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THE EFFECTS OF PLANT DENSITY, SPECIES PROPORTION AND POTASSIUM–PHOSPHORUS FERTILIZATION ON INTERFERENCE BETWEEN *TRIFOLIUM INCARNATUM* AND *LOLIUM MULTIFLORUM* WITH LIMITED NITROGEN SUPPLY

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SUMMARY

(1) Growth and reproductive performance of mixtures of the annual species *Trifolium incarnatum* and *Lolium multiflorum* were studied in experiments in which proportion of each species, overall plant density, and potassium and phosphorus supply were combined factorially in a replacement design. The plants were grown in pots.

(2) The proportion of the two species which results in the greatest total yield and the greatest increase in yield relative to the pure species yield (complementation) depends upon density and nutrition. The increase in relative yield in mixture was most pronounced at high density and low potassium and phosphorus supply.

(3) The log of the production of an average individual was a nearly linear function of the log of the density of each species for a given fertilizer supply, but the density of individuals of the same species was always more important than the density of the other species in accounting for average individual production.

(4) For a given density, *Trifolium incarnatum* individuals generally showed greater yield when competing with *Lolium multiflorum* than when competing with others of their own species, but average yield of *Trifolium incarnatum* individuals was higher in monoculture than in mixtures with one-sixth *Lolium multiflorum*.

INTRODUCTION

The role of interference in plant communities is still not well understood. It is not always clear which aspects of the biology of a species allow it to coexist with other competing species, to become extinct, or to dominate and cause the exclusion of other species in a given area (Harper 1967). The concept of 'competitive ability' (Sakai 1955) was an attempt to express a plant species' overall competitive relationship to other species, but such a concept is practically useless in nature, because it will have meaning only with respect to a given species and environmental regime. The goal of the student of plant interference is twofold: to discover whatever general laws may exist, and to explain and predict outcomes of interference in natural and agricultural situations.

Experimental studies of plant interference have usually focused on the effect of one biotic or abiotic factor on the growth or reproduction of one or several competing populations of plants. The factor which has been studied most extensively is density (e.g. Kira,

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Ogawa & Sakazaki 1953; Hodgson & Blackman 1956; Holliday 1960; Harper & McNaughton 1962; Palmblad 1966; Puckridge & Donald 1967). Effects of density in monoculture have been studied to determine optimum spacing for crops. Other factors which have been studied include species proportions (de Wit 1960, 1961; van den Bergh 1968), pattern (Sakai 1957), timing (Sagar 1959; Harper 1961; Haizel & Harper 1973), light (Donald 1958), propagule size (Black 1958), and concentration of specific nutrients (Titman 1976). Because of the possibility of interactions between these factors, one has to guess as to whether generalizations from these experiments will be applicable to situations which differ in factors other than those upon which the experiment focused. This may be one reason why generalizations about plant interference in experimental conditions have often not been useful in making predictions about field performance.

One method of assessing the performance of two species or varieties in mixture and in monoculture is the 'replacement series' (de Wit 1960). It has been employed and extended by others (e.g. Hall 1974a, b). By varying the proportions of two species, but keeping the overall density constant, it is possible to predict the outcome of competition between a mixed population of the two species without actually continuing each experiment for many generations. The relative yield is the yield of a species in mixture divided by its yield in monoculture, and the relative yield total (RYT) is the sum of the relative yields. If RYT < 1, then elimination of one species is the expected result, but if RYT > 1, then individuals are benefiting from the mixture, and equilibrium coexistence should be the result. An assumption here is that a difference in some other factor such as density or nutrient supply will not fundamentally alter the interaction between the two groups, i.e. the replacement series diagram will look the same in different conditions. That nutrient supply does affect the performance of a replacement series was shown by Hall (1974b), and Harper (1965) found that in some mixtures of two varieties of flax, the tendency of a variety to gain or suffer in mixture was reversed by a change in density. Harper's conclusions seem to be the result of individual observations, and therefore not statistically based, but if it could be shown that changes in density commonly change the interference interaction between two species or varieties, then our thinking about plant interference would be considerably altered. One implication here is that a change in density which in itself does not favour one species or another (e.g. non-selective herbivory or an increase or decrease in the supply of a nutrient which is not differentially utilized) might still affect the outcome of the competition.

