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COMPETITION AND COEXISTENCE IN A NORTH CAROLINA GRASSLAND

III. MIXTURES OF COMPONENT SPECIES

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SUMMARY

(1) Six species from a mown field were grown in mixtures of two and three species in pots in the glasshouse, using the experimental design of de Wit. The mixtures differed in the identity of the component species and their relative proportions, in total density, in the number of species in each mixture, and in soil conditions and the time of year during which they were grown.

(2) Density had little effect upon the outcome of competition between species. Lowered density appeared to increase the yield in mixtures.

(3) Three two-species mixtures were each grown in a series of differing proportions. In mixtures containing *Plantago lanceolata* and *Poa pratensis*, the species which formed a smaller proportion of the mixture had larger individuals. This would tend to promote the coexistence of these two species.

(4) Soil fertility and time of year affected the intensity and outcome of competition. In two of six pairs of species, one species was dominant in one environment, but the other species became dominant in another environment. This may mean that spatial variation in soil conditions and seasonal variation in the environment are responsible for the coexistence of some of the species.

(5) The results of each two-species mixture may be summarized by identifying one species as the competitive dominant and the other as the competitive subordinate; when these summaries are combined a consistent, linear, order of all of the species results for each season and level of soil fertility. The order of the species differs between seasons and between fertility levels.

(6) The results of mixtures of three species were well-predicted from the results of two-species mixtures by both the model of de Wit and a linear model incorporating the relative proportions of each species in the three-species mixtures.

INTRODUCTION

Studies of the relationships among species in a mown field in North Carolina have revealed a pattern of diffuse competition among these herbaceous plant species, together with a high degree of spatial and temporal heterogeneity in their occurrence and growth (Fowler 1981; Fowler & Antonovics 1981). With the exception that the species are divided into two groups, each of which has a clearly differentiated seasonal pattern of growth, the nature of the factors that permit these species to coexist remains obscure. The present paper explores the dynamics of the interactions amongst a selected subset of the species of this community, and the nature of the coexistence of these species, by means of competition experiments in pots in the glasshouse. The intensity and direction of competition between these species was measured, and the stability of competitive relationships under different total densities, proportions of different species in multi-species mixtures, soil conditions

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and seasons was investigated. The design used in these experiments was that of de Wit (1960). This design has been widely used in agronomic studies, but less often in the investigation of natural or semi-natural communities (see Trenbath 1974). The present study therefore is also a test of the usefulness of such experiments in the investigation of plant communities.

SPECIES

Two separate experiments were made. The first, conducted during March to August 1977, involved five species; *Anthoxanthum odoratum* and *Poa pratensis* (grasses), and *Plantago lanceolata*, *Rumex acetosella* and *Salvia lyrata* (forbs) (nomenclature follows Radford, Ahles & Bell 1968). The second, conducted during October 1977 to May 1978, involved the first four of these species (but not *Salvia lyrata*) and *Cerastium glomeratum*, a forb. All of these species are commonly found in lawns, pastures, and mown fields in the Piedmont of North Carolina, and all were abundant in the mown field studied previously (Fowler & Antonovics 1981). This field will be referred to as 'the field site'.

Cerastium glomeratum is a small winter annual, branching from a single stem. All the rest of these species are herbaceous perennials. *Plantago lanceolata* and *Salvia lyrata* form rosettes, *Rumex acetosella* spreads vigorously by means of rhizomes, *Anthoxanthum odoratum* is a tufted (i.e. bunch) grass, and *Poa pratensis*, although capable of vegetative spread by lateral tillers, is much more localized in its growth than is *Rumex acetosella*.

METHODS

Mixtures and pure stands of these species were grown in an unheated glasshouse in plastic pots, 16·5 cm in diameter and 13 cm deep. with perforated bases. The pots were filled to 10 cm depth with soil (described later). This depth corresponded to the (shallow) rooting zone of these species in the field site. Plants were grown from seed collected from the field site unless otherwise noted. A surplus of seed was sown, and seedlings thinned to the desired density 6 weeks after sowing. At this time ramets of *Rumex acetosella* were added (first experiment only). At the termination of each experiment, above-ground biomass of each species separately was harvested by clipping at the soil surface. Material was dried for 48 h at 65 °C and weighed. All results are given as above-ground dry biomass (g) of a single species in a single pot.

First experiment

The first experiment was sown on 25–28 March 1977. Non-varietal commercial seed of *Poa pratensis* from Central Carolina Farmers, Durham, North Carolina, was used, and *Rumex acetosella* was added to the pots as ramets collected from the field site. Each ramet consisted of one small stem with associated roots. The soil consisted of equal parts of clay, *Sphagnum* peat and 'Perlite' without added nutrients. No further nutrients were added during the course of the experiment. All pots were clipped three times, at monthly intervals, to simulate the regular mowing at the field site. The pots were watered at irregular intervals corresponding to the occurrence of rain and the pattern of water stress at the field site, as estimated from the degree of wilting and leaf rolling observed there and the time of day at which it occurred. The plants were crowded in the pots, the soil was relatively infertile, and the watering was restricted, which resulted, as intended, in plants which appeared quite similar to ones growing at the field site, i.e. small, low-growing and non-succulent. At the end of August there was a severe drought and watering was reduced accordingly. The resultant water stress in the pots was so severe that some of the plants died, so the experiment was ended on 31 August 1977.

