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SPECIATION PATTERNS IN PREDOMINATELY SELF-POLLINATED MEDITERRANEAN ANNUALS

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Abstract

Many groups of annual plants in the Mediterranean basin are characterized by self-pollination. It is suggested that the breeding system operating in these plants affected considerably their mode of speciation. It is argued that the reproductive isolation barrier caused by selfing frequently initated sympatric speciation in these autogamous plants - a mode of speciation that cross-pollinated plants rarely achieve.

Introduction

One of the principal adaptations which characterize plant-life in the Mediterranean region is annual habit. Indeed, a large proportion of the plant species which grow in the countries bordering the Mediterranean Sea are annuals. Richest in this life-form seem to be the East Mediterranean countries. Thus about 50% of the species listed in *Flora Palaestina* (ZOHARY 1966, 1972; FEINBRUN-DOTHAN 1978, 1986) are annuals. Many of them are short-lived ephemerals.

Strongly associated with the annual habit is self-pollination. In sharp contrast to their perennial neighbours (which are overwhelmingly allogamous), a large proportion of the Mediterranean annual species are predominately self-pollinated. The exact amount of selfers in the Mediterranean flora has not been assessed yet, but it is considerable. An unpublished survey carried out by the present author in Israel revealed that at least half (and may be even 60%) of the annual species native to this country are selfers.

Autogamous plants can be recognized in the field and distinguished from allogamous plants by a syndrome of morphological traits (frequently a family specific syndrome), which structures the flowers for automatic self-fertilization. Very common arrangements are: (i) Placing of the anthers and the stigmas close together. (ii) Shedding of pollen before the openning of the flower bud. (iii) Reduction of the flower size and of the amount of pollen in the anthers. (iv) Full fruit-set even when single plants are isolated or prevented from cross-pollination, indicating the absence of self-incompatibility or other devices that safegard cross-pollination. When needed, self-pollination can be confirmed (and quantified) by genetic tests, which determine the amount of inbreeding in populations with the help of molecular genetic markers.

As already suggested by STEBBINS (1956), and by JAIN (1976), autogamy seems to be a derived situation. Very probably it has evolved independently - again and again - in different allogamous stocks. Furthermore, in numerous genera native to the Mediterranean region, autogamy seems to be rather old. It commonly characterizes not a single species, but clusters of closely related taxa. In fact, series of closely related autogamous species (comprising whole taxonomic subsections, sections, or even entire genera) are the rule rather than the exception. The genera *Aegilops*, *Triticum*, *Avena*, *Lens*, *Pisum*, *Bromus*, *Vicia*, *Trifolium*, *Medicago* or *Anthemis* provide good examples for such clustering. The first five genera contain only (or almost only) autogamous species. In the other five genera, entire taxonomic sections have this pollination system. Significantly, some of these clusters contain numerous species. Thus in the genus *Aegilops* (which comprises 22 species, see SLAGEREN 1994), all but one species are selfers. So are all the 27 species grouped in Sect. *Spirocarpos* of *Medicago* (HEYN 1963), and the 9 species placed in Sect. *Trichocephalum of Trifolium* (ZOHARY and HELLER 1984). Such wide species divergence indicates a long history of evolution under the breeding system of self-pollination.

The present paper examines the patterns of speciation in the Mediterranean autogamous plants. More specifically, it tries to assess how different is the origin of species under self-pollination, compared to what happens under cross-pollination. In other words, in what ways speciation in these selfers differs from that of their out-crossed counterparts.

Traits that characterize self-pollinated plants

Predominately self-pollinated species show several features which are totally (or almost totally) lacking in cross-pollinated species. The following traits seem to affect (or to reflect) the mode of speciation in selfers.

Reproductive isolation caused by selfing

The shift from cross-pollination to self-pollination introduces, automatically, isolation between lines and/or between species. When selfing is predominant (and the amount of occasional cross-pollination does not exceed few promils or few percents), the reproductive isolation introduced by this breeding system is indeed considerable. It blocks gene-exchange between taxa as effectively as other kinds of reproductive isolation barriers - such as strong cross incompatibility, hybrid inviability or hybrid sterility. (For enumeration of the various reproductive isolation mechanisms found in plants see GRANT 1981: 112).

As already argued by LEVIN (1978) and by GRANT (1981: 114), isolation due to autogamy should be included the list of the isolating mechanisms operating in plant speciation. What has not been yet fully considered is the fact that this type of reproductive isolation is a potent element for initiating speciation. Being part of the breeding system, isolation due to autogamy is omni-present in self-pollinated plants. It facilitates speciation from its very beginning, introducing separation already among inbred lines growing side by side. In other words, the reproductive isolation barrier caused by self-pollination renders the autogamous plants suitable for sympatric speciation. This is an advantage their allogamous counterparts do no have.

The units of selection

In addition to the introduction of a special reproductive isolation barrier, the shift from cross-pollination to self-pollination also effects selection patterns. Cross-pollinated populations usually contain considerable amount of genetic variation, and in each sexual cycle their genes are recombined. As a consequence of this repeated reshuffling, the units of selection in out-crossers are mostly the individual genes. Also selfers frequently maintain large amount of genetic variation in their populations. But self-fertilization moulds their gene-pools into true breeding lines, and structures their genetic variation in tightly kept gene combinations. In selfers, the units of selection are therefore not the individual genes but rather the homozygous genotypes. Competition is largely between the various inbred lines which build the population. The small amount of cross-pollination (which exists in almost all selfers) maintains their ability to produce (and test) new gene combinations, and thus keeps their genetic flexability.