The purpose of this work is to examine the effects of both density and of nutrient supply on a replacement series of two species.

METHODS

Species

The species chosen were a grass and a legume: *Lolium multiflorum* Lam. and *Trifolium incarnatum* L. These species are known to be able to coexist and the grass–legume relationship has been much investigated. Grass growth is often limited by nitrogen, whereas legumes with nitrogen-fixing symbionts are usually limited by some other nutrient or light. For example de Wit & van den Bergh (1965) grew grass and legume species together and found that the relative yield total was increased in mixtures. Individuals of these species are able to coexist and even to benefit from having as their neighbours members of the other species.

Both species are annual, so a direct measure of reproduction is practicable. *Lolium* *multiflorum* is grown as a seed crop in the Willamette Valley of western Oregon and is also amongst the most important weeds in the fields of other local annual crops such as *Trifolium incarnatum*. The interaction between these two species represents an annual agricultural version of the perennial grass–legume dominated communities.

Experiments

Plants were grown from seed in 10-inch (25-cm) diameter plastic containers of 15-l volume in a glasshouse at Eugene, Oregon. The soil used was a low fertility silty loam representative of much of the Willamette Valley. To ensure that nitrogen, potassium and phosphorus were the only potentially limiting elements, lime was added at the rate of 530 g dolomitic lime and 177 g calcium carbonate lime per cubic metre of soil, and trace elements were added at the rate of 17·6 g per cubic metre of soil. The soil was also inoculated with a small amount of commercial clover *Rhizobium*.

The experimental variables were:

(i) density (6, 18, 60 individuals per pot, in the arrangement described below; the mean distance between plants was 9·2, 5·3 and 2·9 cm respectively);

(ii) proportions of the two species (6:0, 5:1, 3:3, 1:5, 0:6);

(iii) phosphorus and potassium fertilization (with and without 70 g commercial 'superphosphate' and 51 g 'sulphate of potash' per cubic metre of soil).

Thus there were 3 × 5 × 2 = 30 treatments. Each was replicated four times, and all 120 pots were placed at random on several glasshouse benches. Pots were well spaced so that plants in one pot could not shade those in another pot. A population of plants will behave differently with differing spatial patterns (Harper 1965), an effect which has plagued plant population growth experiments. A uniform pattern such as rows or hexagonal arrays may also be undesirable. For these experiments, a random pattern was produced within a circle the size of the pots' soil surface. For monoculture of six plants per pot, a seed was planted at each of 15 points. Fourteen days after sowing, the seedlings were thinned to six. The reverse of the order in which the points were generated was used to decide which individuals were to be removed, so that, as far as possible, the seedling pattern was random and the same in each pot at a given density. Thus transplanting was unnecessary. The planting patterns for low-density mixtures were a randomly chosen subset of the 15 points and the points for the minority species in a biased mixture were a subset of points for one species in the 50:50 mixture. The same procedure was followed at the higher densities where more random points were added to the lower-density pattern, so the lower-density pattern was a subset of the higher-density pattern. At the highest density it was not possible to identify individual positions with confidence, so the plants were thinned to the desired density randomly, although the standard pattern was used for sowing. Planting seeds took a long time, so the four replicates were sown on consecutive days (26–30 April 1976). Harvesting was similarly spread over 4 days (30 August – 2 September 1976) so that each unit had the same length of time for development.

