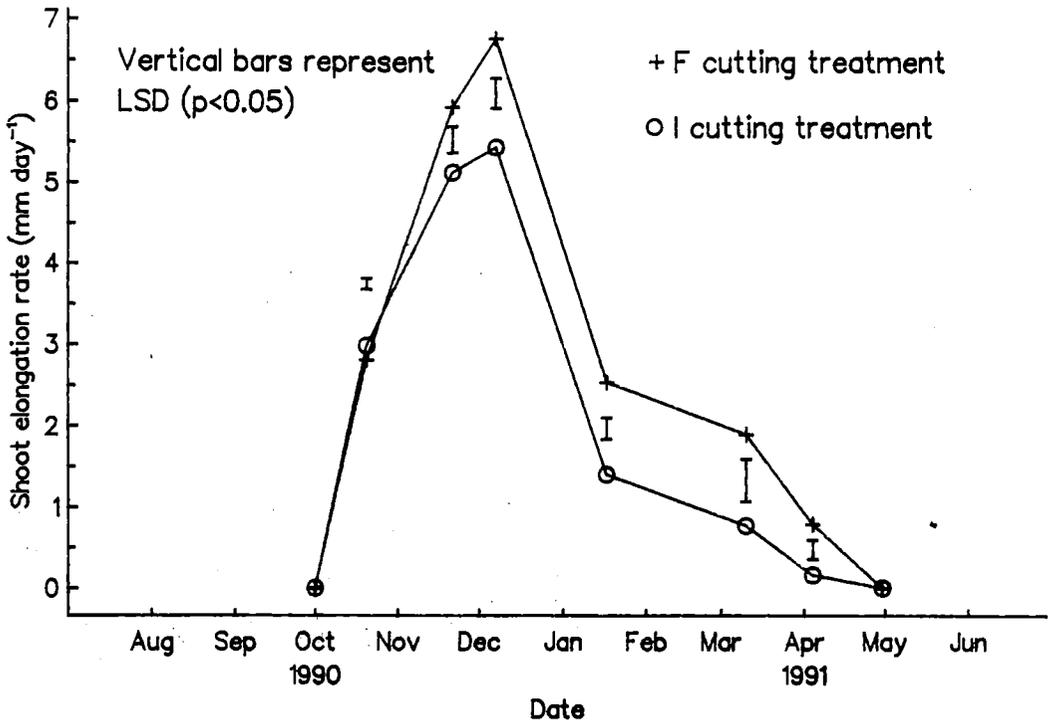


Fig. 3.16 Mean shoot elongation rate and soil water content – Springston trial, 1989/90 growth season.

(a) Shoot elongation rate



(b) Volumetric water content of soil

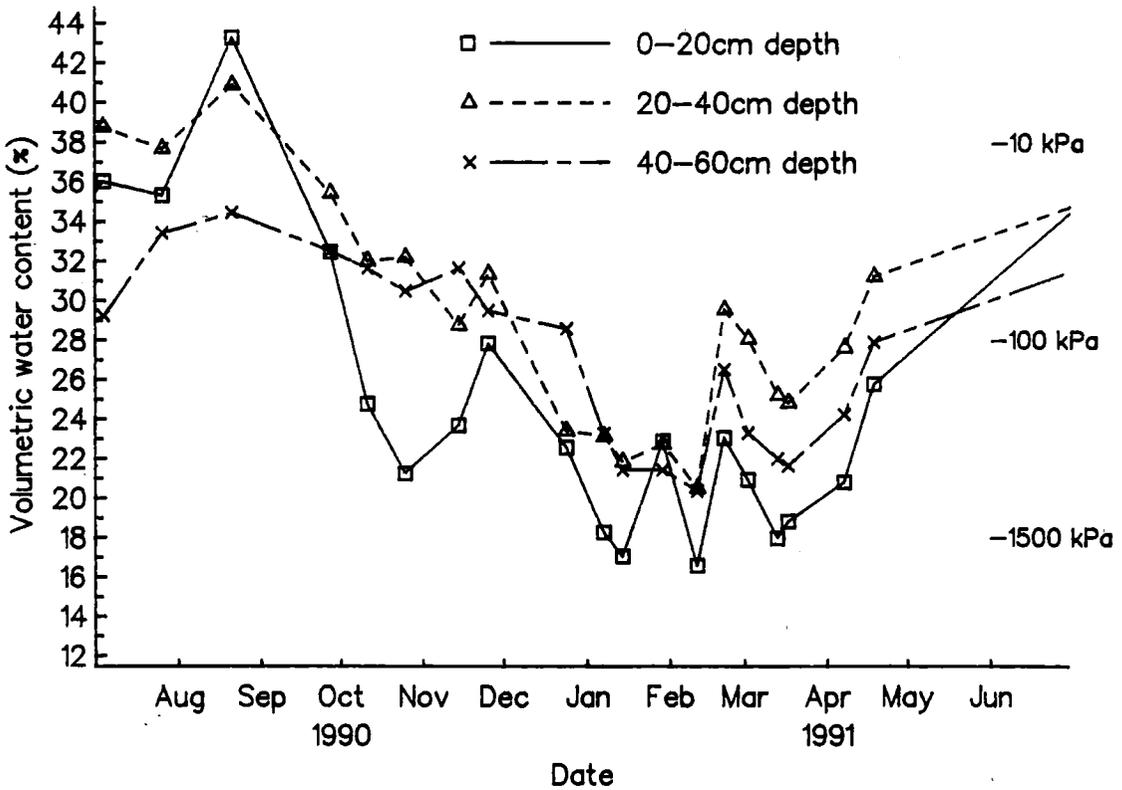


Fig. 3.17 Mean shoot elongation rate and soil water content – Springston trial, 1990/91 growth season.

Soil moisture characteristics derived from the data of Watt and Burgham (1992) and Grewal (1991) are presented in Table 3.27.

Table 3.27 Soil moisture characteristics of Wakanui soil (Watt and Burgham 1992; Grewal 1991)

Depth (cm)	Volumetric water contents (%) at different soil matric potentials		
	-10 kPa (field capacity)	-100 kPa (Limit of readily available water)	-1500 kPa (Permanent wilting point)
0-20	35.7	26.9	16.9
20-40	33.1	29.2	20.3
40-60	32.8	30.0	21.6

Water contents at matric potentials of -10 kPa (field capacity), -100 kPa (limit of readily available water) and -1500 kPa (permanent wilting point) for the 0-20 cm soil layer are indicated on Figs 3.16(b) and 3.17(b). A fall in soil matric potential below field capacity, (i.e. below -10 kPa) can cause a significant decrease in plant growth (Sands and Rutter 1959; Jarvis 1963). Decreases in matric potential may be particularly important in the surface soil layer where, because of their likely adverse effect on nutrient uptake generally (Newman 1974; Garwood and Williams 1967a & b) and P uptake in particular (Fisher 1980; Ozanne 1980). Water content of the 0-20 cm layer declined to permanent wilting point for much of the January - March period of both growth seasons (Figs 3.16(b) and 3.17(b)).

3.3.4.3 Effect of shoot type on shoot length

In the 1989/90 growth season, lengths of terminal, mid-stem and basal shoots were measured (Section 3.2.6.1).

A summary of the analysis of variance of shoot length for the I cutting treatment is presented in Table 3.28(a). There was a significant rate of P effect, as shown previously for both cutting treatments combined (Table 3.26; Fig. 3.15). There was also a significant effect of shoot type and a significant rate of P × shoot type interaction. Shoot length was greatest for basal shoots (mean = 37.3 cm) less for terminal shoots (mean = 31.2 cm) and

least for mid-stem shoots (mean = 16.1 cm) (Table 3.28).

Table 3.28 Effects of rate of P, rate of N and shoot type on gorse shoot length - I treatment 1989/90

(a) Summary of analysis of variance table

Source of variation (treatment or interaction)	Level of significance
P	***
N	ns
P × N	*
Shoot type	***
P × shoot type	**
N × shoot type	ns
P × N × shoot type	ns

See Table 3.7 for description of significance levels

(b) Shoot length (cm) - shoot type means

Shoot length	Shoot type †			L.S.D. (p<0.05)
	T	M	B	
	31.2	16.1	37.3	

(c) Shoot length (cm) - P × shoot type means

Shoot type †	Rate of P					L.S.D. (p<0.05)
	P0	P1	P2	P3	P4	
T	18.6	29.8	33.8	36.4	36.9	7.1
M	9.7	13.9	18.5	19.6	18.7	
B	24.0	38.0	35.7	51.3	37.4	

† Shoot type: T = terminal, M = mid-stem, B = basal

The nature of the response to increasing rate of P appeared to vary with shoot type. For terminal and mid-stem shoots, length increased significantly with increasing rate of P, before reaching a plateau at the higher rates (Table 3.28(c)). For the basal shoots, however, shoot length increased significantly up to the P3 rate of P, then declined significantly at the P4 rate.

It is not possible to quantify the contributions of different shoot types to dry matter yield because numbers of the different shoot types were not estimated.

3.3.5 Effect of rate of N application on nitrate reductase activity of shoot and root tissue of gorse

3.3.5.1 I Cutting treatment, 22 Dec 1990

NRA (Nitrate reductase activity) per unit dry weight was significantly greater at the high rate of N than at the nil rate, (Table 3.29(a) and (b)). This occurred even though 2 mol l^{-1} KCl-extractable N concentrations in the soil were low, and were not significantly greater in the high N compared with the low N treatment (Table 3.30). The low extractable N concentrations reflect the fact that the most recent application of N had been 38 days prior to the date of assay. The effect of plant part was nonsignificant, as was the rate of N \times plant part interaction (Table 3.29(a)).

3.3.5.2 F Cutting treatment, 28 Feb - 1 Mar 1991

For this set of assays, the effect of N treatment on NRA was significant at only $p = 0.08$ (Table 3.29(a)), with NRA again tending to be greater at the high rate of N than the nil rate (Table 3.29(b)).

Table 3.29 Effect of rate of N application on rate of NRA in gorse - Springston trial

(a) Summary of analyses of variance - levels of significance (p)

Source of variation (treatment or interaction)	Level of significance (p) Cutting treatment, date	
	I, Dec 1990	F, Feb 1991
N	0.026	0.080
Plant part	0.440	0.013
N × plant part	0.138	0.832

(b) Effect of N treatment on rate of NRA ($\mu\text{ mol NO}_3\text{ h}^{-1}\text{ g}^{-1}\text{dwt}$) (means for all plant parts)

Cutting treatment, date	N treatment		L.S.D. ($p < 0.05$)
	Nil	High	
I, Dec 1990	0.027	0.086	0.031
F, Feb 1991	0.097	0.146	0.040

(c) Effect of plant part on rate of NRA ($\mu\text{mol NO}_3\text{ h}^{-1}\text{ g}^{-1}\text{dwt}$)(means for both N treatments)

Cutting treatment, Date	Plant part			L.S.D. ($p < 0.05$)
	New shoot	Old wood	Root	
I, Dec 1990	0.041	0.060	0.069	0.046
F, Feb 1991	0.060	0.109	0.195	0.083

NRA per unit dry weight was greater at this assay time than for the previous time (Table 3.29(b) and (c)) presumably reflecting the greater KCl-extractable N values in February 1991 compared with Dec 1990 (Table 3.30). The greater soil N concentrations in Feb 1991 compared with Dec 1990 probably reflect the more recent application of N fertilizer in Feb 1991 (11 days previously) compared with Dec 1990 (38 days previously) (Section 3.2.1.2.2). 2 mol l^{-1} KCl-extractable $\text{NO}_3\text{-N}$ concentrations were significantly greater in the high N than in the nil N treatment (Table 3.30).

Table 3.30 2 mol l⁻¹ KCl-extractable N in soil (0-15 cm depth) ($\mu\text{g N g}^{-1}$ soil)

Cutting treatment, Date	Form of N	N treatment		L.S.D. ($p < 0.05$)
		Nil N ($\mu\text{g N g}^{-1}$ soil)	High N	
I, Dec 1990	NO ₃	0.12	1.13	1.37
	NH ₄	4.6	8.6	6.6
F, Feb 1991	NO ₃	22.5	74.5	27.3
	NH ₄	60.0	129.0	102.0

Although mean NH₄-N concentration was greater in the high N treatment than in the nil N treatment, the difference was not statistically significant (Table 3.30).

At this assay time there was a significant effect of plant part on NRA, with NRA per unit dry weight being greatest in roots followed by old wood and new shoots (Table 3.29(c)).

3.3.6 Effect of N treatment on N₂-fixing (acetylene reducing) activity

N₂-fixing (acetylene reducing) activity was measured in soil cores from nil N and high N plots on 17 March 1991 (Section 3.2.11). Mean N₂-fixing activity in soil cores from the nil N plots was numerically greater than that in cores from the high N plots (Table 3.31), but the difference was not statistically significant ($p = 0.145$). Both 2 mol l⁻¹ KCl-extractable NO₃-N and NH₄-N were significantly greater in the high N than in the nil N treatment (Table 3.31).

Two of the plots on which acetylene reduction assays were done, were also assayed 10 days earlier, with almost identical results, suggesting that N₂-fixing activity was not increasing with time in the high N plots (due to depletion of soluble N).

Table 3.31 Effect of N treatment on N_2 -fixing (acetylene reducing) activity and 2 mol l^{-1} KCl-extractable N

	N treatment		L.S.D.
	nil N	High N	
Acetylene reduction ($\mu\text{mol C}_2\text{H}_2 \text{ h}^{-1}$ per 10 cores)	0.450	0.234	0.331
2 mol l^{-1} KCl-extractable $\text{NO}_3\text{-N}$ ($\mu\text{g g}^{-1}$)	34	202	104
2 mol l^{-1} KCl-extractable $\text{NH}_4\text{-N}$ ($\mu\text{g g}^{-1}$)	70	171	42

3.4. DISCUSSION

3.4.1 Dry matter yield of gorse - responses to applied P and N

Annual dry matter (DM) yield of gorse was very responsive to applied P in both growth seasons of the trial (Figs 3.3 and 3.4). In the first year of the trial (annual rainfall = 590 mm) dry matter yields from the F cutting treatment were relatively low, increasing from 451 kg ha^{-1} with no applied P to a maximum of 2508 kg ha^{-1} at 88 kg P ha^{-1} (Fig 3.3(a)). In the second growth season of the trial (annual rainfall = 601 mm) dry matter yield of the frequently cut gorse increased from 5053 kg ha^{-1} without P fertilizer to a maximum of 9452 kg ha^{-1} at 123 kg P ha^{-1} (total P applied over both seasons) (Fig 3.3(b)). The corresponding dry matter response for uncut gorse was from 10890 kg ha^{-1} without P fertilizer to 18516 kg ha^{-1} at 124 kg P ha^{-1} (Fig 3.4). Rickard and Radcliffe (1976) report mean annual dryland (annual rainfall = 771 mm) production of pasture receiving $250 \text{ kg superphosphate ha}^{-1}$ (approximately 22 kg P ha^{-1}) to be $5870 \text{ kg DM ha}^{-1}$. Even in the F cutting treatment without applied P, gorse in its second growth season produced approximately this amount of dry matter. The frequently cut gorse supplied with adequate fertilizer P and the uncut gorse with or without fertilizer P exceeded it by large amounts. Maximum annual dry matter yield of uncut gorse in its second growth season (18516 kg ha^{-1}) was similar to that of 19500 kg ha^{-1} reported by Radcliffe (1986) for browsed gorse which had received

applications of superphosphate and lime.

The effects of applied N (split application of $200 \text{ kg ha}^{-1} \text{ year}^{-1}$) on annual dry matter yields were nonsignificant for both the F and I cutting treatments (Sections 3.3.2.3 and 3.3.2.4), indicating that the symbiotic N_2 -fixing system of gorse was able to meet the N needs of the plants under the conditions of this trial. The $\text{P} \times \text{N}$ interactions were also nonsignificant (Sections 3.3.2.3 and 3.3.2.4) indicating that even at low or nil rates of applied P there was no response to applied N. This may suggest that P did not directly stimulate symbiotic N_2 fixation as is sometimes claimed for legumes (e.g. Israel 1987). Alternatively the lack of response to N at P0 may have been due to P deficiency while at P4 it may have been due to P induced N_2 fixation.

When harvests of the F cutting treatment plots are considered individually, there was a significant negative response to N at the final harvest (Table 3.7). Mineral N is known to depress nodulation and N_2 fixation in a wide range of legumes (e.g. Munns 1968; Heichel and Vance 1979; Dean and Clark 1980; Wong 1980; Allos and Bartholomew 1955; Allos and Bartholomew 1959; Pate 1977). It is probable that fertilizer N depressed nodulation and N_2 fixation (Section 2.4.1, Figs 5.6 and 5.8) immediately after its application, but then after a period of depletion, soil N concentrations may have been insufficient to maintain growth at a rate comparable to that in the nil N treatment. The plants would then presumably have to invest resources in increasing their N_2 -fixing capacities. There could have been a lag period while this occurred (Hume and Withers 1985) during which time plant growth would be limited by low N concentrations. The apparently adequate shoot N concentrations in the high N compared with the nil N treatment does not necessarily negate this suggested mechanism. The difference in yield could reflect slower growth when the applied N was exhausted and before the N_2 -fixing system was re-activated. The growth lost was not subsequently made up and therefore the shoot N concentration did not decline.

3.4.2 Contrasting responses of gorse and white clover to external P supply

3.4.2.1 Shape of response curves

Under conditions of low available soil P, gorse was highly responsive to P fertilisation (Figs 3.1 and 3.4, Table 3.7, Section 3.3.2.4). This is consistent with the findings of Thompson (1974) and Ivens and Mlowe (1983). However the authors cited used only two rates of applied P (nil and high), and therefore provided no information about the shape of the P response curve of gorse.

The shape of the P response curve of gorse appeared to differ from that of white clover (Figs 3.1, 3.2). White clover yield generally continued to increase significantly with increasing rate of P application up to the highest rate of P applied (Fig 3.2). There was no evidence of any tendency for yield to decline at high rates of P. The relationships between yield and rate of P application were therefore well described by the exponential diminishing response curves fitted (Fig 3.2, Table 3.9). For gorse the relationship between yield and rate of P application was best described using quadratic curves, reflecting the tendency for gorse yield to reach a maximum and then decline slightly within the range of P rates applied (Fig 3.1, Table 3.9).

Response curves where yield either levels off or declines with high concentrations of nutrients, have been reported by other authors (e.g. Loneragan and Asher 1967; MacLeod 1969; Shimsi 1969; Boyd 1970; Eck 1984). Loneragan and Asher (1967) found that very high P uptake in solution culture was associated with reduced growth in 3 species, including clover. Such effects may result from phosphate retarding the uptake and translocation of micronutrients such as Zn, Fe and Cu (Mengel and Kirkby 1987). However the concentrations of P in gorse shoots at the highest rate of P were not high compared with other plants, including white clover (Figs 3.9 and 3.10) and did not suggest that such effects were likely. Nutrients other than P and N which were likely to limit plant growth at the trial site (K, S and Mo) were supplied as a basal application (Section 3.2.5), therefore it is unlikely that the tendency for gorse yield to decline at the highest rate of P was associated with a deficiency of any of these nutrients. Also, any nutrient deficiency suffered by gorse would presumably also affect white clover, which showed no tendency for yield decline at the highest rate of P. Gorse plants in the trial were under moisture stress for significant

periods throughout the trial (Figs 3.16 and 3.17), but again it can be argued that if moisture stress had combined with the P4 rate of P to cause a decline in gorse yield a similar effect should have occurred for white clover. Also, soil moisture stress was greatest in the second half of each growth season, and there was no correspondingly increased tendency for decline in yield at the P4 rate of P in the second half of either growth season (Fig 3.1). In the presence of white clover, P application has been found to depress gorse growth, because of competition from the clover (Hartley and Popay 1982). This was probably not a major factor in this trial as particular care was taken to minimise competition for light when the gorse plants were small, by regular defoliation of the clover. Also the effect was apparent in the uncut treatment in the second year of the trial when white clover had been virtually shaded out of the high P plots (P2-P4).

3.4.2.2. Soil P requirement for maximum growth

Gorse appeared to require less applied P than white clover in order to reach its yield potential under the conditions of this trial (Figs 3.1, 3.2). For gorse there was no significant increase in yield beyond the P3 rate of applied P (Olsen P = 23.1 and 20.5 $\mu\text{g g}^{-1}$ for 1989/90 and 1990/91 respectively, Table 3.6). In contrast white clover was responsive to increasing rate of P up to the P4 rate (Olsen P = 42.7 and 38.7 $\mu\text{g g}^{-1}$ for 1989/90 and 1990/91 respectively) and possibly beyond (Fig 3.2, Table 3.6).

3.4.2.3 Capacity to reach growth potential without applied P

From autumn 1990 onwards the responsiveness of gorse to applied P was less than that of white clover i.e. gorse had a greater capacity for growth without applied P, relative to its growth with non-limiting P supply, than white clover, under the conditions of this trial (Section 3.3.2.2, Table 3.10).

A similar comparison was observed between the shrub legume tagasaste (*Chamaecytisus palmensis*) which is tolerant of low fertility (Fitzgerald 1980) and the high soil fertility demanding red clover (*Trifolium pratense*), where responsiveness to applied P was approximately 0.63 for tagasaste compared with 0.84 for red clover (estimated from the data of Voon (1986)). The value for red clover was very similar to the values for white clover in the Springston field trial from autumn 1990 onwards (0.85-0.87, Table 3.10). The value

for tagasaste appeared to be a little greater than that for gorse in the second growth season (0.36-0.54, Table 3.10) but this could be explained by the fact that it was growing in soil with lower Olsen P concentration ($4 \mu\text{g g}^{-1}$) compared with gorse in the Springston trial ($9.0 \mu\text{g g}^{-1}$ in 1989/90, $7.3 \mu\text{g g}^{-1}$ in 1990/91, Table 3.6).

In the first growth season of the trial gorse and white clover had similar responsiveness to applied P (0.74-0.85 and 0.74-0.86 respectively, Table 3.10). Gorse was more responsive to applied P early on compared with later in the trial (Table 3.10) because initially the plants were small, would have had a relatively undeveloped root system and consequently would have been less able to exploit the P contained in unfertilized soil. In the second growth season gorse became much less responsive to applied P (0.36-0.54, Table 3.10), presumably because root system development had enabled it to better exploit soil P and made it less dependent on surface applied P. In contrast, white clover was established at the site before the trial began, but the site did not become clover-dominant until it was sprayed with grass-killer at the beginning of the trial. As the white clover population increased, it would have tended to have increased its potential to respond to applied P, but its increases in P responsiveness from spring 1989 were not significant.

The responsiveness of gorse to applied P in the I (uncut) cutting treatment was similar to that in the F (cut twice yearly) cutting treatment (Table 3.10), suggesting that plants in the two cutting treatments had similar abilities to absorb P from unfertilized soil.

The lower requirement for P in order to reach maximum yield (Section 3.4.2.2), and the greater growth of gorse in unfertilized soil relative to its growth potential, in comparison with white clover is consistent with its reputation as a species which tolerates low soil fertility and grows well under these conditions (Meeklah 1979; Dancer *et al.* 1977a; Roberts *et al.* 1981). Conversely the poor growth of white clover in the absence of P fertilizer and its lesser ability (compared with gorse) to reach its growth potential in the absence of applied P is consistent with its acknowledged role as a high fertility demanding species (Dunlop and Hart 1987) which has a relatively limited ability to adapt to low fertility (low N and P) soil conditions (Mouat 1983). It has been found that other shrub legumes (broom (*Sarothamnus scoparius*), tagasaste, Russell lupin (*Lupinus polyphyllus*), and yellow tree lupin (*Lupinus arboreus*)), also grow well compared with pasture legumes such as white and red clover, under low fertility conditions (Dancer *et al.* 1977a, Fitzgerald 1980; Voon 1986).

Paynter (1990), comparing yellow serradella (*Ornithopus compressus*) with other legumes, associated its ability to produce 90% maximum yield under conditions of low available soil P with its greater ability to absorb P from the soil (similarly to gorse in this trial, Table 3.25) and its greater ability to translocate P to shoots (also similarly to gorse, Section 4.4.2.2).

The lesser responsiveness of gorse to applied P (0.36-0.54) compared with white clover (0.85-0.87) in the second year of the trial (Table 3.10), where both species were grown together was consistent with findings from the lime/P experiment where gorse and white clover were grown separately (responsiveness = 0.74 and 0.95, for gorse and white clover respectively, Table 4.12). The greater responsiveness of both species in the pot trial would be expected because of the lower Olsen P concentration ($4 \mu\text{g g}^{-1}$, Table 4.1) compared with the field trial ($7-9 \mu\text{g g}^{-1}$, Table 3.6). Also, responsiveness in the field would tend to be lower than in pots because in the field roots can absorb nutrients from a greater volume of soil than they can in pots. In the field trial it might have been expected that the close proximity of gorse and white clover may have influenced their individual responses to applied P because of the apparently greater ability of gorse to absorb P from low fertility soils (Tables 3.11 and 3.25). However, the relative responses of gorse and white clover to applied P when grown together in the field trial were consistent with those when the species were grown separately in pots. This suggests that the negative effects of P application on gorse growth in the presence of pasture, and in particular white clover, (Thompson 1974; Hartley and Popay 1982) may have been due to competition for light rather than nutrients.

3.4.3 Abilities of gorse and white clover to acquire P from unfertilized soil

When the fitted curve, yield vs rate of P applied is extrapolated back to the point at which it intercepts the x-axis, the magnitude of the negative intercept is an indication of the ability of the particular plant species to acquire P from the unfertilized soil in the units used for rate of P application (kg P ha^{-1} in this case) (Ozanne 1980). It can be seen (Table 3.11) that, from autumn 1990 onwards, gorse appeared to be able to acquire more P from the unfertilized soil than white clover. This is consistent with the greater ability of gorse to reach its growth potential in the absence of P fertilizer compared with white clover, as discussed in the previous section. The lesser P-acquiring ability of gorse in spring 1989 is probably due to its relatively undeveloped root system at this early stage of the trial (as

discussed in the previous section). The values obtained for the P-acquiring ability of gorse appear to be similar for both frequently and infrequently cut gorse (Table 3.11).

A comparison of P uptake during spring 1990 indicated that gorse had the ability to take up approximately three times as much P per unit time as white clover (0.0424 and 0.0149 kg ha⁻¹ day⁻¹ respectively (Table 3.25).

The apparently greater ability of gorse to acquire P under the unfertilized conditions of this trial further reinforces the reputation of gorse as a tolerator of low soil fertility (e.g. Meeklah 1979) which frequently has the role of a pioneer species (Dancer *et al.* 1977a; Roberts *et al.* 1981).

Gorse absorbed more P from unfertilized low P soil than white clover, regardless of whether the species were grown separately or together. On unfertilized soil gorse absorbed 2.8 times more P than white clover (Table 3.25) when both species were grown together in the field. When the two species were grown separately in pots, gorse absorbed 1.6 times as much P as white clover (Table 4.20). The greater P uptake by gorse relative to white clover in the field compared with pots is probably due to the greater volume of soil available to the roots of field grown gorse. However, because gorse was also able to take up more P than white clover from within the restricted volume of a pot (Table 4.20, Section 4.4.2.1) it may also be reducing the amount of P taken up by the white clover, via direct competition.

3.4.4 P uptake and internal efficiency of P use

At most sampling times, P concentration in the foliage of both gorse and white clover increased progressively with increasing rate of applied P, up to the highest rate (Figs 3.5, 3.7, 3.9 and 3.10). The increases in P concentration with increase in rate of P application were generally well described by exponential (diminishing response) curves.

Exceptions to the two previous statements occurred for both cutting treatments at the final harvest (April 1991, Figs 3.5 and 3.7) and this anomaly is discussed in Section 3.4.5.

P concentration in gorse shoots was less than that in white clover shoots at all rates of P in Jan 1990 and at all except for the nil rate of P in Dec 1990 (Figs 3.9 and 3.10). Thus gorse

was more internally efficient than white clover at using P for dry matter production.

3.4.5 Critical P concentrations

Critical shoot P concentrations are defined here as those concentrations associated with 90% maximum yield, according to the concept of Macy (1936), Andrew (1960) and Andrew and Robins (1969a).

Growth of gorse was slow in its first season (1989/90) compared with that in the second season (1990/91) (Fig. 3.1), similarly to some other perennial legumes (Andrew and Jones 1978). Andrew and Jones (1978) state that critical nutrient concentrations based on the slow first seasons growth may be misleading. Therefore the value for critical shoot P concentration calculated from the spring 1990/91 data, when the plants were growing more rapidly, is probably more reliable than those calculated from the 1989/90 data (Table 3.21).

The apparent anomaly of the autumn 1991 value is discussed later in this section.

The best estimate of critical P concentration of gorse (Dec 1990, when young shoots were growing vigorously) appeared to be less than that for white clover in this trial and less than values for white clover and lucerne calculated by other authors (Table 3.32). It has been found that legume species with relatively low critical P concentrations tend to be those having greatest P uptake per unit soil mass and which reach maximum yield at relatively low rates of applied P (Andrew and Robins 1969a). This is similar to the contrast between gorse and white clover presented here, where gorse had a relatively low critical P concentration, but was able to absorb more P from unfertilized low fertility soil than white clover which had a relatively greater critical P concentrations (Tables 3.25, 3.21 and 3.32).

The low gorse shoot P concentrations observed in April 1991 for both the F and I cutting treatments were less than those at the Dec 1990 sampling time (Figs. 3.5 and 3.7). This situation may have arisen because Dec 1990 was a time of rapid growth (requiring relatively greater shoot P concentration) compared with April 1991 which was a time of almost no growth (Fig. 3.17).

Table 3.32 Critical shoot P concentration - comparison of gorse with other temperate legumes

Species	Reference	Critical shoot P concentration (%)
Gorse	This trial (F cutting treatment)	0.19
Gorse	This trial (I cutting treatment)	0.18
White clover	This trial	0.35
White clover	McNaught 1970	0.30
White clover	Cornforth and Sinclair 1984	0.35
Lucerne	Andrew and Robins 1969a	0.24
Lucerne	Cornforth and Sinclair 1984	0.26

Another factor which may have contributed to low shoot P concentrations in April 1991 was the low soil water content, particularly in the surface layer, which existed during the January to March period prior to the April harvest (Fig. 3.17, Section 3.3.4.2.). Low soil water content can have adverse effects on nutrient uptake generally (Newman 1974; Garwood and Williams 1967a & b) and on P uptake in particular (Fisher 1980; Ozanne 1980).

There may also have been loss of P from plants because of the shedding of seed which had occurred during the February to April period. This is important because there tends to be an accumulation of P in flowers (and ultimately seeds) at the expense of leaves, stems and roots (Robinson and Jones 1972) which increases the potential for loss of P via seed shedding. Flowers and seeds on the gorse shoots at harvest were included in the subsamples taken for chemical analysis.

As in the 1990/91 growth season, soil moisture levels in the 1989/90 season were low (even lower than in 1990/91, Figs 3.16 and 3.17) during the January to March period, and loss of seed occurred during the February to April period. Unlike the 1990/91 season, shoot P concentrations at the second harvest (31 May 1990) were similar to those at the first harvest (Fig 3.5). However, it is possible that P concentrations were low in April 1990 but that P uptake increased when surface soil water contents increased in April to May (Fig 3.16).

Considering the above discussion on the relatively low P concentrations in April 1991, the best estimates of critical P concentration for the 1990/91 growth season appear to be as follows:

- a) For the F cutting treatment, critical P concentrations are probably best estimated using the yield and P concentration data from the spring 1990 period when rapid growth occurred, and avoiding the period later in the season when growth rate and soil water contents were low.
- b) For the I cutting treatment the best estimate of critical P concentration appears to be that based on total 1990/91 dry matter production (most of which would have been produced in the spring early summer period (Fig 3.17)), combined with the P concentrations of Dec 90 (which represent the period of most active growth, when soil moisture conditions were more favourable than during the late summer autumn period). An important prerequisite for estimating critical concentrations of an element is the absence of other limiting factors (Andrew and Robins 1969a), such as would have existed in the form of low surface soil water contents and therefore relative nutrient unavailability during January to March 1991. Therefore the gorse P concentrations measured for April 1991, are probably unsuitable for the estimation of critical concentrations.

Critical P concentrations in gorse shoots were similar for the F (0.19%) and I (0.18%) cutting treatments and less than for white clover shoots (0.35%) (Table 3.32). The efficient internal use of P in the production of dry matter by gorse compared with the high fertility demanding white clover (Dunlop and Hart 1987) appears to be one of the mechanisms enabling it to thrive under conditions of low soil fertility.

3.4.6 N nutrition of gorse and white clover

3.4.6.1 Internal efficiency of N use

At both the Jan 1990 and Dec 1990 sampling times, N concentration in new shoots was substantially lower for gorse than white clover (Tables 3.19 and 3.20; Figs 3.9 and 3.10). Mean new shoot N concentrations for gorse and white clover respectively were 2.03% and 3.73% in Jan 1990, and 2.68% and 3.72% in Dec 1990. Thus gorse was more efficient at

using N acquired (either by symbiotic fixation or uptake from the soil) in the production of dry matter. - This finding is consistent with the data of Gebru (1989) who also found that gorse (mean = 2.13%) and a range of other shrub legumes had lower herbage N concentrations than white clover (3.52%) and lucerne (*Medicago sativa*) (2.70%). Lambert *et al.* (1989d) also reported low N concentrations for gorse (1.9%) and other shrub legumes compared with concentrations normally associated with species such as white clover which are reputedly demanding of high fertility.

3.4.6.2 Effect of rates of P and N on N concentration and N content - gorse and white clover

For both gorse and white clover, N concentration in new shoots generally increased significantly with increasing rate of applied P (Tables 3.15 and 3.17, 3.19 and 3.20; Figs 3.6, 3.8, 3.9 and 3.10). Similar effects of increasing rate of applied P on N concentration of legume herbage have been observed elsewhere e.g. Andrew and Robins (1969b) for a range of pasture legumes (several tropical and one temperate). There is some evidence that applied P enhances symbiotic N₂ fixation over and above any effect on the plant generally (e.g. Israel 1987). However most authors conclude that the evidence for this is not clearcut and express the view that P supply has its effect on the symbiotic N₂-fixing system primarily via effects on the host plant and photosynthate supply (eg Munns 1977; Robson 1978; Robson and Bottomly 1991). In this trial P × N interactions which were generally non-significant or occasionally positive (Tables 3.15, 3.17, 3.19 and 3.20; Fig 3.8) indicate that correcting P deficiency did not increase N supply to gorse (Robson and Bottomly 1991; Section 2.2.4).

Applied N either had no significant effect on or increased shoot N concentration of gorse and white clover (Tables 3.15, 3.17, 3.19 and 3.20). However the fact that increases in shoot N concentration were not accompanied by increased yields (Section 4.1), indicates that luxury consumption occurred (Macy 1936). The greater increase in mean shoot N concentration accompanying N application in white clover compared with gorse shoots (Table 3.20) suggests a greater tendency for luxury N uptake in white clover.

The explanation for relatively low shoot N concentrations in April 1991 compared with December 1990 (Figs. 3.6 and 3.8) may be similar to that offered for the low P values

(Section 3.4.5); namely that April 1991 was a period of almost nil growth in contrast to the rapid growth (requiring relatively greater shoot N concentration) recorded in December 1990 (Fig. 3.17), and that dry soil conditions may have reduced N uptake (Newman 1974; Garwood and Williams 1967a & b) and symbiotic N₂ fixation (Gibson 1977).

The decrease in shoot N concentration in April 1991 compared with December 1990 was proportionately less than the decrease in shoot P concentration (Figs 3.5, 3.6, 3.7 and 3.8). For the F cutting treatment, mean P and N concentrations in April 1991 were reduced to proportions of 0.48 and 0.69 respectively of their values in December 1990. For the I cutting treatment the equivalent proportions were 0.43 and 0.63 for P and N concentrations respectively. This is in agreement with the finding of Fisher (1980), working with *Stylosanthes humilis*, that the adverse effect of moisture stress on nutrient uptake is greater than on symbiotic N₂ fixation.

Shoot N contents for both the F and I cutting treatments showed quadratic responses to increasing rates of P application similar to those for dry matter yield (Figs 3.12, 3.14, 3.3 and 3.4).

N content was never significantly affected by N application (Sections 3.3.3.6.1 and 3.3.3.6.2). This reinforces the finding discussed previously for dry matter production (Section 3.4.1), that the symbiotic N₂-fixing system of gorse is able to meet the N requirements of the plant, under the conditions of this trial (Section 3.4.1).

3.4.6.3 Effect of N application on nitrate reductase activity (NRA)

The application of 200 kg N ha⁻¹ year⁻¹ (as NH₄NO₃) resulted in increased NRA in new shoots, old wood and roots of gorse in the field (Table 3.29). In February 1991 there were significant differences in NRA between plant parts, with greatest activity in roots, followed by old wood and new shoots. There were no significant N × plant part interactions indicating that the partitioning of NRA between plant parts was proportionally similar at both the nil and high N treatments. This contrasts with the finding of Andrews *et al.* (1984) that for temperate legumes the proportion of total NRA in the shoot increased as available nitrate increased. It should be noted, though, that the rates of NRA measured in this trial (Table 3.29) were very low compared with those of Andrews *et al.* (1984). This may have

been due to the fact that the first assay was done 38 days after the application of N fertilizer and soil nitrate levels were very low (Section 3.3.5.1; Table 3.30) and that on the second occasion, although soil nitrate levels were much greater (Table 3.30), the surface soil was very dry (Fig 3.17) and the nitrate may have been largely unavailable.

3.4.6.4 Effect of N application on N₂-fixing activity

Acetylene reduction assays were done on 5 nil N and 5 high N plots (Section 3.2.11.1). In three of the high N plots N₂-fixing activity was very low, but in the other two N₂-fixing activity was similar to that in the nil N plots, with the result that N₂-fixing activity in the high plots was not significantly lower overall than in the nil N plots (Table 3.31). A possible reason for the high N₂-fixing activity in two of the high N plots is low soil water content (Fig 3.17) which may possibly have lead to unavailability of the nitrate that was present in the soil (Table 3.31). It has been found that growth and nutrient uptake by legumes are more adversely affected by moisture stress than symbiotic N₂ fixation (Ahmed and Quilt 1980; Fisher 1980).

3.4.7 Effects of cutting frequency on yield, P and N concentrations, and P and N contents

3.4.7.1 Effects of cutting frequency on yield

For the 1990/91 growth season alone and for the 1989/90 and 1990/91 growth seasons in total, uncut gorse produced over twice as much dry matter as gorse cut twice-yearly (Table 3.13, Figs 3.3 and 3.4). The probable reason for this is that the uncut gorse was able to maintain a greater leaf area index, and was therefore able to acquire more carbon from the atmosphere and produce more dry matter. In contrast the twice-yearly cut gorse had the bulk of its photosynthetic area removed every time it was cut, and, particularly in the second growth season, never approached the degree of canopy closure which existed in the uncut plots, even at the ends of the intervals between cutting. There was almost complete canopy closure at the end of the second growth season in uncut plots receiving the higher rates of applied P (light interception measured in one P4 plot was 99.4% in full sunlight and 97.0% under overcast conditions). In the frequently cut plots there were always parts of the plots with no gorse canopy cover. It is well established that increased photosynthetic

surface area leads to increased growth rates and to increases in rates of other specifically energy demanding processes such as N_2 fixation (eg. Ryle *et al.* 1985). Lambert *et al.* (1989a) also observed much greater dry matter yield when gorse was cut infrequently (annually) compared with frequently (4 times per year). Rows of gorse plants were trimmed to 68 cm height and 43 cm width (Lambert *et al.* 1989a). Similar effects of cutting on yield have been observed for a range of other shrub legumes: tagasaste, tree medic (*Medicago arborea*), broom, and black locust (*Robinia pseudoacacia*) (Lambert *et al.* 1989a; Gebru 1989).

Thus, in a situation where it was being browsed by animals, it appears that dry matter yield of gorse would be considerably reduced compared with unbrowsed gorse.

3.4.7.2 Effect of cutting frequency on P concentration and P content

Cutting treatment had small but significant effects on mean P concentration with frequently cut gorse (F cutting treatment) having slightly higher P concentration in new (current growth seasons) shoots than uncut (I cutting treatment) gorse in December 1990 (0.19 and 0.17% for F and I respectively) and April 1991 (0.09 and 0.07% for F and I respectively) (Table 3.18). The reason for this is not clear, but it may be a dilution effect resulting from the much greater growth of the uncut compared with the twice-yearly cut plants (Sections 3.4.1 and 3.4.7.1). Radcliffe (1986) also observed greater P concentration in green foliage from smaller plants (regrowth from burning) than in green foliage from larger bushes (1-2 m tall, which were progressively grazed by goats down to about 30cm height). Mean P concentrations were 0.17% and 0.07% respectively for the small and large plants (Radcliffe 1986).

Cutting treatment had no significant effect on total P content for either the 1990/91 growth season or the two growth seasons combined (1989/91) (Section 3.3.3.6.3, Table 3.24), even though dry matter production in the I cutting treatment was more than twice that in the F cutting treatment (as discussed in Section 3.4.7.1). Thus, plants in both cutting treatments had similar capacities for P uptake and they also had similar critical P concentrations during the period of vigorous spring growth (0.19% and 0.18% for the F and I treatments respectively, Table 3.21). This suggests that in the I treatment, greater internal efficiency of P use and therefore greater growth compared with the F treatment occurred because of

the greater potential for translocation of P to new, actively growing shoot tips from older shoot tissue. The P contained in harvested shoot tissue was lost to the frequently cut plants, whereas the uncut plants appeared to be able to make more efficient use of the P taken up by transferring it from old to new tissue. P is readily translocated within plants (Bouma 1967; Morard 1970)). Dry matter production of gorse appeared to be limited by P availability up to the P3 rate of P (Figs 3.3 and 3.4).

3.4.7.3 Effect of cutting frequency on N concentration and N content

Cutting treatment had a significant effect on shoot N concentration only in April 1991 (Table 3.18), with mean N concentration being greater in the F treatment (1.86%) than in the I treatment (1.70%). Radcliffe (1986) also measured greater N concentrations in green foliage of smaller plants (mean = 2.8%, regrowth after burning) compared with larger gorse plants (mean = 1.8%, 1-2 m tall plants which were then reduced in size by goat grazing).

The N content of gorse shoots was significantly greater for the I treatment than the F treatment, for both the 1990/91 growth season alone and for both the 1989/90 and 1990/91 seasons combined, unlike P content which was very similar for the two cutting treatments (Table 3.24). N content was greater in the I treatment because greater growth by far outweighed slightly lower shoot N concentration compared with the F cutting treatment (Tables 3.13 and 3.18). Gorse growth was not limited by N supply (Table 3.8(b), Section 3.3.2.4), therefore the need to maximise the internal efficiency of N use by redistribution between plant parts was probably not so great as for P. Greater growth in the I cutting treatment resulted in a dilution effect and consequently slightly lower shoot N concentrations compared with the F cutting treatment.

3.4.8 Effects of rate of P, rate of N and cutting frequency on shoot growth

In both growth seasons shoot length increased with increasing rate of P but did not respond to N fertilization (Fig 3.15; Table 3.26). In the second growth season, shoot length was greater in the F than the I cutting treatment, and shoot length was less responsive to increasing rate of P application in the I cutting treatment than in the F cutting treatment. The interaction between rate of P and cutting treatment is illustrated in Fig 3.15(b). This suggests that the greater dry matter yield in the I compared with the F cutting treatment, and

the dry matter response to P in the I treatment, were largely the result of increased number rather than length of shoots. This is consistent with observation of the plants, although shoot counts were not done.

The responses of shoot length to the treatments in the trial were sufficiently similar to those of dry matter yield to suggest that rate of shoot elongation is a reasonable indication of rate of dry matter production within cutting treatments (Figs 3.3, 3.4 and 3.15).

3.4.9 Seasonal growth pattern of gorse

In both growth seasons of this trial most of the annual growth took place during the spring (Figs 3.16 & 3.17). One possible reason for the reduction in rate of shoot elongation during summer and autumn was low soil water content resulting in moisture stress and reduced nutrient availability (Section 3.3.4.2). Water contents of all three soil layers for which water content was measured (0-20 cm, 20-40 cm and 40-60 cm) were reduced to values which would be expected to cause reduced plant growth during the summer/autumn period (January to April) of both growth seasons (Sands and Rutter 1959; Jarvis 1963; Section 3.3.4.2). Low soil water contents may also cause decreased growth via reduced nutrient availability (Section 3.3.4.2), as discussed in Section 3.4.5.

The reduction in rate of shoot elongation may also be due, at least in part, to the reproductive cycle of the plant, with summer/autumn flowering and seed set being associated with decreased vegetative growth.

Lambert *et al.* (1989a) observed most dry matter production in summer (416 g m⁻¹ row) followed closely by spring (344 g m⁻¹ row) with very little in autumn (32 g m⁻¹ row) and winter (25 g m⁻¹ row). Rainfall at the site used by Lambert *et al.* (1989a) was approximately 1200 mm per year (compared with approximately 600 mm per year at the Springston trial reported here) and was reasonably evenly spread throughout the year. Comparison of data between the two trials suggests that summer growth of gorse at the Springston site reported here may have been curtailed because of dry soil conditions. However, even at the wetter site of Lambert *et al.* (1989a) there was little autumn growth, suggesting that gorse produces most of its annual dry matter during the spring summer period regardless of rainfall.

In summary, it appears that there may have been two factors operating to reduce summer/autumn growth:

- a) Low soil water contents, sufficient to reduce growth because of moisture stress and reduced nutrient availability.
- b) A change from a primarily vegetative growth phase to a primarily reproductive one, where flowering and seed set are associated with reduced vegetative growth.

The above two factors may be linked, because a degree of water stress can promote reproductive development in perennial legumes (such as white clover and lucerne) at the expense of vegetative growth (Zaleski 1970; Noggle and Fritz 1983).

3.4.10 Likely ability of gorse to withstand browsing

To be useful as a forage for goats, gorse must be able to regrow readily following browsing. The shoot growth data indicate that gorse should be able to withstand browsing by animals such as goats:

- a) Gorse produced abundant new shoots at the beginning of each growth season, which arose in all positions from the base of the plant to the terminals of the previous seasons shoots (visual observation).
- b) There was vigorous growth of shoots arising from a variety of positions (base of plant, mid-stem, terminal of previous seasons stem, Table 3.28). Greatest growth was recorded for basal and terminal shoots (Table 3.28).
- c) There was vigorous regrowth of plants defoliated to 20 cm height (Fig 3.1(b),(c) and (d)). Vigorous regrowth has also been measured by others (e.g. Radcliffe 1986; Lambert *et al.* 1989a).

3.5 CONCLUSIONS

- a) Gorse in its second growth season was more productive than unirrigated pasture
- b) Dry matter production was greatest in spring - early summer under the dryland conditions of this trial.
- c) Under conditions of low available soil P, gorse was very responsive to applied P, but less so than white clover.
- d) The P response curves of gorse differed from those of white clover. Whereas dry matter yield of gorse tended to decrease at high rates of P application, dry matter yield of white clover kept increasing over the range of P rates applied in this trial.
- e) Gorse had a much greater ability to acquire P from unfertilized soil than white clover.
- f) Gorse used P and N more efficiently in the processes of growth than white clover.
- g) The critical shoot P concentration of gorse (0.19%) was less than that of white clover (0.35%).
- h) Applied N ($200 \text{ kg ha}^{-1} \text{ year}^{-1}$) did not increase dry matter yields of gorse (or white clover) indicating that its symbiotic N_2 -fixing system provided sufficient N for the plant's requirements under the conditions of this trial.
- i) Over the two years of this trial dry matter production by uncut gorse was more than twice that of gorse cut twice yearly, presumably because uncut plants were able to maintain a greater leaf area index.
- j) Under the conditions of this trial, growth appeared to be limited by P uptake. The ability of uncut gorse to transfer P from old to new shoots, in combination with greater leaf area index, appeared to enable it to produce twice as much dry matter as gorse cut twice yearly.

CHAPTER 4

EFFECTS OF AVAILABLE PHOSPHORUS AND SOIL ACIDITY ON GORSE AND WHITE CLOVER GROWTH

4.1 INTRODUCTION AND AIMS

Gorse is present on over one million hectares of land in Zealand (Blaschke *et al.* 1981). It occupies a wide range of habitats, but is most abundant in extensively managed grassland and scrubland, particularly in low fertility hill country (Hunter and Blaschke 1986), and under medium to high rainfall (Bascand 1973). Soils on much of the land occupied by gorse (including northern, central and southern yellow brown earths, central yellow brown loams, and central and southern yellow grey earths) tend to be P deficient and have low pH (Gibbs *et al.* 1968; Raeside *et al.* 1968; During 1984; Hunter and Blaschke 1986). Thus gorse appears to tolerate low soil fertility and pH.

