Letters to the Editor

Transposable Elements in Inbreeding and Outbreeding Populations

YOUNG *et al.* (1994) recently found that a putative transposable element (*Lyt1*) is present at high abundance in the genomes of individuals sampled from a group of red-fruited species of *Lycopersicon*, and at a much lower abundance in green-fruited species of this genus. Similar or somewhat lower abundances were found in *Solanum* species believed to be closely related to *Lycopersicon*, and even lower abundances were found in less closely related *Solanum* species. These authors hypothesize that the red-fruited group of *Lycopersicon* species evolved from green-fruited species. As discussed in their paper, this is consistent with other information on these species, including crossability and allozyme genetic distances, though not with data on mitochondrial DNA. The high transposable element abundances in red-fruited species may thus be an ancestral character shared between the species.

We here point out that the two groups of species differ in their levels of inbreeding (RICK 1984). The red-fruited species (*Lycopersicon esculentum*, *cheesmanii*, *pimpinellifolium*) lack self-incompatibility, and several are known to have high autogamous selfing rates, while the green-fruited species include self-incompatible (*L. hirsutum*, *penelli*, *peruvianum*) or facultatively outcrossing (*L. chmielewski*, *chilense*) species, as well as the autogamous *L. parviflorum*. Although the outcrossing rates of these species have in general not been estimated using segregation of polymorphic genetic markers in families (see RITLAND and JAIN 1981; RITLAND 1990), inferences from flower sizes and degrees of stigma exertion are supported by data showing lower genetic diversity within putatively inbreeding populations (RICK 1984; MILLER and TANKSLEY 1990) and, in some cases, by fixation indices consistent with high inbreeding (RICK 1984). According to RICK's (1984) review, high levels of genetic diversity, suggesting frequent outcrossing, are found in all the green-fruited species included in the study of YOUNG *et al.* (1994), with the exception of the self-compatible, inbreeding *L. hirsutum* accession LA407.

It is therefore possible that the different transposable element abundances are related to the differences in selfing rates in the two groups of plants. Ectopic exchange between transposable elements (LANGLEY *et al.* 1988; MONTGOMERY *et al.* 1991) is a mechanism that might cause such a relationship. Chromosome rearrangements produced by such exchanges during meiosis probably contribute an important portion of the deleterious effects of transposable elements, and there is evidence that it may be a major mechanism for stabi-

lizing the number of elements that genomes can harbor (LANGLEY *et al.* 1988; MONTGOMERY *et al.* 1991; CHARLESWORTH *et al.* 1994). There is evidence in *Drosophila* that ectopic exchange is less frequent in chromosomal homozygotes than in heterozygotes, possibly because a heterozygous element at a given location is more likely to search for a pairing partner elsewhere in the genome (MONTGOMERY *et al.* 1991). If this is a general phenomenon, the higher levels of homozygosity in inbreeding species should lead to lower frequencies of ectopic exchange than in comparable outbreeders.

It is important to note that there are still a number of unanswered questions concerning the mechanisms of ectopic exchange, which bear on our suggestion. In particular, the relation between the rate of normal meiotic exchange and the frequency of ectopic exchange is still somewhat unclear. The data of MONTGOMERY *et al.* (1991) suggest that a significant fraction of ectopic exchange events in *Drosophila* are meiotic in origin and that their frequency is increased by heterozygosity, consistent with our proposal. In yeast, both ectopic and regular exchange are much more frequent in meiosis than mitosis, but there is little evidence for an effect of heterozygosity on ectopic exchange (PETES and HILL 1988). Evidence on both of these points is lacking in plants.

Transposable element abundances in inbreeding populations that have reached equilibrium for these elements should therefore be higher than in outcrossing populations. While this process has not been formally modeled, theoretical analysis of random-mating populations has shown that containment of the spread of transposable elements by ectopic exchange leads to higher equilibrium abundances in genomic regions with lower frequencies of exchange (LANGLEY *et al.* 1988), and the *Drosophila* data suggest that such a relationship is indeed observed (CHARLESWORTH *et al.* 1994). There is thus little doubt that the restriction of effective recombination by selfing would cause a similar effect. In addition, the lower effective population sizes of highly selfing species, due to direct effects of the breeding system itself and to the enhanced effects of selective sweeps and background selection against deleterious mutations (CHARLESWORTH *et al.* 1993), may also lead to higher abundances of transposable elements due to the effective weakening of selection against their presence (CHARLESWORTH and CHARLESWORTH 1983).

