

Lewis D. Comparative incompatibility in angiosperms and fungi.

Advan. Genet. 6:235-85, 1954.

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A comparative and comprehensive treatment is given for seven genetic systems of self-incompatibility, four in flowering plants and three in fungi. [The *SC*⁹ indicates that this paper has been cited in over 160 publications since 1955.]

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This review summarized 18 years of my work and thought at the John Innes Horticultural Institution. Self-incompatibility was, and still is, important in fruit production and was of genetical interest because the controlling gene had many alleles, each conferring a unique recognition between pollen and style.

I was given complete freedom to work and started to show that the striking effect of autotetraploidy that nullified the recognition process and made a plant self-compatible was due to interactions between the products of different alleles in diploid pollen. By serological methods, the I-gene product was shown to be a serologically active protein. Using the self-style as a highly sensitive selector of I-gene mutations, I showed that the gene was a complex of two and probably three closely linked genes, one active in the pollen and another in the style; all the mutations were to loss of activity to self-compatibility. No new active alleles were found despite the sensitivity of the method to 10⁻⁸ and the large number of alleles in wild populations. This caused some controversy about the efficiency of the style for selecting new active alleles, which might be the result of a series of mutational changes in the genome.

All this and much work of others was set in context in the review. But an important factor in the timeliness of the review was the discovery of the new sporophytic system by Babcock and Hughes¹ and Gerstel² in the US, and Bateman³ and Crowe⁴ in my own laboratory. This system combined multiple alleles with maternal control of the pollen, a hypothetical combination that I had foreseen⁵ but

arrogantly dismissed as improbable and beyond the capacity of the gene, a mistake I hope not to make again.

Fungi were included in the review because of the frustration of not finding active new allelic mutants in plants. I turned to the higher fungi, which have a similar multi-allelic system and a more direct cellular barrier. A *Coprinus* species collected from the wild was the foundation stock of what became a standard genetic organism in several laboratories. But, even in this organism, only breakdown mutants rather than allelic mutants were obtained.

The review also described the application of self-incompatibility to plant improvement. The commercial production of F₁ hybrid vegetables was the outcome of the new sporophytic system. The commercial exploitation of my own self-compatible mutants of the sweet cherry, *Prunus avium*, has left me with only the review and mixed feelings. The practical application in Britain suffered from political considerations and what the late C.D. Darlington called the "dead hand on discovery."^{6,7} Fortunately, the unique I_c gene was sent to the Canadian Department of Agriculture and developed by Lapins into the first commercial self-compatible sweet cherry, *Stella*.⁸

My work was recognised one year after the review by my election to Fellowship of the Royal Society and later by my invitation to the Quain Chair of Botany at University College London.

The originality and significance of the review were mainly in its comparative approach, which was enhanced by the treatment of four different genetic systems, including the newly discovered sporophytic system, in plants and three systems in fungi.

It may be significant that de Nettancourt, in his specialist book on the subject,⁹ makes 141 references in the text to 24 of my papers. The "classical" review is referred to only five times. The most frequently quoted is a paper with a highly contentious hypothesis on unilateral incompatibility that stimulated many disparagements.¹⁰ It would appear from this that the main reason for the high rating of a review is that it is (too often) an easy way of quoting the literature with the added bonus of an authoritative backing for quotation.

I have, with S.C. Verma and M.I. Zuberi (manuscript), recently reexamined the sporophytic system and have found a second gene *G* that is complementary to the well-established *S* gene and is gametophytic in its action. Current work of others has turned to molecular aspects and gene isolation; the most recent contribution¹¹ is a good example and contains useful references to recent research and reviews.

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