Gorse is reputed to be a calcifuge (Chater 1931; Meeklah 1979), and to have a soil acidifying effect by increasing soil humus levels in the field (Grubb and Suter 1970). Lime application was found to reduce emergence of container and field grown seedlings (probably because of competition from other species) (Phung *et al.* 1984), to either retard or increase the growth of container and field grown seedlings (Thompson 1974; Phung *et al.* 1984), to retard the growth of mature (0.5 m tall) plants in containers (Thompson 1974), and to enhance seedling nodulation (Phung *et al.* 1984).

Container grown gorse seedlings were responsive to P fertilization (single rates were compared with a nil rate) (Thompson 1974; Ivens and Mlowe 1983). Applied P resulted in an increased shoot:root ratio and an increased nodule number which was correlated with shoot weight (Ivens and Mlowe 1983).

The specific aims of this glasshouse trial were as follows:

- 1) To determine the tolerance of gorse to very low available P concentrations, and to compare its responsiveness to increasing rates of P with that of white clover.

- 2) To determine the tolerance of gorse to low soil pH and high soluble Al, and its responsiveness to liming in comparison with white clover.
- 3) To determine the effects of very low soil pH, high soluble Al and low available P on symbiotic N₂-fixing activity of gorse and white clover.

4.2 EXPERIMENTAL

4.2.1 Soil

The soil used in this experiment was material from the eluvial (E) horizon of a Katrine soil (Andic Haplorthod). Some chemical properties of this soil material are in Table 4.1. This soil was chosen because it has an extremely acid pH, contains much soluble Al and has little available P.

4.2.2 Trial design

The relative responses of gorse (*Ulex europaeus* L.) and white clover (*Trifolium repens* L.) to P fertilizer and lime were investigated in a pot experiment. Four rates each of applied P and lime, including zero rates of each, were factorially combined. There were four replicates of each treatment combination which were set out in 4 blocks. White clover and gorse pots were located in opposite halves of the blocks. Within half blocks pots receiving the different lime and P treatment combinations were located randomly and were re-randomised at regular intervals throughout the experiment.

4.2.2.1 Phosphorus treatments

P application rates were based on a P sorption isotherm (Appendix 4.1; Fox and Kamprath 1970) and are shown in Table 4.2. It was intended that the P2 rate of P would be sufficient for near maximum growth (Section 3.2.1.2.1).

Table 4.1 Chemical properties of soil - Katrine E. Horizon

pH (H ₂ O)	C (%)	N(%)	C/N	Olsen P (µg/g)	P retention (%)	Phosphate Ex. SO ₄ (µg/g)
4.2	2.3	0.10	23	4	50	2

CEC	Sum bases	Cation exchange (NH ₄ OAc @ pH7 me.%)					KCl Ex. Al (me.%)	0.02M CaCl ₂ -Al (ppm)	Reserve (me.%)	
		%BS	Ca	Mg	K	Na			Mg _r	K _c
15.7	1.04	7	0.75	0.27	0.02	0.00	13.8	80.4	3.4	0.36

Table 4.2 Phosphorus treatments - Lime/P experiment

Phosphorus Treatment	Target concentration of P in soil solution (ppm)	Rate of P applied (mg g ⁻¹ equivalent dry wt of soil)
P0	-	0
P1	0.1	0.186
P2	0.2	0.270
P3	0.3	0.325

P was applied in the form of calcium dihydrogen orthophosphate ($\text{Ca}(\text{H}_2\text{PO}_4)_2$), which was mixed uniformly throughout the soil 4 days before planting.

4.2.2.2 Lime treatments

Lime application rates based on a lime/pH curve (Appendix 4.2) and are shown in Table 4.3. The lime/pH curve was determined by adding progressively increasing quantities of CaCO_3 to 100 g equivalent dry weight of field moist soil (water content = 33.6%). The CaCO_3 was mixed uniformly throughout the soil. The lime/pH curve was based on pH measurements after 14 days, by which time pH had stabilised.

Table 4.3 Lime treatments - Lime/P experiment.

Lime rate	pH target	Rate of CaCO_3 applied (g 100g ⁻¹ equivalent dry wt of soil)
L0	4.34	0
L1	5.10	0.255
L2	5.80	0.685
L3	6.50	1.12

The lime (CaCO_3) was mixed uniformly throughout the soil to be used for the trial, 20 days before planting.

4.2.3 Plant culture

4.2.3.1 Planting

Planting was done on 9 November 1989. Plastic pots were used which had a total capacity of about 1.4 litres. 1150 g equivalent dry weight of field moist soil (water content = 33.6%) was packed into each pot. Plastic liners were used to prevent leaching of nutrients from the pots.

Because of its low germination percentage compared with white clover, and because it tended to germinate slowly over several weeks, the gorse seed was pregerminated (Section 3.2.3.1)

Pregerminated gorse seeds were planted into holes made at 4 uniformly spaced locations (2 seedlings per planting location) in each plot. For the white clover pots the soil was packed into the pots, except for sufficient to provide a layer approximately 3 mm deep over the surface of the pot. A minimum of 2 seeds were planted at each of 4 planting locations (same as for gorse) and then covered with the remaining soil. Because the white clover seeds had a very high germination percentage (93%), and because they germinated very rapidly and uniformly, they were not pre-germinated. At the first true leaf stage seedlings of both species were thinned to 4 per pot.

In order to be able to monitor changes occurring in the soil in the absence of plants, two fallow pots were packed for each lime/phosphorus treatment combination. The fallow pots were smaller because of the limited quantity of soil remaining. Each contained 515 g equivalent dry weight of soil.

4.2.3.2 Watering

Pots were regularly weighed and water applied to maintain a water content equivalent to a soil matric potential of -5 kPa (gravimetric water content = 38.6%). The water content at -5 kPa was determined using a tension table apparatus.

4.2.3.3 Rhizobial inoculation

Rhizobia were first applied 14 days after planting. Both the gorse and white clover plants were inoculated using peat cultures suspended in deionised water.

The gorse plants were inoculated with the same strain of *Bradyrhizobium* used for the Springston field trial (Section 3.2.3.2). Five ml of a suspension containing approximately 3.5×10^8 rhizobia was applied to the base of each plant. Numbers of rhizobia were determined by dilution plate counts (Sirockin and Cullimore 1969).

The white clover plants were inoculated using a commercial peat culture of *Rhizobium* strain cc275e. Five ml of a suspension containing approximately 5×10^8 rhizobia was applied to the base of each plant.

A second inoculation was done on day 43. Approximately 1.6×10^8 rhizobia were applied to the base of each gorse plant, and 3.3×10^8 to the base of each white clover plant.

4.2.3.4 Basal nutrient solutions

To ensure that nutrients other than P and N were not limiting growth, nutrient solutions were applied at rates and times shown in Table 4.4. When the first nutrient solution was applied (day 27), gorse plants were typically 1-2 cm tall and had about 3 true leaves. White clover was at the first trifoliate leaf stage. B and Fe were applied separately from the other nutrients. Quantities of nutrients were designed to be well in excess of total plant requirements. The final nutrient application took place shortly after the first cut. Fallow pots received the same quantities of nutrients per unit weight of soil as the larger pots.

Table 4.4 Basal nutrient solutions Lime/P experiment

Element	Stock Solution	day 27		day 44		day 66		day 84	
		stock/l (ml)	element/pot (mg)						
K	KCl (1 mol l ⁻¹)	51	100						
K S	K ₂ SO ₄ (0.5 mol l ⁻¹)			51.2	100 41	25.6	50 20.5	128	250 102.6
Mg S	MgSO ₄ (1 mol l ⁻¹)	16	19.4 25.6	16	19.4 25.6	8	9.7 12.8	20.6	25 33.0
Mn	MnCl ₂ (10 g Mn/l)	10	5	10	5				
Zn	ZnCl ₂ (6 g Zn/l)	10	3	10	3				
Cu	CuCl ₂ (6 g Cu/l)	10	3	10	3				
Mo	Na ₂ MoO ₄ (1 g Mo/l)	6	0.5						
Co	CoCl ₂ (0.2 g Co/l)	10	0.1						
B	Na ₂ B ₄ O ₇ (1.2 g B/l)	10	0.6	10	0.3				
Fe	EDTA Ferric monosodium salt (3.334 g Fe/l)	60	5						

All nutrients apart from B and Fe were applied together, and the volume of nutrient solution applied at each application time was 50ml. B and Fe were applied in 25ml volumes at each application time.

4.2.3.5 Glasshouse temperatures

Mean maximum/minimum glasshouse temperatures over the period of the experiment were 28.5/15.0°C up to the first harvest and 30.0/17.0°C between the first and second harvests.

4.2.4 Acetylene reduction assays

4.2.4.1 Incubation and gas sampling

Acetylene reduction assays were done on all pots, entire replicates at a time for individual species during the week before the final harvest of that species. Intact plants in pots were incubated for exactly 2 hours between approximately 11.00 a.m. and 1.00 p.m. (N.Z. daylight saving time). Incubation temperatures varied slightly from day to day but were always within the range 20-26°C. The temperature range during individual incubation periods was generally less than 2°C. Pots were enclosed in 5 litre gas-tight "Polypails". The lids were fitted with rubber septa to allow for introduction of acetylene (C_2H_2) and sampling of gases. 350 ml of air was replaced by acetylene to give a pC_2H_2 (partial pressure of C_2H_2) of approximately 0.08 atmospheres. At the end of the incubation period, gas in the containers was mixed using a large syringe, and three 1 ml gas samples were taken using disposable plastic syringes. The syringes were sealed for storage by plunging their needles into rubber bungs. Samples were stored for no longer than five hours before analysis.

4.2.4.2 Gas analysis

Gas samples were analysed for ethylene and acetylene using a Shimadzu GC-8A gas chromatograph fitted with a flame ionisation detector. Attached to this was a Shimadzu C-R3A Chromatopac integrator which printed out peak areas and retention times. The column was 0.5 m long, made from 6 mm internal diameter stainless steel tubing, and packed with "Haye Sep N" 80/100 mesh. The conditions for analysis of the gas samples were as follows:

Temperature programme: isothermal

Column temperature: 80°C

Injector and detector temperatures: 110°C

Carrier gas flow rate: 30 ml per minute

4.2.4.3 Calculation of ethylene production

C_2H_4 concentrations were calculated as described by Sinclair 1973, with reference to standards containing concentrations of C_2H_4 and C_2H_2 covering the range of concentrations found in the samples.

The standards were made up in 50 ml conical flasks sealed with Gallenkemp "suba seals". To ensure that there was no leakage 2 ml of mercury was injected into the flasks, and they were stored upside down with the mercury covering the suba seals. The C_2H_2 and C_2H_4 were introduced into the flasks through the suba seals using high precision gas-tight syringes.

4.2.5 Harvests

Plants were first harvested on days 77 (white clover) and 78 (gorse). The plants were cut level with the tops of the pots (3.5 cm above soil level). White clover regrew more rapidly than the gorse, so the clover pots had their final cut on day 110, before the gorse pots on day 125. At the final harvest plants were cut at soil level. The soil in the pots was then cut in half vertically. The roots were washed from one half, while the other half, after removal of the large roots, was retained for future analysis. After rinsing thoroughly, shoot and root samples were dried to constant weight at 70°C.

4.2.6 Chemical analysis of plant and soil samples

Unless otherwise stated, methods of analysis of plant and soil samples are as described in section 3.2.12.

CaCl₂-Al

Measurement of CaCl₂-Al was based on the method of Hoyt and Nyborg (1972). Ten g of soil was shaken on an end-over-end shaker for 1 hour with 20 ml of 0.02 mol l⁻¹ CaCl₂. The supernatant was filtered (Whatman no. 42 filter paper) and Al concentration in the filtrate determined using atomic absorption spectroscopy.

Shoot element concentrations apart from N and P

Shoot element concentrations apart from N and P (Table 4.21) were determined using X-ray fluorescence (XRF).

4.2.7 Statistical analysis

Analyses of variance were done as described in Section 3.2.14. For the CaCl_2 -Al data (Table 4.7) the following transformation gave residuals which best satisfied the analysis of variance assumptions : transformed value = $\ln(\text{value} + 3)$.

Genstat incorporates a powerful algorithm for the analysis of unusual designs. There was a need to use this because plant P and N, and Olsen P were measured for only 10 of the 16 lime and P treatment combinations, and CaCl_2 -Al was measured for 13 of the 16 treatment combinations (Tables 4.7 and 4.8; Figs 4.5-4.8). For these sets of data the treatment sum of squares for the 10 or 13 treatment combinations was separated by the use of contrast matrices into partitions corresponding to the following effects:

lime - linear response

lime - quadratic response

lime - cubic response, which is not emphasised in this analysis as it can only be appropriately considered if there are more than four levels of a factor. Hence it is referred to as lack of fit (Steel and Torrie 1980).

P - linear response

P - quadratic response

P - cubic response (referred to as lack of fit)

Lime linear response \times P linear response

Orthogonal polynomials were calculated to derive the appropriate contrast coefficients.

Near maximum growth of both gorse (Section 4.3.2.1) and white clover was obtained at the L1 rate of lime and P1 rate of P application (Tables 4.2 and 4.3). Because of the lack of intermediate rates between L0 and L1, and P0 and P1, response curves are not presented. It was felt that additional points in these regions would be needed in order to properly determine the shape of such curves.

4.3 RESULTS

4.3.1 Effects of treatments on soil properties

4.3.1.1 pH

Increases in rate of lime application resulted in increases in pH (Table 4.5). Species and rate of P also had significant effects on soil pH (Table 4.5). At the end of the experiment, mean pH in the white clover pots (5.01) was less than that in the gorse pots (5.14).

The species \times lime, species \times P and lime \times P interactions were all significant (Table 4.5).

With regard to the species \times lime interaction (Table 4.5(b)), pH in the white clover pots was lower than that in the gorse pots at all rates of lime, but the differences appeared to increase with increase in lime rate from L0 to L1 to L2 and then decline at L3. The differences appeared to be greatest in those lime treatments where plant growth was greatest (Table 4.5(b), Figs 4.1 and 4.2).

Increasing rates of P were associated with significantly increased soil pH in gorse pots, but not in white clover pots (Table 4.5(c)). pH in white clover pots was significantly less than in gorse pots at all but the P0 rate of P, where there was very little clover growth (Table 4.5; Figs 4.1 and 4.2).

At the L0 rate of lime, there was a significant increase in pH from the P0 to the P1 rate of P, but no further increase with increasing rate of P (Table 4.5(d)). At the L1 and L2 rates of lime there were no significant increases in pH with increasing rate of P. At the L3 rate of lime, pH at the P2 rate of P was greater than at the P0 or P3 rates (Table 4.5(d)).

Table 4.5 Effects of species, and rates of lime and P application on soil pH - lime/P experiment

(a) Summary of analysis of variance table (end of experiment, excluding fallow pots)

Source of variation (treatment or interaction)	Level of significance
Species	*
Lime	***
P	*
Species × lime	*
Species × P	***
Lime × P	***
Species × lime × P	ns (p=0.051)

Note: Significance levels are shown by *** (p<0.001), ** (p<0.01), * (p<0.05) and ns (nonsignificant).

(b) Soil pH - species × rate of lime means

Species	Rate of lime				LSD (p<0.05)
	L0	L1	L2	L3	
Gorse	4.00	4.61	5.33	6.62	All means: 0.062
White clover	3.92	4.48	5.14	6.52	Within species: 0.048

(c) Soil pH - species × rate of P means

Species	Rate of P				LSD
	P0	P1	P2	P3	
Gorse	5.08	5.14	5.17	5.18	All means: 0.062
White clover	5.02	5.01	5.04	4.98	Within species: 0.048

Table 4.5 continued

(d) Soil pH - rate of lime \times rate of P means

Rate of lime	Rate of P				LSD
	P0	P1	P2	P3	
L0	3.86	3.98	3.98	4.01	0.068
L1	4.54	4.51	4.57	4.56	
L2	5.26	5.22	5.24	5.23	
L3	6.54	6.59	6.62	6.52	

Soil pH values for all treatments at the end of the experiment are presented along with pH of the fallow pots and pH at the beginning of the experiment (Table 4.6). No statistical analysis was done on the data from the beginning of the experiment because there was no replication, or on the fallow pots (2 replicates only). At the L0-L2 rates of lime, pH in the fallow pots appears similar to that in the beginning samples (Table 4.6). At the L3 rate of lime, pH values in the fallow pots appear to be slightly less than in the beginning samples. pH values in the gorse pots at the end of the experiment appeared to be generally similar to values in the fallow pots, but values in the white clover pots tended to be slightly lower, especially where there was rapid clover growth (i.e. treatments L0 P2-P3; L1 P1-P3; L2 P1-P3) (Table 4.6; Figs 4.1 and 4.2).

Table 4.6 Soil pH, all treatments lime/P experiment

Treatment	Beginning of experiment	End of experiment		
		Fallow pots	Gorse pots	Clover pots
L0 P0	3.96	3.89	3.90	3.82
P1	4.01	4.08	3.98	3.99
P2	4.05	4.16	4.04	3.93
P3	4.02	4.13	4.09	3.94
L1 P0	4.68	4.52	4.56	4.53
P1	4.69	4.71	4.60	4.42
P2	4.72	4.72	4.66	4.49
P3	4.70	4.71	4.63	4.49
L2 P0	5.41	5.23	5.28	5.25
P1	5.43	5.33	5.34	5.10
P2	5.43	5.44	5.35	5.12
P3	5.41	5.42	5.36	5.10
L3 P0	6.97	6.51	6.58	6.50
P1	6.91	6.65	6.63	6.56
P2	6.99	6.61	6.64	6.61
P3	6.91	6.58	6.63	6.41
LSD (within species comparisons)			0.083	0.108
LSD (between species comparisons)			0.104	

4.3.1.2 Soluble Al

The influence of species, lime and P on 0.02 mol l⁻¹ CaCl₂-extractable Al (CaCl₂-Al) concentrations are summarised in Table 4.7. CaCl₂-Al had been reduced to very low concentrations at the L2 rate of lime (mean = 0.8 µg g⁻¹), well below concentrations at which Al toxicity might be expected (>3 µg g⁻¹) (Edmeades *et al.* 1983; Hume *et al.* 1988). Also, dry matter yield had ceased to increase with increase in rate of lime application beyond the L2 rate (Figs 4.1 and 4.2). Therefore CaCl₂-Al concentration was measured for the L0-L2 rates of lime only, except at the P2 rate of P, when the L3 rate of lime was included as a check on Al concentration at the greatest rate of lime and at adequate P for near maximum plant growth.

Increasing rates of lime application caused substantial decreases in CaCl₂-Al (Table 4.7(b)). There was also a significant effect of rate of applied P on CaCl₂-Al (Table 4.7(a)). Within rates of lime, increasing rates of P resulted in significant decreases in CaCl₂-Al

except where Al concentrations were very low to begin with (L2 and L3 rates of lime) (Table 4.7(b)). The pattern of change in $\text{CaCl}_2\text{-Al}$ with increase in rate of P for the L1, white clover samples was different from that for gorse at the same lime rate or for either species at the L0 rate of lime application (Table 4.7(b)). This appears to have contributed to the significant lime \times P, P \times species and lime \times P \times species interactions (Table 4.7(a)) and will be discussed in relation to plant growth in Section 4.4.4.

There was a significant effect of species on $\text{CaCl}_2\text{-Al}$ at the end of the experiment ($p = 0.004$), with final concentrations of $\text{CaCl}_2\text{-Al}$ being less in gorse pots (mean = $22.8 \mu\text{g g}^{-1}$) than in white clover pots (mean = $26.7 \mu\text{g g}^{-1}$) (Table 4.7).

$\text{CaCl}_2\text{-Al}$ concentrations in soils growing gorse appeared to change little throughout the experiment but appeared to increase when white clover was grown (no statistical analysis was done on analyses of samples from the beginning of the experiment (before potting) because these were not replicated) (Table 4.7).

Table 4.7 Effects of species lime and P on soluble Al ($\text{CaCl}_2\text{-Al}$) - lime/P experiment

(a) Summary of analysis of variance table (end of experiment only)

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	**			
Treatment (lime & P)	***			
Lime		***	***	***
P		***	***	ns
Lime \times P	***			
Treatment \times species	***			
Lime \times species		***	***	***
P \times species		***	ns	ns
Lime \times P \times species	*			

See Table 4.5 for description of significance levels

The data were log-transformed as follows: transformed value = $\ln(\text{value} + 3)$

Table 4.7 continued

(b) 0.02 mol l⁻¹ CaCl₂-extractable Al (µg Al g⁻¹ soil) - lime/P experiment

Treatment	Beginning of experiment	End of experiment	
		gorse	white clover
LOP0	92.3	95.4 (4.59)†	99.5 (4.63)
P1	69.1	67.1 (4.25)	69.5 (4.28)
P2	59.7	57.5 (4.10)	68.6 (4.27)
P3	54.7	48.6 (3.94)	64.5 (4.21)
L1P0	7.1	8.0 (2.39)	8.4 (2.43)
P1	5.5	6.6 (2.26)	13.6 (2.81)
P2	4.7	5.4 (2.12)	10.1 (2.57)
P3	4.5	5.0 (2.07)	9.4 (2.51)
L2P0	0.7	0.7 (1.30)	0.7 (1.31)
P1	0.7	0.7 (1.31)	1.0 (1.39)
P2	0.6	0.7 (1.31)	1.0 (1.39)
P3	0.7	0.5 (1.25)	1.0 (1.38)
L3P2	0.2	0.1 (1.14)	0.3 (1.18)
‡ LSD p<0.05 (within species comparisons)		(0.08)	
‡ LSD p<0.05 (between species comparisons)		(0.09)	

† Numbers in brackets are means of log-transformed values

‡ LSD's for use with means of log-transformed values

4.3.1.3 Available P

Available phosphorus (Olsen P) was measured for all rates of P at the L0 and L1 rates of lime, because dry matter yield generally responded to lime only up to the L1 rate of application (Figs 4.1 and 4.2). Olsen P concentrations were also measured for the L2P2 and L3P2 treatments, to follow any effects of the higher rates of lime at an adequate rate of P for vigorous plant growth.

Olsen P concentrations increased with increasing rate of P application (Table 4.8). Rate of lime application also had a significant effect on Olsen P, with concentrations tending to decline with increase in lime rate from L0 to L1, but not at the P0 rate of P (Table 4.8). There was also a significant effect of species on Olsen P with final values being less in white clover (mean = $41 \mu\text{g g}^{-1}$) than gorse pots ($46 \mu\text{g g}^{-1}$) (Table 4.8). The significant rate of P \times species interaction appeared to arise as a result of similar Olsen P concentrations for the two species at the P0 rate of P, but greater concentrations in gorse compared with white clover pots at the P1-P3 rates of applied P (Table 4.8).

For the reasons given previously, statistical analysis was not done for the beginning of experiment or fallow pot data. However, there appears to have been a slight decline in Olsen P concentration in the fallow pots compared with the samples taken at the beginning of the experiment for all except the P0 rate of applied P (Table 4.8(b)). Olsen P concentrations in the gorse pots appear to have been similar to those in the fallow pots, whereas those in the clover pots appear to have been less except at the P0 rate of applied P (Table 4.8).

Table 4.8 Effects of species, and rates of lime and P on available P (Olsen P) - Lime/P experiment

(a) Summary of analysis of variance table (end of experiment only)

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	**			
Treatment (lime and P)	***			
Lime		***	***	***
P		***	ns	ns
Lime × P	***			
Treatment × species	***			
Lime × species		ns	ns	ns
P × species		***	ns	ns
Lime × P × species	ns			

See Table 4.5 for description of significance levels

(b) Olsen P ($\mu\text{g g}^{-1}$) - lime/P experiment

Treatment	Beginning of experiment	Fallow pots	End of experiment	
			Gorse pots	Clover pots
L0P0	4	4	4	4
P1	49	44	44	41
P2	70	61	61	53
P3	84	73	73	65
L1P0	3	4	3	4
P1	46	43	41	34
P2	62	58	57	49
P3	74	68	69	58
L2P2	64	61	55	50
L3P2	61	54	56	50
LSD $p < 0.05$ (within species comparisons)			2.6	
LSD $p < 0.05$ (all comparisons)			2.8	

4.3.2 Plant growth

4.3.2.1 Shoot growth

Patterns of shoot growth were similar at both harvests, for both gorse and white clover. Therefore discussion of shoot growth will be confined to total shoot growth from the two harvests. (Mean shoot weights of gorse and white clover were 1.21 and 3.80 g respectively at the first harvest and 2.22 and 4.23 g respectively at the final harvest.)

An initial analysis of variance was done including both species. There were indications of unequal variance for the two species and highly significant ($p < 0.001$) species \times lime, species \times P and species \times lime \times P interactions. Therefore separate analyses of variance were done for the two species (Table 4.9):

Table 4.9 Effects of rates of lime and P application on total shoot dry weight of gorse and white clover, lime/P experiment - summary of analyses of variance for individual species

Source of variation (treatment or interaction)	Level of significance	
	Gorse	Clover
Lime	***	***
P	***	***
Lime \times P	**	***

See Table 4.5 for description of significance levels.

Mean shoot dry weight of white clover (8.04 g) was significantly greater than that of gorse (3.43 g) ($p < 0.001$).

For gorse, at the L0 rate of lime, there were significant increases in shoot weight with increase in rate of P, up to the P3 rate of P (Fig 4.1(a)). In contrast, at the L1-L3 rates of lime, shoot weight increased significantly with increase in rate of P from the P0 to the P1 rate, with no further significant change at the P2 and P3 rates.

At the P0 rate of applied P, gorse shoot weight increased progressively from the L0 to the L2 rate of lime (Fig 4.1(a)). At the P1 and P2 rates of P, shoot weight increased

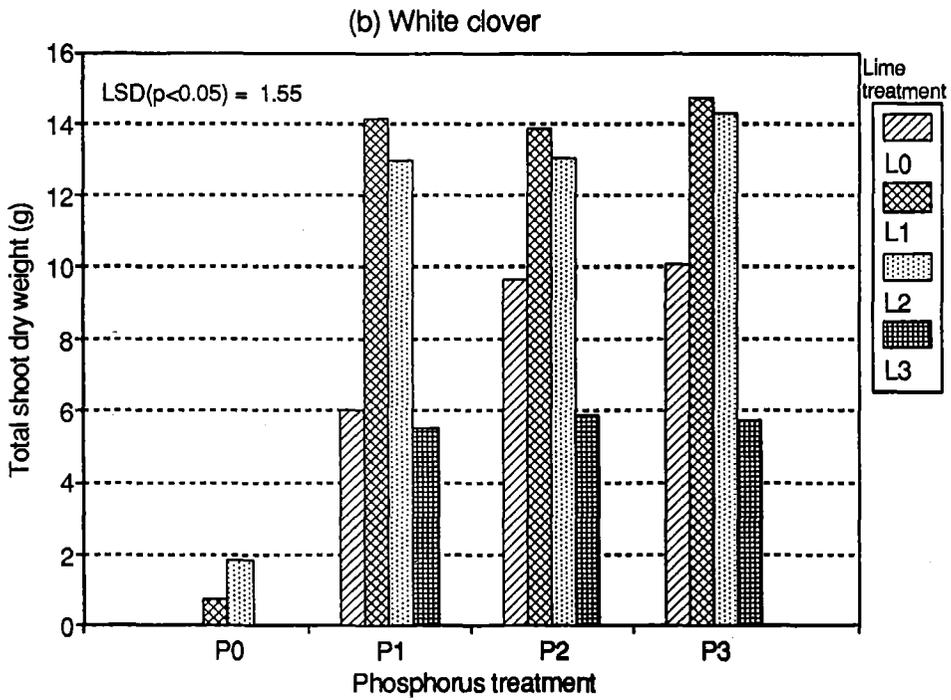
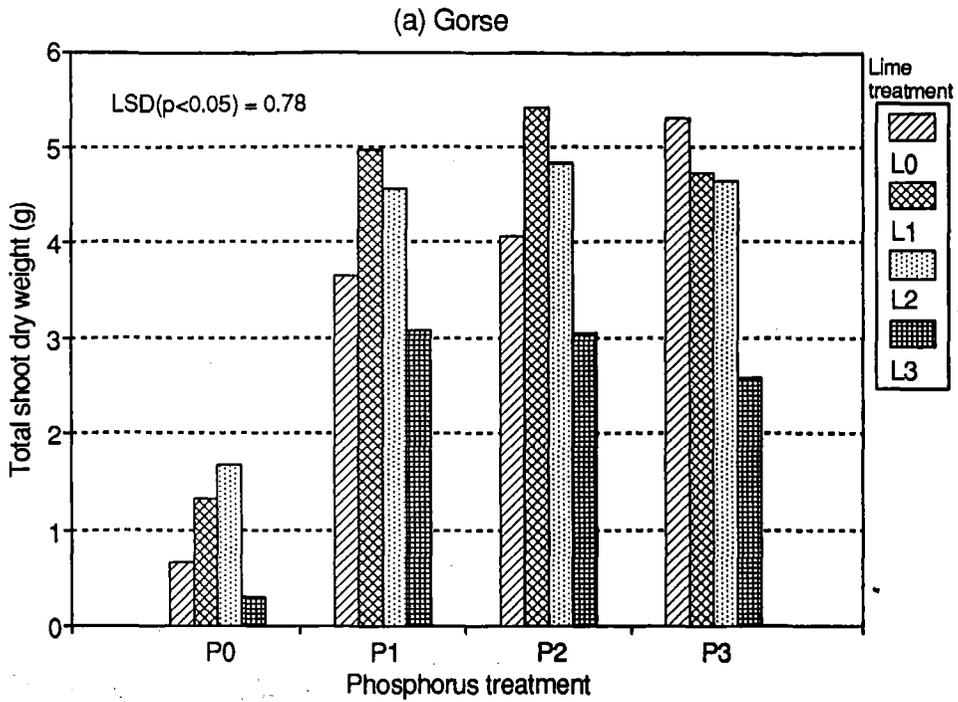


Fig. 4.1 Effects of rate of phosphorus and rate of lime application on total shoot dry weight of gorse and white clover (g per pot) grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

significantly from the L0 to the L1 rate of lime, showed no significant change at the L2 rate of lime, then declined sharply at the L3 rate of lime (Fig 4.1(a)). At the P3 rate of applied P, shoot growth was similar at the L0-L2 rates of lime, but again declined sharply at the L3 rate (Fig 4.1(a)).

For white clover at the L0 rate of lime, there were significant increases in shoot dry weight only up to the P2 rate of P (Fig 4.1(b)). The P3 rate of P did not compensate for the absence of lime as it did in the LOP3 treatment for gorse. At the L1-L3 rates of lime, shoot growth responses to increasing rates of P followed similar patterns to those described for gorse (Fig 4.1).

Responses of white clover shoot weight to increasing rates of lime followed similar patterns to those for gorse except for a positive response to the L1 rate of lime at the P3 rate of P (Fig 4.1).

The responsiveness of white clover to both lime and P appeared to be greater than that for gorse, where responsiveness is defined as the increase in dry matter yield gained in response to applied lime or P, divided by near maximum dry matter yield. This concept will be treated more thoroughly in section 4.3.2.4

For this experiment, near maximum yield is defined as dry matter yield which is not significantly less than the greatest achieved. The lowest Olsen P concentration associated with near maximum yield of gorse was $41 \mu\text{g g}^{-1}$ (L1P1 treatment) (Fig 4.1(a); Table 4.8). The lowest pH and greatest $\text{CaCl}_2\text{-Al}$ concentration associated with near maximum yield of gorse were 4.09 and $48.6 \mu\text{g g}^{-1}$ respectively (LOP3 treatment) (Fig 4.1(a), Tables 4.6 and 4.7).

Near maximum yield of white clover (L1P1 treatment) was associated with Olsen P = $34 \mu\text{g g}^{-1}$, pH = 4.42 and $\text{CaCl}_2\text{-Al} = 13.6 \mu\text{g g}^{-1}$ (Fig 4.1(b), Tables 4.6-4.8).

Significant depression in gorse growth (compared with the greatest achieved in this experiment) was associated with Olsen P = $3 \mu\text{g g}^{-1}$ (L1P0 treatment), pH = 3.98 and $\text{CaCl}_2\text{-Al} = 67.1 \mu\text{g g}^{-1}$ (LOP1 treatment) (Fig 4.1(a), Tables 4.6-4.8).

Significant depression in white clover growth was associated with Olsen P = 4 $\mu\text{g g}^{-1}$ (treatment L1P0), pH = 3.99 and $\text{CaCl}_2\text{-Al} = 69.5 \mu\text{g g}^{-1}$ (L0P1 treatment) (Fig 4.1(b), Tables 4.6-4.8).

Olsen P and $\text{CaCl}_2\text{-Al}$ values refer to soil samples taken after the second harvest; in some instances these properties were differentially affected by species (Tables 4.6-4.8). For example CaCl_2 in the L1P1 treatment, associated with near maximum white clover growth, was increased from 5.5 $\mu\text{g g}^{-1}$ at the beginning of the experiment to 13.6 $\mu\text{g g}^{-1}$ at the end (Table 4.7).

4.3.2.2 Root growth

An initial analysis of variance was done including both gorse and white clover. As for shoot dry weight there were indications of unequal variance for the two species and significant species \times lime, species \times P ($p < 0.001$ for both) and species \times lime \times P ($p < 0.01$) interactions. Therefore separate analyses of variance were done for the two species (Table 4.10).

Table 4.10 Effects of rates of P and lime application on total root dry weight of gorse and white clover, lime/P experiment - summary of analyses of variance for individual species

Source of variation (treatment or interaction)	Level of significance	
	Gorse	Clover
Lime	***	***
P	***	***
Lime \times P	ns	**

See Table 4.5 for description of significance levels

For gorse, the response patterns of root growth to increasing rates of applied P (Fig 4.2) were generally similar to those of shoot growth (Fig 4.1), except that at the L0 rate of lime there was no significant increase in root growth beyond the P1 rate of applied P (similarly

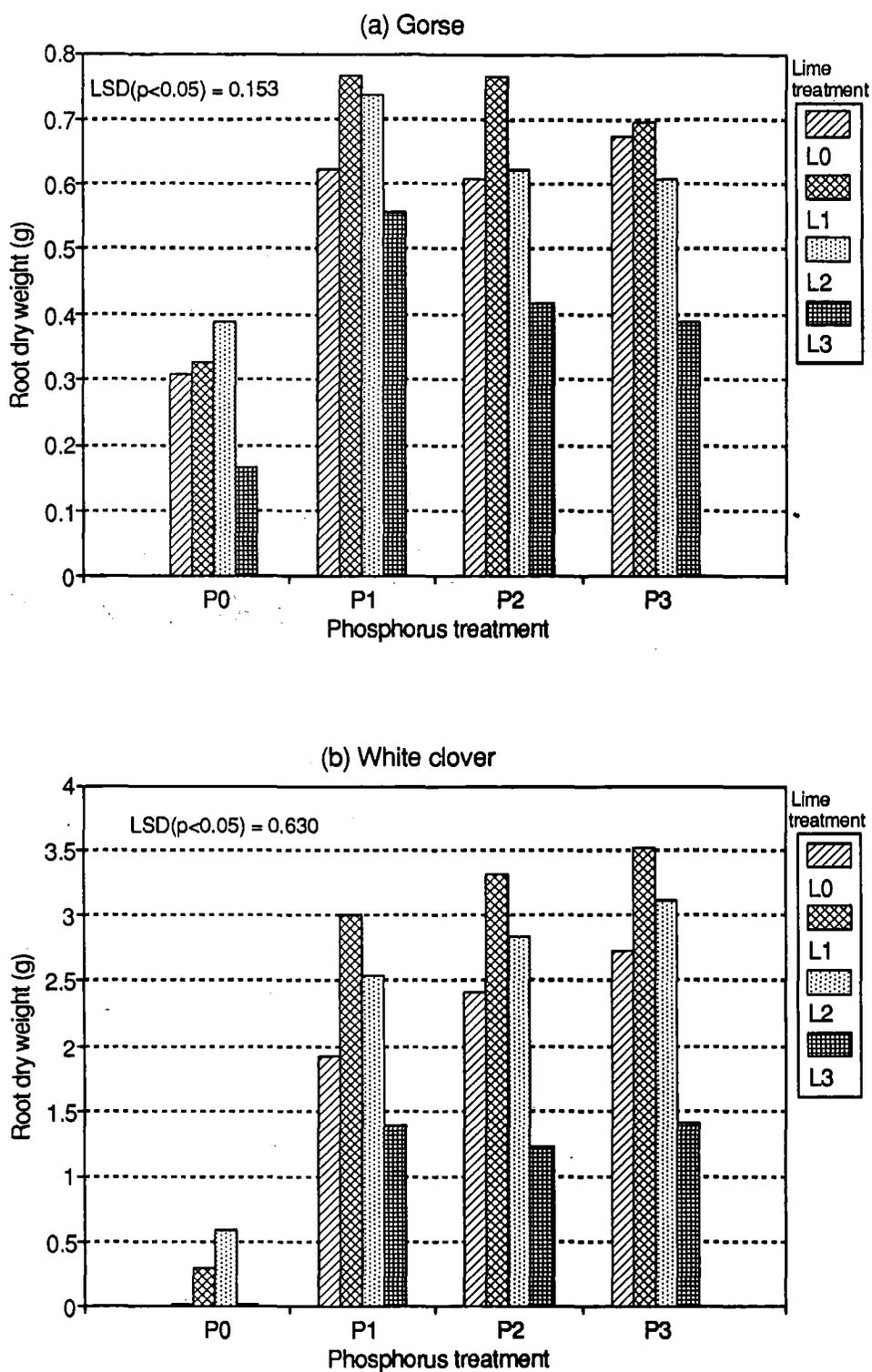


Fig. 4.2

Effects of rate of phosphorus and rate of lime application on root dry weight of gorse and white clover (g per pot) grown the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

to the L1 and L2 rates of lime), whereas shoot weight increased up to the P3 rate. This was reflected in the lack of a significant lime \times P interaction for gorse root weight (Table 4.10). Root growth responses to lime for gorse also generally followed the same pattern as for shoot growth. For gorse, the responsiveness (as defined in section 4.3.2.1) of root growth to increasing rates of lime and P appeared to be lower than that of shoot growth (Figs 4.1 and 4.2)

For white clover, the response patterns of root growth to increasing rates of lime and P (Fig 4.2) were very similar to those for shoot growth (Fig 4.1).

Near maximum root growth of both gorse and white clover (definition analogous to that for near maximum shoot growth in previous section) was associated with the same Olsen P concentrations, pH values and $\text{CaCl}_2\text{-Al}$ concentrations as near maximum shoot growth (Section 4.3.2.1, Figs 4.1 and 4.2, Tables 4.6-4.8). Depression in root dry matter yield of gorse and white clover were also associated with the Olsen P, pH and $\text{CaCl}_2\text{-Al}$ values associated with depression in shoot dry matter yield (Fig 4.2; Tables 4.6 - 4.8).

4.3.2.3 Shoot:root ratio

Shoot:root ratio was calculated from shoot and root weight at the final harvest. There was a significant species effect on shoot:root dry weight ratio (Table 4.11), with the ratio being significantly greater for gorse (mean = 4.0) than for white clover (mean = 2.3). There were also significant effects of lime and P and significant species \times P and lime \times P interactions (Table 4.11). For gorse alone, there were significant lime and P effects on shoot:root ratio, and a significant lime \times P interaction. In contrast, for white clover there was no significant P effect (Table 4.11).

The main features of the shoot:root ratio data are as follows:

- 1) The shoot:root ratio of gorse increased with increase with increase in rate of P from P0 to P1, at the L0 rate of lime application, but that of white clover did not (Fig 4.3).
- 2) Shoot:root ratio of gorse increased with increase in rate of lime from L0 to L1 at the P0 rate of applied P, then declined from L2 to L3 (Fig 4.3). It appeared that lime and P

application had similar effects in raising shoot:root ratio of gorse. At the P2 rate of P there was an increase in shoot:root ratio from the L0 to the L2 rate of lime (Fig 4.3).

3) There were no significant increases in shoot:root ratio of white clover with increasing rates of P application, except at the L3 rate of lime.

4) For white clover, the increase in shoot:root ratio associated with the increase in lime rate from L0 to L2 at the P0 rate of applied P, was not matched by a similar response to applied P as occurred with gorse (Fig 4.3). Shoot:root ratio declined in the L3P0 treatment. At the P1 to P3 rates of P, shoot:root ratio increased from the L0 to the L3 rates of lime. The high ratios at L3 were associated with decreases in dry matter yield (Fig 4.1).

5) P responses at the L3 rate of lime were different from those at other lime rates, for both species (Fig 4.3). At the L3 rate of lime both species were more responsive to P and reached near maximum shoot:root ratio at higher rates of P compared with the L0 to L2 rates of lime.

Table 4.11 Effects of rates of lime and P application on shoot:root dry weight ratio of gorse and white clover, lime/P experiment - summary of analysis of variance tables for species together and individually

Source of variation (treatment or interaction)	Level of significance		
	Gorse and clover	Gorse	Clover
Species	***		
Lime	***	**	*
P	***	***	ns
Lime × P	***	***	*
Species × lime	ns		
Species × P	***		
Species × lime × P	ns		

See Table 4.5 for description of significance levels.

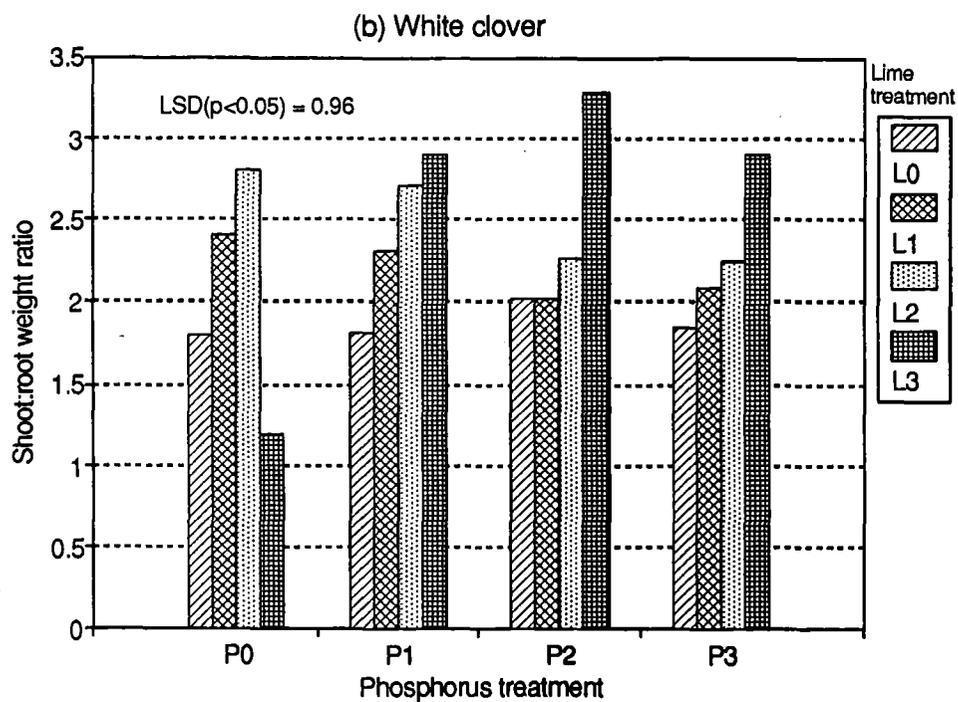
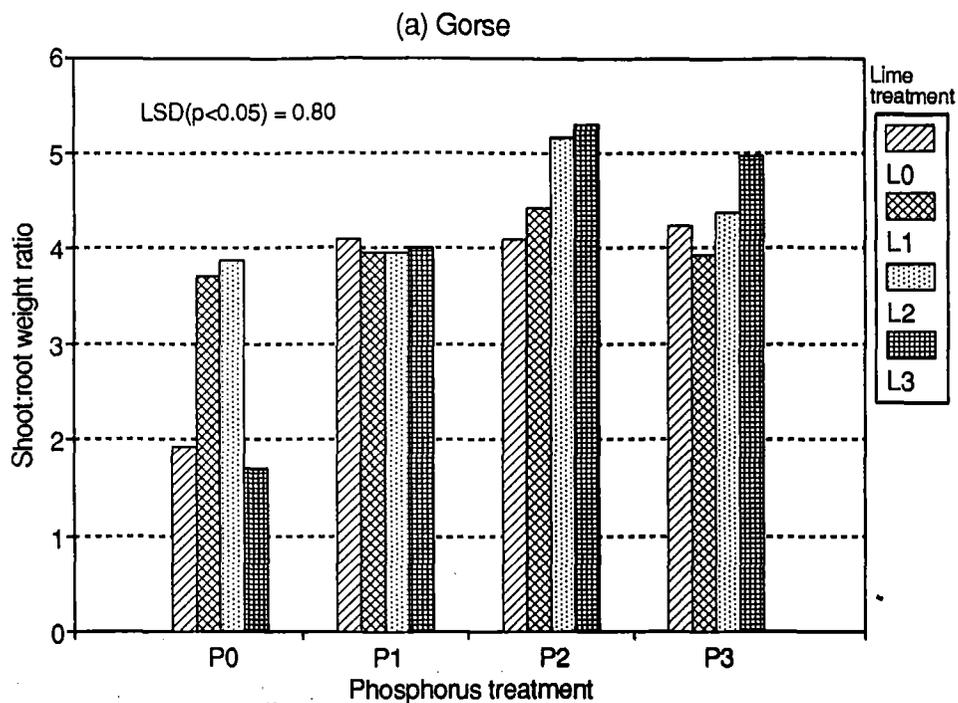


Fig. 4.3

Effects of rate of phosphorus and rate of lime application on the shoot:root dry weight ratio of gorse and white clover grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

4.3.2.4 Responsiveness of gorse and white clover to applied P and lime

The responsiveness of gorse and white clover to applied P and lime are compared in Tables 4.12 and 4.13. Responsiveness is defined in Section 3.2.14. In this experiment Y_0 is the yield without applied P or lime, and Y_m is near maximum yield (defined in Section 4.3.2.1) achieved by the application of lime or P. Curves were not fitted to the data in this experiment (Section 4.2.7), so values for Y_m were taken from treatments which appeared to support near maximum yield rather than from fitted curves as in Section 3.2.14. The treatments upon which Y_0 and Y_m are based are shown in Tables 4.12 and 4.13. Interpretation of responsiveness values is discussed in Section 3.3.2.2.

Table 4.12 Responsiveness of gorse and white clover to applied P - lime/P experiment (based on treatments L1P0 and L1P1)

Plant part (dry weight)	Responsiveness to applied P (Section 4.3.2.4)		Significance of between species differences
	Gorse	White clover	
Total shoot	0.74	0.95	***
Root	0.57	0.91	***
Total plant	0.71	0.94	***

See Table 4.5 for description of significance levels.

The values for responsiveness to applied P (Table 4.12) are based on treatments L1P0 (Y_0) and L1P1 (Y_m). The L1 rate of lime was used because it generally appeared to support most growth for both species and therefore appeared to allow the greatest response to applied P (Fig 4.1).

P responsiveness of gorse was significantly less than that of white clover in terms of total shoot weight (both harvests), root weight and total plant weight (shoot weight both harvests plus root weight).

Table 4.13 Responsiveness of gorse and white clover to applied lime - lime/P experiment (based on treatments L0P1 and L1P1)

Plant part (dry weight)	Responsiveness to applied lime (Section 4.3.2.4)		Significance of between species differences
	Gorse	White clover	
Total shoot	0.27	0.56	**
Root	0.22	0.37	ns
Total plant	0.26	0.53	*

See Table 4.5 for description of significance levels.

The calculation of responsiveness to lime was based on treatments L0P1 (\bar{Y}_o) and L1P1 (\bar{Y}_m). Gorse was significantly less responsive to applied lime than white clover in terms of total shoot and total plant weight, but the difference in responsiveness in terms of root weight was not significant (Table 4.13).

4.3.3 Symbiotic N_2 -fixing activity

Symbiotic N_2 -fixing activity on a per pot basis was significantly greater for white clover (mean rate of acetylene (C_2H_2) reduction = $14.9 \mu\text{mol h}^{-1}$) than for gorse (mean rate of C_2H_2 reduction = $5.4 \mu\text{mol h}^{-1}$). However the main reason for this difference appeared to be the greater dry matter yield of white clover compared with gorse. In order to remove the effect of plant weight, rates of N_2 -fixing activity are presented on a unit plant weight basis. When considered on this basis, there was no significant effect of species on N_2 -fixing activity (Table 4.14).

In the combined analysis of variance all treatment effects and interactions apart from the main effect of species were significant (Table 4.14).

For gorse there were significant lime and P effects and a significant lime \times P interaction, whereas for white clover the main effect of lime was nonsignificant (Table 4.14).