Second experiment

The second experiment was sown on 21–24 October 1977 and harvested on 10–13 May 1978. Because plants grew more slowly in colder weather, only one clipping was necessary, corresponding to the single mowing at the field site during this period. The dry weights reported for this experiment include material from this clipping, as the inclusion of this material should improve the sensitivity of the results to early interference among individuals. Inclusion of clippings could perhaps affect the nature of the results in some cases. This possibility was tested by comparing analyses of data which did not include clippings with analyses of data which did. No differences were evident except the loss of significance in some cases. Four environments were imposed, two levels of water availability and two levels of soil fertility, in a factorial design. In the first watering regime, W, the plants were watered in the same way as in the first experiment, that is, as dictated by field conditions. These pots received more water than did those in the first experiment because of the cooler, wetter weather during this period. Plants in the W regime in the second experiment frequently wilted, reversibly, during the day in April and May, as did plants at the field site. There were however no drought-induced deaths in this experiment. In the second watering regime, WW, pots were kept at field capacity. In the first fertility regime, −F, pots received no added fertilizer. In the second, +F, a total of 500 ml of a solution of 'Peters 20-20-20' brand fertilizer was added to each pot (0·36 g per pot of each of total N, P_2O_5 and K_2O), 50 or 100 ml at a time, during the course of the experiment. Fertilizing was spaced over the course of the experiment to simulate the gradual release of nutrients in a natural ecosystem.

DESIGN AND ANALYSIS OF EXPERIMENTS

Design

The treatments used in the two experiments are shown in Table 1. Each treatment was replicated five times, once in each of five blocks arranged along a bench. Pots were arranged randomly within a block. Each pot contained one, two or three species, and a total of one, three, six or twelve individual plants, and, in the second experiment, was subject to one watering regime and one fertility regime.

Analysis

The experimental design and analysis used here are based upon those of de Wit (1960) and van den Bergh (1968). The growth of individual plants in mixtures of species is compared with the growth of individuals in pure stands (monocultures) at the same overall density. The total density of all plants is held constant and only the proportions of the different species differ. This design provides a method of measuring the effects of interference (competition) amongst species despite the often large differences in absolute yield between different species.

From the yield (above-ground biomass) of each species in each pot, the total number of individuals in the pot and the proportions of each species in the pot after the initial

TABLE 1. Design of experiments.

	Proportions	Number of species	Environment* (water, soil)	Species†	Number of treatments‡
First experiment					
A	12:0	1	W, −F	*A, Pl, P, R, S*	5
B	6:0	1	W, −F	*Pl, P, S*	3
C	3:0	1	W, −F	*Pl, P, S*	3
D	1:0	1	W, −F	*Pl, P, S*	3
E	6:6	2	W, −F	All combinations§ of *A, Pl, P, R, S*	10
F	3:3	2	W, −F	*Pl–P, Pl–S, P–S*	3
G	8:4 and 4:8	2	W, −F	*Pl–P, Pl–S, P–A*	6
H	4:4:4	3	W, −F	All combinations of *A, Pl, P, R, S*	10
Second experiment					
I	12:0	1	W, −F	*A, Pl, P, R*	4
J	6:6	2	W, −F	All combinations of *A, Pl, P, R*	6
K	4:4:4	3	W, −F	All combinations of *A, Pl, P, R*	3
L	12:0	1	WW, −F	*A, Pl, P, R*	4
M	6:6	2	WW, −F	All combinations of *A, Pl, P, R*	6
N	12:0	1	W, +F	*A, Pl, P, R*	4
O	6:6	2	W, +F	All combinations of *A, Pl, P, R*	6
P	12:0	1	WW, +F	*A, Pl, P, R*	4
Q	6:6	2	WW, +F	All combinations of *A, Pl, P, R*	6

* Watering treatments: W, to simulate field conditions; WW, to field capacity. Soil treatments: −F, no added fertilizer; +F, with added fertilizer. See text for details.

† Species symbols: *A, Anthoxanthum odoratum; Pl, Plantago lanceolata; P, Poa pratensis; R, Rumex acetosella; S, Salvia lyrata.*

‡ There were five replicates of each treatment.

§ Number of species combined is shown in the third column.

thinning, two variables were calculated, relative yield per plant, *RYP*, and relative yield total, *RYT*. These variables are defined in the following way. First, let

p = initial proportion of species i in a mixture,
q = initial proportion of species j in a mixture,
r = initial proportion of species k in a mixture,

so that

$p + q = 1$ in a mixture of two species, and

$p' + q' + r' = 1$ in a mixture of three species (where the 'prime' notation is used to indicate a three-species mixture).

Now define

Y_{i} = yield of species i in a pure stand of species i,
Y_{ij} = yield of species i in a mixture of species i and j,
Y_{ijk} = yield of species i in a mixture of species i, j and k,

and so on, all values being per pot. Given a constant total density, then

$$RYP_{\mathrm{ij}} = Y_{\mathrm{ij}}/(pY_{\mathrm{i}}) \text{ and}$$
$$RYP_{\mathrm{ji}} = Y_{\mathrm{ji}}/(qY_{\mathrm{j}}).$$

Relative yield per plant in a mixture of three species is calculated in an analogous fashion:

$$RYP_{ijk} = Y_{ijk}/(p'Y_i).$$

Relative yield per plant may be interpreted as the average performance of an individual in a mixture in comparison with the average performance of an individual of the same species in a pure stand of the same total density. Relative yield per plant as calculated here is closely related to the relative yield (RY) as defined by de Wit (1960):

$$RYP_{ij} = pRY_{ij}.$$

The relative yield total, RYT, is the weighted average of the relative yields of the mixture components:

$$RYT_{ij} = pRYP_{ij} + qRYP_{ji} \text{ and}$$
$$RYT_{ijk} = p'RYP_{ijk} + q'RYP_{jik} + r'RYP_{kij}.$$

If the growth of an individual is unaffected by the identity of the neighbouring individuals, then $RYP_{ij} = 1{\cdot}0$; but $RYP_{ij} > 1{\cdot}0$ implies that individuals of species i suffer less interference from individuals of species j (between-species competition) than they do from individuals of their own species (within-species competition); and $RYP_{ij} < 1{\cdot}0$ implies that within-species competition is less than that between species. For example, a value of 1·20 for RYP_{ij} indicates a 20% average increase in biomass of individuals of species i as a result of growing in a mixture with species j, rather than in a pure stand of species i.

