

The three C's – competition, coexistence and coevolution – and their impact on the breeding of forage crop mixtures

J. Hill

Broneirian, Llanbadarn Road, Aberystwyth, Dyfed SY23 1HB, Wales, UK

Received August 12, 1989; Accepted August 30, 1989

Communicated by P. M. A. Tigerstedt

“In the badlands, where nature is rarely kind, they (the animals) make their meagre resources serve them and so find their way without fighting” (Chatwin 1987)

Summary. The role of competition, coexistence and coevolution in the formation of plant communities is discussed, particularly in relation to the breeding of improved grass/legume mixtures. Competition occurs whenever the demand for a particular resource outstrips supply, with the pressures generated within a species expected to exceed those between species. These pressures must be withstood before populations can coexist within a community. This is accomplished by a process of niche diversification, arising from temporal or spatial differences between the populations, that enables them to draw on resources not readily available to their competitors. Coexistence is crucial to the success of any breeding programme designed to raise the productivity of grass/legume pastures, because it enables components to adapt not only to the environment which they share, but also to each other. A strategy that improves the “general ecological combining ability” of one or both components by a process of recurrent or reciprocal recurrent unilateral adaptation may prove successful, particularly if existing niche differences are increased thereby. Although both processes may give rise to populations which have apparently coevolved, only those resulting from reciprocal recurrent selection will meet the criteria of specificity and reciprocity.

Key words: Competition – Coexistence – Coevolution – White clover – Perennial ryegrass

Competition

Many definitions of competition have been put forward. That proposed by Milne (1961), however, is probably the

most widely accepted and acceptable, even though, like the above quotation, it relates to animal competition. Competition will occur whenever and wherever the demand for a shared resource exceeds its availability, since competition is the endeavour by two or more individuals to secure the measure each requires of a resource which is in limited supply. Those individuals who obtain this measure survive, those which fail, perish. In plants, competition usually occurs for nutrients, water or light, resources which de Wit (1960) collectively refers to as “space”. Since individuals with similar morphologies will make comparable demands upon the available environmental resources (Mather 1961; Caligari 1980), the stresses engendered by intraspecific competition are expected, and have been shown to be greater than those induced by interspecific competition (Connell 1983; Hill et al. 1987; Hill and Michaelson Yeates 1988). If different populations are to coexist within a community, however, these competitive stresses must somehow be avoided, minimised or tolerated; or as Harper (1977) states, an evolutionary solution to the problems posed by these stresses must be sought.

Niche diversification and coexistence

Within a community, competing populations maintain a stable coexistence by niche differentiation, where a niche is defined as “the range of values of environmental factors that are necessary and sufficient to allow a species to carry out its life history” (James et al. 1984). A species would normally be expected “to occupy a geographic region that is directly congruent with its niche distribution”. At best, however, niche theory offers a simplistic view of how competition can sustain a pattern of resource partitioning among coexisting species (Roughgar-

den 1983a). Niches may be differentiated spatially or temporally, as when species have different rooting depths or use resources successionaly throughout the growing season. Several theoretical studies have demonstrated how species competing for renewable resources can coexist. They may actually occupy different niches or become specialized users of a particular resource (Lawlor and Maynard Smith 1976), especially if, as expected, the effects of intraspecific competition are greater than those of interspecific competition (Antonovics 1978; Berendse 1983; Vance 1984, 1985; Pacala 1988).

Alternatively, Aarssen and Turkington (1985a) believe that natural selection will leave species competing for the same resource with similar interspecific competitive abilities. Evidence from natural pastures, showing a progressive similarity in the competitive ability of the species with increasing age of pasture, is cited in support of their hypothesis (see also Fowler 1981, 1982; Roughgarden 1983b). By contrast, Kelley and Clay (1987) detected differences in interspecific competitive ability between two coexisting perennial grass populations, though they used a different measure of competitive ability than Aarssen and Turkington. However, the estimates of competitive ability obtained by Aarssen and Turkington, Fowler, and Kelley and Clay measure the combined effects of intra- and interspecific competition. Separation of these effects requires the inclusion in the experimental design of an appropriate density series of monocultures (see, e.g. Mather and Caligari 1981; Spitters 1983; Firbank and Watkinson 1985), in addition to the conventional substitution series of mixtures often used to assay the effects of competition (de Wit 1960).

Niche diversification will be underpinned by genetic changes within populations resulting from the action of directional, stabilizing or disruptive selection (Mather 1953, 1973). Directional selection will operate initially, provided there is no environmental heterogeneity within the territorial range of the population. As the environmental optimum (adaptive peak) is approached, selection will act to stabilize the population around this optimum, thereby reducing the level of variability. Any physical or biotic discontinuities within the environment will effectively divide that population into a number of subpopulations. Disruptive selection will operate with respect to the original population, though within these subpopulations, as they move towards their respective optima, directional and then stabilizing selection will act as before. If the selected classes are interdependent, disruptive selection may lead to polymorphism, as in a dioecious species. Where these classes are independent, reproductive isolation may result providing, amongst other things, that suitable habitats are separated in time or space, that sufficient heritable variation exists within the constituent populations and that individuals mate locally within their chosen habitats (Mather 1955; Thoday and Gibson

1962; Rice and Salt 1988). Adaptive peaks will be occupied by the fittest members of a population, while selection will be strongest against those individuals whose phenotype places them in an adaptive valley (see also Brown and Vincent 1987, in relation to competitive speciation).