Table 4.14 Effects of rates of lime and P application on symbiotic N₂-fixing activity per unit whole-plant dry weight (N₂-fixing activity ratio), lime/P experiment - summary of analysis of variance tables

Source of variation (treatment or interaction)	Level of significance		
	Gorse and clover	Gorse	Clover
Species	ns		
Lime	***	***	ns
P	***	***	***
Lime × P	*	**	*
Species × lime	***		
Species × P	**		
Species × lime × P	***		

See Table 4.5 for description of significance levels

The main features of the N₂-fixing activity data are as follows:

- 1) N₂-fixing activity per unit whole-plant dry weight (N₂-fixing activity ratio) increased substantially in both species with increase in rate of P from P0 to P1 and then tended to remain on a plateau with further increases in rate of P (Fig 4.4).
- 2) For both species N₂-fixing activity ratio increased significantly with increase in lime rate up to L2 at the P0 rate of P (Fig 4.4).

It appeared that lime application was able to partially compensate for the absence of applied P, but that P could fully compensate for the absence of lime (because near maximum N₂-fixing activity per unit dry weight was achieved in the absence of applied lime in the LOP1 treatment) in terms of N₂-fixing activity (Fig 4.4).

- 3) For gorse only, there was a substantial decline in N₂-fixing activity ratio at the L3 rate of applied lime at all rates of applied P (Fig 4.4).

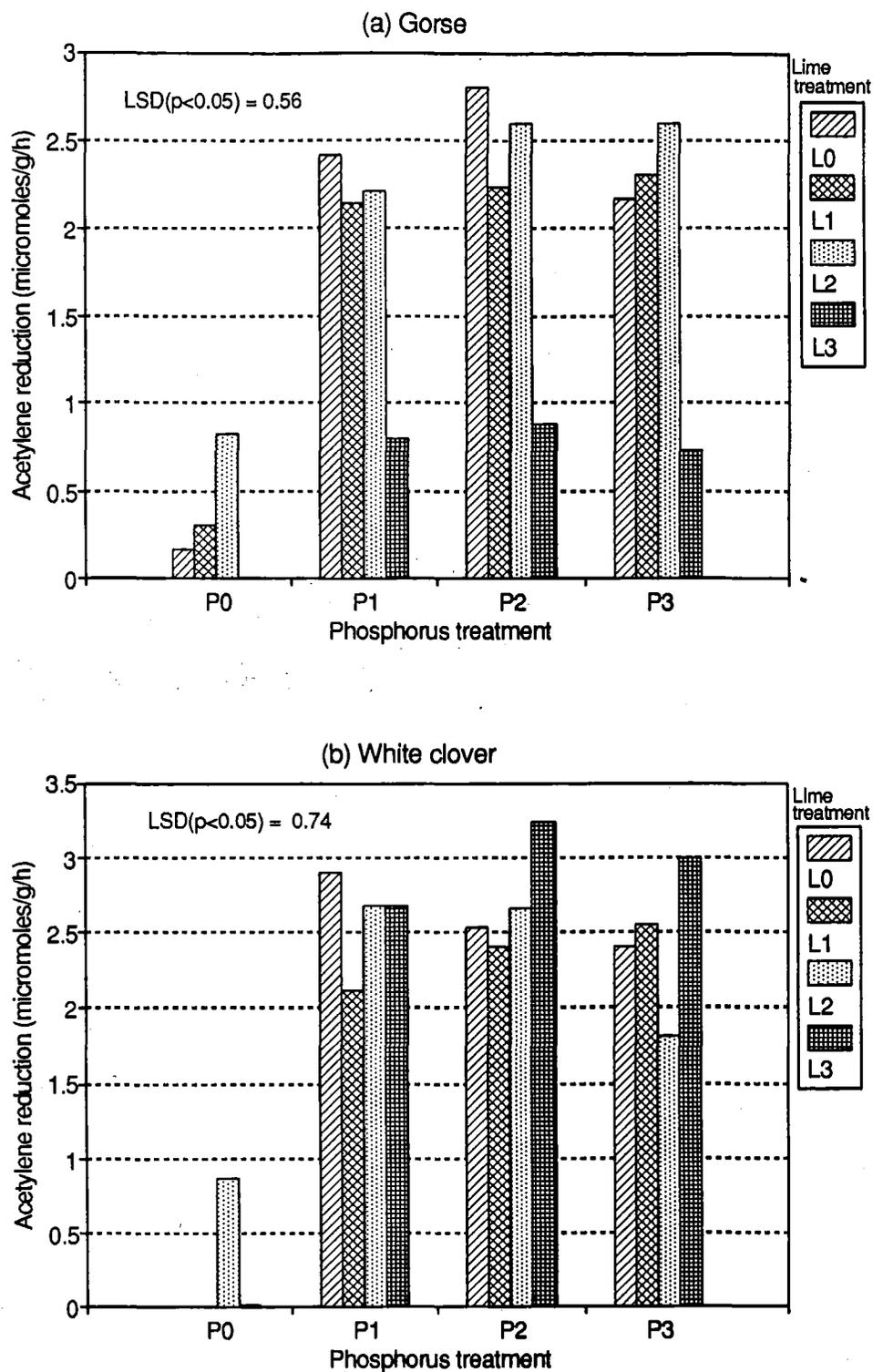


Fig. 4.4

Effects of rate phosphorus and rate of lime application on nitrogen-fixing (acetylene-reducing) activity per unit whole-plant dry weight (N_2 -fixing activity ratio) of gorse and white clover (micromoles acetylene per g per hour) grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

4.3.4 Plant P and N concentration

The effects of lime and P treatments on shoot P and N concentrations were similar at both harvest times for both gorse and white clover. (The main difference between harvest times was that P concentration in gorse shoots in the L0P0 treatment was less at harvest 1 than at harvest 2). Also shoot P concentrations at harvest 2 are more directly comparable with the root P concentrations than shoot P concentrations at harvest 1. Therefore, to avoid repetition, shoot P concentrations from harvest 2 only are presented. Using a rationale analogous to that used in Section 4.3.1.3, P analyses were done on plant material from treatments L0P0-P3, L1P0-P3, L2P2 and L3P2 only. Because of the omission of some treatments the design was unbalanced, and the analysis of variance was done as described in section 4.2.7.

4.3.4.1 Shoot P concentration

There was a significant effect of species on shoot P concentration (Table 4.15) with P concentration being significantly greater in white clover (mean 0.28%) than in gorse shoots (mean 0.24%). At P rates resulting in near maximum plant growth (P1 and P2, Figs 4.1 and 4.2), gorse generally had lower P concentrations than white clover (Fig 4.5, pooled LSD = 0.037). The effects of both lime and P rate, and the lime \times P, species \times lime and species \times P interactions were all significant (Table 4.15).

At the L0 rate of lime, P concentration in gorse shoots increased with increase in rate of applied P up to the P2 rate (Fig 4.5(a)). At the L1 rate of lime, however, there was no significant increase in shoot P concentration except at the P3 rate of P (Fig 4.5(a)). Within P treatments, there were no significant responses to rate of lime, except at the P2 rate of P, where P concentration for the L0 rate of lime was greater than for the other 3 rates (Fig 4.5(a)).

At the L0 and L1 rates of lime, P concentration in white clover shoots increased progressively with increasing rate of P application up to the P2 rate of P (Fig 4.5(b)). This contrasts with the response pattern for gorse where the only response to applied P, at the L1 rate of lime, was to the P3 rate which was above that associated with yield responses in either species (Figs 4.5 and 4.1).

Table 4.15 Effects of lime and P application rate on P concentration in gorse and white clover shoots, lime/P experiment, harvest 2 - summary of analysis of variance table

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	*			
Treatment (lime and P)	***			
Lime		***	ns	ns
P		***	ns	ns
Lime × P	***			
Treatment × species	***			
Lime × species		***	ns	ns
P × species		***	***	ns
Lime × P × species	ns			

See Table 4.5 for description of significance levels

Lime (L1 rate only) increased the concentration of P in clover shoots when no fertilizer P was applied.

Increases in yield of white clover associated with increase in rate of P were more closely associated with increase in shoot P concentration than those of gorse. In the L1P0 treatment, P concentration in gorse shoots, under conditions of P deficiency was similar to that in the L1P1 treatment, which was associated with near maximum yield (Table 4.16; Fig 4.1(a)). In contrast, for white clover, P concentration increased along with dry matter yield from treatments L1P0 to L1P1 (Table 4.16; Fig 4.1(b)). A similar effect was observed in the comparison between the LOP0 and LOP1 treatments (Table 4.16).

Shoot P concentration associated with near maximum dry matter yield (L1P1 treatment for both species) was less for gorse (0.22) than white clover (0.28%) (Table 4.16).

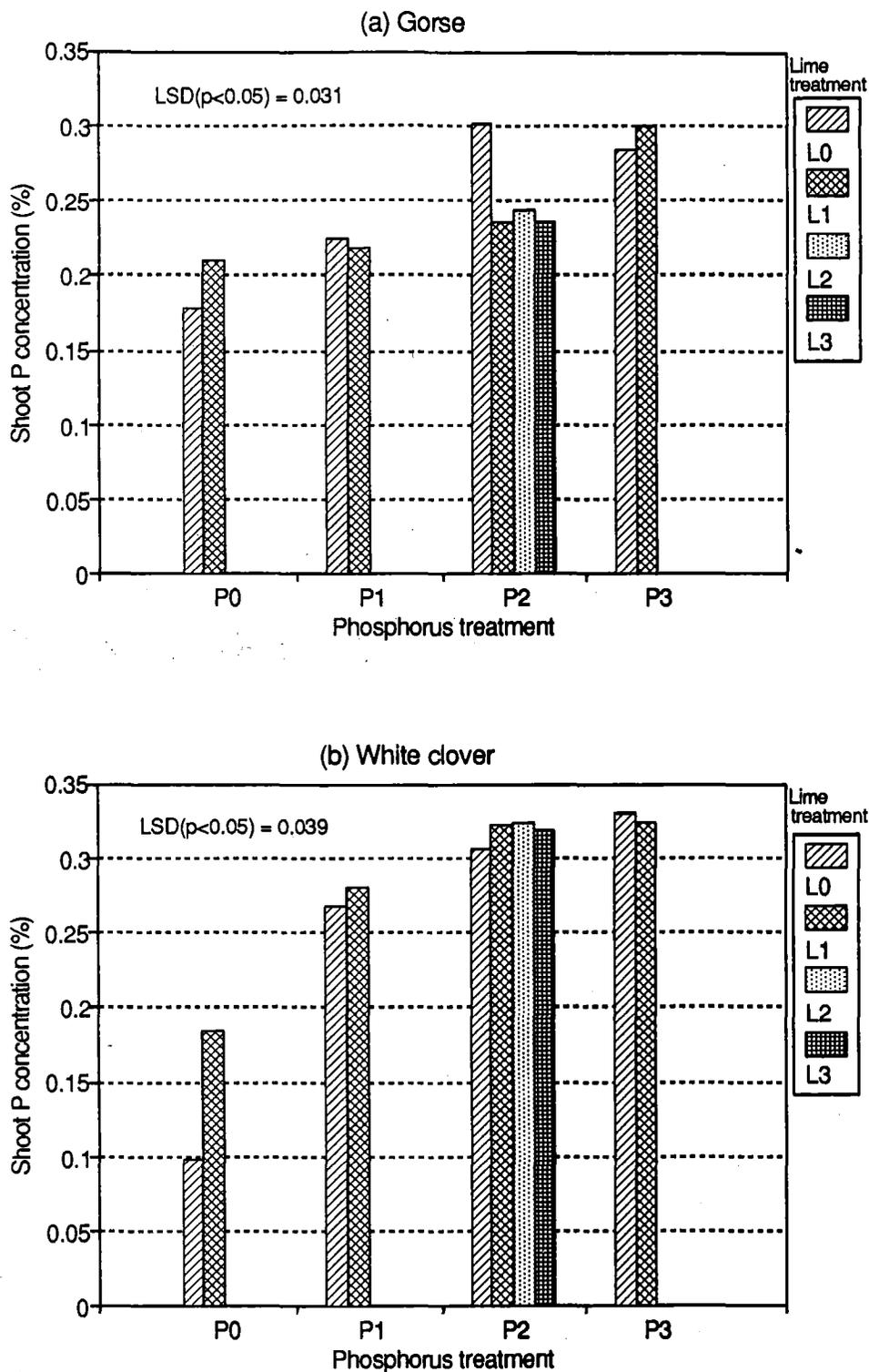


Fig. 4.5

Effects of rate of phosphorus and rate of lime application on shoot phosphorus concentration (harvest 2) of gorse and white clover grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

Table 4.16 A comparison of the effects of soil P availability on shoot P concentration in gorse and white clover shoots - lime/P experiment

Treatment	Shoot P concentration (%)		LSD (p<0.05)
	Gorse	White clover	
LOP0	0.18	0.10	0.036
LOP1	0.22	0.27	
L1P0	0.21	0.19	
L1P1	0.22	0.28	

4.3.4.2 Root P concentration

There was no significant overall effect of species on root P concentration. However there were interactions between species and rates of lime and P application (Table 4.17). Rates of lime and P application both significantly affected root P concentration but the lime \times P interaction was nonsignificant (Table 4.17).

Table 4.17 Effects of lime and P application rate on P concentration in gorse and white clover roots, lime/P experiment - summary of analysis of variance table

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	ns			
Treatment (lime and P)	***			
Lime		***	ns	*
P		***	*	ns
Lime \times P	ns			
Treatment \times species	***			
Lime \times species		**	**	ns
P \times species		ns	*	ns
Lime \times P \times species	ns			

See Table 4.5 for description of significance levels

At the L0 and L1 rates of lime, root P concentration of both species increased progressively with increasing rate of P from P0 (mean = 0.12% for both gorse and white clover) to P3 (means = 0.38 and 0.33% for gorse and white clover respectively) (Fig 4.6). Within rates of P for both species, increase in lime rate from L0 to L1 did not significantly affect root P concentration (Fig 4.6). At the P2 rate of P, the L3 rate of lime decreased P concentration in gorse roots and increased P concentration in white clover roots compared with the L0 rate (Fig 4.6). Root P concentration associated with near maximum growth (in the L1P1 treatment for both species) was 0.24 and 0.23% for gorse and white clover respectively.

4.3.4.3 Shoot N concentration

There was a significant species effect on shoot N concentration (Table 4.18), with shoot N concentration being greater in white clover (mean = 3.45%) than in gorse (mean = 2.84%). Shoot N concentration was less for gorse than white clover at all combinations of lime and P rate except for L0P0 where that for gorse was greatest (Fig 4.7, pooled LSD = 0.33).

Table 4.18 Effects of lime and P application rate on N concentration in gorse and white clover shoots, lime/P experiment, harvest 2 - summary of analysis of variance table.

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	**			
Treatment (lime and P)	***			
Lime		ns	**	**
P		***	***	*
Lime × P	***			
Treatment × species	***			
Lime × species		ns	***	**
P × species		***	ns	ns
Lime × P × species	***			

See Table 4.5 for description of significance levels

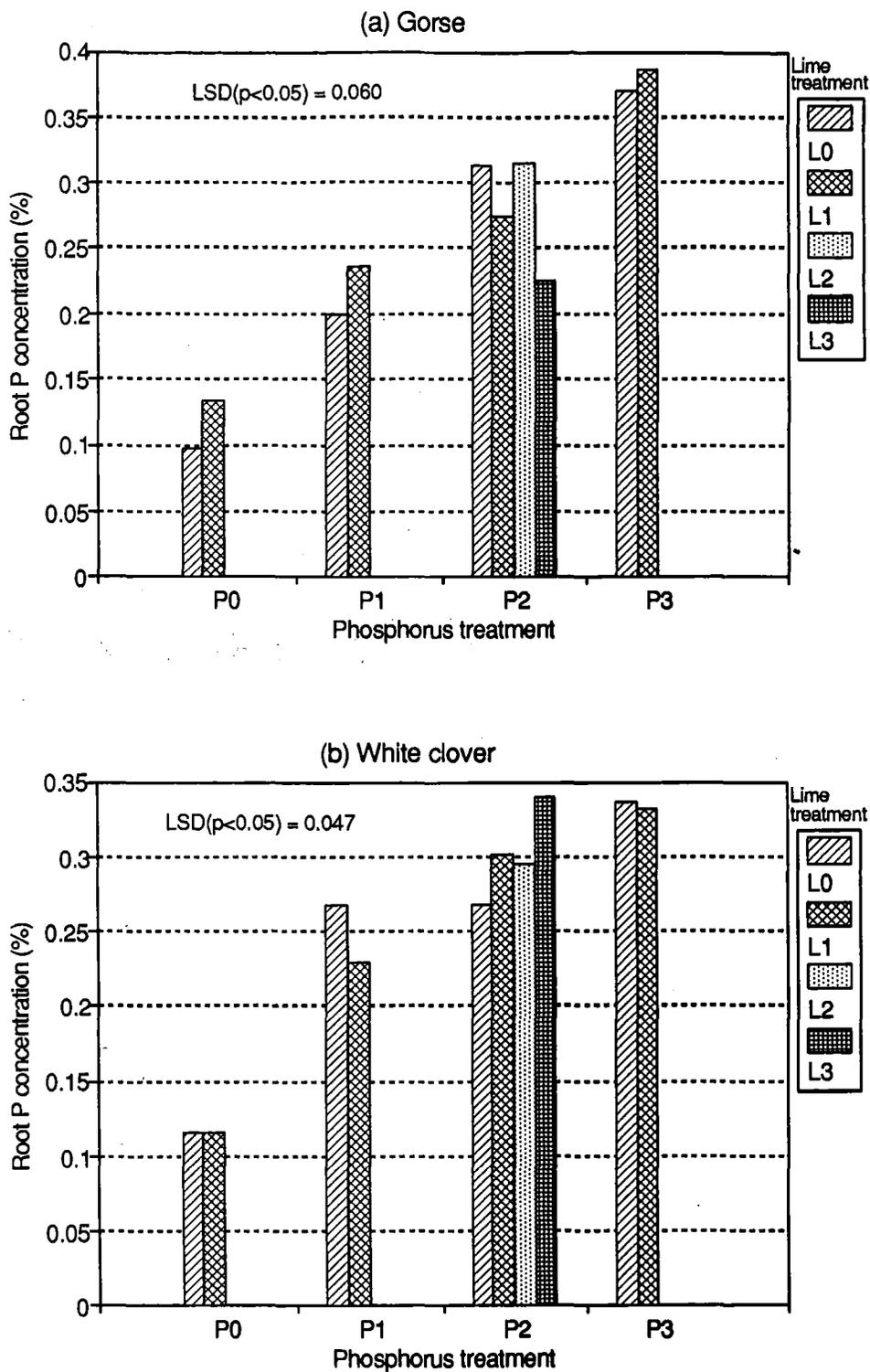


Fig. 4.6

Effects of rate of phosphorus and rate of lime application on root phosphorus concentration of gorse and white clover grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

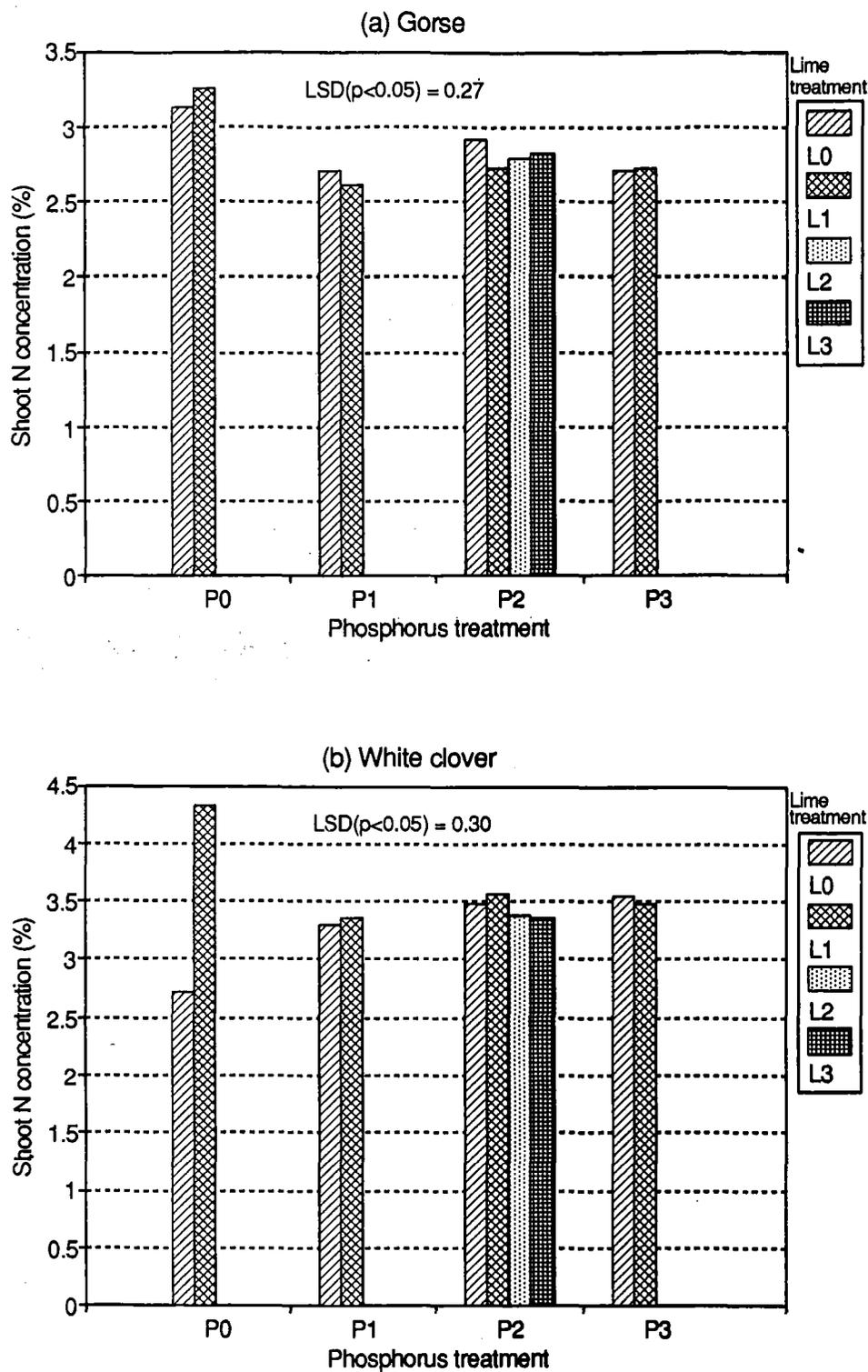


Fig. 4.7

Effects of rate of phosphorus and rate of lime application on shoot nitrogen concentration (harvest 2) of gorse and white clover grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

Shoot N concentration was significantly affected by rates of both lime and P and there were significant lime \times P, lime \times species, P \times species and lime \times P \times species interactions (Table 4.18).

Within rates of lime, shoot N concentration in gorse was generally significantly greater at the P0 rate of P than at other rates (Fig 4.7(a)). Excluding the L0P0 treatment, white clover followed the same pattern (Fig 4.7). In the L0P0 treatment, however, shoot N concentration of white clover was significantly lower than in all other treatments (Fig 4.7(b)).

Rate of lime application did not affect shoot N concentration in gorse. Lime (L1 rate) increased shoot N concentrations in white clover only in the absence of applied P (Fig 4.7(b)).

4.3.4.4 Root N concentration

Root N concentration was significantly greater in white clover (mean = 2.15%) than in gorse (mean = 1.77%) (Table 4.19). Root N concentration was less for gorse than white clover at all combinations of lime and P rate except for L0P0 where that for gorse was greater (Fig 4.8, pooled LSD = 0.22).

Root N concentration was significantly affected by rates of lime and P and there were significant lime \times P, lime \times species and P \times species and lime \times P \times species interactions (Table 4.19).

An increase in lime application rate (L0 to L1) resulted in a small but significant increase in root N concentration of gorse in the absence of applied P (Fig 4.8(a)). Otherwise root N concentration was fairly uniform across treatments. An increase in lime rate (L0 to L1) increased root N concentration of white clover in the absence of applied P, and P increased root N concentration in the absence of applied lime (Table 4.8(b)). Lime and P seemed to be able to substitute for each other with regard to their effect in raising root N concentration of white clover (Fig 4.8(b)).

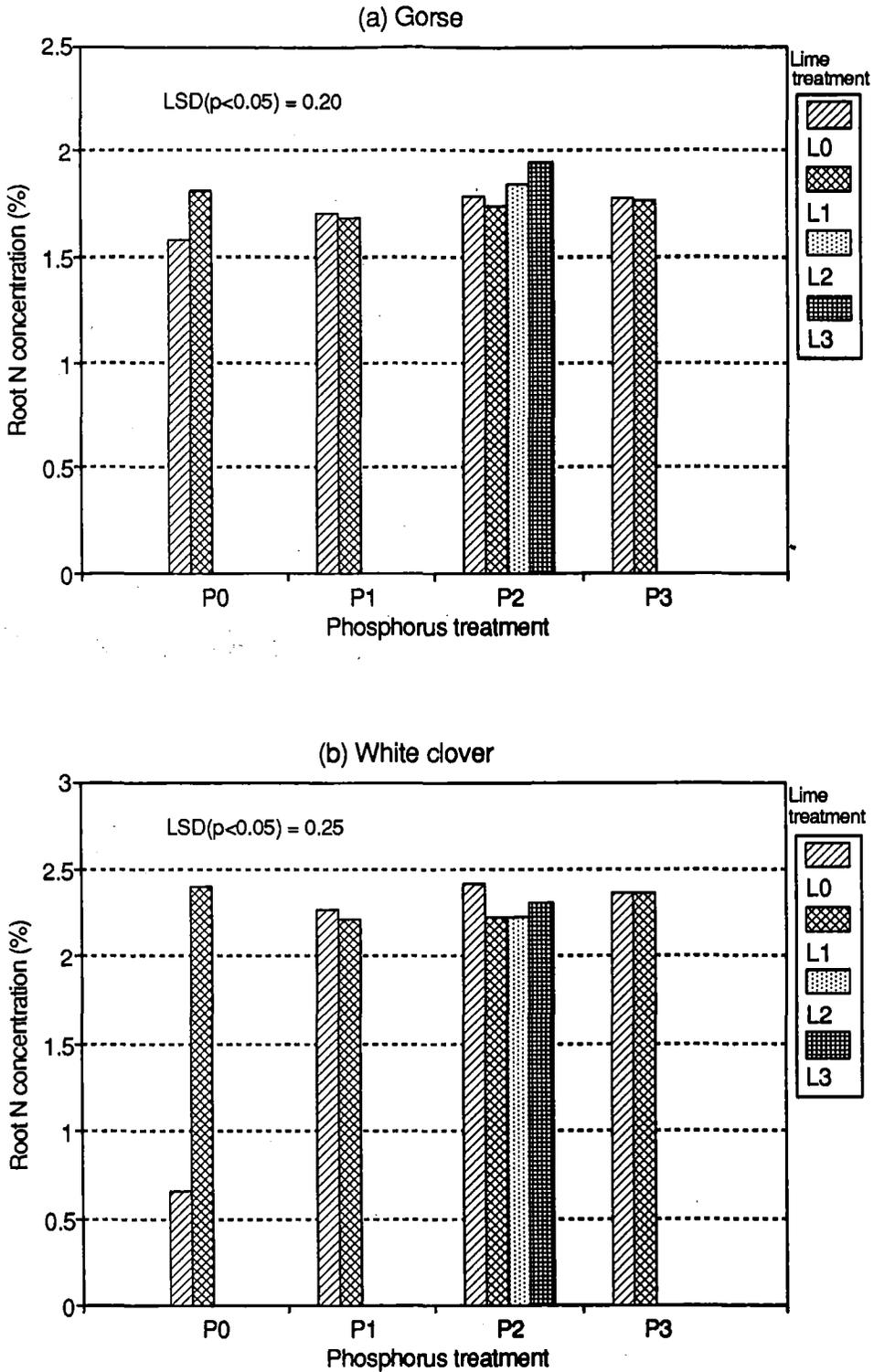


Fig. 4.8

Effects of rate of phosphorus and rate of lime application on root nitrogen concentration of gorse and white clover grown in the E horizon from a Katrine soil. Phosphorus and lime treatments are shown in Tables 4.2 and 4.3 respectively.

Table 4.19 Effects of lime and P application rate on N concentration in gorse and white clover roots; lime/P experiment - summary of analysis of variance table

Source of variation (treatment or interaction)	Overall effect	Components		
		Linear	Quadratic	Lack of fit
Species	***			
Treatment (lime and P)	***			
Lime		***	**	*
P		***	*	ns
Lime × P	***			
Treatment × species	***			
Lime × species		ns	**	*
P × species		***	**	ns
Lime × P × species	***			

See Table 4.5 for description of significance levels.

4.3.4.5 Total P uptake under conditions of low P availability

The abilities of gorse and white clover to take up P, under conditions of low available P, are compared in Table 4.20. The comparison was made in the L1P0 treatment because greatest growth of both gorse and white clover appeared to occur at the L1 rate of lime over the range of P rates applied (Figs 4.1 and 4.2). The P uptake values represent total P uptake throughout the experiment (shoot P, harvests 1 and 2, plus root P), and are presented alongside the corresponding Olsen P concentrations, $\text{CaCl}_2\text{-Al}$ concentrations and pH values at the end of the experiment (Table 4.20). Because harvest date differed for the two species, total P uptake was expressed as uptake per day, rather than as a total.

The ability of gorse to take up P under the conditions applying in the L1P0 treatment was significantly greater than that of white clover (Table 4.20). In contrast, when the rate of P applied was increased without corresponding decreases in $\text{CaCl}_2\text{-Al}$ or increases in pH, P uptake of white clover was much greater than that of gorse (Table 4.20).

Table 4.20 Comparative abilities of gorse and white clover to take up soil P under conditions of very low and relatively high availability - lime/P experiment

	Species	Treatment	
		L1P0	L1P1
P uptake ($\mu\text{g pot}^{-1}$ day^{-1}): mean (s.e.)	Gorse	26.2 (2.6)	101 (8)
	Clover	16.1 (5.8) [n=4]	372 (25) [n=4]
Olsen P ($\mu\text{g g}^{-1}$) (end of expt.)	Gorse	3	41
	Clover	4	34
$\text{CaCl}_2\text{-Al}$ ($\mu\text{g g}^{-1}$) (end of expt.)	Gorse	8.0	6.6
	Clover	8.4	13.6
pH (end of expt.)	Gorse	4.56	4.60
	Clover	4.53	4.42

4.3.5 Effect of lime rate on element concentration of gorse and white clover shoots at a high concentration of available P

Gorse and white clover shoots were analysed for a range of major and micro-nutrients using X-ray fluorescence (Table 4.21). Optimum ranges for white clover nutrient concentrations (Cornforth and Sinclair 1984) are presented alongside the nutrient concentrations in Table 4.21. Optimum ranges or critical values for gorse are not available. However, P and N concentrations in gorse shoots tend to be less than for white clover (Figs 4.5 and 4.7) and estimated critical values for P and N concentration were less for gorse than white clover (Table 3.21). Concentrations of a range of nutrients in gorse shoots (Radcliffe 1986) tended to be low compared with optimum ranges for white clover (Cornforth and Sinclair 1984). Therefore it is probably reasonable to assume that optimum nutrient concentrations for gorse are less than those for white clover.

Increasing rates of lime application were associated with decreasing shoot Al and increasing shoot Ca and Mo concentrations in both species. Ca concentration in both species and Mo concentration in white clover were always above the optimum range for white clover (Cornforth and Sinclair 1984) (Table 4.21). Mo concentrations in gorse shoots were below the optimum range for white clover at the L0 rate of lime. It is therefore possible that increase in yield of gorse with increase in lime rate from L0 to L1 was associated with

decrease in Al or increase in Mo concentration, and that the corresponding increase in white clover yield was associated with decrease in Al concentration (Table 4.21; Figs 4.1 and 4.2).

Table 4.21 Effect of rate of lime application on element concentrations in gorse and white clover shoots under conditions of high available P (P2 rate, Table 4.8).

Element	Species	Lime treatment				LSD p<0.05	Optimum range for white clover †
		L0	L1	L2	L3		
K (%)	Gorse	3.62	3.09	3.38	3.82	0.59	2.0-2.4
	Clover	3.55	2.88	3.48	3.77		
Mg (%)	Gorse	0.24	0.17	0.16	0.15	0.063	0.18-0.22
	Clover	0.45	0.42	0.32	0.28		
Ca (%)	Gorse	0.398	0.689	0.749	0.833	0.144	0.4-0.5
	Clover	0.713	1.635	2.071	2.286		
S (%)	Gorse	0.24	0.21	0.24	0.25	0.035	0.27-0.32
	Clover	0.27	0.24	0.27	0.28		
Al (%)	Gorse	0.0254	0.0183	0.0151	0.0134	0.0078	-
	Clover	0.0383	0.0276	0.0230	0.0173		
Mn (ppm)	Gorse	205	158	157	97	28	25-30
	Clover	258	207	122	95		
Cu (ppm)	Gorse	5	4	4	4	1.8	6-7
	Clover	9	9	9	10		
Zn (ppm)	Gorse	104	67	34	16	10	16-19
	Clover	105	74	29	27		
Fe (ppm)	Gorse	148	113	116	113	21	50-65
	Clover	161	142	158	150		
Mo (ppm)	Gorse	0.1	1.1	4.9	19.8	5.2	0.15-0.20
	Clover	1.7	2.3	7.1	11.5		
B (ppm)	Gorse	44	39	42	48	-	25-30
	Clover	30	32	36	41		

† Optimum ranges quoted are those of Cornforth and Sinclair (1984) for white clover.

As a check on soil contamination of the plant samples, Ti concentrations were measured. These were within the analytical precision of the spectrometer employed (Philips PW1400, S. Winter pers. comm.) and were not significantly ($p>0.05$) affected by lime treatment,

indicating that the samples were largely free from soil contamination. Therefore the Al concentrations presented can be regarded as reliable.

Concentrations of K, Mg, Ca, Mn, Cu, Zn, Fe, Mo and B in white clover shoots were within or above the optimum range throughout the range of lime treatments applied (Table 4.21).

S concentration in white clover was at the low end of the optimum range, but showed no trend with lime rate (Table 4.21). Mg, Mn, Zn and Fe concentrations in white clover shoots showed a downward trend with increasing lime rate, but never fell below the optimum range and therefore do not provide an obvious explanation for the decline in dry matter yield at the L3 rate of lime application (Table 4.21; Figs 4.1 and 4.2).

K, Ca, Mn, Zn, Fe and B concentrations in gorse shoots were always within or above the optimum range for white clover. Mn, Zn and Fe showed a downward trend with increasing rate of lime, but because they never fell below the optimum range for white clover, do not provide an obvious explanation for the decline in yield at the L3 rate of lime (Table 4.21; Figs 4.1 and 4.2). S and Cu concentrations in gorse shoots tended to be a little below the optimum range for white clover, but showed no clear trend with lime rate (Table 4.21). Gorse shoot Mg concentration declined with increasing lime rate, and at the L3 rate was below the optimum range for white clover. However the optimum range for gorse may be lower than that for white clover, and also the decline in Mg concentration with increase in lime rate from L2 to L3 was minimal (Table 4.21). Therefore low Mg concentration doesn't provide an obvious explanation for decline in dry matter yield of gorse at the L3 rate of lime. S and Cu concentrations in gorse shoots were below the optimum range for white clover but showed no trend with rate of lime application (Table 4.21).

4.4 DISCUSSION

4.4.1 Effects of rates of P and lime application on gorse and white clover growth

4.4.1.1 Shoot and root weight

Gorse and white clover responded in different ways to the lime and P treatment combinations applied (Sections 4.3.2.1 and 4.3.2.2; Figs 4.1 and 4.2). At the L0 rate of lime, shoot weight of gorse increased significantly and progressively up to the P3 rate of P, achieving a yield similar to that in the L1P1 treatment. At the L1-L3 rates of lime there were no responses to rate of P above P1. It appears that, in the absence of applied lime, P was acting as a liming agent in addition to supplying P to the plant. From the L0P0 treatment to the L0P3 treatment pH increased only slightly (from 3.90 to 4.09) but $\text{CaCl}_2\text{-Al}$ decreased from 95.4 to 48.6 $\mu\text{g Al g}^{-1}$ soil (Tables 4.6 and 4.7). Al toxicity has been identified as the major factor limiting plant growth in many acid soils (Adams and Pearson 1967; Foy 1974) and has been found to reduce growth of a range of legume species in pots containing soil (McLeod and Jackson 1965; Munns 1965c; Evans and Kamprath 1970) and in the field (Mahoney *et al.* 1983) (Section 2.3.2). Applied P tends to interact with Al to form polymers or precipitates, thereby reducing monomeric Al concentrations in soil solution and hence reducing Al toxicity (Munns 1965b; Blamey *et al.* 1983; Dodd *et al.* 1992) (Section 2.3.4.2). At the L1 rate of lime, the P1 rate of P was sufficient to produce near maximum yield. Therefore at the L0 rate of lime it appears that the increase in P application rate from P1 to P3 resulted in increased yield by reducing Al toxicity. Shoot P concentration did increase with increasing rate of P up to P2, but from the P1 rate of P and above was always greater than that associated with near maximum yield (0.22%, L1P1 treatment) (Fig 4.5).

White clover responded similarly to gorse in that shoot weight increased with increase in rate of P at the L0 rate of applied lime, but only significantly up to the P2 rate (Fig 4.1). Unlike gorse, white clover did not reach its yield potential without the application of lime (Fig 4.1(b)). This suggests that white clover is more sensitive to Al toxicity than gorse, but the evidence is not conclusive because pH was slightly less and $\text{CaCl}_2\text{-Al}$ greater than for the gorse pots in the L0P3 treatment by the end of the experiment (Tables 4.6 and 4.7). Therefore it is not possible to say whether or not white clover would have reached its yield

potential if $\text{CaCl}_2\text{-Al}$ concentration had been reduced to the values measured in the gorse pots. However both species did have the same conditions at the beginning of the experiment and the relative shoot dry weight of white clover in the LOP3 treatment (5.11 g) compared with the L1P1 treatment (7.10 g) at the first harvest (when presumably less soil acidification would have occurred) was almost identical to that at the final harvest (4.99 g in the LOP3 treatment compared with 7.04 g in the L1P1 treatment). At the L1 to L3 rates of lime there were no significant increases in dry matter yield with increasing rate of P beyond the P1 rate (Fig 4.1).

The P treatments raised available concentrations more than was originally intended (Section 4.2.2.1) and it would have been advantageous to have had a rate between P0 and P1, i.e. a rate insufficient for near maximum growth.

Responses to lime rate followed similar trends for both species, with shoot dry weight tending to increase with increase in lime rate from the L0 to the L1 rate, then decline from the L2 to the L3 rate (Fig 4.1). However, gorse appeared to be less responsive to lime than white clover (Fig 4.1) (discussed in Section 4.4.1.2). Also, at the P3 rate of P gorse did not respond to lime at all, as discussed earlier in this section, whereas for white clover the P3 rate of P did not compensate for the lack of applied lime.

Root growth in both species followed similar response patterns to rates of lime and P as shoot growth, except that root weight of gorse appeared to be less depressed by low available P than shoot weight (Figs 4.1(a) and 4.2(a)). Dry matter yield responses of both gorse and white clover to increasing rates of lime, at an adequate concentration of available P for plant growth, (P2 rate of applied P, Table 4.8), were associated with progressively decreasing shoot Al concentrations (Table 4.21). This, along with the negative interaction between lime and P responses discussed earlier in this section, suggests that the increases in dry matter resulting from increases in rate of lime application were associated with decreases in Al toxicity.

At the L3 rate of applied lime, shoot and root dry matter yields of both species declined substantially in comparison with yields at the L2 rate. Dry matter yield of gorse appeared to decline less than that of white clover (Figs 4.1 and 4.2), which is not completely consistent with the reputation of gorse as a calcifuge (Grubb and Suter 1970; Zabkiewicz

1976; MacCarter and Gaynor 1980) (Section 2.1.3.2). The decline in gorse and white clover yields at the L3 rate of lime may have been the result of a nutrient imbalance, but analyses of shoot tissue of the two species gave no clear indication of this (Section 4.3.5). Shoot Mg, Mn, Zn and Fe concentrations decreased with increase in rate of lime application for both species (Table 4.21). Mn, Zn and Fe concentrations did not fall below the optimum range for white clover shoots (Cornforth and Sinclair 1984), even at the L3 rate of lime, and therefore do not provide an obvious explanation for the observed decline in yield.

At the L3 rate of lime, Mg concentration in white clover shoots was greater than the optimum range for white clover, but at the L1-L3 rates of lime Mg concentration in gorse shoots was less than the optimum range for white clover shoots, being lowest at the L3 rate (Table 4.21). However the optimum range for gorse may well be lower than that for white clover, and also there was little decline in Mg concentration with increase in lime rate from L1 to L3. For these reasons, and the fact that Mg concentrations were above optimum in white clover shoots, low Mg concentration does not provide an obvious explanation for the decline in dry matter yield of either species at the L3 rate of lime.

Shoot Mo increased markedly to very high concentrations from the L2 to the L3 rates of lime (Table 4.21). However Mo can be taken up in much greater amounts than those needed without toxic effects (Mengel and Kirkby 1987). Mo concentrations in the range 1000-2000 ppm were associated with Mo toxicity symptoms in tomato leaves (Johnson 1966). Therefore Mo toxicity is also unlikely to be the cause of depressed growth at the L3 rate of lime. B availability decreases with increasing rate of lime (Mengel and Kirkby 1987), but shoot B concentration for both species was above the optimum for white clover and did not decline with increasing rates of lime.

4.4.1.2 Available P concentrations, soluble Al concentrations and pH values associated with near maximum growth and yield depression

Near maximum yield of both species was achieved in the L1P1 treatment (Figs 4.1 and 4.2), at similar Olsen P concentrations (41 and 34 $\mu\text{g g}^{-1}$ for gorse and white clover respectively) (Table 4.8). Near maximum yield of white clover achieved in the L1P1 treatment, was associated with pH = 4.42 and $\text{CaCl}_2\text{-Al} = 13.6 \mu\text{g g}^{-1}$. However, near maximum yield of gorse was also achieved in the L0P3 treatment under conditions of lower pH and greater

CaCl₂-Al concentration (pH = 4.09 and CaCl₂-Al = 48.6 µg g⁻¹) (Tables 4.6 and 4.7). Because available P at the P1 rate of P was greater than desired and because there were no rates of P between P0 and P1 it is not possible to precisely determine critical available P (Olsen P) concentrations for gorse and white clover (Section 4.2.7). A similar problem exists for the rates of lime. Because both gorse and white clover performed so well at low pH it would have been desirable to have additional rates of lime between L0 and L1 (Table 4.3). The soil pH (4.42) at which white clover achieved near maximum yield was within the range of estimated critical values of Edmeades *et al.* (1983) (4.4-4.7) but tended to be a little lower than those associated with near maximum yield by Hume *et al.* (1988) (4.8-5.4). The CaCl₂-Al concentration associated with near maximum white clover yield (13.6 µg g⁻¹) appeared greater than the critical range (3.0-5.0 µg g⁻¹) of Edmeades *et al.* (1983) and also greater than the range of values associated with near maximum yield (1.7-9.7 µg g⁻¹) of Hume *et al.* (1988). It should be remembered, however, that CaCl₂-Al was lower at the beginning of the experiment (5.5 µg g⁻¹) in the L1P1 treatment.

The lowest soil pH (4.09) at which gorse reached near maximum yield (L0P3 treatment) was less than that for white clover (4.42) (Table 4.6) and the corresponding CaCl₂-Al concentration (48.6 µg g⁻¹) was greater than that for white clover (13.6 µg g⁻¹) (Table 4.7). These pH values were less and the CaCl₂-Al concentrations considerably greater than those which would be expected to result in Al toxicity in white clover (Edmeades *et al.* 1983; Hume *et al.* 1988). The indication is that gorse is more tolerant of low pH and high soluble Al than white clover, but the evidence is not conclusive because of the lack of lime applications rates between L1 and L0 and the consequent lack of pH values between 4.42 and 3.99 (L1P1 and L0P1 treatments respectively), and CaCl₂-Al concentrations between 13.6 (L1P1 treatment) and 64.5 µg g⁻¹ (L0P3 treatment) (Tables 4.6 and 4.7).

4.4.1.3 Responsiveness of gorse and white clover to applied P and lime

In this experiment the responsiveness of gorse, in terms of shoot dry weight, to applied P was 0.74 (Section 4.3.2.4; Table 4.12). These values are similar to those obtained in the first year of the Springston field trial (0.74-0.85), despite the fact that Olsen P concentrations at the P0 rate of P were slightly lower in this pot experiment (3-4 µg g⁻¹) than in the Springston trial (7-9 µg g⁻¹). Values in the second year of the Springston trial were much lower (Table 3.10) presumably because, with the development of a more

extensive and deep root system, gorse became less dependent on applied P.

The lower responsiveness of gorse (0.74) compared with white clover (0.95) in this experiment (Table 4.12) followed a similar pattern to that shown by the data of Voon (1986), where the low soil fertility demanding shrub legume tagasaste (*Chamaecytisus palmensis*) was less responsive to applied P (estimated responsiveness = 0.63), than the high fertility demanding red clover (*Trifolium pratense*) (estimated responsiveness = 0.84). The pot trial of Voon (1986) was done using soil of similar Olsen P concentration ($4 \mu\text{g g}^{-1}$) to that in this experiment.

In this trial gorse was less responsive to P application than white clover (in terms of shoot, root or whole-plant growth) (Table 4.12). This is consistent with data from the Springston trial (Table 3.10) and indicates that gorse has a greater ability to reach its growth potential under conditions of low available soil P than white clover. The greater ability of gorse to absorb P from soil with very low available P concentration, compared with white clover (Table 4.20), probably contributes to its lower responsiveness to P. The lower responsiveness to P of gorse compared with white clover is consistent with its reputation as a species which tolerates and grows relatively well under low fertility conditions (Chater 1931; Egunjobi 1969; Meeklah 1979; Dancer *et al.* 1977a; Roberts *et al.* 1981) in contrast to white clover which is regarded to be a high fertility demanding species (Dunlop and Hart 1987).

Gorse was also less responsive to lime than white clover (in terms of shoot and whole-plant dry weight) (Table 4.13). The relatively good growth of gorse under conditions of low pH and high soluble Al is consistent with its reputation as a calcifuge (Grubb and Suter 1970; Zabkiewicz 1976; MacCarter and Gaynor 1980) and its tendency to inhabit soils with pH in the range 4.0-6.0 (Meeklah 1979; Grime *et al.* 1988) (Section 2.1.3.2). In contrast, white clover is considered to be only moderately tolerant to soil acidity and soluble Al (Andrew *et al.* 1973; Pinkerton and Simpson 1981; Edmeades *et al.* 1991a & b; Section 2.3.2).

4.4.1.4 Dry matter partitioning between shoot and root

The shoot:root ratio of gorse approximately doubled with increase in rate of lime from the L0P0 to the L1P0 treatment, or from the L0P0 treatment to the L0P1 treatment (Fig 4.3). The application of either P or lime had similar effects in increasing shoot:root ratio. It is well known that shoot:root ratios tend to be lower under conditions of P deficiency (Shank 1945; Loneragan and Asher 1967; Fohse *et al.* 1988) (Section 2.2.3.1), and P deficiency has been found to promote root elongation (Anuradha and Narayanan 1991). An increase in P availability could explain the increase in shoot:root ratio from the L0P0 to the L0P1 treatment. A corresponding small increase in shoot P concentration was observed (Figs 4.5 and 4.6). The increase in shoot:root ratio with increase in lime rate at the P0 rate of applied P may also result from increased P availability. Phosphate and monomeric Al ions react in solution to form polymers and precipitates (Blamey *et al.* 1983) and Al toxicity often manifests itself as an apparent P deficiency (Munns 1965a) (Section 2.3.4.2). Thus reduction of the Al concentration in soil solution may increase P availability. The slight increases in shoot and root P concentration between the L0P0 and L1P0 treatments (Figs 4.5 and 4.6) may have resulted from increased P availability because of decreases in soil solution Al concentration. The ability of gorse to decrease its shoot:root ratio under conditions of very low P availability may have enhanced its ability to take up P and thereby maintain an adequate shoot P concentration in the L0P0 treatment (Figs 4.3 and 4.5).

In contrast, for white clover there were no significant increases in shoot:root ratio with increase in soil P, except at the L3 rate of lime which will be discussed later in this section.

