Genet. Res., Camb. (1996), **68**, *pp.* 165–173 *With 7 text-figures* Copyright © 1996 Cambridge University Press

Evolution of amphimixis and recombination under fluctuating selection in one and many traits

ALEXEY S. KONDRASHOV* AND LEV YU. YAMPOLSKY
Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, USA

(*Received 6 June 1995 and in revised form 14 May 1996*)

Summary

Both stabilizing and directional selection acting on one or many quantitative traits usually reduce the genetic variance in a polymorphic population. Amphimixis and recombination restore the variance, pushing it closer to its value under linkage equilibrium. They thus increase the response of the population to fluctuating selection and decrease the genetic load when the mean phenotype is far from optimum. Amphimixis can have a short-term advantage over apomixis if selection fluctuates frequently and widely, so that every genotype often has a low fitness. Such selection causes high genetic variance due to frequent allele substitutions, and a high load even with amphimixis. Recombination in an amphimictic population is maintained only if selection is usually strong and effectively directional. A modifier allele causing free recombination can have a significant advantage only if fluctuations of selection are such that the load is substantial. With smaller fluctuations, an intermediate recombination rate can be established, either due to fixation of alleles that cause such a rate or due to the stable coexistence of alleles causing high and low recombination. If many traits simultaneously are under fluctuating selection, amphimixis and recombination can be maintained when selection associated with individual traits is weaker and the changes in their mean values are smaller than with a single trait. Still, the range of changes of the fitness optima in each trait must be at least of the order of the trait's standard deviation, and the total load must be high.

1. Introduction

Amphimixis and recombination can be beneficial in an infinite population under a changing environment because they destroy linkage disequilibria created by epistatic selection (see Kondrashov, 1993). The corresponding Environmental Deterministic (ED) hypotheses can be subdivided into two subclasses. *Non-responsiveness* hypotheses claim that destruction of disequilibria is beneficial because it reduces the response of a population to frequent and relatively small fluctuations of selection, while *better responsiveness* hypotheses postulate that this destruction is beneficial because it increases the response to rarer and wider fluctuations, or to invariant directional selection (Barton, 1995).

'Narrowing' selection (Shnol & Kondrashov, 1993) acting on a quantitative trait reduces the genetic variance below its linkage equilibrium level by creating

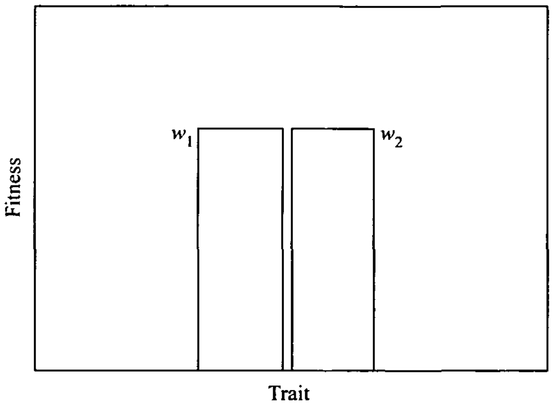

Fig. 1. Under selection with fluctuating fitness function amphimixis can be advantageous only if every genotype sometimes has a low fitness. With all-or-nothing truncation selection, this is the case when there is at least a pair of fitness functions, $w_1(x)$ and $w_2(x)$, each describing selection at some moments of time, which do not overlap.

---

* Corresponding author. Telephone: +1(607) 254-4221. Fax: +1(607) 255-8088. e-mail: ask3@cornell.edu.

