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Two theories of sex and variation

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For almost the whole history of evolutionary biology, sex has been thought of as creating preadaptation to an uncertain future, either permitting species to adapt more quickly or enabling individual females to produce a few unexpectedly fit offspring. The demise of this powerful idea dates from theoretical difficulties noted by Maynard Smith[73], and was completed by the overwhelming hostility of the comparative evidence: it is parthenogenesis, and not outcrossed sexuality, that prevails in harsh, uncertain, disturbed and novel conditions[10]. The comparative evidence points instead to a quite different role for sex, concerned with the efficient exploitation of the full range of possibilities presented by a diverse environment. Two theories of this sort have been especially prominent. The first is the Tangled Bank[10], which descends from the economic analogies of Ghiselin[38] and is related to the sib-competition models introduced by Williams[105] and elaborated by Maynard Smith[74] and Price and Waser[86]. In its simplest form, the Tangled Bank holds that the state of the environment varies widely from place to place on a very local scale, such that different genotypes are optimal at different sites. Since each site can support only a few individuals, the uniform progeny of an asexual female will compete intensely with one another for the same set of resources, while the progeny of a sexual female, which by virtue of their diversity will be able to exploit a much wider range of sites, will compete amongst themselves less intensely and thus achieve greater overall success. In this way, a narrowly specialized asexual clone cannot replace a diverse sexual lineage, despite its greater reproductive efficiency.

A formal population model (Bell[10] and Bell, in preparation) identifies two processes which are crucial to the maintenance of sexuality. Imagine a subdivided population with each local group contributing to a common pool of dispersive propagules. Each local group inhabits a diverse environment, in which the performance of a given genotype varies from site to site. Because the high local fitness of a successful genotype may not be reproducible when it is transferred to some other random site, it may be advantageous to break up even successful genotypes by recombination. At the same time, the total contribution made by each local group to the common pool will depend on the effectiveness with which the whole range of available sites is exploited, and will therefore increase as the genetic variance of the group increases. Mixed groups created by sexual diversification will therefore outyield genetically uniform clones. The Tangled Bank therefore involves both interaction between genotype and environment and interaction between genotypes.

The Red Queen, descending eventually from the theme introduced by van Valen[101], was first adequately stated for the special case of sex by Jaenike[58] and later formalized by Glesener[39], Hamilton[47], Hutson and Law[56], and Bell[10]. It attributes the success of sexuality to the continual necessity to respond to the shifting challenge of antagonists such as predators and parasites. Since such antagonists will always be able to counteradapt eventually to any given genotype in the prey or host population, sex is necessary to recreate resistance in the progeny by producing new combinations of genes. Sex is equally necessary to the predators and parasites, which need to respond effectively to these counteradaptations, and the cycle of adaptation and counteradaptation continues indefinitely.

In formal population models, the crucial feature of the Red Queen is the negative correlation between the fitness of a genotype and its frequency at some time in the past. If the fitness of a genotype defined by the alleles present at two (or more) loci is a decreasing function of its past frequency, then not only are the allele frequencies at these loci likely to cycle through time, but the coefficient of linkage disequilibrium will also cycle, changing regularly from positive to negative and back again. This greatly favors the maintenance of sexuality, since the passage from coupling to repulsion genotypes, or vice versa, is greatly facilitated by meiotic recombination. We can validate this conclusion by building a model with three loci; current fitness is determined at two of the loci, and for any given genotype is a decreasing function of the past frequency of that genotype, while the third locus is segregating for a series of alleles whose only effect is to alter the rate of recombination between the two fitness loci. A model of this sort was analyzed by Bell[10], who found, as expected, that alleles at the third locus which suppressed recombination were counterselected, and that in general alleles favoring intermediate rates of recombination were favored, confirming the analytical results of Hutson and Law[56].

The Red Queen can be restated in terms which make it directly comparable with the Tangled Bank. There is an interaction between genotype and environment, though 'environment' is in this case a year (or some other appropriate measure of time) rather than a site. There is also an interaction between genotypes, since a population whose genetic composition is continually changing will outyield an invariant clone. The two theories thus equally involve complex genetic interactions, but differ in the source of these interactions. This perspective immediately suggests that the analysis of variance components in short-term experiments and observations may both show whether either theory is plausible, and may help to distinguish between them.

The Tangled Bank and the Red Queen are not merely two possibilities drawn by historical accident from a long list of possible theories. Rather, they represent two alternative opinions about variation, the former stressing spatial and the latter temporal heterogeneity in the environment. It will be a recurring theme in this review that the problem of how sex is maintained and the problem of how variation is maintained are, if not identical, at least very closely related. The dichotomy between these two theories is therefore of great interest. I have previously published an extensive comparative analysis of theories of sex[10], and shall not discuss the comparative evidence further here. Instead, I shall show how short-term experimental and observational techniques can be used to evaluate the worth of the Tangled Bank and Red Queen theories, independently of comparative predictions.

Variation in space and time

The basic concept invoked by both the Tangled Bank and the Red Queen is that the relative fitness of a genotype depends on the conditions in which it is reared. More precisely, when the relative fitnesses of a number of genotypes are measured under different experimental treatments there will be a substantial genotype x treatment interaction, showing that the ranking of relative fitnesses changes with treatment. This interaction is the familiar genotype x environment (GxE) interaction of quantitative genetics; I shall often refer to 'treatment' rather than 'environment' when the variance is created by some premeditated manipulation.