Analysis of variance was used to compare the effects of between-species and within-species competition. A separate analysis of variance was made on the yields of each species, at each density, proportion, and fertilizer and watering regime, but including results both of pure stands and of mixtures with the various competing species. Pure stand yields were first multiplied by 1/2 (mixtures of two species) or 1/3 (mixtures of three species). For example, the yields of the twelve-plant pure stands of *Plantago* (treatment A, Table 1) multiplied by 1/2 and the yields of *Plantago* in the four 6:6 mixtures (treatment E) of which it was a component provide the data for one analysis of variance. Variances between treatments were tested for homogeneity of variance within each analysis of variance by the F-max test. None showed significant heterogeneity. Two way analysis of variance was then performed. The two main effects were treatment and replicate (block), with the interaction providing the residual variance. The treatment means and the estimates of mean square errors from these analyses of variance were used in subsequent t-tests and Scheffé multiple comparison tests to compare the yield of each species in each mixture with its yield in pure stand. Relative yield per plant was calculated from the treatment means. A mixture yield significantly different from 1/2 (or 1/3) of the comparable pure stand yield is equivalent to a relative yield per plant significantly different from 1·0. The Scheffé multiple comparison test, as used here, is conservative, while the t-test overestimates the improbability (P-value) of a particular difference because it makes no allowance for multiple testing. Consequently, both tests were used. In all cases the Scheffé test showed significance at $P < 0{\cdot}05$ only when the t-test showed significance at $P < 0{\cdot}01$.

Relative yield totals were calculated on a pot by pot basis and averaged according to the following equations:

$$RYT_{ij} = \left[\sum_{u=1}^{n} (RYT_{iju})\right]/n \text{ and}$$

$$RYT_{ijk} = \left[\sum_{u=1}^{n} (RYT_{ijku})\right]/n,$$

where u = number of the replicate (1, 2, 3, 4 or 5) and n = number of replicates = 5.

When two species are grown in several different proportions, but at the same total density, the results may also be presented in the form of 'ratio diagrams' (de Wit 1960), in which the (final) output quotient is plotted against the (initial) input quotient (p/q) using a logarithmic scale on both axes. The output quotient, Q, is given by

$$Q = (Y_{iju}/Y_i)/(Y_{jiu}/Y_j).$$

The line that fits these points is usually straight or slightly sigmoid (Braakhekke 1980). A straight line with a slope of 1·0 indicates that one of the species consistently outcompetes the other. A slope less than 1·0 implies that a stable equilibrium exists, a situation commonly described as 'negative frequency dependent' or 'stabilizing frequency dependent' (Harper 1977; Braakhekke 1980) because the performance of each species improves as its proportion in the mixture is decreased. The equilibrium point may be located by determining where the fitted line crosses the line that goes through the origin and has a slope of 1·0 (i.e. where the output quotient equals the input quotient). Linear regressions were calculated from the log-transformed input and output quotients and the resultant slopes tested for significant deviations from 1·0.

RESULTS

The effects of density

Three of the five species, *Plantago lanceolata*, *Poa pratensis*, and *Salvia lyrata*, were each planted in pure stands at each of several densities in the first experiment (treatments A–D, Table 1). As expected, the yield increased with increasing density (Fig. 1). This increase was not significant, however, in *Plantago*. The expected form of these curves is asymptotic, the asymptote being the maximum possible yield per pot. Only three individuals of *Plantago* were necessary to reach the maximum yield. In all cases a density of twelve plants per pot was sufficient to reach the asymptote under these conditions; hence the planting density of twelve plants per pot used in the other treatments was sufficient to ensure that all available space was being used. At least three plants of *Poa pratensis* or *Salvia lyrata* are necessary for this.

The effect of density upon competition between species was examined in those pairs of species grown at two densities: mixtures of *Plantago lanceolata*, *Poa pratensis* and *Salvia lyrata* grown in 3 : 3 and 6 : 6 mixtures (treatments E and F, Table 1) and in pure stands of six and twelve plants per pot (treatments A and B, Table 1). The effect of density upon both yield and relative yield per plant was slight: the results at the two densities were quite similar (Table 2). The correlation coefficient between RYP_{ij} in the 3 : 3 mixture and RYP_{ij} in the 6 : 6 mixture, calculated over all six RYP values, is 0·92. The mean relative yield per plant was not significantly different in the two sets of mixtures ($P > 0·5$) nor were any pair of relative yield per plant values significantly different between the two sets of mixtures.

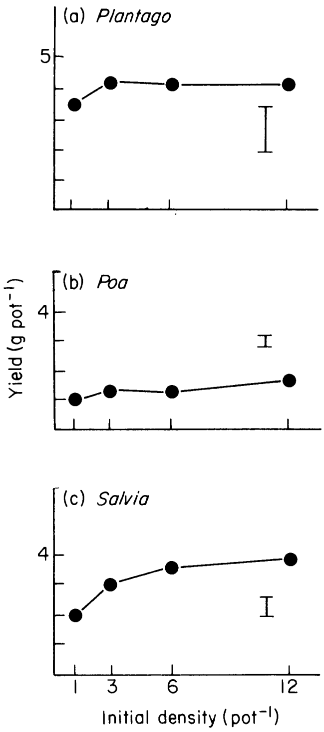

Fig. 1. The relationship between density and yield in pure stands of (a) *Plantago lanceolata*, (b) *Poa pratensis* and (c) *Salvia lyrata* grown in 16·5-cm diameter pots in a glasshouse. The least significant difference ($P < 0·05$) is shown as a bar in each graph.

Table 2. Yield and relative yield per plant of 6:6 and 3:3 mixtures in the first experiment. Pure stand yields (italicized) have been multiplied by 1/2 so that they are comparable with other values. Yields significantly different from the pure stand value shown, and relative yields per plant significantly different from 1·0 are indicated by significance symbols: *, $P < 0·05$; **, $P < 0·01$ (t-test); †, $P < 0·05$; ††, $P < 0·01$; (Scheffé test).