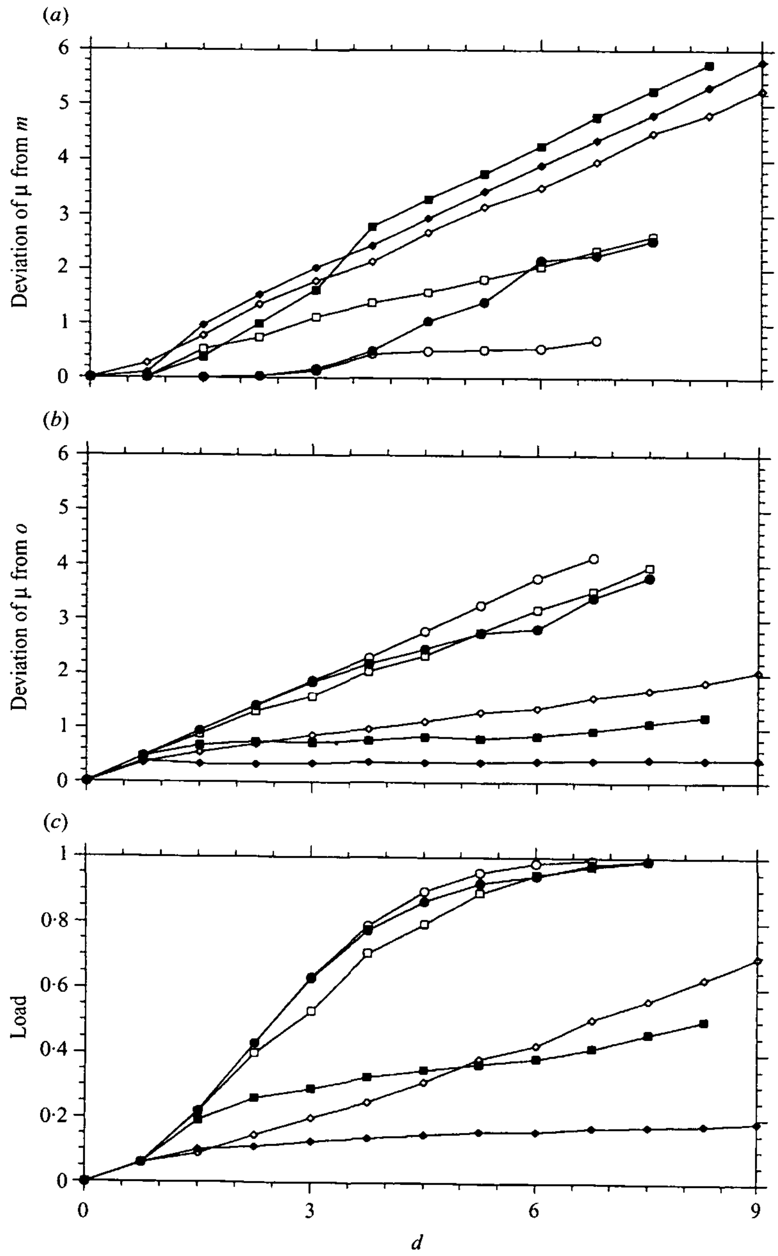

Fig. 2. The average deviation of the mean value (μ) of the trait from m (a) and from o (b), and the genetic load corresponding to the geometric mean fitness (c) with $n = 1$, $S = 1{\cdot}5$, and $\tau = 20$ (circles), 80 (squares), and 320 (diamonds) in the amphimictic (filled markers) and apomictic (open markers) populations as functions of d (compare with figure 3 in KY-96).

repulsion linkage disequilibria, while amphimixis and recombination move it closer to this level by destroying them and thus increase the resulting changes in the trait mean value (Mather, 1943; Fraser, 1957; Felsenstein, 1965; Eshel & Feldman, 1970; Crow, 1992; Charlesworth, 1993). Both directional selection (if the increase in fitness caused by two beneficial alleles in the same genotype is less than the product of their individual effects, i.e. if they interact sub-multiplicatively or with diminishing returns epistasis) and stabilizing selection are usually narrowing (see Shnol & Kondrashov, 1993).

Under invariant stabilizing selection, the higher variance becomes deleterious after the population mean reaches the fitness optimum. Under invariant directional selection strong enough to provide a short-term (Maynard Smith, 1978) advantage for amphimixis, the higher variance is beneficial but the mean value of the trait changes rapidly and irreversibly. Apparently this is not common in nature, although if many traits are selected simultaneously a short-term advantage may be consistent with slow evolution in each of them (Maynard Smith, 1988, p. 62; Crow, 1992).

Thus, the better responsiveness hypotheses are more plausible under fluctuating selection (Mather, 1943; Treisman, 1976; Maynard Smith, 1980, 1988; Korol & Preygel 1989; Crow, 1992; Charlesworth, 1993; Korol *et al.* 1994), either directional or stabilizing (when the population mean is far from the optimum, stabilizing selection becomes effectively directional and the increase in variance is beneficial). A short-term advantage of amphimixis requires that no phenotype has high fitness for a long time (Fig. 1; Treisman, 1976). Maintenance of recombination in an amphimictic population may require even more stringent conditions (Charlesworth, 1993).

Here we will supplement the recent analytical results of Charlesworth (1993) and Barton (1995) by investigating a computer simulational model of the evolution of amphimixis and recombination under fluctuating selection acting on one or many quantitative traits.

2. Model

The basic model was described in Kondrashov & Yampolsky (1996; hereafter KY-96). To consider the evolution of recombination, we added a modifier locus R, which does not mutate, does not influence fitness directly, is unlinked to the selectable loci, and determines the recombination rate. An allele r_k caused k cross-overs in independent random places in the single linkage group (chromosome) that carried all the selectable loci. Thus, r_0 caused complete linkage in this chromosome, while r_∞ caused free recombination. Different modes of dominance at R were studied.

In the case of many (n) traits, we assumed that each one is controlled by a separate set of l loci, so that the total number of selectable loci was $l*n$. With limited recombination, all these loci were arranged linearly in one chromosome (l loci responsible for the first trait first, then l loci responsible for the second trait, etc.). The fitness of a phenotype X, $w(X)$, depended on the distance of X from the optimum O (both X and O are, of course, n-dimensional vectors). With Euclidean metrics $X = \sqrt{\Sigma(x_i - o_i)^2}$, while with module metrics $X = \Sigma|x_i - o_i|$, where o_i and x_i are the optimal and the actual values of the ith trait, respectively. The middle phenotype M (with coordinates m_i), occupies the centre of the range of changes in O. The maximal deviation of o_i from m_i is d, and the maximal distance of O from M is D. With Gaussian stabilizing selection $w(X) = \exp(-(X-O)^2/2S^2)$, while with truncation stabilizing selection $w(X) = 1$ if $|X-O| \leqslant T$ and 0 otherwise.

For periodically fluctuating selection we assumed

$$o_i(t) = m_i + d\sin\{2\pi[t/\tau + i/n]\} \qquad (1)$$

(compare with equation 1 in KY-96). According to eqn (1), different o_i deviate maximally from the corresponding m_i at different moments, so that the distribution of the values of o_i does not change much with time. The THINK C programs are available on request.

