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BIOTIC SPECIALIZATION BETWEEN NEIGHBOURING GENOTYPES IN *LOLIUM PERENNE* AND *TRIFOLIUM REPENS* FROM A PERMANENT PASTURE

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SUMMARY

(1) Recent studies suggest that the genotype may be an important functional unit of community variation. This raises the principal question addressed in this study: does micro-evolution occur differentially within a single population in response to interactions with different neighbouring genotypes of a second species?

(2) Samples of *Lolium perenne* and *Trifolium repens* were collected as neighbouring pairs from four different localities in a 40-year-old pasture. Each grass-genet-type was planted, as cloned ramets, in competition with each clover-genet-type in all possible combinations. Cumulative dry-weight production was recorded for the two components separately for 1 year.

(3) Each clover-genet-type generally produced more dry weight when grown with the grass-genet-associate with which it was collected than with others. The converse was true for the grass genets. The grass yielded more than the clover in all combinations, but members of natural-neighbouring genet pairs contributed more equitably to the total yield than other pairs. Natural-neighbouring pairs, however, did not differ significantly in total yield from pairs of non-natural neighbours.

(4) The results suggest the presence of precisely-defined biotic specialization in several neighbouring genotype pairs, all belonging to the same two species in different localities of a single community. Because natural neighbours did not have the highest combined yields, biotic specialization cannot, however, be interpreted as indicating niche differentiation. Interpretation instead focuses on the more even distribution of yield in combinations of natural neighbours, reflecting that natural neighbours have more balanced competitive abilities for contested resources than do non-natural neighbours. A mechanism which may generate this relationship between *Lolium perenne* and *Trifolium repens* is proposed, based on the relatively high mobility of *T. repens* clones through stolon extension, and the opportunity for concomitant competition and beneficence (through nitrogen enrichment from symbiotic *Rhizobium*) between these two species.

(5) This study suggests that natural selection, in contexts of competition, may result in more balanced competitive abilities for contested resources instead of niche differentiation and that this may be an important evolutionary mechanism of coexistence in plant communities.

INTRODUCTION

Darwin (1859) stated that 'We have reason to believe that species in a state of nature are closely limited in their ranges by the competition of other organic beings' (p. 145), and that there is a 'deeply-seated error of considering the physical conditions of a country as the most important [for its inhabitants]; whereas it cannot be disputed that the nature of the other species with which each has to compete, is at least as important, and generally a far more important element of success' (p. 406). This emphasis on the role of interactions

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between species has been central to the development of evolutionary theory. Yet, it is surprising that most studies of within-species or within-population differentiation in plants have been dominated by what Harper (1977) has called 'Wallacian' forces or abiotic selection pressures in the environment—see reviews by Hamrick (1982) and Turkington & Aarssen (1984). It has been argued by Burdon (1980) that the tremendously variable nature of the local biotic environment may act to produce and maintain a high level of variation in plant populations (see parallel arguments by Glesener & Tilman (1978) for terrestrial animals). Even though plant–plant interactions might be expected to produce the necessary conditions which would result in local-scale population differentiation there have been remarkably few attempts to search for and document such effects.

Local-scale differentiation as a result of biotic interactions between species has been demonstrated by Linhart (1974), Watson (1974, cited in Antonovics 1978), Turkington (1979), and Turkington & Harper (1979a). These studies provide evidence of Darwinian forces of natural selection in nature and have demonstrated fine-scale genetically-based variation within single populations representing biotic specialization to neighbouring species. Some authors, however, have stressed that the genotype, rather than the species, may be an appropriate unit of community diversity (Antonovics 1976; Raven 1976; Harper 1982; Aarssen & Turkington 1983; Turkington & Aarssen 1984). At this fine scale, Allard & Adams (1969) showed that lines of barley, that had persisted together in mixtures over many generations, on average yielded higher in mixed than in pure stands. In contrast, lines that had no history of interaction generally showed no difference in yields in mixture compared with pure stands. Joy & Laitinen (1980) demonstrated a similar phenomenon with *Phleum pratense* and *Trifolium pratense*. Can such fine scale biotic specialization be detected between neighbouring genotypes in a natural community? Such a question calls for a view of the plant community as a mosaic of evolving components (Antonovics 1976) or local neighbourhoods in which, not the particular species, but the particular genotypes of different neighbours dictate the nature of biotic interaction and thus set the pattern of community evolution.