When a series of genotypes is raised under two treatments, their performances in the two treatments will be correlated to some extent. If there is no G × E interaction, this correlation will be large and positive, being less than $+1$ only because of measurement error. Theories of sex, whether Tangled Bank or Red Queen, require that the correlation should be zero or negative, at least for certain combinations of treatments, since it is only when the ranking of relative fitnesses tends to be reversed that there is a straightforward advantage for breaking up the parental genome.

This argument applies to the performance of genotypes when grown in pure culture, and deals with the interaction between genotype and treatment while ignoring any interaction between genotypes when grown together in mixed culture. If sex is to be favored, interactions between genotypes should occur, and must lead to the superiority of mixed over pure cultures with respect to yield, rate of increase, or some other measure of performance directly related to Darwinian fitness. This will be the case if different genotypes facilitate one another's growth, while individuals having the same genotype are antagonistic.

These two arguments suggest that there are two basic experimental procedures for detecting possible short-term advantages for sex and varibality.

1) Transplantation. If there is a large G × E interaction then the relative performance of a genotype will be altered substantially by moving it to a random site or by growing it under different random conditions. The Tangled Bank and the Red Queen differ with respect to the sort of transplant which is expected to produce this effect: essentially, the Tangled Bank predicts a large effect from transplanting between sites, and the Red Queen from transplanting between years. Another way of putting this is to say that if there is a large G × E interaction, the Tangled Bank predicts that the variance of treatments between sites will be much greater than that between years, while the Red Queen makes the reverse prediction. Naturally, the units of time involved are not necessarily years, and the definition of a site will also vary according to the organism involved.

2) Mixture. If there is a large positive interaction between genotypes then the combined yield of a mixture will exceed the average yield of its constituents in pure culture. The Tangled Bank and Red Queen differ in the type of mixture expected to be the more effective; the Tangled Bank predicts a large effect from a mixture of genotypes at a site or sites within a given year, and the Red Queen from a mixture over time, each site being occupied by a pure culture in any given year, the genotype of the culture being changed between years.

The literature of interactions between genotypes and between genotype and environment is very large, with papers scattered through the fields of population genetics, biometrical genetics, evolutionary biology, agronomy and stockbreeding. No critical review exists, and it would be impracticable to attempt an exhaustive treatment here; instead, I shall attempt to identify the major categories of evidence and survey some of the major empirical findings.

Interaction between genotype and treatment

The occurrence and magnitude of G × E interaction. Most large-scale studies of variation involving many combinations of strains and treatments turn up substantial interactions. Some of the most extensive work has been done with crop plants and domestic animals. Blyth et al.[14] analyzed data on 49 wheat cultivars grown in 63 environments and found that about 22% of the total variance in yield was contributed by G × E interaction. In another very large experiment with cauliflower, involving 12 genotypes and 36 environments, about 10% of the total variance in time to maturity and about 42% of the variance in the weight of the flowering head was contributed by G × E interaction[62]. A similar unpublished study on lettuce involving 13 varieties in eight field environments (Gray, cited by Kesavan et al.[62]) found that only about 2% of the variance in time to maturity but about 24% of variance in head weight was attributable to G × E interaction. Witcombe and Whittington[106] found a substantial interaction for germination rate in *Brassica* seedlings grown at different temperatures. In some cases, the results are less consistent. For characters of economic importance in poultry, for instance, some authors (e.g. Hill and Nordstrog[53], Nordstrog and Kempthorne[76] and Osborne[80]) found rather large and consistent G × E interactions, but others found interactions for some characters and not for others (e.g. Gowe[41] and Gutteridge and O'Neill[46]), while others found no interactions at al.[1, 42, 71]. In general, characters which are close to biological fitness (such as seed yield in cereals) usually seem to have substantial G × E interaction, while characters less highly correlated with fitness (e.g. fleece weight in sheep, King and Young[66]) often have little or none. The retention of substantial interaction variance in many economically important characters, however, is doubly significant because one of the main aims of selective breeding is to remove this source of variance in order to create strains which perform uniformly well in a wide range of environments.

Extensive work on variation in plants under non-agricultural conditions has been done on *Nicotiana, Arabidopsis* and *Papaver*. Perkins and Jinks[84] grew 10 inbred lines of *Nicotiana* in 16 soil environments and found small but significant line × soil type interactions, which accounted for about 4% of the total variance in time to flowering and final height. In a large and carefully analyzed experiment, Pooni et al.[85] found widespread genotype × microenvironment interactions in *N. rustica*. In *Arabidopsis*, large experiments involving inbred lines and their hybrids have shown substantial G × E interaction[83, 102–104]; Westerman and Lawrence[104] remark that although the G × E interaction is small relative to the total phenotypic variance, it is large relative to the genetic variance. Zuberi and Gale[112] studied 11 metrical traits in 20 inbred lines of *Papaver dubium* grown under 16 combinations of fertilizer treatment, and found large G × E interactions for three of the traits, including fruit number, the trait closest to fitness; they comment that the relative fitness of different genotypes will probably change very markedly with changes in the natural environment.

