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 Main features of Spore killer

 systems in Neurospora.

Meiotic drive is a general term for any process that results in a "driven" gene being represented disproportionately in the progeny of heterozygotes for reasons unrelated to the selective advantage or disadvantage of the driven gene for individuals carrying it. The process can be accomplished either by preferential segregation during meiosis or by lowered recovery (through death or dysfunction) of meiotic products that do not carry the driven gene (reviewed by Zimmering et al. 1970). The latter mechanism is exemplified by Segregation distortion in Drosophila (reviewed by Sandler and Golic 1985), by transmission ratio distortion involving the t complex in mice (reviewed by Bennett 1986) and also by Spore killer in Neurospora, which provides the best understood example of meiotic drive in fungi.

Two chromosomal factors called Spore killer (symbolized Sk-2^K and Sk-3^K) have been found in nature in Neurospora intermedia and have been introgressed into N. crassa. Sk-2^K will be used as an example in the following summary. Unreferenced information is from Turner and Perkins (1979), Raju (1979), or Turner and Perkins, unpublished.

1. When a Spore killer strain is crossed with the standard wild type or with any other strain that is sensitive to killing (Sk-2^K x Sk-2^S), only four ascospores survive in each ascus (Fig. 1A). The survivors are Spore killers. When Spore killer is crossed by Spore killer (Sk-2^K x Sk-2^K), all eight ascospores survive (Fig. 1B). Thus presence of Sk-2^K results in death of ascospores that receive Sk-2^S but not of those that receive Sk-2^K. Ascus development in Sk-2^K x Sk-2^K is indistinguishable from that in Sk-2^S x Sk-2^S (Fig. 1C).

2. Sk-2^K shows 1:1 Mendelian segregation, 100% first division segregation, and linkage to centromere markers of linkage group III.

3. Killing does not depend on which strain is used as female and which as fertilizing parent. Reciprocal crosses are alike.

4. No difference between Sk-2^K and Sk-2^S has been detected in the vegetative phase. When heterokaryon-compatible strains are used, forced heterokaryons containing nuclei of both types in the same cytoplasm are vigorous and healthy. Likewise, meiosis and ascus differentiation are normal in heterozygous crosses where killing will occur.

5. Abnormalities are seen only after Sk-2^S nuclei are sequestered in an ascospore. Sk-2^S nuclei which would otherwise die are rescued if an Sk-2^K nucleus or chromosome is enclosed within the same ascospore wall. This occurs in the disomics that occur sporadically in Neurospora crosses. Rescue also occurs in multinucleate giant ascospores, which can be obtained regularly from Sk-2^K x Sk-2^S crosses by using mutants, such as Ban, that affect ascus development. Upon germination, the giant spores produce mixed cultures which include both Sk-2^K and Sk-2^S progeny. The Sk-2^S progeny can be recovered in pure culture from the mixture.   They appear to be undamaged and unchanged.

Figure 1. Manifestation of Spore killer in rosettes of developing asci at various stages of maturation. Neurospora crassa (x 350).

A. KILLER x SENSITIVE (Sk-2^K x Sk-2^S. Each mature ascus contains four large ascospores (Sk-2^K) and four small aborted ascospores (Sk-2^S). The asci with dark ascospores are more mature than those with lighter ascospores. The few asci not showing the 4 : 4 pattern are still immature.

B. KILLER x KILLER (Sk-2^K x Sk-2^K). Ascospore delimitation and growth are normal, but some ascospores may fail to pigment fully. This behavior is also seen in the absence of Sk-2^K in normal wild-type crosses and is distinct from the ascospore death seen in asci heterozygous for Sk-2^K, as in A.

C. SENSITIVE x SENSITIVE (Sk-2^S x Sk-2^S). Ascus development in homozygous Sk-2^S x Sk-2^S crosses is indistinguishable from that in Sk-2^K x Sk-2^K. Laboratory wild-type strains of N. crassa are all Sk-2^S. The following stocks were used: A. DP No. 3120 (FGSC No. 3114 could be used) x FGSC 2221. B. FGSC 3673 x DP NO. 3213 (FGSC 3674 could be used). C. FGSC 2220 x FGSC 2221.

6. Postmeiotic nuclear divisions are not necessary for killing to occur. The Four-spore mutation Fsp-1 eliminates a postmeiotic mitosis in many asci, but half the ascospores are still aborted in four-spored asci of crosses heterozygous for Sk-2^K.

7. When Sk-2^K is crossed with a non-killer strain, crossing over is blocked in a 30 unit region that starts just right of cum and extends across the centromere to the right of leu-1 (Figure 2). The recombination block appears not to be due to an inversion. Marker sequence and crossing over frequencies are normal in Sk-2^K x Sk-3^K (Campbell and Turner, 1987).