Shoot:root ratio of white clover increased significantly with increasing rate of lime. Disregarding temporarily the values associated with the L3 rate of lime, shoot:root ratio increased progressively with increasing rate of lime at the P0 and P1 rates of P, but not at the P2 and P3 rates of P (Fig 4.3). Shoot:root ratios may have increased with increase in lime rate because of decreasing Al toxicity. Reduction in root growth is often the first observable effect on plants affected by Al toxicity (Clarkson and Sanderson 1969). Al toxicity has been found to affect root morphology. It has been found to reduce root elongation (Munns 1965b), lateral root weight and root length per unit weight (Sartain and Kamprath 1975), the ratio of fine root length per unit shoot weight (Pinkerton and Simpson 1981), and root hair formation (Wood *et al.* 1984) (Section 2.3.2). The efficiency of roots

in absorbing P is found to be related to rate of root growth (Khaswaneh and Copeland 1973), root surface area (Jeffery 1967), and the presence of root hairs via their effect on root surface area (McLachlan 1976; Haynes and Ludecke 1981; Itoh and Barber 1983) (Section 2.2.2). Therefore reduction in Al toxicity by liming may have enabled improved root growth and morphology, enhanced P uptake and ultimately increased shoot:root ratio because of the improved P status of the plant (Loneragan and Asher 1967; Fohse *et al.* 1988) (Section 2.2.3.1) In support of this explanation shoot P concentration increased significantly with increased rate of lime application from treatments L0P0 to L1P0 (Fig 4.5(b)). However if shoot:root ratio of white clover was increasing in response to increased P availability with increasing lime rate, increased ratios in response to increasing rates of P would also be expected, but this was not the case (Fig 4.3).

At the L3 rate of lime pH was 6.5 or greater and $\text{CaCl}_2\text{-Al}$ concentrations were very low ($0.3 \mu\text{g g}^{-1}$ or less) at the P2 rate of P (Tables 4.6 and 4.7). Therefore pH or $\text{CaCl}_2\text{-Al}$ are unlikely to be directly involved in the plant responses obtained at this rate of lime. As suggested in Section 4.4.1.1, a nutrient imbalance caused by the high rate of lime application may be involved. Chemical analysis of gorse and white clover shoots from the P2 rate of P and all rates of lime gave no clear indication of why root and shoot dry matter yields of both species were depressed at the L3 rate of applied lime. They also give no clear indication of why the shoot:root ratio of white clover might be greater at the L3 rate of lime than at other rates of lime at the P2 rate of P (Fig 4.3, Table 4.21). The increases in shoot:root ratio with increasing rate of P at the L3 rate of lime for both species (Fig 4.3) suggest increases in nutrient availability (Chung *et al.* 1982). With the data available it is not possible to satisfactorily explain the effects observed at the L3 rate of lime.

4.4.2 P uptake and internal efficiency of use

4.4.2.1 P uptake

As in the Springston field trial (Section 3.4.3, Table 3.25), gorse grown in pots in this experiment had the ability to take up more P under conditions of low P availability than white clover (Section 4.3.4.5). Average rates of P uptake without applied P (L1P0 treatment) were 26.2 and 16.1 μg per pot per day for gorse and white clover respectively (Table 4.20). Thus, gorse would be expected to have a competitive advantage over white

clover under conditions of low soil fertility and this was shown in the field where both species were competing for nutrients (Table 3.25). Characteristics associated with the ability of plants to take up P from a given volume of soil are root length and surface area, rate of root growth, the presence of root hairs and their length (Jeffrey 1967; Khasawneh and Copeland 1973; McLachlan 1976; Haynes and Ludecke 1981; Itoh and Barber 1983) and effective mycorrhizal associations (Hattingh et al. 1973; Abbot and Robson 1982) (Section 2.2.2). It is not possible to say what mechanism is employed by gorse to enable it to acquire more P than white clover under conditions of very low available P (Olsen P = 3-4 $\mu\text{g g}^{-1}$).

Under conditions of high P availability (Olsen P = 34-41 $\mu\text{g g}^{-1}$) (L1P1 treatment) white clover had a much greater rate of P uptake per unit time than gorse (Table 4.20), and would therefore be expected to have a competitive advantage over gorse under these conditions. The greater P uptake by white clover under conditions of abundant applied P is reflected in the lower Olsen P concentrations in white clover pots compared with gorse pots at the end of the experiment.

4.4.2.2 Maintenance of adequate shoot P concentration under conditions of low P availability

Under conditions of low P availability (P0 treatment) gorse was better able to maintain shoot P concentration at a level close to that associated with near maximum dry matter yield (L1P1 treatment) than white clover. Gorse shoot P concentration in the L1P0 treatment was not significantly less and that in the L0P0 treatment was only slightly less than in the L1P1 treatment (Fig 4.5). In contrast white clover shoot P concentrations at the P0 rate of applied P were substantially less than in the L1P1 treatment (Fig 4.5). Legumes differ in their ability to translocate P from roots to shoots under conditions of low available P, and their ability to do this is associated with greater shoot growth (White 1972; Kee 1981; Paynter 1990). Gorse appears to be better able to translocate P from root to shoot at low available soil P, compared with white clover, and this is reflected in its greater shoot growth under these conditions (Figs 4.5 and 4.1). As discussed in Section 4.4.1.4 the ability of gorse to maintain shoot P concentration may have been related to its decreased shoot:root ratio in the L0P0 treatment.

4.4.2.3 Internal efficiency of P use

Where efficiency of P use is defined as the amount of dry matter produced per unit of P contained in the plant (Section 2.2.3) then plants having relatively lower P concentration will have relatively greater efficiency of P use. Gorse was found to have lower shoot P concentrations than white clover at most combinations of lime and P rate which resulted in near maximum dry weight (Figs 4.5 and 4.1). The lowest rate of applied P at which near maximum yield for both species was achieved was in the L1P1 treatment. Therefore the P concentration in this treatment is probably the best estimate of critical P concentration which can be obtained from the data in this experiment. In the L1P1 treatment, where both species produced near maximum yield, mean P concentration in gorse shoots (0.22%) was significantly less than that in white clover shoots (0.28%) (Fig 4.5). As rate of P application increased beyond that required for near maximum yield, both shoot and root P concentration tended to increase further (Figs 4.5 and 4.6) leading to a decline in efficiency of P use. The relative efficiency of P use in gorse compared with white clover, which was also observed in the Springston field trial (Sections 3.4.4 and 3.4.5), may be a key factor in the ability of gorse to thrive under conditions of low available P. It is considered that efficiency of P use may be more important than ability to acquire P in determining dry matter productivity (McLachlan 1976). This section continued overleaf.

4.4.3 N₂ fixation and N use

4.4.3.1 N₂-fixing activity

For both gorse and white clover, N₂-fixing activity per unit whole-plant dry weight (N₂-fixing activity ratio) was generally unaffected by lime rates from L0-L2, at adequate rates of P (P1-P3) (Fig 4.4). This indicates that the effect of soil acidity in depressing plant growth, under favourable conditions of available P, was not occurring via an adverse effect on symbiotic N₂ fixation in either species. There is substantial evidence that Al toxicity directly affects symbiotic N₂ fixation of sensitive species via adverse effects on rhizobial multiplication and nodulation, decreased number of infection sites, and reductions in nodule number and weight (Wood *et al.* 1984; de Carvalho *et al.* 1981). Al toxicity has been found to depress growth of legumes more severely when they are dependent on symbiotic N₂ fixation than when they are provided with mineral N (Munns 1965a; de Carvalho *et al.*

4.4.2.3 continued

Other authors have suggested that slow growth rates, and therefore low demand for P, are more important than internal efficiency of P use in the adaption of species to low available P concentrations (Chapin and Bielecki 1982; Chapin *et al.* 1982; Blair and Wilson 1990). However, species or accessions adapted to adequate P conditions produced either a similar amount (Chapin *et al.* 1982) or more dry matter (Chapin and Bielecki 1982; Blair and Wilson 1990) than those adapted to low P conditions, at low P concentrations. In contrast, gorse in this experiment (Section 4.3.4.5, Fig 4.1) and in the Springston field trial (Section 3.3.3.6.4, Figs 3.1(c) and 3.2(c)) took up more P and produced as much or more dry matter than the higher fertility demanding white clover under conditions of very low available P. Also, in the Springston field trial, annual dry matter production of unfertilized or P-fertilized gorse in its second growth season was similar to or greater than that of pasture, depending on fertilizer rate and cutting treatment (Section 3.4.1). Thus, it appears that gorse has high potential growth rates over a wide range of available P concentrations compared with white clover or grass/clover pasture, and that internal efficiency of P use rather than inherently slow growth is a key factor in its adaption to conditions of low available P.

Note: References quoted in this addition can be found at the end of the alphabetical list of references, on page 290.

1981). However for more tolerant species the effect of Al toxicity on symbiotic N_2 fixation may not be any greater than that on the host plant (Munns 1965a; Munns *et al.* 1981). Gorse and white clover in this experiment, by virtue of the apparent tolerance of their symbiotic N_2 -fixing systems to Al, appear to fall into the category of more tolerant species.

Applied P increased N_2 -fixing activity ratio at all rates of lime and for both species. The increase in N_2 -fixing activity ratio (at the P0 rate of P) with increase in lime rate from L0 to L2 is unlikely to be a direct result of increase in pH or decrease in Al toxicity, because pH was lower and $CaCl_2$ -Al greater in the L0P1 treatment compared with all but the L0P0 treatment, with no corresponding depression of N_2 -fixing activity per unit plant weight (Fig 4.4). It is more likely that Al is having an indirect effect by reducing P availability (Munns 1965b; Clarkson 1966; Dodd *et al.* 1992). Effects of P supply on the symbiotic N_2 -fixing system of legumes are well documented (Shaw *et al.* 1966; Gates 1974; Wagner *et al.* 1978; Zaroug and Munns 1979; Hart 1979; Section 2.2.4). However, there is conflicting evidence as to whether P deficiency has a direct effect on the symbiotic N_2 -fixing system of legumes, or whether it has its effect primarily via the host plant (e.g. Israel 1987; Robson and Bottomley 1991).

Superficially the evidence from this experiment suggests that P had a direct effect on the symbiotic N_2 -fixing systems of gorse and white clover in addition to that on the host plant, because of the reduction in N_2 -fixing activity ratio without applied P. However shoot and root N concentrations at the P0 rate of P were similar to those at higher rates, except for white clover in the L0P0 treatment (Figs 4.7 and 4.8). It is possible that plant growth rates were sufficiently depressed at the P0 rate of P to enable the plants to obtain most or all of their required N from the soil, thereby reducing the need for symbiotic N_2 fixation. There is no obvious explanation for the difference in white clover shoot N concentration between the L0P0 treatment and the L1P0 treatment (Figs 4.7 and 4.8), because N_2 -fixing activity ratio was nil in both cases.

There is also no obvious explanation for the depression in N_2 -fixing activity ratio at the L3 rate of lime in gorse but not in white clover (except at the P0 rate of P) (Fig 4.4).

4.4.3.2 Internal efficiency of N use

Shoot and root N concentration in gorse was significantly less than that of white clover at all treatments for which N concentration was measured, except for the L0P0 treatment (Figs 4.7 and 4.8). In the L1P1 treatment, near maximum yield was associated with shoot N concentrations of 2.60 and 3.35% for gorse and white clover respectively. Thus it appears that gorse is more efficient than white clover at using N (acquired from the soil or by symbiotic fixation) in the processes of growth. This indicates that gorse would be better able to survive in a low N situation because its energy requirement for N uptake, N₂ fixation and internal N use would be less than that of white clover.

4.4.4 Soil acidifying effects of gorse and white clover

White clover had a significant acidifying effect on the soil (resulting in decreased pH and increased CaCl₂-Al) compared with gorse. This effect was particularly marked where there was vigorous white clover growth. For example, at the L1 rate of lime, the increases in CaCl₂-Al in white clover pots relative to gorse pots were greatest at the P1-P3 rates of P where growth was also greatest (Table 4.7; Fig 4.1). At the end of the experiment, pH values and CaCl₂-Al concentrations in the gorse pots tended to be similar to those in the fallow pots or those at the beginning of the experiment.

The soil acidifying effect of gorse reported by Grubb *et al.* (1969) was not observed in this experiment.

4.5 CONCLUSIONS

- 1) Gorse was less responsive to applied P than white clover.
- 2) Under conditions of low available soil P, gorse was able to take up more P from the soil than white clover, within the restricted volume of a pot.
- 3) Gorse appeared to respond to low soil available P concentrations by lowering its shoot:root ratio.

- 4) Gorse used both P and N more efficiently in the production of plant dry matter, compared with white clover and appeared better able to maintain adequate shoot P concentrations at low available soil P concentrations than white clover.
- 5) Gorse was less responsive to applied lime than white clover, and appeared to be less sensitive to soluble ($0.02 \text{ mol l}^{-1} \text{ CaCl}_2$ -extractable) Al than white clover.
- 6) N_2 -fixing activity on a plant dry weight basis was similar for both gorse and white clover. It did not appear to be any more sensitive to soil acidity than the host plant for either species.
- 7) White clover had a significantly greater soil acidifying effect than gorse, which appeared to have no such effect.

CHAPTER 5

EFFECTS OF NITRATE CONCENTRATION ON GORSE AND WHITE CLOVER GROWTH

5.1 INTRODUCTION AND AIMS

Nitrogen is the element which most frequently limits crop growth (Quispel 1974; Yates 1976; Fowden 1979). Fertile soils may contain as much as 6.7 tonnes of combined N per hectare, but only a few kg of this will be in plant available mineral forms (Stevenson 1965). The atmosphere contains an abundant supply of gaseous nitrogen (N_2); approximately 78,500 tonnes over each hectare of land area (Stevenson 1965).

A small minority of plants can use atmospheric N_2 (via fixation) as a source of N (Stewart 1966). One very important group of N_2 fixing plants is the legumes. Legumes belong to the family Fabaceae which consists of between 12 000 and 14 000 species (Burns and Hardy 1975). Legumes account for almost half the annual quantity of N fixed by biological systems (Evans and Barber 1977).

Gorse is a legume and is therefore able to meet all or part of its N requirement via symbiotic N_2 fixation. Egunjobi (1969), in a successional study on a low fertility hill country soil, found that the most productive stage of regrowth (following burning) both in terms of biomass production and N accumulation was the early phase when gorse was dominant. Older stages, when gorse shared dominance with manuka (*Leptospermum scoparium*) and when kamihi (*Weinmannia racemosa*) was dominant, were less productive (Egunjobi 1969). Soil N concentration was greatest under gorse because of the capture of atmospheric N_2 by fixation and the large amount of litter deposited. Gorse litter stimulates N mineralisation more than litters from other species (Goma-Tchimbakla and Roze, 1985). Dancer *et al.* (1977a) also observed relatively high rates of N accumulation in gorse stands on kaolin mining wastes (coarse sand and gravel). N accumulation under gorse was higher than for other woody legume (broom or lupin) communities (Dancer *et al.* 1977a). Gorse, by virtue of its role as a nitrogen-fixing pioneer species appears to have the ability to accelerate soil development and plant succession. However, following application of P, K and lime, N accumulation rates by forage legumes (white clover and red clover (*Trifolium*

pratense)) were 70% higher than the maximum rate estimated for gorse on sand waste (Dancer *et al.* 1977b). N is found to inhibit gorse seedling nodulation and reduce seedling growth and survival (Thompson 1974; Hartley and Phung 1979, 1982). Ivens and Mlowe (1983) observed no response to applied N (as urea) either in terms of increased growth or decreased nodulation. Established plants however have been found to rapidly adapt to use applied N (Thompson 1974). In a situation where gorse seedlings were competing with grass species applied N was found to depress gorse seedling numbers. Conversely where grass establishment was poor, N increased gorse seedling numbers (Hartley and Popay 1982). Thus it appears that gorse will readily take up and use applied N. However, when N is applied in the presence of competing grass species, gorse loses its competitive advantage as a N₂-fixer and its growth is depressed.

The nature and magnitude of legume responses to applied N vary widely with species, as do the effects of applied N on symbiotic N₂-fixation. These topics are reviewed in greater detail in the Literature Review (Section 2.4).

In order to investigate further the N₂-fixing capacity of gorse, and its ability to use mineral N, a sand culture experiment was done with the following aims:

- 1) To compare the growth responses of gorse and white clover to increasing concentrations of nitrate.
- 2) To compare the relative abilities of gorse and white clover to meet their own N needs via symbiotic fixation.
- 3) To compare the capacities of gorse and white clover to use large external solution N concentrations.

5.2 EXPERIMENTAL

5.2.1 Trial Design

The trial was set up as a randomised block design with 7 nutrient solution nitrate concentrations, 2 plant species: gorse (*Ulex europaeus* L.) and "Grasslands Huia" white clover (*Trifolium repens* L.), and 4 replications. The concentrations of nitrate used are shown in Table 5.1.

Table 5.1 Nitrate treatments - rates of nitrate experiment

Treatment Code	Nitrate concentration (mmol l ⁻¹ as NaNO ₃)
00	0
SO	0
0.5	0.5
1	1.0
5	5.0
10	10.0
20	20.0

Starter N (0.5 mmol l⁻¹) was applied up to day 28 in all treatments except "00".

The nitrate concentrations in this experiment were intended to cover the range found in soils. Under natural conditions nitrate commonly occurs at concentrations of 1 mmol l⁻¹ or less in the interstitial water of soils, although in arid areas greater concentrations may build up (Russell 1973). In agricultural soils nitrate concentrations can be as high as 20 mmol l⁻¹ because of the addition of N fertiliser (Russell 1973; Reed and Hageman 1980; Young and Aldag 1982).

In the early stages of the experiment, when the plants were very small, depletion of nitrate between nutrient solution replacements (Section 5.2.3) would have been minimal. At the end of the experiment, for both species, it was estimated that plant uptake would have been at least matched by nitrate application in the 5.0 mmol l⁻¹ nitrate treatment. Therefore at nutrient solution nitrate concentrations of 5.0 mmol l⁻¹ or less, nitrate would have been considerably depleted between nutrient applications. At 10 and 20 mmol l⁻¹ nitrate, there would have been a considerable excess of nitrate supplied over nitrate uptake. Estimates of N uptake were based on plant dry weights, estimated relative growth rates (0.052 and 0.080 g g⁻¹ day⁻¹ for gorse and white clover respectively), and plant N concentrations. Analysis of effluent from the pots at the end of experiment indicated almost complete depletion of nitrate in the 0.5 and 1.0 mmol l⁻¹ treatments, but that some nitrate remained in the 5 mmol l⁻¹ treatment. Nitrate concentrations in the 10 and 20 mmol l⁻¹ treatments tended to increase slightly over the interval between nutrient applications, indicating that

water uptake plus evaporation exceeded nitrate uptake.

Gorse and white clover pots were kept separate within each block. Within each block, the individual gorse and clover pots were re-randomised weekly, and the position of the gorse and clover pots, as groups, were randomly relocated.

5.2.2 Plant Culture

5.2.2.1 Seed

The gorse seed source was the same as that for the Springston field trial (Section 3.2.3.1). Fifteen hundred seeds were pre-germinated as for the Springston trial (Section 3.2.3.1). "Grasslands Huia" white clover seeds were sown directly, without pre-germination.

5.2.2.2 Growth Medium and Pots

Plants were grown in coarse quartz sand, obtained from the Walton Park Sand Co Ltd, Dunedin. The sand was thoroughly washed to remove fine material. 2045 g equivalent dry weight of sand occupying a volume of 1230 cm³ was packed into 1.4 litre free-draining plastic pots. The bottoms of the pots were lined with fibreglass insect mesh (mesh size 1.2 × 1.8 mm) to prevent loss of sand. The water holding capacity of the sand in the pots, and the particle size distribution of the sand are shown in Table 5.2. A water release curve done for a slightly finer sand than the one used in this experiment indicates that almost all of the water held by the sand was readily available (Hume 1981).

Table 5.2 Physical properties of quartz sand used in rates of nitrogen experiment

(a) Water holding properties of 2045g equivalent dry weight of sand packed in pots to a volume of 1230 cm³

* Water holding capacity	296 ml
Gravimetric water content	14.5%
Volumetric water content	24.1%

* Water held against gravity after saturation then free drainage for 16 hours

(b) Particle size distribution

International classification	Size (mm)	% by weight (air dry)
Gravel	>2	15.5
Coarse sand	1-2	40.7
	0.5-1	33.5
	0.25-0.5	8.1
Fine sand	0.125-0.25	2.2
	0.063-0.125	0.17
Silt and clay	<0.063	trace

5.2.2.3 Planting

Gorse

The moist sand was packed into the pots and levelled. Holes were made at each of 4 evenly spaced planting positions using a template. Two germinated gorse seeds were placed in each hole and covered over with about 2 mm of sand.

White clover

All but 100 g moist weight of sand was packed into the pots. At least 2 seeds were placed in each of the 4 planting positions (same as for gorse). The remaining 100 g of moist sand was then placed evenly over the surface.

One hundred ml of deionised water was sprinkled onto the surface of each pot and the pots

were covered with sheets of heavy paper to reduce moisture loss. The pots were sprayed daily with deionised water to keep the surface of the sand moist.

Pots were kept moist before transfer to a glasshouse when the seedlings were emerging (day 2 from planting for gorse, day 4 for white clover). At the first true leaf stage, plants were thinned to 4 per pot.

5.2.2.4 Watering

After planting, and between nutrient applications, pots were watered with deionised water (conductivity = 1-2 μMho).

Pots were watered to their weight at water holding capacity so that nutrients would not be lost (an allowance was made for the weight of plant material present).

5.2.2.5 Glasshouse Temperature

Mean daily maximum/minimum temperatures in the glasshouse over the period of the experiment were 25.0/13.5°C. Because the experiment was run over the winter/early spring period, overheating in the glasshouse was not a problem and there was little day-to-day variation in temperature.

5.2.3 Nutrient Solutions

The elemental composition of the nil N nutrient solution is shown in Table 5.3. The compounds and stock solution used are shown in Appendix 5.1. The nitrate treatments were applied as sodium nitrate (Table 5.1). The quantity of nutrient solution applied at each application was 400 ml, well in excess of the amount needed to completely flush out the solution already in the pot.

During the establishment and inoculation phase, the nutrient solution applied was the nil nutrient solution (Table 5.3) plus 0.5 mmol l⁻¹ N, except for the 00 treatment which was given no starter N. The timing of initial nutrient applications and inoculations are shown in Table 5.4. At the time of first application of the nitrate treatments, the gorse seedlings

had 4 true leaves and the white clover seedlings had their first trifoliate leaf. From day 28 nutrient solutions were replaced 5-daily up to day 53, 4-daily to day 57, 3-daily until day 69 and 2-daily until the end of the experiment. Nutrient solutions were always replaced the day before acetylene reduction or nitrate reductase assays were done, even when this meant advancing the normal schedule.

Table 5.3 Elemental composition of nil N nutrient solution.

Element	Concentration (ppm)
P	38.7
K	205.3
Mg	24.3
S	96.6
Ca	100.2
Zn	0.250
Cu	0.100
B	0.500
Mn	0.500
Mo	0.050
Co	0.010
Fe	3.000
Cl	177.3
Na	0.024

Table 5.4 Timing of operations during establishment - Rates of nitrate experiment.

Operation	Time - days from sowing	
	gorse	white clover
1st nutrient application	6	10
1st inoculation	7	11
2nd nutrient application	16	18
2nd inoculation	16	18
1st nitrate treatment	28	28

5.2.4 Rhizobial Inoculation

Both plant species were inoculated twice (Table 5.4) using peat cultures suspended in deionised water.

The gorse plants were inoculated with the same strain of *Bradyrhizobium* used for the Springston field trial and the lime/P experiment (Section 3.3.3.2). Five ml of suspension, containing approximately 3.5×10^7 rhizobia, was applied to the base of each plant at each inoculation (rhizobial numbers were determined by dilution plate counts).

The white clover plants were inoculated with a commercially available *Rhizobium* strain (cc275e). Suspensions were made up containing the same quantity of peat as for the gorse and five ml, containing a minimum of 3.5×10^8 rhizobia, was applied to the base of each plant at each inoculation time (rhizobial numbers were supplied by the manufacturer).

On day 30, a number of spare plants, which had been grown and inoculated in the same way as the experimental plants, were examined to check that nodulation had occurred. The data are recorded in Table 5.5. The plants appeared to be well nodulated. All of the plants observed had nodules, and gorse nodules appeared to be larger than those of white clover. Many of the nodules had pink centres, indicating the presence of leghaemoglobin and N_2 -fixing activity (Stewart 1966).

Table 5.5 Stage of development and nodule number of gorse and white clover plants at day 30 - rates of nitrate experiment

	Gorse (n=9)	White clover (n=19)
Stage of plant development	Fourth true leaf	First trifoliate leaf
Plant height (cm) mean	2.5	3.6
s.e.	0.35	0.53
Nodule number mean	5.4	7.9
s.e.	3.0	2.4
Number pink nodules mean	2.6	6.5
s.e.	2.3	3.0

5.2.5 Acetylene Reduction Assay

5.2.5.1 Incubation, sampling and gas analysis

Acetylene reduction assays were done two replicates at a time, 3 days before the final harvest. Pots were incubated for exactly 2 hours beginning at approximately 12.30 pm. Incubation temperatures were in the range 18-20°C. Other incubation conditions, sampling and gas analysis were as described in Section 4.2.4.

5.2.6 Final Harvest

The white clover pots were harvested on days 89 and 90, and the gorse pots on days 124 and 125. Individual species were harvested before they became too large relative to the size of the pots. White clover grew more rapidly than gorse and therefore was harvested at a younger age.

Roots were floated free from the sand in water. The shoots and roots were separated and rinsed in deionised water. Sub-samples of both shoots and roots were taken for measurement of nitrate reductase activity. The number and dry weight of nodules were measured on a further representative sub-sample of root from each plant (approx. 10% of total weight). All plant material was dried to constant weight at 70°C.

5.2.7 Nitrate Reductase Assay

Reagents and assay conditions were those described by Andrews *et al.* (1984), except that the samples were incubated for 30 instead of 20 minutes.

5.2.7.1 Procedure

Immediately following removal of the plants from their pots, plant material was rinsed in deionised water and dried. Representative subsamples of both root and shoot (0.5-0.7 g fresh weight) were taken and cut into pieces about 2 mm long or 2 mm square in the case of white clover leaflets.

The subsamples were placed in 10 ml of phosphate buffer and incubated for 30 minutes under the conditions described by Andrews *et al.* (1984). One ml samples were taken at the beginning and end of the incubation period.

The samples were analysed for nitrite colorimetrically as described by Mackereth *et al.* (1978). Rates of nitrate reductase activity were expressed on a plant dry weight basis.

5.2.8 Statistical Analysis

Analyses of variance were done as described in Section 3.2.14.

When considering responses of individual species to nitrate, the species were analysed individually. In order to study interactions between species and nutrient solution nitrate concentration, and differences between species, analyses were done including both species, where species was the main plot treatment and nitrate concentration was the sub-plot treatment in a split plot design.

In no instance was there a significant difference between the 00 and S0 treatments. For the purpose of curve fitting therefore, curves were fitted to the means of all treatments, including both nil nitrate treatments. For ease of presentation mean values for treatments 00 and S0 are presented in Figs 5.2, 5.3, 5.5, 5.7 and 5.9.

The following relationships were calculated for treatment means and those giving the best fit used:

$$y = a + bx$$

$$y = a + bx + cx^2$$

$$y = a + b(\ln(x+0.325)) + c(\ln(x+0.325))^2$$

$$y = a + br^x$$

$$y = a + b\sqrt{x} + cx$$

The approach to curve fitting used in this experiment was a functional one (Hunt 1978), where the only concern is that the fitted curves adequately describe the trends in the data. Comparisons made between parameters of fitted curves (e.g. asymptotes (a) for the relationship $y = a + br^x$) were based on *t* tests.

Responsiveness, critical shoot N concentration and the nutrient solution N concentration at which 90% maximum yield is achieved are useful parameters in biological terms (Sections 5.3.1, 5.3.2.1 and 5.3.2.2). Responsiveness is defined in Section 3.2.14. In this experiment Y_m was taken to be the maximum point of the fitted response curve, of the form $y = a + b\sqrt{x} + cx$. Nutrient solution N concentration associated with 90% maximum yield was also determined using the fitted yield response curve. Critical shoot N concentration was the N concentration associated with 90% maximum yield and was determined using a quadratic curve fitted to a plot of dry matter yield versus P concentration. Estimates for these parameters were formed in the same way as estimates of responsiveness and P acquisition for the Springston field trial (Section 3.2.14).

5.3 RESULTS

5.3.1 Growth and dry matter partitioning

Nutrient solution nitrate concentration significantly affected shoot and root weight of both gorse and white clover (Table 5.6). There was no species \times N concentration interaction for either shoot or root weight, suggesting that responses to increasing solution nitrate concentration were similar for both species (Fig 5.1).

Table 5.6 Effect of nutrient solution N (nitrate) concentration on shoot and root weight of gorse and white clover

Source of variation (treatment or interaction)	Level of significance		
	Shoot	Root	shoot:root ratio
species	***	***	ns
N	***	***	**
species \times N	ns	ns	ns

Significance levels are shown by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$) and ns (nonsignificant).

For shoot, root and total plant growth, the relationship $y = a + b\sqrt{x} + cx$ gave a consistently better fit than the other relationships tested. This curve type is useful for describing data

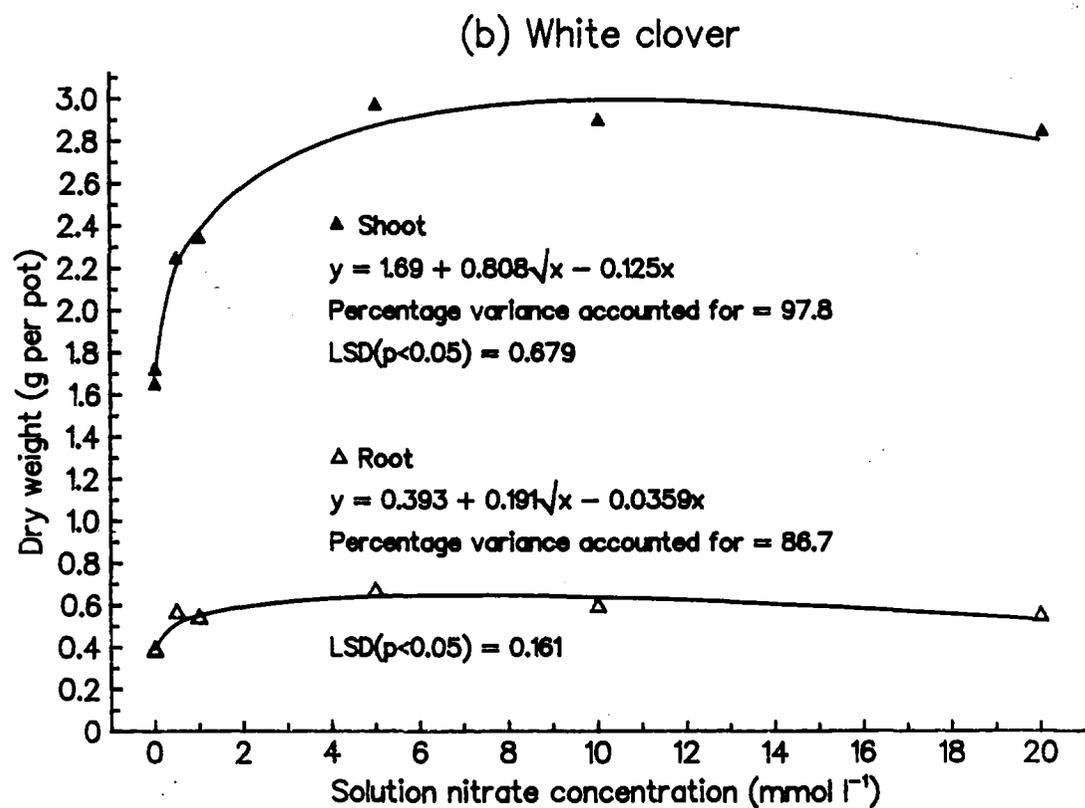
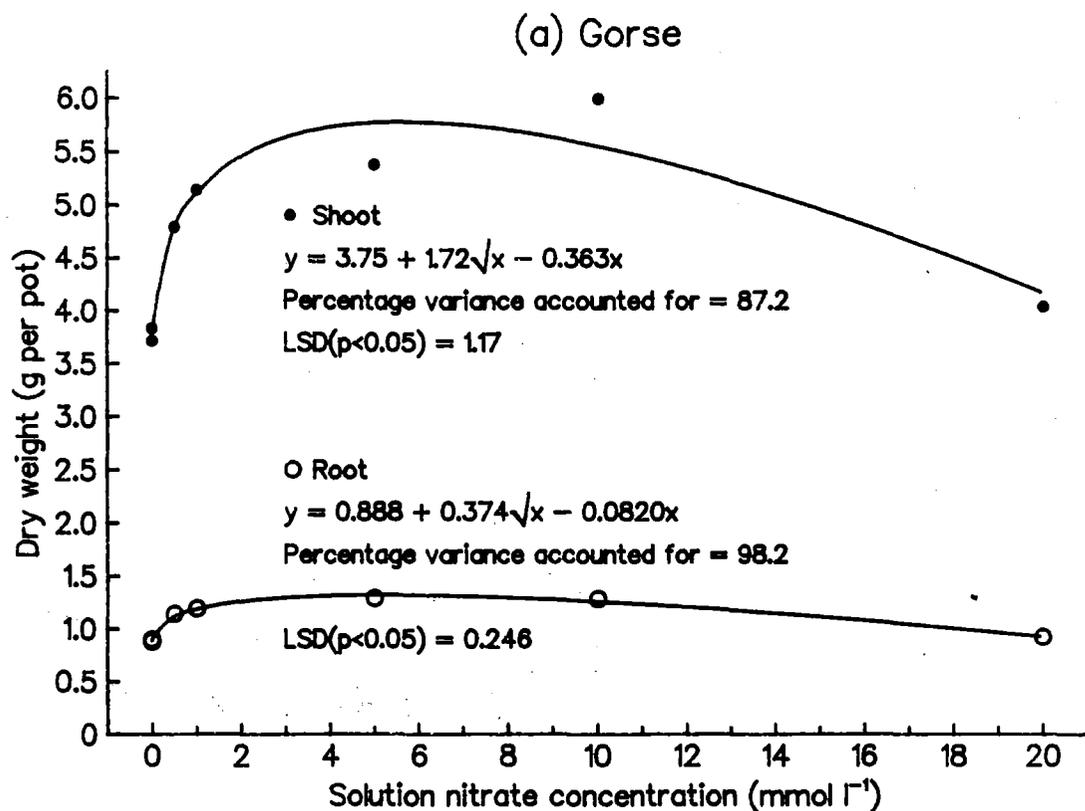


Fig. 5.1 Effect of nutrient solution nitrate concentration on shoot and root weight of gorse and white clover – rates of nitrate experiment.

which are not symmetrical about the maximum, as in this experiment where there were rapid increases in dry matter yield with increase in solution nitrate concentration followed by gradual declines at high nitrate concentrations (Fig 5.1). Gorse shoot and root weights increased significantly with increase in solution nitrate concentration and, according to the fitted curves, reached 90% of maximum yield at 1.22 and 1.03 mmol l⁻¹ nitrate respectively (Fig 5.1(a); Table 5.7).

Table 5.7 Nitrate concentration at 90% maximum dry matter yield and responsiveness of gorse and white clover to increasing nitrate concentration

Variable (dry weight)	Parameter	
	Nitrate concentration at 90% maximum yield (mmol l ⁻¹) Estimate (se)	Responsiveness (Section 3.3.2.2) Estimate (se)
Gorse shoot	1.22 (0.29) *	0.35 (0.056) ns
Clover shoot	2.86 (0.22)	0.44 (0.056)
Gorse root	1.03 (0.25) ns	0.32 (0.049) ns
Clover root	1.72 (0.42)	0.39 (0.067)
Gorse whole-plant	1.18 (0.28) *	0.35 (0.053) ns
Clover whole-plant	1.58 (0.64)	0.43 (0.057)

Significance levels of differences between species are shown by * (p=0.05) and ns (nonsignificant).

There were significant declines in both shoot and root weight at 20 mmol l⁻¹ nitrate (Fig 5.1(a)). White clover shoot and root weights also increased significantly with increase in solution nitrate concentration, but reached 90% maximum yield at greater (significant for shoot weight only) nitrate concentrations (2.86 and 1.72 mmol l⁻¹ for shoot and root weight respectively) than for gorse (Fig 5.1(b); Table 5.7). There was no significant decline in shoot or root weight of white clover at 20 mmol l⁻¹ nitrate (Fig 5.1(b)). Responsiveness (Ozanne 1980, defined in Sections 5.2.8 and 3.2.14) of gorse shoot weight to increasing solution nitrate concentration was 0.35 (Table 5.7). This means that gorse, entirely dependent on symbiotic N₂ fixation (nil nitrate concentration), produced 65% of the maximum shoot dry weight obtained when abundant N was supplied. Responsiveness of white clover shoot weight was 0.44, meaning that white clover dependent on symbiotic N₂ fixation produced

56% of the shoot dry matter obtained at maximum yield (Table 5.7). The responsiveness of gorse to increasing solution nitrate concentration was not significantly less than that of white clover (Table 5.7).

Shoot:root ratio of white clover increased significantly with increase in solution nitrate concentration but there was no clear trend for gorse (Table 5.6; Fig 5.2). There was no significant difference in mean shoot:root ratio between the species (4.35 and 4.57 for gorse and white clover respectively).

5.3.2 Plant nitrogen

5.3.2.1 Shoot and root nitrogen concentration

Shoot %N increased significantly with increasing nutrient solution nitrate concentration for both gorse and white clover and there was a significant interaction between solution nitrate concentration and species (Table 5.8; Fig 5.3). For white clover, there were progressive increases in shoot N concentration up to 10 mmol l⁻¹ nitrate, where a plateau was reached. For gorse however the increases were not consistent, and the only value which was greater than most of the others was that at 20 mmol l⁻¹. This appears to have resulted from the decline in shoot weight (Fig 5.1) rather than enhanced N uptake (Fig 5.4).

Table 5.8 Effect of nutrient solution N (nitrate) concentration on shoot and root N concentration of gorse and white clover

Source of variation (treatment or interaction)	Level of significance	
	%N shoot	%N root
Species	***	***
N	***	**
Species × N	***	ns

See Table 5.6 for description of significance levels

Shoot N concentration was significantly less for gorse (mean = 3.16%) than for white clover, (mean = 4.48%) at all solution nitrate concentrations (Table 5.8; Fig 5.3(a)).

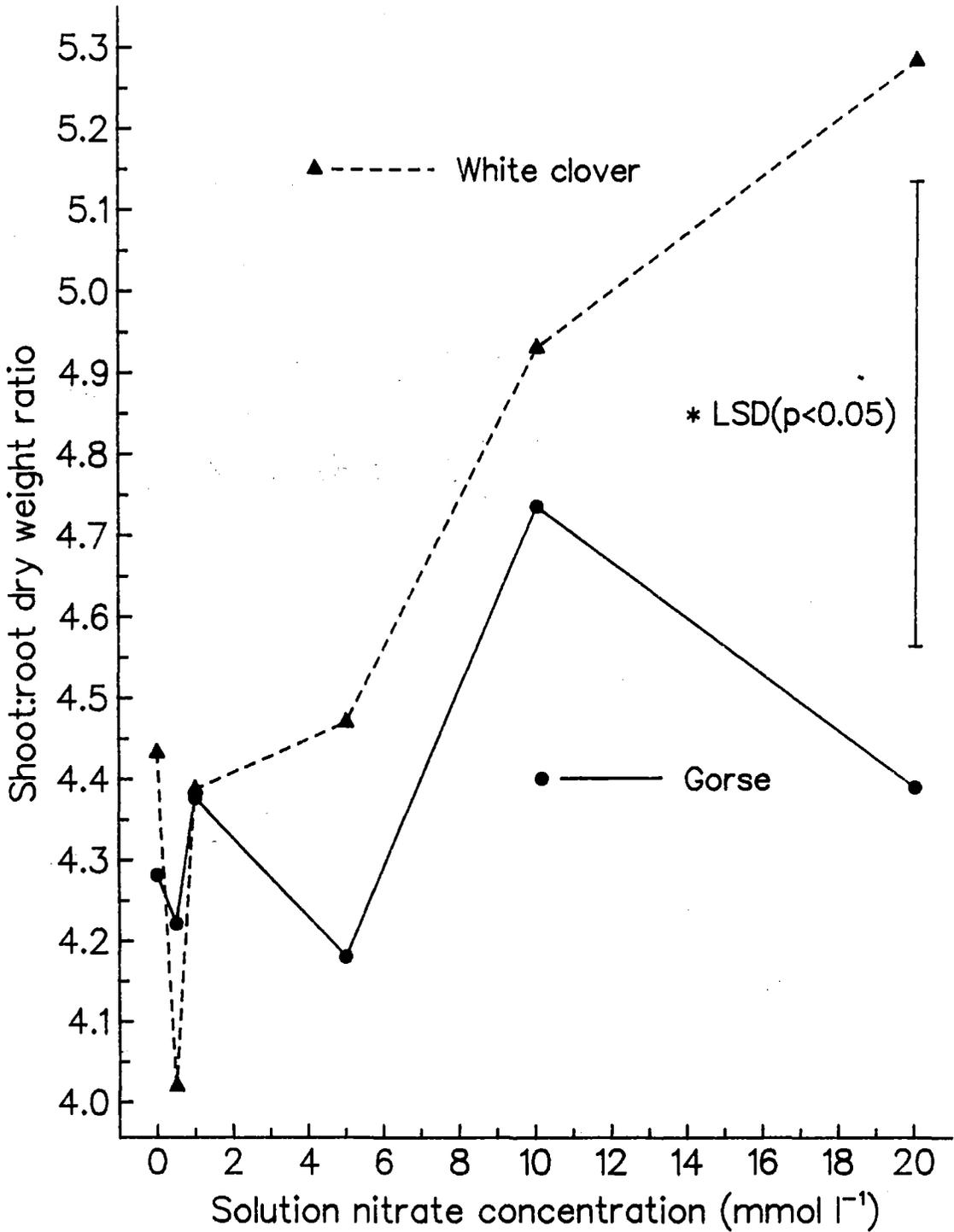


Fig. 5.2 Effect of nutrient solution nitrate concentration on shoot:root ratio of gorse and white clover – rates of nitrate experiment.
* LSD pooled for both species.

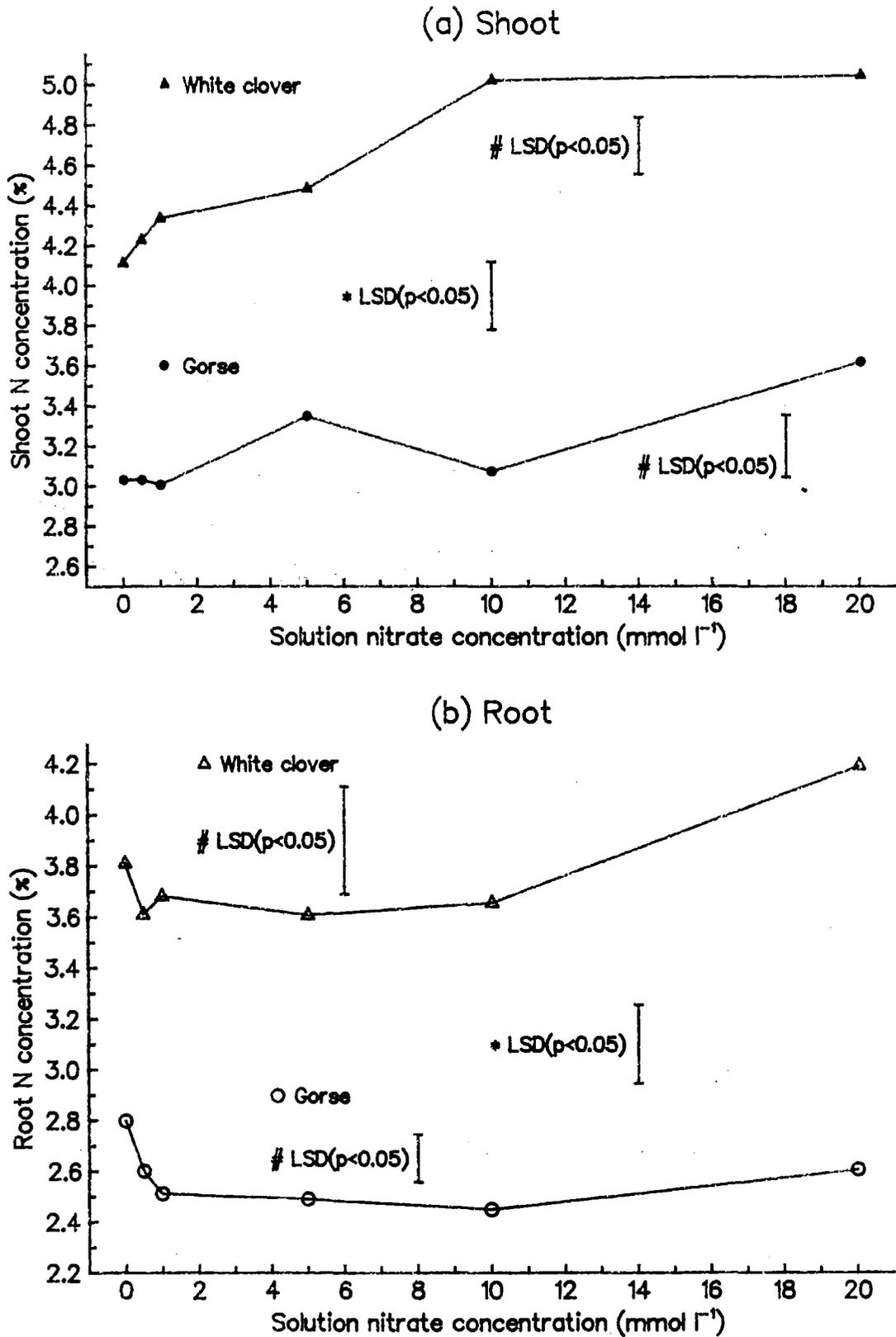


Fig. 5.3 Effect of nutrient solution nitrate concentration on N concentration in shoots and roots of gorse and white clover – rates of nitrate experiment.

* LSD pooled for both species.

LSD for individual species.

The critical shoot N concentration (at 90% maximum yield) for gorse (2.79%) was also significantly less than that for white clover (4.62%) ($p < 0.001$). Nitrate concentration had a significant effect on root N concentration (Table 5.8). However the differences were small (Fig 5.3(b)). The main feature of the root N concentrations was the large species effect (Table 5.8), with N concentration being significantly less in gorse roots (mean = 2.61%) than in white clover roots (mean = 3.77%) at all solution nitrate concentrations (Fig 5.3(b)). For whole-plant N concentration, the effect of species and the patterns of response to increasing nutrient solution nitrate concentrations for both species, were very similar to those for shoot N concentration (Table 5.8; Fig 5.3).

5.3.2.2 Shoot, root and whole-plant nitrogen content

For shoot, root and whole-plant N content, there were significant effects of species and nutrient solution nitrate concentration, but no species \times nitrate interaction (Table 5.9).

Table 5.9 Effect of nutrient solution N (nitrate) concentration on N content of gorse and white clover

Source of variation (treatment or interaction)	Level of significance		
	Shoot N content	Root N content	Whole-plant N content
Species	**	**	**
N	***	***	***
Species \times N	ns	ns	ns

See Table 5.6 for description of significance levels.

For shoot, root and whole-plant N content of both species, the relationship giving best fit was, as for plant dry weight, that using the square root transformation ($y = a + b\sqrt{x} + cx$).

Gorse shoot and root N content both increased with increasing nutrient solution nitrate concentration and according to the fitted curves, reached 90% of maximum at 1.61 and 0.57 mmol l⁻¹ nitrate respectively (Fig 5.4(a)). There were significant declines in N content as nitrate concentration was increased to 20 mmol l⁻¹ (Fig 5.4(a)).