3. Results

(i) *Amphimixis versus apomixis: one trait*

When not stated otherwise, we used the default parameters from KY-96. Figure 2 presents the data on the deviations of the mean value of the trait μ from m (Fig. 2*a*) and o (Fig. 2*b*), and on the genetic load (Fig. 2*c*). In the amphimictic population the deviation of μ from o is smaller, while its deviation from m is larger, so that amphimixis facilities the response to selection, due to higher genetic variance (see KY-96). Figure 2 is based on the data from a single run, observed from generation 3d during 5d generations. The results of different runs were very similar (data not reported).

Not surprisingly, this better responsiveness of amphimixis leads to a lower load when $d > S$. Amphimicts outcompete apomicts with twofold reproductive advantage (Maynard Smith, 1978) if $(1-L_{\text{amp}})/[2(1-L_{\text{apo}})] > 1$, where L_{amp} and L_{apo} are the values of the load, in terms of geometric mean fitness, in the two populations. This requires $L_{\text{apo}} > 0{\cdot}5$, which does not happen if there is a phenotype which always has high fitness (a compromise strategy), i.e. if $d < S$ (Fig. 2*c*). When selection changes frequently ($\tau = 20$), L_{apo} grows rapidly when d becomes larger than S, but L_{amp} is only slightly lower than L_{apo}. In contrast, when selection changes rarely ($\tau = 320$) only very large d leads to high L_{apo}. The advantage of amphimixis appears most readily with an intermediate frequency of fluctuations ($\tau = 80$). In

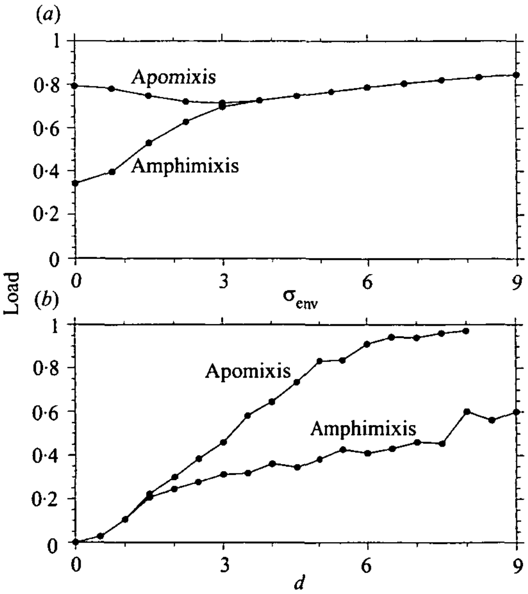

Fig. 3. The genetic load corresponding to the geometric mean fitness in the amphimictic and apomictic population (*a*) under the same parameters as in Fig. 2 ($S = 1{\cdot}5$, $d = 4{\cdot}5$ and $\tau = 80$) but with non-zero environmental variance, and (b) under the same parameters as in Fig. 2 ($S = 1{\cdot}5$, $\tau = 80$), but with alleles having arbitrary effects (compared with figures 6 and 7 in KY-96).