Previous studies have shown that different clones of *Trifolium repens* vary in response to particular grass species (Turkington 1979; Turkington & Harper 1979a). However, information about the properties of biotic interactions and ensuing micro-evolutionary patterns is incomplete without an investigation of reciprocal responses between natural neighbours. Reciprocal responses of natural neighbours reflect the extent to which each component is compatible in the presence of the other; i.e. the potential of two species or genotypes to continue interaction with one another, or to coexist. In the work presented here, the occurrence of local population differentiation is studied at the level of reciprocal responses between natural genotype neighbours from interacting populations of *Lolium perenne* and *Trifolium repens* from a permanent pasture.

METHODS

Experimental design

Four different genet pairs of *Lolium perenne* L. and *Trifolium repens* L. (designated L1,T1; L2,T2; L3,T3; L4,T4) were collected as physical neighbours from four widely separate locations in a 1939-sown pasture (40 years old) in British Columbia described in Aarssen & Turkington (1985). These samples were collected from areas where there was abundant overlap in their percentage cover frequencies. The pairs were collected as two whole plants (including root material) and each genet type was propagated separately in a glasshouse for 4 months by the periodic separation of tillers or cutting of stolon pieces followed by replanting as ramets of the original clone. Plastic pots (26·5 cm top diameter; 30·5 cm deep) were used, containing a standard potting mixture of 50% peat, 25% sand and 25% perlite with the following nutrients added per 35 l of potting mix: 85 g fertilizer (18% N, 6% P_2O_5, 12% K_2O) (9 months slow release), 110 g dolomite lime, 45 g gypsum, 4·5 g trace elements (boron, copper, iron, manganese, molybdenum, zinc). The nutrients were added at half the recommended rate to ensure that they were not available in abundance. Each pot had a 2·5-cm border in which seeds of *Dactylis glomerata* L. were sown at a high density to serve as an outer buffer zone and to contain the study plants by preventing clover stolons from growing over the edge of the pot and to keep leaves of test plants from adjacent pots from interacting. The appropriate height to achieve this was monitored by varying the height at which the *D. glomerata* border was clipped. The *D. glomerata* border zone was separated below ground from the central zone by a plastic sleeve.

To prevent repetition, the three experimental species will be referred to by their generic names only in the remainder of this paper.

Three weeks after sowing the *Dactylis* border, eight individual ramets of each grass type were planted per pot with eight of each clover type in all possible sixteen paired-genotype combinations. In a given pot, plants were arranged in a grid with four central transplants (two of each species) surrounded by the remaining ramets which served as an inner-buffer zone. Thus, each of the four central transplants was surrounded by four transplants of the other species. Each combination of clover genotype and grass genotype was replicated three times and the pots were arranged randomly in a temperature-controlled glasshouse. The pots were watered whenever the soil surface became dry, which was about two to three times each week. Once every 3 or 4 weeks the plants, including the *Dactylis* border, were clipped to approximately 3 cm to simulate grazing. The clippings from the four central transplants were collected, dried and weighed separately according to species. Twelve months after planting the ramets, the total above ground parts of the four central transplants were harvested, dried and weighed and the weights of the two components were added to the respective cumulative totals.

Data analysis

A component yield quotient (CYQ) was calculated for each L,T genet combination as follows:

$$\text{CYQ} = Y/Y'$$

where Y is the observed value for the lower yielding component and Y' is the observed value for the higher yielding component. In all combinations, *Trifolium* was Y and *Lolium* Y'. The CYQ is compared among genet combinations and therefore has strictly relative value. It assumes that a measure of the relative contribution of the two components to the combined yield reflects their capacity to persist together relative to the same measure for other combinations. Data were tabulated as shown in Table 1 for grass yields, clover yields, total yields and CYQ values. Each of these variables was subjected to the following linear model in the analysis of variance:

$$Y_{ijk} = \mu + r_i + c_j + \delta_{ij} d_i + e_{ijk}$$

where, Y_{ijk} is a value for the observed variable (i.e. total yield, component yield or CYQ); i is the row number; j is the column number; k is the replicate number; μ is the mean of the

TABLE 1. Tabular model used in the analysis of variance of interactions between genotypes of *Lolium perenne* (grass) and *Trifolium repens* (clover) in a British Columbia pasture (see text for description).