Apart from selection pressures exerted by those environmental factors operating within its territorial range, local pressures generated by neighbours have a role to play in community formation (Harper 1978; Turkington and Harper 1979; Burdon 1980). This point was emphasised by Breese and Hill (1973) when re-analysing data from competition diallel experiments using the linear regression technique devised by Yates and Cochran (1938) for the analysis of genotype-environment interactions. The re-analysis of data published by Williams (1962) proved particularly interesting, because one of the six competitors grown – species 2 – behaved anomalously. Reviewing the numerous analyses to which these data have been subject, Trenbath (1978) disclosed that species 2 was the only legume among these competitors.

Conventional wisdom suggests there is a feedback between coexistence and niche divergence, with the former promoting the latter and the latter prolonging the former. However, Connell (1980) maintains that any link between them is purely coincidental. He contends that independent, competing species coexist only after each has adapted to separate niches elsewhere. In this chicken and egg situation it is difficult to envisage how a species can slot into a niche which has been shaped in part by competitors with whom it has not previously coexisted. Conceivably, however, specific species combinations may carve out a niche with the same general features, leaving coexistence to carry out the fine tuning afterwards.

Coevolution

Whatever the interrelationships between niche divergence and coexistence, species must coexist before they can coevolve. The definitions of coevolution and its consequences vary. Thus, coevolution occurs when a trait of one species evolves in response to a trait of another species, which trait has itself evolved in response to the trait in the first species (Janzen 1980). It is a process that occurs between species and populations within a community (Orians and Paine 1983), which encompasses both specificity and reciprocity. This definition may be somewhat restrictive, because if only one species diverges coevolution has not occurred (Futuyma and Slatkin 1983a). Diffuse coevolution relaxes the criterion of specificity to include the evolution of a particular trait in one or more species in response to a trait or suite of traits

in several other species (Janzen 1980; see Roughgarden 1979; Futuyma and Slatkin 1983 b for a discussion of coevolution).

Connell (1980) and Snaydon (1985) suggest that the potential for coevolution is greatest between interdependent species at different trophic levels, where one species must coexist with the other for its survival, such as in predator/prey or host/parasite relationships. These relationships provide examples of coexistence and coevolution, even though the participants are not competing for limited resources in the generally accepted sense of this term. Clearly it would be an unwise evolutionary strategy for the predator to eliminate its prey or for the parasite to kill its host. Evolution records many "arms races" between predator and prey, as natural selection favours prey with the best defences and predators with the best killing equipment (but see Abrams 1986).

Unlike predator/prey and host/parasite relationships, symbiosis benefits both partners. The mutual adjustments engendered by coexistence may enable scarce resources to be utilized more efficiently, or lead to the capture of resources that would otherwise be unattainable. Once established, natural selection will stabilize the symbiosis, because the partnership is fitter than the sum of its component parts.

Opportunities for independent plant species to coevolve will be limited and will depend upon their exploitation of the available niches. As already explained, these niches may be differentiated spatially or temporally, and may reflect environmental heterogeneity created by the recurrence of a factor, such as drought, or the imposition of a management regime, such as cutting or grazing. The selection pressures exerted by these factors will, as described earlier, lead to genetic changes that promote the coexistence of the constituent populations within the community. Although concomitant changes may occur in several cohabiting populations, these may represent no more than the response of individual populations to a common factor. Inevitably, such changes will be confounded with coevolution, as previously defined.

As a community diversifies into the available niches, it becomes relatively non-successional and ecologically stable (Silvertown 1980, 1987; Berendse 1983), and hence able to withstand external disturbances and invasion by other species (Roughgarden 1979; Loeschke 1985). Of greater agronomic interest, however, is the suggestion that coevolved competitors jointly use resources more efficiently and have a higher productivity than species which have not coevolved (Roughgarden 1979; Futuyma and Slatkin 1983 c). But do they? This question, and the issues which it raises, will be considered primarily in relation to the breeding of forage crops. Particular emphasis will be placed upon white clover/perennial ryegrass mixtures because of the environmental impact they are likely to have on British agriculture.