Among fungi, Fripp and Caten[37] found substantial G × E interactions for the growth-rate of *Schizophyllum commune* dikaryons, while Butcher et al.[20] obtained a similar result for comparisons of growth-rate and cleistothecial production between compatibility groups of *Aspergillus nidulans*.

Relatively little work on animals has been directed to the measurement of G × E interaction, but it has usually been found when it has been looked for. Young[111] found substantial interaction for body weight and litter size of three strains of mice reared under four combinations of temperature and food level; Falconer and Latyszewski[35] got a similar result for two strains and two food levels. Laboratory populations of fruitflies and flour beetles often show G × E interactions, which are described under the appropriate headings below.

The examples I have described above are only a small fraction of those it would be possible to extract from the literature. They suffice, however, to show that the G × E interaction is often substantial, and therefore that the performance of a genotype under one set of conditions will often by a poor predictor of its performance under different conditions.

The correlation between genotype and environment. If the relative fitness of genotypes varies between sites the result is likely to be local adaptation, with different genotypes prevailing in different types of site; thus, G × E interaction is likely to lead to G × E correlation, and the existence of this correlation is indirect testimony to the existence, and the strength, of the interaction. Local adaptation has been the subject of some of the best empirical work in evolutionary biology, including the classical studies of heavy metal tolerance in *Agrostis,* industrial melanism in moths and crypsis in the snail *Cepaea.* These studies are especially valuable, both because they have identified the selective agents responsible for the G × E correlation and because they have shown that selection coefficients can change drastically over very small distances. Thè Park Grass Experiment at Rothamsted is particularly revealing, since this concerned differences in soil nutrient status which are directly relevant to the spatial heterogeneity commonly encountered by natural populations of plants. It has been described in a series of papers by Snaydon and Davies[24–28, 93–95]. They showed that the response of plants from different field plots to soil pH and nutrient status was related to the treatment the plots had received over the past 100 years. In general, plants from sites to which a given nutrient had been supplied could respond to high levels of that nutrient when grown in sand culture, whereas plants from unfertilized plots could not. The result was a pronounced physiological differentiation between plots, directly related to the local selective pressures exerted by the experimental treatments. It seems likely that these experimentally induced patterns are similar to the patterns observed in natural plant communities; Imam and Allard[57] for instance, found that '... variability in wild oats in California takes the form of a mosaic in which highly localized differentiations are superimposed in a complicated way on patterns of differentiation associated with larger geographical areas' (p. 59). Although there are many such accounts of spatial differentiation on a very local scale in plants and sessile animals, I have found no corresponding accounts of temporal differentiation, such that particular genotypes are associated with particular types of year. The closest approach is made by seasonal fluctuations, such as those of inversion frequencies in natural population of *Drosophila.*

Selective response. A general implication of the presence of substantial G × E interaction is that progress under selection will depend on the environment in which selection is practised. This is important in applied genetics, since it means that not only the pattern of selection but also the environment in which selection is applied must be specified to ensure high and consistent yield. From our point of view, it is another technique of demonstrating G × E interaction which highlights its role in producing local adaptation. Negative results, in which selective gains were independent of the environment in which selection was practised, have been reported for growth and size in mice[23], rats[81] and *Drosophila,* but similar experiments by other authors have given positive results for mice[34, 35] and flour beetles[52, 110]; Orozco[79] gives a particularly careful account of G × E interaction during selection for oviposition rate in *Tribolium.*

Sites and years as sources of interaction. The ubiquity of G × E interaction, while strengthening the case for a leading role of spatial or temporal heterogeneity in the maintenance of sex and genetic variation, does not help us to distinguish between the Tangled Bank and the Red Queen. In fact, I have been unable to find any extensive comparison of the relative contributions of sites and years to the interaction variance. Gooding et al.[40] found that sites and years were about equally important for plant size, crown number, inflorescences per crown and fruits per inflorescence in strawberries. Killick and Simmonds[64] give broader information, unfortunately for a character (specific gravity of potato tubers) which is of large economic but little biological importance; they conclude that while both years and localities may give rise to large interactions, years are generally the more important. Indeed, they refer (without authorities) to a general belief among agronomists that this is usually the case. But even if this were true, it must be remembered that differences between sites can be largely eliminated in agricultural practice by manuring, pesticide application and so forth, while differences between years are less easily dealt with. A more promising line of attack, for natural populations, is to argue that where G × E interaction is substantial the relative importance of sites and years will depend on the variance of the treatment variates over sites and years. It is my strong impression, which I cannot substantiate, that variance between sites within years is usually much larger then variance between years within sites.

Direct transplant experiments. The crucial experiment is the transplanting of individuals from their home site to an alien site, their performance being compared with that of individuals having the same genotype which are transplanted back into their home site. While planting from natural sites into a common garden, with the object of demonstrating the existence of 'ecotypes', has often been done, reciprocal transplant and replant experiments are relatively rare. With the exception of the classical work on heavy-metal tolerance, the most extensive is probably that reported by Davies and Snaydon[28], using *Anthoxanthum* in the Rothamsted Park Grass Experiment. They found that plants survived longer, produced more tillers and produced more dry matter when planted back into their home plots than when transplanted to ecologically contrasting plots. The differences were large; the average half-life of plants put into alien plots, for example, was eight months, while that of plants put back into their home plots was two years. Davies and Snaydon calculated selection coefficients against the alien transplants as 1 – (performance on alien plot)/(performance on home plot); for 18-month survival these varied from 0.09 to 0.77 with a mean of 0.36, and similar values were found for tiller number and plant size. This demonstrates very powerful local selection, though admittedly within a system deliberately engineered to provide sharp ecological contrasts.