Yield (g pot^{-1})	6:6 Mixtures Competing species					3:3 Mixtures Competing species		
Reference species	*A*	*Pl*	*P*	*R*	*S*	*Pl*	*P*	*S*
Anthoxanthum	*1·42*	1·21	1·28	2·28††	2·47††			
Plantago	1·87	*2·04*	2·24	3·02*	3·93†	*2·04*	2·15†	3·59†
Poa	0·61**	0·81	*0·82*	1·33††	1·33††	0·78	*0·59*	1·10††
Rumex	0·30††	0·50†	0·54†	*0·94*	0·94			
Salvia	0·98†	0·41††	0·91†	2·82**	*1·98*	0·35††	0·90††	*1·82*

Relative yield per plant	6:6 Mixtures Competing species					3:3 Mixtures Competing species		
Reference species	*A*	*Pl*	*P*	*R*	*S*	*Pl*	*P*	*S*
Anthoxanthum	1·00	0·85	0·90	1·61††	1·74††			
Plantago	0·92	1·00	1·10	1·48*	1·92†	1·00	1·05†	1·76†
Poa	0·74**	0·98	1·00	1·62††	1·62††	1·32	1·00	1·87†
Rumex	0·32††	0·53†	0·57†	1·00	1·00			
Salvia	0·50†	0·21††	0·46†	1·43**	1·00	0·19††	0·49††	1·00

The effects of differing proportions

The values of relative yield per plant of the 4 : 8 and 8 : 4 mixtures (treatment G, Table 1) were generally consistent with the results of the 6 : 6 mixtures (Table 3). Of the three pairs of species tested, only *Plantago lanceolata–Poa pratensis* had a slope significantly ($P <$ 0·05) different from 1·0 in the linear regression of log-transformed output quotient on log-transformed input quotient (Fig. 2). There was no apparent effect of differing proportions on the two other mixtures. The slope of the line fitted by regression to the *Plantago–Poa* data is 0·50. Hence individuals of *Plantago* grew larger in mixtures in which the proportion of *Plantago* was smaller, and individuals of *Poa* grew larger in mixtures in which the proportion of *Poa* was smaller (Table 3), that is, both species

TABLE 3. Yield and relative yield per plant of 8 : 4 and 4 : 8 mixtures of three pairs of species in the first experiment. (Relative yield per plant of 6 : 6 mixtures is that given in Table 2.)

Species	Yield (g pot^{-1})		Relative yield per plant		
Mixture:	8*Pl*:4*P*	4*Pl*:8*P*	8*Pl*:4*P*	6*Pl*:6*P*	4*Pl*:8*P*
Plantago	2·37	1·82	0·88	1·10	1·34
Poa	0·61	0·90	1·13	0·98	0·83
Mixture:	8*A* :4*P*	4*A* :8*P*	8*A* :4*P*	6*A* :6*P*	4*A* :8*P*
Anthoxanthum	1·69	0·91	0·90	0·90	0·96
Poa	0·48	1·11	0·89	0·74	1·02
Mixture:	8*Pl*:4*S*	4*Pl*:8*S*	8*Pl*:4*S*	6*Pl*:6*S*	4*Pl*:8*S*
Plantago	3·53	4·02	1·30	1·92	2·95
Salvia	0·24	0·73	0·18	0·21	0·28

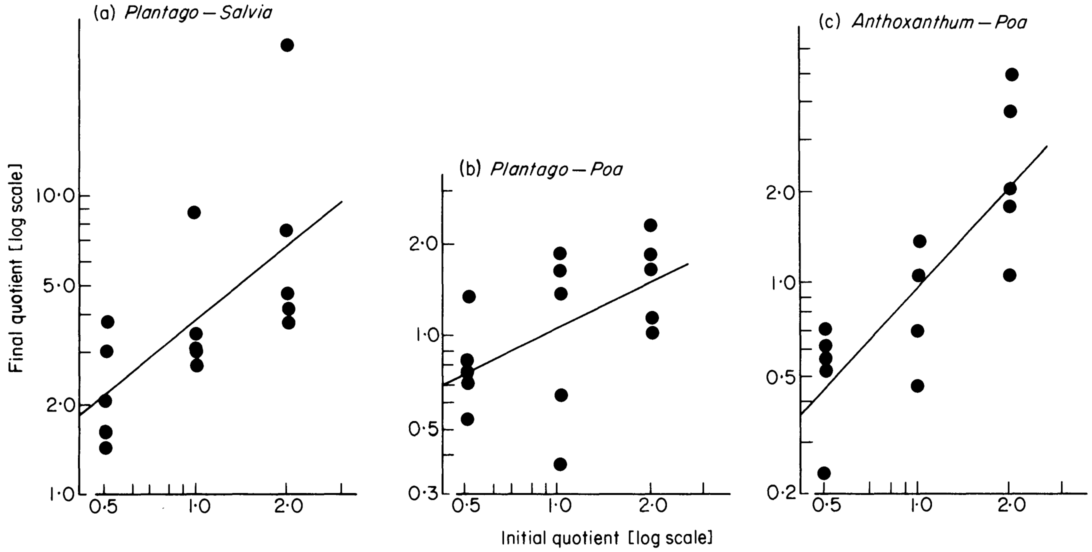

FIG. 2. Ratio diagrams of three two-species mixtures: (a) *Plantago lanceolata–Salvia lyrata*; (b) *P. lanceolata–Poa pratensis*; (c) *Anthoxanthum odoratum–P. pratensis*. The initial, x, and final, y, quotients of the two species in each pot are plotted on logarithmic scales. Linear regressions using the log-transformed data are shown. The equations are (a) $\log y = 1{\cdot}00 + 0{\cdot}83 \log x$; (b) $\log y = 0{\cdot}03 + 0{\cdot}50 \log x$; (c) $\log y = 0{\cdot}00 + 1{\cdot}12 \log x$. Only the slope, 0·50, of the *Plantago–Poa* mixture (b) differs significantly ($P <$ 0·05) from 1·0, indicating that in this mixture the rarer species has the competitive advantage and that a stable equilibrium exists.

