

THE GROWTH, DISTRIBUTION AND NEIGHBOUR RELATIONSHIPS OF *TRIFOLIUM REPENS* IN A PERMANENT PASTURE

II. INTER- AND INTRA-SPECIFIC CONTACT

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SUMMARY

(1) A contact sampling method for detecting physical contacts between species in a permanent pasture is used to define the position of *Trifolium repens* within the vegetation, and also to define relationships between other species. A modification of the method is used to examine both inter- and intra-specific contacts.

(2) The two methods together revealed seasonal variations in the relationships between neighbours.

(3) *Trifolium repens* regularly failed to contact grasses as often as expected by chance, with the notable exception of *Lolium perenne*.

(4) Leaves of *Trifolium repens* made contacts within the canopy that were primarily interspecific, whereas the grasses exhibited mostly intraspecific and intraclonal contacts.

(5) All species monitored showed asynchronous growth cycles. This finding is interpreted as a form of temporal exclusion which permits cohabitation of the various species.

(6) The study emphasizes the role of growth form and seasonality in determining the way an individual plant senses biotic pressures.

INTRODUCTION

Explanations of the behaviour of plants and animals must come ultimately from consideration of the evolutionary forces that have determined fitness. In any resource-limited community, the activities of other organisms (competition and predation) are likely to dominate the immediate fitness of individuals, i.e. their relative chance of leaving descendants. In the case of plants, because of their relative immobility, the critical associates and competitors will usually be physical neighbours. It is known that the growth rate and reproductive activity of individual plants can be rather precisely determined by the placement and stages of development of neighbours. The closest neighbours are the most important (among plants of approximately equal size), and up to 70% of the variation in reproductive output of individual sand-dune annuals can be accounted for by the neighbours present within a radius of 2 cm (Mack & Harper 1977). Any description of vegetation that is to be interpreted in relation to the biological properties of the species

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present should therefore emphasize the way individuals meet their immediate environment of neighbours.

An individual leaf, tiller or shoot in a pasture may have three kinds of neighbour:

- (a) another species (interspecific);
- (b) a member of the same species but a different genetic individual (genet) (intra-specific, intergenetic);
- (c) a part of the same genet or clone (intraspecific, intragenetic).

In practice, it is extremely difficult to distinguish between (b) and (c) in a grassland where genets of so many species form clones with no permanent physical connection. We do not attempt to make this distinction here—but detailed mapping of leaf-mark morphs within the same pasture (Cahn & Harper 1976) has shown, for *Trifolium repens*, that intraspecific and intergenetic intermingling is on such a fine scale that intraspecific neighbours are likely to be from different clones. The three different categories of neighbour represent different types of neighbour influence—they will have quite different selectional effects and evolutionary consequences.

Although plants are usually rooted in position and so have clearly defined neighbours, the spatial relationships between species are not fixed immutably, even in a supposedly stable community. Clonal migration and seedling establishment contribute to a spatial flux. Differences in the seasonal pattern of growth may also be expected to contribute a seasonal flux in the relative importance of different species as neighbours. Numerous workers have stressed the dynamic nature of this flux in grassland, e.g. Lieth (1960), Kershaw (1973), Grubb (1977), Turkington & Harper (1979). The overall composition of the community is the summation of these phases, and cyclical phases represent fluctuation about a mean value. Some elements of the cyclical vegetational changes in grassland are controlled and directed by seasonality.

A crude estimate of which plants are 'close neighbours' can be obtained by determining physical contacts made within the canopy (Turkington & Harper 1979) or in the soil (Litav & Harper 1967). A procedure for studying canopy contacts has been developed for interspecific contacts (Turkington & Harper 1979), derived from a method of Yarranton (1966). The present paper further modifies and extends this method to examine the inter- and intra-specific contacts that are made within an area of permanent grassland, and to display seasonal variation in the relationship between neighbours. Yarranton's original method of plotless sampling was designed specifically to investigate interspecific association. As adapted for use with higher plants (Turkington & Harper 1979), the method used records of the species contacted by each sampling point ('point' samples) together with the next *different* species contacting the first, nearest to the sampling point ('contact' samples). In the present study Yarranton's original method was used, but the procedure was varied to the extent that records were made of the first 'point' sample and of the nearest 'contact' sample *irrespective of whether it was of the same species or not*.