Intra-specific chromosomal polymorphism:

Cytogenetic studies have revealed that Mediterranean self-pollinated annual species may contain several (sometimes even numerous) chromosomal types, differing from one another by reciprocal translocations, inversions or similar chromosomal rearrangements. The following three cases illustrate this kind of intra-specific chromosomal polymorphism:

Rich polymorphism of this kind has been discovered in the wild lentil, Lens orientalis (2n=2x=14). Fifteen samples of this wild progenitor, collected in the Near East, were tested cytogenetically (LADIZINSKY al. 1984). They were found to contain six distinct translocation types. Crosses between the different chromosomal types were rather easy to make, but because of chromosomal structural hybridity the F1 hybrids were semi-sterile.

Similar intra-specific translocation differences (mainly among homeologous chromosomes) have been encountered in wild emmer wheat *Triticum dicoccoides* (2n=4x=28), sometimes even among lines co-habiting the same location. Several other members of the wheat group (such as *Aegilops peregrina*, 2n=4x=28) also revealed rich polymorphism of this kind.

A most extreme intra-specific chromosomal polymorphism has been found in the diploid *Vicia sativa* species complex (ZOHARY & PLITMANN 1981). Three chromosomal numbers (2n=10, 12 & 14) have been detected in this morphologically variable complex (seven subspecies have been recognized). Furthermore, not less than 22 distinct karyotypes were distinguished by HOLLINGS & STACE (1974) in only one of its subspecies (subsp. *nigra*, which contains both 2n=12 and 2n=10 forms). Again, different chromosomal forms of *V. sativa* complex frequently grow together, and crosses between the various types can still be made. Yet in many cross-combinations (particularly between plants having different chromosomal numbers) the F1 hybrids are largely sterile. However, even from such hybrids, some F2 and F3 derivatives have been recovered.

All in all, under the system of self-pollination intra-specific chromosome polymorphism is probably a rather common feature. Chromosomal rearrangements, once spontaneously induced, have a good chance to quickly establish themselves in separate homozygous lines. It is therefore not surprising that researchers, engaged in cytogenetic examinations of self-pollinated species, occasionally stambled on such intra-specific polymorphism. This even when only few collections were tested. In contrast, very little intra-specific chromosomal polymorphism of this kind (polyploidy excluded) has been detected in allogamous plants. Under cross-pollination uniformity seems to be the rule; and it is expected to be so. After all, in panmictic populations, natural selection would quickly weed out newly produced translocations, inversions or similar chromosomal mutations - because individuals heterozygous for such rearrangements are semi-sterile.

Sympatry

Self-pollinated plants seem to differ from cross-pollinated plants also in their patterns of distribution. In allogamous plants, most closely related species occupy - as a rule - separate territories. Moreover, geographic isolation is largely responsible for keeping such out-crossers apart. When brought together, such closely related (and often vicarious) species tend to massively hybridize and sometimes even to fuse. In contrast, autogamous plants in the Mediterranean flora exhibit entirely different distribution patterns. Under the breeding system of self-pollination, most closely related species are frequently sympatric. In other words, Mediterranean selfers not only evolved clusters of closely related species. Members of such species groups commonly grow side by side, and still maintain their morphological individuality and taxonomic distinction. The genus *Aegilops* provides a well studied example of this kind of sympatry. Here, three, four, or even half a dozen of closely related species often form mixed stands (ZOHARY, 1965). Similar co-habitation occurs in *Medicago, Trifolium, Vicia, Bromus*, and numerous other selfers.

Discusion

A main difference between self-pollinated plants and cross-pollinated ones is the presence - in the formers - of a reproductive isolation barrier caused by selfing; while in outcrossers this isolating mechanism does not exist. In terms of speciation, the impact of this addition seems to be considerable: (i) Under self-pollination, this type of reproductive isolation is part of the breeding system and is omnipresent. (ii) Therefore, isolation caused by selfing efects speciation from the very start. It brings about isolation not only between well diverged taxa, but also between conspecific inbred lines growing together in the same locations. In contrast, in cross-pollinated plants,a build-up of isolation - under sympatric conditions - rarely happens. As amply argued by MAYR (1963: 482), speciation in panmictic organisms is usually initiated by geographic isolation. In conclusion, in self-pollinated plants the introduction of reproductive isolation due to autogamy can subtitute for geographic separation. It creates a background for the initiation of speciation also under sympaty. This seems to explain why co-habitation of the same territory by closely related taxa is so common among the Mediterranean self-pollinated plants; while in their cross-pollinated counterparts closely related species usually occupy separate territories.

Another characteristic feature unique to self-pollination, is the ease by which new chromosomal mutations are able to establish themselves. Chromosomal rearrangements in which no loss of chromosome material has occurred (e.g. reciprocal translocations or inversions) would be particularly tolerated under this breeding system; and "fixed" (as new, homozygous, stractural lines) in only very few generations. Such tolerance could lead, in selfers, to a relatively rapid build up of chromosomal divergence also under sympatric conditions. Significantly, once such chromosomal polymorphism is established, it further enhances sympatric speciation. It augments the initial reproductive isolation brought about by autogamy also by a barrier of hybrid sterility.

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