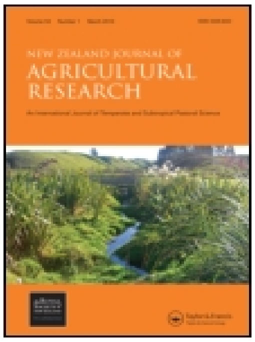

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Variation in partitioning and percentage nitrogen and phosphorus content of the leaf, stolon, and root of white clover genotypes

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Abstract As part of a programme to breed a productive white clover (*Trifolium repens* L.) tolerant of low soil phosphorus (P) levels, 98 white clover and 2 *Lotus pedunculatus* Cav. genotypes were examined for partitioning of P, nitrogen (N), and dry matter within the plant, and for concentration of P and N within leaves, stolons, and roots. Genotypes were grown in pots with either 300 or 2000 mg P per kg soil. Differences among genotypes for % P content and partitioning of P within the plant did not result in differences in dry matter response to added P fertiliser between genotypes. Genotypes that allocate a high proportion of total P to shoots and have low shoot % P were large-leaved and had high herbage yields, but a low proportion of dry matter in stolons suggested that they would be non-persistent in grazed, low P swards. Genotypes collected from hill country swards had a high proportion of dry matter in stolons but were low yielding, had a high shoot % P and a low N/P ratio. There was sufficient variation among genotypes to suggest that selections of persistent plants that have a low harvest index, low shoot % P, and high N/P ratio may be successful.

Keywords white clover; phosphorus; plant nutrition; nitrogen; screening; genotypes; roots; stolons; shoots

INTRODUCTION

In New Zealand, white clover survival and yield are often limited by the low level of available phosphorus (P) in soils (Suckling 1976). With the increasing price of P fertilisers, attempts are being made to breed a white clover that can tolerate low soil P levels and still be productive.

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The success of such an objective is partly dependent upon finding white clover genotypes that differ in their P nutrition. They may differ in P uptake, translocation, utilisation, re-distribution, partitioning within the plant, or a combination of such factors. Ultimately it is hoped that such differences in P nutrition will result in improved clover tolerance and yield on P deficient soils. Because of this, initial pot trials compared the shoot dry matter yield at a high and a low soil P level of a range of white clover genotypes (Caradus & Dunlop 1978; Caradus et al. 1980). However, the variation in yield resulting from differences in P nutrition was small (i.e., there was no genotype × P interaction). Hence this study was undertaken to compare not only dry matter yield but also the partitioning of P within the shoots, stolons, and roots of white clover genotypes grown at 2 soil P levels.

It was thought that a plant able to tolerate grazing in low soil P conditions should have a low dry matter harvest index (i.e., the proportion of the plant that is eaten) and should thus be able to conserve P. Such a plant would probably have many stolons, short petioles, and a low shoot to root ratio. In a competitive grass sward, plants capable of rapidly absorbing P added as fertiliser, conserving or storing it in the roots or stolons, and later releasing it to the shoot when soil P availability is again low would have an advantage. Thus the aim was to examine many white clover genotypes for differences in partitioning of P and dry matter within the plant, and in concentration (percentage) of P. Since a major reason for incorporating clovers into pasture is their ability to fix nitrogen (N), the partitioning of N within the plant and the amount of N fixed per unit P absorbed were also determined.

Definition of terms

'Shoot' refers to all leaves, petioles, and unrooted stolons. 'Stolon' is the remaining, rooted, above-ground material. 'Root' is all below-ground plant material. 'Percentage' P and N always refers to the concentration of these elements in the plant material. 'Proportion' of P always refers to the amount of P in a certain plant part (shoot, stolon, or root) divided by the total amount of P.

Table 1 Origin, leaf size (measured at the end of the experimental period), and total dry weight (leaf, stolon, root) at final harvest of 98 white clover genotypes and 2 lotus genotypes. Each value is the mean of 2 phosphorus levels.

Genotype number	Origin	Leaflet width (mm)	Total dry weight (g)
1	Tihoi, West Taupo Road	8.7	1.48
2	Tokaroa Beach	7.3	4.09
3	Bethells Beach, Auckland	5.2	0.49
4	Bethells Beach, Auckland	6.5	1.94
5	Bethells Beach, Auckland	6.2	1.64
6	Kuratau, Lake Taupo	11.0	3.94
7	Desert Road (Turangi)	9.5	3.84
8	Tokaroa	10.3	4.11
9	Turangi Beach, Auckland	7.7	1.29
10	Bethells Beach, Auckland	5.8	1.67
11	Waiouru	14.3	5.22
12	Tokaroa	8.0	0.59
13	Vinegar Hill	12.3	3.08
14	Waiouru	11.0	4.18
15	Vinegar Hill	7.2	1.89
16	Bethells Beach, Auckland	5.7	2.27
17	Desert Road (Turangi)	8.0	2.11
18	Desert Road (Waiouru)	11.0	6.56
19	Desert Road (Waiouru)	13.5	8.23
20	Taupo–Tokaroa Highway	10.5	2.27
21	Origin unknown	17.3	25.77
22	'Kent wild white'	7.2	7.41
23	'Kent wild white'	8.3	7.69
24	'Kent wild white'	8.5	3.25
25	'Kent wild white'	6.2	3.58
26	'Kent wild white'	7.3	3.87
27	G18	18.8	19.34
28	G18	19.8	17.15
29	G18	19.0	18.12
30	G18	14.7	15.43
31	G18	17.3	14.77
32	G18	13.0	11.22
33	'Grasslands Huia'	14.0	16.11
34	'Grasslands Huia'	11.2	10.31
35	'Grasslands Huia'	12.8	10.05
36	'Grasslands Huia'	12.5	8.44
37	'Grasslands Huia'	12.5	9.91
38	'Grasslands Huia'	10.3	7.06
39	'S.100 Nomark'	12.3	9.69
40	'S.100 Nomark'	10.5	6.76
41	'S.100 Nomark'	10.0	4.69
42	'S.100 Nomark'	15.0	12.13
43	'S.100 Nomark'	9.7	6.49
44	'S.100 Nomark'	10.2	7.27
45	'Regal'	27.5	33.12
46	'Regal'	21.2	25.41
47	'Regal'	21.2	27.04
48	'Rega'l	21.3	22.12
49	'Regal'	19.8	25.14
50	'Regal'	18.7	22.81
51	Tahora[1]	6.3	2.62
52	Ararata	5.7	1.72
53	Mohoenui	9.2	2.36
54	Mangatainoka	7.2	2.37
55	Te Awa	5.8	1.19
56	Te Pohue	7.5	1.31
57	Kereru Station	8.5	1.24

