

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

IV. FINE-SCALE BIOTIC DIFFERENTIATION

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SUMMARY

(1) Ramets of *Trifolium repens* were sampled from sites in a field of permanent pasture dominated by a mosaic of *Lolium perenne*, *Holcus lanatus*, *Cynosurus cristatus* and *Agrostis tenuis*. After multiplication of the ramets in a glasshouse, they were transplanted back into the original swards in all combinations of clover 'type' and site of origin. The pre-existing vegetation on the sites was either destroyed by herbicide or left as a control.

(2) Clover 'types' were also transplanted into experimental sown swards of the four grass species.

(3) Differences were found in aggressiveness of the grass swards and species, and between the clover 'type', and these were most clearly expressed in the growing swards. Most striking was a 'principal diagonal effect', in which each clover 'type' made most growth when transplanted back into its sward of origin—or into a pure stand of the grass that had dominated that sward.

(4) This is interpreted as a micro-evolutionary response of clover to the diversifying selection imposed by a variety of grass neighbours, and is discussed in relation to the ecological significance of the outbreeding habit and 'Sisyphean fitness'.

INTRODUCTION

The study of micro-evolution in flowering plants has concentrated upon the formation of edaphic and climatic ecotypes—locally-differentiated populations fitted to local peculiarities of the physical environment (e.g. Turesson 1922; Kruckeberg 1951; McMillan 1956; Snaydon & Bradshaw 1961; Antonovics, Lovett & Bradshaw 1967). The physical components of the environment, together with predators, constitute the forces of selection; these might be called 'Wallacian' forces (Darwin & Wallace 1858). In contrast, Darwin's description (Darwin 1859) of the processes of natural selection emphasized far more forcibly the biotic processes that result from population pressures, i.e. competitive interaction both inter- and intra-specific. A 'Darwinian' might expect micro-evolution to be dominated by biotic interactions, but there has been little search for biotic ecotypes. One exception is a study by Watson (1969), in which she showed that populations of *Potentilla erecta*, growing in neighbouring areas of *Molinia*- and *Agrostis*-dominated

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grassland, were different when compared both as transplant material and as seed progeny growing in an experimental garden. This is suggestive evidence for the formation of biotic ecotypes, and it can be argued that the differentiation within *Potentilla* was due to the different selective pressures imposed by the presence of *Molinia* or *Agrostis*. An alternative explanation, however, could be that the very conditions that caused one area to be dominated by one grass and the other by another, were the same conditions that selected for divergence in *Potentilla erecta*.

Striking evidence that genetic differentiation occurs within a population of a single species comes from the studies of Allard & Adams (1969), who showed that lines of barley that had persisted together in mixture over many generations had the property of yielding more reliably in mixture than in pure stands, and more reliably than lines that had no history of co-evolution. Kannenberg & Allard (1967) have shown that *Festuca microstachys*, an obligate inbreeder, maintains high genetic diversity within its population, and it can be argued that this is maintained by the competitive exclusion of like individuals and the favouring of neighbours with subtle co-evolved differences.

This paper describes an experiment designed to examine the extent of the differentiation that occurs within a population of *Trifolium repens* in an old permanent-grassland site in North Wales. The hypothesis tested was that the various species of grass in the pasture exert different selective pressures on populations of *T. repens*, and the experiments were designed to discover whether samples of clover taken from the neighbourhood of different grasses differed in their ability to grow in the presence of those same species.

METHODS

The site chosen for study was the same 1-ha field of permanent grassland described by Sarukhán & Harper (1973), by Turkington & Harper (1979a, b) and Turkington *et al.* (1979c), and at which studies had been made of the leaf-mark polymorphism in *Trifolium repens* (Cahn & Harper 1976a, b).