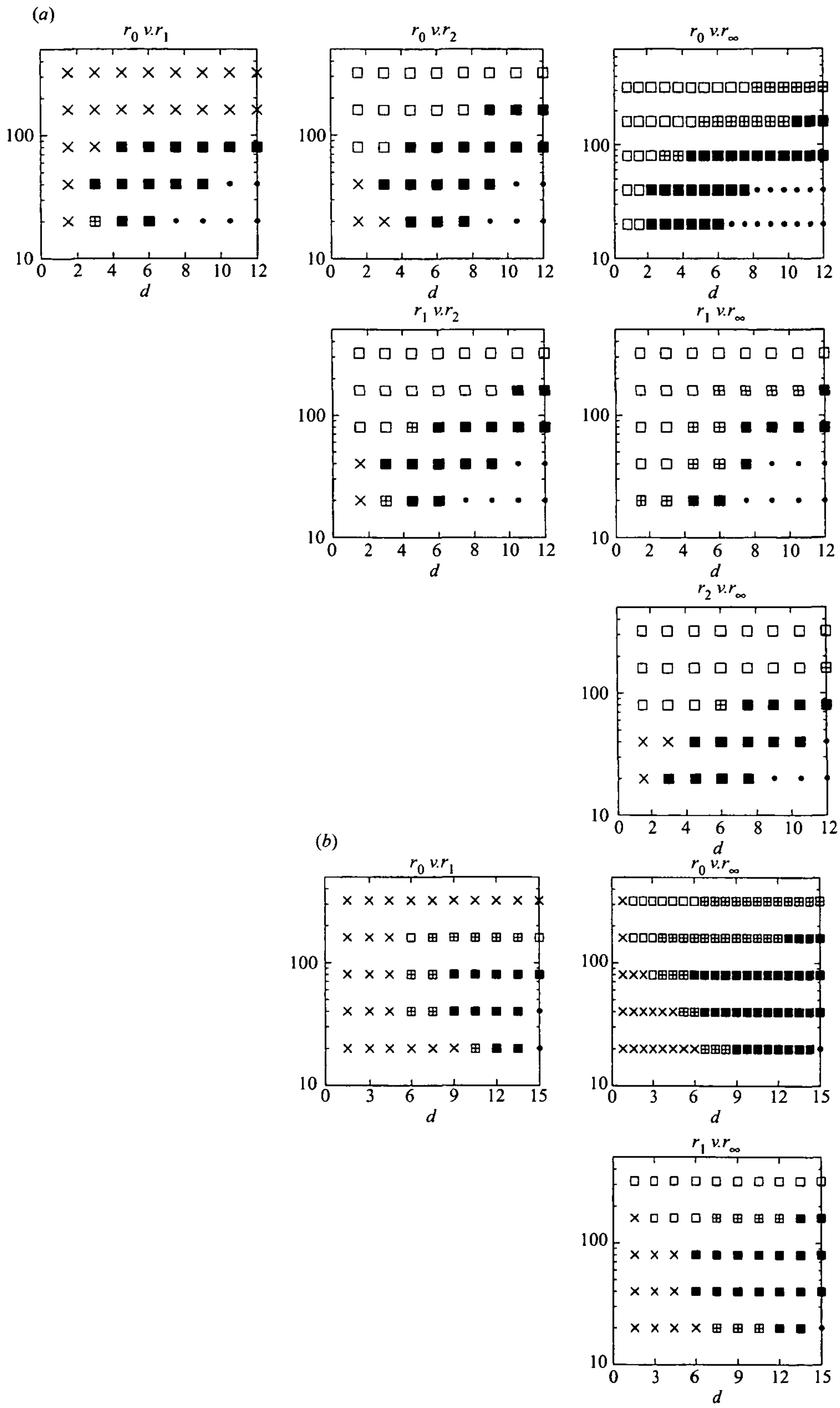

Fig. 4. Evolution at the R locus under the same conditions as in Fig. 2 with $S = 1{\cdot}5$ (*a*) or $S = 3{\cdot}0$ (*b*). Fixations of alleles causing more and less recombination are denoted by black and white squares, respectively; their stable coexistence is denoted by crossed squares, their neutral coexistence (selection at R too weak to be detected) is denoted by crosses, and extinction of the population is denoted by dots. Only a pair of alleles, marked above the corresponding pictures, was present in each case. With $d = 0$, selection at R was always too weak to be detected, although r_0 probably won eventually (Charlesworth, 1993).

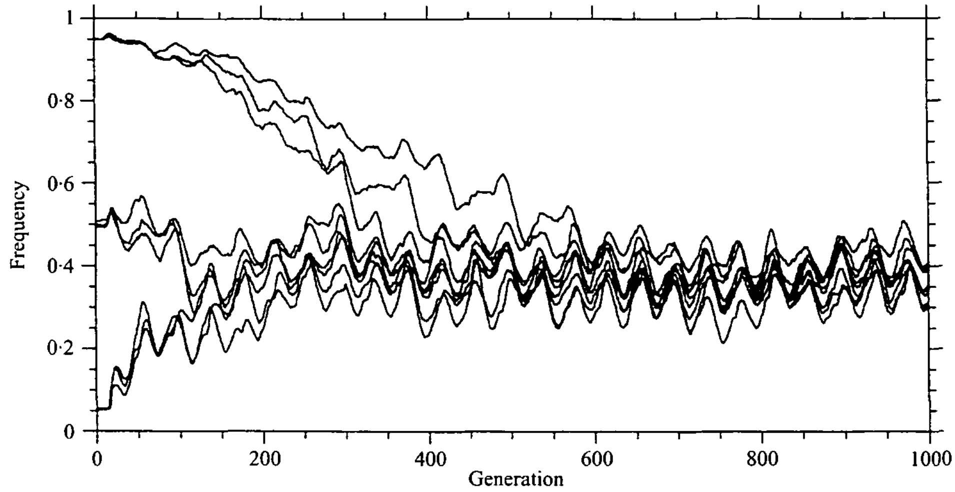

Fig. 5. Dynamics of the frequency of allele r_∞, coexisting with allele r_0 with $S = 1{\cdot}5$, $\tau = 80$ and $d = 3{\cdot}75$ in nine runs (three with initial frequency of 0·05, three with 0·5, and three with 0·95).

all cases, the L_{amp} required for the protection of amphimixis was high (at least $\sim 0{\cdot}3$). Of course, without the twofold advantage of apomixis, $L_{\mathrm{amp}} < L_{\mathrm{apo}}$ is sufficient for the protection of amphimixis. An advantage of amphimixis disappears only when $S \ll 1$ (data not reported).

If the mutation rate u is not much smaller than N^{-1}, allele fixations are rare and some variability is usually present at a locus, while with $u < 0{\cdot}01N^{-1}$ even an amphimictic population can run out of variability and die out when $d \gg S$. In contrast, with a high u (perhaps unrealistic) even an apomictic population can adapt rapidly, due to new mutations. Thus, $u \sim 0{\cdot}1N^{-1}$ (as in Fig. 2) usually leads to the largest advantage of amphimixis (data not presented). Truncation stabilizing selection, as well as random fluctuations of the fitness optimum, led to roughly the same advantage of amphimixis (data not reported; see Charlesworth, 1993).

The advantage of amphimixis increased slightly with the number of loci that influence the trait (data not reported). In the presence of environmental variance the advantage of amphimixis requires even wider fluctuations of fitness optimum, such that $d > \sqrt{(S^2 + \sigma_{\mathrm{env}}^2)}$, because, with smaller d, the population fails to respond to fluctuating selection (Fig. 3*a*). In contrast, a continuous Gaussian distribution of allele effects has little effect on the advantage of amphimixis (Fig. 3*b*).