Table 1 (continued)

Genotype number	Origin	Leaflet width (mm)	Total dry weight (g)
58	Para Para	5.3	1.58
59	Mangaweka	5.8	0.95
60	Kereru Station	9.7	1.72
61	Otangawai	5.3	1.30
62	Rewa	7.5	1.36
63	Antawa, Parianga	6.3	2.14
64	Ararato	6.7	1.24
65	Kereru Station	11.7	1.65
66	Matawai	7.8	1.33
67	Tarata	6.8	2.18
68	Isla Bank	7.0	2.13
69	Isla Bank	5.8	1.35
70	Tahora[1]	8.0	0.97
71	Kereru Station	9.7	2.03
72	Manweka	5.5	1.27
73	Rere	9.8	1.67
74	Te Awa	5.8	0.85
75	Ararato	7.3	4.06
76	Ngawapurua District	6.8	2.23
77	Te Hue Station	8.0	3.23
78	Isla Bank	8.8	3.84
79	Kereru Station	8.3	1.95
80	Aramatai	6.3	2.55
81	Te Hue Station	7.7	1.79
82	Te Awa	8.5	1.28
83	Rewa	7.0	1.45
84	Para Para	5.7	1.38
85	Ararata	6.7	2.48
86	Piopio	6.0	0.77
87	Te Awa	6.8	1.77
88	Te Awa	5.0	10.33
89	Rewa	7.3	1.61
90	Rewa	7.8	1.53
91	Rewa	7.2	1.54
92	Ngawapurua District	5.8	1.42
93	Tarata	5.7	0.50
94	Tarata	7.2	1.82
95	Te Hue Station	5.2	1.37
96	Te Awa	7.2	2.01
97	Rewa	7.7	1.87
98	Tahora[1]	5.3	0.46
99	Maku lotus	12.8	13.41
100	Maku lotus	12.2	10.37
	P	***	***
	$LSD_{0.05}$	1.6	-
	$LSR_{0.05}$	-	×1.9

[1] Place of origin, not a cultivar name.

MATERIALS AND METHODS

Ninety-eight genotypes of *Trifolium repens* L., covering the range of known morphological variation, and 2 genotypes of *Lotus pedunculatus* Cav. cv. Maku were examined. Their origins are given in Table 1. Genotypes 1–20 were collected from roadsides, genotypes 22–50 were from 5 cultivars, and genotypes 51–98 were part of an extensive collection of hill country white clovers made by Mr F. E. T. Suckling (Suckling & Forde 1978).

Plants were initially grown in pots of fertile potting mix until 12 stolon tips could be removed from plants of each genotype to form roots in a