Cuttings were taken from three different clones of *T. repens* in each of four sites in the experimental field. The sites represented areas of high density of *Agrostis tenuis* (79.6% cover), *Cynosurus cristatus* (56.5% cover), *Holcus lanatus* (94.6% cover) or *Lolium perenne* (96.4% cover). The positions of sampling are shown in Fig. 2(c)–(f) in Turkington & Harper (1979a). The cuttings were rooted and propagated under glasshouse conditions, and, after 3 months, were further subdivided by taking cuttings (approximately 2.5 cm of stolon with one trifoliate leaf and an associated axillary bud) which were transplanted into 2.5-cm-diameter 'jiffy' pots filled with field soil.

Each of the four populations of *Trifolium repens* prepared in this way was thus derived from the bulked ramets of three clones. The four populations are distinguished in this paper by a subscript, e.g. *T. repens*_(Lolium), refers to clover sampled from plots dominated by *Lolium perenne*.

The rooted shoots of *Trifolium repens* (phytometers) were transplanted into plots in the field swards, in the sixteen combinations of the four populations of clover phytometers and the four sites of origin. Thus *T. repens*_(Lolium) was planted back into the *Lolium*-dominated site and also into the sites dominated by *Holcus*, *Agrostis* and *Cynosurus*. At each of the four sites there were twenty-four plots, 30 × 30 cm, separated by 10-cm-wide guard strips. Twelve of the plots had been treated with 'Paraquat' (di-pyrrilidium chloride, 6 ml l⁻¹) to destroy the existing sward before the transplants were introduced.

Ten phytometers from a bulk population were transplanted into each plot. Thus at each of the four sites the experimental design involved 2 sward treatments (control and chemically denuded) \times 4 bulk clonal populations of *T. repens* \times 3 replicates; the positions of the twenty-four plots were completely randomized with respect to each other. The phytometers were introduced in early May 1974, and observed at 2–4-week intervals until May 1975. At the end of the experiment, the shoots, including stolons of the surviving phytometers, were harvested and dry weights were measured. The denuded plots were kept bare (except for the phytometers) by repeated hand-weeding.

At the same time that phytometers from the four clover bulk populations were introduced into the field plots, a second experiment was carried out in which further phytometers from the bulk populations were planted into deliberately-sown swards. Forty-eight boxes (40 \times 30 \times 10 cm) were filled with soil from the experimental field and left in a glasshouse for 3 months. These were weeded continually and the soil was stirred periodically to stimulate the germination of dormant weed seeds. Twelve of the boxes were then sown with seed of *Agrostis tenuis*, twelve with *Cynosurus cristatus*, twelve with *Holcus lanatus* and twelve with *Lolium perenne* S23. The seeding rate was 4.17 g seed per box. The seed was obtained from Milne Masters, Chester.

Four months after the grass seeds had been sown, phytometers of each of the four clover 'types' were planted into each of the four grass swards, i.e. *T. repens*_(Lolium) was planted into pure swards of *Agrostis tenuis*, *Cynosurus cristatus*, *Holcus lanatus* and *Lolium perenne*; *T. repens*_(Cynosurus), *T. repens*_(Holcus) and *T. repens*_(Agrostis) were planted similarly. Five phytometers were planted into each box. Each combination of clover 'type' and grass species was replicated three times, and the layout was a completely randomized block in a cool glasshouse. The boxes were watered daily, and once every 2 weeks the swards were clipped to approximately 3 cm to simulate a grazed pasture and to maintain the plants in a vegetative condition. Twelve months after the introduction of the transplants, the above-ground parts of the clover plants were removed from the swards, dried and weighed.

RESULTS

The growth of clover 'types' in denuded plots

On the denuded plots there was no significant difference between the different clover 'types' either in weight or in the number of surviving transplants (Tables 1(a) and 2). There were, however, significant differences ($P < 0.05$) between sites in total dry weight of clover, though not in the number of survivors. The interaction between clover 'type' and site was significant ($P < 0.01$) for total dry weight but not for the number of survivors (See Table 2).