Sward dynamics of grass/legume mixtures

White clover (*Trifolium repens*) is the most widely used forage legume in British agriculture. Apart from seed crops, it is invariably grown in mixtures with a companion grass, usually perennial ryegrass (*Lolium perenne*). In the absence of nitrogenous fertilizer, a symbiotic relationship is established between white clover and the appropriate rhizobium species, as a result of which atmospheric nitrogen is converted ultimately into plant protein. Where nitrogenous fertilizer is applied, white clover will rely on this source of nitrogen rather than use the symbiotic pathway (Rys and Mytton 1985; Mytton and Rys 1985), even though the companion grass utilises mineral nitrogen more efficiently than the legume (Chestnutt and Lowe 1970; Frame and Newbould 1984). This will lead, amongst other things, to increased competition for light. Although the effects of this competition are indirect (Woledge et al. 1984), the white clover content of the pasture is inevitably decreased. Selective grazing and the removal of stolon material by sheep will likewise reduce the clover content of a sward (Evans and Williams 1987).

Within this symbiotic relationship, Harper (1978) regards the white clover as having an "escapist" growth habit, enabling it not only to seek out ecologically compatible grass genotypes or species, but also presumably to avoid those which are relatively incompatible. Alternatively, it could be argued that white clover colonises nitrogen-deficient niches, where it can withstand competition from its neighbouring grasses and fixes atmospheric nitrogen, which subsequently becomes available to the grass following the decay of plant parts. The original niche, now enriched with nitrogen, is taken over by the grass, leaving the clover to use its stoloniferous growth habit to seek out a more suitable niche. Once the grass has depleted the available nitrogen, the cycle can begin again. This relationship allows white clover preemptive use of a resource for which it would otherwise be at a competitive disadvantage. Not only does this symbiosis promote the coexistence of grass and clover, it also uses a renewable source of nitrogen, although, to sustain this role, a pasture should contain between 30% and 50% white clover (Harris and Thomas 1973).

Observations on sown and natural pastures indicate that selection operates as expected. In sown pastures the establishment year is characterized by a mortality rate of up to 90% (Charles 1961; Langer et al. 1964; Kays and Harper 1974) and, although much of this mortality occurs at random, a genetic component cannot be ruled out (Antonovics 1978). This mortality is accompanied by the elimination of some species (Charles 1961; Roughgarden 1983 b) and a decrease in variability among the survivors (Charles 1970; Aarssen and Turkington 1985 b). Thus, a pasture composed initially of several sown species and

cultivars eventually settles down to a narrow range of species and genotypes, provided the management remains constant (Charles 1961). Furthermore, a comparison of survivors with the original population discloses significant differences between them for several characters (Charles 1970, 1971, 1972), indicating that a genetic shift has occurred. This shift, coupled with the reduction in variability, is precisely what would be expected if directional and stabilizing selection have been acting within the pasture.

After the establishment phase, genotypic variation may play a diminishing role in the advance to, and maintenance of, a dynamic balance between the sward components (Breese et al. 1965). The nature and magnitude of these genetic changes will depend upon the reproductive biology of the species, and whether any gaps in the pasture are plugged by the vegetative spread of existing genotypes or by seedling recruitment. Asexual reproduction will result in the slow depletion of genotypes, so that the expression of mature sward characteristics may depend upon adaptive extranuclear variation which is transmissible to daughter tillers (Breese et al. 1965). Genetic variability being the essence of future evolution, it is vital that all populations within the community retain some heritable variation. Seedling recruitment, though sporadic, is one such mechanism (Burdon 1980; Aarssen and Turkington 1985b). Others include selection pressures exerted by neighbours (Burdon 1980) and intergenotypic interactions (Seaton and Antonovics 1967; Allard and Adams 1969; Kelley and Clay 1987). Indeed, Allard and Adams believe the frequency of these interactions in plant associations is such that they may be among the major forces maintaining genetic diversity in populations.

Experimental evidence

Experimental evidence for reciprocal adaptation is sparse and easily confused with unilateral adaptation (Janzen 1980). Moreover, the available evidence suggests that diffuse coevolution rather than coevolution between pairs of species has played a more prominent role in community formation (Futuyma and Slatkin 1983c). There is also a danger of applying the wrong criteria to judge whether coevolution has occurred. Coevolution in the strict sense is concerned with improving the genetic fitness of the participants, not with increasing their agricultural productivity. As Harper (1978) states, "many of the processes that favour members of one species over another – in respect of leaving more descendants than their neighbours, may lead in a direction quite opposite to that of agronomic optimisation." The evolutionary and plant breeding concepts of coevolution may not, therefore, be synonymous.

Nevertheless, experimental evidence suggests that mixtures based on components with a history of coexistence may have higher yields. Thus Allard and Adams (1969), working with cereals, found that genotypes of barley selected in a mixed population produced several mixtures with large and significant yield increments, relative to their pure stand yield. By comparison, increments produced by mixtures based on pure bred varieties were small and non-significant. Moreover, this increase in mixture yield was not achieved at the expense of monoculture performance, as the pure stand yield of some of these genotypes was equal or possibly superior to that of the best commercial variety tested. As Allard and Adams observed, "selection in such mixed populations favours the survival of genotypes – that are good competitors and at the same time good neighbours." Several experiments with grass/legume mixtures based on coexisting components gave similar results (Turkington and Harper 1979; Joy and Laitinen 1980; Aarssen and Turkington 1985c; Evans et al. 1985, 1989), though Collins and Rhodes (1989) found that not all the clovers grown in their experiment performed well with its coexisting grass. Some of these studies have apparently detected localised adaptations in white clover in response to a particular grass neighbour (Turkington and Harper 1979; Aarssen and Turkington 1985c), whilst reciprocal accommodation by the grass has also been demonstrated, at least for part of the experimental duration (Evans et al. 1985, 1989). None of these results provide convincing evidence of coevolution, however (Snaydon 1985).