(ii) *Recombination: one trait*

Figure 4 shows the outcomes of competition between co-dominant (in a heterozygote, recombination rate was determined with probability 0·5 by either allele) alleles of R. Three initial frequencies of modifier allele were used (0·05, 0·5 and 0·95) and at least five runs were performed for each, usually giving the same results. When $d < S$, selection at R is either negligible (because of very low variability) or acts against recombination, while with $d > S$ recombination can be selected for. Free recombination was selected for when $L_{\mathrm{amp}} > \sim 0{\cdot}3$, but still the advantage of amphimixis was often not sufficient to overcome the twofold advantage of apomixis (compare Figs. 2*c* and 4). Recombination was favoured most with $\tau = 20$ or 40 under $S = 1{\cdot}5$, and with $\tau = 40$ or 80 under $S = 3{\cdot}0$. With $d > S$, but not sufficient to favour free recombination, intermediate recombination rates were established, due to either fixation of alleles causing such rates or stable coexistence of two alleles causing a high and a low rate (Fig. 5).

With $S < 0{\cdot}3$ recombination was not favoured, because the increase in variance always led to lower fitness. The properties of alleles causing three or more chiasmata were very similar to those of r_∞. Dominance of an r allele led, as expected,to the decreased efficiency of selection when this allele was frequent (data not reported).

As with the advantage of amphimixis, non-zero environmental variance increases the range of o fluctuations required for the advantage of recombination. For example, if $S = 1{\cdot}5$ and $d = 6{\cdot}0$, allele r_∞ replaced r_0 only when $\sigma_{\mathrm{env}} < 1{\cdot}5$ ($\tau = 20$) or $\sigma_{\mathrm{env}} < 2{\cdot}0$ ($\tau = 40$), i.e. when d exceeded $\sqrt{(S^2 + \sigma_{\mathrm{env}}^2)}$ more than twofold, while with higher σ_{env} selection at R was difficult to detect (compare with Fig. 4*a*).

(iii) *Amphimixis versus apomixis: many traits*

The data on genetic load in the amphimictic and apomictic populations under fluctuating selection acting on 10 traits are presented in Fig. 6. If all o_i reach their maximal deviation from m_{eq} at the same time, D would be $d\sqrt{n}$. However, here $D \approx 0{\cdot}7d\sqrt{n}$ because according to eqn (1) different o_i deviate from m_i maximally at different moments. Thus, $D = 0{\cdot}7d\sqrt{10} \approx 2d$. Therefore, with increasing d the load is already substantial when $d = 0{\cdot}5S$, but amphimixis, has a significant advantage only when $d > S$. With

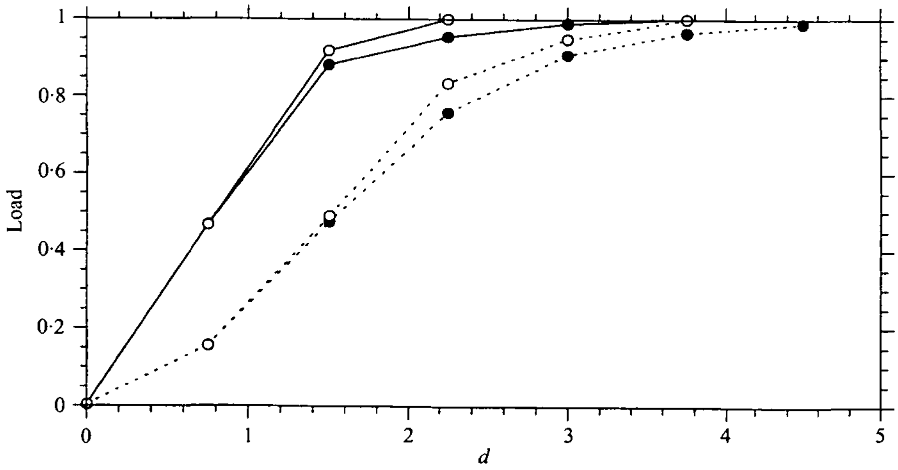

Fig. 6. The geometric mean genetic load in the amphimictic (filled markers) and apomictic (open markers) population with fluctuating selection acting on 10 traits, $\tau = 80$ and $S = 1{\cdot}5$ (continuous lines) and $S = 3{\cdot}0$ (dotted lines).

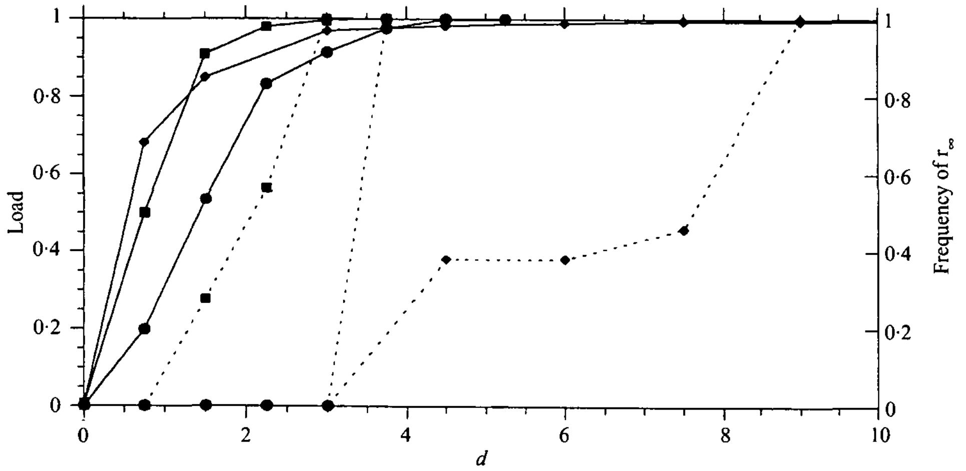

Fig. 7. The geometric mean genetic load (continuous lines) and frequency of the allele r_∞ after 7τ generations (dotted lines) under fluctuating selection acting on 10 traits with $S = 1{\cdot}5$, $\tau = 20$ (circles), 80 (squares) and 320 (diamonds), and different values of d. Initially only the alleles and r_0 and r_∞ were present.

such d the load is very high even with amphimixis. Under shorter and longer periods of selection fluctuations the pattern was similar (data not reported).