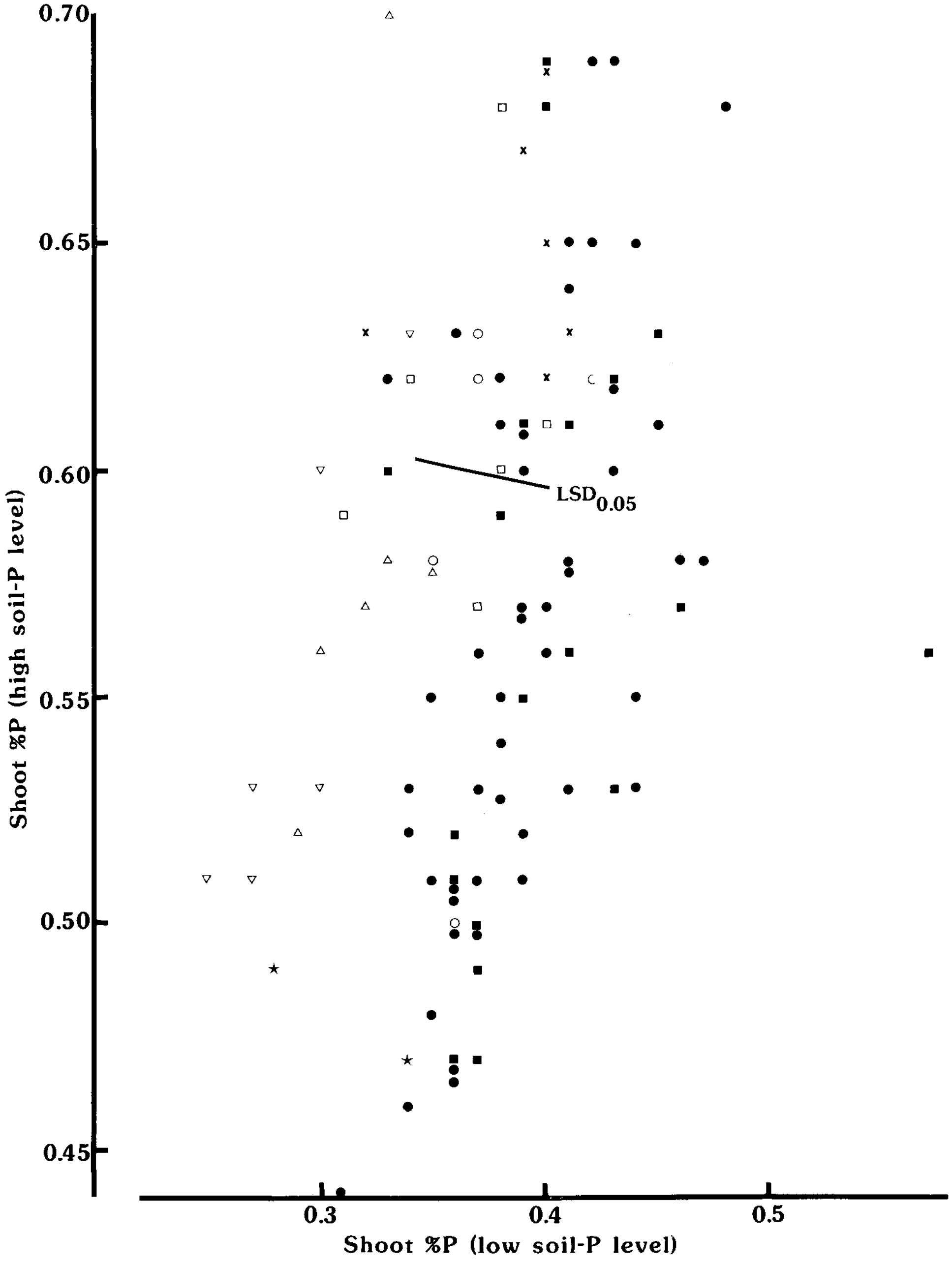


Fig. 1 Shoot % P content of genotypes grown at high P (2000 mg P per kg soil) and low P (300 mg P per kg soil). White clover genotypes collected from hill country swards are denoted by ●, from roadsides ■, from cultivars Kent wild white ○, S.100 Nomark □, Huia ×, G18 Δ, and Regal ∇, and from *Lotus pedunculatus* cv. Maku ★.

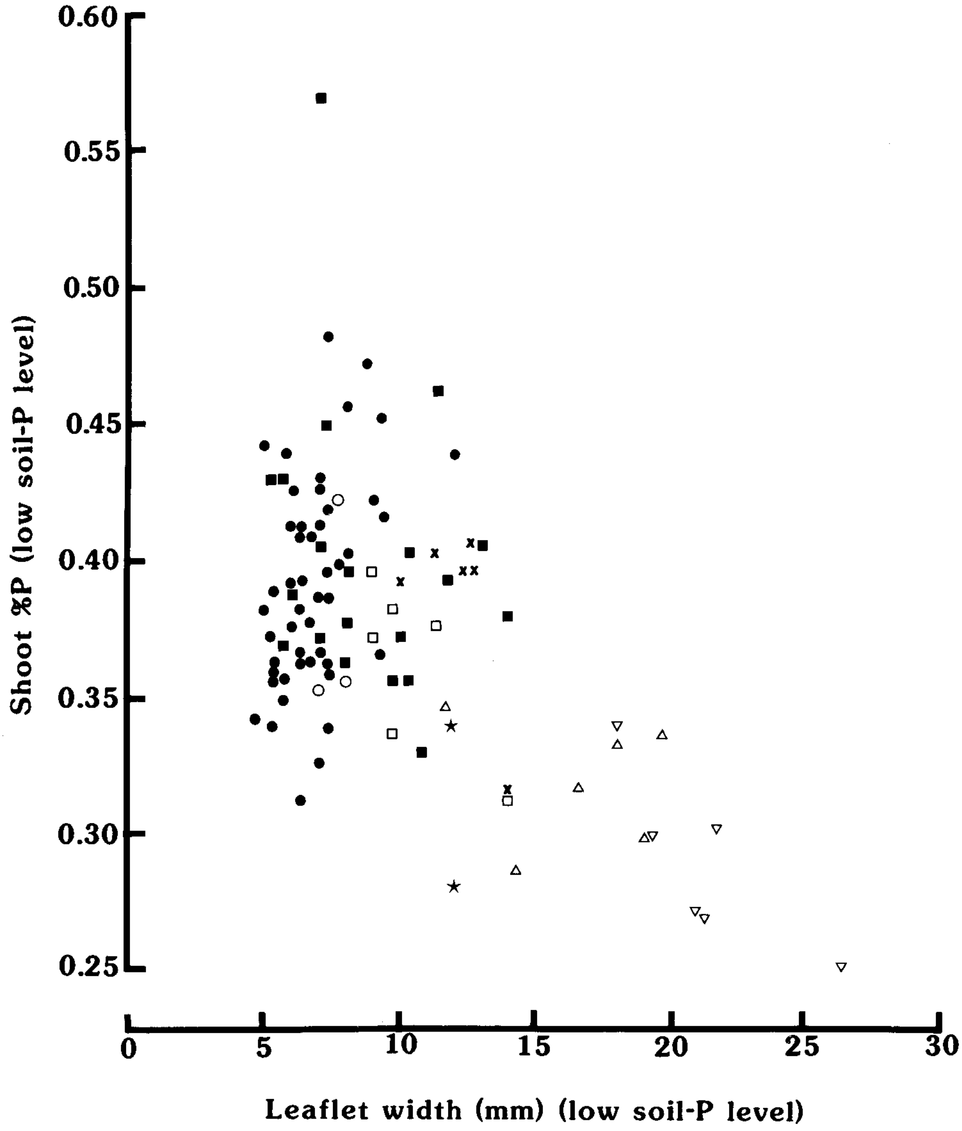


Fig. 2 Correlation of leaflet width *v*. shoot % P, at harvest 3, of genotypes grown at 300 mg P per kg soil ($r = -0.55$, $P<0.01$). For key to symbols see Fig. 1.