An especial interest lies in the principal diagonal of the data matrix—this represents the performance of clover 'types' transplanted back into the sites from which they had been derived. The values in the principal diagonal represent a balanced orthogonal component of the total sum of squares in an ANOVA, and it is possible, therefore, to test for the significance of departures from the mean that are due to this specific component of the interaction table. In the denuded plots the mean yield of plots in the principal diagonal was significantly higher ($P < 0.05$) than in the remaining combinations of clover 'type' and site. The mean weight of clover transplanted back into its own sites was 135.6 g, compared with 104.7 g in other combinations of 'type' and site.

TABLE 1. Yields (g) and survivorship (in parentheses) of phytometers of *Trifolium repens* 'types' sampled from four sites in the experimental field and transplanted back into all combinations of 'type' and site; the performances of 'type' transplanted back into their original sites are shown in heavy print on the principal diagonal of each matrix; all values are means of three replicates

Clover 'type'	<i>Lolium perenne</i>	Sites dominated by:			Clover 'type' mean
		<i>Holcus lanatus</i>	<i>Cynosurus cristatus</i>	<i>Agrostis tenuis</i>	
(a) Denuded plots					
<i>T. repens</i> _(Lolium)	169.6 (1.0)	90.0 (0.9)	103.0 (0.93)	77.4 (0.93)	110.0 (0.94)
<i>T. repens</i> _(Holcus)	106.0 (0.97)	125.4 (0.97)	109.4 (0.9)	116.5 (1.0)	114.3 (0.96)
<i>T. repens</i> _(Cynosurus)	146.1 (1.0)	102.3 (0.9)	140.0 (0.97)	61.9 (0.97)	112.6 (0.96)
<i>T. repens</i> _(Agrostis)	92.9 (0.9)	112.0 (0.97)	138.5 (1.0)	107.5 (1.0)	122.7 (0.97)
Site mean	128.7 (0.97)	107.4 (0.93)	122.7 (0.95)	90.8 (0.98)	
		L.S.D. 5% = 28.0 (0.064)			
(b) Control vegetated plots					
<i>T. repens</i> _(Lolium)	0.51 (0.33)	0.05 (0.10)	0.53 (0.40)	0.24 (0.20)	0.33 (0.26)
<i>T. repens</i> _(Holcus)	0.30 (0.10)	0.35 (0.27)	0.34 (0.30)	0.94 (0.43)	0.48 (0.28)
<i>T. repens</i> _(Cynosurus)	0.50 (0.17)	0.08 (0.13)	0.87 (0.63)	0.20 (0.33)	0.41 (0.32)
<i>T. repens</i> _(Agrostis)	0.57 (0.40)	1.15 (0.73)	1.29 (0.70)	1.83 (0.68)	1.21 (0.63)
Site mean	0.47 (0.25)	0.41 (0.31)	0.76 (0.51)	0.81 (0.41)	
		L.S.D. 5% = 0.23 (0.144)			
(c) Sown grass plots					
<i>T. repens</i> _(Lolium)	64.8	18.3	27.1	49.1	39.8
<i>T. repens</i> _(Holcus)	25.4	32.3	29.0	27.5	28.5
<i>T. repens</i> _(Cynosurus)	30.2	22.3	68.4	43.2	41.0
<i>T. repens</i> _(Agrostis)	39.7	32.7	38.9	71.9	45.8
Grass species mean	40.0	26.4	40.9	47.9	
		L.S.D. 5% = 7.1			

TABLE 2. The levels of significance of main effects and interactions in an experiment in which four bulk populations ('types') of *Trifolium repens* were planted as phytometers into four sites in (a) denuded natural swards, (b) control natural swards and (c) deliberately sown swards; the values for the principal diagonal represent the significance of clover yield of phytometer types transplanted back into the site from which they had originated compared with other parts of the interaction table

Degrees of freedom		Clover 'type'	Site	Clover × site	Principal diagonal
		3	3	9	1
Denuded sites	Dry weight yield	NS	*	**	*
	Survivorship	NS	NS	NS	NS
Control sites	Dry weight yield	**	**	*	***
	Survivorship	**	**	NS	*
Experimental sown swards	Dry weight yield	**	**	**	*****
	Survivorship	NS	NS	NS	NS

Probability levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *****, $P < 0.00001$; NS, not significant.