Experiments in natural systems rather strongly support the Rothamsted result. Turkington and Harper[100] transplanted *Trifolium* clones between and within different plant associations in a single old field. They found that shoots planted back into the same association usually had greater vegetative yield than those planted into different associations; even more strikingly, shoots planted into deliberately sown swards of the same grass with which they were associated in the field had almost twice as great a yield as those planted into an alien sward. Lovett Doust[70] performed reciprocal transplants of *Ranunculus* clones between adjacent woodland and grassland sites and found that those replanted in their home site generally grew faster and produced more leaves and ramets than those transplanted to an alien site. Antonovics and Primack[6] made reciprocal transplants of *Plantago* between six field sites. They found that seedling survival was indifferent to the transplant site, but that growth and fecundity were generally greater in home than in alien sites. McGraw and Antonovics[72] moved snowbed and fellfield ecotypes of *Dryas* over a distance of about 100 m and found that in 10/11 comparisons of fitness components (pollination success, seed germination, seedling and adult viability) seedlings replanted into their home site were superior to those moved to alien sites.

These experiments provide direct evidence of the site-specific adaptation required by the Tangled Bank. So far as I know, there are no comparable experiments in which genotypes are stored, either as seeds or as vegetative material, and transplanted between years.

The correlation between treatments as a function of their difference. A conventional analysis will show whether or not a significant G × E interaction occurs in any particular case, but it cannot predict in advance whether or not an interaction will occur. We must be able to make such a prediction, however, if we wish to make general statements of how a given shift in place or time will affect the ranking of genotypic fitness.

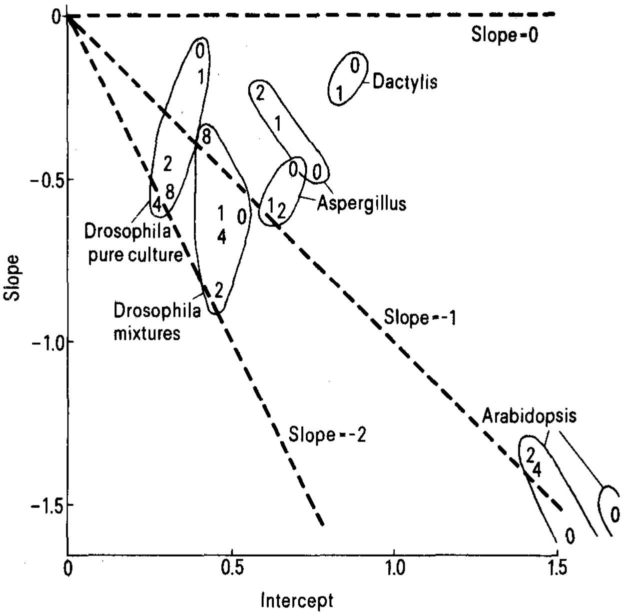
Suppose that we have measured the fitness w of a number of clones or inbred lines i in each of two sets of conditions, j and k. We wish to know the relationship between the genotypic fitnesses in the two treatments, w_{ij} and w_{ik}. If j and k are nearly the same, the w_{ij} and w_{ik} will be closely related, with a correlation coefficient of about unity. Conversely, if j and k are very different then we expect the correlation to be smaller. Indeed, if j and k are sufficiently different the correlation between w_{ij} and w_{ik} may drop to zero or even become negative.

This argument implies that the correlation between genotypic fitness under different conditions is a decreasing function of the difference between the conditions. There are two difficulties with this approach, which I have dealt with as follows.

1) The first concerns the array of environments, or treatments; the way in which the difference between treatments is measured has not been defined. The analysis must not depend on the particular units (degrees Centigrade, individuals per square meter, or whatever) used to express the difference between the treatments, which suggests the use of some dimensionless number. Moreover, we are not concerned with the difference between the treatments in terms of temperature, crowding or whatever, but only with the differences as expressed by the difference in performance of the strains under test. I propose that an appropriate statistic is the proportion of all the variance in performance over the two treatments being compared which is accounted for by the variance of the treatment means (i.e. the evironmental variance, as a fraction of the whole). If the difference in treatment has little effect on performance, so that the variance of strains within a treatment is large relative to the difference between the treatment means, then this measure will be close to zero. On the other hand, if the difference in treatment has a very large effect on performance, so that the variance of strains within a treatment is small relative to the difference between the treatment means, then the measure will be close to unity. In this way, we can scale the effect of the treatment in a way which can be applied consistently to any particular sort of manipulation. This approach is similar to that taken by Hull and Gowe[54], who suggested from poultry-breeding data that G × E interaction is likely to be large when the variation due to treatment is large relative to the nongenetic variation within treatments, or when the genetic variance between the groups which are subdivided and subjected to different treatments is large relative to the total phenotypic within-treatment variance.