A possible factor that might operate in the opposite direction is selection for regulation of transposition

rate. CHARLESWORTH and LANGLEY (1986) showed that the conditions for the spread of elements with reduced rates of transposition are easier to satisfy in populations with lower rates of genetic recombination, as with selfing or asexual organisms. It is not clear whether, over the long term, this would eliminate the effect of ectopic exchange that we have suggested. In any event, an increase in abundance as a result of relaxation of the effects of ectopic exchange would be likely to take place before the evolution of reduced transposition could occur. Further modeling is required to investigate the relative importance of these processes.

The possibility of a relationship between transposable element abundance and inbreeding does not contradict the suggestion that the red-fruited species all derive from green-fruited ancestors having lower abundances of the transposable element. It is quite possible that the more selfing species did indeed all evolve from an ancestor that had high element abundance, but an explanation of the maintenance of this state is required. The hypothesis that high inbreeding has been a factor can provide this, as well as explaining why high abundance should have evolved in the first place. If there were no difference between the two groups of species other than their having started with different numbers, *i.e.*, if there were no effect of breeding system on the level of element abundance, then the species would probably diverge in abundance over time. In other groups, such as *Drosophila*, there is evidence for considerable divergence in element abundances between closely related species (YOUNG 1979). As the three red-fruited species studied were all estimated to have very similar abundances (41–46 elements per genome) and the five green-fruited species were also quite homogeneous (2–8 copies per genome), the data suggest some systematic difference other than ancestry alone.

In view of this striking difference between the *Lycopersicon* species, it would probably be interesting to carry out more such studies of the abundance of transposable elements, making use of the existence of related species with contrasting levels of inbreeding. It would also be interesting to test whether the difference in element abundance in *Lycopersicon* is found for other transposable element families in the genomes of these species. With the recent discovery of transposable element families with widespread distributions among plants (*e.g.*, VOYTAS *et al.* 1992; BUREAU and WESSLER 1992, 1994), further tests should be possible. If the differences in abundances found by YOUNG *et al.* (1994) are unrelated to differences in breeding system, differences in the opposite direction should sometimes be seen when these species are studied, and in comparisons using other groups of plant species. An apparent case counter to the above prediction of increased abundance in highly inbreeding populations is the highly selfing plant *Arabidopsis thaliana*, which has low abundances of the elements that have so far been studied,

at least in laboratory populations (VOYTAS *et al.* 1990; FLAVELL *et al.* 1994). Without comparisons of the abundance of the same elements in related outbreeding populations, however, the finding of low abundance is uninformative about any possible relationship of abundance to breeding system. To date, most comparative studies of plant transposable elements have been confined to showing their widespread presence (*e.g.*, FLAVELL *et al.* 1992, 1994), and it is usually unclear to what extent differences between species are due to differences in abundance *vs.* sequence divergence.

Comparisons could also be done in animal genera that include both inbreeding and outcrossing species, *e.g.*, the genus *Caenorhabditis*. Transposable elements are present in the two hermaphrodites *Caenorhabditis elegans* (*e.g.*, LIAO *et al.* 1983) and *C. briggsae* (HARRIS *et al.* 1990). The breeding systems of these species have not been studied in natural conditions, but both are presumed to be highly inbreeding (BAIRD *et al.* 1992). However, no data on transposable elements are available from isolates from natural populations, and as far as we are aware, none are available from dioecious (gonochoristic) species. Such comparisons could provide tests of whether levels of inbreeding influence transposable element abundances. It may also be worthwhile to test whether abundances differ between closely related outbreeding species that differ in recombination frequency. The hypothesis that ectopic exchange is an important factor limiting element numbers predicts that species with lower recombination should have greater element numbers. As there are large differences in recombination frequency per nucleotide among *Drosophila* species (DOBZHANSKY and POWELL 1975; ALEXANDER 1976; OHNISHI and VOELKER 1979; KRIMBAS 1993), such a study is feasible in that genus.

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