With random fluctuations in O, L_{amp} was even higher under the conditions necessary for the advantage of amphimixis. However, the minimal D required for this advantage was slightly lower than under periodic fluctuations according to eqn (1), because here all position of O inside the multidimensional cube $(m_i - d \leqslant o_i \leqslant m_i + d)$ are possible (data not reported).

(iv) *Recombination: many traits*

Some data on the outcomes of evolution at the R locus with fluctuating selection acting on 10 traits are presented in Fig. 7. As with a single trait, an increased range of optimum fluctuations favours free recombination, while the period most favourable to it is 80. Even with such τ, free recombination wins only when selection changes so rapidly that the load is very high. However, some recombination can be maintained with a smaller load, although it still must be at least $\sim 0{\cdot}5$. As with one trait, a stable polymorphism at the R locus can be established with intermediate d (data not reported).

4. Discussion

(i) *When does fluctuating stabilizing selection maintain amphimixis?*

Amphimixis may have an advantage when every genotype is sometimes maladapted (Fig. 1). In our model this happens when $d > \sim \surd(S^2 + \sigma_{\text{env}}^2)$ (Figs. 2, 3). The advantage of amphimixis appears when fluctuations of o are ~ 2 times wider than that required for increased genetic variance, because this advantage depends on simultaneous allele substitutions, while even isolated substitutions increase the variance (compare Fig. 2*c* with figure 3 in KY-96). Fluctuations must be also frequent enough, thus causing a substantial load even in an amphimictic population, because otherwise apomicts can adapt using fresh mutations. However, if fluctuations are too frequent the advantage of amphimixis disappears, because the population cannot respond to selection. Apparently, intermediate frequencies of fluctuation are most favourable to amphimixis (Fig. 2*c*). The exact mode of selection and its fluctuations are not critical.

Thus, our results are in a qualitative agreement with those of Charlesworth (1993). However, his analytical predictions should be used with caution, because he did not take into account the dramatic increase in the variance due to changing selection (KY-96). Although both deterministic and stochastic factors were involved in our simulations, we believe that, because our populations were very large, the advantage of amphimixis and recombination we observed was mostly deterministic.

In nature, the width of the fitness curve S usually exceeds σ because: (i) the data suggest that for many traits $S \sim 10\sigma$ (Turelli, 1984; Endler, 1986), (ii) with $S < \sigma$ the load can be too high even when $\mu = o$ and (iii) it is difficult to imagine a factor that can maintain $\sigma > S$ (see KY-96). If so, $d > \surd(S^2 + \sigma_{\text{env}}{}^2)$ implies $d \gg \sigma$. Thus, because fluctuations of o cause fluctuations of μ with only a slightly smaller amplitude (Fig. 2*a*, *b*), if amphimixis is maintained by fluctuating selection acting on one quantitative trait, the ranges of changes of fitness optimum and of the mean value of this trait must exceed its standard deviation.

When selection acts on many traits, the compromise strategy is absent when $D > S$. With the Euclidean metric $D = d\surd n$, and this requires $S < d\surd n$. With $n \rightarrow \infty$, $S < \sigma\surd n$ would cause too high a load, because the proportion of a multivariate Gaussian distribution with the same variance σ^2 of each trait and with no covariances (this assumption is justified if disequilibria are not high) inside a sphere with its centre at the mean and radius $\sigma\surd n$ approaches 50%, while spheres with slightly smaller or larger radii contain $\sim 0\%$ and $\sim 100\%$ of the distribution, respectively (this follows from the weak law of large numbers, because all components of the distribution are independent and identically distributed). Thus, if the load is not too high, when $D > S$ the range of changes in o_i, $2d$, must exceed 2σ. The same is true for the module (and probably any other reasonable) metric, where $D = dn$, and, as $n \rightarrow \infty$, 50% of the population deviates from the mean by less than $0{\cdot}798\sigma n$ ($0{\cdot}798 = \surd(2/\pi)$ is the mean absolute value of a variable with a standardized Gaussian distribution).

Thus, even with many traits, amphimixis may have an advantage without excessive load only if the range of changes of fitness optima in individual traits exceeds their standard deviations. However, selection associated with each trait can be weak (its intensity declines as $\surd n^{-1}$), so that the changes in mean values of individual traits can be small if n is large and the fluctuations of O are frequent.

Fluctuating selection acting on many traits may favour amphimixis more because in this case the movements of O can be effectively irreversible (e.g. circular), although each o_i changes back and forth. Thus, the trajectory of O may be free of 'returns', which are unavoidable with $n = 1$, which favour apomixis and linkage. However, we did not observe (Figs. 2*c*, 6) a better protection of amphimixis with $n > 1$. In contrast, it was protected only when the genetic load was very high even in the amphimictic population.