2) The second difficulty concerns the array of genotypes. Whatever combination of treatments we choose, it is not unlikely that some genotypes will perform badly in both; this is especially likely when working with inbred lines. It is possible, though less likely, that a few types will be markedly superior in almost all conditions. This would tend to create large positive correlations for almost any combination of treatments, even if the bulk of the data, concerning more centrally located genotypes, showed negative correlation. Since this result would have little relevance to natural populations, in which unconditionally inferior genotypes are unlikely to occur, it is desirable to investigate the effect of removing extreme genotypes. I have done this by calculating for each genotype the sum of squared deviations from the treatment means, and excluding the genotype with the greatest sum. If two genotypes are to be excluded, the procedure is repeated for the new data set created by the removal of the single most extreme genotype; and so forth, for any desired number of exclusions.

We expect to find that as the variance between treatment means becomes large relative to the variance between strains within treatments, the correlation between genotypic fitnesses under the two treatments will fall. By analyzing several combinations of treatments for a given array of genotypes, we can calculate the linear regression of the correlation between genotypic fitnesses, Corr, on the variance component attributable to the difference between treatment means, PV. Having estimated the parameters of $\mathrm{Corr} = b_0 + b_1 \mathrm{PV}$, it follows that the correlation becomes zero when $\mathrm{PV} = -b_0/b_1$ (granted that b_1 is negative), and will be negative for greater values of PV. Thus, if $b_1 = -b_0$ the correlation between genotypes reaches zero when the variance within treatments is negligible compared with the variance between treatment means; if $b_1 = -2b_0$ then the correlation reaches zero when the variance is equally distributed within and between treatments; while if $b_1 > -b_0$ the correlation is always positive. The results from a number of studies involving fairly large numbers of genotypes under a variety of treatments are mapped in the figure. (It should be emphasized this is a map rather than the regression of two variates, since neither correlations and variance components nor slopes and intercepts are statistically independent.) There is a tendency, though not a very strong one, for the slope b_1 to become more negative when extreme genotypes are excluded, as was anticipated. Leaving this aside, two major conclusions can be tentatively drawn. First, the regressions are all negative, showing that high fitness in one treatment becomes progressively less likely to be repeatable under a second treatment as the two treatments become more different. Secondly, in most cases the correlation remains positive no matter how extreme the difference between the treatments. This is by no means conclusive, since there may be manipulations which do induce negative correlations; indeed, the correlations are predominantly negative for rather large treatment effects on larval viability in *Drosophila,* while the only direct plot of genotypic fitnesses I have found in the literature[65] shows a striking negative correlation. However, what this small data set suggests is that if genotypes are moved from their home sites to alien sites within the range of tolerance of the species the correlation between their fitness in the two sites, though usually positive, will be small. More extensive experiments designed specifically to test this hypothesis would be of great interest.



An attempt to describe the effect of a change of environment on the relative fitness of a genotype. Each data set analyzed consists of the performance of a number of clones or inbred lines under a number of different treatments. For each possible pairwise comparison between treatments I calculated the correlation between genotypic fitnesses, *Corr,* and the proportion of the variance contributed by the difference between treatment means, *PV.* I then estimated the intercept b_0 and the slope b_1 of the linear regression $Corr = b_0 + b_1 PV$. This procedure was repeated with the most extreme *n* genotypes removed from each comparison, where the greatest value of *n* used depended on the number of genotypes in the experiment. The results are mapped in the figure; a solid line surrounds the estimates for each case, with a number indicating how many genotypes were removed from the data defore analysis. The broken lines indicate various slopes. If the data map below the line of zero slope, the correlation between genotypic fitnesses in different treatments declines as the treatments become more different. If they map below the line with slope -1, the correlation becomes negative for treatments which are sufficiently different: if they map below the line with slope -2, the correlation becomes negative when less than half the variance in the data is due to the difference between treatment means. Authorities are as follows. *Drosophila* pure strains (19 inbred lines, 6 density treatments) and mixtures (19 inbred lines, 5 density treatments, using larval viability, Lewontin[16]). *Aspergillus* (5 compatibility groups 12 combinations of medium, pH and temperature), using cleistithecium production (upper) and colony growth rate (lower), Butcher et al.[20]. *Dactylis* (5 strains, 10 combinations of site and harvest frequency), using yield of dry matter, Breese[16]. *Arabidopsis* (33 inbred lines, 3 temperatures), using flowering time (right) and fruit production (left), Westerman and Lawrence[104]; doubtless because of the small number of treatments this analysis gave large positive values for the intercept and large negative values for the slope, but in this and the other cases intercept = –slope as a rough general rule.

Interactions between genotypes

The overall properties of mixtures. Antagonism between individuals of the same genotype and facilitation between individuals with different genotypes will create greater rates of increase and higher asymptotic densities in mixtures than in pure cultures of a single strain. A common way of comparing mixtures with pure strains is to compare the yield of the mixture with the mean of the yields of its components in pure culture; this is valid only when the strains are mixed in equal proportions and the composition of the mixture does not change between sowing and harvest. A more severe test is to compare the yield of the mixture with that of the component having the greater yield in pure culture; if the mixture is superior then facilitation has been proven, but a failure to obtain this result does not prove the absence of facilitation.