showed 'negative frequency dependent' behaviour. The calculated stable equilibrium for this pair of species is 1·15 *Plantago* : 1·00 *Poa.*

The effects of differing soil environment

Four species, *Plantago lanceolata*, *Poa pratensis*, *Anthoxanthum odoratum* and *Rumex acetosella*, were grown in four different soil environments in the second experiment, in pure stands and two-species mixtures (treatments I, J and L–Q, Table 1). The four environments resulted in significant differences in yield in each species in each mixture and in each pure stand (judged by one way analyses of variance on each species in each mixture or pure stand, in most cases with an overall F value of $P < 0{\cdot}001$). Yields were always greatest in the WW, +F and W, +F regimes, and lowest in the WW, −F and W, −F regimes, in all mixtures and pure stands (Table 4). The fertilizer addition appeared to be the key factor, as the WW, +F and W, +F regimes did not result in significantly different yields and the WW, −F and W, −F regimes did not result in significantly different yields in most mixtures and pure stands. In many cases both of these were true.

In many instances soil environment affected competition between species (Table 4). In the second experiment, *Poa pratensis* was in all cases competitively dominant to *Plantago lanceolata*: *Poa* had relative yields per plant greater than 1·0 in all four environments and *Plantago* had relative yields per plant less than 1·0 in three of the four environments. In the first experiment, however, *Plantago* was competitively dominant to *Poa*, although not significantly so. Very similar results were obtained from the *Plantago–Anthoxanthum odoratum* mixtures. The relative yields per plant were more variable in the *Plantago–Rumex acetosella* mixtures. The reversal of competitive dominance between the unfertilized (−F)

TABLE 4. Yield and relative yield per plant of 6 : 6 mixtures in four treatments, (a)–(d), in the second experiment. Pure stand yields (italicized) have been multiplied by 1/2 so they are comparable with other values. Yields significantly different from half the yield of the pure stand of the same species and relative yields per plant significantly different from 1·0 are indicated. Significance conventions as in Table 2; treatment symbols as in Table 1.

	Yield (g pot^{-1}) Competing species				Relative yield per plant Competing species			
Reference species	*A*	*Pl*	*P*	*R*	*A*	*Pl*	*P*	*R*
(a) W, −F								
Anthoxanthum	*3·38*	4·64†	5·00†	4·36*	1·00	1·37†	1·48†	1·29*
Plantago	0·98††	*2·28*	1·45†	1·91	0·43††	1·00	0·64†	0·84
Poa	0·76††	2·17*	*1·63*	1·69	0·46††	1·33*	1·00	1·04
Rumex	1·30	1·95	2·18	*1·76*	0·74	1·11	1·24	1·00
(b) WW, −F								
Anthoxanthum	*3·49*	4·36*	5·32††	5·06†	1·00	1·25*	1·52††	1·45†
Plantago	1·09††	*2·18*	1·63**	1·68*	0·50††	1·00	0·75**	0·77*
Poa	0·92††	2·44*	*1·90*	1·63	0·48††	1·28*	1·00	0·86
Rumex	0·89†	2·72	2·51	*2·41*	0·37†	1·13	1·04	1·00
(c) W, +F								
Anthoxanthum	*5·18*	6·36	7·12*	8·00†	1·00	1·23	1·37*	1·54†
Plantago	4·68	*4·33*	4·57	7·10*	1·08	1·00	1·05	1·64*
Poa	2·18†	4·40††	*3·12*	4·39††	0·70†	1·41††	1·00	1·41††
Rumex	2·15††	1·96††	3·57†	*5·08*	0·42††	0·39††	0·70†	1·00
(d) WW, +F								
Anthoxanthum	*5·98*	6·69	9·46†	9·38†	1·00	1·12	1·58†	1·57†
Plantago	3·69*	*5·84*	3·26*	6·62	0·63*	1·00	0·56*	1·13
Poa	2·57*	4·80*	*3·73*	3·92	0·69*	1·29*	1·00	1·05
Rumex	2·96††	3·12††	4·20	*5·22*	0·57††	0·60††	0·80	1·00

environments of the second experiment (*Rumex* dominant), on the one hand, and the fertilized (+F) ones of the second experiment and the (unfertilized) environment of the first experiment (*Plantago* dominant), on the other, resulted in relative yields per plant significantly different from 1·0. In all environments *Anthoxanthum* was competitively dominant to *Poa*, although relative yields per plant of *Poa* were much lower in the unfertilized environments of the second experiment. *Rumex* was dominant to *Poa* in the unfertilized environments of the second experiment and competitively subordinate in the fertilized ones and in the environment of the first experiment. In all environments *Anthoxanthum* was dominant to *Rumex*, although relative yield per plant was quite variable.

The first experiment also included *Salvia lyrata*, which was competitively subordinate to all species except *Rumex*. The second experiment also included *Cerastium glomeratum*, a winter annual. This species grew so poorly in mixtures that it was not possible to recover enough of it from the mixtures to dry and weigh. This species grew well in pure stands, however. Relative yields of the other species in mixtures with *Cerastium* were high, from 1·5 to more than 2·0, as if the individuals were growing in a pure stand at half density.

The effects of increasing the number of species in a mixture

All possible three-species combinations of the five species in the first experiment, and of the four species in the second experiment, W, −F regime only (treatments H and K, Table 1) were grown at an overall density of twelve plants per pot and equal proportions of the three species, that is, as 4 : 4 : 4 mixtures. The appropriate comparisons in each experiment are therefore between the yield of each species in the mixture and 1/3 the yield of that species in the appropriate pure stand. The results of the three-species mixtures were quite similar to those of the two-species mixtures (Tables 2, 4, 5 and 6).