(ii) *When does fluctuating stabilizing selection maintain recombination?*

Under constant selection tight linkage is ultimately favoured (see Zhivotovsky *et al.* 1994), although recombination can enjoy a temporary advantage if the population is initially far from the selection optimum (Bergman & Feldman, 1990). An allele causing free recombination can win if selection changes so rapidly that it is effectively directional most of the time (Fig. 4). Our results are consistent with those of Maynard Smith (1988, figure 3), who observed that the allele that increases recombination rate won only under wide fluctuations of O which caused wide fluctuation of μ. Contrary to his opinion (p. 59), the lag load (see Maynard Smith, 1978) that corresponds to the geometric mean fitness is a useful predictor of the evolution of recombination. Under truncation selection the immediate advantage of a higher variance requires the load (i.e. the proportion truncated) to be above 0·5. However, the conditions where recombination is selected for are less restrictive, because a higher variance makes selection more efficient, so that after selection an allele for higher recombination is on the better genetic background (see Barton, 1995; Charlesworth & Barton, 1996). With the less extreme linear selection, free recombination can be advantageous under any load (Kondrashov, 1984, figure 1).

We observed a significant advantage of free recombination only when selection fluctuated widely, thus causing a load no less than $\sim 0{\cdot}3$ (Figs. 4, 7). The same is true if recombination is maintained by the mutational deterministic mechanism, although the conditions may be a little lighter (Charlesworth, 1990). Korol & Preygel (1989) and Korol *et al.* (1994) showed that an allele that increases recombination can be selected for when the geometric mean lag load is $\sim 0{\cdot}2$. Perhaps, free recombination can be advantageous under a low load, for example if in many generations selection is simply absent, but the magnitude of this advantage should be small. In a multichromosomal genome, crossing-over probably can be selected for only when free recombination enjoys a substantial advantage.

With smaller, but still substantial, fluctuations an intermediate recombination rate can be established due either to the fixation of the corresponding modifier allele or to a polymorphism (Fig. 5). In this case the load would be lower with free recombination, which provides one more example of the violation of Karlin–McGregor (1972) principle. Such polymorphism in a similar ED model was first observed by Korol & Preygel (1989) and Korol *et al.* (1994), while Charlesworth (1993, equation 7) concluded that intermediate ESS recombination rates are possible. A similar polymorphism was described by Kondrashov (1984, figure 5) in the mutational deterministic model.

(iii) *Stabilizing versus directional fluctuating selection*

Contrary to the opinion of Maynard Smith (1980, 1988), fluctuating stabilizing and directional selection maintain amphimixis and recombination by the same mechanism (Charlesworth, 1993; Barton, 1995). Both are usually narrowing (non-narrowing directional selection does not maintain amphimixis), and restoration of the variance improves the response to directional selection and to stabilizing selection when μ deviates from O (therefore, only fluctuating stabilizing selection maintains amphimixis).

However, the maintenance of amphimixis and recombination under directional selection implies even larger changes of μ. Under invariant directional selection, μ changes indefinitely. The advantage of amphimixis under selection with fluctuating direction requires that some phenotypes are maladapted because they are 'too big' under one direction of selection and 'too small' under the other direction, because otherwise there would be phenotypes that always have a high fitness. Minimal fluctuations of μ will occur under fluctuating directional selection consisting of two regimes: (i) $w_1(x) = 1$ if $x < a$ and 0 otherwise and (ii) $w_2(x) = 1$ if $x > a$ and 0 otherwise, where a is some trait value. Even if the switches between w_1 and w_2 occur every generation, the amplitude of μ changes would be $\sim \sigma$, while the load exceeds 0·5. If fluctuating directional selection acts on very many traits, the maintenance of amphimixis is consistent with small changes in the mean values of individual traits (Crow, 1992).

(iv) *How plausible is the mechanism?*

Any environmental hypothesis on the maintenance of amphimixis and recombination depends on conditionally beneficial genetic variability (Kondrashov & Turelli, 1992; Kondrashov, 1993; Judson, 1995). Theoretically, several factors can protect such variability (see KY-96), but we do not know yet how common it is. Some of these factors can actually diminish the advantage of amphimixis, by helping apomicts to adapt. New mutations do so by creating new genotypes, while frequency-dependent selection does so by preserving many clones.

The main falsifiable prediction of any ED hypothesis is that every genotype must experience frequent episodes of low fitness. There are no direct data supporting this assertion, but currently it cannot be ruled out. In addition, the ED scenario considered here requires that:

(1) Fluctuating selection is strong, causing a high load, and usually effectively directional (even if formally stabilizing), because most of the time μ deviates substantially from o. In contrast, the data apparently suggest that quantitative traits are usually under weak stabilizing selection with μ close to o (Turelli, 1984).

(2) The genetic variance is much higher than it would be under invariant selection, because of frequent allele substitutions (compare figure 3 in KY-96 with Figs. 2*c* and 4).

(3) The mean values of the traits involved change at least by $\sim \sigma$ regularly, unless their number is very high, because the range of the optimum changes must be $\sim \sigma$, at the very least. The observed rates of evolution of the mean values of most traits are usually very low. Of course, only some traits must experience such changes, so we may be watching the wrong traits.

(4) The parameters of fluctuating selection fit in a narrow zone. If the range of the optimum changes is too narrow (and/or its period is too long), apomixis does well, while if it is too wide (and/or the period is too short) the genetic load is prohibitively high even in the amphimictic population with free recombination (Figs. 2*c*, 3*b*, and 6). We see no reason why fluctuating selection should be fine-tuned to provide a substantial advantage to amphimicts without killing them.