The bulk of the available information comes from inbred lines of crop plants, especially cereals. According to Simmonds[92], 'the performance means of mixtures (of cereal varieties) are often equal to the means of the components but they sometimes exceed them, and occasionally even exceed the higher component; they are rarely inferior to the means of the components'. The impression of a general tendency to facilitation is strengthened by reviewing particular cases. Engelke[32] combined five varieties of wheat in five combinations at various proportions and found that the yield of 11/13 mixtures exceeded that of the higher-yielding component (by up to nearly 20%). Nuding[77] compared the performance of four wheat varieties with that of the six possible equal mixtures at seven sites over three years. He found that all six mixtures exceeded the component means, though not significantly for any individual case, while pooling the data showed that the mixtures had a slightly (about 3%) but significantly greater yield than the pure cultures. Frankel[36] found little difference between mixtures and pure strains; Borlaug[15] got mixed results form various mixtures of backcrosses from a standard wheat cultivar, 8/21 cases showing superiority of the mixture over the component means and 4/21 inferiority, with overall a 2.8% increase in yield being attributable to mixture. Jensen[59] found that mixtures of oat varieties generally exceeded the component means by about 5% but were slightly inferior to the better pure strain. Sandfaer[89] tested three oat mixtures and found that all were superior to the component mean and one exceeded the better component. Griffiths[43] found that twelve mixtures all equalled or exceeded the better component. In experiments with barley, Sandfaer[89] used six equal mixtures of four varieties and found that five exceeded the component mean and one the better component, giving an average gain in gross yield of about 5% overall. Gustaffson[44] conducted a careful study of three mixtures of barley cultivars and found them generally to produce more spikes, more grains and heavier grains than in pure culture; one mixture was intermediate between the two components, but the other two both exceeded the better component by about 2%. Roy[88] grew mixtures of two high-yielding rice varieties and found that all exceeded the component mean while two exceeded the better component by 11–20%. In a larger experiment he compared 31 mixtures of varieties; only two mixtures were significantly different from their component means, both being greater. Allard[3] reported a rare contradictory case in lima beans, where four equal mixtures of three varieties were each a little less productive than the component means. Hanson et al.[48] found that mixtures of bluegrass clones exceeded component means by about 5%; England[33] sowed six mixtures of four varieties of herbage grasses and found that they consistently yielded more than the pure strains, often exceeding the component means by more than 10%, all the significant differences (9/24 comparisons) being in this direction. In cotton, a widely-sown mixture of diploid and tetraploid strains performs better than either component over a wide variety of conditions[55]. According to Khan et al.[63], both flax and linseed often do better in mixture than in pure stand.

A few experiments have been done using insects in laboratory culture. Mixtures of karyotypes of *Drosophila pseudo-obscura* generally yield more flies than pure cultures, whether the design enforces crowding among larvae[9] or among adults[30]. These results might conceivably be due to the superiority of chromosomal heterozygotes, but by obtaining similar results at a temperature at which the heterozygotes are known not to be superior Battaglia and Smith[8] showed that the increase in yield is an effect of mixture. In a further experiment, Dobzhansky et al.[29], found that thin uncrowded cultures the rate of increase of chromosomally polymorphic cultures exceeded that of pure cultures. This effect seems to disappear under very favorable conditions, when pure cultures attained very high rates of increase[78]. Klearsey[61] found that the viability of *D. melanogaster* is greater in mixed than in pure culture at low or moderate density, but less at high density; an interaction with density was also found by Lewontin[69], who found facilitation of larval viability in mixed culture only at intermediate densities. Sokal and Sullivan[96] found that one strain of housefly did a little better and another strain a little worse in mixed than in pure culture; Bhalla and Sokal[12], working with a different mutant, found that its performance in mixed culture 'furnishes a clear-cut demonstration of mutual facilitation among genotypes'. Finally, in a rare experiment with domestic animals, Moav and Wohlfarth[75] found that the growth rate of carp is greater in mixed than in pure cultures, and showed that this was due to the greater genetic values of growth rate in mixed ponds.

A particularly interesting and relevant experiment was performed by Ellstrand and Antonovics[31], who compared the success of blocks of clonally and sexually propagated tillers from semi-natural populations of the grass *Anthoxanthum*. The sexual tillers had greater survivorship and fecundity in each of two independent experiments, presumably because of their greater variability.

There are persistent suggestions that, aside from any difference in mean yield, mixtures are also less variable in performance than pure strains. This has been claimed, for instance, in cotton[55], wheat[92], corn[97], lima beans[3] and fruitflies[9], but there seems to be too little hard evidence to permit a confident generalization.

The relevance of experiments involving arbitrary mixtures of pure strains can be questioned, on the grounds that facilitation is scarcely to be expected between genotypes which have never before interacted. The results with crop plants are, on this view, all the more convincing, since they concern genotypes which have actually been seen selected for their performance in pure culture. Seaton and Antonovics[90] found that mixtures of wild-type and mutant *Drosophila* yielded more than pure strains only after a period of selection in mixture.

The bulk of the evidence, therefore, points unequivocally towards the general superiority of mixtures. All the examples cited above are mixtures sown in one place at one time, and are therefore consistent with the correlation between variation and yield required by the Tangled Bank. The practice of crop rotation shows that mixtures in time may also enhance yield, but I know of no experiments which use temporal mixtures of varieties rather than species, and the Red Queen therefore receives no direct experimental support.