The soil was kept moist, and the plants grown to maturity. Seeds were collected from the *Lolium** plants as they matured by cutting off the matured spikes. Honey bees were introduced into the glasshouse to pollinate the *Trifolium**, but pollination and seed production were erratic. Dried inflorescences were collected from the *Trifolium* plants at harvest, and their weight was used as a measure of reproductive output. After 127 days, all

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* The generic name is used alone for convenience.

the remaining above-ground parts of both species were harvested, dried, and weighed. During the later stages of development, aphids and whiteflies were controlled with malathion and nicotine sulphate.

RESULTS

Trifolium *production*

Both inflorescence and shoot production of the whole *Trifolium* population in a pot were influenced by all three factors (density, proportion of *Lolium*, and fertilizer supply) (Tables 1 and 2). There is also some indication of a density–fertilization interaction, and that addition of potassium and phosphorus had a greater effect at high density than it had at low density (Fig. 1). When considered per individual plant, inflorescence and shoot production were influenced by overall density and fertilization (Tables 3 and 4) and inflorescence production showed a significant ratio–density interaction (Fig. 2).

TABLE 1. Analysis of variance of weight of inflorescences produced by *Trifolium incarnatum* populations grown in mixture with *Lolium multiflorum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	2228	2	< 0·001
B. Species proportion	2644	3	< 0·001
C. Fertilizer supply	1743	1	< 0·001
Interactions			
A × C	139	2	0·06
Other interactions (not significant)	300	15	
Residual	1742	72	

TABLE 2. Analysis of variance of weight of above-ground shoots produced by *Trifolium incarnatum* populations grown in mixture with *Lolium multiflorum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	19 636	2	< 0·001
B. Species proportion	40 555	3	< 0·001
C. Fertilizer supply	24 037	1	< 0·001
Interactions			
A × C	2759	2	0·006
Other interactions (not significant)	2483	15	
Residual	17 754	72	

TABLE 3. Analysis of variance of weight of inflorescences per *Trifolium incarnatum* individual grown in mixture with *Lolium multiflorum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	29·10	2	< 0·001
B. Species proportion	3·33	3	N.S.
C. Fertilizer supply	22·06	1	< 0·001
Interactions			
A × B	11·82	6	0·002
A × C	4·10	2	0·022
Other interactions (not significant)	6·11	9	
Residual	36·89	72	

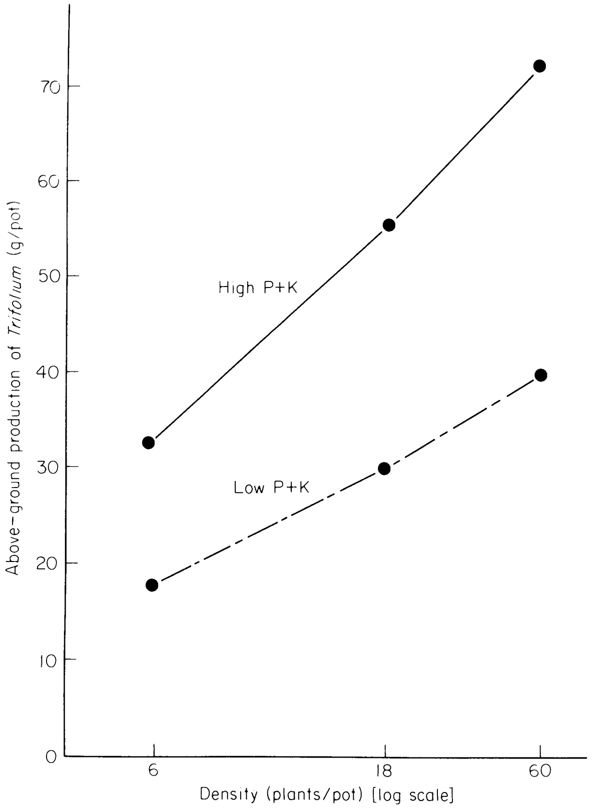

FIG. 1. Above-ground production of *Trifolium incarnatum* populations in experiments: the effects of different density and fertilizer supply.