The growth of clover 'types' in control vegetation

In the vegetated plots the clover transplants made much less growth, presumably because of the aggressiveness of the grasses. However, the main effects of clover 'type' and site and the interactions were much more marked than in the denuded plots. Both total dry weight and the number of survivors differed between clover 'type' ($P < 0.01$). Most of the difference between 'types' was accounted for by the relatively vigorous growth of *T. repens*_(Agrostis) in swards, though it was not particularly vigorous in denuded plots.

Clover growth differed between sites ($P < 0.01$). The interaction of clover 'type' and site was again significant, but the most interesting feature is the very high significance of the principal diagonal. Secondary to the effect of *Agrostis tenuis*, each clover 'type' made most growth when transplanted back into its sward of origin (Table 1(b) and 2). The mean yield of clover 'types' transplanted into their own sites was 0.89 g and into alien sites 0.52 g (significant at $P < 0.001$).

In the vegetated sites the number of surviving phytometers differed both between clover 'types' ($P < 0.01$) and between sites ($P < 0.01$). The interaction as a whole was not significant, but the principal diagonal effect was significant at $P < 0.05$. The reduced survivorship of the phytometers in the vegetated swards contrasted very strongly with their behaviour in the denuded swards, where no significant effect of clover 'type', site or interaction could be detected in survivorship. It is a mistake to interpret survivorship as a fundamentally different effect from growth of survivors. The growth of clover was so much depressed in the control swards that death or survival may reflect no more than marginally negative or marginally positive relative growth rates.

The growth of clover 'types' in sown swards of single species

The growth made by phytometers of the four clover types in sown swards of the four grasses is shown in Fig. 1 and in more detail in Tables 1(c) and 2. The order of aggressiveness of the four grass species (measured by the growth of clover summed over the four clover types) was *Agrostis tenuis* > *Cynosurus cristatus* > *Lolium perenne* > *Holcus lanatus*. The influence of associated grasses on clover growth was significant at $P < 0.01$. Similarly, the four clover populations can be ranked according to their growth in the presence of the grasses: *T. repens*_(Agrostis) > *T. repens*_(Cynosurus) > *T. repens*_(Lolium) > *T. repens*_(Holcus)—the differences are significant at $P < 0.01$. The interaction 'type' and site is again significant at $P < 0.01$. The most striking result from this experiment was the very high yields of clover when each 'type' was grown in mixture with the grass species that had dominated the area from which the clover was sampled in the field; the principal diagonal contributes overwhelmingly to the total sum of squares in the interaction table. The mean yield of clover in principal diagonal interactions was 59.4 g, and in other interactions 31.9 g ($P < 0.00001$).

DISCUSSION

It is well-known that grasses differ in their aggressiveness towards *Trifolium repens* (Chestnut & Lowe 1970). Clones of *Poa pratensis* differ in the competitive ability they display in mixtures with *T. repens* (Myers & Garber 1942). *Trifolium repens* is suppressed more by taller-growing, more productive strains of *Poa pratensis* than by shorter-growing, less productive strains (Ahlgren, Smith & Nielsen 1945). The aggressiveness of strains of *Poa pratensis* towards clover was only weakly correlated