The results obtained by Mytton (1975), relating to the interaction of clover genotype with strain of rhizobium, are relevant here. Relatively high- and low-yielding genotypes were selected from each of four white clover cultivars, together with their associated strain of rhizobium. All 64 combinations of clover genotype and rhizobium strain were grown in a diallel arrangement. Those combinations inoculated either with their own strain or with the strain from the other genotype of the same cultivar gave significantly higher clover dry matter yields than those combinations inoculated with a strain from another cultivar. Moreover, clover genotype had a greater impact upon yield than strain of rhizobium. Further analysis suggests that, although high-yielding clover genotypes inoculated with any of the high-yielding strains may produce some outstanding combinations, those associations between these same genotypes and low-yielding strains apparently give significantly better than average combinations more reliably.

Implications for plant breeding

The breeding of varieties intended for use in mixtures clearly requires a strategy different from that used in

conventional varietal improvement programmes, where the aim is to identify superior genotypes on the basis of their performance in pure stands. It is unlikely that genotypes selected in this way will possess biological characters conducive to synergism (Allard and Adams 1969). If the "ecological combining ability" (Harper 1967; Allard and Adams 1969) of the mixture components is to be improved, they must be exposed to the combined effects of intra- and interspecific competition during their breeding and development, so that each may exert selective pressures upon the other (Allard and Adams 1969; Donald 1978; Hill et al. 1987; Hill and Michaelson-Yeates 1987; Evans et al. 1989). Indeed, the composite cross used by Allard and Adams was derived from 31 barley varieties and had subsequently undergone 18 generations of natural selection. Wolfe (1985) suggests a comparable breeding strategy for the development of cereal breeding lines for use in mixtures. Because the pure-line mentality has produced material vulnerable to biotic and physical stresses, Wolfe advocates a breeding programme based on mass selection within each generation, leaving the extraction of pedigree lines for a later stage in the programme. According to Wolfe, the end result would be mixtures buffered against the vagaries of the environment, including diseases, which nevertheless retain essential quality characteristics. This should reduce the usage of fungicides, with consequent economic and environmental benefits.

Allard and Adams, and Wolfe are seeking to improve the "ecological combining ability" of mixtures of genotypes from inbreeding cereal species. However, their annual cycle, coupled with the requirement for uniform ripening in such crops, virtually precludes improvements in the temporal compatibility of these genotypes. Forage mixtures pose different problems, as they are based upon perennial, outbreeding species that often have a strong gametophytic incompatibility system. In forage mixtures it is the "ecological combining ability" of populations, rather than individual genotypes, which is being improved. Even though the breeding objectives may be similar in both types of mixture, the precise means by which they are attained will therefore differ. Improvements in the "ecological combining ability" of forage mixtures may be achieved by increasing both the temporal and spatial compatibility of the components (Rhodes 1981). In white clover/perennial ryegrass mixtures, the two constituents already enjoy a measure of temporal separation by virtue of their contrasting growth rhythms. Thus, the pursuance of a breeding strategy which reduces this temporal separation, without a compensatory improvement in spatial compatibility, is to be deprecated. Indeed, if clover is to contribute effectively to the pasture, the two effects should reinforce rather than oppose each other, e.g. by withholding nitrogenous fertilizer, and using a grass companion that allows more light to penetrate the

canopy. In fact, Evans et al. (1985, 1989) used just such a grass companion, selected for long, rigid leaves and erect tillers, in one of their sets of grass/clover mixtures. The yields of these mixtures were intermediate between those based on coexisting components on the one hand, and those having S. 23 as grass companion on the other hand.

Like genetic combining ability, "ecological combining ability" may be partitioned into a general effect, measuring the average expression of a character in all mixtures having a common component, expressed as a deviation from the experimental mean, and a specific effect due to the residual deviations of individual mixtures. Provided those characters promoting "general ecological combining ability" can be identified, exhibit additive genetic variation and are not strongly negatively correlated with other important characters, it should be possible to combine them in one component, as presumably happened during the selection of the grass cultivar used by Evans et al. (1985, 1989). Molecular genetical techniques can help here, because with the development of molecular markers such as isozymes or, more recently, restriction fragment length polymorphisms (RFLPs), it is possible to map the genome of a species in much greater detail. Such markers may be used to locate those quantitative trait loci (QTLs) that affect the genetic expression of the character concerned (Stuber et al. 1987; Stuber 1989; Melchinger 1989; Knapp 1989). However, having identified those QTLs of interest, the formidable practical task of assembling this information into a new variety remains.