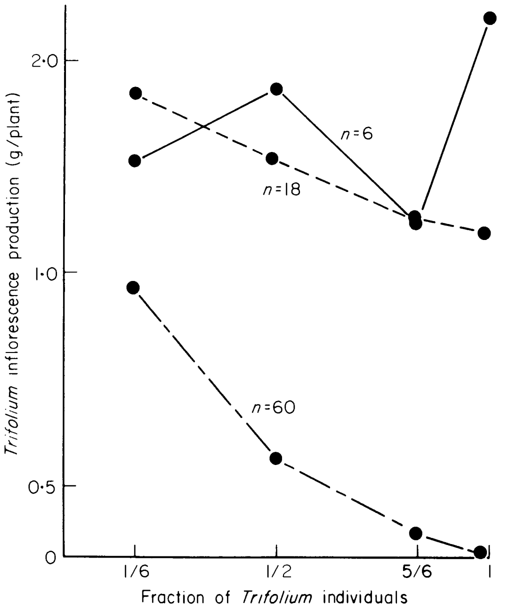

FIG. 2. Inflorescence production of *Trifolium incarnatum* individuals in experiments: the effects of different density and of proportion of *Lolium multiflorum*.

TABLE 4. Analysis of variance of weight of above-ground shoots per *Trifolium incarnatum* individual grown in mixture with *Lolium multiflorum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	688	2	< 0·001
B. Species proportion	99	3	N.S.
C. Fertilizer supply	382	1	< 0·001
Interactions (not significant)	308	17	
Residual	1363	72	

Lolium *production*

The total production of *Lolium* inflorescences by the whole population in a pot was significantly influenced only by the supply of fertilizer and by the ratio of *Lolium* to *Trifolium* (Table 5). The weight of inflorescences produced by a *Lolium* individual showed a significant interaction between overall density and proportion of *Lolium* (Table 6). There was large-scale variation in the seed production of *Lolium* plants because of the variability in the time of flowering and seed-set. Many individuals were just beginning to produce spikes when the other individuals had senesced.

TABLE 5. Analysis of variance of weight of inflorescences produced by a *Lolium multiflorum* population grown in mixture with *Trifolium incarnatum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	0·263	2	N.S.
B. Species proportion	2·587	3	0·012
C. Fertilizer supply	0·921	1	0·044
Interactions (not significant)	3·13	17	
Residual	15·851	72	

TABLE 6. Analysis of variance of weight of inflorescences per *Lolium multiflorum* individual grown in mixture with *Trifolium incarnatum*

Source of variation	Sum of squares	d.f.	*P*
Main effects			
A. Overall density	0·029	1	N.S.
B. Species proportion	0·703	2	< 0·001
C. Fertilizer supply	0·486	3	< 0·001
Interactions			
B × C	0·524	6	< 0·001
Other interactions (not significant)	0·132	11	
Residual	1·175	72	

Relationship between production and density

In general, log density of each species and log of individual production were related in a linear fashion. Regressions of log individual above-ground and inflorescence production of *Trifolium* plants on log density of *Lolium* and *Trifolium* accounted for 40 – 50% of the variation in *Trifolium* production (Table 7). Individual *Lolium* inflorescence production was highly variable within each group of replicates and the slope of the regression of log

TABLE 7. Linear regressions of log of production per *Trifolium* individual on log of density of *Trifolium* and *Lolium*; non-significant terms ($P > 0{\cdot}05$) omitted

Linear regression equation	r^2
No P or K added:	
$\log Y_{ci} = 0{\cdot}375 - 0{\cdot}388 \log (N_c + 1) - 0{\cdot}128 \log (N_r + 1)$	0·37
$\log Y_{ca} = 1{\cdot}03 - 0{\cdot}425 \log (N_c + 1) - 0{\cdot}221 \log (N_r + 1)$	0·44
P and K added:	
$\log Y_{ci} = 0{\cdot}676 - 0{\cdot}478 \log(N_c + 1)$	0·46
$\log Y_{ca} = 1{\cdot}32 - 0{\cdot}546 \log(N_c + 1)$	0·52

Y_{ci} = mean dry weight of inflorescence per individual *Trifolium* plant (g).
Y_{ca} = mean dry weight of above-ground shoots per individual *Trifolium* plant (g).
N_c = density of *Trifolium* (individuals per pot).
N_r = density of *Lolium* (individuals per pot).

production on log density was not significantly different from zero. The log of the individual above-ground production of *Lolium* was well explained as a function of log density of the two species (Table 8).