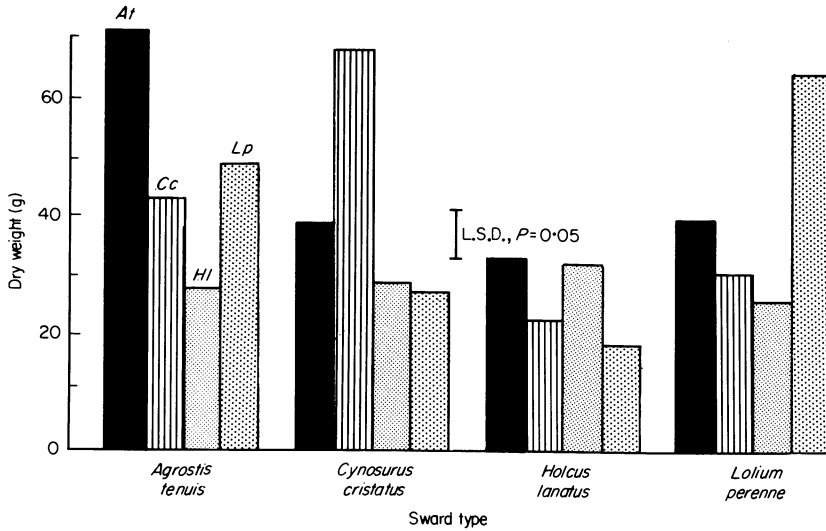


FIG. 1. The dry weight of plants of *Trifolium repens* from a permanent grassland sward, sampled from patches dominated by four different perennial grasses and grown in all combinations of mixture with the four grass species. Clover 'types': At, *Agrostis tenuis*; Cc, *Cynosurus cristatus*; HI, *Holcus lanatus*; Lp, *Lolium perenne*.

with the yield of the grass, so presumably factors other than simply growth rate influence the interaction. There is also evidence that species of grass affect *T. repens* and *Poa pratensis* differentially (Charles 1968). Four considerations lead one to suspect that, if biotic differentiation occurs within populations of a species, it might be expected to occur in *T. repens* in the studied pasture.

(1) Hill (1977) has shown that different strains of *Lolium perenne* elicit quite different growth responses and phenotypes from a single clone of *T. repens*, in a complex interaction between the response to the grasses and the source of nitrogen—mineral or rhizobial. This suggests that species and strains of grass will exert different selective forces on *T. repens* when they grow together.

(2) Natural populations of *T. repens* are genetically extremely diverse (Cahn & Harper 1967a, b), obligately outbreeding (Williams 1931) and, in permanent grasslands, live in a mosaic of other species—mainly grasses (Turkington & Harper 1979a).

(3) Clover clones from the studied pasture vary in aggressiveness—as measured by their reaction to a standard clone (Turkington *et al.* 1979c).

(4) The pasture is at least 60 years old. It is perhaps not surprising if, in this time, fine-scale micro-evolution has occurred in which clover strains have been selected by the different grasses that are part of their normal day-to-day neighbourhood.

The aggressiveness of the field vegetation was measured by comparing clover growth in chemically denuded and control vegetated swards, and in all sites the presence of actively-growing vegetation strongly depressed the growth of clover phytometers. However, the clover was more depressed in some sites than others. In the denuded swards there was variation in clover growth: expressed as the order of reduction of clover growth, the growth was most depressed in the order:

Agrostis sward > *Holcus* sward > *Cynosurus* sward > *Lolium* sward.

This effect was significant only at $P = 0.05$. Although the denuded sites differed in hospitality to clover, the presence of a growing sward greatly depressed and forced a quite different order on the growth of the phytometers. Clearly, the growing sward provides a hostile environment for clover; this was shown particularly in the low survivorship of phytometers (Table 1(a) and (b)). The order of aggressiveness of the living grass swards as measured by the survivorship of transplants was:

Holcus sward > *Lolium* sward > *Cynosurus* sward > *Agrostis* sward.

The differences were significant at $P < 0.01$.

In the artificially-sown swards the different grasses suppressed clover growth differentially, giving an order of aggressiveness of:

Holcus > *Lolium* > *Cynosurus* > *Agrostis*.

This was significant at $P < 0.01$, and the same as the order observed in the natural swards. Thus, although the natural swards were not pure and the sown swards were grown from commercial seed samples, the order of aggressiveness of grass species towards clover remained the same in the two experiments.