Traits contributing to "specific ecological combining ability" will be harder to identify since, by definition, they are likely to vary from mixture to mixture. Furthermore, too great a reliance on "specific ecological combining ability" could prove disastrous if one of the components is attacked by a viral or fungal pathogen.

Grass/legume pastures have formed an integral part of temperate grasslands for some considerable time. It is only recently, however, that the potential of coexistence for improving pasture stability and productivity has been recognised (Hill 1977). Despite a growing awareness of the need to improve their "ecological combining ability", none of the extant perennial ryegrass or white clover cultivars have been bred specifically for use in mixtures. Potential white clover cultivars are usually evaluated in mixtures with a standard perennial ryegrass variety, however.

Within grass/clover mixtures, coexistence is possible at two levels, grass/legume and legume/rhizobium. Experimental evidence suggests that efforts to improve symbiotic productivity should centre on the legume, providing an effective, indigenous strain of rhizobium is available to infect the clover. Increased grass/legume yields are most likely to be achieved by concentrating on those

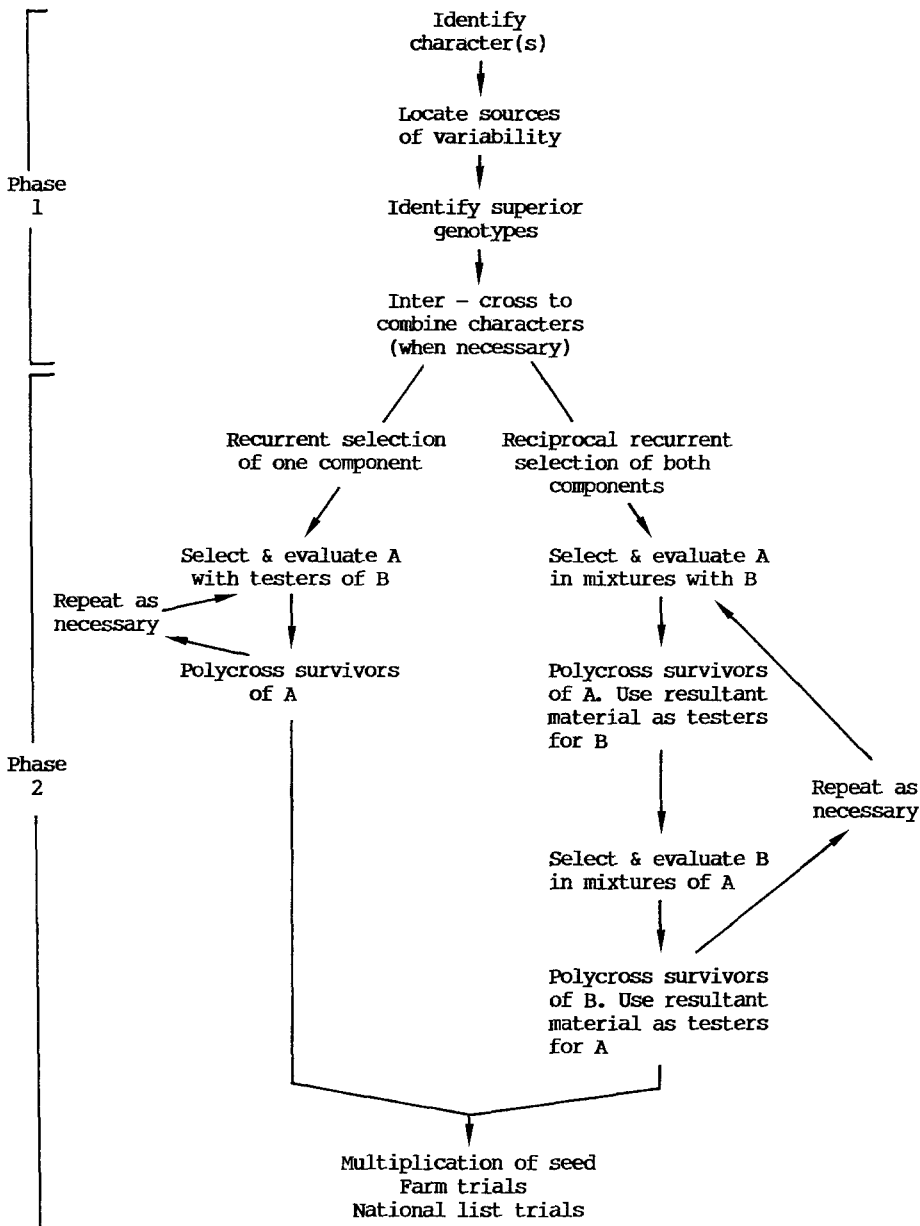


Fig. 1. Outline of a breeding and selection programme for improving the "general ecological combining ability" of mixture components A and/or B