The effect of input frequency. Mutual facilitation between genotypes implies that the fitness of a genotype will be greatest when it is rare, and when in consequence it interacts mostly with members of other genotypes. Thus, in the experiments on mixtures of *Linum* by Khan et al.[63] the flax and linseed varieties were sown in three different proportions, allowing the authors to show that the superiority of mixtures was accompanied by frequency-dependence of fitness within the mixture. A particularly clear result was obtained by Birley and Beardmoore[13], who varied temperature and density as well as the input frequency of genotypes at an esterase locus in *Drosophila*. They found not only significant effects of input frequency on fitness, but also significant interactions between input frequency and treatment.

While instances of frequency dependence are too numerous to review here, the relevance of natural mixtures of clones in asexual organisms must be pointed out. It is difficult to see how such mixtures could persist, unless a clone has greater than average fitness when it is rare. In fact, the number of clones in grass communities often declines with time, perhaps eventually leaving only the single best genotype[22,49,50,60]. However in fertile lowland habitats populations are often highly polyclonal[21,51]. Bell[10] concludes that populations of asexual animals such as anemones, rotifers and cladocerans are usually, though not invariably, polyclonal.

Proximal causes of the superiority of mixtures. The mechanism of facilitation is often unknown. In some crop plants, differential resource utilization has been suggested; in Gustafsson's barley experiments, for instance, the superiority of mixtures was attributed to differential exploitation of the soil, one type having a shorter but more branched root system than the other (Wettstein, cited by Gustafsson[45]). In bluegrass, Hanson et al.[48] suggested that the components of high-yielding mixtures have complementary morphologies, e.g. sod formers and taller grasses.

A much more common explanation of the superiority of mixtures is that they resist pests and pathogens more effectively than pure stands. Besides a great deal of more or less anecdotal evidence for the sensitivity of pure stands (e.g. Simmonds[91] for banana; Borlaug[15] for maize; Borlaug[15] and Thorpe[99] for wheat; review in Adams et al.[2]) there is some quantitative evidence that both the incidence of pathogen damage[98, 109] and the rate of increase of pathogens[11, 17, 19, 67] is lower in mixed than in pure stands. The properties of monocultures, with special reference to the susceptibility of genetically uniform strains of crop plants and domestic animals to damage by pathogens, has been brillantly reviewed by Barrett[7]. From the opposite perspective, it is generally true that biological control (usually by insects) is more likely to be effective with asexual than with sexual weeds[18].

A particularly extensive and important experiment was conducted by Wolfe and Barrett[107, 108], who compared 37 different three-cultivar mixtures of spring barley, involving 25 cultivars in all, with the performance of their components when grown alone. Of 47 possible comparisons, 39 showed the mixtures to equal or exceed the component mean, while in 26 cases the yield of the mixture exceeded that of the highest-yielding component when grown alone. Overall, the effect of mixture was an increase in yield of 6.5%. However, the effectiveness of mixture varied with the degree of pathogen damage: at seven sites with little or no mildew infection the superiority of mixtures was about 3%, while in 10 sites with heavy mildewing it was about 9%. This suggests that, out of a total yield increase of about 10% associated with these rather simple mixtures, about two-thirds is attributable to increased resistance to pathogens and about one-third to other factors, including enhanced resource utilization. The implication of pathogens in the superiority of mixtures immediately suggests the Red Queen as a possible explanation.

It must be emphasized, however, that the Red Queen is not necessarily a theory about pathogens, nor is pathogen resistance necessarily evidence for the Red Queen. What the Red Queen states is that the function of sex and variability is to enable a response in time to pathogen pressure to be made. The Tangled Bank can refer to pathogens as well as to any other ecological variate, but predicts that current diversity is in itself a sufficient protection against pathogens. The operational difference between the two hypotheses is as follows. If we compare a pure strain with a mechanical mixture of genotypes, we expect the mixture to do better, perhaps because of resistance to pathogen attack. The Tangled Bank predicts that a mixture sown in one place at one time should be effective; the Red Queen predicts that a temporal mixture should be effective, a different genotype being sown in each year. The crucial experiment would be the comparison of a mechanical mixture of clonal genotypes with a sexual population; the Tangled Bank predicts that both will do equally well, whereas the Red Queen predicts that the sexual population, with its greater capacity for adaptive change, will do better. In fact, most of the observations refer to mechanical mixtures sown in a single season, and therefore support the Tangled Bank as much as the Red Queen. The only observations that directly suggest a role for the Red Queen are the greater effectiveness of biological control for apomictic weeds and the fact that parasites almost always manage eventually to overcome disease resistance based on one or two loci, so that the only effective agronomic strategy is then to introduce a new resistant variety. In neither case, however, it is clear that coevolutionary response rather than high current variation is crucial for success.

The effect of neighbors. A particularly elegant and vulnerable experiment to test for mutual facilitation between different genotypes is to measure the performance of a test plant when surrounded by related or unrelated neighbors. Any increase in yield associated with the presence of unrelated neighbors is a conclusive demonstration of facilitation. The classical experiment was done by Allard and Adams[4], using a 3 × 3 planting design to evaluate the effect on the central test plant of its eight neighbors. Their results are summarized in the table. When cultivars of barley or wheat were used there is a small (1–4%) but significant and highly consistent increase in the yield of the test plant when its neighbors belong to a different variety or varieties. An even clearer result, giving a 5–6% increase in yield, was obtained by drawing neighbors from the genotypes produced by intercrossing varieties of wheat. A similar result was obtained by Antonovics and Ellstrad[5] for *Anthoxanthum* under semi-natural conditions. Tillers were transplanted into blocks or rows in such a way that each was surrounded by genetically similar or dissimilar neighbors. Plants with dissimilar neighbors had greater reproductive output, the effect being much greater than that in Allard and Adams' cereals;