1 : 1 soil-sand mix (2 ppm Truog P). After 18 days (on 13 August 1979) 6 similar stolon tips per genotype were weighed fresh and planted individually into pots with a soil surface area of 530 cm^2 (23 × 23 cm) and a depth of 30 cm. The soil was a B horizon Egmont sandy loam, a free draining, low N, highly P retentive soil (New Zealand Soil Bureau 1968). Three weeks before stolon tips were transplanted, adequate amounts of all nutrients except N and P were mixed into the soil. Phosphorus as superphosphate (9% P) was mixed into the soil at rates of 300 mg P per kg soil (low P) and 2000 mg P per kg soil (high P). In a preliminary experiment it was found that the addition of more than 2000 mg P per kg soil did not give further increases in yield. Soil was not sterilised and no extra *Rhizobium* inoculum was added. Previous studies (Caradus et al. 1980) have shown

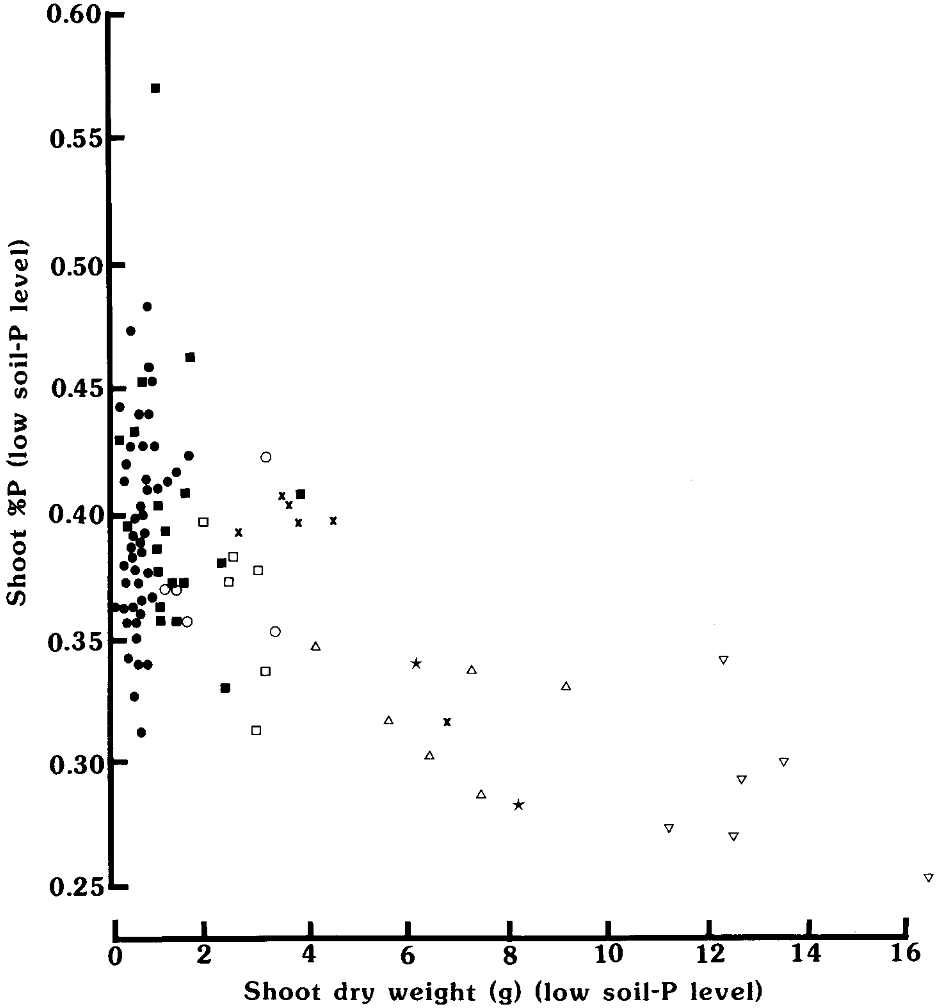


Fig. 3 Correlation of shoot dry weight *v.* shoot % P, at harvest 3, of genotypes grown at 300 mg P per kg soil ($r = -0.61$, $P < 0.01$). For key to symbols see Fig. 1.

that good nodulation of white clover occurs in this soil.

There were 3 replicates of each genotype at each P level (giving a total of 600 pots). Pots were completely randomised in high and low P pair, in a glasshouse. Pots were watered daily from the top. Shoots were harvested after 8, 12, and 16 weeks. At each shoot harvest, leaves, petioles, and unrooted stolons were removed, dried, and weighed. This shoot material was considered the part of the plant available to the grazing animal. At the final harvest (16 weeks), stolons and roots were harvested separately, dried, and weighed. Dried shoot, stolon, and root material from the final harvest was ground and analysed separately for total N and P content. As an indicator of plant type, leaflet width was measured before the final shoot harvest. One recently opened leaf was measured per plant. This technique is well documented (Ahlgren & Sprague 1940; Hawkins 1959; Caradus 1977, 1981).

Weekly maximum and minimum temperatures were recorded. Before the first shoot harvest they were 30 ± 1.1 °C and 7 ± 1.5 °C respectively; between the first and second harvests 30 ± 2.1 °C and 9 ± 1.5 °C; and between the second and final harvests 33 ± 1.3 °C and 12 ± 1.9 °C.