Three-species mixtures provide a test of the predictability of the interactions among species in a mixture of three species from knowledge of the interactions between pairs of species. De Wit has proposed a model for the growth of plants in mixtures which can be used to calculate the relative yield per plant in mixtures of three or more species from yields in two-species mixtures. This model is based upon an analogy with the gas laws (de Wit 1960). In the present terminology, his model states that, in a two-species mixture,

$$
\begin{aligned}
Y_{ij} &= Y_i\,[p/(p + q/c_{ij})]\\
Y_{ji} &= Y_j[q/(q + p/c_{ji})]
\end{aligned}
$$

where c_{ij} and c_{ji} are fitted constants. Substituting and solving,

$$
\begin{aligned}
c_{ij} &= [(1-p)RYP_{ij}]/[1-pRYP_{ij}]\\
&= [(1/2)RYP_{ij}]/[1-(1/2)\mathrm{RYP}_{ij}] \text{ and}\\
c_{ji} &= [(1-q)RYP_{ji}]/[1-qRYP_{ji}]\\
&= [(1/2)RYP_{ji}]/[1-(1/2)RYP_{ji}].
\end{aligned}
$$

The yield of a three-species mixture at the same total density is calculated to be

$$Y_{ijk} = Y_i\,[p/(p' + q'/c_{ij} + r'/c_{ik})].$$

Substituting,

$$
\begin{aligned}
RYP_{ijk} &= 1/(p' + q'/c_{ij} + r'/c_{ik})\\
&= 1/[(2/3)(1/RYP_{ij} + 1/RYP_{ik} - (1/2))].
\end{aligned}
$$

TABLE 5. Yield and relative yield per plant of 4:4:4 mixtures in the first experiment. Yields significantly different from one-third of the pure stand yield of the same species, and relative yields per plant significantly different from 1·0 are indicated. Significance conventions as in Table 2.

Yield (g pot^{-1})

Species	Competing species *A–Pl*	*A–P*	*A–R*	*A–S*	*Pl–P*
Anthoxanthum	–	–	–	–	0·91
Plantago	–	1·34	1·82	1·57	–
Poa	0·40	–	0·66	0·57	–
Rumex	0·35*	0·23**	–	0·25**	0·33*
Salvia	0·28†	0·45**	0·33†	–	0·31†
	Pl–R	*Pl–S*	*P–R*	*P–S*	*R–S*
Anthoxanthum	1·08	1·30*	1·29	1·12	1·81††
Plantago	–	–	1·55	1·81	2·69**
Poa	0·45	0·77*	–	–	1·06††
Rumex	–	0·31**	–	0·33*	–
Salvia	0·46**	–	1·18	–	–

Relative yield per plant

Species	Competing species *A–Pl*	*A–P*	*A–R*	*A–S*	*Pl–P*
Anthoxanthum	–	–	–	–	0·96
Plantago	–	0·99	1·34	1·16	–
Poa	0·81	–	1·29	1·12	–
Rumex	0·57*	0·37**	–	0·40**	0·53*
Salvia	0·22†	0·34**	0·25†	–	0·23†
	Pl–R	*Pl–S*	*P–R*	*P–S*	*R–S*
Anthoxanthum	1·14	1·37*	1·35	1·17	1·91††
Plantago	–	–	1·14	1·33	1·98**
Poa	0·89	1·48*	–	–	2·02††
Rumex	–	0·50**	–	0·53*	–
Salvia	0·35**	–	0·90	–	–

TABLE 6. Yield and relative yield per plant of 4:4:4 mixtures in the second experiment, W, –F environment (see Table 1). Yields significantly different from one-third of the pure stand yield of the same species (italicized), and relative yields per plant significantly different from 1·0 are indicated. Significance conventions as in Table 2.

Yield (g pot^{-1})

Species	*A–Pl*	*A–P*	Competing species *A–R*	*Pl–P*	*Pl–R*	*P–R*	Pure stand yield × 1/3
Anthoxanthum	–	–	–	3·33*	4·26††	3·74†	*2·25*
Plantago	–	0·92†	0·80††	–	–	1·45	*1·52*
Poa	0·82*	–	0·57††	–	1·18	–	*1·09*
Rumex	0·46†	0·85	–	1·03	–	–	*1·17*

Relative yield per plant

Species	*A–Pl*	*A–P*	Competing species *A–R*	*Pl–P*	*Pl–R*	*P–R*
Anthoxanthum	–	–	–	1·48*	1·89††	1·66†
Plantago	–	0·60†	0·53††	–	–	0·96
Poa	0·75*	–	0·52††	–	1·08	–
Rumex	0·39†	0·73	–	0·88	–	–

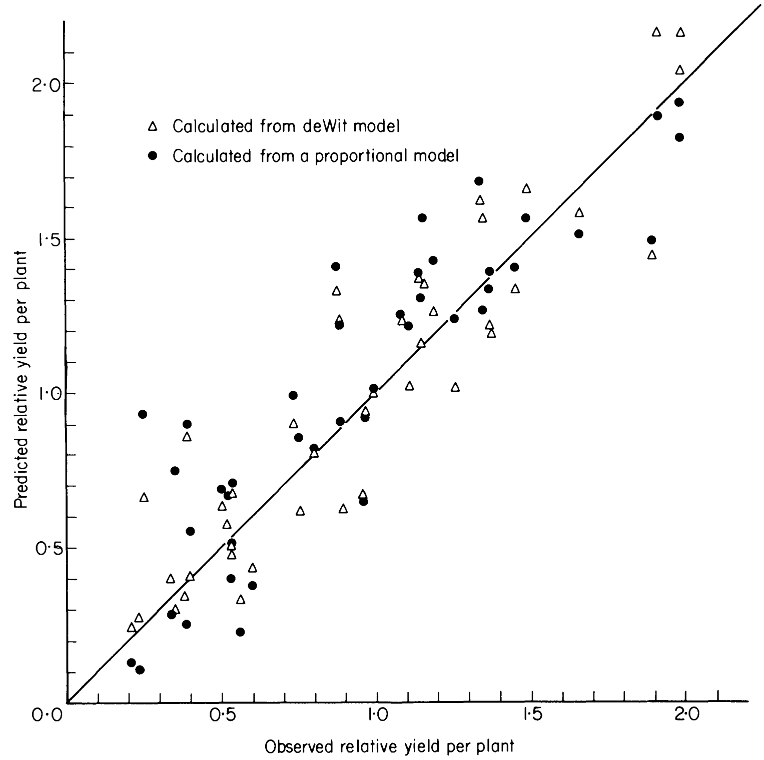

FIG. 3. Predicted and observed values of relative yield per plant in mixtures of three species. Triangles, values calculated using the de Wit model; circles, values calculated using a proportional model (see text). The line is that which would be obtained if there were perfect agreement between observed and calculated values.