Summary of the results obtained by Allard and Adams[4] from an experiment to measure the effect of genetically similar and dissimilar neighbors on a target plant

Neighbors	Barley vars		Wheat vars		Wheat genotypes	
	Mean	SD	Mean	SD	Mean	SD
1) All eight of a single different type	101.54* n = 24	2.529	102.10** n = 24	2.598	104.5** n = 16	4.379
2) Equal numbers (four each) of same type and another type	101.16* n = 24	1.581	101.36** n = 24	1.517	–	
3) Two of same type; two each of three different types	101.95* n = 8	1.258	103.78** n = 8	1.436	–	
4) One of same type; one each of seven different types	–		–		106.31** n = 16	4.600

The mean and SD are estimated from 25 replicates of each design, and refer to yield of seed relative to yield = 100 when surrounded by eight neighbors of the same type. On this basis, t-tests for significance of the excess of yield over 100 are shown by * $p < 0.01$, ** $p < 0.001$.

although there were statistical difficulties arising from highly skewed fitness distributions, substitution of unlike for like neighbor appeared to be associated with a doubling of fitness, an astonishing result.

Conclusions and suggestions

The evidence that I have very briefly reviewed above strongly suggests the general occurrence of substantial interactions between genotypes and between genotype and environment. These short-term observations and experiments therefore run parallel to comparative work showing that sex is associated with stable heterogeneous environments, and the confluence of these two independent streams of evidence argues very strongly that either the Tangled Bank or the Red Queen, or both, are crucial to the maintenance of sex and variation. Unfortunately, the data do not seem sufficient decisively to eliminate one of these two possibilities; genotypic fitness may interact substantially with time or place or both. Indeed, both hypotheses may be required for a satisfactory solution to the problem, and experiments such as those conducted by Wolfe and Barrett[107] show how the variance in yield between mixtures and pure lines might be partitioned between the two effects.

The most effective designs are the reciprocal transplant-replant and the effect-of-neighbor experiments I have described above, and it is very desirable not only that more of these should be performed, but also that they should be capable of detecting between-year effects. A different type of experiment, however, has not to my knowledge been attempted: the comparison of mechanical mixtures with sexual populations within a single site, to evaluate the relative importance of current variation and selective response. It would be necessary to use a short-lived outbreeding organism which can be propagated vegetatively or by apomictic seed. From a diverse initial sample from natural populations, a large number of genotypes are extracted and propagated clonally. Each site within a block of sites is then stocked at the beginning of each generation in one of five ways:

1) same clone;
2) different random clone;
3) same mixture of clones;
4) different random mixture of clones;
5) the indefinite mixture generated by random-mating the surviving individuals in proportion to their fecundity.

From the mean performance of individuals from each of these five treatments, we can then identify four types of effect.

A) The effect of temporal mixture, estimated by the excess of 2 over 1.

B) The effect of contemporary mixture, estimated by the excess of 3 over 1.

C) The interaction of A with B, estimated by the excess of 4 over 1 not explained by the excess of 2 or 3 over 1.

D) The effect of appropriate genetic response, generated by selection, estimated by the excess of 5 over 4.

The main effects A and B identify any advantage to the random dispersal of genotypes in time or space; if both are substantial then it is not unlikely that the interaction C will also be important. The final effect D is intended to show whether outbred sexuality is more or less effective in enhancing the properties of mixtures than deliberate randomization. The results of such an experiment would be interesting on general grounds, showing whether the Red Queen (effects A and D) or the Tangled Bank (effect B) or both (effect C) were supported by the properties of different kinds of mixture. They might also have some practical utility in suggesting the best ways of constructing mixed crops. It would obviously be very instructive to run such experiments so that spatial heterogeneity within sites or exposure to an appropriate pathogen were deliberately contrived. It is, I believe, very desirable that the extensive comparative work on sexuality should be supplemented by increased effort to devise short-term experimental tests of the rival theories.

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The adaptive significance of sexuality

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Summary. A theory of sexuality and polymorphism is proposed in which diversity at the molecular level is the adaptive response of multicellular organisms to the challenge of microparasites that have smaller genomes, shorter generation times and which can evolve more quickly than their hosts. The theory has implications for genetically homogenized crops and other cultivated plants as well as for immunology. A different function of sexuality is proposed for microorganisms that reproduce both asexually and sexually. Several possible experimental tests are discussed. Mathematical modelling techniques are outlined qualitatively and compared with game-theoretical methods which may be interpreted as simplifications of population dynamic and genetic equilibria. Some results about equilibria, stability and extinction in the population dynamics of polymorphic host-parasite populations are referenced.

Key words. Recombination; sex; parasites; pathogens; immune system.

1. Introduction

Birds do it, bees do it, plants, algae, protozoans, bacteria, and last but not least: mammals and *Homo sapiens*. Much of the entire biosphere is engaged in sexual recombination. The near universality of sexual recombination lets one suspect a common cause or function.

It has been argued that sex speeds up evolution by bringing together rare advantageous mutations[26, 27, 63]. Kimura and Ohta[42] have stated this effect dramatically: 'Sexual