The fluctuations of selection required by ED hypothesis may occur because of biotic interactions between populations (see Hamilton *et al.* 1990), instead of being imposed by non-biological forces. Still, any fluctuating selection can be presented as a fitness function changing with time. The only difference that biotic interactions could make is to ensure that selection possesses the parameters most advantageous for amphimixis, but it is not clear why this should be the case.

Environmental fluctuations, especially caused by biotic factors, are probably asynchronous in different places. Thus, under widely fluctuating selection we should find large differences between mean values of quantitative traits and, even if these values temporarily coincide, between the frequencies of alleles at the loci involved, among different populations of the same species. We are not aware of any data on geographical variability that cannot be explained by permanent differences between conditions in different locations.

Thus, the ED hypothesis considered here leads to several predictions that are not impossible to test experimentally. Before this is done, it is premature to decide what role is played by fluctuating selection in the maintenance of amphimixis and recombination.

The study reported in this and the accompanying paper was initiated on a suggestion by James Crow. We thank Thomas Nagylaki, Deborah Charlesworth, Martin Morgan, John Willis, Joel Peck and David Houle for discussions. Brian Charlesworth and Nick Barton made several very useful suggestions while reviewing these papers. Our work on these papers was partly supported by a Fellowship from the University of Chicago to A.S.K. and by NSF grant DEB-9417753.

References

Barton, N. H. (1995). A general model for the evolution of recombination. *Genetical Research* **65**, 123–144.

Bergman, A. & Feldman, M. W. (1990). More on selection for and against recombination. *Theoretical Population Biology*, **38**, 68–92.

Charlesworth, B. (1990). Mutation–selection balance and the evolutionary advantage of sex and recombination. *Genetical Research* **55**, 199–221.

Charlesworth, B. (1993). Directional selection and the evolution of sex and recombination. *Genetical Research* **61**, 205–224.

Charlesworth, B. & Barton, N. H. (1996). Recombination load associated with selection for increased recombination. *Genetical Research* **67**, 27–41.

Crow, J. F. (1988). The importance of recombination. In *The Evolution of Sex: An Examination of Current Ideas* (ed. R. E. Michod & B. R. Levin), pp. 56–73. Sunderland: Sinauer.

Crow, J. F. (1992). An advantage of sexual reproduction in a rapidly changing environment. *Journal of Heredity* **83**, 169–173.

Endler, J. A. (1986). *Natural Selection in the Wild.* Princeton, NJ: Princeton University Press.

Eshel, I. & Feldman, M. W. (1970). On the evolutionary effect of recombination. *Theoretical Population Biology* **1**, 88–100.

Felsenstein, J. (1965). The effect of linkage on directional selection. *Genetics* **52**, 349–363.

Fraser, A. S. (1957). Simulation of genetic systems by automatic digital computers. II. Effects of linkage on rates of advance under selection. *Australian Journal of Biological Science* **10**, 492–499.

Hamilton, W. D., Axelrod, R. & Tanese, R. (1990). Sexual reproduction as an adaptation to resist parasites: a review. *Proceedings of the National Academy of Sciences of the USA* **87**, 3566–3573.

Judson, O. P. (1995). Preserving genes: a model of the maintenance of genetic variation in a metapopulation under frequency-dependent selection. *Genetical Research* **65**, 175–191.

Karlin, S. & McGregor, J. (1972). Towards a theory of the evolution of modifier genes. *Theoretical Population Biology* **5**, 59–105.

Kondrashov, A. S. (1984). Deleterious mutations as an evolutionary factor. I. The advantage of recombination. *Genetical Research* **44**, 199–214.

Kondrashov, A. S. (1993). Classification of hypotheses on the advantage of amphimixis. *Journal of Heredity* **84**, 372–387.

Kondrashov, A. S. & Turelli, M. (1992). Deleterious mutations, apparent stabilizing selection and maintenance of quantitative variation. *Genetics* **132**, 603–618.

Kondrashov, A. S. & Yampolsky, L. Yu. (1996). High genetic variability under the balance between symmetric mutations and fluctuating stabilizing selection. *Genetic Research* **68**, 157–164.

Korol, A. B. & Preygel, I. A. (1989). The increase of recombination in the multilocus system under changing environment. *Genetika* **25**, 923–931 (in Russian).

Korol, A. B., Preygel, I. A. & Preygel, S. I. (1994). *Recombination, Variability and Evolution.* London, Chapman & Hall.

Maynard Smith, J. (1978). *The Evolution of Sex.* Cambridge: Cambridge University Press.

Maynard Smith, J. (1980). Selection for recombination in a polygenic model. *Genetical Research* **35**, 269–277.

Maynard Smith, J. (1988). Selection for recombination in a polygenic model: the mechanism. *Genetical Research* **51**, 59–63.

Shnol, E. E. & Kondrashov, A. S. (1993). Effect of selection on the phenotypic variance. *Genetics* **134**, 995–996.

Treisman, M. (1976). The evolution of sexual reproduction: a model which assumes individual selection. *Journal of Theoretical Biology*, **60**, 421–431.

Turelli, M. (1984). Heritable genetic variation via mutation–selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical Population Biology* **25**, 138–193.

Zhivotovsky, L. A., Feldman, M. W. & Christiansen, F. B. (1994). Evolution of recombination among multiple selected loci: a generalized reduction principle. *Proceedings of the National Academy of Sciences of the USA* **91**, 1079–1083.