The four clover 'types' did not differ significantly in the denuded swards, but behaved very differently in the natural and sown swards. The order of aggressiveness, measured by clover growth was:

(a) In control vegetated plots: $T. repens_{(Agrostis)} > T. repens_{(Holcus)} > T. repens_{(Cynosurus)} > T. repens_{(Lolium)}$ (significant at $P < 0.01$).

(b) In sown plots: $T. repens_{(Agrostis)} > T. repens_{(Cynosurus)} > T. repens_{(Lolium)} > T. repens_{(Holcus)}$ (significant at $P < 0.01$).

The order was slightly altered in the two experiments but not significantly. The great vigour of $T. repens_{(Agrostis)}$ and the relative weakness of $T. repens_{(Lolium)}$ appeared in both experiments, though the relative status of $T. repens_{(Holcus)}$ and $T. repens_{(Cynosurus)}$ was less clear.

The most remarkable feature to emerge from the experiments was the strength of the interaction between site and clover 'type' in the field, and between grass-associate and clover 'type' in the sown plots. The interaction was mainly accounted for by the principal diagonal component of the interaction table, i.e. each clover 'type' performed best, on average, when grown in the site from which it had originally been sampled, or in association with the grass species that dominated that site. This points to a finer and more subtle specialization of organism to environment than had previously been recognized within plant communities.

The 'principal diagonal effect' appears in the denuded plots, though relatively weakly (total interaction $P < 0.01$, principal diagonal $P < 0.05$). In an earlier comparison of establishment and growth of a standard seed population sown into denuded plots in the same sites, no differences between sites had been detected (Turkington *et al.* 1979c). The interaction between clover 'type' and site in the denuded sward suggests that the effects of each dominant grass on clover are expressed at least partially through the soil. It is perfectly clear, however, that the major part of the 'principal diagonal effect' is only expressed in a living sward—whether natural or deliberately sown: it then contributes overwhelmingly to the interaction as a whole. In the natural sward the total interaction is significant at $P < 0.05$ and the principal diagonal at $P < 0.001$. In the sown sward the total interaction is significant at $P < 0.01$ and the principal diagonal at $P \ll 0.00001$.

If the studies had been made with a grass or some other dicotyledonous herb it would have been conventional (though probably wrong) to ignore pests, pathogens, mycorrhiza and other symbionts in interpreting plant-plant interactions. This easy path is denied in a study of *Trifolium repens*, because the species has been so intensively studied, and it is well-known not only that it forms strain-specific associations with *Rhizobium* (Mytton 1975), but also that its vigour is strongly dependent on mycorrhizal associations (Tinker & Sanders 1975). Mycorrhizal association may be especially important in the studied field as the phosphate level is low (Turkington & Harper 1979a). However, the fact that the 'principal diagonal effect' is shown so clearly in the sown-plot experiment suggests that subtle microbial interactions are less likely to explain the field observations. For the sown-plot experiment the clover transplants had been multiplied in a standard soil and the swards had been sown in the same soil—a mixed sample taken from mole-hills in the field: the opportunities for subtle microbial site effects were effectively removed. Nevertheless, it was in the sown-plot experiment that the 'principal diagonal effect' was strongest.

The most likely interpretation of the experimental results is that micro-evolution of *T. repens* has occurred in response to the differing selection pressures exerted by the different species of grass. It has been shown that the seasonal rhythm of growth of the grasses is very different—especially as viewed by the frequency of clover-grass contacts though the year (Turkington & Harper 1979b). Moreover, clover experiences predominantly interspecific contacts (mainly with grasses) in the sward, which suggests that they play a critical part in its 'struggle for existence'. A previous study has shown that *T. repens* tends to be associated rather seldom with *Agrostis tenuis* and *Holcus lanatus* which, at a fine scale, exclude clover from their close tussocks. The very high aggressiveness of the clover clones sampled from *Agrostis* (and to a lesser extent from *Holcus*) fit well with this interpretation—only the more vigorous forms persist in close association with these grasses. In contrast, *T. repens* is intimately associated in the field with *Lolium perenne* (Turkington & Harper 1979a); this close cohabitation has been interpreted as due to the looser tussock of *L. perenne* and the marked asynchrony of growth cycle (and so reduced level of mutual interference) of these two species. This interpretation fits well with the finding that *T. repens*_(Lolium) has weak general aggressiveness towards the grasses.