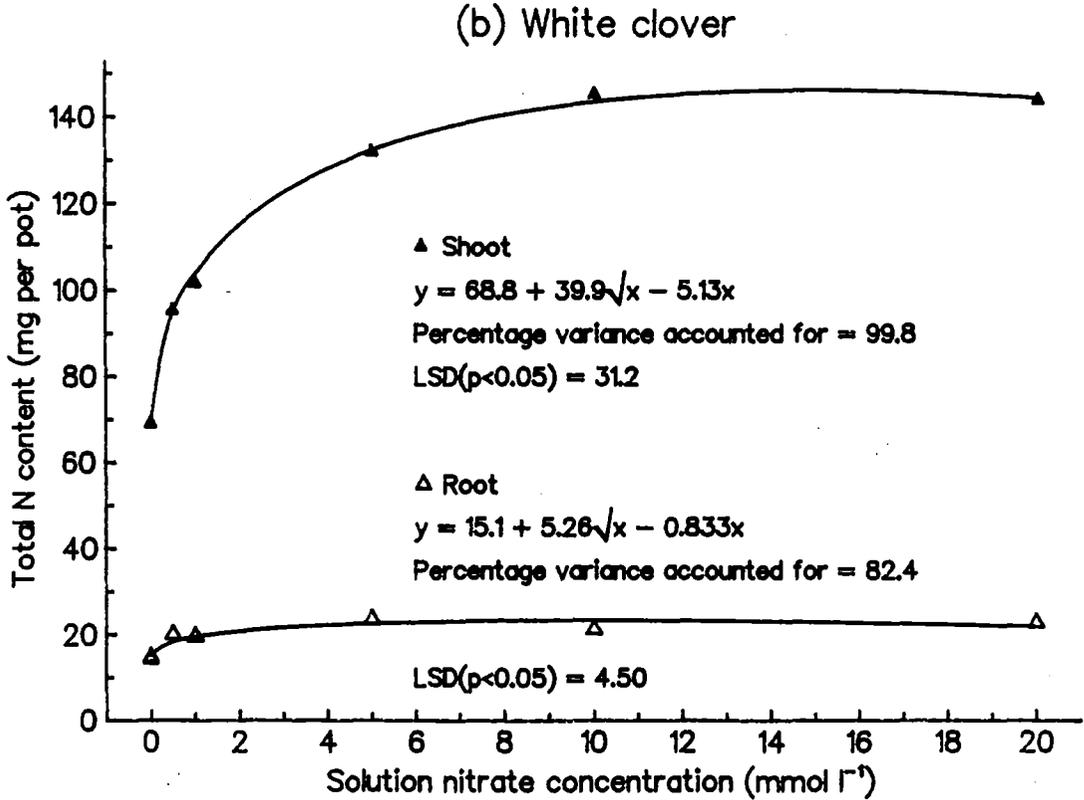
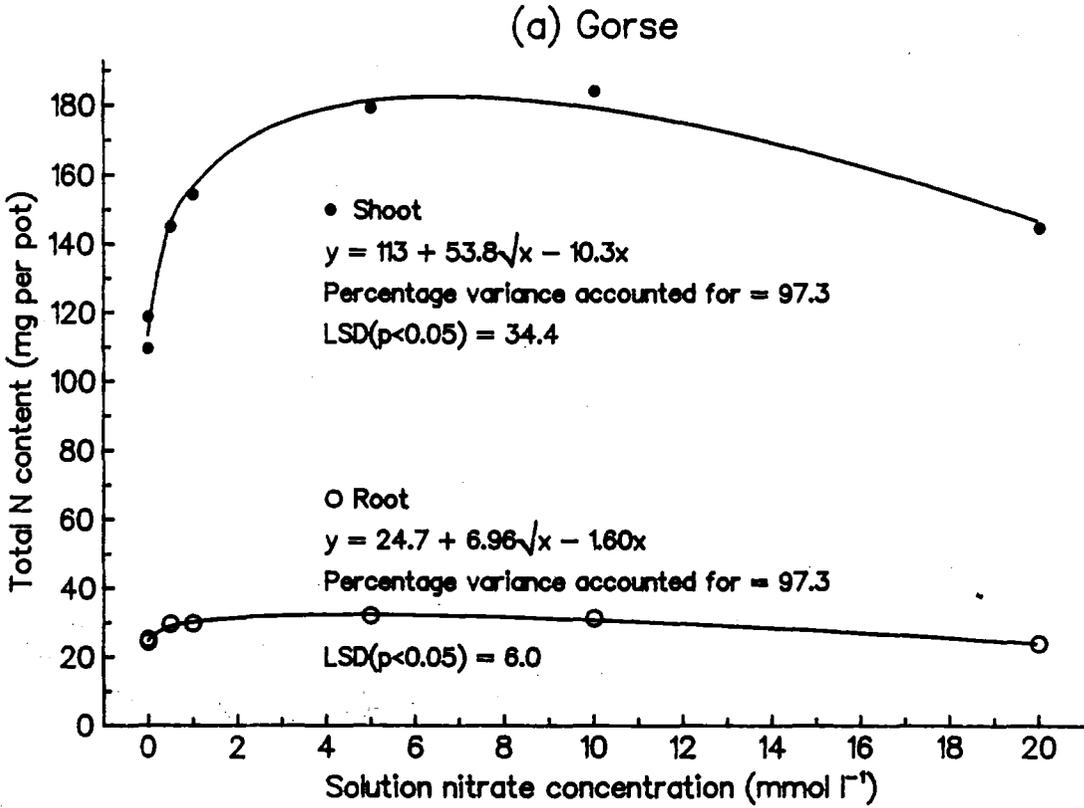


Fig. 5.4 Effect of nutrient solution nitrate concentration on total N content of gorse and white clover – rates of nitrate experiment.

White clover shoot and root N content also increased significantly with increasing nutrient solution nitrate concentration reaching 90% of maximum at 5.05 and 2.29 mmol l⁻¹ nitrate respectively (derived from fitted curves) (Fig 5.4(b)). For white clover the N contents of shoots and roots effectively reached a plateau at approximately 10 mmol l⁻¹ nitrate (Fig 5.4(b)). In contrast with gorse, there was no significant decline in shoot or root N content as nitrate concentration was increased to 20 mmol l⁻¹ (Fig 5.4). Total plant N for both species very closely followed the pattern described for total shoot N.

The nutrient solution N concentrations at which plants reached 90% maximum N content were significantly less ($p < 0.05$) for gorse than white clover for roots only. The lack of significance for shoot N was largely due to a high standard error associated with the estimates for white clover shoots. A probable cause of this is the relatively gentle slope (and therefore insensitivity) of the response curve for white clover shoots at the point of 90% maximum yield (Fig 5.4). Estimates of solution N concentration at 80% maximum shoot and whole-plant N content (where the curves had greater slope) were significantly less for gorse than white clover (Table 5.10).

Table 5.10 Nitrate concentration at 80% maximum N content and responsiveness of gorse and white clover (in terms of N content) to increasing nitrate concentration

Variable (N content)	Parameter	
	Nitrate concentration at 80% maximum N content (mmol l ⁻¹) Estimate (se)	Responsiveness (Section 3.3.2.2) Estimate (se)
Gorse shoot	0.52 (0.19) *	0.38 (0.049) *
Clover shoot	2.25 (0.82)	0.54 (0.050)
Gorse root	0.03 (0.08) ns	0.23 (0.051) ns
Clover root	0.62 (0.31)	0.36 (0.056)
Gorse whole-plant	0.42 (0.17) *	0.36 (0.049) *
Clover whole-plant	1.97 (0.69)	0.51 (0.050)

Significance levels of differences between species are shown by * ($p < 0.05$) and ns (nonsignificant).

In terms of shoot and whole-plant N content, gorse was significantly less responsive to

increasing nutrient solution nitrate concentration than white clover (Table 5.10). Focusing on whole-plant N content, gorse totally dependent on symbiotic N₂ fixation achieved 64% of the maximum N content achieved when supplied with nutrient solution nitrate (Table 5.10). In contrast, white clover dependent on symbiotic N₂ fixation achieved only 49% of the maximum N content achieved when it was supplied with nutrient solution nitrate (Table 5.10).

5.3.3 Nodulation and Nitrogen fixing activity

5.3.3.1 Nodulation

Nodule number and weight on a whole-plant dry weight basis and individual nodule mass were significantly affected by plant species and nutrient solution nitrate concentration (Table 5.11). The species × nitrate concentration interaction was significant only for nodule number per unit whole-plant dry weight (nodule number ratio) (Table 5.11).

Table 5.11 Effect of nutrient solution N (nitrate) concentration on nodule number and dry weight on a whole-plant dry weight basis (nodule number ratio and nodule weight ratio), and on individual nodule mass

Source of variation (treatment or interaction)	Level of significance		
	Nodule number ratio	Nodule weight ratio	Individual nodule mass
Species	**	**	**
N	***	***	***
Species × N	*	ns	ns

See Table 5.6 for description of significance levels.

For gorse, nodule number ratio did not decline significantly with increases in nutrient solution nitrate concentration (Fig 5.5). In contrast, nodule number ratio of white clover decreased substantially with increases in solution nitrate concentration; being significantly greater than that for gorse at low concentrations (0 and 0.5 mmol l⁻¹), but similar from 1 to 20 mmol l⁻¹ nitrate (Fig 5.5).

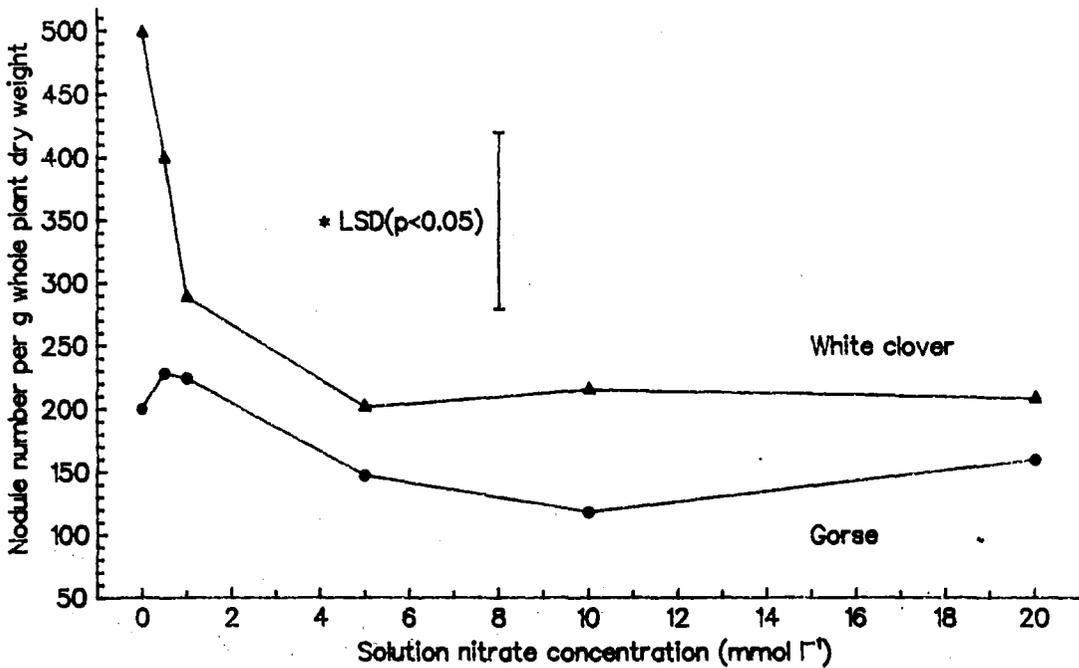


Fig. 5.5 Effect of nutrient solution nitrate concentration on number of nodules per unit whole plant dry weight (nodule number ratio) – rates of nitrate experiment.
* LSD pooled for both species.

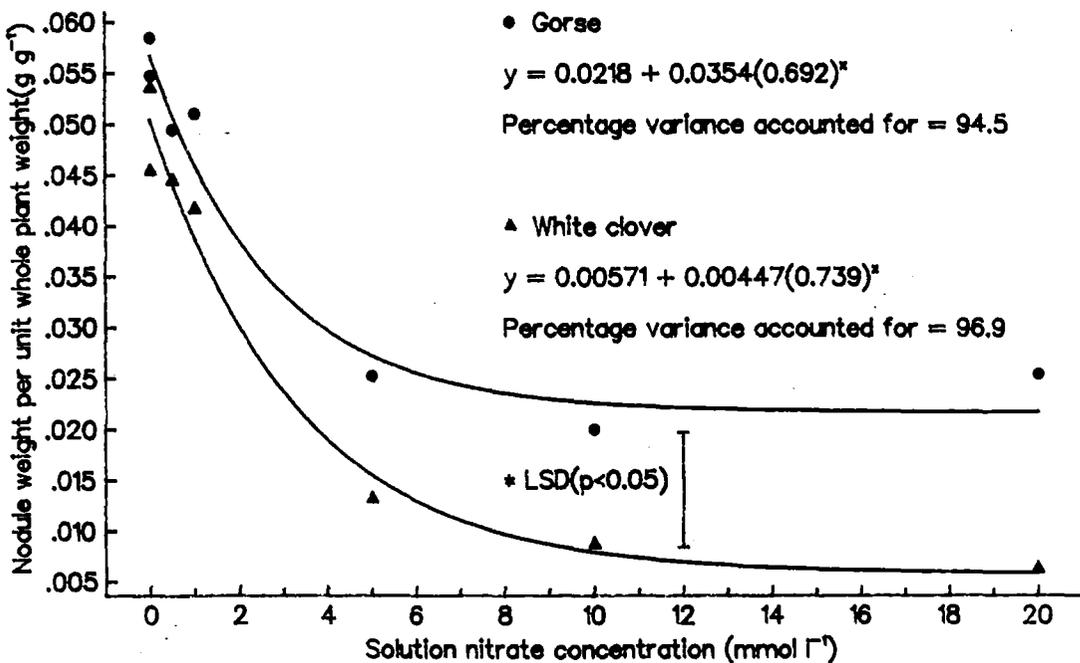


Fig. 5.6 Effect of nutrient solution nitrate concentration on nodule dry weight per unit whole plant dry weight (nodule weight ratio) – rates of nitrate experiment.
* LSD pooled for both species.

Nodule weight on a unit whole-plant dry weight basis (nodule weight ratio), and individual nodule mass were significantly affected by species and nutrient solution nitrate concentration, but there was no significant species \times nitrate concentration interaction (Table 5.11).

Nodule weight ratio decreased exponentially with increasing nitrate concentration for both species (Fig 5.6). The major decrease in nodule weight ratio for both species occurred from 1 to 5 mmol l⁻¹ nitrate. Whereas at nutrient solution nitrate concentrations of 0 to 1 mmol l⁻¹, nodule weight ratios were similar for both species, at greater nitrate concentrations (5 to 20 mmol l⁻¹) nodule weight ratio was significantly greater for gorse than white clover (Fig 5.6).

Based on the fitted curves, nodule weight ratios at a solution nitrate concentration of 0 mmol l⁻¹ were 0.0572 and 0.0504 g g⁻¹ for gorse and white clover respectively (Fig 5.6). The rate of decline in nodule weight ratio with increase in solution nitrate concentration were not significantly different between both species (Fig 5.6). However the suppression of nodule weight ratio at high solution nitrate concentrations was significantly less ($p < 0.001$) for gorse than for white clover, with asymptotes at 0.0218 and 0.0057 g g⁻¹ for gorse and white clover respectively (Fig 5.6). The degree of nodulation at 0.5 mmol l⁻¹ nitrate compared with 20 mmol l⁻¹ nitrate, for gorse compared with white clover is illustrated in Plates 5.1 and 5.2.

Individual nodule mass declined significantly with increase in solution nitrate concentration for both gorse and white clover, but the decrease was larger for gorse (Fig 5.7). At all nitrate concentrations nodule mass was significantly greater for gorse than for white clover (Fig 5.7).

5.3.3.2 Symbiotic N₂-fixing activity

Symbiotic N₂-fixing activity was expressed on a plant dry weight basis in order to avoid effects merely due to differences in plant dry weight.

Nutrient solution nitrate concentration had significant effects on N₂-fixing activity per unit whole-plant dry weight (N₂-fixing activity ratio), but there was no significant effect of species and no significant species \times rate of nitrate interaction (Table 5.12).

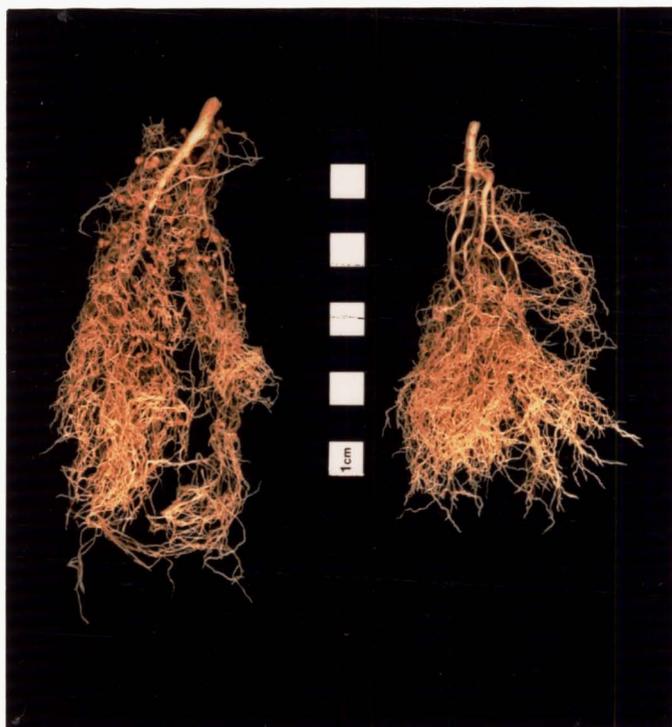


Plate 5.1 Gorse root systems showing degree of nodulation at 0.5 mmol l⁻¹ (left) and 20 mmol l⁻¹ nitrate (right).



Plate 5.2 White clover root systems showing degree of nodulation at 0.5 mmol l⁻¹ (left) and 20 mmol l⁻¹ nitrate (right).

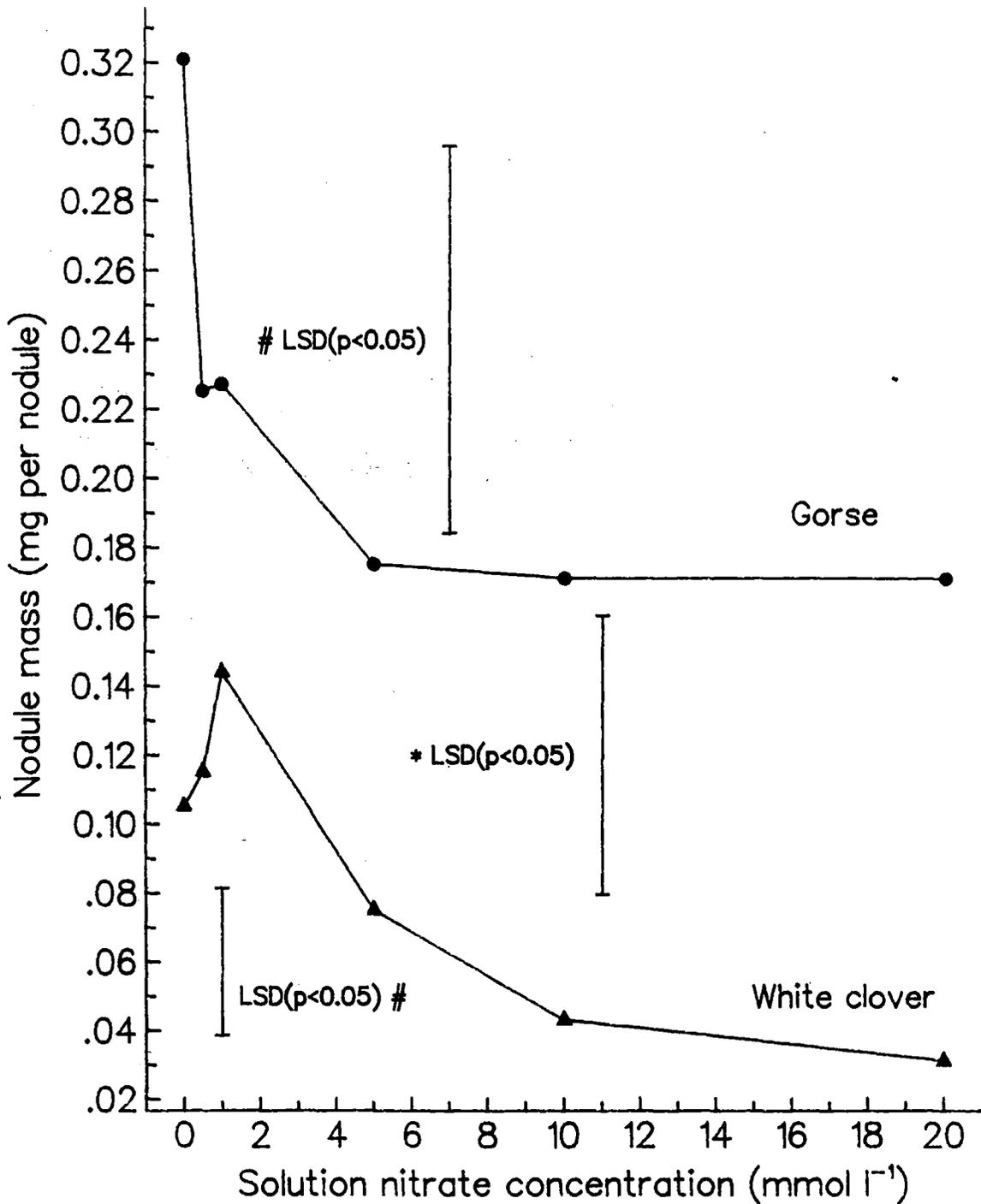


Fig. 5.7 Effect of nutrient solution nitrate concentration on individual nodule mass of gorse and white clover — rates of nitrate experiment.
 * LSD pooled for both species.
 # LSD for individual species.

The fitted curves (Fig 5.8) indicate that N_2 -fixing activity ratio decreased exponentially with increase in solution nitrate concentration for both species. Based on the asymptotes to the fitted curves, the increasing solution nitrate concentrations depressed N_2 -fixing activity ratio to a significantly lower level in white clover ($0.30 \mu\text{mol g}^{-1} \text{h}^{-1}$) than in gorse ($1.19 \mu\text{mol g}^{-1} \text{h}^{-1}$) ($p < 0.01$).

Nutrient solution nitrate concentration significantly affected N_2 -fixing activity per unit nodule weight (specific N_2 -fixing activity). Analysis of variance on an individual species basis (because variance was much greater for white clover than gorse) showed that specific N_2 -fixing activity of both gorse and white clover declined significantly, in a linear manner ($p < 0.001$ for gorse and $p = 0.024$ for white clover), with increasing solution nitrate concentration (Fig 5.9). The slopes were similar, being -2.28 ($se = 0.46$) for gorse and -3.85 ($se = 1.71$) for white clover.

Table 5.12 Effect of nutrient solution N (nitrate) concentration on N_2 -fixing activity of gorse and white clover

Source of variation (treatment or interaction)	Level of significance	
	N_2 -fixing activity per pot	N_2 -fixing activity per unit whole-plant dry weight
Species	*	ns
N	***	***
Species \times N	ns	ns

See Table 5.6 for description of significance levels.

5.3.4 Nitrate reductase activity

5.3.4.1 Specific nitrate reductase activity

Analyses of variance of nitrate reductase activity (NRA) were done on both untransformed and log-transformed values. Analyses of the log-transformed values are presented because they better fulfil the underlying assumptions for analyses of variance (Section 3.2.14).

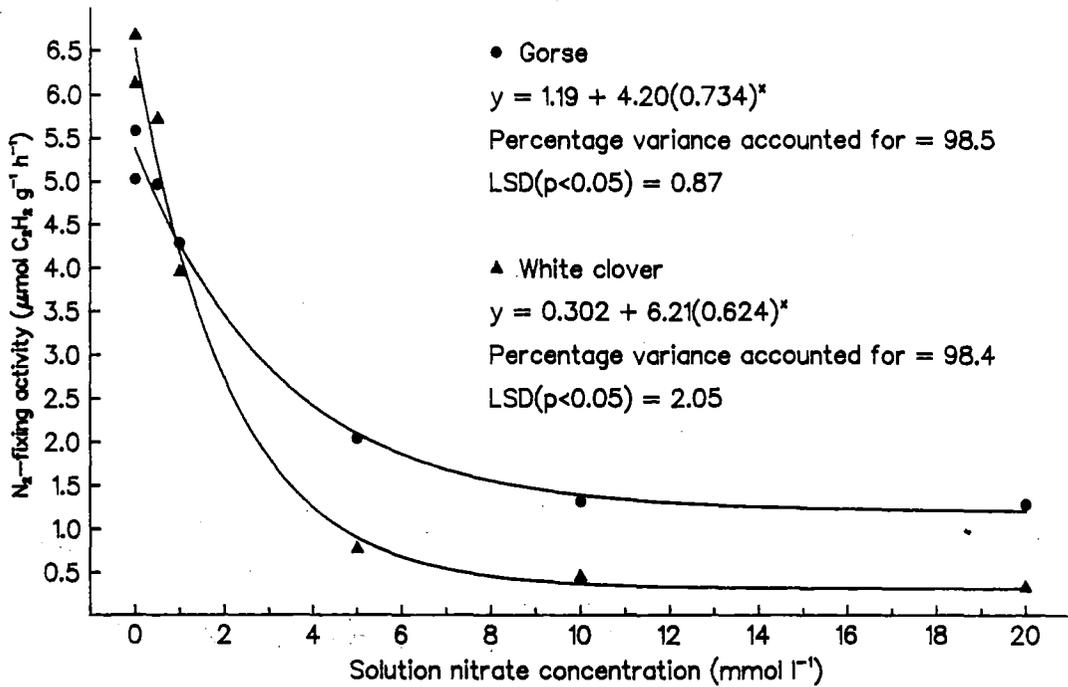


Fig. 5.8 Effect of nutrient solution nitrate concentration on N_2 -fixing (C_2H_2 -reducing) activity per unit whole plant dry weight – rates of nitrate experiment.

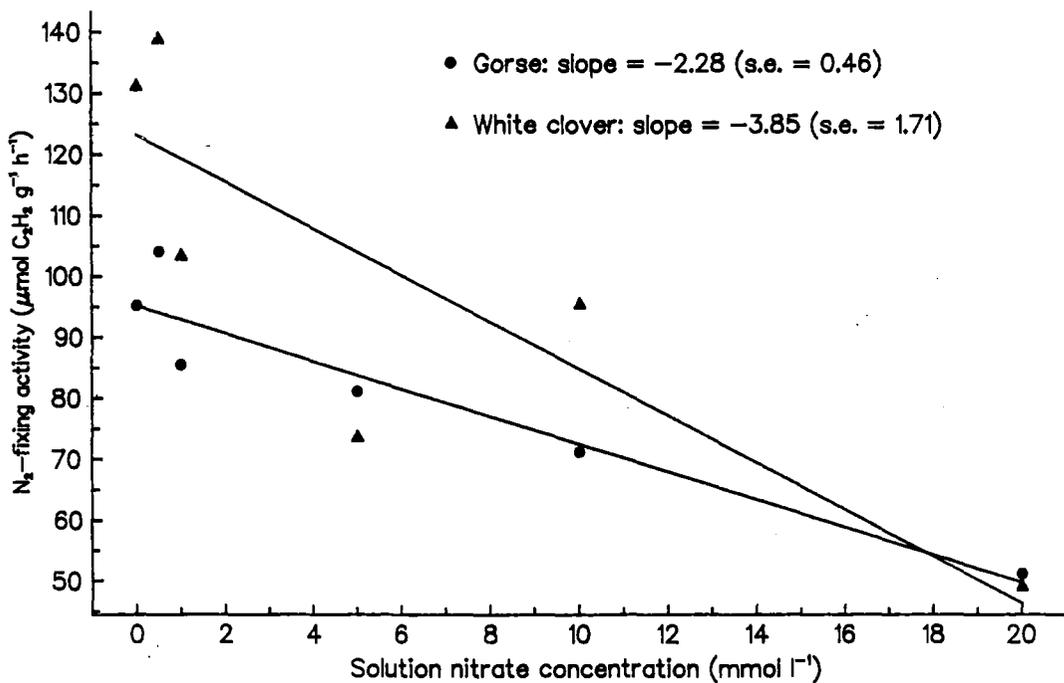


Fig. 5.9 Effect of nutrient solution nitrate concentration on N_2 -fixing (C_2H_2 -reducing) activity per unit nodule dry weight – rates of nitrate experiment.

Nutrient solution nitrate concentration significantly affected specific NRA (NRA per unit dry weight) of both roots and shoots (Table 5.13). The effect of species was not significant in either case, and there was a significant species \times rate of nitrate interaction for specific NRA of roots only (Table 5.13).

Table 5.13 Effect of nutrient solution N (nitrate) concentration on specific nitrate reductase activity (NRA) of gorse and white clover

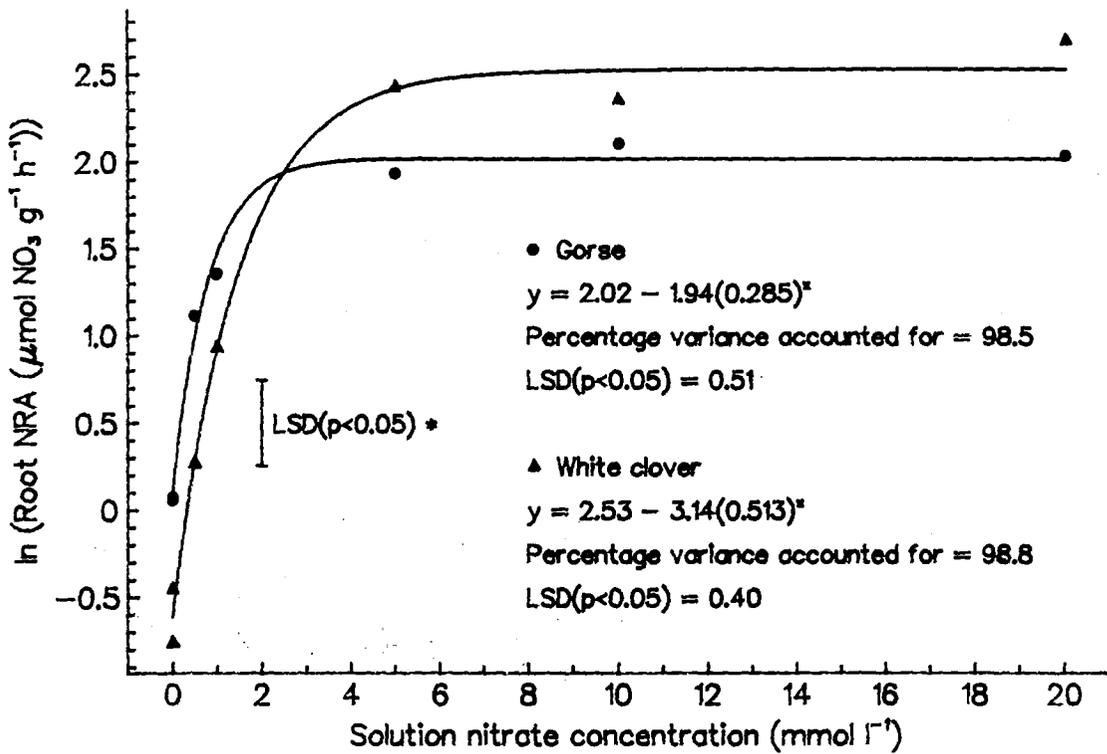
Source of variation (treatment or interaction)	Level of significance	
	NRA g ⁻¹ root	NRA g ⁻¹ shoot
Species	ns	ns
N	***	***
Species \times N	***	ns

See Table 5.6 for description of significance levels.

For both gorse and white clover specific root NRA increased rapidly from near zero at the nil nitrate concentration and began to plateau at about 2 mmol l⁻¹ nitrate for gorse and 5 mmol l⁻¹ for white clover (Fig 5.10(a)). Specific root NRA was greater for gorse than white clover at low solution nitrate concentrations (less than 1 mmol l⁻¹), but less for gorse than white clover at high nitrate concentrations (5 mmol l⁻¹ or greater) (Fig 5.10(a)). The fitted curves of the form $y = a + br^x$ indicate that specific root NRA increased more rapidly in gorse than white clover with increase in solution nitrate concentration (the parameter "r" was significantly less for gorse than white clover, $p < 0.05$, Section 5.2.8) (Fig 5.10(a)). The fitted curves also indicate that specific root NRA plateaued at a significantly lower level in gorse than white clover (the asymptote "a" was significantly less for gorse than white clover, $p < 0.01$) (Fig 5.10(a)).

For both species, specific shoot NRA increased rapidly with increasing solution nitrate concentration from 0 to 5 mmol l⁻¹, with no further significant increase above 5 mmol l⁻¹ (Fig 5.10(b)). As for specific root NRA, the fitted curves indicate that specific shoot NRA plateaued at a significantly lower level in gorse than white clover ($p < 0.01$) (Fig 5.10).

(a) Root



(b) Shoot

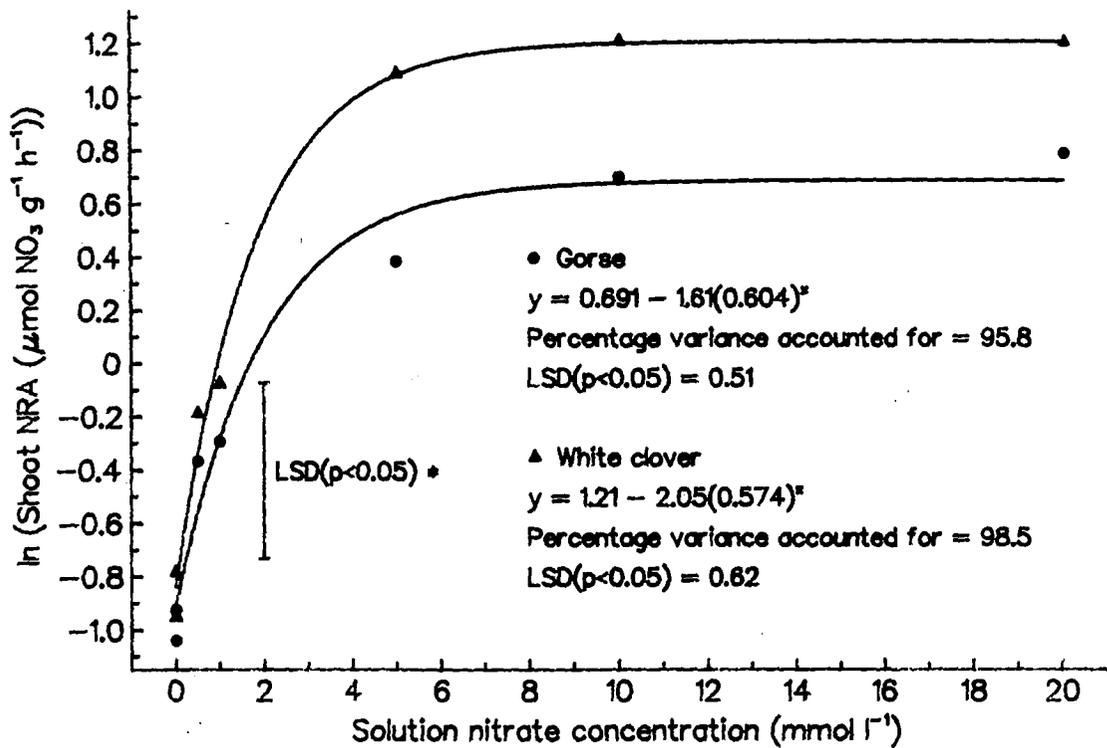


Fig. 5.10 Effect of nutrient solution nitrate concentration on shoot and root NRA (nitrate reductase activity) of gorse and white clover – rates of nitrate experiment.
 * LSD pooled for both species.

For both species, specific NRA in the roots was substantially greater than that in the shoots ($p < 0.001$ in both cases, based on paired t tests). Mean specific root and shoot NRA values for gorse were 4.51 and 0.91 $\mu\text{mol nitrate g}^{-1} \text{h}^{-1}$ respectively, and for white clover were 5.91 and 1.79 $\mu\text{mol nitrate g}^{-1} \text{h}^{-1}$ respectively.

5.3.4.2 Distribution of nitrate reductase activity between root and shoot

Analyses of variance were done on the ratio of total shoot NRA:total root NRA. When both gorse and white clover were analysed together there were no significant effects or interactions (Table 5.14). When gorse was analysed alone, however, there was a significant solution nitrate concentration effect (Table 5.14).

Table 5.14 Effect of nutrient solution N (nitrate) concentration on distribution of NRA between roots and shoots (NRA shoot/NRA root) of gorse and white clover - summary of analyses of variance (done on log-transformed values, Section 3.2.14)

Source of variation (treatment or interaction)	Level of significance		
	Gorse and clover	Gorse	White clover
Species	ns		
N	ns	**	ns
Species \times N	ns		

See Table 5.6 for description of significance levels.

For gorse the proportion of NRA in the shoots increased with increasing nutrient solution nitrate concentration (Fig 5.11).

In contrast the distribution of total NRA between root and shoot for white clover did not differ significantly with nitrate concentration.

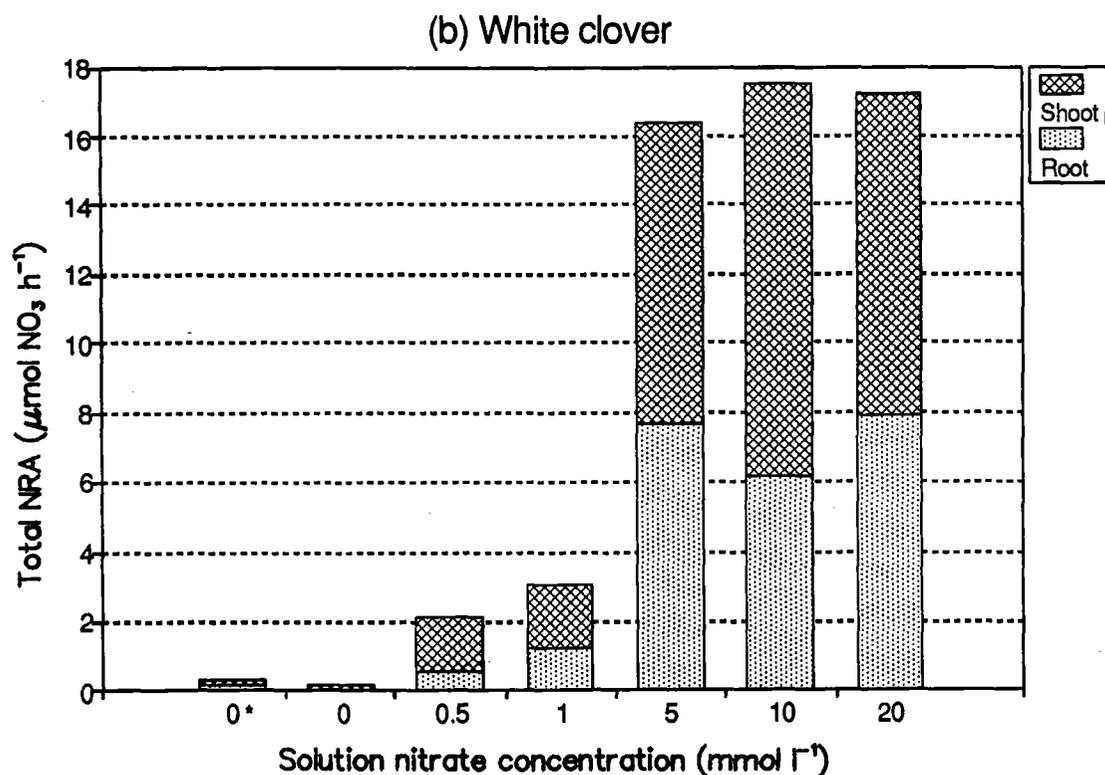
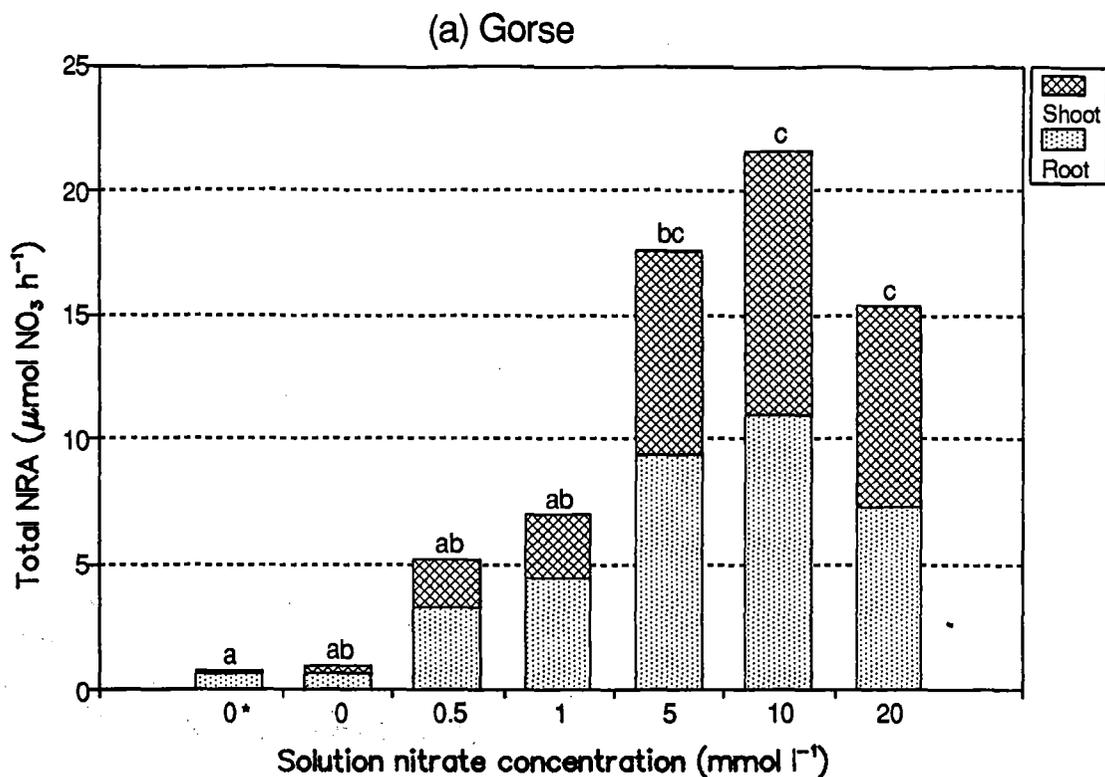


Fig. 5.11 Effect of nutrient solution nitrate (NO_3) concentration on the distribution of NRA (nitrate reductase activity) between root and shoot of gorse and white clover – rates of nitrate experiment. Different letters at the tops of bars indicate significant differences between treatments within species (LSD $p < 0.05$) in the ratio shoot:root NRA.

* Plants not supplied with starter N, unlike other treatments (Section 5.2.1).

5.4 DISCUSSION

5.4.1 Effects of nutrient solution nitrate concentration on growth and N accumulation

Both gorse and white clover showed growth responses to increasing concentrations of nutrient solution nitrate (Fig 5.1), consistent with responses to combined N by a range of other nodulated legumes (e.g. Munns 1968; Heichel and Vance 1979; Dean and Clark 1980). The energy requirement for nitrate assimilation has been found to be less than that for symbiotic N₂ fixation, enabling more photosynthate to be retained as dry matter in nitrate-fed plants (Finke *et al.* 1982). Hence legumes frequently give dry matter yield responses to increasing supply of combined N.

Gorse appeared to have a lower solution nitrate concentration requirement for 90% maximum dry matter yield (shoot or whole-plant) than white clover (Table 5.7). This suggests that gorse may be able to thrive a little better than white clover in environments where there is little combined N. Nutrient solution nitrate concentrations were not significantly different at 90% maximum N accumulation for the two species, apparently because of the gentle slope of the white clover curve at this point (Fig 5.4) and the consequently high standard error (Section 5.3.2.2). However, the solution nitrate concentration at which gorse reached 80% maximum accumulation was significantly less than that for white clover (Table 5.10) suggesting that gorse has a greater capacity to satisfy its own demands for N under conditions of little mineral N, compared with white clover (Fig 5.4).

In terms of dry matter yield gorse was not significantly less responsive to increasing nutrient solution nitrate concentration than white clover (Table 5.7). However in terms of whole-plant N content gorse was significantly less responsive than white clover (Table 5.10). This indicates that gorse had a relatively greater capacity to acquire N via symbiotic fixation, relative to its growth potential in terms of weight of nitrogen, compared with white clover. Other work has also demonstrated that the capacity of gorse to accumulate N is great relative to other species (Egunjobi 1969; Dancer *et al.* 1977b). Responsiveness to combined N of a range of legume species are compared with gorse and white clover from this experiment in Table 5.15. In terms of dry matter yield, gorse in this experiment appeared to be less responsive to increases in N supply than all of the other legumes listed, except

cowpea (*Vigna unguiculata*). In terms of whole-plant N content gorse is also less responsive to combined N than most of the other legumes listed (except soybean (*Glycine max*), *Vicia faba* and cowpea) (Table 5.15).

Thus gorse appears to have a high capacity to provide for its own N demands via symbiotic fixation, relative to other legumes. This finding is consistent with other findings that gorse frequently functions as a pioneer species and is a very productive coloniser of growth media having little combined N and low fertility generally (Egunjobi 1969; Dancer *et al.* 1977a & b; Fitzgerald 1980; Roberts *et al.* 1981).

The N concentrations in gorse shoots and roots were less in gorse than in white clover at all nutrient solution nitrate concentrations (Fig 5.3). Also, the estimated critical shoot N concentration associated with 90% maximum yield was significantly less for gorse (2.79%) than for white clover (4.62%) (Section 5.3.2.1). It appears, therefore, that gorse was more efficient than white clover at using N in the processes of growth; i.e. gorse produced more dry matter per unit N than white clover. Greater internal efficiency in the using of N should release energy resources for other plant processes and possibly lead to increased growth. This effect could be especially important in legumes because of the greater energy requirement for symbiotic N₂ fixation compared with nitrate reduction (e.g. Finke *et al.* 1982).

For gorse the decline in dry weight observed at 20 mmol l⁻¹ nitrate was associated with a tendency for increase in shoot N concentration with increasing nutrient solution nitrate concentration (Fig 5.3). It is possible that the decline in dry weight was caused by the increase in N concentration. Three possible causes of decreased dry matter yield with increasing solution nitrate concentration are (Andrews *et al.* 1989):

- 1) Increased nitrate concentrations within the plant caused an ion imbalance which resulted in decreased growth.
- 2) Increased reduced N concentrations within the plant, which resulted in Fe deficiency and leaf chlorosis.
- 3) Competition for energy between nitrate assimilation and C fixation, resulting in a

reduction in the amount of C available for growth.

Table 5.15 Responsiveness to applied N in terms of whole-plant dry weight, shoot dry weight and whole-plant N content. Plants solely dependent on symbiotic N₂ fixation are compared with plants supplied with abundant mineral N.

Plant (age in days)	Whole-plant Dry weight	Shoot Dry weight	Whole-plant N content	Reference
Gorse (125)	34	34	36	This experiment
White clover (90)	41	43	50	This experiment
Lucerne (70)	53	-	45	Allos & Bartholomew (1959)
Birdsfoot trefoil (70)	44	-	55	
Red clover (flowering)	39	-	39	Koter (1965a)
White clover	62	59	-	Ryle <i>et al</i> (1979b)
Sweet clover (70)	70	-	56	Allos & Bartholomew (1959)
Ladino clover (70)	69	-	67	
Soybean (70)	52	-	21	
Soybean	69	68	-	Ryle <i>et al.</i> (1979a)
<i>Vicia faba</i>	-	-	23	Richards & Soper (1979)
<i>Vicia faba</i>	-	-	19	Hill-Cottingham & Lloyd-Jones (1980)
Cowpea	30	27	-	Summerfield <i>et al</i> (1977)
Cowpea	29	30	0	Ryle <i>et al.</i> (1979a)
Sainfoin (flowering)	55	56	-	Koter (1965a)
Sainfoin (flowering)	50	57	45	Koter (1965b)
Sainfoin (143)	55	67	57	Hume (1981)

There was no evidence of leaf chlorosis in either gorse or white clover to support explanation 2. Mechanisms 1 or 3 could explain the declines in yield at high nitrate concentration. If mechanism 3 was involved it could explain the apparently greater depression of gorse yield compared with white clover at 20 mmol l⁻¹ N (Fig 5.1). Because of the architecture of its photosynthetic tissue compared with that of white clover, gorse probably has a lesser photosynthetic area relative to its dry weight, and hence a lesser capacity for harvesting C from the atmosphere than white clover. This may render gorse more vulnerable to any reduction in C assimilation, such as that caused by competition for energy by nitrate reduction, as suggested above.

Neither the mode of N nutrition (dependence on symbiotic N₂ fixation or uptake of nitrate N) nor the solution nitrate concentration significantly affected the shoot:root ratio of gorse (Fig 5.2). In contrast, the shoot:root ratio of white clover increased with increase in solution nitrate concentration (Fig 5.2). The effect of mode of N nutrition and N concentration on dry matter distribution between shoot and root appears to differ between legume species. Koter (1965a & b) observed a greater shoot:root ratio in sainfoin (*Onobrychis viciifolia*) supplied with combined N compared with sainfoin dependent on symbiotic N₂ fixation. The same effect was not observed for red clover (*Trifolium pratense*) by the same author. The findings of Turner (1922), Brouwer (1962) (birdsfoot trefoil), Cassman *et al.* (1980) (soybeans), Summerfield *et al.* (1977) and Atkins *et al.* (1980) (both with cowpea), Hildebrand *et al.* (1981) (winged bean (*Psophocarpus tetragonolobus*) and soybean) and Hume and Withers (1985) (sainfoin), suggest a change in dry matter partitioning in favour of the shoot in plants supplied with combined N compared with plants dependent on symbiotic N₂ fixation, similar to that observed for white clover in this experiment.

Summary

(a) Gorse reached 90% maximum dry matter yield and 80% maximum whole-plant N content at lower nutrient solution N concentrations than white clover. Gorse appeared to have a greater capacity to satisfy its own demands for N under conditions of little mineral N, compared with white clover.