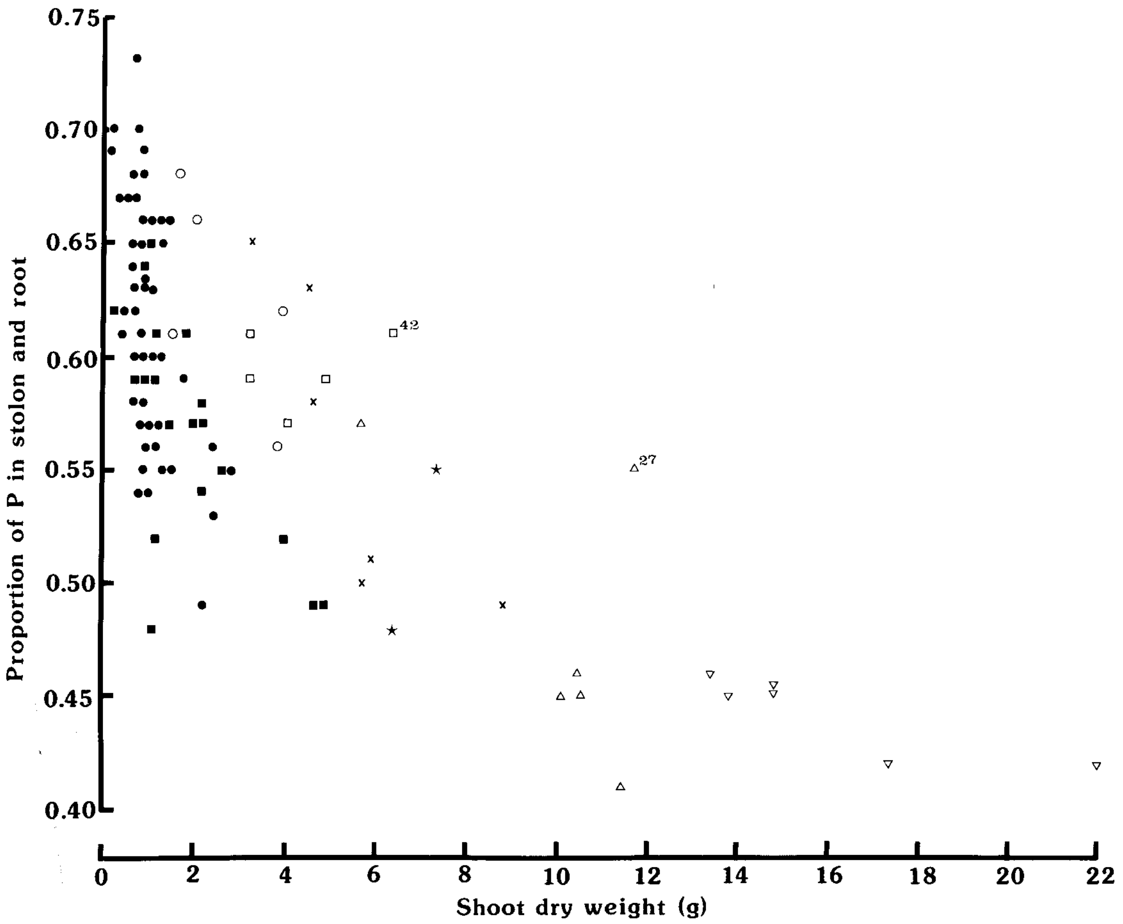


Fig. 4 Correlation of shoot dry weight at harvest 3, against proportion of P in stolons and roots of genotypes ($r = -0.75$, $P<0.01$). Values are means of 2 soil P levels. For key to symbols see Fig. 1.

RESULTS

Dry weight

There were large differences ($P<0.001$) among genotypes for shoot yields at each harvest, and for stolon and root weights at the final harvest. Total (shoot + stolon + root) dry weight at the final harvest (Table 1) varied among genotypes by 7200%. The genotypes with the highest dry weights were those with the largest leaf sizes ($r = +0.92$, $P<0.001$) — namely the cultivars Regal and G18.

There were no significant genotype × P interactions for any dry weight measurements.

Morphology

The leaf sizes of genotypes collected from hill country swards (genotypes 51–98) were generally smaller than those of the bred cultivars, S.100, Huia, G18, and Regal (Table 1). Roadside collections (genotypes 1–20) were more variable, but included some of the smallest leaved genotypes.

There were significant ($P<0.001$) differences among genotypes for proportion of dry matter in shoots, stolons, and roots; but genotype × P interactions were not significant. Large-leaved genotypes had a high proportion of shoot ($r = +0.71$, $P<0.01$) and a low proportion of stolon ($r = -0.74$, $P<0.01$) compared with small-leaved types. Proportion of root was unrelated to genotype leaf size ($r = -0.25$, NS).

Phosphorus content

There were significant ($P<0.001$) differences among genotypes, and significant ($P<0.001$) interactions between genotypes and P level for % P