The matrix of observed 'point' and 'contact' samples contains elements that can be analysed as a variety of 2×2 contingency squares. The original form of contact analysis uses data arranged in 2×2 contingency tables (Type I) of the form shown in Fig. 1. In this case, where two species are strongly associated, high values of χ^2 will be significant, and both positive and negative associations are detected. In the modified method, both intra- and inter-specific contacts are recorded, and it is possible to assemble the data in two different forms of contingency square (Types II and III—Figs 2 and 3). The arrangement of information in Type II contingency tables (Fig. 2) is appropriate for

		Species A	
		+	-
Species B	+	(a)	(c)
	-	(b)	(d)

FIG. 1. Contingency square I. This examines (a) contacts of species A with B; (b) contacts of species A with species other than B (or no contact); (c) contacts of species B with species other than A (or no contact); (d) contacts not involving species A and B (or no contact).

		Point-sampled species	
		A	Others
Contact-sampled species	A	(a)	(c)
	Others	(b)	(d)

FIG. 2. Contingency square II. This examines (a) contacts of species A with A; (b) contacts of species A with other species; (c) contacts of other species with A; (d) contacts not involving species A.

		Point-sampled species	
		A	B
Contact sampled species	A	(a)	(c)
	B	(b)	(d)

FIG. 3. Contingency square III. This examines (a) contacts of species A with A; (b) contacts of species A with B; (c) contacts of species B with A; (d) contacts of species B with B.

studying the relative frequency of intraspecific contacts. When intraspecific contacts are more common than random expectation, *high* values of χ^2 are obtained. The Type III contingency table (Fig. 3) is appropriate for comparing the frequency of chosen species-pairs.

There are no 'no contacts' in contingency squares II and III. Two different measures of interspecific association are obtained by using contingency squares I and III. The two measures differ in important ways: I compares contacts between defined species with other contacts (or 'no contacts'), III compares contacts between defined species-pairs with intraspecific contacts.

In the course of determining the matrix of plant-to-plant contacts, the hits made by the point samples represent a measure of species-abundance in the pasture—an estimate of cover. This is biased, like all the other samples, in favour of species high in the canopy, because it is based on the first species hit by the sampling point at each position. The data can be used, however, for a comparison of the abundance of species in the pasture as measured by sampling points, with the abundance measured by contacts (the 'plant's eye view' of the pasture).

METHODS

The study was made in the same 1-ha field of permanent grassland described by Sarukhán & Harper (1973). For the collection of contact data by the original method (and analysis by contingency square I), fifty-two 1-m² (2 × 0.5 m) quadrats were distributed over the field in a systematic arrangement at the sampling points shown in Fig. 2(a) of Turkington & Harper (1979). The peripheral areas of the field, in which the vegetation was affected by hedges, trees, etc., were eliminated from the survey area so as to leave a visually more homogeneous community. This precaution was taken so as to reduce the effect contributed by infrequent species and to reduce the amount of sampling needed. Twenty-five contact samples were recorded per quadrat, so that 1300 contact samples were recorded in each survey. A sample data matrix is shown in Turkington (1975). One such matrix was prepared for each quadrat, and the totals from the fifty-two quadrats were then summed to give a master matrix for each sampling date.

The survey was repeated at 2-monthly intervals over a period of 16 months. The last 4 months permitted an overlap of three surveys to determine if trends revealed in the first year were being reflected in the preliminary stages of the second cycle.

For the collection of contact data by the modified method (i.e. including intraspecific contacts), twenty-five further contact samples were recorded within the same fifty-two quadrats described above. In all, 1300 contact samples were recorded in each of seven surveys conducted over a period of 1 year. A sample matrix is shown in Table 1.

RESULTS

Interspecific contacts made by Trifolium repens (original method—ignoring intraspecific contacts)

Seasonal variation

Figure 4 shows the variation in interspecific contacts made by *Trifolium repens* with its immediately-neighbouring grass species over a period of 16 months from July 1973 to

November 1974. The graphs are appropriate for illustrating magnitudes of variation and not for formal statistical comparison. Two points are immediately obvious:

(i) the frequency of contacts with any one grass species varied throughout the year, and
 (ii) the yearly pattern of contacts made by *T. repens* was different for each of the grasses. *Trifolium repens* regularly failed to contact grass as often as expected by chance—with the notable exception of *Lolium perenne*, which was positively associated with *Trifolium repens* over the 16-month period of study, though the association was not significant ($P < 0.05$) at any single sampling date.