Differences in aggressiveness of clover clones from different parts of the field had been detected first (Turkington *et al.* 1979c) by comparing them against a standard clone of clover. The present experiments made with quite independently-sampled clones, and tested in mixtures with grasses, confirm the presence of biotically-adapted strains in *T. repens*. It is not possible without breeding experiments to determine whether these differences are genetic or persistent cytological effects. Breese, Hayward & Thomas (1965) have shown that intracloonal selection can be a powerful force in pasture grasses, and it may occur in *T. repens*. However, the fact that all the studied clonal bulk populations had been multiplied for 4 months before the experiment began, in the same soil and glasshouse environment and in the absence of grasses, makes a 'training' interpretation less likely than a genetic interpretation. Certainly the sampled sites were too far apart for them to have contained the same clones. The simplest interpretation of the observations is that the genetic diversity of white clover in this old pasture is maintained in part by diversifying selection from the variety of neighbouring grass species. It would be interesting to look for a similar effect among the grasses, though their generally tighter, tussock-forming habit of growth would usually deny them the opportunity permitted to clover for continual wandering within a co-adapted mosaic of the pasture.

Within the community of permanent grassland, the clones of *Trifolium repens* are long-lived, and continually migrate by stoloniferous growth through the sward. A great diversity of clones is present, as is indicated by the high frequency and close intermixing of clones with different leaf-mark polymorphism (Cahn & Harper 1976a). The input of new genets through seedling establishment in such swards is exceptionally rare, or seems to occur only where there is localized soil disturbance. The present experiments suggest that, in addition to the known polymorphisms of leaf mark, cyanogenesis, *Rhizobium* strain-sensitivity and incompatibility, there is a further level of diversity associated with the ability to compete with particular species of grass. The presence of a variety of different important grasses within the same pasture presumably provides an equal number of different specialized selective forces. The stoloniferous habit of *Trifolium repens* permits its genets continually to track change in the distribution pattern of the associated grass species. It is now well-known that two components of a mixed population can exert selective forces upon each other that result in rapid mutual shifts in niche occupation (Seaton & Antonovics 1967; Barker 1971). Such experimental studies have been made in the laboratory with *Drosophila*. The experiments described here appear to be the first indication of the fine-scale development of such biotic ecotypes in nature.

Discussion has recently started about the significance of outbreeding in the context of the fitness displayed by organisms as individuals (e.g. Williams 1975). Williams suggests circumstances in which fit individuals—those that leave most descendants—represent unusual combinations of genes that are rarely re-assembled after outbreeding and recombination. In a fiercely-selective environment that is patchy in space and time, fit genotypes are repeatedly reselected from a wide array of recombinants. The specialized clover–grass co-adaptation revealed by the present experiments suggests just such special high fitness—and on this interpretation, the fitness qualities might not be easily displayed in a progeny test. Williams (1975) writes about ‘Sisyphean fitness’—in which each generation of progeny faces anew the selective process that picks out the individuals of high fitness. In a long-lived community in which fit individuals live long and physically ‘track’ favourable places in the species-mosaic, new and successful genets may only colonize if they differ in some critical way from those already established. This interpretation was anticipated by Stebbins (1958) ‘If, . . . a population remains constant in size, and its individuals are so long-lived that they produce progeny in far greater numbers than are able to survive, then the advantage will go to those individuals which are able to produce a relatively small proportion of highly fit descendants, even at the expense of a large number of poorly adapted progeny’. This would seem to describe exactly what we know of the behaviour of white clover in old pastures.

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