		Clover type			
		T1	T2	T3	T4
Grass type	L1	$\mu + d_1$	$\mu + c_2$	$\mu + c_3$	$\mu + c_4$
	L2	$\mu + r_2$	$\mu + r_2 + c_2 + d_2$	$\mu + r_2 + c_3$	$\mu + r_2 + c_4$
	L3	$\mu + r_3$	$\mu + r_3 + c_2$	$\mu + r_3 + c_3 + d_3$	$\mu + r_3 + c_4$
	L4	$\mu + r_4$	$\mu + r_4 + c_2$	$\mu + r_4 + c_3$	$\mu + r_4 + c_4 + d_4$

cell in row 1, column 1 assuming no diagonal effect; r_i is a variable for row effect (i.e. component of the observation due to the effect of row i); c_j is a variable for column effect (i.e. component of the observation due to the effect of column j); d_i is a variable for diagonal effect (i.e. component of the observation due to the effect of principal diagonal position i); δ_{ij} has a value of 1 if $i = j$ and a value of 0 if $i \neq j$ (i.e. a diagonal effect is incorporated if the observation is in a principal diagonal cell); e_{ijk} is a random normal variate with zero mean.

The overall test had the null hypothesis:

$$H_0\colon r2 = r3 = r4 = c2 = c3 = c4 = d1 = d2 = d3 = d4 = 0.$$

(i.e. no row, column or diagonal effects). Analysis was aimed mainly to detect whether there were any significant diagonal effects in the data, allowing also for any possible row or column effects. Where the analysis revealed no significant row or column effects, an overall test was generated with the null hypothesis:

$$H_0^1\colon d1 = d2 = d3 = d4 = 0$$

(i.e. assuming row and column effects are zero). For individual diagonal effects the following null hypotheses were tested:

$$H_0^1\colon d1 = 0, H_0^2\colon d2 = 0, H_0^3\colon d3 = 0, H_0^4\colon d4 = 0.$$

RESULTS

The results of dry weight production for *Trifolium* and *Lolium* in all genet-pair combinations are shown in Tables 2 and 3, respectively. The null hypothesis of no row,

TABLE 2. Yields (g dry weight) of transplants of *Trifolium repens* (T*x*), each collected with a natural neighbouring genet of *Lolium perenne* (L*x*) from four sites in a pasture sown in 1939 in British Columbia and planted in all combinations of clover type and grass type in pots. The performances of the clover types with their natural neighbouring grass types are shown on the principal diagonal; all values are means of three replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming row and column effects: for the overall test, $P = 0·004$.

		Grass associate			
		L1	L2	L3	L4
Clover producer	T1	3·32	2·25	1·00	0·94
	T2	2·95	3·25	1·73	0·99
	T3	1·68	1·43	3·38	1·39
	T4	2·15	1·07	1·84	2·97

$P_1 = 0·210$; $P_2 = 0·130$; $P_3 = 0·007$; $P_4 = 0·009$.

TABLE 3. Yields (g dry weight) of transplants of *Lolium perenne* (L*x*), each collected with a natural neighbouring genet of *Trifolium repens* (T*x*) from four sites in a pasture sown in 1939 in British Columbia and planted in all combinations of clover type and grass type in pots. The performances of the grass types with their natural neighbouring clover types are shown on the principal diagonal; all values are means of three replicates; the probability levels given are the attained significance levels for the four diagonal elements assuming row and column effects; for the overall test, $P = 0{\cdot}013$.

		Clover associate			
		T1	T2	T3	T4
Grass producer	L1	6·45	15·22	23·01	8·03
	L2	7·11	9·59	10·13	5·21
	L3	11·38	6·53	5·63	8·94
	L4	12·71	7·92	10·71	7·44

$P_1 = 0{\cdot}009$; $P_2 = 0{\cdot}242$; $P_3 = 0{\cdot}043$; $P_4 = 0{\cdot}663$.