8. Neutral (resistant) strains that neither kill nor are killed are found in nature (Turner, 1977). In the best analyzed example, resistance segregates as a single chromo-somal gene called r(Sk-2)-l, in IIIL. Recombination of markers in the III-centromere re-gion is blocked in Sk-2^K x r(Sk-2)-l but not in Sk-2^S x r(Sk-2)-l (Campbell and Turner, 1987). A gene r(SK-3)-l, which confers resistance specifically to Sk-3^K, resembles r(Sk-2)-l in its map location and effect on recombination. The existence of neutral strains that are resistant only to Sk-2^K or only to Sk-3^K provides one basis for treating the two Spore killers as distinct entities. r-(Sk-2)-l and r(Sk-3)-l confer complete resistance, but different neutral strains from nature form a spectrum from slight to complete resistance.

9. Sk-3^K, the other killer allele identified in N. intermedia resembles Sk-2^K in all of the characteristics described above. But Sk-3^K differs from Sk-2^K in all specificity of killing and resistance. Although Sk-3^K does not kill Sk-3^K, it is sensitive to killing by Sk-2^K and vice versa. In crosses between Sk-2^K and Sk-3^K, all ascospores abort in most of the asci.

10. Rare survivors are found from Sk-2^K x Sk-3^K, however. These usually occur as black ascospore-pairs. Some of them contain both Sk-2^K and Sk-3^K nuclei; these apparently start-ed as disomic or heterokaryotic ascospores. Other survivors have characteristics unlike either parent; these have been shown to be recombinant and are apparently aneuploid.

11. Both Sk-2^K and Sk-3^K are rare in nature. Sk-2^K has been found four times (in Borneo [twice], New Guinea and Java), and Sk-3^K only once (in New Guinea). Laboratory strains are sensitive to both Sk-2^K and Sk-3^K, as are most of 1400 tested wild-collected isolates of N. intermedia and N. crassa. Numerous strains that are resistant to killing by Sk-2^K or by Sk-3^K have been found in N. intermedia from the Eastern Hemisphere (Turner, 1977), and two isolated examples of Sk-2^K-resistant N. crassa are known, one from North America and one from India.

12. A similar Spore killer, Sk-1^K, has been found in N. sitophila. Sk-1^K differs from Sk-2^K and Sk-3^K by showing 5% second-division segregation. Sk-1^K and Sk-1^S are about equally frequent in wild-collected N. sitophila from many parts of the world. No neutral strain has been found. Attempts to introgress Sk-1^K into N. crassa have failed. The chromosomal location of Sk-1^K is unknown, as is its effect on recombination.
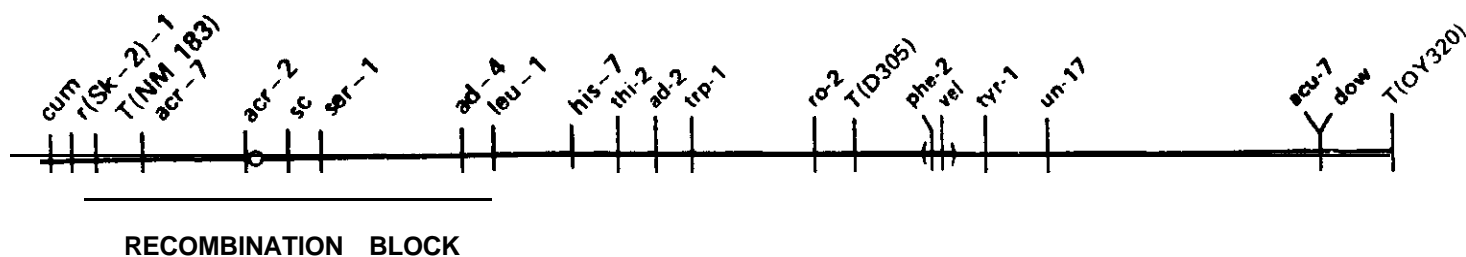

RECOMBINATION BLOCK

Figure 2. Genetic map of linkage group III showing extent of the recombination block that results when one of the Spore killers is heterozygous

Similar systems in related organisms._ Chromosomally located Spore killing systems are also known in two other Pyrenomycetes. In _Podospora anserina_, two unlinked spore-abortion genes behave exactly as would be expected if their mechanism of killing were the same as for Sk-2^K and Sk-3^K in Neurospora (Padieu and Bernet, 1967). In _Giberella fujikuroi_ (_Fusarium_ _moniliforme_), a majority of wild isolates contain a chromosomally located Spore killer factor (Kathariou and Spieth, 1982).

These fungal Spore killers resemble typical meiotic drive systems in higher plants and animals in being manifested postmeiotically by differential survival of spores or gametes (reviewed by Zimmering _et al._ 1970). (For recent examples in plants, see Tsujimoto and Tsunewake 1985, Finch _et al._ 1984, Scoles and Kibirge-Sebunya 1983 and references therein.)

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