In marked contrast, there was strong negative association ($P < 0.001$) of *T. repens* with *Agrostis tenuis*, *Dactylis glomerata* and *Holcus lanatus*, and weaker negative association with *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Cynosurus cristatus* and *Poa trivialis*.

The 16-month survey period enabled the frequency of contacts between species for July to November 1973 to be compared with the frequency of contacts during July to November 1974. On testing for heterogeneity, the null hypothesis, that the two periods are homogeneous, was not rejected in any instance. This means that the two samples may be considered homogeneous. Although there are large numerical discrepancies

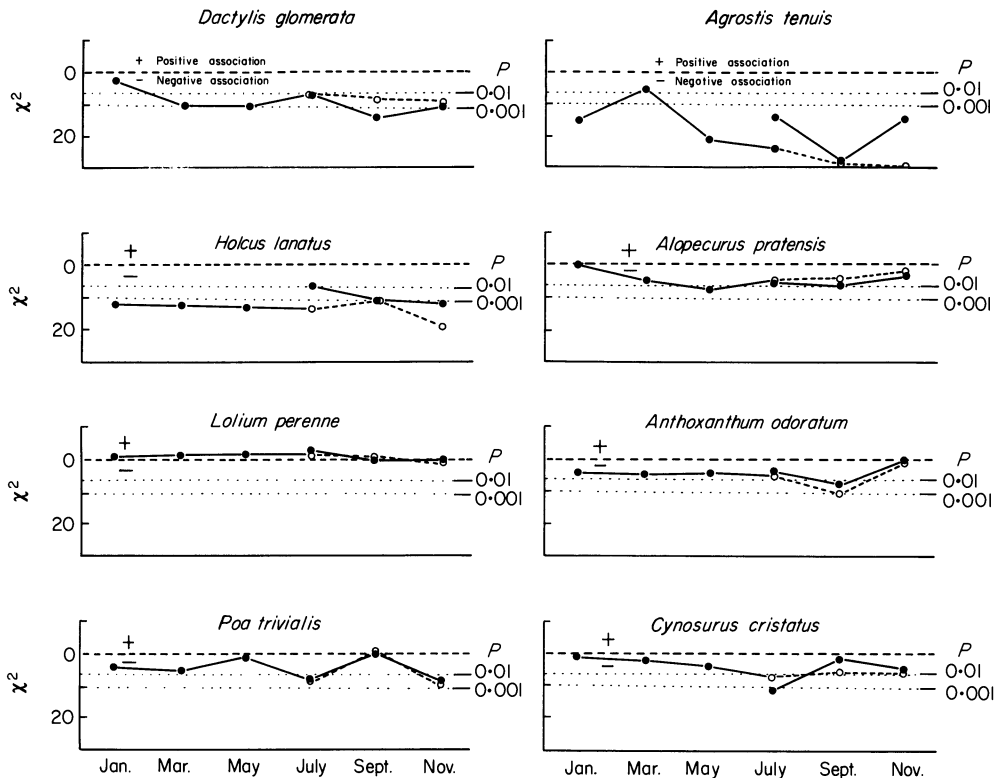


FIG. 4. χ^2 values for interspecific association between *Trifolium repens* and eight named grasses over a period of 16 months from July 1973 to November 1974. ●—●, July 1973 to July 1974; ○---○, July 1974 to November 1974. The data are calculated by the original method, i.e. intraspecific contacts were ignored. The χ^2 values indicate the magnitude of positive and negative association; values corresponding to probability levels of 0.01 and 0.001 are shown.

between χ^2 values, these occur when the χ^2 values themselves are high and large numerical differences in χ^2 then represent only small differences in probability.

The correlation between the frequency of interspecific contacts and the percentage cover of species in the pasture

Figure 5 shows the changes in composition of the pasture throughout one year, measured by the frequency of point samples (*not* by plant-to-plant contacts). Correlation coefficients were calculated between these measures of pasture composition in the different sites and the χ^2 values of contact association shown in Fig. 4. The correlation coefficients obtained are shown in Table 2. Six values are significant at the 5% level, the most interesting being (i) that where *Agrostis tenuis* is abundant, *Lolium perenne* and *Trifolium repens* make very frequent contacts; and (ii) that where *L. perenne* is abundant there are very few contacts made between *A. tenuis* and *T. repens*. It is also interesting that where there is a high percentage representation of *Poa trivialis* and 'other species' (dicotyledonous herbs and infrequent grasses) there are very infrequent contacts between *L. perenne* and *T. repens*. Whenever the percentage representation of *Lolium perenne* is high, clover makes contact with the remaining species less often than expected by chance. In plots where there is a high representation of *Agrostis tenuis*, *Cynosurus* and *Holcus lanatus*, *T. repens* usually makes disproportionately frequent contacts with the remaining grasses.