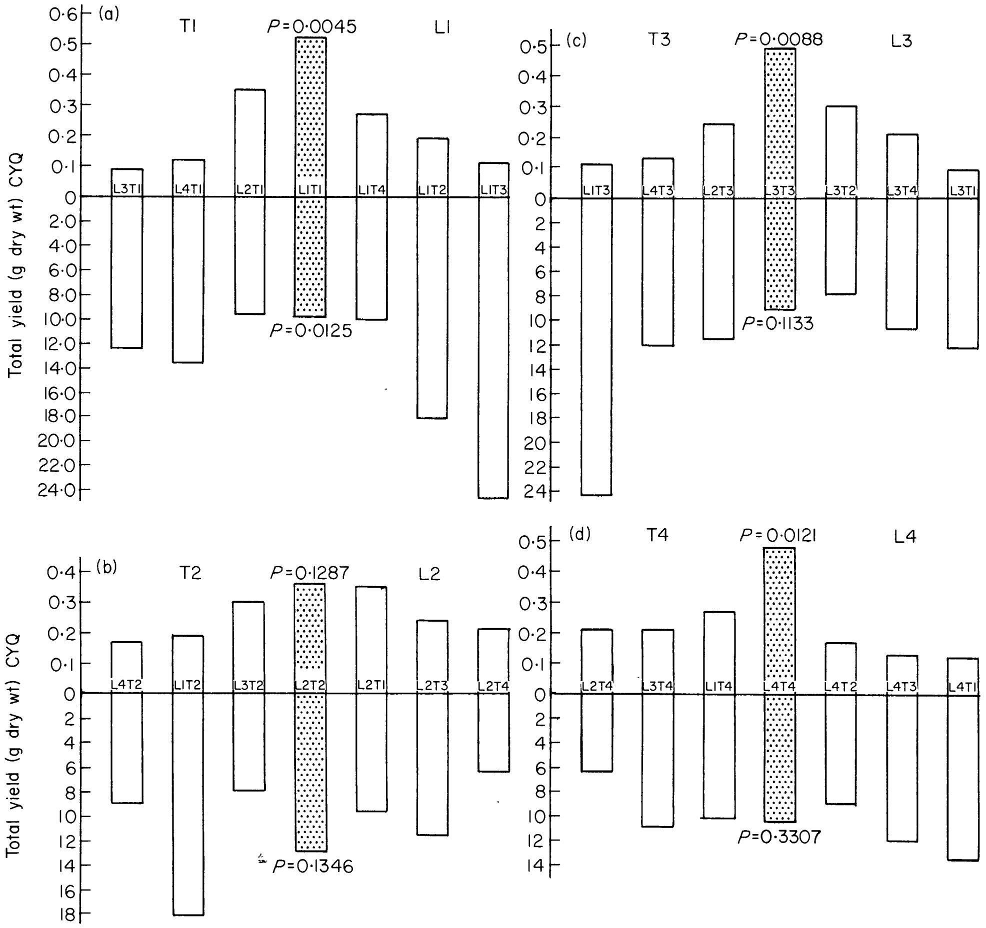

FIG. 1. Component yield quotient (CYQ) (dry weight of *Trifolium* divided by that of *Lolium*) and total yields for different genet type combinations of *Lolium perenne* and *Trifolium repens*. Graphs show the values for the four combinations of natural neighbours (stippled bar graphs (▨)), compared with all other combinations involving (a) L1 or T1, (b) L2 or T2, (c) L3 or T3, (d) L4 or T4. All values are means of three replicates.

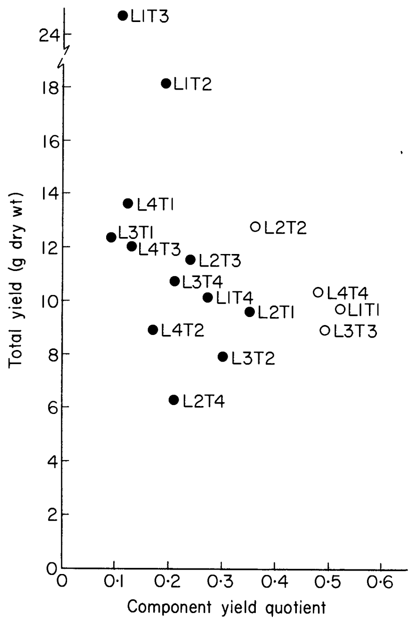

FIG. 2. Relationship between total yield and component yield quotient (CYQ) for different genet type combinations of *Lolium perenne* and *Trifolium repens*. The values for the naturally neighbouring genet pairs (●) collected from the four sites in the experimental field are indicated by unfilled circles (○). All values are means of three replicates.

column or diagonal effects was rejected in both cases. For each genet pair Lx,Tx, the yield of T (clover) in any combination involving Lx or Tx was generally highest in the natural neighbouring combination; L3,T3 and L4,T4 showed significant ($P < 0{\cdot}05$) diagonal effects (Table 2). The converse was true for *Lolium*; yield was lowest in the natural neighbouring genet combination and significant diagonal effects were found for L1,T1 and L3,T3 (Table 3).