(b) In terms of dry matter yield and whole-plant N content, gorse appeared to have a relatively greater capacity to meet its own requirements when solely dependent on symbiotic

N₂ fixation, than a range of other legumes.

(c) Gorse was more efficient than white clover at using N in the processes of growth.

These characteristics are all consistent with the suggested role of gorse as a low soil fertility tolerating plant which can thrive in nitrogen deficient situations (Chater 1931; Egunjobi 1969; Dancer *et al.* 1977a; Roberts *et al.* 1981; Section 2.1.3.2).

5.4.2 Effect of nutrient solution nitrate concentration on nodulation and N₂-fixing activity

Increases in nitrate concentration affected nodulation and N₂-fixing activity to different degrees in gorse and white clover.

Nodule dry weight per unit whole-plant dry weight (nodule weight ratio) was similar for both species when totally dependent on symbiotic N₂ fixation, but was less for white clover than gorse at nitrate concentrations of 5.0 mmol l⁻¹ or greater (Section 5.3.3.1, Fig 5.6). The nodule weight ratio retained by gorse at a solution nitrate concentration of 20 mmol l⁻¹ was 45% of that of plants totally dependent on symbiotic nitrogen fixation. The corresponding percentage for white clover was 13%. Thus, it appears that gorse has a greater ability to maintain nodule weight under conditions of high nitrate concentration than white clover. For gorse the decline in nodule weight ratio was primarily a result of decreases in individual nodule mass, whereas for white clover there were substantial decreases in both nodule number per unit whole-plant dry weight (nodule number ratio) and individual nodule mass (Figs 5.5 and 5.7). Depression of nodulation in the presence of combined N has been observed in a wide range of legumes grown in solution or sand culture (Munns 1968; Heichel and Vance 1979; Wong 1980; Streeter 1982) and in the field (Dean and Clark 1980; Saito *et al.* 1984). As in this experiment, other researchers have also found that the sensitivity of nodulation and N₂ fixation to combined N varies between species (e.g. Allos and Bartholomew 1959). For both gorse and white clover the major depression in nodule weight occurred between nutrient solution nitrate concentrations of 1.0 and 5.0 mmol l⁻¹. That is, a supply of combined N sufficient to completely meet the needs of the plants (Section 5.2.1) resulted in a substantial decrease in nodule weight ratio in both species. At solution nitrate concentrations above 5 mmol l⁻¹ there was no further significant

decrease in nodule weight ratio with increase in solution nitrate concentration (Fig 5.6). That is, the decrease in nodule weight ratio was not proportional to nitrate concentration. This suggests that the mechanism resulting in a reduced nodule weight ratio was related to decreased demand for fixed N, rather than a direct effect of solution nitrate concentration, because the response of total N content to increasing solution nitrate concentration levelled off at about the same nitrate concentration as nodule weight ratio (5 mmol l⁻¹, Figs 5.4 and 5.6).

The similar nodule weight ratios for the two species, when both were solely dependent on symbiotic N₂ fixation, were reflected in similar rates of symbiotic N₂-fixing activity per unit whole-plant dry weight (N₂-fixing activity ratio) (Section 5.3.3.2; Figs 5.6 and 5.8). The patterns of change in N₂-fixing activity ratio with increases in nutrient solution nitrate concentration followed a pattern similar to that for nodule weight ratio (Figs 5.8 and 5.6), and as for nodule weight ratio, N₂-fixing activity ratio was depressed proportionally more for white clover than gorse. The N₂-fixing activity ratio retained by gorse at a solution nitrate concentration of 20 mmol l⁻¹ was 24% of that at 0 mmol l⁻¹ nitrate, whereas the equivalent proportion for white clover was 5%. These proportions compared with those for nodule weight illustrate a tendency for decline in N₂-fixing activity per unit nodule weight with increases in solution nitrate concentration (Fig 5.9). The declines in symbiotic N₂-fixing activity per unit whole-plant dry weight with increasing solution nitrate concentration are consistent with other findings that combined N, particularly nitrate, is found to substantially reduce N₂-fixing activity in a wide range of legumes (Oghoghorie and Pate 1971; Pate 1977; Hojjati *et al.* 1978), even where a symbiotic N₂-fixing system is established before the application of combined N (Allos and Bartholomew 1955 & 1959; Copeland and Pate 1969; Latimore *et al.* 1977; Dean and Clark 1980; Wong 1980; Streeter 1986; Dakora *et al.* 1992).

The ability of gorse to maintain greater nodule weight and N₂-fixing activity ratios would give it a competitive advantage under conditions of fluctuating available soil N. Under conditions of low available N, following conditions of abundant available N, it would be required to expend less resources in re-establishing its symbiotic N₂-fixing system than species such as white clover which had lost a greater proportion of their N₂-fixing capacity.

5.4.3 Nitrate assimilation

The very low NRA values for shoots and roots of both species at 0 mmol l⁻¹ nitrate (Fig 5.10) are consistent with the finding that constitutive (non-nitrate induced) NRA does not occur in either gorse or white clover (Andrews *et al.* 1990).

At low solution nitrate concentrations (<1 mmol l⁻¹) specific root NRA was greater for gorse than white clover, perhaps indicating that gorse has a greater ability to take up N under conditions of little mineral N. This is consistent with its suggested role as a species which is able to thrive in nitrogen deficient situations (Dancer *et al.* 1977a; Roberts *et al.* 1981). Root and shoot NRA per unit dry weight both increased significantly between 0 and 0.5 mmol l⁻¹ nitrate and continued to increase up to 5 mmol l⁻¹ nitrate (Fig 5.10). The patterns of change in NRA with change in nitrate concentration were similar for shoots and roots of both species. They did not appear to follow the suggested pattern for temperate legumes that at low nitrate concentrations (about 1 mmol l⁻¹) NRA occurs almost exclusively in roots, and that NRA in the shoot becomes progressively more important as nitrate concentration increases between 1 and 20 mmol l⁻¹ (Andrews *et al.* 1984; Andrews 1986). For both species NRA per unit dry weight was significantly greater in roots than shoots, but because shoot weights were substantially greater than root weights both root and shoot had a substantial role in nitrate reduction for both species (Fig 5.11). For gorse the ratio of total shoot NRA:total root NRA did increase with increasing nitrate concentration, in line with the suggested pattern for temperate legumes but for white clover it did not (Fig 5.11). White clover particularly, and to a lesser extent gorse, followed the pattern described for tropical species (Andrews *et al.* 1984; Andrews 1986) where the ratio of total shoot NRA:total root NRA remains approximately constant with increase in nitrate concentration.

NRA and N₂(C₂H₂)-fixing activity appeared to compliment each other in this experiment, similarly to the situation described by Silsbury (1987). N₂-fixing activity was high at nutrient solution nitrate concentrations of <1 mmol l⁻¹ and declined to a low level at solution nitrate concentrations of 5 mmol l⁻¹ (Fig 5.8). Approximately the reverse happened for NRA, with low rates up to solution nitrate concentrations of 1 mmol l⁻¹ and high rates at 5 mmol l⁻¹ and greater (Fig 5.10). As combined nitrogen becomes available, both species showed a switch in emphasis from symbiotic N₂ fixation to nitrate assimilation, presumably because less energy per unit N is required for the latter process compared with the former (Section

2.4.1) (Finke *et al.* 1982).

5.5 CONCLUSIONS

- 1) Gorse was responsive to increasing nitrate concentrations, within the range normally found in natural and agricultural soils. Unlike white clover however, high nitrate concentrations (at the top of the range which can temporarily occur in highly fertilized soils) depressed gorse growth and N accumulation.
- 2) Gorse reached near maximum growth at lower solution nitrate concentrations than white clover.
- 3) Gorse used N in the processes of growth more efficiently than white clover i.e. it produced more dry matter per unit N acquired.
- 4) In terms of whole-plant N content, gorse was less responsive to increases in nutrient solution nitrate concentration than white clover.
- 5) Nodulation and $N_2(C_2H_2)$ -fixing activity decreased in an exponential manner with increasing nitrate concentrations for both gorse and white clover. However the symbiotic N_2 -fixing system of gorse appeared to be more tolerant of increasing nitrate concentrations than that of white clover. The fall-off in nodule weight and N_2 -fixing activity with increasing nitrate concentration was less severe in gorse compared with white clover.
- 6) At solution nitrate concentrations $<1 \text{ mmol l}^{-1}$, specific root NRA for gorse was greater than that for white clover. NRA increased rapidly with increasing nitrate concentration in both gorse and white clover. NRA was inversely related to $N_2(C_2H_2)$ -fixing activity for both species.
- 7) Partitioning of NRA between root and shoot did not completely follow the pattern thought to be typical for temperate legumes. For both species the proportion of total NRA associated with the shoot was substantial throughout the range of nitrate concentrations provided. However gorse did partially follow the pattern thought to

be typical for temperate legumes in that the proportion NRA in the shoot increased with-increases in solution nitrate concentration.

Items 2 and 3 above are both consistent with the suggested role of gorse as a low fertility tolerating plant which is able to thrive in environments having little mineral N (Section 2.1.3.2). The fact that specific root NRA of gorse was greater at low nitrate concentrations than that of white clover is perhaps an indication that gorse is better able to take up combined N under conditions where there is little mineral N. Its maintenance of relatively high rates of N_2 -fixing activity and relatively high proportions of nodule weight at high nitrate concentrations compared with white clover, would give gorse an advantage in situations where the quantity of available combined N was fluctuating.

CHAPTER 6

GROWTH OF ESTABLISHED GORSE ON A SOIL CHRONOSEQUENCE IN NORTH WESTLAND

6.1 INTRODUCTION AND AIMS

In earlier experiments of this study, specific aspects of gorse nutrition were examined. In this study the growth and nutrition of mature gorse were examined in a range of natural edaphic conditions, but with common climate.

The study was done using a chronosequence of soils at Larry River, North Westland. The area chosen for the study had established gorse bushes, which were predominantly growing as individuals rather than as a dense stand. Bushes in the 4-5 year age range were chosen for the study, because gorse is at its most rapid stage of growth at this age (Egunjobi 1969). Also it is more difficult to ascertain the age of bushes as they become older (greater than 6-7 years) (R.J. Hill pers. comm.).

The approach used attempted to relate gorse growth to edaphic factors in natural situations. The advantage of this approach is that real situations are studied. Major disadvantages are the large number of factors which may influence gorse growth and hence possible relationships between cause (edaphic factor) and effect (gorse growth or nutrient concentration). In a designed experiment all factors are held constant except those being manipulated by the experimenter, and when analysing results it is possible to focus on responses to the specific treatments applied. In this study, bush growth and element composition of new shoots were measured in different edaphic conditions. An attempt is made to relate gorse growth to some chemical properties of topsoils and to the pedology of the soil chronosequence under study.

Specific aims were as follows:

- 1) To measure productivity of established gorse, in a natural environment, under differing edaphic conditions.

- 2) To attempt to identify specific soil factors which may be limiting the growth of gorse.
- 3) A subsidiary aim was to examine relationships between total shoot dry matter production and easily measured components of growth, with a view to developing a rapid means of assessing gorse growth.

6.2 EXPERIMENTAL

6.2.1 Site and physiography

The site chosen for this work was a soil sequence on a river terrace system in the Inangahua Valley, North Westland. The specific terrace sequence used was that at Larry River described by Ross *et al.* (1977). A site was chosen on the West Coast because of its relatively high rainfall compared with Canterbury. Because soil moisture was less likely to be limiting gorse growth at such a site, any effects of soil fertility on gorse growth should consequently be more apparent. Mean annual rainfall recorded at Reefton (approx. 11 km from the site) is 1919 mm. Areas of gorse with bushes in the 4-6 year age range were chosen on the four main soil series of the chronosequence, namely Hokitika, Ikamatua, Ahaura and Okarito.

The sequence of soils studied are described in terms of physiographic units as follows (Mew *et al.* 1975) (the associated soil series are shown in brackets):

1) River flats (Hokitika series):

The river flats are relatively small strips of land not far above the level of the river, and subject to comparatively frequent flooding. They are underlain by recent river alluvium which includes gravels, sands and silts derived from granite, schist, indurated sandstone and a variety of Tertiary rocks.

2) Main post-glacial terrace (Ikamatua series):

The main post glacial terrace is separated from the river flats by a low scarp and is now out of reach of all but the largest floods. Like the river flats, this terrace is underlain by recent river alluvium.

3) Low and intermediate glacial outwash terraces (Ahaura and Okarito series respectively). The low and intermediate glacial outwash terraces were formed during the Pleistocene glacial and interglacial periods, and were subsequently dissected. They were formed during the Otiran and Waimean periods of glaciation and covered with outwash gravels sands and silts from the nearby Victoria and Paparoa ranges (Tan 1971, Mew *et al.* 1975). A proportion of loess is also thought to be present on the intermediate terrace (Mew *et al.* 1975).

6.2.2 Fertilizer history

The Hokitika soil was located on islands in the bed of Larry River. As such it was a completely unfertilized site. The Ikamatua soil also had no known history of fertilizer application.

The Ahaura site has a history of annual applications of either superphosphate, 30 or 50% potash superphosphate or 20% potash sulphur superphosphate. All three have been used in various years at application rates ranging from 250 kg ha⁻¹ to 375 kg ha⁻¹. In addition, lime (0.5 tonne ha⁻¹) was applied every 3 years up to 1987.

The Okarito soil has received two known applications of fertilizer: 375 kg ha⁻¹ sulphur superphosphate (8% P, 20% S) in 1984, and 375 kg ha⁻¹ of "Westland Pakihi Starter" (superphosphate containing additional S, B, Cu, Co and Mo) in 1985.

6.2.3 Estimation of bush age

The age of gorse bushes was estimated from the branching structure of the bush. A new set of stems is produced during each growth season, and it is possible to reliably estimate age by this means for bushes up to 6-7 years old (R.J. Hill pers. comm.). The ages estimated in this way were checked against estimates using growth rings and were found to be accurate.

6.2.4 Estimation of gorse growth

Gorse growth from the previous season was estimated during the winter period when the plant had stopped growing.

In winter 1989 a minimum of 10 bushes on each of the soil series Hokitika, Ikamatua, Ahaura and Okarito were destructively harvested. In 1990 the Ahaura series was discarded, because the area used in 1989 had been cleared of gorse. For each of the soils, the bushes measured were selected from an area, close to the profile description for that soil (Section 6.2.7). The bushes chosen were growing individually, rather than in close association with others and they were predominantly in the 4 to 5 year age range. On the Okarito soil the bushes were chosen from both the drier and wetter areas of the site. Initial data recorded for each bush were its age, its total height, and diameter North-South and East-West.

Shoots produced in the previous growing season (new shoots) were cut out of a 0.1 m² circle on top of the bush. The fresh weight of material from the circle was recorded and it was retained for dry matter determination, shoot length measurement and chemical analysis. The purpose of making measurements using the 0.1 m² circle was to investigate their possible use in rapidly estimating gorse growth without destructively harvesting whole bushes. The possibility of estimating gorse growth using weight of shoots from the 0.1 m² circle, in combination with bush size measurements, is explored in Appendix 6.1. The bushes were then cut at ground level and the cut material was separated into new (green) shoots and older material (brown stems). Fresh weights of material in both of these categories were recorded. From each terrace a composite sample of brown stems was taken for dry matter determination. Notes were made about bush shape.

6.2.5 Plant sampling and chemical analysis

Material cut from the 0.1 m² circles during the winters of 1989 and 1990 was subsampled for chemical analysis. So that the sub-sample would be representative, the shoots were lined up in order of size. Sufficient whole shoots were then chosen to provide an adequately sized sample and to represent the range of shoot sizes present.

On December 14-15, 1989 shoot samples from the 4 terraces at Larry River were collected for chemical analysis. Fifty new shoots were taken from about 1.7 m height from each of 10 bushes on each of the terraces being studied. At the time of sampling the shoots were in the period of active spring growth.

Analysis of plant samples for N were done using a semi-micro Kjeldahl method (Blakemore *et al.* 1987; Section 3.2.12.1). Determinations of all other elements (Table 6.9) were done using X-ray fluorescence.

6.2.6 Soil sampling and analysis

Composite 0-7.5 and 7.5-15 cm soil samples were taken from each area of gorse studied at each of the harvest times (winters 1989 and 1990), using a 2.3 cm diameter stainless steel coring device. The cores were taken from close to the harvested bushes. On the Okarito soil in 1989, separate samples were taken from waterlogged and relatively dry areas. In 1990 it was not possible to obtain an adequate sample from the waterlogged areas because they were too wet.

Soil samples were analysed according to the methods of Blakemore *et al.* (1987).

6.2.7 Soil profile descriptions

The soil profile was described for each of the four soils included in this study. The edge of each pit dug for the purpose of soil profile description was approximately 20 cm from the base of a 5-7 year old gorse bush. The distribution of gorse roots down each profile was assessed by digging a hole of known cross-sectional area (3000-4000 cm²) and removing the gorse roots from known depth increments. The gorse roots were washed and dried to constant weight at 70°C.

6.2.8 Statistical analysis

Statistical analysis was done using analysis of variance techniques as described in Section 3.2.14.

6.3 RESULTS

6.3.1 Soil pattern

The soils studied constitute a sequence where the main soil-forming factor was time (Mew *et al.* 1975). Weathering and leaching increases in the sequence Hokitika series, Ikamatua series, Ahaura series and Okarito series. The Okarito series contains more finer textured material, thought to be of loessial origin (Ross *et al.* 1977), than the other soils (Tables 6.1, 6.2, 6.3 and 6.4).

6.3.1.1 Profile descriptions

Soil conditions may restrict both the total volume of soil containing roots or the intensity of roots within that total volume. Both may influence the supply of water and nutrients to the plant. The total volume of soil containing roots may be restricted by a shallow soil, a dense horizon or an anaerobic layer. The intensity of roots within the total rooted volume depends on the proportion of stones within the soil and the distribution of pore-sizes within the fine material. Rooting volume is defined as the volume of soil, within the total rooted volume, which is able to be explored by roots for the absorption of water and nutrients.

Profile descriptions for the 4 soils in the chronosequence are given in Tables 6.1-6.4, and photographs of the profiles are presented in Plates 6.1-6.4. Some features of significance for plant growth are:

Hokitika soil (Table 6.1, Plate 6.1):

- a) Much reduced rooting volume because of the large volume occupied by stones and gravel.
- b) No physical impediment to rooting depth or water movement.
- c) Lack of fine material would adversely affect moisture storage and transmission (Hillel 1982).

Note: This soil was quite variable. At some locations there was a layer of loamy sand at the surface (Table 6.1) while at others there were large stones and sand right to the surface.

Ikamatua soil (Table 6.2, Plate 6.2):

- a) Good rooting volume (comparatively few stones).
- b) No physical impediment to rooting depth or water movement.
- c) No mottles, indicating lack of anaerobic conditions.

Ahaura soil (Table 6.3, Plate 6.3):

- a) Reduced rooting volume due to stoniness (Rooting volume would be less than Ikamatua but greater than Hokitika).
- b) No physical barrier to rooting depth or water movement, but very distinct textural change at 52 cm.

Okarito soil (Table 6.4, Plate 6.4):

- a) Textural limitation to root growth at 27-51 cm
- b) An iron pan occurring at 51 cm would limit rooting depth and restrict the downward movement of water. The presence of mottles indicates anaerobic conditions above the pan. In times of high rainfall, water is probably perched above the pan.

Table 6.1Hokitika series - soil profile description

Landform: vegetated island bar

Location: Edge of Larry River, 1.7 km southeast of Larry River road bridge

Grid reference: NZMS 260 L30 196 101

Vegetation: dense gorse

Drainage class: well drained

Profile:

A	0-2 cm	dark greyish brown (10YR 4/2); loamy sand; moderately-strongly developed medium granular structure; loose; few coarse, many medium-fine roots; clear smooth boundary;
C1	2-13 cm	grey-brown (2.5Y 5/2); sand; single grained; loose; many medium-fine roots; abrupt wavy boundary;
bA	13-15 cm	dark greyish brown (10YR 4/2); loamy sand; weakly developed medium granular structure; loose; many medium-fine roots; abrupt wavy boundary;
C2	15-22 cm	pale olive brown (2.5Y 5/3); sand; single grained; loose; many medium-fine roots; abrupt wavy boundary;
b2A	22-40 cm	dark greyish brown (10YR 4/2); loamy sand; loose consistence; many medium-fine roots; gradual irregular boundary;
2C	40-100 ⁺ cm	very gravelly stony coarse sand; loose; many fine roots.

Table 6.2**Ikamatua series - soil profile description**

Landform: Low river terrace

Location: Near State Highway 69, 800 m southwest of Larry River road bridge.

Grid reference: NZMS 260 L30 179 109

Vegetation: scattered gorse, pasture

Drainage class: well drained

Profile:

- | | | |
|-----|----------|--|
| Ah | 0-8 cm | brown to dark brown (10YR 4/3); small gleyed zones occur in horizon (5Y 4/1) with associated ochreous mottles (few, fine, faint 7.5YR 4/4)
sandy loam with few fresh rounded granite and greywacke stones; well developed medium granular structure; slightly sticky, slightly plastic; many fine roots; clear wavy boundary; |
| AB | 8-17 cm | yellowish brown (10YR 5/4); small gleyed zones occur in horizon (5Y 4/1) with associated ochreous mottles (few, fine, faint 7.5YR 4/4)
sandy loam; well developed medium nutty structure; weak; brittle failure, non-sticky, slightly plastic; many fine roots; abrupt wavy boundary; |
| Bw | 17-27 cm | yellowish brown (10YR 5/4);
sandy loam; weakly developed coarse blocky breaking to moderate fine blocky structure;
weak; brittle failure, non-sticky, slightly plastic;
common very fine roots; abrupt wavy boundary; |
| 2BC | 27-32 cm | pale olive brown (2.5Y 5/3);
medium sand; weak medium blocky breaking to single grain structure; loose; brittle failure, non-sticky, non-plastic;
few medium roots; abrupt wavy boundary; |

- 3BC 32-38 cm yellowish brown (10YR 5/4);
loamy sand; weakly developed coarse blocky structure; weak;
brittle failure, non-sticky, non-plastic;
few medium roots; abrupt wavy boundary;
- 4BC 38-51 cm pale olive brown (2.5Y 5/3);
medium sand; weakly developed medium blocky structure
breaking to single grains; loose; brittle failure, non-sticky,
non-plastic; abrupt wavy boundary;
- 5BC 51-63 cm yellowish brown (10YR 5/4);
loamy sand; weakly developed coarse blocky structure; weak;
brittle failure, non-sticky, non-plastic;
common medium roots; abrupt wavy boundary;
- 6C 63-95 cm very gravelly stony coarse sand clasts rounded, fresh greywacke
and granite; single grains; non-sticky, non-plastic;
many medium and fine roots at top.

Plate 6.1 Hokitika loamy sand



Plate 6.2 Ikamatua sandy loam



Table 6.3**Ahaura series - soil profile description**

Landform: Low aggradation terrace of Ikamatua River.

Location: K & D Williams farm, state highway 69, 5.4 km north of Reefton

Grid reference: NZMS 260 L30 142 042

Vegetation: manuka, gorse, pasture

Drainage class: well drained

Profile:

- Ah1 0-14 cm dark greyish brown (10YR 4/2);
sandy loam; strongly developed coarse nut and fine crumb structure; weak; brittle failure, non-sticky, slightly plastic consistence;
many coarse roots; clear wavy boundary;
- Ah2 14-29 cm brown (10YR 5/3);
very stony sandy loam, clasts rounded moderately weathered granite; strongly developed fine nut and crumb structure; loose; non-sticky, slightly plastic; many coarse roots; abrupt smooth boundary;
- Bw 29-52 cm yellowish brown (10YR 5/6);
moderately stony sandy loam, clasts rounded slightly weathered granite and greywacke; strongly developed fine nut structure; weak; brittle failure, non-sticky, slightly plastic;
many medium roots; abrupt wavy boundary;
- BC1 52-65 cm dark yellowish brown (10YR 4/4);
very stony gravel, clasts rounded weathered granite and greywacke; loose; very weakly cemented, non-sticky non-plastic; single grained; common thin distinct patchy (7.5YR 3/3) iron/organic coatings; on stones, abundant fine roots;
- BC2 65-99 cm pale yellowish brown (10YR 6/4);
moderately stony gravel, clasts rounded, fresh granite and greywacke; single grained; loose; very weakly cemented, non-sticky, non-plastic; few very fine roots.

Table 6.4**Okarito series - soil profile description**

Landform: Intermediate aggradation terrace of Ikamatua River

Location: Near forestry road 1.3 km south of Larry River road bridge

Grid reference: NZMS 260 L30 185 101

Vegetation: Scattered gorse, pasture

Drainage class: very poor

Profile:

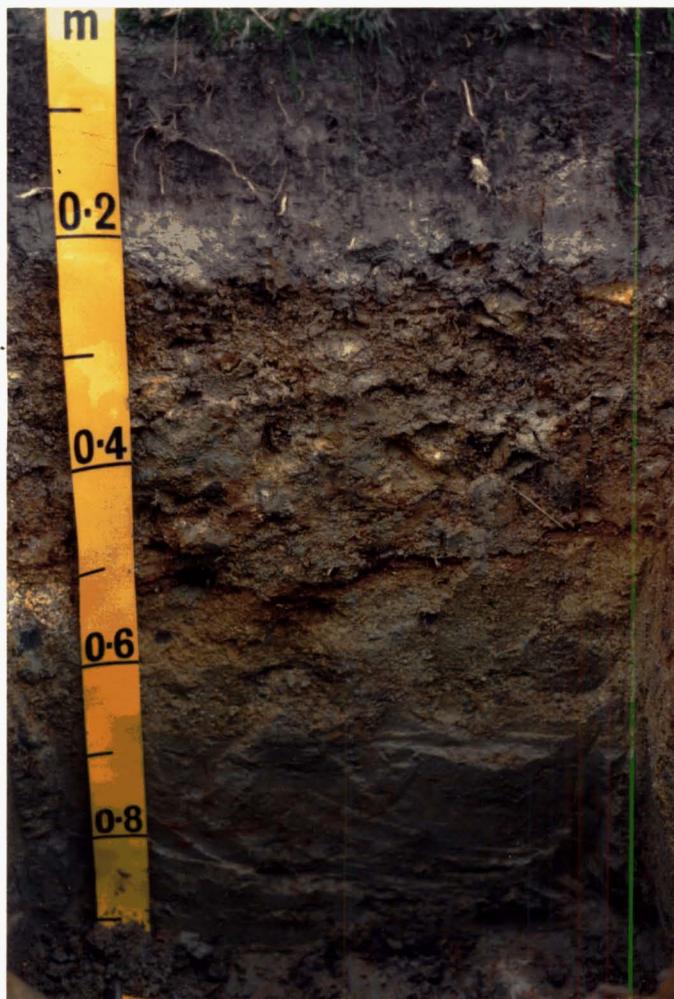
Ahg	0-15 cm	brownish grey (7.5YR 4/1); silt loam; moderately developed fine blocky structure; weak; semi-deformable failure, slightly sticky, moderately plastic; common medium roots; clear wavy boundary;
Er	15-24 cm	pale grey (5Y 7/2); slightly stony sandy loam moderately weathered sub-round stones; weakly developed coarse blocky breaking to moderately developed fine blocky structure; firm; brittle failure, moderately sticky, moderately plastic; common coarse distinct (7.5YR 4/1) mottles (worm casts); few fine roots; clear wavy boundary;
Bhf	24-27 cm	brownish black (7.5YR 3/2); very stony sandy loam angular and sub-rounded yellowish brown (10YR 5/6) stones; single grained; moderately cemented; common fine roots; diffuse, irregular boundary;
Bf	27-51 cm	orange and pale grey (5Y 7/2 and 7.5YR 6/8); very stony sandy loam pale grey stones; massive; slightly cemented; few medium roots; sharp wavy boundary;
Bfm	5mm thick	very dark reddish brown (2.5YR 2/3); moderately cemented iron pan sharp wavy boundary;
2Cf	52-66 cm	bright yellowish brown (2.5YR 7/6); slightly gravelly coarse sand; non-sticky, non-plastic; clear wavy boundary;

- 3C 66-94 cm pale olive grey green (5Y 6/2);
— medium sand; non-sticky non-plastic; common distinct coarse
(5YR 5/6) mottles; clear irregular boundary;
- 4C 94+cm weakly weathered stones not described.

Plate 6.3 Ahaura sandy loam



Plate 6.4 Okarito silt loam



6.3.1.2 Soil chemical properties

Percent total carbon and nitrogen values generally increased up the chronosequence (Tables 6.5 and 6.6). The ratings for soil chemical properties given in this section are those of Blakemore *et al.* (1987). Olsen P concentrations tended to be low to very low, and increase with increasing soil age (Tables 6.5 and 6.6). Phosphate-extractable sulphate was very low to low in the Ikamatua and Okarito soils and low to medium in the Ahaura soil (reflecting fertiliser inputs). No phosphate-extractable sulphate was detected in the Hokitika soil (Tables 6.5 and 6.6). Extractable sulphate values appeared to reflect fertilizer inputs (Section 6.2.2).

Cation exchange capacity (CEC) increased with increase in soil age and was very low to low in the Hokitika soil, low to medium in the Ikamatua soil, medium in the Ahaura soil and medium to high in the Okarito soil (Tables 6.5 and 6.6). Exchangeable Ca was greater in the Okarito soil (medium to high in the 0-7.5 cm layer) than in the other three soils (low in the 0-7.5 cm layer). Exchangeable Mg was very low to low in all soils but appeared to be very slightly greater in Hokitika and Okarito soils. Exchangeable K was very low to low in all soils in both years, except for the 0-7.5 cm sample from the wet area of the Okarito soil, which was in the medium range. Exchangeable K appeared to be slightly greater in the Okarito soil than in the Ikamatua soil, followed by the Hokitika and Ahaura soils (Tables 6.5 and 6.6). The sharply declining reserve K and Mg (K_c and Mg_c) values from the Hokitika to Okarito soils reflects the effect of increased weathering and leaching with increasing soil age. The decrease in these values indicates a reduction in long term K and Mg supplying power with soil age (Metson *et al.* 1956; Metson and Brooks 1975) due to increased leaching.

Soil pH tended to decrease with increase in soil age, being greater in the Hokitika soil than in the other three soils (Tables 6.5 and 6.6). Exchangeable Al also tended to increase with increase in soil age up to the Ahaura soil, (where it was greatest), but then decline in the Okarito soil (Tables 6.5 and 6.6). $0.02 \text{ mol l}^{-1} \text{ CaCl}_2$ -extractable Al was also greatest in the Ahaura soil followed by the Ikamatua soil and then the Okarito and Hokitika soils (Tables 6.5 and 6.6).

Lower pH, greater percent total C and N, and greater CEC in the samples from the wet

Table 6.5 Chemical properties of soils - Larry River chronosequence 1989

Soil series	Sample depth (cm)	pH (H ₂ O)	C (%)	N (%)	C/N ratio	Olsen P (µg g ⁻¹)	P retention (%)	Phosphate ext. SO ₄ (µg g ⁻¹)
Hokitika	0-7.5	5.6	2.6	0.10	26	6	11	0
	7.5-15	5.8	1.0	0.05	20	2	9	0
Ikamatua	0-7.5	5.2	4.7	0.26	18	7	28	3
	7.5-15	5.3	3.0	0.17	18	4	28	0
Ahaura	0-7.5	5.1	8.8	0.48	18	11	67	12
	7.5-15	5.1	7.0	0.39	18	7	72	15
Okarito - dry - wet	0-7.5	5.6	8.3	0.38	22	10	30	3
	7.5-15	5.4	4.5	0.16	28	4	38	2
	0-7.5	5.0	15.6	0.61	26	21	14	5
	7.5-15	4.8	11.6	0.44	26	16	13	1

Soil series	Sample Depth (cm)	Cation exchange (NH ₄ OAc @ pH 7 me. %)							KCl-Ext. Al (me.%)	0.02mol l ⁻¹ CaCl ₂ ext. Al (µg g ⁻¹)	Reserve (me. %)	
		CEC	Sum Bases	%BS	Ca	Mg	K	Na			Mg _r	K _r
Hokitika	0-7.5	7.6	4.41	58	3.06	1.01	0.32	0.02	0.2	4.4	44	0.27
	7.5-15	4.7	2.42	51	1.82	0.48	0.11	0.01	0.1	1.5	39	0.28
Ikamatua	0-7.5	12.2	4.21	35	3.14	0.62	0.40	0.05	0.7	5.1	31	0.28
	7.5-15	9.2	2.28	25	1.88	0.24	0.13	0.03	1.1	7.6	30	0.28
Ahaura	0-7.5	22.3	4.18	19	3.35	0.43	0.31	0.09	2.0	13.1	15	0.18
	7.5-15	20.9	2.57	12	2.13	0.20	0.20	0.04	2.5	17.2	17	0.20
Okarito -dry -wet	0-7.5	23.7	16.1	68	14.8	0.73	0.43	0.10	0.1	1.8	1.4	0.15
	7.5-15	13.2	5.03	38	4.65	0.19	0.14	0.05	1.0	3.0	1.7	0.17
	0-7.5	30.6	17.4	57	15.8	0.94	0.54	0.13	0.1	3.2	0.6	0.08
	7.5-15	25.2	10.8	43	9.99	0.49	0.23	0.06	0.2	3.0	0.2	0.08

Table 6.6 Chemical properties of soils - Larry River chronosequence 1990

Soil series	Sample depth (cm)	pH (H ₂ O)	C (%)	N (%)	C/N ratio	Olsen P (µg g ⁻¹)	P retention (%)	Phosphate ext. SO ₄ (µg g ⁻¹)
Hokitika	0-7.5	5.6	1.3	0.09	14	2	8	0
	7.5-15	5.8	0.56	0.04	14	1	6	0
Ikamatua	0-7.5	5.3	4.5	0.29	16	7	26	3
	7.5-15	5.1	2.6	0.21	12	3	24	1
Okarito	0-7.5	5.3	7.8	0.25	31	14	12	3
	7.5-15	5.0	5.3	0.46	12	10	23	2

Soil series	Sample depth (cm)	Cation exchange (NH ₄ OAc @ pH 7 me.%)							KCl-Ext. Al (me.%)	0.02M CaCl ₂ -ext. Al (µg g ⁻¹)	Reserve (me.%)	
		CEC	Sum bases	%BS	Ca	Mg	K	Na			Mg _r	K _c
Hokitika	0-7.5	6.0	3.34	56	2.30	0.70	0.30	0.04	0.2	2.8	37	0.53
	7.5-15	3.1	1.63	53	1.09	0.36	0.14	0.04	0.2	2.2	35	0.51
Ikamatua	0-7.5	11.8	3.83	32	2.72	0.59	0.42	0.10	0.9	4.5	30	0.34
	7.5-15	9.3	1.95	21	1.54	0.23	0.13	0.05	1.6	9.8	30	0.35
Okarito	0-7.5	18.1	10.7	59	9.41	0.64	0.48	0.16	0.3	2.7	0.9	0.15
	7.5-15	13.4	4.87	36	4.48	0.20	0.15	0.04	1.1	4.4	0.8	0.13

compared with the dry areas of the Okarito soil reflect greater amounts of undecomposed organic material in the wet areas (Table 6.5). Olsen P also appeared to be greater in the wet compared with the dry areas (Table 6.5).

6.3.2 Gorse growth

Plants were measured during the winter periods of 1989 and 1990, when gorse was not growing. Bushes were chosen and measurements were done as described in section 6.2.4.

Bush age was used as a covariate in all analyses of variance. For bush height in 1989, the effect of age was significant and the means presented (Table 6.7) are adjusted for covariance. For bush height in 1990 and for all other growth measurements for both years, the effect of the covariate was nonsignificant so the actual means are presented (Table 6.7, Figs 6.1 and 6.2).

Table 6.7 Effect of soil series on the size and growth of gorse plants

Variable (mean)	Year	Significance of soil series effect (p)	Soil Series				LSD (p<0.05)
			Hokitika	Ikamatua	Ahaura	Okarito	
Total height (cm)	1989	0.061	169	179	158	171	-
	1990	0.221	183	182		168	-
Mean diameter (cm)	1989	0.016	130	152	141	111	25
	1990	0.013	107	155		115	33
New shoot dry weight (g per bush)	1989	<0.001	1373	2654	1906	1185	542
	1990	<0.001	598	1827		894	408
Old wood (>1yr) dry weight (g per bush)	1989	<0.002	1479	2462	1489	1381	599
	1990	0.020	1002	2125		1508	766
Total dry weight (g)	1989	<0.001	2852	5116	3395	2566	1071
	1990	<0.001	1600	3951		2402	1113
Circle dry weight (g)	1989	0.003	271	484	387	306	116
	1990	<0.001	162	413		237	101
Shoot no. per 0.1m ²	1989	0.597	45	49	40	44	-
	1990	0.573	42	51		50	-
Mean shoot length per 0.1m ² (cm)	1989	0.011	36.4	41.6	41.8	31.6	6.9
	1990	0.057	29.8	34.5		24.7	-
Total shoot length per 0.1m ² (cm)	1989	0.041	1580	2021	1690	1284	512
	1990	0.046	1177	1714		1126	505
Maximum shoot length per 0.1m ² (cm)	1989	0.308	59.1	66.9	71.6	59.5	-
	1990	0.007	55.3	69.3		50.4	11.6

6.3.2.1 Height and diameter

Differences in bush height between soil series were not significant at the 5% level in either year but the effects of soil series on mean bush diameter was significant in both years (Table 6.7). In 1989, bush diameter (mean of measurements North - South and East - West) ranged from 111 cm on the Okarito soil to 152 cm on the Ikamatua soil (Table 6.7). Bush diameter was significantly greater on the Ikamatua and Ahaura soils than on the Okarito soil. Bush diameter for the Hokitika soil lay in the middle of the range and was not significantly different from the diameters for the other soils (Table 6.7). In 1990 the pattern was similar with bush diameter on the Ikamatua soil (155 cm) being significantly greater than on the Hokitika or Okarito soils (107 and 115 cm respectively) (Table 6.7).

6.3.2.2 Total bush weight

6.3.2.2.1 New shoots

The weights of new shoots for 1989 and 1990 represent dry matter yields from the 1988/1989 and 1989/90 growth seasons respectively (Table 6.7). The effect of soil series on weight of new (<1 year old) shoots was highly significant in both years (Figs 6.1 and 6.2, Table 6.7).

In 1989 dry matter yield ranged from 1185 g per bush on the Okarito soil to 2654 g per bush on the Ikamatua soil. Dry matter yield on the Ikamatua soil was significantly greater than that on the Ahaura soil, which in turn was significantly greater than that on the Okarito soil (Table 6.7). Dry matter yield on the Hokitika soil was between those on the Ahaura and Okarito soils, but not significantly different from either (Table 6.7).

In 1990, dry matter yield was again significantly greater on the Ikamatua soil (1827 g per bush) than on the Okarito or Hokitika soils (894 and 598 g per bush respectively) (Table 6.7). In 1989 dry matter yield on the Hokitika soil was slightly (but nonsignificantly) greater than on the Okarito soil whereas in 1990 the reverse was true. (Table 6.7).

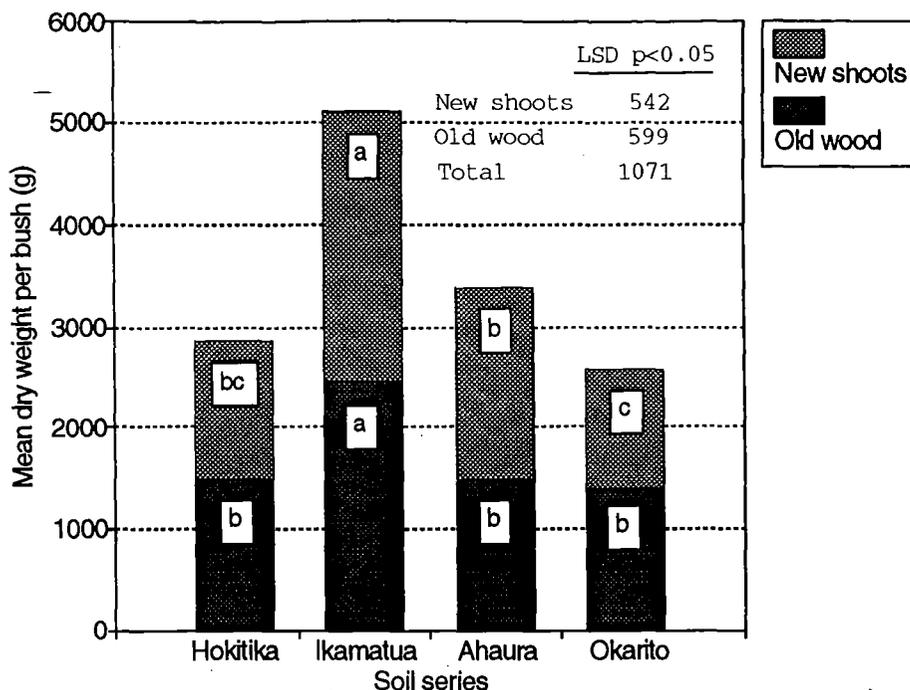


Fig 6.1 Gorse growth - Larry River soil chronosequence, 1989. Different letters within tissue age indicate significant differences between soils (LSD $p < 0.05$).

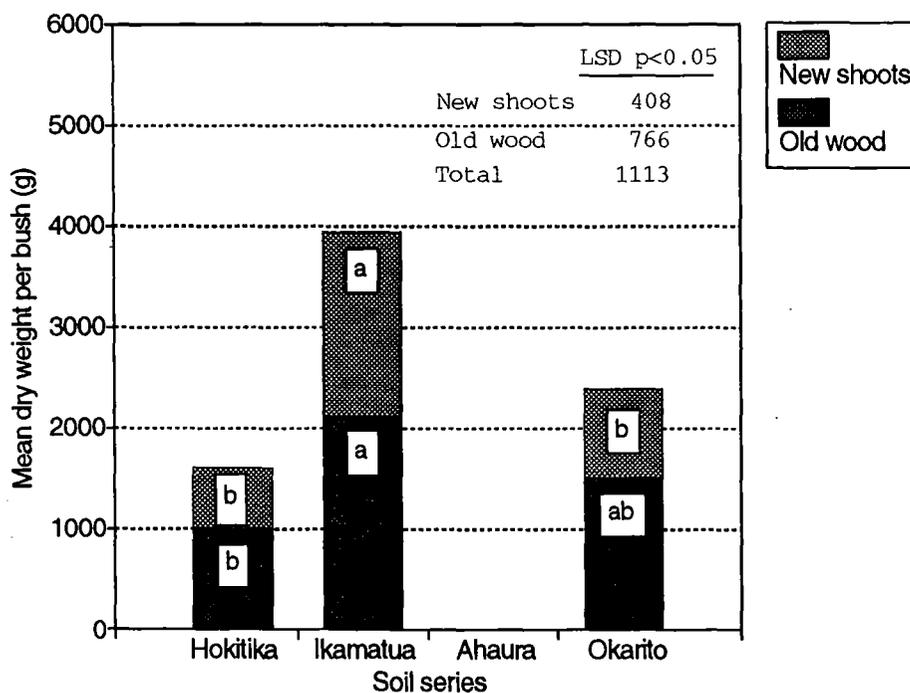


Fig 6.2 Gorse growth - Larry River soil chronosequence, 1990. Different letters within tissue age indicate significant differences between soils (LSD $p < 0.05$).

6.3.2.2.2 Old wood

Soil series had significant effect on the weight of old wood (>1 year old stems) in both years (Table 6.7). In 1989 the weight of old wood ranged from 1381 g per bush on the Okarito soil to 2462 g per bush on the Ikamatua soil, and was significantly greater on the Ikamatua soil than on the other three soils (Table 6.7, Figs 6.1 and 6.2). In 1990 the weight of old wood was greater on the Ikamatua soil (2125 g per bush) than on the Hokitika soil (1002 g per bush), with that on the Okarito soil in between the two extremes and not significantly different from either (Table 6.7; Figs 6.1 and 6.2).

6.3.2.2.3 Total bush weight

Soil series had significant effects on total bush weights in both 1989 and 1990, as would be expected from results presented in the previous two sections. In 1989 total bush dry weight ranged from 2566 g on the Okarito soil to 5116 g on the Ikamatua soil, and was significantly greater on the Ikamatua soil than on the other three soils (Table 6.7, Figs 6.1 and 6.2). In 1990 the pattern was similar, with bush weight being significantly greater on the Ikamatua soil (3951 g) than on the Okarito and Hokitika soils (2402 and 1600 g respectively) (Table 6.7, Figs 6.1 and 6.2).

6.3.2.3 0.1 m² circles

Shoot weights from the 0.1 m² circles were significantly affected by soil series in both years (Table 6.7). In 1989, shoot weight within a 0.1 m² circle was significantly greater for the Ikamatua soil (484 g) than the Hokitika soil (271 g), with that for the Ahaura and Okarito soils being between the two extremes but not significantly different from either (Table 6.7). In 1990 shoot weight from the cut circle was significantly greater for the Ikamatua soil (413 g) than for the Okarito or Hokitika soils (237 and 162 g respectively) (Table 6.7).

Shoot number within the 0.1 m² circle was not significantly affected by soil series (Table 6.7). This was partly a reflection of the large amount of variability in these data. Mean shoot length, total shoot length and maximum shoot length approximately followed the pattern of quadrat dry weight, but differences were not so pronounced (Table 6.7). The possibility of using data from the 0.1 m² circles, in combination with bush size data, to

estimate bush growth, is explored in Appendix 6.1.

6.3.2.4 Productivity on land area basis

Mean gorse productivity values on a land area basis, for the area actually covered by gorse canopy are given in Table 6.8. The figures in Table 6.8 indicate that under the low fertility conditions existing in the chronosequence of soils studied, gorse was still able to produce up to 14 600 kg dry matter per hectare.

Table 6.8 Gorse productivity on land area basis

Soil series	Growth season	Mean productivity of gorse (kg dry matter ha ⁻¹)
Hokitika	1988/89	10430
	1989/90	7210
Ikamatua	1988/89	14600
	1989/90	9530
Ahaura	1988/89	12150
	1989/90	-
Okarito	1988/89	12270
	1989/90	8310

6.3.3 Nutrient concentrations in shoots

Chemical analysis was done on new shoots i.e. shoots produced during the most recent growth season. Concentrations of the major nutrients, the micro nutrients Mn, Cu, Zn and Fe and also Al, Na, Cl and Si are presented in Table 6.9.

6.3.3.1 Macronutrients

Shoot N concentrations were not significantly different between soils at any sampling time (Table 6.9).

Shoot P concentrations did not differ significantly at the winter or spring 1989 sampling

times, but at the winter 1990 sampling time, concentrations were greater on the Okarito soil than on the Hokitika or Ikamatua soils.

Shoot K and Mg concentrations both declined significantly with increasing soil age (Table 6.9). K concentration declined progressively with increasing age at every sampling time, whereas Mg levels declined progressively with age in the Hokitika, Ikamatua and Ahaura soils, but tended to increase slightly for the Okarito soil.

The effect of soil series on shoot Ca concentration was significant at the 5% level at the spring 1989 and winter 1990 sampling times, but only at the 5.2% level at the winter 1989 sampling time (Table 6.9). Ca concentration was greatest on the Okarito soil at all sampling times and least on the Ahaura, Hokitika and Ikamatua soils in winter 1989, Spring 1989 and winter 1990 respectively (Table 6.9).

At the winter 1989 sampling time shoot S concentration was significantly greater on the Ahaura soil than on the other three soils (Table 6.9). The pattern was similar at the Spring 1989 sampling time, except that S concentration on the Okarito soil was not significantly less than that on the Ahaura soil or greater than that on the Hokitika or Ikamatua soils. In winter 1990, when the Ahaura soil was not included there was no significant effect of soil series on foliage S concentration (Table 6.9).

6.3.3.2 Micronutrients

Shoot Mn, Cu and Zn concentrations all tended to decline with increasing soil age, tending to be greater on the Hokitika and Ikamatua soils than on the Ahaura and Okarito soils. Shoot Fe concentration also tended to decline with increasing soil age, except for the Ahaura samples which had relatively greater concentrations than their neighbours in the chronosequence (Table 6.9).

6.3.3.3 Other elements

Shoot Al concentrations were significantly affected by soil series at the winter and spring 1989 sampling times but not at the winter 1990 sampling time (Table 6.9). Where the effect of soil series was significant, shoot Al concentration was lower on the Okarito than on the

other three soils (Table 6.9)

Na, Cl and Si concentrations are presented for completeness but will not be discussed.