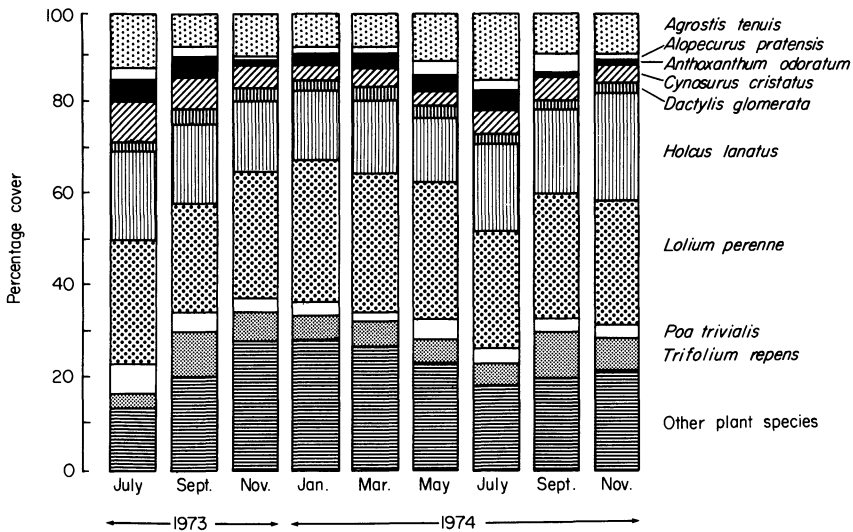


FIG. 5. Percentage cover of the most abundant species in the experimental field over the course of 1 year, based on the first hits made by vertical point samples (see text).

*Interspecific contacts made by Trifolium repens
(estimated by the modified method and contingency square analysis III)*

This form of analysis shows again (Fig. 6) that there is variation in contact frequency between *T. repens* and the various grasses throughout the year, and this yearly pattern is different in form and scale for different grass species. There are two general patterns:—

(i) The frequency of interspecific contacts is low between June and August, rises fairly consistently to a peak in December, then declines equally consistently to the original low level in the June–August period. This pattern is shown by contacts of *T. repens* with *Lolium perenne*, *Holcus lanatus*, *Cynosurus cristatus*, *Agrostis tenuis* and *Alopecurus pratensis*.

(ii) The frequency of interspecific contacts reaches a peak in April–June, declines to December, and rises to a new peak in the early summer. This pattern is shown by *Dactylis glomerata* and *Anthoxanthum odoratum*. It is perhaps noteworthy that the lowest frequencies of interspecific contacts (for the first pattern) and the highest frequencies of interspecific contacts (for the second pattern) are not concentrated in one particular summer month, but are spread over June (*Anthoxanthum odoratum*, *Holcus lanatus*, *Lolium perenne*), July (*Cynosurus cristatus*, *Dactylis glomerata*) and August (*Agrostis tenuis*, *Alopecurus pratensis*).

TABLE 2. Correlation coefficients of the relative representation by cover over the 16-month period (July 1973 to November 1974) for each of the species listed against the variation of χ^2 values for frequency of contact with *Trifolium repens* for each of the species