Component yield quotient (CYQ) values simultaneously incorporate the neighbour-specificity of L for T, and T for L. For each genet pair type Lx,Tx, the CYQ was higher than in any other combination involving Lx or Tx (Fig. 1). Significant ($P < 0{\cdot}05$) diagonal effects were obtained for L1,T1, L3,T3 and L4,T4. There was little neighbour specific pattern for total (L plus T) yields of the combinations; the L1,T1 combination showed the only significant diagonal effect (Fig. 1). There appears to be some negative relationship between total yield and CYQ in combinations involving L1 or T1 (Fig. 1a) and in combinations involving L3 or T3 (Fig. 1c). For the data as a whole, the four natural neighbouring genet pairs had the highest CYQ values but did not differ significantly from the other combinations in terms of total yield (Fig. 2).

DISCUSSION

Genet pairs of *Lolium* and *Trifolium* which were sampled together as immediate neighbours in the field had higher component yield quotients than those in which the two components came from different neighbourhoods. The CYQ reflects the capacity to avoid competitive exclusion or the probability of coexistence for one genet combination relative to another. The term makes no assumption about mechanisms. Those combinations in which the superior component vastly out-yielded the inferior component have a lower probability of coexistence (reflected by a lower CYQ) than combinations in which the two components were more similar in their performance. Ecological combining ability (Harper 1977) implies a high probability of coexistence due to some degree of niche separation, affording some measure of escape from competition. The result is that combinations with more ecological combining ability have a higher total yield in combination than those with less ecological combining ability (e.g. Seaton & Antonovics 1967; Allard & Adams 1969; Remison & Snaydon, in Snaydon 1978; Joy & Laitinen 1980). In the present study, however, an interpretation of the results in terms of ecological combining ability is not justified. Combinations with the highest CYQ did not have the highest total yields (Fig. 2). The higher CYQ of natural neighbouring genets is instead due to the fact that the performance of each clover genet was generally highest with its natural neighbouring grass genet (which parallels the findings of Turkington & Harper (1979a) with respect to clover response to natural neighbouring grass species as opposed to genets), but that the performance of each grass genet was generally lowest with its natural neighbouring clover genet. The result is that the differential in performance of the highest yielding component (which was always the grass) and the lowest yielding component (which was always the clover) was least in genet pairs which were natural neighbours. The consequence of this is a higher CYQ for these genet pairs but not a higher total yield.

The results support the interpretation of an alternative consequence of selection in systems of competition—one which reduces the differential in relative competitive power for contested resources, i.e. selection for 'competitive' combining ability (Aarssen 1983). This process may occur independently of any change in the extent of niche overlap. From the present results, relative competitive ability appears to be genotype specific; the factors that govern high CYQ for one pair of neighbouring *Lolium–Trifolium* genets may not be the same factors that govern a high CYQ for a different neighbouring pair from a different neighbourhood in the community.

The processes generating this higher CYQ for natural neighbours have not been investigated, but several factors may be considered. Differences in the relative mobility of the species may provide a partial explanation. The relatively mobile, wandering, phenotype of *Trifolium* permits it to sample neighbourhoods of grass genotypes much more rapidly than the relatively immobile *Lolium*. This permits *Trifolium* effectively to 'seek out' compatible neighbourhoods of particular grass genotypes, presumably those which impose the least competitive conditions. Further, the results suggest that these neighbourhoods are ones in which no member imposes an overbearing threat on the relative fitness of others through having a superior ability to exploit contested resources. This course of selection is especially likely if niche requirements are not readily partitionable. Clover genotypes with the most challenging relative competitive abilities would be expected to leave the most descendants and therefore increase in local frequency. The exact course of selection would depend on the type of competition imposed by particular grass genotypes. Grass genotypes would therefore face the strongest competition from the locally adapted clover genets that belong to the same neighbourhood and hence perform more poorly in their presence than with alien clover genets from other neighbourhoods. The converse would be true for clover genotypes. In the face of an adversely altered competitive environment, fitness in the clover is enhanced by the ability of the genotype to migrate through lateral spread.