The calculated values for each RYP_{ijk} and the results of the 6 : 6 mixtures (Tables 2 and 4) are shown in Fig. 3. The Pearson product moment correlation coefficient is 0·92.

A simple proportional model is almost as good a predictor of relative yield per plant in three-species mixtures as is the model of de Wit, and needs fewer assumptions. Such a model may be constructed as follows.

Assume that all individuals in a pot interact, unaffected by their position in the pot. The effect of a mixture is to increase or decrease the size of an individual, relative to individuals in a pure stand. This increase is d_{ij}, such that

$$d_{ij} = RYP_{ij} - 1,$$

where i is the species considered and j the competing species. In a two-species mixture of equal proportions, such as the 6 : 6 mixtures grown in these experiments, half (actually six-elevenths, in these pots) of the individuals with which an individual of species i competes are of species j and half (actually five-elevenths) are of the same species, i. In a three-species mixture, only one-third of competing individuals are of species j. As d_{ij} is the increment associated with a proportion of j of 1/2, it therefore must be corrected for the reduced proportion of species j in the three-species mixture, so

$$\begin{aligned} d'_{ij} &= (q'/q)\, d_{ij} \\ &= [(1/3)/(1/2)]\, d_{ij} \\ &= (2/3)\, d_{ij}, \end{aligned}$$

where d'_{ij} = corrected increment, q' = proportion of species j in the three-species mixture, and q = proportion of species j in a two-species mixture at the same total density.

In a three-species mixture there is also another competing species, species k. Therefore

$$\begin{aligned} d'_{ik} &= (r'/r)\, d_{ik} \\ &= [(1/3)/(1/2)]\, d_{ik} \\ &= (2/3)\, d_{ik}, \end{aligned}$$

where r' = proportion of species k in the three-species mixture, and r = proportion of species k in a two-species mixture at the same total density.

The resulting calculated relative yield per plant is

$$\begin{aligned} RYP_{ijk} &= 1 + \mathrm{d}'_{ij} + d'_{ik} \\ &= 1 + 2/3(RYP_{ij} + RYP_{ik} - 2). \end{aligned}$$

Values calculated from this equation and the results of the 6:6 mixtures (Tables 2 and 4) had a correlation coefficient of 0·88 (Fig. 3) with the observed values (Tables 5 and 6). The correlation coefficients of the two models are not sufficiently different to be a basis for preferring one model to the other.

Relative yield totals

Relative yield totals were calculated for all treatments. All treatments had values quite close to 1·0. The average relative yield total of 6:6 mixtures was 1·01 ($s^2 = 0{\cdot}01$, $n = 34$) and of 4:4:4 mixtures was 0·96 ($s^2 = 0{\cdot}01$, $n = 14$). The possible exception to this generalization is the 3:3 mixtures of the first experiment (mean $RYT = 1{\cdot}12$, $s^2 = 0{\cdot}01$, $n = 3$). Two of the three values contributing to this mean value were relatively large (1·18 and 1·19).

DISCUSSION

The six species studied commonly grow adjacent to one another. They are persistent components of the plant communities found in pastures, lawns and mown fields and, in particular, were important members of the mown field that served as the reference field site for these experiments. These glasshouse experiments therefore represent simplications of a natural community in which species were extracted and grown under conditions in which the density and proportion of species were controlled and much of the natural spatial heterogeneity of the environment removed. The reduction in complexity provides an opportunity to isolate and measure the interactions among these species. It must be remembered, however, that the cost of this simplication is that the interactions occur in the environment provided by pots in a glasshouse, and therefore that the extrapolation of conclusions from glasshouse to natural community must be cautious.

Variations in density had the expected effect upon monospecific stands, but did not have a major effect upon competition between species. Halving the density, from twelve to six plants per pot, resulted on average in only a 12% change in the relative yield per plant, although the actual yield per plant almost doubled in most cases. A change in the relative proportions of two species in a two-species mixture had a greater effect upon the performance of an individual relative to its performance in a pure stand. Of particular interest is the existence of a 'negative frequency dependent' response on the part of both species in one of the three mixtures tested (*Plantago lanceolata–Poa pratensis*), as it reveals a mechanism whereby the two species can coexist, if these responses also occur in natural communities. The cause of this relationship is probably a reversal of competitive dominance during the growing season because these two species have different phenology

(Fowler & Antonovics 1981). 'Negative frequency dependent' responses by both members of a mixture have also been reported for species of *Papaver* (Harper & McNaughton 1962) and *Avena* (Marshall & Jain 1969). In neither of these instances was the cause evident.

Species interact in nature not only at a variety of densities and relative proportions. but also in a matrix of surrounding individuals of many other species. It may be that in some communities competition among the component species is an emergent property of the community as a whole, and hence not predictable from the behaviour of pairs of species. Evidence of the unpredictability of the interactions among species in multi-species mixtures was found in a field study of these species (Fowler 1981). The apparent cause was the difference among species in rates of vegetative spread, which resulted in the pre-emption of open space by two species with rapid vegetative spread, one of them *Rumex acetosella.* In these glasshouse experiments, however, the values of relative yield per plant in three-species mixtures calculated from the results of the two-species mixtures agreed excellently with the measured values. Both the model proposed by de Wit (1960) and a simple proportional model gave very good agreement between calculated and measured values. It seems that the confined space of the pots does not provide the opportunity for significant amounts of vegetative spread into open spaces, and that no other mechanism operated in the pots to provide unpredictable responses.