Relative representation by cover	<i>Agrostis tenuis</i>	<i>Alopecurus pratensis</i>	<i>Anthoxanthum odoratum</i>	<i>Cynosurus cristatus</i>	<i>Dactylis glomerata</i>	<i>Holcus lanatus</i>	<i>Lolium perenne</i>	<i>Poa trivialis</i>
<i>Agrostis tenuis</i>	0.11	0.37	-0.08	0.78*	-0.18	—	0.71*	0.39
<i>Alopecurus pratensis</i>	0.26	0.41	0.70	0.36	-0.10	-0.34	0.33	-0.51
<i>Anthoxanthum odoratum</i>	-0.26	0.69	0.30	—	0.15	-0.23	0.29	-0.39
<i>Cynosurus cristatus</i>	0.46	0.29	0.33	0.65	0.35	-0.45	0.51	0.04
<i>Dactylis glomerata</i>	-0.36	0.66	-0.17	0.30	0.44	-0.34	0.50	0.04
<i>Holcus lanatus</i>	0.51	0.22	-0.16	0.63	0.01	0.58	0.48	0.45
<i>Lolium perenne</i>	-0.76*	-0.15	-0.07	-0.54	-0.37	-0.15	-0.30	-0.30
<i>Poa trivialis</i>	0.08	0.31	-0.03	0.56	-0.02	-0.52	-0.80*	-0.02
<i>Trifolium repens</i>	0.63	0.01	0.47	-0.40	0.47	0.09	-0.54	-0.52
Other species	-0.32	-0.35	-0.36	-0.80*	0.02	0.22	-0.82*	-0.12

* $P < 0.05$.

Intraspecific contacts for selected species (contingency square analysis II)

There is great variation between species in their frequency of intraspecific contacts (Fig. 7); e.g. leaves of *Trifolium repens* have a consistently low frequency of intraspecific encounter, whereas for *Holcus lanatus* the situation is quite different—its contacts are overwhelmingly intraspecific. The other species, i.e. *Agrostis tenuis*, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Dactylis glomerata*, *Lolium perenne* and *Poa trivialis*, are more variable through time. Again two general patterns emerge: one in which the frequency of intraspecific contacts rises to a peak in the summer months of June (*Dactylis glomerata*) and July (*Cynosurus cristatus*, *Anthoxanthum odoratum*), and declines during the September–December period; and a second pattern in which the intraspecific contact-frequency rises to a peak in the winter months of December (*Trifolium repens*)

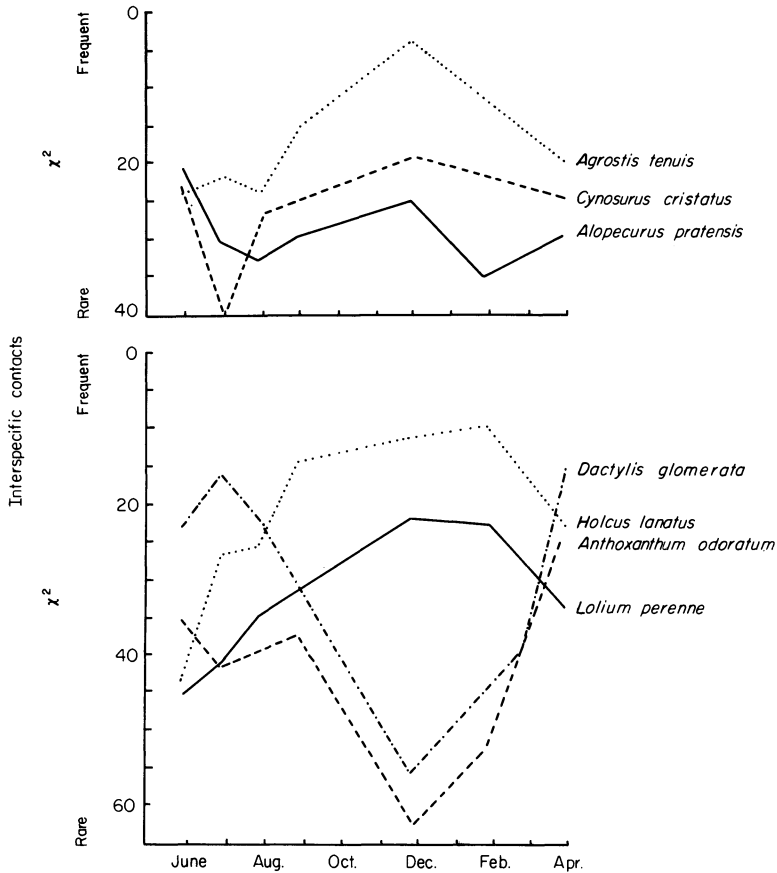


FIG. 6. χ^2 values for interspecific association between *Trifolium repens* and seven grasses over a period of 1 year. The data are calculated using Contingency square III. All associations are less frequent than random expectation.

and February (*Holcus lanatus*, *Lolium perenne*), and declines during the summer period. Clearly, the growth cycles of the species are asynchronous. Although two general patterns can be recognized, no two species have synchronous cycles.