This raises a further question concerning why the grass does not escape or respond in like manner through selection for improved relative competitive ability in these neighbourhoods. First, its relative immobility does not permit escape from the relatively mobile clover. Secondly, the clover may provide a nitrogen-rich environment for the grass. This could be a sufficiently strong selective force to favour those genotypes of grass which do not exert stringent competitive pressures on the clover. Grass genets which ultimately leave the most descendants may therefore be those that are competitive enough to avoid exclusion by the clover, but are not so competitive as to suppress or eliminate the source of nitrogen made available by a neighbouring clover. This may be especially important to fitness if available soil nitrogen is scarce. The genotype-specific coadaptation in local neighbourhoods may be further mediated by a complex indirect mutualism involving interaction of particular grass genotypes and particular strains of symbiotic *Rhizobium* in the clover (cf. Hill 1977).

A beneficence of the above sort may place constraints on niche divergence. Niche divergence may not contribute to higher fitness if the mutualistic or commensalistic relationship is lost in the process. Selection may instead result in an equilibration of the reciprocal aggressiveness of the two competing species exploiting a broadly overlapping niche. This would involve selection for increased relative competitive ability in the clover, but decreased relative competitive ability in the grass.

The relative contribution of these various factors in developing this local specialization is worthy of further inquiry, particularly the role of beneficence in defining selectional forces. Ecologists have tended to categorize species interactions into separate types, e.g. predation, commensalism, competition, mutualism. Competition and beneficence have generally been viewed as conflicting extremes of organism interaction and, before about 1960, accounts of the evolutionary process largely dismissed cooperative phenomena as not requiring special attention (Axelrod & Hamilton 1981). Yet two organisms which are competing in one respect, may be co-operating in another. Empirical and theoretical considerations to date have concerned mostly simultaneous within-species competition and co-operation, e.g. in *Drosophila* (Mather 1961) and in sessile invertebrates (Buss 1981). It is argued by Mather (1961) that, insofar as the co-operative function is essential to fitness, a certain minimal contribution to it may be favoured even at the risk of reduction in competitive capacity. There is a paucity of evidence for concomitant positive and negative interactions between species (e.g. Putwain & Harper 1970). Beneficial components of such interactions may, for example, involve protection from herbivores and other pests (Atsatt & O'Dowd 1976) or attraction of pollinators for other species (Thomson 1978; 1980).

Grasses have often been found to be more competitive than white clover for important nutrients such as potassium (see review by Robson & Loneragen 1978). This may result in what has been described as the 'cycle of good and poor clover' (Blaser & Brady 1950). During 'good' clover years the soil nitrogen is increased; hence, grasses start growing very early in the spring of the subsequent year. The resultant competition for potassium may limit the growth of the leguminous associate (hence a 'poor' clover year). In the following year, clover attains more vigorous growth because the grasses face a low nitrogen supply and cannot compete as aggressively for potassium; so the cycle continues. A similar phenomenon has been described in the more detailed 'grassland cycle' of Turkington & Harper (1979b). The selection processes described above may lead to a settling down of such a cycle. Associations between particular species would therefore become more stable with time and this concurs with the findings of Aarssen & Turkington (1985).

The results reported here indicate that, given sufficient genetic variation, micro-evolutionary forces may be so precise that the properties which determine reciprocal adaptation in local neighbourhoods may be neighbour-specific even at the scale of different genotypes of the same species. The interpretation exposes the need for more investigations of the occurrence and role of species interactions which integrate beneficence and competition, and calls for an organism-centred view of community structure and evolution. The traditional view defines a community as the collection of populations occupying a given area, usually thought to affect the distribution and abundance of one another. A more refined approach regards the community as a mosaic of evolving neighbourhoods in which the individual organism is the pivotal unit of interaction (e.g. MacMahon *et al.*, 1978; 1981). This approach is especially suited to sessile organisms since any given individual will interact with others in only a very restricted neighbourhood. The present results suggest that evolutionary changes in the component yield quotient of species mixtures may be a consequence of not only niche differentiation, but also a balancing of competitive abilities and that this may be an important evolutionary mechanism of coexistence in systems of competition (Aarssen 1983).

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