TABLE 8. Linear regressions of log of production per *Lolium* individual on log of density of *Lolium* and *Trifolium*; non-significant terms ($P > 0{\cdot}05$) omitted

Linear regression equation	r^2
No P or K added:	
$\log(Y_{ri} + 1) = 0{\cdot}1 - 0{\cdot}0648 \log(N_r + 1)$	0·39
$\log Y_{ra} = 0{\cdot}873 - 1{\cdot}04 \log(N_r + 1) - 0{\cdot}15 \log(N_c + 1)$	0·84
P and K added:	
$\log(Y_{ri} + 1) = 0{\cdot}13 - 0{\cdot}088 \log(N_r + 1)$	0·35
$\log Y_{ra} = 0{\cdot}789 - 0{\cdot}932 \log(N_r + 1) - 0{\cdot}162 \log(N_c + 1)$	0·71

Y_{ri} = mean dry weight of inflorescence per individual *Lolium* plant (g).
Y_{ra} = mean dry weight of above-ground shoots per individual *Lolium* plant (g).
N_r = density of *Lolium* (individuals per pot).
N_c = density of *Trifolium* (individuals per pot).

DISCUSSION

Within- and between-species competition

The results show that *Lolium* and *Trifolium* can coexist without competitive exclusion under conditions of low available nitrogen. The evidence is strongest for high density: *Trifolium* individuals show greater production amidst *Lolium* than in monoculture, and the effect increases with increasing density (Fig. 2) and with addition of P and K (Fig. 3). Under low N–P–K conditions, log of the individual *Trifolium* inflorescence production and the log of the average above-ground production were approximately linearly dependent on the log of the density of both species. But the density of the *Trifolium* was much more important in determining the individual *Trifolium* plant output (Table 7). Under low N, but high P–K condition, the log of mean *Trifolium* individual production was dependent only on the log of the *Trifolium* density; the log of the *Lolium* density had no significant effect (Table 7). Thus, under high P and K conditions, the *Lolium* density had no significant effect on production by a *Trifolium* individual. Without the addition of P and K, the density of both species was important in determining mean production of a *Trifolium* individual, but the *Trifolium* density still had the larger effect. I conclude

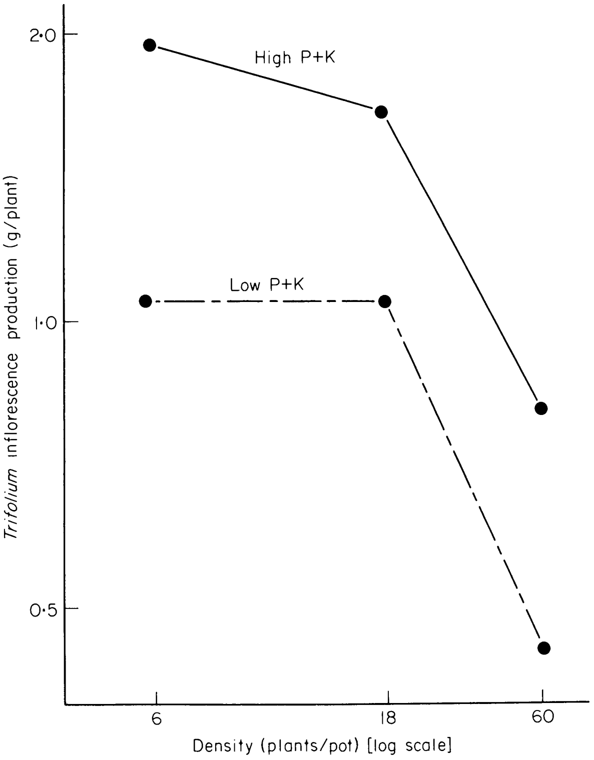

FIG. 3. Inflorescence production of *Trifolium incarnatum* individuals in experiments: the effects of different density and fertilizer supply.