characters that improve the "general ecological combining ability" of one or both components (Fig. 1). Sources of variation for these characters must first be located from a survey of the available genetic material. Within these sources superior genotypes need to be identified, using a mating design suitable for outbreeding species (Hayward 1979). This is followed by a programme of recurrent selection and evaluation aimed at increasing the expression of the characters concerned. If only one component is being improved, a testcross design may be employed to assess the mixtures, using a group of testers appropriate for the selected material and always bearing in mind the role intended for the mixtures in agricultural practice. Survivors from one cycle of selec-

tion could be polycrossed, with the resultant seed forming the starting point for the next cycle. When both components are to be improved, a diallel arrangement of mixtures would be suitable if the number of entries within each component is the same. Otherwise a North Carolina design 2 may be used. Selection could be practised reciprocally on the grass and clover, with improved material from one cycle being used to evaluate the effects of selection on the other component in the next cycle. As improved material becomes available and the number of entries is reduced, both components could be evaluated simultaneously, thereby shortening the selection procedures. On occasion it may be necessary to intercross the source material of one or both components to obtain the

desired combination of characters. The resultant progenies could then be selected as before.

The later stages of the programme cover the multiplication of seed stocks and the evaluation of mixtures in farm trials and by official bodies for National and Recommended Lists. Throughout this programme the prime concern has been the yield of specifically constituted mixtures. This may give the official testing authorities in the UK cause to review their existing procedures for assessing grass/legume mixtures (Collins and Rhodes 1989).

Essentially, improvements in "general ecological combining ability" are being sought by a process of recurrent or reciprocal recurrent unilateral adaptation. Both processes may give rise to populations which have apparently coevolved. Only those subject to reciprocal recurrent selection will meet the criteria of specificity and reciprocity, however. Ideally, the breeding programme should attempt to widen existing niche differences between the components, so that both may contribute to the mixture throughout its productive life. Progress will inevitably be slow, and, as a stop-gap measure until improved material becomes available, mixtures could be generated for assessment by simply growing a range of white clover cultivars with a number of perennial ryegrass varieties, even though this haphazard approach has proved singularly unrewarding in the past. It may, nevertheless, provide information for the main programme, while the routine screening of elite populations for "specific ecological combining ability" could be conducted in this way. Ultimately the forage breeder is aiming to produce perennial ryegrass and white clover cultivars that have complementary "ideotypes" (Donald 1968). This complementarity will vary depending upon the management regime imposed, since different managements, such as cutting or grazing, will generate a different array of niches.

The principles enunciated here also apply to other mixed cropping systems of agriculture, such as those practised in many developing countries. Here too, scant attention is often paid to the agricultural environment in which the material will subsequently be grown (Chirwa 1985). Improving the "ecological combining ability" of the components concerned may therefore increase the productivity of these agricultural systems.

Acknowledgements. I am particularly indebted to Dr. E. L. Breese for the valuable discussions we had together as this paper proceeded through its various drafts. I also wish to thank Dr. L. R. Mytton, Prof. P. D. S. Caligari and Prof. Sir Kenneth Mather, FRS, for reading and commenting upon this script.

References

Aarssen LW, Turkington R (1985a) Competitive relations among species from pastures of different ages. *Can J Bot* 63:2319–2325

- Aarssen LW, Turkington R (1985b) Within-species diversity in natural populations of *Holcus lanatus*, *Lolium perenne* and *Trifolium repens* from four different-aged pastures. *J Ecol* 73:869–886
- Aarssen LW, Turkington R (1985c) Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *J Ecol* 73:605–614
- Abrams PA (1986) Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. *Evolution* 40:1229–1247
- Allard RW, Adams J (1969) Population studies in predominantly self-pollinating species. XIII. Intergenotypic competition and niche differentiation in barley and wheat. *Am Nat* 103:621–645
- Antonovics J (1978) The population genetics of mixtures. In: Wilson JR (ed) *Plant relations in pastures*. CSIRO, East Melbourne, pp 233–252
- Berendse F (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *J Ecol* 71:379–390
- Breese EL, Hill J (1973) Regression analysis of interactions between competing species. *Heredity* 31:181–200
- Breese EL, Hayward MD, Thomas AC (1965) Somatic selection in perennial ryegrass. *Heredity* 20:367–379
- Brown JS, Vincent TL (1987) Coevolution as an evolutionary game. *Evolution* 41:66–79
- Burdon JJ (1980) Intra-specific diversity in natural populations of *Trifolium repens*. *J Ecol* 68:717–735
- Caligari PDS (1980) Competitive interactions in *Drosophila melanogaster*. *Heredity* 45:219–231
- Charles AH (1961) Differential survival of cultivars of *Lolium*, *Dactylis* and *Phleum*. *J Br Grassl Soc* 16:69–75
- Charles AH (1970) Ryegrass populations from intensively managed leys. I. Seedling and spaced plant characters. *J Agric Sci* 75:103–107
- Charles AH (1971) Ryegrass populations from intensively managed leys. II. Reaction to nitrogen and *Poa trivialis* L. *J Agric Sci* 76:233–241
- Charles AH (1972) Ryegrass populations from intensively managed leys. III. Reaction to management, nitrogen application and *Poa trivialis* L. in field trials. *J Agric Sci* 79:205–215
- Chestnutt DMV, Lowe J (1970) Agronomy of white clover/grass swards. *Br Grassl Soc Occas Symp* 6:191–213
- Chirwa RM (1985) Inter- and intra-specific competition in perennial ryegrass-white clover mixtures. MSc thesis, University College of Wales, Aberystwyth
- Collins R, Rhodes I (1989) Yields of white clover populations in mixture with contrasting perennial ryegrasses. *Grass Forage Sci* 44:111–115
- Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Donald CM (1968) The breeding of crop ideotypes. *Euphytica* 17:385–403
- Donald CM (1978) Summative address. In: Wilson JR (ed) *Plant relations in pastures*. CSIRO, East Melbourne, pp 411–420
- Evans DR, Williams TA (1987) The effect of cutting and grazing managements on dry matter yield of white clover varieties (*Trifolium repens*) when grown with S. 23 perennial ryegrass. *Grass Forage Sci* 42:153–159
- Evans DR, Hill J, Williams TA, Rhodes I (1985) Effects of coexistence on the performance of white clover-perennial ryegrass mixtures. *Oecologia* 66:536–539