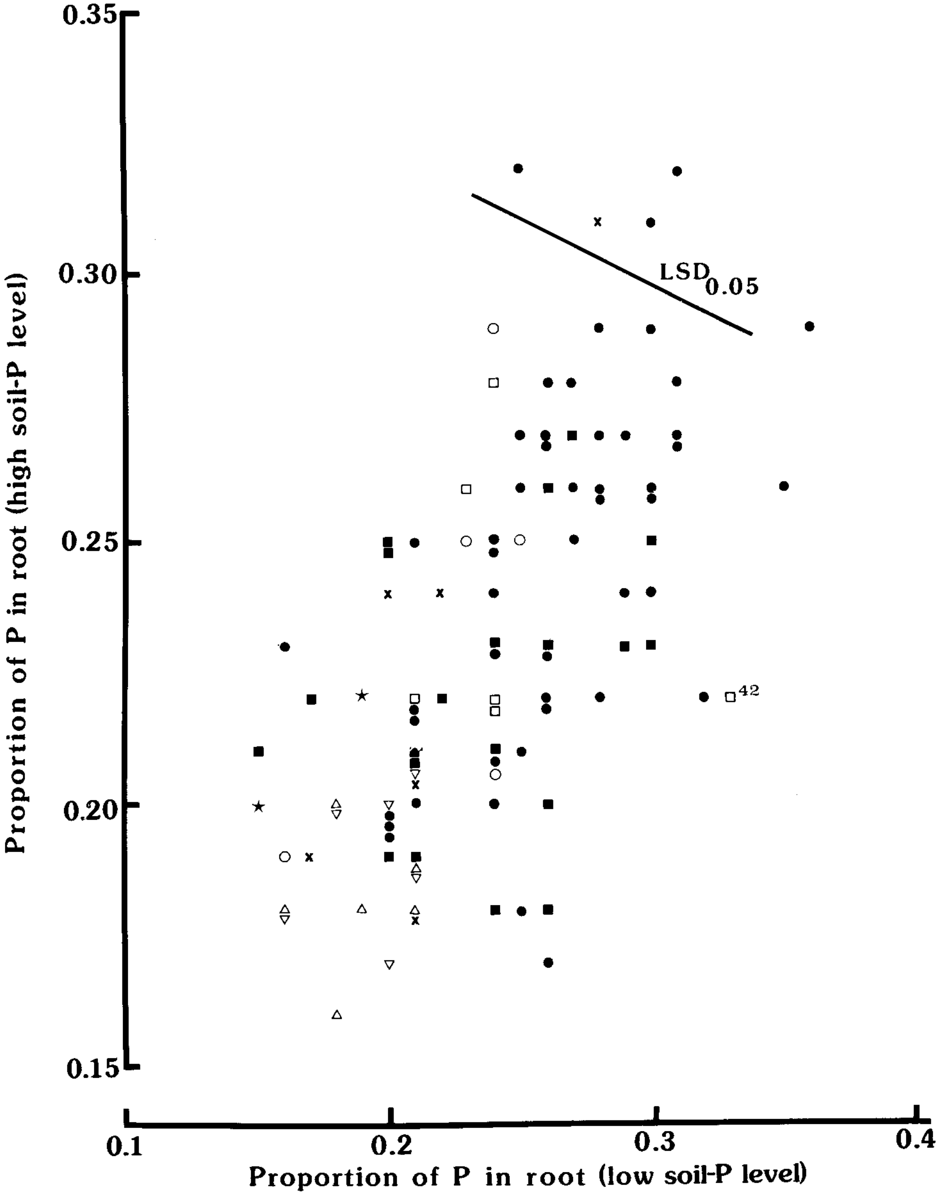
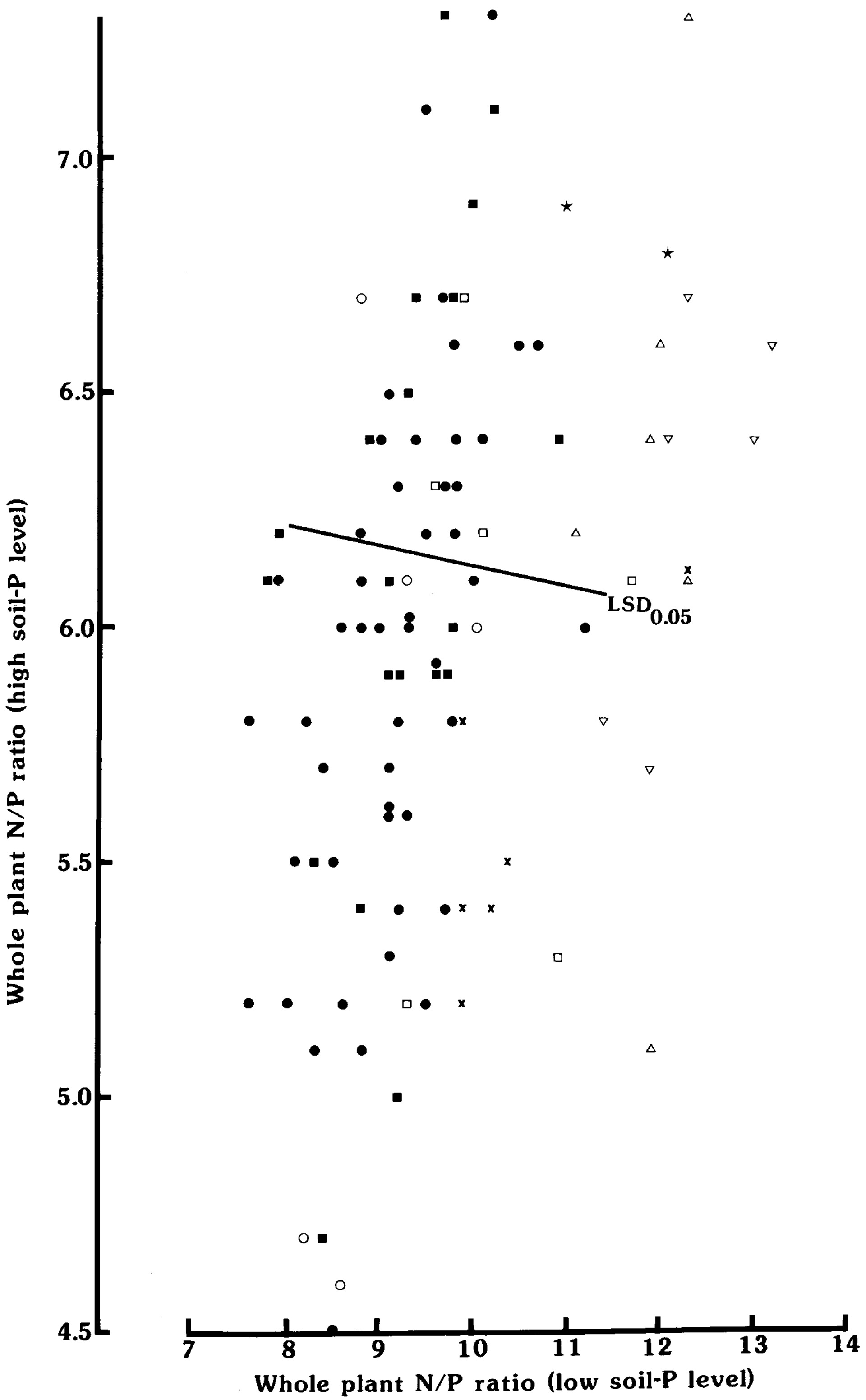


Fig. 5 Proportion of P in root of genotypes grown at high P (2000 mg P per kg soil) and low P (300 mg P per kg soil). Response to P can be measured by the perpendicular distance from the dashed line; populations furthest above the line are most responsive. For key to symbols see Fig. 1.