DISCUSSION

The essential qualities which determine the ecology of a species may only be detected by studying the reactions of its individuals to their neighbours (Harper 1964). '... Accommodating to the presence of "other organisms" occupies a large part of the environmentally-directed genetic information in many species' (Cantlon 1968).

The methods used in the present paper go further than any previously used to describe the structure of a plant community from a 'plant's eye view'. The information relevant to understanding a species' position in a community is the knowledge of the way it experiences (samples) the conditions and pressures that immediately influence it. The present study emphasizes the role of growth form and growth cycle in determining the way in which a genet samples the grain of the community, and so defines the immediate forces of natural selection at the critical level of individual experience.

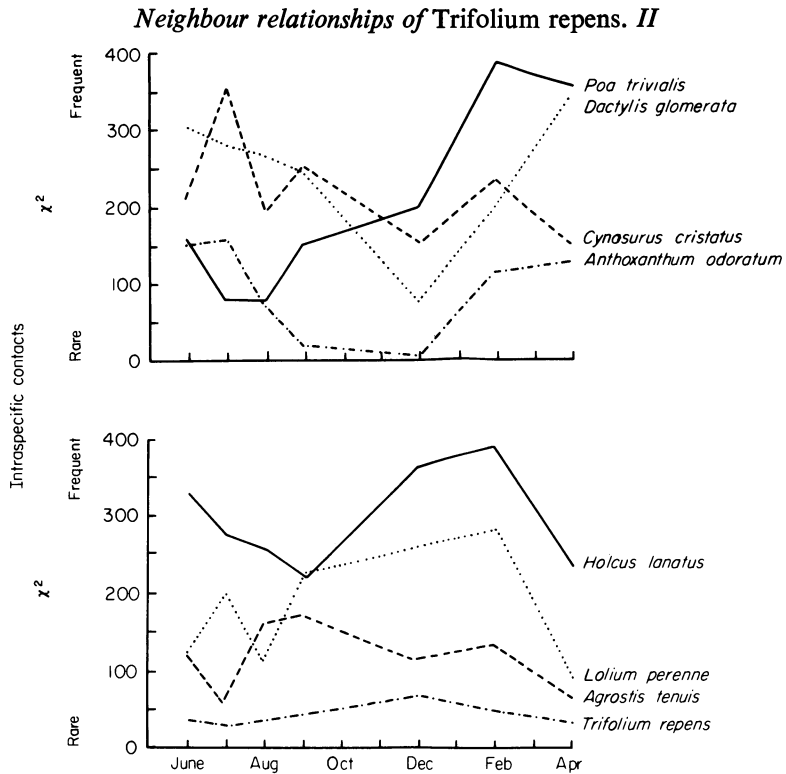


FIG. 7. χ^2 values for intraspecific association of *Trifolium repens* and seven grasses over a period of 1 year. The data are calculated using Contingency square II. All intraspecific contacts are more frequent than random expectation.

Genets of a stoloniferous species such as *Trifolium repens* are continually wandering—their older parts dying while young shoots invade new territory. In contrast, intravaginally-tillering tussock-formers such as *Holcus lanatus*, *Agrostis tenuis*, *Poa trivialis* and *Dactylis glomerata* migrate within the community mainly by establishment from dispersed seed—there is very limited migration as a tussock grows on one side and develops on the other. This difference shows up clearly in Fig. 7: the stoloniferous *Trifolium repens* maintains a consistently low frequency of intraspecific contacts relative to the clumped *Holcus lanatus*, *Lolium perenne*, *Agrostis tenuis*, *Poa trivialis* or *Dactylis glomerata*. Stoloniferous growth minimizes the rigours of intraspecific interaction, while clumping maximizes intraclonal interference. If for any species intraspecific competition is weaker than interspecific effects, survivorship will be greater in clumps, and if intraspecific competition is the greater it will 'pay' to wander and explore.

The growth habit of *Trifolium repens* seems to explain the low frequency of intraspecific contacts made by this species. The growth form of grasses, in contrast, ensures that intraclonal contacts are high, i.e. the most common neighbour for a grass leaf is another leaf of the same plant; the opposite is true for *T. repens*. The stoloniferous habit places leaves in contact with other species, and the stolon may be considered as a mechanism for escape from intraplant competition. The wandering phenotype means that a single genet of white clover may be experiencing quite different biotic selection in different parts of a single genetic individual. The lowest frequencies of interspecific contacts made by *T. repens* are with *Agrostis tenuis*, *Holcus lanatus* and *Dactylis glomerata*, three species that display marked clumping (Hubbard 1968).