that, from the point of view of an average *Trifolium* individual, competition between individuals of the same species is greater than that between individuals of different species, which is a theoretical condition for continued coexistence of competing species. The improvement in performance of *Trifolium* with *Lolium* rather than *Trifolium* as neighbour is greater as density increases.

Competition between individuals of the same species also seems to be more intense for an average *Lolium* individual. The log of the average inflorescence production of a *Lolium* individual was significantly dependent on the log of the *Lolium* density but not on the log of the *Trifolium* density both with and without added fertilizer (Table 8). This effect was more conspicuous for shoot production than for inflorescence production but only because there was less variability among replicates. In both low and high P–K conditions, it was again found that while the log of density of both species was significant in determining average *Lolium* production, the log density of *Lolium* was much more important, both in terms of its coefficient and its contribution in accounting for variation, than was the density of *Trifolium*. These regressions are consistent with the concept of a negative linear relationship between log average plant production and log density.

The relationship between grasses and legumes when nitrogen is in short supply, as in these experiments, suggests that equilibrium coexistence may be possible because of differential resource utilization, such as Titman (1976) has shown to occur amongst diatoms. Under high nitrogen conditions grass has a clear advantage over clover, as many experiments have demonstrated (e.g. Blackman 1938). In addition to the experiments described here, two additional treatments were made, of medium density and 50:50 mixture but with nitrogen as well as potassium and phosphorus added to the soil. In these pots the *Lolium* production was increased by an order of magnitude while *Trifolium* production was halved. Elimination of the *Trifolium* population would be the expected outcome under such conditions (de Wit & van den Bergh 1965).

Factor interaction

In general there was some, but not much, evidence for factor interaction in determining population shoot and inflorescence production except in the case of total *Trifolium* production, where density and fertilization interacted positively. Mean individual production for each species, however, clearly seems to show factor interaction. The superior performance of each species with the other as neighbour is important at high density, but trivial at low density.

The replacement diagrams (Fig. 4) illuminate the effect of density and fertilization on the replacement series. For *Lolium* and *Trifolium* in this experiment, complementation—the increase in yield per individual in mixture over that in monoculture—is greatest at high density. Total *Lolium* production actually increases at high density if ten of the sixty *Lolium* plants are replaced by *Trifolium*.

The *Trifolium* results also suggest an interesting phenomenon. While, in general, a *Trifolium* individual shows greater production when amongst *Lolium* than when amongst *Trifolium*, greater production per individual is observed in monoculture than when there is a small proportion of *Lolium*. This effect was most pronounced at low density, where production of an individual *Trifolium* plant was 79% greater in monoculture than in mixtures which contained one *Lolium* plant. This could be what was observed by Mann & Barnes (1953), who noted that just a few ryegrass individuals had a significant depressing effect on clover production, but this effect did not increase greatly with an increase in the number of ryegrass individuals. This could be due to a combined effect of differential resource utilization, which favours an individual in mixture, and some other interaction, e.g. allelopathy, which favours an individual in monoculture. Perhaps at low density a clover individual does well when surrounded by ryegrass because of a difference in resource utilization, in spite of the allelochemical effect of ryegrass. When there are only a few ryegrass individuals and many clover plants, there is little benefit from this niche difference and chemical products of ryegrass depress clover production somewhat. At high density, however, complementation is the rule: niche differentiation may be more important than chemical or other negative interaction. If this phenomenon occurs it could be quite important in agricultural systems, which are, in general, highly biased mixtures, of monocultures and weeds.