In addition to the effects of proportion, density, and the specific identity of neighbouring individuals, the direction and intensity of competition may also be affected by the physical environment in which it occurs. If the direction of competitive dominance (that is, which member of a pair of species outcompetes the other) is reversed between patches in a site, or between seasons, both species may be able to coexist. The high degree of spatial heterogeneity in the vegetation of the field site and the marked differentiation in seasonality of growth of many of these species (Fowler & Antonovics 1981) suggest that this type of coexistence is important in this community, and the experimental mixtures were therefore subjected to a variety of environments, with different supplies of water and nutrients and, if the two experiments are compared, the season of growth. To increase the likelihood of detecting competitive reversal, the four environments tested were relatively extreme, although not excessively so.

Environment had a major effect upon the interactions between species, affecting the intensity of competition and, in two of the six pairs of species, reversing the direction of competitive dominance. *Rumex acetosella* became the dominant species in competition with *Plantago lanceolata* and *Poa pratensis* only under conditions of low soil fertility. It therefore may persist in the community by exploiting patches of especially low soil fertility. This hypothesis is compatible with the known distribution and biology of *Rumex acetosella* (Putwain, Machin & Harper 1968). This species is also an early colonizer of large empty spaces, by vegetative growth (Fowler 1981), a role that probably also contributes to its persistence. The annual species also invade empty spaces quickly. These include *Cerastium glomeratum*, which has been shown here to be competitively subordinate in all the mixtures tested. In general, competitive interactions among these species appear to be extremely labile, being highly dependent upon both season and soil fertility. It is likely, therefore, that if the experiments had been conducted for longer periods of time, the resulting values of relative yield per plant would have been somewhat different.

A mixture or community that is not theoretically stable (i.e. one that does not have a stable local equilibrium at which all the constituent species coexist) may persist for long periods of time if competitive interactions are close to equality or weak relative to other factors affecting the population dynamics of the component species, In the environments tested here, competitive interactions were often close to equality. Extrapolation of these results to the natural environment is supported by corroborating evidence of generally diffuse competition and hence fairly weak and approximately equal pairwise competitive relationships among these species in the field site (Fowler 1981). It seems probable that, in this community, competitive exclusion is often a slow process and is often overridden by other factors.

In each environment there was a consistent hierarchy of species based upon the magnitudes of the relative yield per plant in the 6:6 mixtures. These were (from competitive dominant to competitive subordinate):

(a) in the first experiment, *Plantago lanceolata* > *Anthoxanthum odoratum* > *Poa pratensis* > *Salvia lyrata* > *Rumex acetosella*;

(b) in the second experiment, fertilized pots, *Anthoxanthum* > *Poa* > *Plantago* > *Rumex*;

(c) in the second experiment, unfertilized pots, *Anthoxanthum* > *Rumex* > *Poa* > *Plantago* > *Cerastium glomeratum*.

At least some of the interactions among these species are dependent upon proportion, and some of the inequalities are very small. Nevertheless each of these three hierarchies is consistent within itself, and therefore competitive dominance is a transitive property of these species. The intensities of the interactions (as measured by relative yield per plant) are however not clearly related to the relative position of the species in the hierarchies. Nor is position in a hierarchy correlated with the size of that species' pure stand yield in the same environment. Consistent hierarchies have been found in other similar studies of species from natural communities (Pemadasa & Lovell 1974; Handel 1978) and, in general, competitive hierarchies are consistent (Harper 1977). It has been suggested (Grime 1977) that competitive interactions will tend to intensify in more favourable environments. This prediction was not supported by the results of my experiments; instead competitive interactions changed with increased fertility in a highly individualistic way.

It is often held as axiomatic that if two species compete for the same resource, the decreased use of that resource by one of the species will be compensated by an equivalent increase in the use of the resource by the other. Different species have different rates of conversion of resources into biomass, and into above-ground parts, which are reflected in their differing pure stand yields. We expect to see, therefore, not an equivalence between the absolute amounts of increase in yield of one species and decrease of the other in a mixture, but an equivalence between the proportional changes in yield of the species in a mixture. The relative yield total reflects the sum of the proportional changes in yield in a mixture, and, if the species compete for the same resources, will be equal to 1·0. If the two species use somewhat different resources, for example, different rooting zones, the proportional gain to individuals of one species from growing in a mixture will be greater than the loss to the other, and the relative yield total will be greater than 1·0. In such a situation, both species may have relative yield per plant greater than 1·0. A relative yield total greater than 1·0 therefore implies some degree of niche differentiation, and hence the possibility of coexistence of the species involved. Relative yield totals greater than 1·0 are rare in agricultural experiments, except when nitrogen fixation by a legume is involved (Trenbath 1974). One would expect them to be more common in mixtures of coexisting species from natural communities, since such species may have coevolved niche differentiation.

For this reason relative yield totals were calculated for all mixtures. Only the mixtures grown at halved density (3:3 mixtures) had relative yield totals appreciably larger than 1·0.

This suggests that differentiation in resource use may lie, not in the eventual use of resources, but in the priority of their use before resources become limiting. Evidently the glasshouse and pot environment did not provide any other opportunities for differential resource use. In no case was the density low enough to provide a significant amount of open space for colonization, nor were the pots large enough to provide a high degree of spatial heterogeneity within a pot. A group of pots receiving different watering or fertilizing regimes, however, can be considered to represent a spatially heterogeneous environment. Therefore the six relative yield totals (one for each two-species mixture) were calculated from the yields of all of the pots of all four of the environments of the second experiment. The largest value (*Poa–Anthoxanthum*) was only 1·06, and the mean of the six values was 1·00, indicating that the same resources were used by all of the species. Differentiation in resource use may of course occur in the natural environment as a result of a division of resources not possible in pots, such as a separation of rooting zones.

The experiments reported here, by isolating elements of the community and simplifying the environment, have tested the importance of a series of factors potentially influencing the outcome of competition between these species. They have revealed aspects of the interactions among these species not readily detectable in the field, and thus satisfactorily complemented the field study.

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