When *A. tenuis* and *H. lanatus* are present in high quantities, *T. repens* is excluded from these centres of intense intraspecific interference. Brown (1939) has commented that clover is less prevalent with the tuft-forming grasses, such as *A. tenuis*, than with species forming more open stands such as *L. perenne*. Here again the stoloniferous growth form of *T. repens* permits the species to escape from a ghetto of intense intraspecific interference. *Holcus lanatus* and *Lolium perenne* are the two most abundant species in our study field, especially during the winter months when a number of species (e.g. *Alopecurus pratensis*, *Anthoxanthum odoratum* and *Cynosurus cristatus*) die back to varying degrees. It is interesting that at this period of very high relative abundance of *Holcus lanatus* and *Lolium perenne*, *T. repens* displays its lowest frequency of contacts with them. This may again be explained primarily in terms of growth forms of the species. The relative abundance of the species is of course also important in determining contact frequency, but only if the growth forms of the species interweave or form a mosaic of many interfaces.

The results from Table 2 suggest that local dominance of *Agrostis tenuis* is incompatible with *T. repens*, but that *T. repens* is accepted in close relationship with locally-dominant *Lolium perenne*. High representation of *L. perenne* in a quadrat is associated with a disproportionately low frequency of interspecific contacts between *T. repens* and all other species, and this suggests that *L. perenne* and *T. repens* rather readily tolerate each other's presence. This argument applies also to *Poa trivialis*, and it may be relevant that the seasonal growth patterns of *Poa trivialis* and *L. perenne* are similar (Vartha 1972).

If, as has been suggested, *Trifolium repens* 'avoids' the interspecific interference of clumped species, the question must now be asked why *T. repens* invariably cohabits so closely with *Lolium perenne* in the field when *L. perenne* itself has an, albeit loose, clumped growth form? The answer appears to lie in the asynchrony of the growth cycles of the two species. Scarisbrick & Ivins (1970) showed that competitive interactions between pasture plants are influenced by seasonal weather conditions. In their studied pasture, the pattern of competition was dominated by the competitive success of *Lolium perenne*, which commences growth in early spring (Blackman 1933). During July and August a depression in growth of *L. perenne* occurs (Anslow 1965), coinciding with the periods when conditions are optimal for the growth of *T. repens* (Blackman 1933). On the whole, if a species is seasonal in growth it would pay to wander among species with asynchronous seasonality. The variation in seasonality of contacts made by clover and the different grasses is clearly shown in Fig. 7. Although there are two primary patterns, i.e. a winter 'high' frequency of intraspecific contacts and a winter 'low', there is great variation, and different species reach their peaks at different times of the season. During the winter period, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Dactylis glomerata* and *Poa trivialis* die back to varying degrees, and the frequency of their intraspecific contacts consequently declines. When these species die back there are more opportunities for the remaining species such as *Agrostis tenuis*, *Holcus lanatus* and *Lolium perenne* to contact intraspecifically.

The present analysis reinforces the findings of the first paper, based on broader-scale studies of ordination and pattern, that biotic interactions may dominate the behaviour of species in the sward. Niche diversification can be recognized in gross correlations with the presence of trees and hedges (Turkington & Harper 1979), in differences in seasonal rhythm between species, and in important fine details of habitat mosaic imposed by growth form.

Recently, Bock (1972) has suggested that the selection forces generated by species-interactions may be largely responsible for the speed of micro-evolutionary change and for the total amount of change. He postulates that interaction between pairs of species is the important source of directional selection required for major evolutionary modification, and that the rate, total amount of change, and final diversity in transpecific evolution are closely correlated with the opportunity for species-interactions of all types. The results presented in this paper suggest that these 'opportunities for species-interactions' are subtly conditioned by the growth form and seasonality of the individuals.

Two lines of enquiry are suggested by the findings: (i) deliberate transplants or sowing of *Trifolium repens* into parts of the sward dominated by different grasses—this might reveal the differing hospitality of grass species as environments for clover growth: (ii) study of plant-to-plant variation of *T. repens* within the pasture, to reveal whether extremely local selection by different grass neighbours affects the genetic structure of the population. These two aspects are discussed in succeeding papers.

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