Fig. 6 *(opposite)* Whole plant nitrogen/phosphorus ratio of genotypes grown at high P (2000 mg P per kg soil) and low P (300 mg P per kg soil). For key to symbols see Fig. 1.


Whole plant N/P ratio (high soil-P level)
7.0
6.5
6.0
5.5
5.0
4.5
LSD0.05
7
8
9
10
11
12
13
14
Whole plant N/P ratio (low soil-P level)

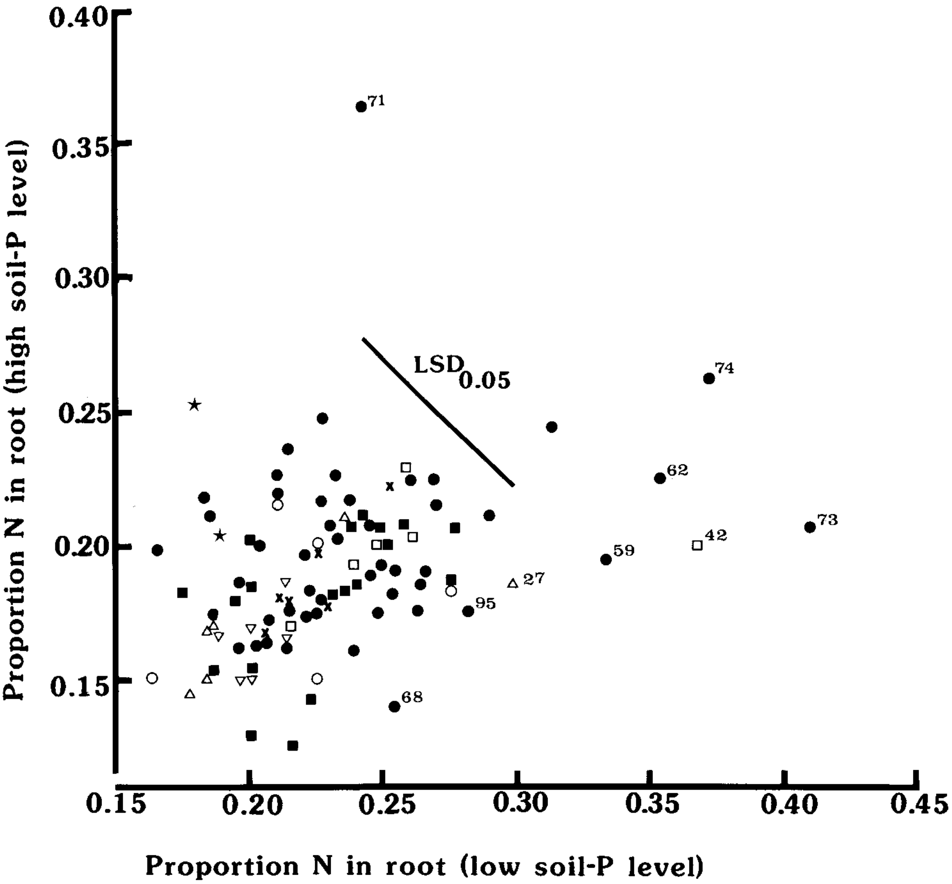


Fig. 7 Proportion of N in root of genotypes grown at high P (2000 mg P per kg soil) and low P (300 mg P per kg soil). For key to symbols see Fig. 1.

content of shoots (Fig. 1), stolons, and roots. Smaller leaved genotypes grown at low P had higher % P levels in shoots (Fig. 2), stolons, and roots than larger leaved genotypes (r = −0.55, −0.77, −0.61 respectively, $P<0.01$). However, when genotypes were grown at high P such correlations were not significant (r = +0.11, −0.20, −0.13 respectively, NS). Shoot % P of hill country genotypes and roadside-collected genotypes were less affected by changes in soil P level than genotypes of the 5 cultivars (Fig. 1). The same effect was observed for stolon % P and root % P.

Shoot % P was negatively correlated with shoot dry weight (e.g., for harvest 3, r = −0.61, $P<0.01$, for plants grown at low P). However, there was variation between genotypes with similar shoot dry weight for % P content of shoots (Fig. 3) — for high yielding genotypes (i.e., dry matter yields >12 g) there was a 34% increase in shoot % P between genotypes with lowest and highest % P contents; and for low yielding genotypes (i.e., dry matter yields <2 g) an 82% increase. It is conceivable that selections could be made of genotypes with similar shoot yields but very different % P contents.

There were significant ($P<0.001$) genotype differences for proportion of P partitioned for shoots and stolons, but there were no significant genotype × P interactions. Proportions of P in shoots, stolons, and roots were significantly correlated with respective proportions of dry matter (r = +0.78 +0.88, +0.71, $P<0.01$). However, this leaves 35–50% of variation unaccounted for, so it may be possible to select for high % P in stolons and roots of genotypes with a low dry matter harvest index. While many genotypes partitioning a high proportion of P below harvestable levels (i.e., in stolons and roots) were not only small-leaved but also low yielding ($r = -0.75$, $P<0.01$, for correlation between proportion of P below harvest level and shoot dry weight), there is still considerable unaccounted variation (approximately 50%) which may allow selection of genotypes with low P harvest index and high shoot yields (Fig. 4). However, only 2 genotypes (27 and 42) had shoot yields greater than 6 g and proportion of P in stolon and root greater than 0.5 — these genotypes were from the cultivars G18 and S.100 respectively.

For proportion of P partitioned to the root there were both significant ($P<0.001$) genotype differences and a significant ($P<0.01$) genotype × P interaction (Fig. 5). Proportion of P in the root was not related to leaf size of genotypes grown at either high P or low P ($r = -0.21$, -0.23 respectively, NS). Genotypes with the highest proportion of P in roots at both P levels were of hill country origin, and those with the lowest were predominantly from the 5 cultivars (Fig. 4). Genotypes with the greatest (towards the far right of the 45° line) or least (towards the far left of the 45° line) ability for increasing proportion of P in the root with a reduction in P supply were either of hill country or roadside origin (Fig. 5). There was, however, also one other genotype (number 42) from the cultivar S.100 which also was able to increase the proportion of P in its root system with a reduction in P supply.