- Evans DR, Hill J, Williams TA, Rhodes I (1989) Coexistence and the productivity of white clover-perennial ryegrass mixtures. *Theor Appl Genet* 77:65–70
- Firbank LG, Watkinson AR (1985) On the analysis of competition with two-species mixtures of plants. *J Appl Ecol* 22:503–517
- Fowler N (1981) Competition and coexistence in a North Carolina grassland. II. The effects of the experimental removal of species. *J Ecol* 69:843–854
- Fowler N (1982) Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. *J Ecol* 70:77–92
- Frame J, Newbould P (1984) Herbage production from grass/clover swards. *Br Grassl Soc Occas Symp* 16:15–35
- Futuyma DJ, Slatkin M (1983a) Introduction. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer Associates, Sunderland, pp 1–13
- Futuyma DJ, Slatkin M (1983b) *Coevolution*. Sinauer Associates, Sunderland
- Futuyma DJ, Slatkin M (1983c) The study of coevolution. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer Associates, Sunderland, pp 459–464
- Harper JL (1967) A Darwinian approach to plant ecology. *J Ecol* 55:247–270
- Harper JL (1977) *Population biology of plants*. Academic Press, London
- Harper JL (1978) Plant relations in pastures. In: Wilson JR (ed) *Plant relations in pastures*. CSIRO, East Melbourne, pp 3–14
- Harris W, Thomas VJ (1973) Competition among pasture plants. III. Effects of frequency and height of cutting on competition between white clover and two ryegrass cultivars. *NZ J Agric Res* 16:49–58
- Hayward MD (1979) The application of the diallel cross to outbreeding crop species. *Euphytica* 28:729–737
- Hill J (1977) Adaptability through mixed sward components. In: Dennis B (ed) *Breeding methods and variety testing in forage plants*. Eucarpia Fodder Crops Section, Roskilde, 1976, pp 87–91
- Hill J, Michaelson-Yeates TPT (1987) Effects of competition upon the productivity of white clover-perennial ryegrass mixtures. *Seasonal trends*. *Plant Breed* 99:251–262
- Hill J, Michaelson-Yeates TPT (1988) The measurement and analysis of competitive ability among populations of white clover and perennial ryegrass. *Theor Appl Genet* 76:361–368
- Hill J, Mather K, Caligari PDS (1987) Analysis of competitive ability among genotypes of perennial ryegrass. II. Effect upon dry matter production. *Euphytica* 36:109–115
- James FC, Johnston RF, Wamer NO, Niemi GJ, Boecklen WJ (1984) The Grinnellian niche of the wood thrush. *Am Nat* 124:17–47
- Janzen DH (1980) When is it coevolution? *Evolution* 34:611–612
- Joy P, Laitinen A (1980) Breeding for coadaptation between red clover and timothy. Five-year report, Hankkija Plant Breed Inst, Finland, pp 151–157
- Kays S, Harper JL (1974) The regulation of plant and tiller density in a grass sward. *J Ecol* 62:97–105
- Kelley SE, Clay K (1987) Interspecific competitive interactions and the maintenance of genotypic variation within two perennial grasses. *Evolution* 41:92–103
- Knapp SJ (1989) Quasi-Mendelian analyses of quantitative traits. In: *Science for plant breeding*. XII Eucarpia Congress, Göttingen. Parey, Berlin Hamburg, pp 51–67
- Langer RHM, Ryle SM, Jewiss OR (1964) The changing plant and tiller populations of timothy and meadow fescue swards. I. Plant survival and the pattern of tillering. *J Appl Ecol* 1:197–208
- Lawlor LR, Maynard Smith J (1976) The evolution and stability of competing species. *Am Nat* 110:79–99
- Loeschcke V (1985) Coevolution and invasion in competitive guilds. *Am Nat* 126:505–520
- Mather K (1953) The genetical structure of populations. *Symp Soc Expl Biol* 7:66–95
- Mather K (1955) Polymorphism as an outcome of disruptive selection. *Evolution* 9:52–61
- Mather K (1961) Competition and co-operation. *Symp Soc Expl Biol* 15:264–281
- Mather K (1973) *Genetical structure of populations*. Chapman and Hall, London
- Mather K, Caligari PDS (1981) Competitive interactions in *Drosophila melanogaster*. II. Measurement of competition. *Heredity* 46:239–254
- Melchinger AE (1989) Locating quantitative trait loci by means of molecular markers. In: Honne BI (ed) *Biometrics in plant breeding*. Eucarpia Biometrics in Plant Breeding Section, Ås, 1988, pp 92–111
- Milne A (1961) Definition of competition among animals. *Symp Soc Expl Biol* 15:40–61
- Mytton LR (1975) Plant genotype × rhizobium strain interactions in white clover. *Ann Appl Biol* 80:103–107
- Mytton LR, Rys GJ (1985) The potential for breeding white clover (*Trifolium repens* L.) with improved nodulation and nitrogen fixation when grown with combined nitrogen. 2. Assessment of genetic variation in *Trifolium repens*. *Plant Soil* 88:197–211
- Orians GH, Paine RT (1983) Convergent evolution at the community level. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer Associates, Sunderland, pp 431–458
- Pacala SW (1988) Competitive equivalence: the coevolutionary consequences of sedentary habit. *Am Nat* 132:576–593
- Rhodes I (1981) The physiological basis of variation in the yield of grass/clover mixtures. *Br Grassl Soc Occas Symp* 13:149–161
- Rice WR, Salt GW (1988) Speciation via disruptive selection on habitat preference: experimental evidence. *Am Nat* 131:911–917
- Roughgarden J (1979) *Theory of population genetics and evolutionary ecology; an introduction*. Macmillan, New York
- Roughgarden J (1983a) Competition and theory in community ecology. *Am Nat* 122:583–601
- Roughgarden J (1983b) The theory of coevolution. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer Associates, Sunderland, pp 33–64
- Rys GJ, Mytton LR (1985) The potential for breeding white clover (*Trifolium repens* L.) with improved nodulation and nitrogen fixation when grown with combined nitrogen. 1. The effects of different amounts of nitrate nitrogen on phenotypic variation. *Plant Soil* 88:181–195
- Seaton APC, Antonovics J (1967) Population inter-relationships. 1. Evolution in mixtures of *Drosophila* mutants. *Heredity* 22:19–33
- Silvertown J (1980) The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *J Appl Ecol* 17:491–504
- Silvertown J (1987) Ecological stability: a test case. *Am Nat* 130:807–810
- Snaydon RW (1985) Aspects of the ecological genetics of pasture species. In: Haeck J, Woldendorp JW (eds) *Structure and functioning of plant populations*. 2. Phenotypic and genotypic variation in plant populations. North Holland, Amsterdam, pp 127–152