Table 6.9 Element concentrations in gorse shoots - West Coast soil chronosequence

Element	Time	Significance of soil series effect (p)	Hokitika	Ikamatua	Ahaura	Okarito	LSD (p<0.05)
N(%)	Winter 89	0.103	1.21	1.28	1.29	1.16	-
	Spring 89	0.070	2.14	2.12	2.28	2.06	-
	Winter 90	0.113	1.26	1.39		1.35	-
P(%)	Winter 89	0.127	0.079	0.083	0.086	0.101	-
	Spring 89	0.276	0.167	0.153	0.169	0.168	-
	Winter 90	0.007	0.086	0.096		0.149	0.040
K(%)	Winter 89	<0.001	0.882	0.773	0.488	0.358	0.121
	Spring 89	<0.001	1.028	0.903	0.812	0.650	0.123
	Winter 90	0.007	0.857	0.809		0.584	0.172
Mg(%)	Winter 89	<0.001	0.139	0.105	0.074	0.124	0.020
	Spring 89	<0.001	0.252	0.201	0.123	0.160	0.030
	Winter 90	<0.001	0.203	0.114		0.126	0.027
Ca(%)	Winter 89	0.052	0.364	0.377	0.315	0.408	-
	Spring 89	<0.001	0.346	0.423	0.349	0.496	0.047
	Winter 90	0.049	0.415	0.359		0.470	0.088
S(%)	Winter 89	<0.001	0.074	0.075	0.099	0.072	0.011
	Spring 89	0.035	0.112	0.117	0.136	0.121	0.017
	Winter 90	0.092	0.076	0.087		0.091	-
Al(%)	Winter 89	<0.001	0.009	0.008	0.010	0.005	0.0023
	Spring 89	<0.001	0.011	0.010	0.009	0.007	0.0017
	Winter 90	0.400	0.009	0.007		0.007	-
Na(%)	Winter 89	<0.001	0.013	0.022	0.054	0.070	0.014
	Spring 89	<0.001	0.028	0.061	0.086	0.135	0.030
	Winter 90	<0.001	0.011	0.021		0.054	0.016
Cl(%)	Winter 89	0.180	0.046	0.050	0.064	0.054	-
	Spring 89	<0.001	0.070	0.112	0.167	0.149	0.027
	Winter 90	0.033	0.032	0.036		0.050	0.014
Si(%)	Winter 89	0.004	0.024	0.017	0.025	0.012	0.0079
	Spring 89	0.007	0.019	0.016	0.014	0.012	0.0040
	Winter 90	0.796	0.018	0.015		0.014	-
Mn(ppm)	Winter 89	<0.001	80.7	106.9	60.5	60.4	23.4
	Spring 89	<0.001	70.1	87.3	54.1	46.2	16.9
	Winter 90	<0.001	125.4	106.5		56.3	27.9
Cu(ppm)	Winter 89	0.005	4.3	4.4	3.3	3.1	0.87
	Spring 89	<0.001	5.7	5.5	3.6	3.2	0.84
	Winter 90	0.936	3.3	3.3		3.4	-
Zn(ppm)	Winter 89	<0.001	28.0	23.1	23.7	15.3	4.9
	Spring 89	<0.001	34.2	31.2	26.1	23.7	4.8
	Winter 90	<0.001	31.6	27.5		19.4	6.2
Fe(ppm)	Winter 89	<0.001	60.0	49.7	75.4	41.1	14.47
	Spring 89	0.002	69.5	53.8	55.5	46.4	11.3
	Winter 90	0.637	52.6	50.7		42.7	-

6.3.4 Distribution of gorse roots in soil profiles

Distribution of gorse roots down the four soil profiles are presented in Figs 6.3 - 6.6. Roots were found to a depth of 90-100 cm for all four profiles (Figs 6.3-6.6). The greatest density of roots in each profile occurred within 18 cm of the soil surface and was associated with the presence of large (5-13 mm diameter) lateral roots. The very high root density in the 9-18 cm depth increment of the Ahaura soil (Fig 6.5) was associated with an unusually large number of these lateral roots. The gorse bush concerned appeared to have regrown from an old stump and this may explain the relatively high weight of large diameter roots near the surface. The density of roots in the 80-95 cm depth increment of the Ahaura soil was $4.8 \text{ mg litre}^{-1}$, similar to the densities in the lowest depth increments of the Ikamatua and Okarito soils (Figs 6.5, 6.4 and 6.6). It appeared to be almost zero only because of the large scale of the x-axis (Fig 6.5).

In all soils the greatest density of roots was close to the surface and tended to decline with depth (Figs 6.3-6.6). The bulge in root density in the 28-40 cm depth increment of the Hokitika soil was associated with a finer textured buried A horizon (Fig 6.3, Table 6.1). The bulge in root density in the 50-65 cm depth increment of the Ikamatua soil was also associated with a finer textured layer compared with the layers above and below it (Fig 6.4, Table 6.2, Plate 6.2). There was no obvious reason for the slight bulge in root density in the 86-100 cm increment of the Hokitika profile. Root density appeared to be greater at depth in the Hokitika profile than for the other three soils. ($35.1 \text{ mg litre}^{-1}$ at the greatest depth increment for the Hokitika soil compared with 4.0, 4.8 and $3.8 \text{ mg litre}^{-1}$ for the Ikamatua, Ahaura and Okarito soils respectively) (Figs 6.3-6.6). Root density was low below the iron pan (52 cm depth) in the Okarito soil, reflecting the limiting effect of this barrier on rooting depth. Some gorse roots did, however get through the iron pan. One way in which they did this was to grow through dead tree roots, which had previously grown through the pan.

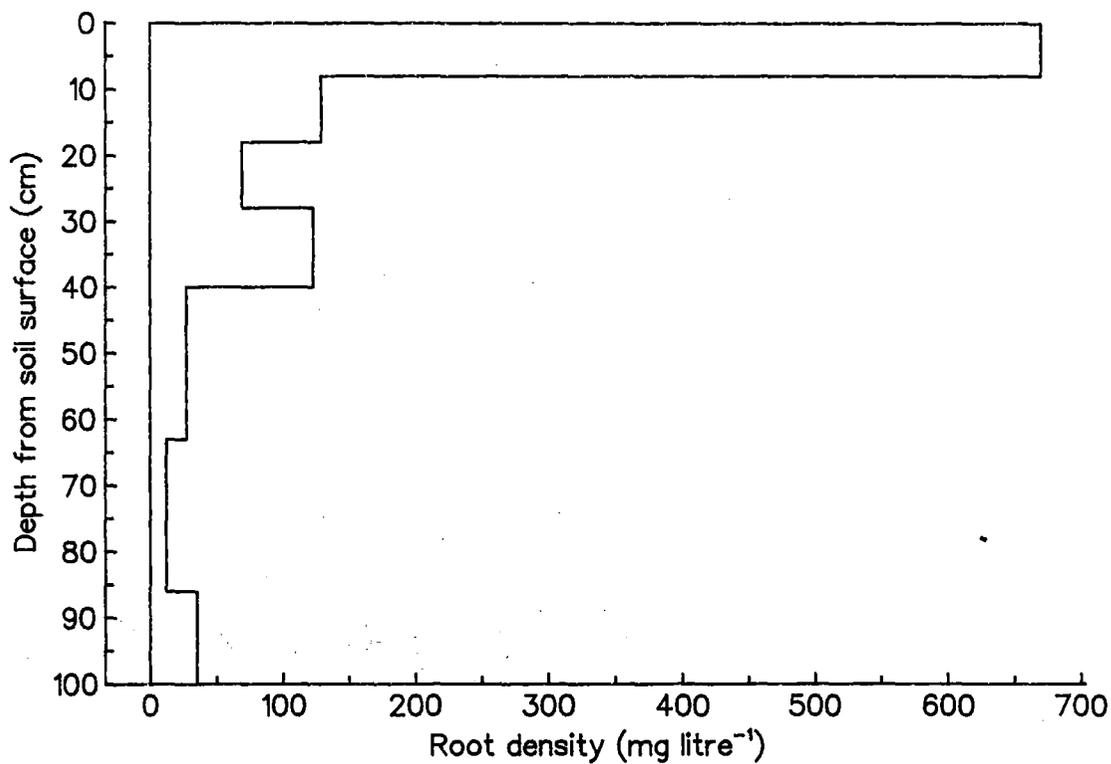


Fig. 6.3 Gorse root distribution – Hokitika soil

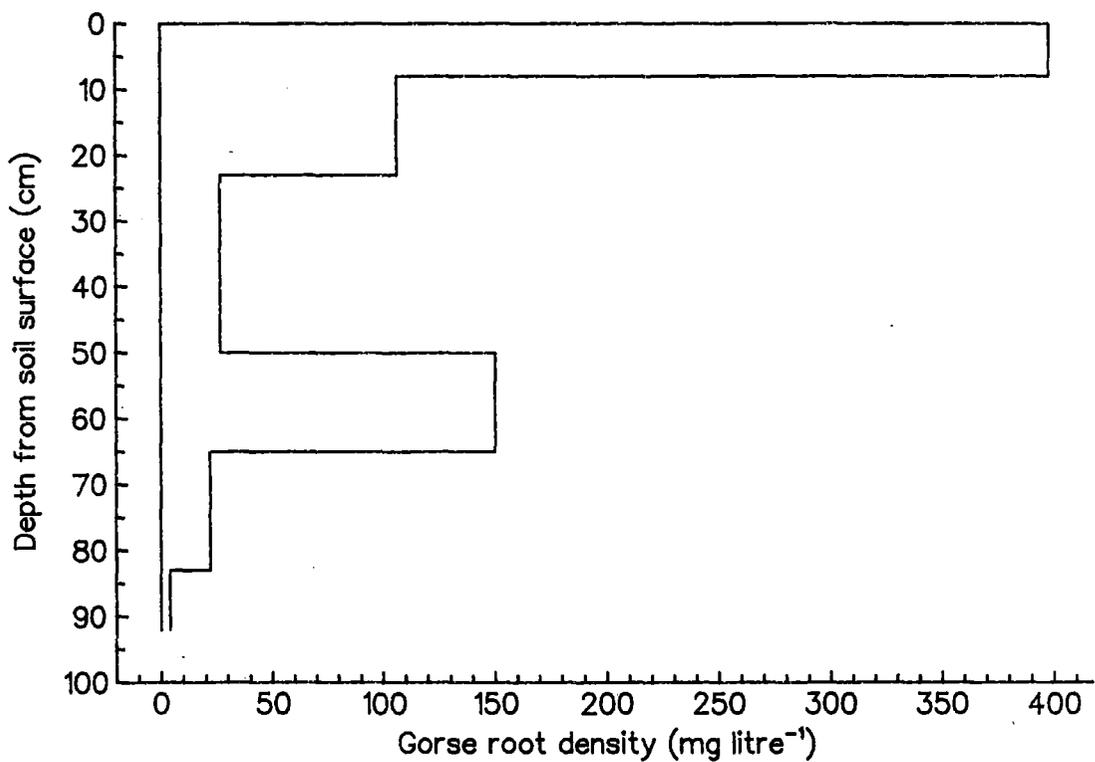


Fig. 6.4 Gorse root distribution – Ikamatua soil

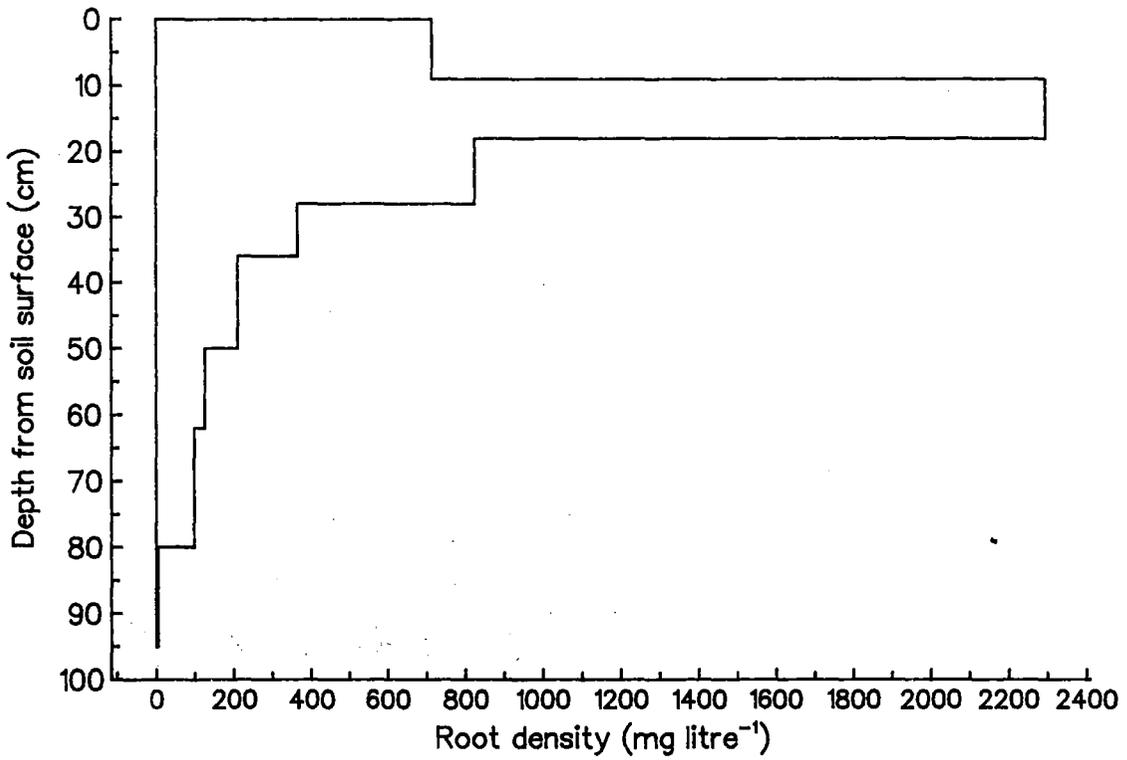


Fig. 6.5 Gorse root distribution – Ahaura soil

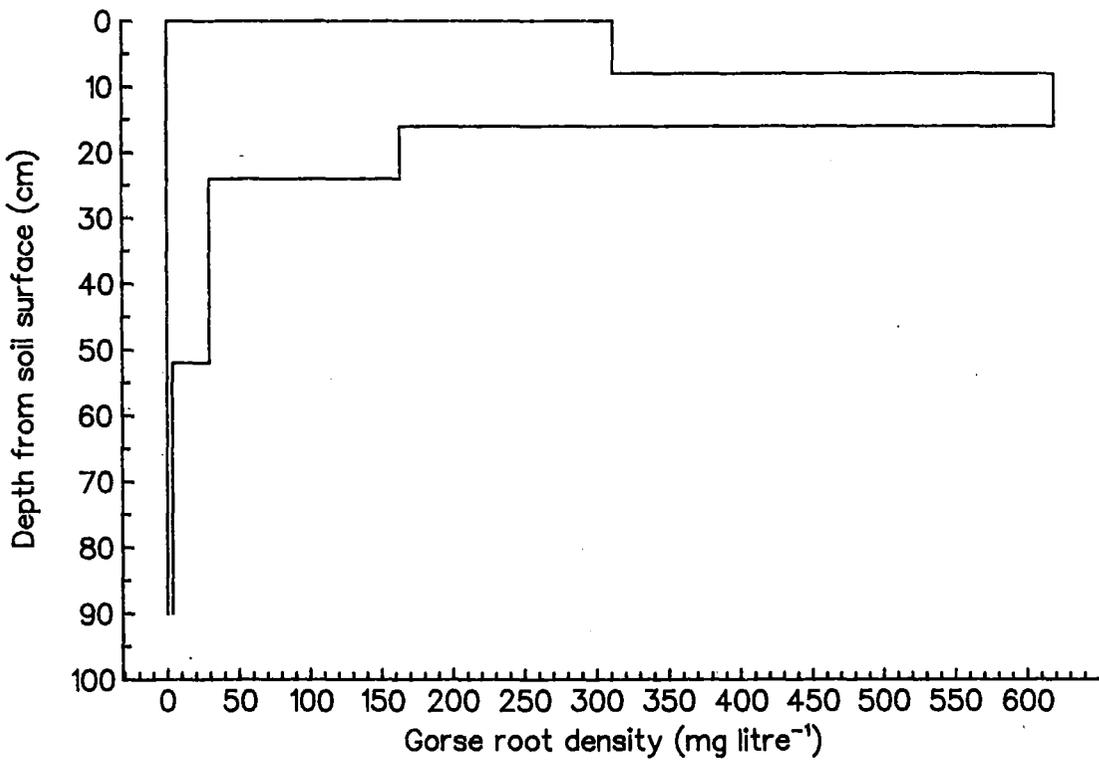


Fig. 6.6 Gorse root distribution – Okarito soil

6.4 DISCUSSION

6.4.1 Soil chemistry

The four soils in the chronosequence studied all had low concentrations of plant nutrients (Tables 6.5 and 6.6; Blakemore *et al.* 1987). There were some small differences between soils.

Olsen P concentrations were greater in the Ahaura and Okarito soils reflecting past fertilizer application (section 6.2.2). Ross *et al.* (1977) found little change in Truog-soluble P up the chronosequence. However total, inorganic, organic and $0.5 \text{ mol l}^{-1} \text{ H}_2\text{SO}_4$ -soluble P were found to decrease with increasing age in the Ikamatua, Ahaura and Okarito soils (Ross *et al.* 1977). The decrease in $0.5 \text{ mol l}^{-1} \text{ H}_2\text{SO}_4$ -soluble P reflects the weathering of acid soluble calcium phosphates, such as apatite, to more soluble forms, and their leaching from the soil (Ross *et al.* 1977; Mew *et al.* 1975). Tan (1971), working with a corresponding soil chronosequence near Reefton, observed similar trends. Thus, although the Ikamatua soil appears to have greatest total and $0.5 \text{ mol l}^{-1} \text{ H}_2\text{SO}_4$ -soluble P, followed by the Ahaura, Hokitika and Okarito soils (Ross *et al.* 1977), this is not reflected in their Olsen (plant-available) P concentrations. Olsen P concentration appeared to be most influenced by fertilizer history.

No phosphate-extractable sulphate was detected in the Hokitika topsoil, reflecting the sandy nature of this material. The relatively high phosphate-extractable sulphate concentrations in the Ahaura soil was a reflection of its fertilizer history (section 6.2.2).

Cation exchange capacity (CEC) in these soils is thought to be largely associated with organic matter contents, rather than with clay contents which tend to be low (Mew *et al.* 1975; Ross *et al.* 1977). Hence CEC tended to increase with soil age, along with increases in soil organic matter (Tables 6.5 and 6.6).

The elevated exchangeable Ca concentrations in the Okarito soil probably reflected the combined effect of past fertilizer application and greater CEC compared with the other soils (Tables 6.5 and 6.6; Section 6.2.2).

The 1 mol l⁻¹ KCl-extractable Al concentrations in the Ahaura soil (up to 2.5 me.% at 7.5-15 cm depth) and CaCl₂-extractable Al concentrations in both the Ahaura and Ikamatua soils (5 to 17 µg g⁻¹) are such that Al toxicity would possibly occur in white clover (Tables 6.5 and 6.6; Edmeades *et al.* 1983; Hume *et al.* 1988). Data from the lime/P experiment (Section 4.3.2.1) indicate that gorse and white clover growth were not reduced by 0.02 mol l⁻¹ CaCl₂-extractable Al concentrations of 48.6 and 13.56 µg g⁻¹ respectively. The value for white clover was measured at the end of the experiment and was greater than that at the beginning of the experiment because of the soil acidifying effect of white clover (Table 4.7). Also, the CaCl₂-Al concentrations quoted were tolerated under conditions of high to very high Olsen P concentration (Table 4.8). Plants growing under the generally low to very low available soil P conditions of this experiment may be less tolerant of Al toxicity because P tends to moderate Al toxicity and conversely Al in solution tends to reduce P availability (Munns 1965b; Clarkson 1966; Dodd *et al.* 1992; Section 2.3.4.2).

Thus it appears that Al toxicity would probably not have adversely affected gorse growth on any of the soils studied, but this is still a possibility because of the low available P concentrations in these soils. Al toxicity may have affected white clover growth on the Ikamatua or Ahaura soils.

The apparently greater chemical fertility of the Okarito site used in this study compared with the other three soils is in contrast to the findings of Ross *et al.* (1977) and Mew *et al.* (1975). Mew *et al.* (1975) describes the Okarito soil as having perhaps the lowest fertility of all soils in the Inangahua depression. They state that most of the nutrients are contained in the organic horizons. Although nutrient concentrations in these horizons may be quite high, the actual quantity of nutrients in the profile may be very low because of the peaty nature and low bulk density of the organic horizons (Mew *et al.* 1975). According to Mew *et al.* (1975) the Okarito soil has severe potential cation deficiencies and a moderate potential trace element deficiency.

The generally low concentrations of nutrients (P, S and exchangeable cations) could limit plant growth on all four soils. However particular chemical properties which could limit growth on any of the four soils compared with the others are as follows:

- 1) Low Olsen P in the Hokitika and Ikamatua soils compared with the Ahaura and

Okarito soils.

- 2) No detectable phosphate-extractable sulphate in the Hokitika soil, and low concentrations in the Ikamatua and Okarito soils compared with the Ahaura soil.
- 3) Low exchangeable Ca concentrations in the Hokitika, Ikamatua and Ahaura soils compared with the Okarito soil.
- 4) Relatively low reserve K and Mg in the Okarito soil.
- 5) Possibly toxic concentrations of soluble Al in the Ahaura soil.

6.4.2 Potential limitations to plant growth

Possible physical limitations to plant growth, based on the soil profile descriptions (Tables 6.1-6.4) are presented in section 6.3.1.1. These along with the soil chemistry data presented in Section 6.3.1.2, and discussed in section 6.4.1, are generally in agreement with the possible limitations for exotic forestry described by Mew *et al.* (1975):

1) Hokitika series:

Slight limitations caused by excessive stoniness and a tendency to dry out in summer, and a moderate limitation due to potential flooding.

Total limitations: slight to moderate.

2) Ikamatua series:

Excessively stony in some cases (not applicable to the site used in this study), and showing a tendency to dry out in summer.

Total limitations: negligible to slight

3) Ahaura series:

Moderate potential cation deficiency and slight potential phosphate and trace element deficiency. Moderate limitation of excessive stoniness and densely packed underlying gravels (from 52 cm in this study), both of which may restrict rooting volume. Slight limitation caused by thin iron pans in some profiles (not in this study) and a tendency to dry

out in summer.

Total limitations: moderate

4) Okarito series:

Severe potential phosphate and cation deficiencies and a moderate potential trace element deficiency. Severe textural limitation to rooting resulting from the massive structured gley horizon commonly observed at a depth of approximately 20 cm, (24 cm in this study) and moderate limitation due to excessive wetness and the presence of iron pans (at 51 cm in this study).

Total limitations: severe

As discussed previously, the Okarito soil used in this study did not appear to be lower in fertility than the other soils. However the chemical data on the Okarito soil may not accurately indicate amounts of nutrients compared with the other soils because of its low bulk density (Mew *et al.* 1975).

6.4.3 Gorse growth and nutrient supply

Gorse growth (Figs 6.1 and 6.2; Table 6.7) was greatest on the Ikamatua soil series which is consistent with the rating of Mew *et al.* (1975) indicating that this was the soil with least limitations in the Larry River chronosequence. Next highest growth was recorded on the Ahaura series, whereas according to Mew *et al.* 1975, it might have been expected that gorse on the Hokitika soil would have out performed gorse on the Ahaura soil. This can probably be explained by the fact that the Hokitika soil used in this study had only a very thin topsoil overlying sand and boulders (Table 6.1, Plate 6.1), in contrast to the somewhat more developed version described by Mew *et al.* (1975). In this study, poorest gorse growth was observed in the most recent (Hokitika) and oldest (Okarito) soils in the chronosequence. Smaller yields on the Okarito soil are consistent with the ratings of Mew *et al.* (1975), which indicate severe chemical and physical limitations.

The pattern of gorse growth on the different soils was similar for the 1988/89 and 1989/90 growth seasons (Figs 6.1 and 6.2). There is no obvious explanation for the apparently greater growth in the 1988/89 season compared with the 1989/90 season. Total rainfall recorded at Reefton (11 km from the site) in the period July 1988 - June 1989 (2278 mm)

was greater than that in July 1989 - June 1990 (1761 mm) (New Zealand Meteorological Service 1988-1990). Probably more importantly, rainfall immediately before and during the spring period when rates of shoot elongation tend to be greatest (Figs 3.16 and 3.17) was much greater in the 1988/89 season than in the 1989/90 season (Fig 6.7). However, rainfall still exceeded potential evapotranspiration (Fig 6.7), suggesting that lower rainfall was not the reason for lower yields in the 1989/90 growth season. Values for potential evapotranspiration are long term averages for Westport (37 km from the study site) which was the nearest location for which such values were available (New Zealand Meteorological Service 1986). It was assumed that rainfall data from Reefton and potential evapotranspiration data from Westport would give a reasonable indication of conditions at the trial site.

Attempts to associate reduced gorse growth with low concentrations of particular elements in its shoot tissue are speculative because of the lack of information on critical nutrient concentrations for gorse. Where it is thought to be useful, element concentrations in gorse shoots from this study will be compared with critical concentrations for white clover. While doing this it should be remembered that while gorse and white clover do have some features in common in that both are legumes, they do have very different growth habits and reputedly different nutritional requirements.

The concentrations of K, Mg, Ca, Mn and Zn in gorse shoots were significantly affected by soil series at every shoot sampling time, the concentrations of P, S, Al, Cu and Fe were affected at one or two sampling times but N concentration was not significantly affected at any sampling time (Table 6.9).

Nitrogen concentrations were not significantly affected by soil series, indicating that gorse growth was not limited by N_2 -fixation or N uptake on the soil series of this chronosequence. N concentrations tended to be slightly lower than found in similarly aged shoots from the Springston field trial (mean from uncut, nil N treatment Dec 1990 = 2.65% (Table 3.17) compared with the mean from all soils in spring (Dec) 1990, of 2.15% in this study (Table 6.9)). Shoot N concentrations in this study also tended to be less than the concentrations for gorse published by Radcliffe (1986).

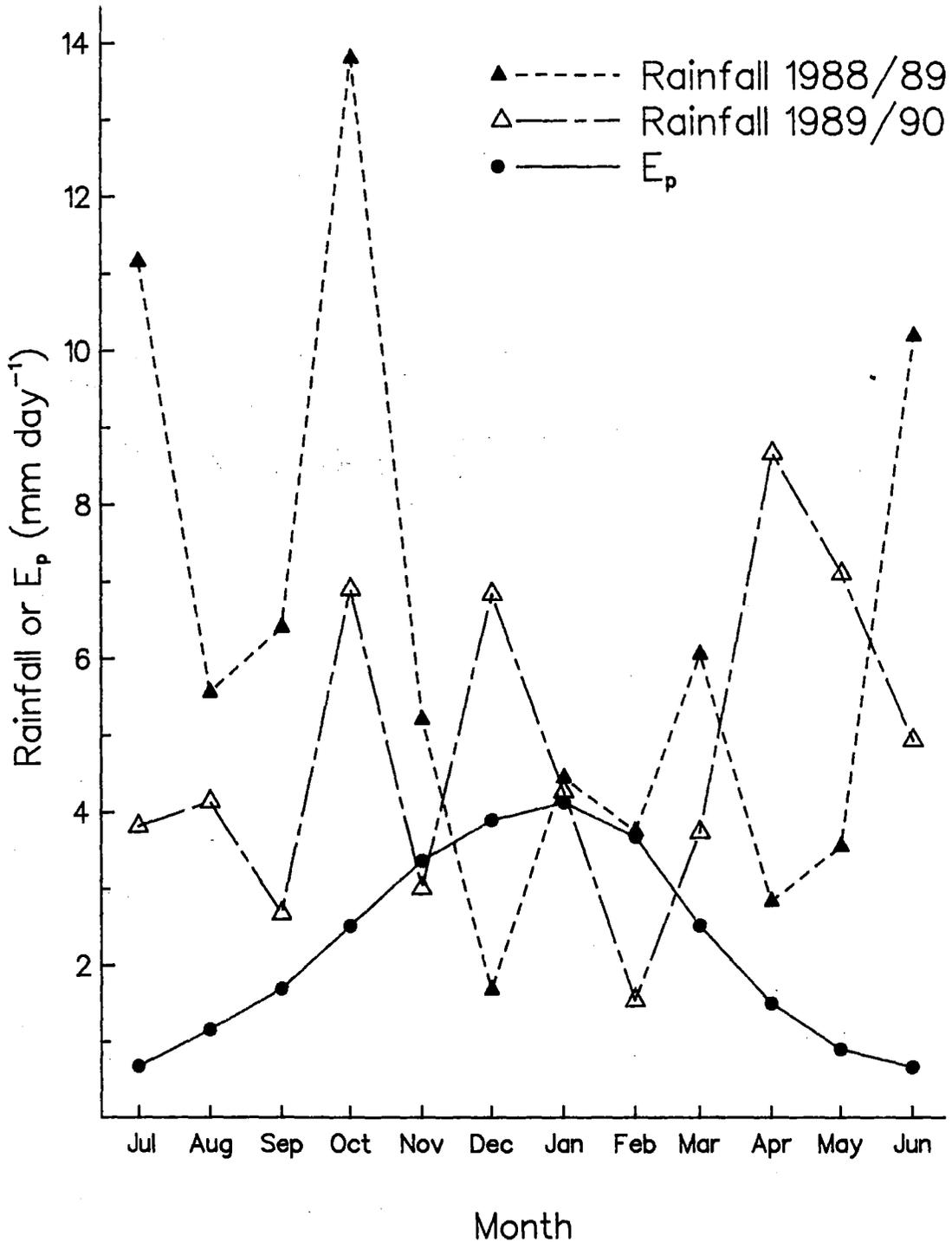


Fig. 6.7 Monthly average rainfall (recorded at Reefton) for the 1988/89 and 1989/90 growth seasons and long term monthly average potential evapotranspiration (E_p) rates for Westport.

Herbage P concentrations (Table 6.9) generally tended not to be significantly affected by the different soils. The greater concentration for the Okarito soil in the winter of 1990 may reflect the greater available P concentrations measured in this soil (Table 6.6), as a similar tendency, albeit not significant, was apparent in the winter of 1989. Alternatively, limitation of growth by some other factor, such as water-logging or deficiency of another nutrient may have enabled greater P concentrations. Most importantly however, P concentrations in actively growing spring shoots were similar for all terraces (Table 6.9). P concentrations in the spring samples (mean = 0.16%) were similar to the critical shoot P concentration for second year uncut gorse in the Springston trial (0.18%) (Table 3.32). This suggests that the spring shoot P concentrations measured in this study were probably adequate for near maximum gorse growth despite generally very low Olsen P concentrations in the soils (Tables 6.5 and 6.6). It also reinforces the finding (Section 4.4.2.2) that pot-grown gorse, in soil with very low available, P was relatively well able to maintain adequate shoot P concentrations (compared with white clover), which was reflected in its lower responsiveness to applied P compared with white clover (Table 4.12). The shoot P concentrations (Table 6.9) were greater than those of Radcliffe (1986) for mature gorse.

Relatively high S concentrations in gorse shoots on the Ahaura soil (Table 6.9) were associated with greater phosphate-extractable sulphate in the soil (Tables 6.5 and 6.6), but were not associated with increase in yield (Figs 6.1 and 6.2). Greatest yield was obtained on the Ikamatua soil which tended to have relatively low shoot S concentrations (Table 6.9, Figs 6.1 and 6.2). Thus, although shoot S concentrations were in the deficient range for white clover (Cornforth and Sinclair 1984) and lower than the summer and autumn values for gorse shoots of Radcliffe (1986), there was no clear relationship between shoot S concentration and dry matter yield.

The generally declining herbage concentrations of K and Mg (Table 6.9) with increasing soil age reflects the decreasing K and Mg supplying power of these soils, as indicated by the decreasing reserve K and Mg (K_e and Mg_e) values (Tables 6.5 and 6.6). However, shoot Mg concentrations on the Ahaura and Okarito soils did not fit into this overall pattern. Gorse shoots on the Ahaura soil had the lowest Mg concentrations, significantly lower than those on the Okarito soil. Although the Okarito soil had by far the lowest Mg_e values, the Ahaura soil had the lowest exchangeable Mg values (in the very low category of Blakemore *et al.* 1987). The spring 1989 values for actively growing shoots on the Hokitika and Ikamatua

soils were within or above the optimum range for white clover (Table 6.9; Cornforth and Sinclair 1984). Concentrations for the Ahaura and Okarito soils were however below this range. It is possible, therefore, that low shoot Mg concentrations could be limiting gorse growth on the Ahaura and Okarito soils.

Gorse shoot K concentrations, without exception, declined with increasing soil age and were lower than the optimum range for white clover (Cornforth and Sinclair 1984). The K values for spring 1989 were less than the spring values of Radcliffe (1986), but the winter values tended to be greater than those reported by Radcliffe. It is possible that low K concentrations could be limiting gorse growth in the Okarito, and perhaps also the Ahaura soils.

Shoot Mn concentrations tended to decline with increasing soil age (Table 6.9), presumably as a result of increased weathering and leaching of this element from the soil. The lower values for the Hokitika soil compared with the Ikamatua soil (in 1989) are probably a result of the very sandy, stony nature of the Hokitika site used. Shoot manganese concentrations were all well above the optimum range for white clover (Cornforth and Sinclair 1984), therefore deficiency of this element is unlikely to have limited gorse growth in this study.

Shoot concentrations of both Cu and Zn also declined with increasing soil development (Table 6.9). Zinc levels were quite high but Cu values were below the optimum range for white clover (Cornforth and Sinclair 1984) and were especially low for the Ahaura and Okarito series. Thus Cu could be limiting growth on these two soils.

Shoot Fe concentrations were lowest for the Okarito soil, being lower than the optimum range for white clover (Cornforth and Sinclair 1984). However, shoot Fe concentration on the Okarito soil was never significantly lower than that on the Ikamatua soil. Thus, limitation of gorse growth on the Okarito soil due to Fe deficiency is possible but not very likely.

Shoot Al concentrations on the Ahaura soil were no greater than those on the Ikamatua or Hokitika soils. Also the shoot Al concentrations in this study (about 0.01%) were substantially less than those associated with no reduction in yield due to soil acidity (Section 4.3.5). These two facts, combined with the fact that the CaCl_2 -Al concentration in the

Ahaura soil (maximum of $17.2 \mu\text{g g}^{-1}$, Table 6.5) was less than the greatest $\text{CaCl}_2\text{-Al}$ concentration associated with near maximum dry matter yield of gorse in the lime/P experiment ($48.6 \mu\text{g g}^{-1}$, Section 4.3.2.1) suggest that the reduction in dry matter yield on the Ahaura soil compared with the Ikamatua soil was not caused by Al toxicity.

To summarise, soil chemistry in combination with shoot element concentrations can be used to provide possible explanations for some of the differences in dry matter yield. For example lower yields on the Ahaura and Okarito soils compared with the Ikamatua soil (Figs 6.1 and 6.2) could be explained by their lower shoot Mg concentrations (Table 6.9) which accompanied the declining Mg_r values with increasing soil age (Tables 6.5 and 6.6). (Low Mg_r values indicate low long term Mg supplying power (Metson *et al.* 1956; Metson and Brooks 1975).) Similarly it is possible that low plant K concentrations (Table 6.9) which were associated with low K_e values (Tables 6.5 and 6.6) could explain lower gorse dry matter production on the Okarito soil and perhaps also the Ahaura soil compared with the Ikamatua soil. It is possible that low plant Cu concentrations could limit growth on the Ahaura and Okarito soils and that low Fe concentrations could limit growth on the Okarito soil. Phosphate-extractable sulphate concentrations suggest that S could limit growth on the Hokitika soil, but shoot S concentrations on this soil were similar to those on the Ikamatua soil.

6.4.4 Other edaphic factors influencing gorse growth on the Larry River soil chronosequence

Differences in gorse growth on this chronosequence of soils did not appear to be closely linked with soil chemistry.

Probably a more convincing explanation of the dry matter yield differences between soils can be gained using the physical characteristics of the soils, and in particular the limiting factors listed in Section 6.3.1.1. The ability of a plant to take up nutrients, as discussed in Section 2.2.2, is closely related to the size (weight or length) and extent of its root system (Loneragan and Asher 1967; McLachlan 1976; Woodhouse *et al.* 1978; Fohse *et al.* 1988). The maximum amount of a nutrient that can come in direct contact with plant roots as they grow through the soil is the amount in a volume of soil equal to the root volume (Barber *et al.* 1963). Nutrients not in direct contact with the root must move through the soil to the

root by mass flow or diffusion in order to be taken up by the plant. Nutrients such as P and K, move through the soil primarily by diffusion because they typically exist at low concentrations in the soil solution, whereas Ca and Mg, because of their typically greater concentrations in soil solution, may be primarily supplied to the surface of the root by mass flow (Barber *et al.* 1963). Nye (1977) concluded that the rates of uptake of N, P and K are limited by their rates of diffusion through the soil. Therefore any factor, which reduces the distance which nutrients must diffuse through the soil to reach the root surface, such as greater root length or volume, must increase the rate of nutrient uptake. Conversely, soil factors which reduce rooting volume such as excessive stoniness, must reduce nutrient and water uptake.

In the Ikamatua soil there was good rooting volume with comparatively few stones and no impediment to rooting depth or water movement. Increased soil volume available to plants due to decrease in aggregate size is found to increase plant yield by increasing nutrient supply (Cornforth 1968a). The Ikamatua soil had a greater depth of fine material than any of the other soils (Tables 6.1-6.4, Plates 6.1-6.4) which would be expected to enhance its nutrient supply and moisture holding characteristics. Plant uptake of nutrients from the soil, especially those which are relatively immobile, such as P, is greater from finer than coarser materials (Wiersum 1962; Cornforth 1968b). In a fine substrate the extensive permeation of roots enhances the uptake of immobile nutrients (Wiersum 1962). Restricted root growth because of large aggregate size particularly impairs the uptake of immobile elements such as P because large, impenetrable aggregates increase the distance which nutrients contained within them must travel in order to reach the root surface (Atkinson 1959; Wiersum 1962). In each of the other three soils there were features which would be expected to adversely affect plant performance. In the Hokitika soil the large volume occupied by stones and gravels would greatly reduce rooting volume, and the lack of fine material would adversely affect moisture storage (Table 6.1, Plate 6.1). In the Ahaura soil the presence of stones, and densely packed gravel below 52 cm (Table 6.3, Plate 6.3) would greatly diminish rooting volume. In the Okarito soil rooting volume would be adversely affected by a massive structured and at times anaerobic gley horizon at 27-51 cm depth and an iron pan at 51 cm would limit rooting depth (Table 6.4, Plate 6.4). In times of high rainfall water would tend to perch above the pan and the resulting water-logged conditions would be expected to adversely affect root growth and symbiotic N₂ fixation (Sprent and Minchin 1983). It can be seen that the iron pan does substantially reduce root density below it, (Fig 6.6), thus

rendering any nutrients below 52 cm depth relatively inaccessible. The importance of rooting depth in determining plant water uptake and growth is emphasised by Pearson (1974). Thus the accessibility of nutrients and water appears to be greatest in the Ikamatua soil and to be limited by physical factors to varying degrees in the Hokitika, Ahaura and Okarito soils.

One interesting feature of root distribution in the Hokitika and Ikamatua soils is the bulge in root density which occurs in both profiles, associated with a layer of relatively finer textured material (Figs 6.3 and 6.4; Tables 6.1 and 6.2). In the case of the Hokitika soil this appeared to be a buried A horizon. The layers of finer textured material would tend to have a greater moisture holding capacity than the layers above and below it, and may also contain more nutrients. The proliferation of roots in zones containing relatively high nutrient concentrations and water contents is well known (Garwood and Williams 1967a & b; McWilliam and Kramer 1968; Strong and Soper 1973).

During the 1988/89 and 1989/90 growth seasons average monthly rainfall generally exceeded average evapotranspiration rates (Fig 6.7). However in two months, December 1988 and February 1990 evapotranspiration was substantially greater than rainfall (by 69 and 60 mm respectively, Fig 6.7).

Available water contents for the soils estimated from moisture release data and experience with other similar soils (T.H. Webb pers. comm.) indicates that the Ikamatua, Ahaura and Okarito soils have available water contents well in excess of the difference between potential evapotranspiration and rainfall for the two months noted. Estimated available water content for the Hokitika soil varies between 40 and 80 mm depending on whether it has a layer of loamy sand at the surface (Table 6.1) or whether it had large stones right to the surface as was often the case. Therefore gorse plants on the Hokitika soil probably suffered short term moisture stress in December 1988 and February 1990, and this may have depressed growth. If the water table of the Hokitika soil is assumed to be at river level this would be well in excess of 1 m depth for most of the growing season. The number of roots reaching the water table, and therefore the amount of water available from it, would probably be small.

Overall, it appears that lack of soil water would not have substantially affected gorse growth on this soil chronosequence. The physical properties of the soils as they affected rooting

volume or rooting depth appear more likely to have affected gorse growth, via their effects on nutrient and water uptake.

6.4.5 Growth potential of gorse

In the two years of this study, dry matter production of gorse ranged from 7210 kg ha⁻¹ on the Hokitika soil in the 1989/90 growth season to 14 600 kg ha⁻¹ on the Ikamatua soil in the 1989/90 growth season (Table 6.8). These dry matter yields compare favourably with the mean annual pasture yield of 10 920 kg ha⁻¹ measured at Westport, North Westland on a soil receiving annual applications of 1000 kg ha⁻¹ of 33% potassic, cobaltised, lime-reverted superphosphate (about 42 kg P, 165 kg K and 56 kg S per ha) (Radcliffe 1975).

The relatively high productivity of gorse on low fertility soils in this study is consistent with its good growth without fertilizer in the Springston trial (10 890 kg dry matter ha⁻¹, Section 3.4.1), and also its acknowledged role as a pioneer species in low fertility situations (Egunjobi 1969; Dancer *et al.* 1977a; Roberts *et al.* 1981) as discussed in section 2.1.3.2.

The efficiency of gorse at fixing N₂ (Section 3.4.1), its relatively high capacity to take up P from unfertilized soil (Section 3.4.3) and its efficient use of P in the processes of growth (Section 3.4.4) as demonstrated in the Springston trial are all consistent with its good growth compared with fertilized pasture on the low fertility soils of the Larry River chronosequence. A comparison between annual P uptake by gorse growing under low soil fertility conditions (this study) and that of highly fertilized pasture (Radcliffe 1975) is shown in Table 6.10.

Table 6.10 A comparison of annual P uptake in gorse and white clover - North Westland

	Gorse (low P soil)	Grass/clover pasture (adequate P soil)
Dry matter yield (kg ha ⁻¹ year ⁻¹)	7210 - 14600	10920
P concentration † (%)	0.09 - 0.08%	0.35%
P uptake (kg ha ⁻¹ year ⁻¹)	6.5 - 11.7	38.2

† P concentrations for gorse are those associated with the dry matter yields given (Hokitika soil 1990 and Ikamatua soil 1989, Tables 6.9 and 6.8).

P concentration for pasture was assumed to be at the lower end of the optimum range for ryegrass and white clover (Cornforth and Sinclair 1984).

It appears that gorse has taken up much less P than the grass/clover pasture but has used it more efficiently in the production of dry matter.

6.5 CONCLUSIONS

- 1) The growth potential of gorse under low soil fertility conditions is similar to that of highly fertilized pasture under North Westland conditions. Internal efficiency of P use appears to be an important factor enabling gorse to thrive on low fertility soils.
- 2) There were possible links between soil fertility and plant performance, but these were not clear cut.
- 3) There were strong associations between the physical nature of the soils and gorse growth. Factors causing reduced rooting volume and rooting depth appeared to result in decreased dry matter yield of gorse. These factors would reduce dry matter yield by reducing water and nutrient uptake.

CHAPTER 7

GENERAL CONCLUSIONS

Gorse appears to possess greater potential for dry matter production than white clover under dryland conditions with either low or high soil chemical fertility. Under dryland conditions in Canterbury gorse in its second growth season, on an unfertilized soil with very low plant available P concentrations and cut twice yearly, produced a similar amount of dry matter ($5053 \text{ kg ha}^{-1} \text{ year}^{-1}$) to pasture ($5870 \text{ kg ha}^{-1} \text{ year}^{-1}$) fertilized with $250 \text{ kg ha}^{-1} \text{ year}^{-1}$ superphosphate. Unfertilized gorse which was uncut, and P-fertilized gorse which was either cut twice yearly or uncut all produced substantially more dry matter (up to $18516 \text{ kg ha}^{-1} \text{ year}^{-1}$) than P-fertilized pasture. On a river terrace sequence in North Westland, established gorse growing on unfertilized soils with very low to low available P concentrations, some of which also had physical limitations to root growth, produced similar amounts of dry matter (ranging from 7210 to $14600 \text{ kg ha}^{-1} \text{ year}^{-1}$) as pasture ($10920 \text{ kg ha}^{-1} \text{ year}^{-1}$) fertilized with $1000 \text{ kg ha}^{-1} \text{ year}^{-1}$ of 33% potassic, cobaltised, lime reverted superphosphate (giving about 42 kg P ha^{-1} , 165 kg K ha^{-1} and 56 kg S ha^{-1}).

Gorse grown on soils with very low available P concentrations was responsive to applied P, but less so than white clover, both in pots (where the two species were grown separately) and in the field (where both species were grown together). Gorse was also able to take up more P than white clover from soils with very low available P concentrations, both in pots and in the field. In the field, a more extensive root system may have enabled gorse to take up more P than white clover, but in the restricted volume of a pot some other mechanism must have been operating, such as greater P uptake per unit length of root, a more effective root architecture or a more effective mycorrhizal association. At very low available P concentrations in the glasshouse (the soil used in the glasshouse had a lower available P concentration than the field trial soil) gorse appeared better able to maintain an adequate shoot P concentration than white clover and this may have contributed to its better growth than white clover in the unfertilized soil.

The shapes of the P responses for gorse and white clover differed. Over the range of P rates used in the Springston field trial, the dry matter response curve for gorse was quadratic in nature with increases in yield with increasing rates of P, but suggesting a tendency for decline at the greatest rate. In contrast, the dry matter response curve of white clover was

exponential in nature, indicating increasing dry matter yield with increasing rates of P, with diminishing-responses at the greatest rates of P but no tendency for decline.

Shoot P concentrations of field grown gorse were generally less than those of white clover at all rates of applied P and critical P concentrations for gorse (0.19%) appeared to be less than those for white clover (0.35%), indicating that gorse was able to use P more efficiently in the processes of growth i.e. produce more dry matter per unit P content than white clover.

It appears that gorse is able to produce more dry matter than white clover on soils with very low available P concentrations because it is able to acquire more P from the soil and use the P taken up more efficiently in dry matter production compared with white clover. This was true both in the field, where gorse and white clover were grown together and in pots where the species were grown separately.

Gorse is not a low fertility demanding species and it is very responsive to applied P. However it does appear to have a competitive advantage under low fertility conditions over higher fertility demanding species such as white clover. This competitive advantage would be particularly important for the survival of gorse at the seedling stage when its growth is slow. Under conditions of low fertility gorse seedlings would have an advantage over potentially faster growing but higher fertility-demanding competitors.

At the end of two years growth in the field gorse which had not previously been cut produced about twice as much dry matter as plants which had been cut back twice each year, but the total P content of plants from the two cutting treatments was similar, indicating similar capacities for P uptake. Critical P concentrations in young shoots were also similar for the two cutting treatments. The ability of infrequently cut gorse to out-yield frequently cut gorse appeared to occur partially because of the greater potential for P translocation from old to young tissue in infrequently cut plants. The P contained in harvested shoots was lost to the frequently cut plants, whereas the infrequently cut plants appeared to make more efficient use of the P taken up by transferring it from old to new tissue. More efficient use of P combined with their greater leaf area index appeared to enable the greater growth of the infrequently cut plants.

Gorse (grown in pots) was less sensitive to soil acidity, and to soluble Al in particular, than

white clover and was less responsive to applied lime. This is a further indication of the competitive-advantage possessed by gorse under conditions of low soil chemical fertility (which frequently includes moderate to strong acidity). N_2 -fixing activity did not appear to be any more sensitive to soil acidity than host plant growth, for either gorse or white clover.

Gorse (grown in sand culture) responded to increasing concentrations of nitrate in nutrient solution within the range normally found in natural and agricultural soils. In terms of dry matter production, gorse and white clover responded similarly to increasing solution concentrations. However in terms of N content, gorse was less responsive to increasing solution nitrate concentration than white clover.

Gorse reached 90% maximum dry matter yield at lower solution nitrate concentration than white clover, suggesting that gorse is better able to thrive with little available combined N than white clover. Unlike white clover, very high nitrate concentrations (at the top of the range which can temporarily occur in highly fertilized soils) depressed gorse growth and N accumulation.

Gorse was similar to white clover in its ability to use available mineral N by increasing its root and shoot NRA, however, unlike white clover, gorse was sensitive to very high nitrate concentrations.