Whole plant N/P ratio (i.e., an indication of the amount of N fixed per unit of P absorbed) differed significantly ($P<0.001$) among genotypes; there was also a significant ($P<0.001$) genotype ×P interaction (Fig. 6). For plants grown at low P, genotypes with larger leaves had a high N/P ratio than smaller leaved genotypes ($r = +0.68$, $P<0.01$); at high P this correlation was not significant ($r = +0.22$, NS). The N/P ratios of hill country genotypes were not reduced as much as those of the large-leaved genotypes with a reduction in P supply.

Nitrogen content

There were differences ($P<0.001$) among genotypes for % N content of shoots, stolons, and roots but there were no significant genotype × P interactions. Genotypes with large leaf sizes generally had the lowest % N shoot and stolon contents compared with small-leaved genotypes ($r = -0.37$, -0.75 respectively, $P<0.01$).

There were significant differences ($P<0.001$) between genotypes for proportion of N in shoots and stolons but again no significant genotype × P interactions. As with proportion of P in these components, significant correlations between leaf size and proportion of N in shoots and stolons ($r = +0.72$, -0.78 respectively, $P<0.01$) were mainly a result of high correlations between leaf size and proportion of dry matter partitioned to shoots and stolons.

Genotypes differed significantly ($P<0.001$) in proportion of N in roots and there was also a significant ($P<0.05$) genotype × P interaction (Fig. 7). Some genotypes, mostly of hill country origin (27, 42, 59, 62, 68, 73, 74, 95) were able to increase the proportion of N in their roots by more than 50% with a reduction in P supply. Genotype 71, also of hill country origin, reduced the proportion of N in its roots by 33% with a reduction in P supply. There were no significant correlations between leaf size and proportion of N in roots under either high P or low P conditions ($r = -0.23$, -0.20 respectively, NS).

DISCUSSION

Differences were found among genotypes for % P content and partitioning of P within the plant, but these did not result in differences in dry matter response to P between genotypes. However, exploitation of variation in % P content and in partitioning of P may be beneficial. Gregg (1979) has shown that there are long periods of the year when pasture P levels on developed hill country are well in excess of plant and animal requirements. He believes that this is an inefficient situation, since where levels of P in herbage are high a large proportion will be returned in dung, often away from the main grazing area. A reduction in either the % P content of pasture or the proportion of P in the grazeable part of the plant may reduce this inefficiency.

Percent P content

Variation in % P content was large and there was also a tendency for more productive genotypes to have lower shoot P contents (Fig. 3). A negative relationship between shoot % P content and dry weight has been observed in other species, e.g., lucerne (Heinrichs et al. 1969) and *Phalaris arundinacea* (Hovin et al. 1978). Unfortunately white clover genotypes with low shoot % P levels and high herbage yields in pots are typical of those that do not persist in hill country pastures (Williams & Caradus 1979). A major reason for this is that they have a low proportion of stolon from which to regrow after grazing. Among the genotypes adapted to hill country conditions there was, however, sufficient variation for selections to be made for reduced shoot % P levels (Fig. 2 and 3).

P partitioning

Although there was considerable variation in the partitioning of P below grazing level, genotypes that partitioned a large proportion of their P into stolons and roots were generally low yielding (Fig. 4). This may be an intractable relationship against which to select.

Few comparisons have been made within species for partitioning of P between shoots and roots in relation to tolerance to low P soils. For beans and tomatoes, Gabelman (1976) found that strains able to use N, P, and K efficiently, contained a larger amount of the limiting element in the roots and less in the leaves. In so-called inefficient strains there was a high level of mobility of these elements, possibly to a point where normal metabolic function was restricted. Other accounts of P partitioning between roots and shoots involve interspecific comparisons (Specht & Groves 1966; Rorison 1968; Biddiscombe et al. 1969; Keay et al. 1970; Barrow 1975; Temple-Smith & Menary 1977; Safaya et al. 1979; Caradus 1980), and all but one show the reverse to the results of Gabelman (1976). The exception is *Scabiosa columbaria*, which has the ability to absorb P in excess of immediate requirements, resulting in high % P levels in its roots (Rorison 1968). In its natural habitat which is basically poor in available P, seasonal flushes of this mineral are known to occur. Accumulation of P at flush times may be adequate to ensure steady growth throughout the year. These seasonal flushes could be likened to fertiliser topdressing of white clover. Although selection for a low proportion of P in grazeable parts of the plant appears to be incompatible with high yields, such selections may improve long-term persistence.

Nitrogen/phosphorus ratio

Genotypes with a low dry matter harvest index had the lowest amount of N fixed per unit of P absorbed ($r = +0.56$, $P<0.01$, for correlation of proportion of dry matter in shoot *v.* N/P ratio of the whole plant meaned over both P levels). While a low harvest index may allow a genotype to survive in grazed, low P swards, such genotypes may require a greater P uptake to fix a unit of N than genotypes with higher harvest indices. Selections for a low harvest index, to ensure persistence, may have to simultaneously consider the ability of genotypes to fix N per unit of P absorbed.

CONCLUSIONS

Selection for a low dry matter and P harvest index may result in low yielding but persistent plants in grazed, P deficient swards. Selections for low shoot % P and a high N/P ratio may result in high yielding but non-persistent plants. It may be difficult to circumvent these relationships by breeding but sufficient variation was found among the genotypes studied to provide some encouragement. The screening of larger numbers of genotypes and the use of multi-character selection techniques may be required to ensure persistent plants with reasonable grazeable yields that conserve P below grazing height and yet produce high levels of N per unit of P absorbed.

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