- Spitters CJT (1983) An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. *Neth J Agric Sci* 31:1–11
- Stuber CW (1989) Marker-based selection for quantitative traits. In: Science for plant breeding. XII Eucarpia Congress, Göttingen. Parey, Berlin Hamburg, pp 31–49
- Stuber CW, Edwards MD, Wendel JF (1987) Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. *Crop Sci* 27:639–648
- Thoday JM, Gibson JB (1962) Isolation by disruptive selection. *Nature* 193:1164–1166
- Trenbath BR (1978) Models and the interpretation of mixture experiments. In: Wilson JR (ed) Plant relations in pastures. CSIRO, East Melbourne, pp 145–162
- Turkington R, Harper JL (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine-scale biotic differentiation. *J Ecol* 67: 245–254
- Vance RR (1984) Interference competition and the coexistence of two competitors on a single limiting resource. *Ecology* 65:1349–1357
- Vance RR (1985) The stable coexistence of two competitors for one resource. *Am Nat* 126:72–86
- Williams EJ (1962) The analysis of competition experiments. *Aust J Biol Sci* 15:509–525
- Wit CT de (1960) On competition. *Versl landbouwk Onderz, Nederlands*, 66 (8) 82 pp
- Woledge J, Dennis WD, Davidson IA (1984) The photosynthesis of white clover and ryegrass in mixed swards. *Adv Photosynth Res* 6:149–152
- Wolfe MS (1985) The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Ann Rev Phytopathol* 23:251–273
- Yates F, Cochran WG (1938) The analysis of groups of experiments. *J Agric Sci* 28:556–580