Critical shoot N concentration for gorse (2.79%) was less than that for white clover (4.62%), and N concentration of gorse tissue was less than that of white clover at all solution N concentrations, indicating that (as for P) gorse used N more efficiently in dry matter production than white clover. The symbiotic nitrogen fixing system of gorse appeared to be able to meet the needs of the plant in the field, where the application of 200 kg N ha⁻¹ year⁻¹ gave no dry matter yield response. For gorse grown in sand culture, nodule weight and N_2 -fixing activity decreased in an exponential manner with increasing nitrate concentration for both gorse and white clover but the symbiotic N_2 -fixing system of gorse appeared to be more tolerant of increasing solution nitrate concentration than that of white clover. The decline in nodule weight and N_2 -fixing activity was less severe in gorse compared with white clover. This suggests that the symbiotic N_2 -fixing system of gorse might be better able to cope with fluctuations in soil N. It may lose less of its N_2 -fixing capacity under conditions of high external solution N concentration and therefore expend

less resources than white clover in re-establishing it under conditions of declining N concentration.

As for available P concentration, gorse was able to use increasing external solution N concentrations but, also as for available P, appeared to be sensitive to very high concentrations.

Dry matter yield of established gorse in North Westland was not clearly linked with soil chemical fertility, but appeared to be more strongly associated with the physical nature of the soils. Factors causing reduced rooting volume and rooting depth (such as stoniness, a massive structured gley horizon and an iron pan) appeared to result in decreased dry matter yield of gorse. These factors would limit dry matter yield by reducing water and nutrient uptake.

Gorse appears to have a competitive advantage under conditions of low soil fertility because it is able to absorb P from very dilute solutions, it can fix enough atmospheric N for its own needs, it uses both of these nutrients efficiently and it tolerates low soil pH. Yields were increased by supplying moderate amounts of extra P and N and by increasing the pH of strongly acid soils. Responses to extra P and N were limited and yields declined when very large applications were made.

The results reported in this thesis have implications for the management of gorse as a pest or as a forage for low input farming systems.

1) It was confirmed that gorse is relatively tolerant of low soil fertility conditions and hence its significance as a pest under these conditions is also confirmed. If economic conditions continue to favour low input pastoral agriculture (low fertilizer inputs and low stocking rates), then increasing infestation of pastoral land by gorse can be expected.

2) Under conditions of high soil fertility, the opportunity to control gorse using pasture management techniques exists only when gorse is at the seedling stage. Growth of gorse is slow at the seedling stage and, under conditions of high fertility, gorse will tend to be out-competed by high fertility demanding species with more rapid initial growth, such as white clover. However when gorse is more mature it has the potential to grow very rapidly and

responds to applications of P and N within the range normally given to pastures.

3) High forage yields of gorse are possible in comparison with pasture under conditions of low soil fertility. However the greatest yields were obtained from uncut plants. If gorse is used as a forage it will be important to achieve an appropriate balance between browsing by animals and retaining sufficient photosynthetic tissue to maintain rapid growth.

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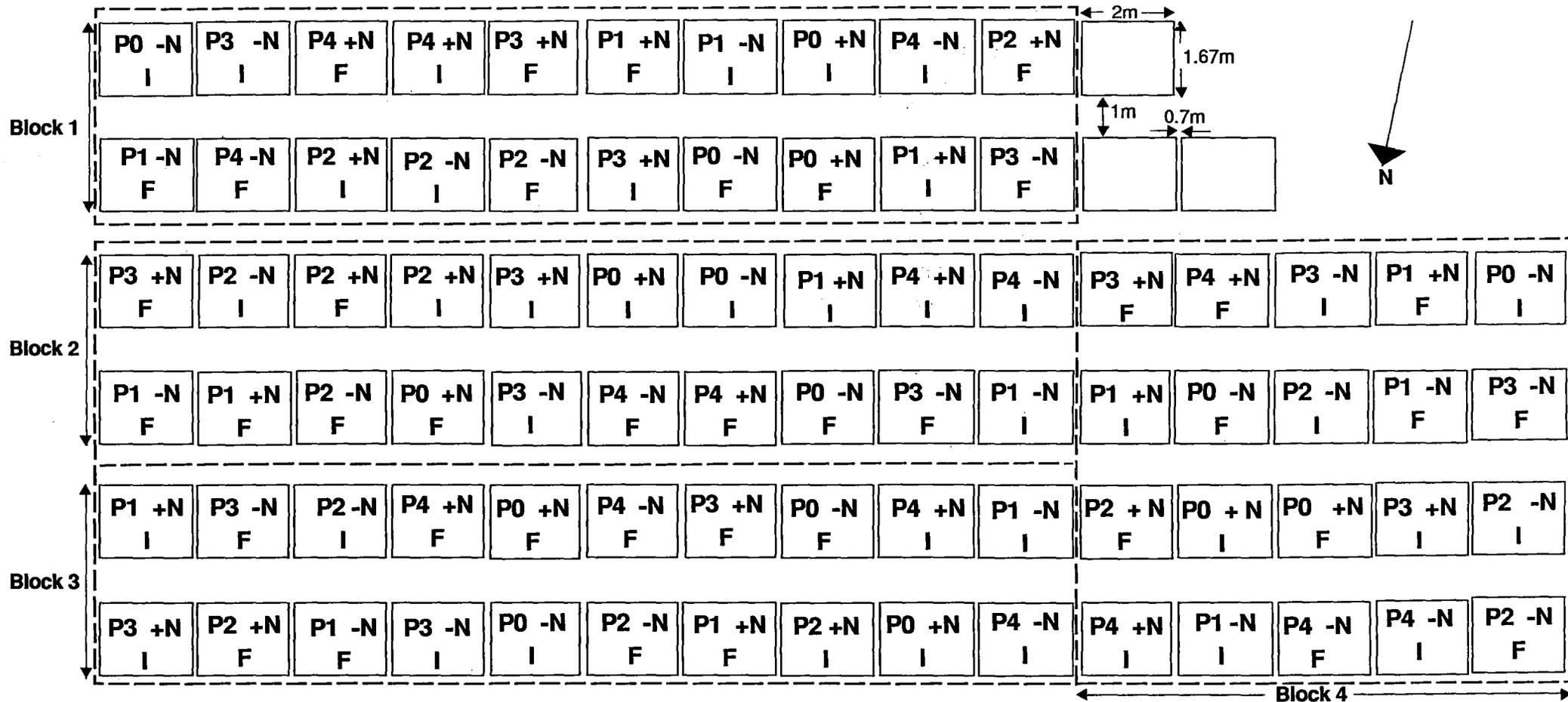
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APPENDICES

Appendix 3.1 Springston gorse trial - layout



Trial design: Randomised block with 4 replicates

Treatments:

5 rates of applied P: P0 - P4 (Table 3.1)

2 rates of applied N: -N (nil) and +N (200kg ha⁻¹ year⁻¹) (Section 3.2.1.2.2)

2 defoliation treatments: F (frequent) and I (infrequent) (Section 3.2.1.2.3)

Appendix 3.2

Determination of rate of P for the P3 treatment, Springston field trial, spring 1989

The P3 rate of P application, designed to give a concentration between 0.20 and 0.25 ppm P in soil solution, was derived using the P sorption isotherm for unfertilized Wakanui silt loam (Fig A1; Fox and Kamprath 1970). Conversion between rate of P on a mass of soil basis and on a surface area basis was done using a soil dry bulk density of 0.956 g cm^{-3} .

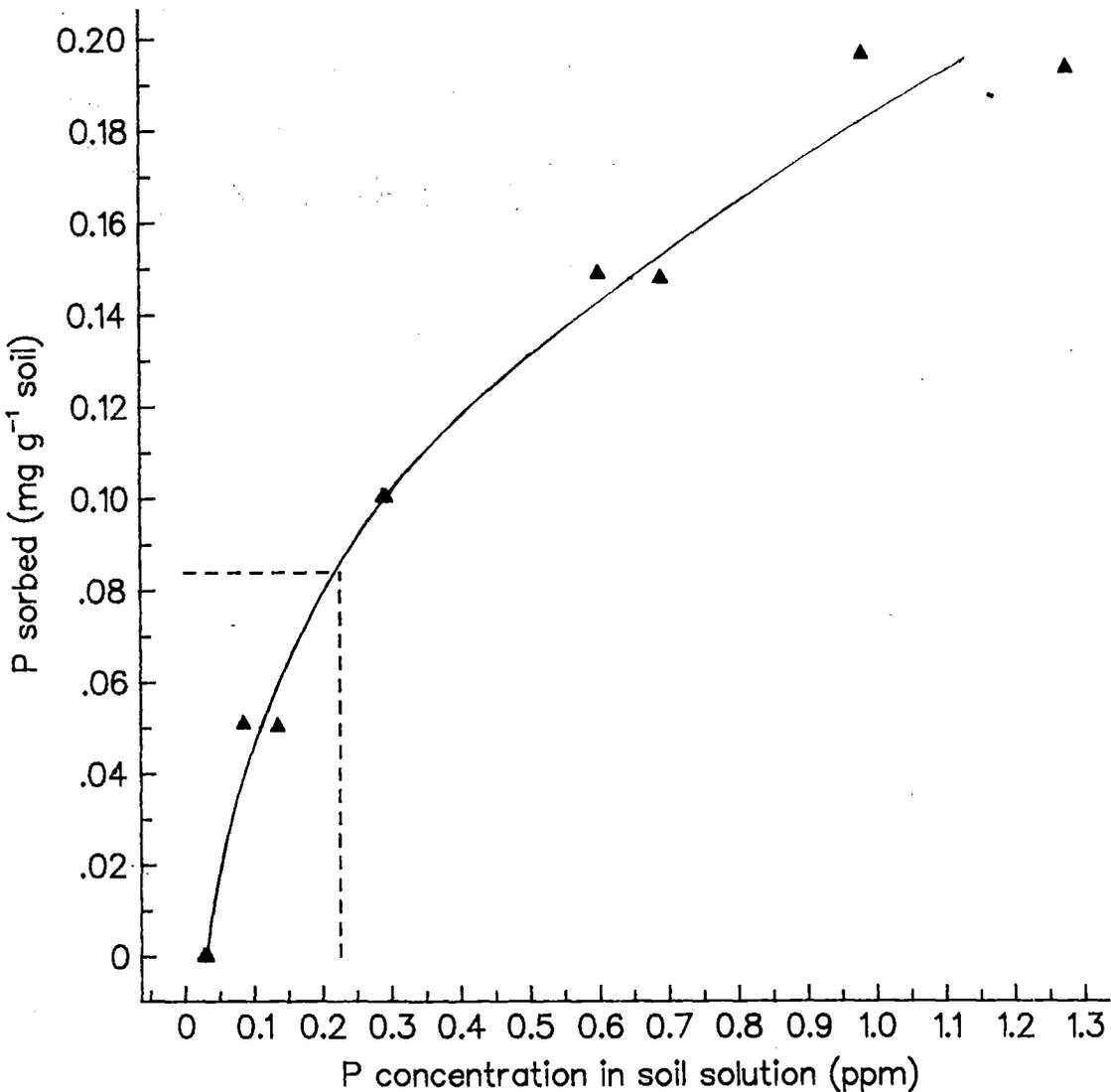


Fig. A1 P sorption isotherm, unfertilized Wakanui silt loam - Springston field trial spring 1989.

Appendix 3.3 Determination of rates of P for the Springston field trial, spring 1990

The aim of the rates of P applied in spring 1990 was to duplicate, as closely as possible, the soil solution P concentrations which existed in spring 1989. P sorption isotherms (Fox and Kamprath 1970) were constructed for composite 0-7.5 cm soil samples from each P treatment, collected during the winter of 1990. Target soil solution P concentrations (x-ordinates) corresponding to the rates of P applied in spring 1989 (y-ordinates) were determined using the P sorption isotherm for the P0 treatment (Fig A2). The rates of P application (expressed as mg g^{-1} on the y-axis) needed to achieve these concentrations for the individual treatments were then determined using the target P concentrations and the P sorption isotherms for the appropriate treatments. Conversions between rates of P on a surface area basis and on a mass of soil basis were done as described in Appendix 3.2.

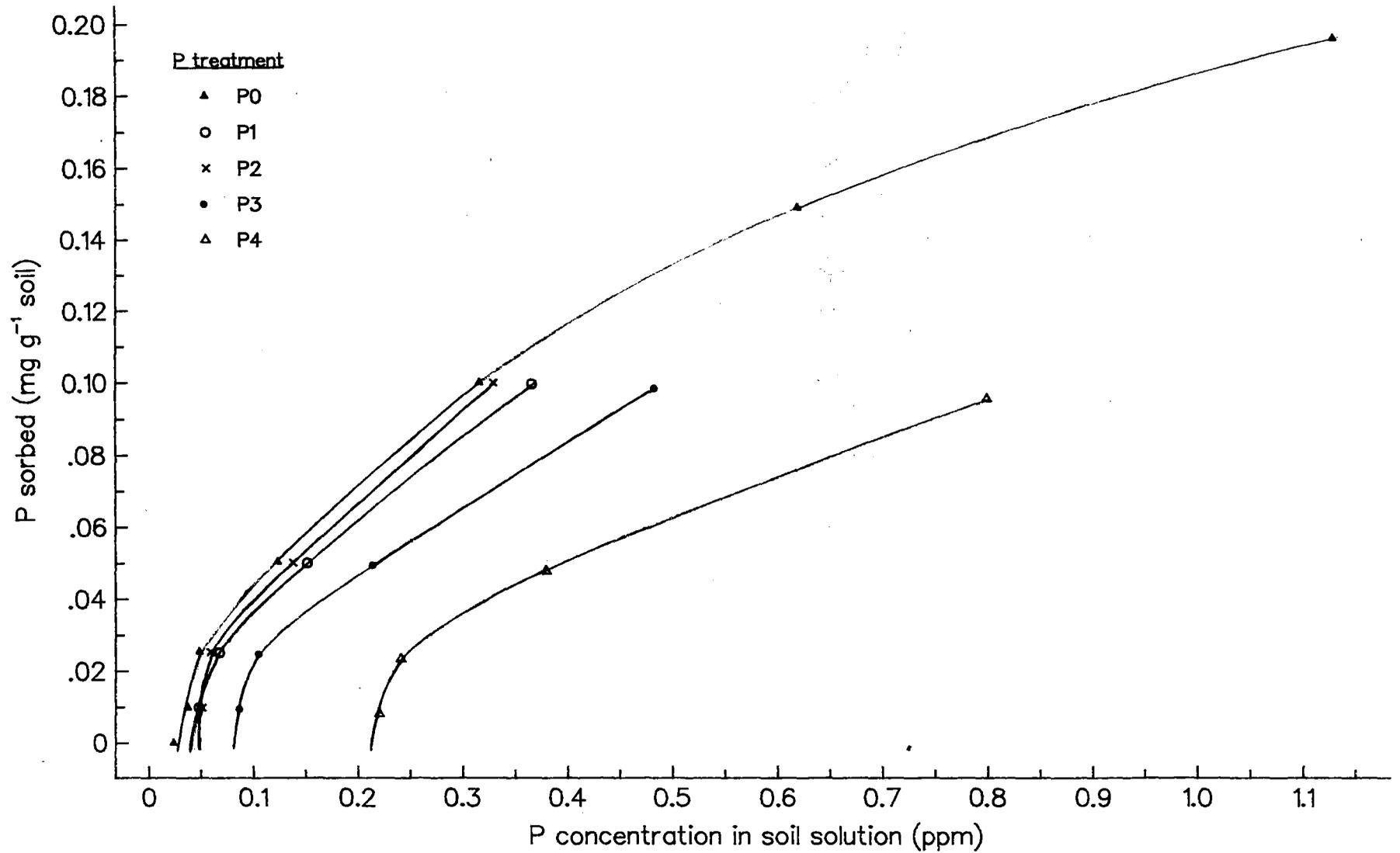


Fig. A2 P sorption isotherms for individual P treatments, Springston field trial, August 1990. Each point is the mean of duplicate determinations.

Appendix 3.4 Soil profile description - Wakanui silt loam (moderately deep phase)

Landform: depression on low terrace

Location: East Maddisons Road, Springston

Grid reference: Infomap 260 M36 612 288

Vegetation: scattered gorse, pasture

Drainage class: imperfectly drained

Profile:

- Ap₁ 0-9cm very dark greyish brown (10yr 3/2); silt loam; weakly developed fine nut structure; friable; many fine and few medium roots; diffuse boundary;
- Ap₂ 9-26cm very dark greyish brown (10yr 3/2); silt loam; common (15-20%) medium (5-15mm) faint strong brown (7.5yr 5/6) mottles; moderately developed medium nut structure; friable; common fine and few medium roots; distinct irregular boundary;
- Bg₁ 26-33cm greyish brown (2.5y 5/2) heavy silt loam many (20-50%) medium prominent strong brown (7.5yr 5/8) mottles; moderately developed medium very coarse blocky structure; very firm; few (5-10%) faint dark greyish brown (10yr 4/2) clay - organic matter coatings on ped faces; common medium worm holes unfilled with very dark greyish brown (10yr 3/2) material; few (<5%) unweathered rounded stones; few fine roots between ped faces; diffuse boundary;
- Bg₂ 33-56cm greyish brown (2.5y 5/2); silt loam; many (20-50%) medium prominent strong brown (7.5yr 5/8) mottles; moderately developed very coarse blocky structure; very firm; common distinct dark greyish brown (10yr 4/2) clay organic matter coatings on ped faces; very few roots between ped faces; distinct wavy boundary;
- 2C 56cm + greyish brown (2.5y 5/2); stony sandy loam; common medium distinct strong brown (7.5yr 5/8); massive; friable; abundant unweathered subrounded greywacke stones; very few fine roots;

on greywacke alluvium.

Appendix 3.5 Effects of selected herbicides on growth and development of gorse seedlings

A. Introduction

It was necessary to investigate weed control options for use on the Springston field trial (Chapter 3) after the establishment of gorse seedlings. Consequently a number of small trials were conducted to test the safety of various chemicals for use with the young gorse seedlings which had been transplanted onto the trial site in the autumn of 1989. The herbicide trials were done during the winter of 1989, to enable herbicide treatment of the trial site in early spring.

B. Experimental

B.1 Plant Culture

Growth medium composition:

bark	800 litres
fine sand	200 litres
Osmocote plus (8-9 month, N:P:K = 16:3.5:10)	500 g
dolomite	6000 g

547 g equivalent dry weight of moist potting mix (water content = 49.0%) was packed into 1.4 litre plastic pots to a volume of 1230 cm³.

Seedlings

Seedlings in the size range 10-15 cm tall were chosen from those left over from the field trial. Sufficient seedlings with single stems were chosen for each trial on the basis of uniformity of height. The seedlings were then ranked in order of size and were allocated to pots in such a way as to minimise the difference in mean seedling size between treatments. Details of seedling culture are given in Chapter 3. Seedlings were planted in the pots, complete with their perlite vermiculite growth medium, but the paper pots were removed.

The seedlings which had previously been located outdoors were placed in a glasshouse where mean maximum/minimum temperatures were 22/16°C. The photoperiod was extended to 16 hours using 400 watt mercury vapour lamps. Within a few days of being placed in the glasshouse, growth of new shoots began.

Watering

The pots were free draining, and were watered daily with tap water according to need.

B.2 Herbicides

Application

Liquid herbicides were applied to the pots using a conveyer belt with a spray nozzle mounted above it, owned by M.A.F., Lincoln. The spray was passed through a 800ZE nozzle at a pressure of 210 kPa. Belt speed was 1 metre per second. These settings gave a rate of application equivalent to 200 litres per hectare. This application mechanism enabled equivalent field rates to be accurately applied to the pots. Granular herbicides were applied by weight, based on the surface area of the pots. The granules were spread uniformly over the surfaces of the pots.

Chemicals tested

Details of the herbicides tested and rates applied are listed in Table 1.

B.3 Measurement of treatment effects

Effects of herbicide treatment on growth were estimated by measuring shoot elongation and plant weight. One terminal and one side shoot were tagged on each plant. These were measured at the time of herbicide application and again after approximately 2 and 4 weeks. At the end of each trial plants were cut at soil surface level and tops were dried to constant weight at 70°C and weighed.

Table 1 Details of herbicides tested for use on field trial

Commercial name	Application rate		Groups of plants controlled	Absorption; activity
	litres ha ⁻¹ †	kg AI ha ⁻¹ ‡		
Alloxol S	10.0	2.0	grasses	green tissue
Fusilade	6.0	1.5	grasses	
Gallant	15.0	1.5	grasses	
Simazine	6.0	3.0	grasses, broadleaf weeds	roots of germinating seedlings; prevents photosynthesis
Atrazine	20.0	10.0	broadleaf weeds, grasses	leaves and roots; prevents photosynthesis
Versatill	1.4	0.42	clover, broadleaf weeds	leaves, stem, roots; interferes with cell elongation
Tramat	15.0	3.0	grass, clover, broadleaf weeds	shoots and roots
	kg ha ⁻¹ †			
Classic (Liquid)	0.18	0.045	clover, broadleaf weeds	foliage and roots; inhibits cell division and growth
Velpar (granules)	5.0	1.0	grasses, broadleaf weeds	mainly roots; inhibits photosynthesis
Casoron (granules)	100.0	6.75	grass, broadleaf weeds	mainly roots; acts on growing points and root tips
Prefix (granules)	100.0	7.5	grass, broadleaf weeds	mainly roots; inhibits germination, acts on growing points and root tips

† litres or kg per hectare of product ‡ AI = active ingredient

C. Herbicide trial 1

The herbicides Alloxol S, Fusilade, Gallant, Gallant + Simazine, Gallant + Atrazine and Versatill were applied to three pots (replicates) each. The first 3 herbicides are grass killers. Simazine and atrazine were included to broaden the range of weeds which would be controlled and Versatill was included because of its ability to control clovers and broadleaf weeds. Twelve days after transplanting, spray treatments were applied at the rates shown in Table 1.

Data from this trial are shown in Table 2.

Table 2 Results from herbicide trial 1

Treatment	Mean total shoot weight at 70 days (g per pot)	Mean shoot elongation (mm)	
		0-14 days	14-30 days
Control	28.9 a	89 ab	113 a
Alloxol S	25.3 ab	95 a	91 ab
Fusilade	22.9 b	75 b	86 b
Gallant	26.1 ab	73 b	95 ab
Gallant + Simazine	18.7 c	83 ab	100 ab
Gallant + Atrazine	2.24 e	31 c	-8 c
Versatill	7.97 d	39 c	0 c

Note:

- 1) Times in days are times from herbicide application.
- 2) Values within columns followed by different letters differ at the 5% level of significance according to Fisher's least significant difference (LSD).
- 3) The negative shoot elongation for Gallant + Atrazine over the 14 - 30 day period was caused the wilting of growing tips.

At day 70 after herbicide application the Gallant and Alloxol S treated plants were not significantly smaller (in terms of shoot dry weight) than the controls but plants in all other treatments were (Table 2). From 0 to 14 days shoot elongation in all treatments except for

Alloxol S and Gallant + Simazine was less than that in the control treatment (Table 2). From day 14 to day 30 shoot elongation of all treatments except Alloxol S, Gallant and Gallant + Simazine was less than that in the control treatment (Table 2).

D. Herbicide trial 2

The second trial focused on herbicides with potential for controlling clover and broadleaf weeds. The herbicides used were in two categories: those that can be sprayed onto some legumes without serious damage, namely Trammat (used to control white clover in "Grasslands" Maku lotus seed crops) and Classic (used to control clovers and broadleaf weeds in lucerne); and those that are applied to the ground in granule form, and do not come in contact with the foliage, namely Velpar, Prefix and Casoron. Rates applied are shown in Table 1. These herbicides were applied to 2 separate groups of plants. One group had been transplanted into pots and brought into the glasshouse 32 days before application (Trial 2a). A second group were transplanted and placed in the glasshouse the day before application (Trial 2b). The former group had new shoots which were typically >20cm in length, whereas the latter group were just beginning to produce new shoots at the time of application.

The results of these two trials are shown in Tables 3 and 4. In Trial 2a, the number of replicates varied with treatment and these are shown in Table 3. In Trial 2b there were 2 replicates per treatment.

In the trial with large seedlings (Table 3), Velpar was the only herbicide treatment which did not significantly decrease shoot weight, but several treatments (Tramat, Velpar, Prefix and Casoron) did not significantly decrease shoot elongation. In the trial with small seedlings and newly emerging shoots (Table 4) Trammat and Classic were the only two herbicide treatments which did not result in significantly decreased shoot weight and Trammat was the only treatment showing no decrease in shoot elongation.

Table 3 Results from herbicide trial 2a

Treatment (no. of pots)	Mean total shoot weight at 43 days (g per pot)	Mean shoot elongation (mm)	
		0-15 days	15-29 days
Control(4)	35.17	90	53
Tramat (3)	28.50 s	77 ns	48 ns
Classic (3)	25.23 s	20 s	18 s
Velpar (2)	32.66 ns	102 ns	53 ns
Prefix (2)	26.12 s	67 ns	32 ns
Casoron (2)	24.06 s	79 ns	37 ns

Note:

- 1) Times in days are times from herbicide application.
- 2) s and ns indicate whether a particular mean differs significantly (s) from the control, or whether the difference is not statistically significant (ns) (LSD $p < 0.05$).

Table 4 Results from herbicide trial 2b

Treatment	Mean total shoot weight at 43 days (g per pot)	Mean shoot elongation (mm)	
		0-15 days	15-29 days
Control	19.14a	107 a	93 a
Tramat	16.64ab	112 a	66 ab
Classic	16.32ab	39 c	39 b
Velpar	10.03c	86 ab	57 b
Prefix	14.16bc	56 bc	46 b
Casoron	10.21c	63 bc	44 b

See notes 1) and 2) for Table 2.

E. Field test - Versatill

A very small field test was done after the results of Herbicide trial 1 was known. Versatill had severely affected gorse growth if sprayed onto the foliage. However there was a possibility of applying this herbicide using a wick applicator, thus avoiding contact with gorse foliage. This trial was done to determine if there would be any adverse effects on gorse growth via root uptake.

Two 1.33 m long plots (each containing 8 plants) were marked out in the double row of gorse plants along the northern border of the Springston trial site. Herbicide solutions were made up as follows:

Versatill - 1:3 (chemical:water)

Roundup - 1:2 (chemical:water)

Versatill was applied alone and in 50:50 combination with Roundup. The addition of Roundup would broaden the range of weed species controlled. The chemicals were applied using a wick applicator. The wick was wiped over the weeds present until there was moisture visible on the leaves. Care was taken not to touch the gorse plants. Within each treated area 2 shoots (1 terminal and 1 side shoot) were tagged on each of 4 plants. Four control plants were also tagged. Shoot elongation was measured at about monthly intervals during the whole 1989/1990 growth season. Most active growth occurred during the first 2 months following herbicide application, so shoot elongation for this period is presented in Table 5.

Table 5 Results from Versatill wick application test

Treatment	Mean shoot length at 71 days (mm) (n=8)	Standard error of mean
Control	95	36
Versatill	22	30
Versatill + Roundup	32	50

Note: Time in days is the time from herbicide application.

It appeared that both versatill and versatill + roundup were taken up by the gorse roots in sufficient quantities to severely reduce shoot elongation. Thickening of shoots was also

observed (Table 6).

F. Visual symptoms of herbicide treatment on gorse

Visual symptoms observed in both glasshouse trials, and the field test are shown in Table 6.

Table 6 Visual symptoms following herbicide treatment

<u>Herbicide</u>	<u>Symptom(s)</u>
Alloxol S	None
Fusilade	Some browning of prickles on new growth (2 plants only)
Gallant	Small areas of dead tissue near the tips of broad leaves near the base of several plants. Noted 2 weeks from spraying. No further symptoms with time. No apparent effect on growth.
Gallant + Simazine	As for gallant above
Gallant + Atrazine	As for gallant, above but also discolouration and wilting of growing tips. Eventually many plants died.
Versatill - glasshouse	New stems and growth tips pale, new stems distorted-wavey, thickened and stiff compared with control. Some shoots eventually died.
Versatill - field	Yellowing and thickening of shoots. Death of some shoots.
Tramat	Death of leaf tips and distortion of growing tips (both older and younger shoots).
Classic	Stunting and thickening of growth tips and stems
Velpar	Killed some plants in the group with smaller new shoots (group with older shoots o.k.)
Prefix	Yellowing, starting at growth tips and progressing down the shoots.
Casoron	Same as for Prefix, but more severe.

The only herbicide treatments which did not show significant visual symptoms of damage were Alloxol S, Fusilade, Gallant and Gallant + Simazine.

G. Choice of herbicide for use on the Springston field trial

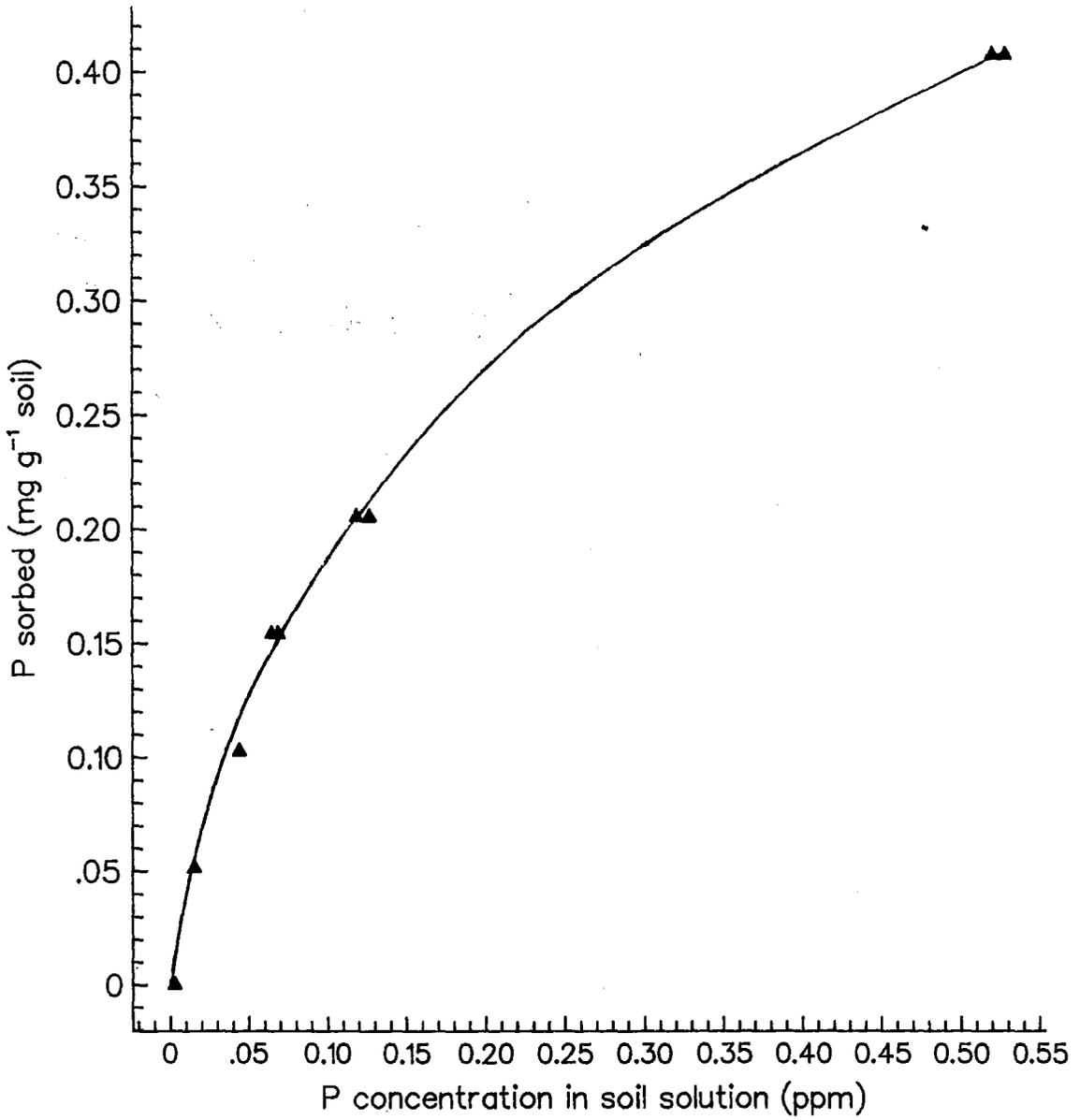
Based on the yield and shoot elongation data (Tables 2, 3, 4 and 5) and the visual symptoms of damage (Table 6), the only two herbicides suitable for use on the Springston field trial (Chapter 3) appeared to be the grass killers Alloxol S and Gallant because they no had significant effect on gorse growth and showed only minor or no visual symptoms of damage to gorse shoots. Gallant was chosen from these two herbicides because of advice received suggesting that it would give best control of the range of grass species present at the trial site. Further, a disadvantage with Alloxol S was that it was no longer being manufactured, so that if it was used and a repeat application to was needed, it may have been necessary to switch to a different herbicide for the second application.

Because of their effects on gorse growth and the visual symptoms of shoot damage observed, none of the herbicides suitable for controlling clovers and broadleaf weeds were considered to be safe for use on the field trial (Tables 1 - 6).

Appendix 3.6 Monthly Rainfall - Springston Trial

Month	Rainfall (mm)		
	Year		
	1989	1990	1991
January		22.4	80.5
February		27.5	78.4
March		52.7	1.6
April	46.4	25.9	100.2
May	113.3	54.4	43.3
June	53.3	39.7	82.9
July	52.2	30.7	
August	63.0	103.3	
September	32.8	20.3	
October	103.9	25.1	
November	21.4	59.1	
December	80.6	18.7	

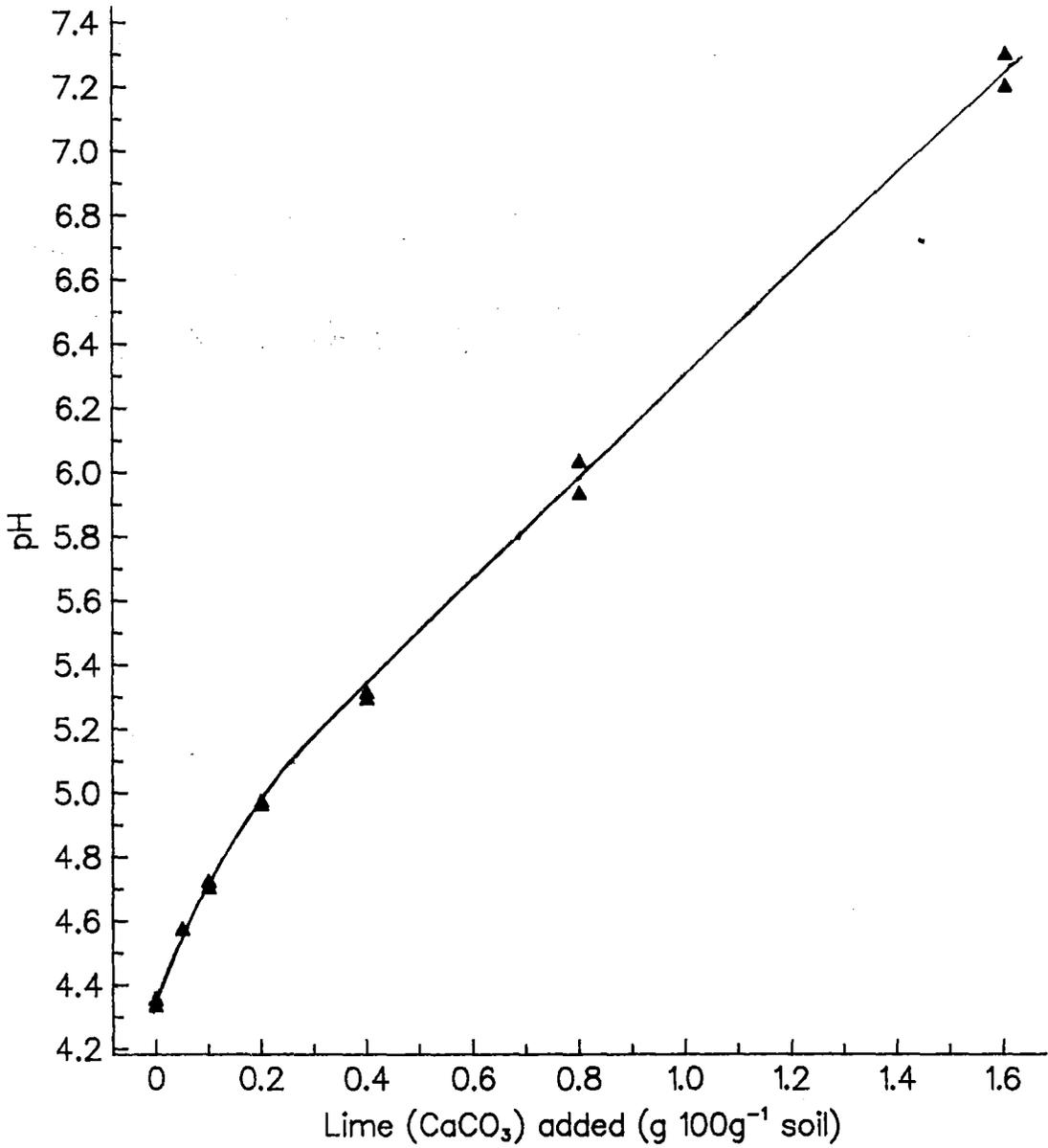
Appendix 4.1

P sorption isotherm for the E horizon from a Katrine soil
- lime/P experiment

Appendix 4.2

Lime/pH curve for the E horizon from a Katrine soil

- lime/P experiment



Appendix 5.1 Composition of zero N nutrient solution - rates of nitrate experiment

Compound & stock solution concentration	Amount of stock solution per litre of nutrient solution (ml)
Macroelements	
KH_2PO_4 (1 mol l ⁻¹)	1.25
K_2SO_4 (1 mol l ⁻¹)	4.0
MgSO_4 (1 mol l ⁻¹)	1.0
CaCl_2 (1 mol l ⁻¹)	2.5
Microelements	
$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (1.10g l ⁻¹)	1.0
$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ (0.393g l ⁻¹)	1.0
H_3BO_3 (2.86g l ⁻¹)	1.0
$\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$ (2.03g l ⁻¹)	1.0
$\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$ (0.126g l ⁻¹)	1.0
$\text{CoSO}_4 \cdot 7\text{H}_2\text{O}$ (0.0477g l ⁻¹)	1.0
EDTA - ferric monosodium salt (19.7g l ⁻¹)	1.0

Note: Micronutrients apart from Fe were combined into one stock solution.

Appendix 6.1 Estimation of gorse growth using cut 0.1 m² circles and bush size measurements

A. Introduction

As part of the North Westland field work (Chapter 6) it was desired to develop a relatively quick and reliable method of estimating gorse growth, rather than having to destructively harvest whole bushes. Correlations of dry matter yield with bush size measurements and the possibility of using the 0.1 m² circle shoot weights combined with bush size measurements to estimate annual dry matter yield were examined. The methods for making the 0.1 m² circle and bush size measurements are described in Section 6.2.4.

B. Results and discussion

Correlations of new shoot dry weight with estimated bush age and individual bush size and 0.1 m² circle (circle) measurements are presented in Table 1. In both growth seasons new shoot dry weight was correlated most highly with mean bush diameter, followed by circle dry weight.

Table 1 Correlations of total new shoot dry weight with bush size and 0.1m² circle (circle) measurements

Variable	Correlation (r) with new shoot dry weight	
	1989 (n=41)	1990 (n=30)
Age	-0.158	0.366
Total height	-0.079	0.475
Mean diameter	0.727	0.666
Circle dry weight	0.508	0.604
Shoot number in circle	0.181	0.236
Mean shoot length in circle	0.348	0.233
Total shoot length in circle	0.386	0.415
Maximum shoot length in circle	0.217	0.551

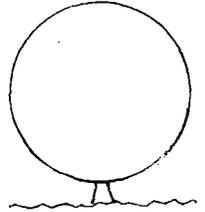
An attempt was made to combine circle dry weight with other measurements, for example

bush surface area and volume based on bush dimensions. In some cases log transformations increased the correlation coefficients. Correlation coefficients were calculated for individual years and for the 1988/89 and 1989/90 data combined. Bush shapes A,B and C were chosen to approximate the shapes of bushes at the study sites. Surface areas and volumes for the three shapes were calculated as follows:

Shape A) Sphere based on mean bush diameter (d)

$$\text{Spherical surface area of bush (s.a.A)} = 4\pi(d/2)^2$$

$$\text{Spherical volume of bush (vol.A)} = 4/3\pi(d/2)^3$$



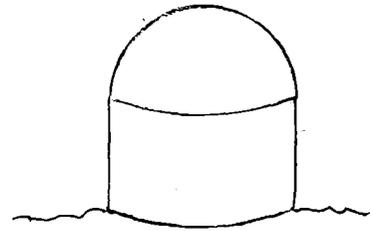
Shape B) Hemisphere on top of cylinder, based on mean bush diameter (d) and bush height (h).

$$\text{Surface area of hemisphere on cylinder (s.a.B)}$$

$$= (s.a.A)/2 + (\pi d(h-d/2))$$

$$\text{Volume of hemisphere on cylinder (vol.B)}$$

$$= (\text{vol.A})/2 + (\pi(d/2)^2 \times (h-d/2))$$



Shape C) Inverted cone with hemisphere on top, based on mean bush diameter (d), bush height (h) and slant height of cone (l).

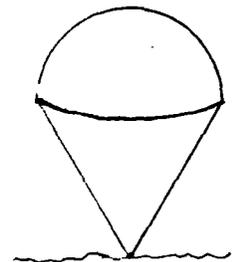
$$\text{Surface area of hemisphere on cone (s.a.C)}$$

$$= (s.a.A)/2 + (\pi(d/2)l)$$

$$\text{Volume of hemisphere on cone (vol.C)}$$

$$= (\text{vol.A})/2 + (1/3\pi(d/2)^2 (h-d/2))$$

$$(l^2 = (h-d/2)^2 + (d/2)^2)$$



Correlations between new shoot dry weight and circle dry weight multiplied by bush surface area or volume (assuming 3 different bush shapes as above) are presented in Table 2. Correlations were almost always best if both sets of variables were untransformed or both log-transformed, so the correlations shown are from sets of data treated in these two ways.

Table 2 Correlations of total new shoot dry weight with estimates of new shoot dry weight based on circle dry weight \times bush surface area or volume

Estimate of dry weight	Correlation coefficient (r) of estimated dry weight with total new shoot dry weight		
	1989 (n=41)	1990 (n=30)	1989 & 1990 (n=71)
Circle d.wt. \times s.a.A (1)	0.884	0.817	0.851
(2)	0.864	0.917	0.903
Circle d.wt. \times vol.A (1)	0.873	0.709	0.775
(2)	0.861	0.901	0.888
Circle d.wt. \times s.a.B (1)	0.775	0.892	0.818
(2)	0.750	0.911	0.863
Circle d.wt. \times vol.B (1)	0.883	0.891	0.837
(2)	0.830	0.933	0.895
Circle d.wt. \times s.a.C (1)	0.855	0.874	0.855
(2)	0.835	0.922	0.896
Circle d.wt. \times vol.C (1)	0.867	0.817	0.824
(2)	0.860	0.926	0.901

(1) indicates both variables untransformed.

(2) indicates both variables \log_{10} -transformed.

The combination of circle dry weight with bush surface area or volume estimates gave better correlations with new shoot dry weight than circle dry weight or individual bush dimensions alone (Tables 1 and 2).

For the 1989 and 1990 data combined, circle dry weight multiplied by bush surface area, assuming a spherical bush shape (shape A), was most highly correlated with annual growth (new shoot dry weight), when both sets of variables were log-transformed (Table 2).

Other shapes gave similarly high correlations, but because the correlation involving spherical surface area was greatest and this was also the simplest shape, this was chosen for further discussion.

The relationship between new shoot dry weight and new shoot dry weight estimated by circle dry weight \times spherical surface area (s.a.A) is as follows, where E = estimated new shoot dry weight:

$$\log_{10} (\text{new shoot dry weight (g)}) = 0.682 \log_{10} E + 0.269 \quad r = 0.903$$

(E = circle dry weight (g m⁻²) \times s.a.A (m²))

A scatter plot of the data is shown in Fig. A3 which confirms that there is a good linear relationship between \log_{10} (new shoot weight) and \log_{10} (estimated new shoot weight). For the purpose of estimating gorse growth in the field, it would be more useful to use circle fresh weight than circle dry weight. The equivalent relationship using circle fresh weight was as follows:

$$\log_{10} (\text{new shoot fresh weight}) = 0.068 \log_{10} E + 0.707 \quad r = 0.893$$

C. Conclusions

In the areas of gorse covered by this study, dry matter production from the previous growth season could have been estimated from measurement of bush diameter and the weight of new shoots from within a 0.1m² circle on the tops of bushes. A sample of shoots would need to be taken for calculation of dry matter percentage, in order to calculate total dry weight. It would not be necessary to do this for each bush because dry matter percentage was reasonably uniform between bushes.

The relationships discussed here did cover a range of edaphic conditions and bush shapes (these tended to vary both between and within soil series). However they only covered quite a narrow range of bush age. If the procedure described is to be used to estimate gorse growth, it should be tested further, particularly for bushes of differing age.

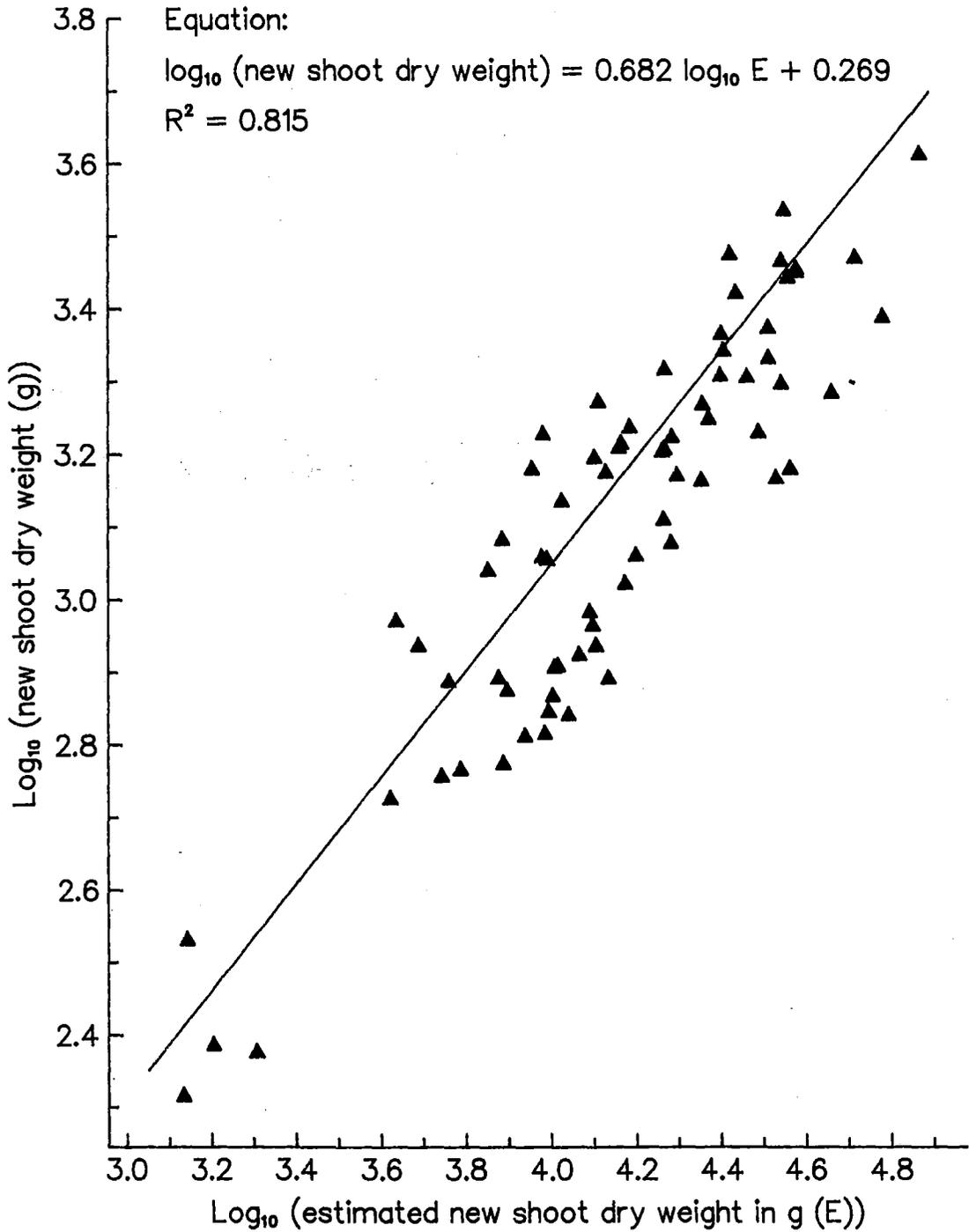


Fig. A3 Scatter plot of $\log_{10}(\text{new shoot dry weight})$ vs $\log_{10}(\text{estimated dry weight})$. Estimated dry weight (E) = circle dry weight (g) \times spherical surface area of bush (m^2).