Another interesting result is that the total *Lolium* output of the populations was influenced by the proportions of the two species, but not by the overall density: the *Lolium* is limited by nitrogen, and as few as six individuals are capable of exhaustively exploiting the available nitrogen in the experimental containers. Some benefits to *Lolium* from *Trifolium* clearly exist at high density, where grass population production actually increases as the proportion of *Trifolium* changes from zero to one-sixth. It is likely that some of the nitrogen fixed by the legume's symbionts is becoming accessible to the grass. This provides an interesting contrast to the behaviour of the *Trifolium* population when mixed with a few *Lolium* individuals.

The hypothesis that the results of replacement series experiments may be affected by overall density and nutrition has been confirmed.

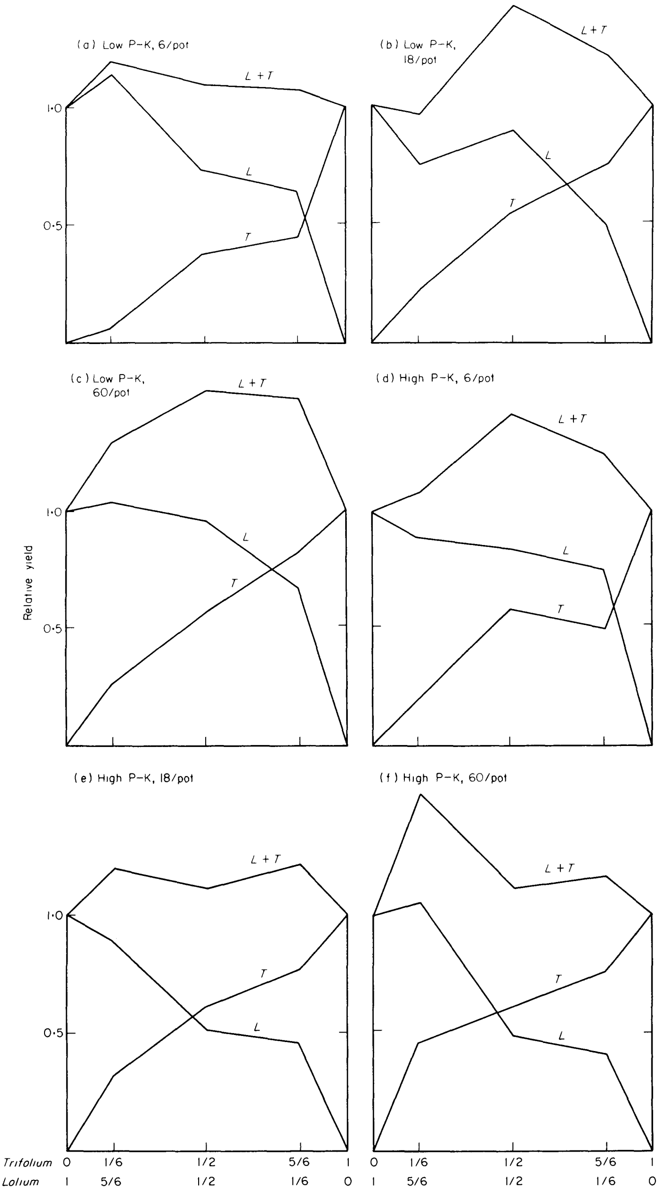

FIG. 4. Replacement diagrams for each density–fertilization combination. Each point is the mean of four replicates. 'Yield' is population above-ground shoot production. Relative yield for a species is (yield in mixture)/(yield in monoculture). *T*, *Trifolium incarnatum*; *L*, *Lolium multiflorum*; *L* + *T*, relative yield total (RYT). (a)–(c), low supply of P and K; (d)–(f), high supply of P and K. (a) and (d), six plants/pot; (b) and (e), eighteen plants/pot; (c) and (f), sixty plants/pot.

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