Bridging a Gap Between Related Fields of Research: Pistil-Pollen Relationships and the Distinction Between Incompatibility and Incongruity in Nonfunctioning Host-Parasite Relationships

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Intimate relationships between partners exist in several forms. In higher plants such a relationship occurs between pistil and pollen. Research on this relationship is extensive, and interpretations of the mechanisms for nonfunctioning of the relationship have been discussed for many years (see the references cited in reference 14).

A comparable situation occurs in the similar relationship between host and parasite. Here too, the discussion on interpreting mechanisms for nonfunctioning—called mechanisms for resistance—has been extensive, but in spite of the many models presented, insight into this elusive subject is still incomplete (2,5–10,19,21,23–26). It is striking that in both discussions even the same terms are used, such as "different levels of specificity" or "one incompatibility system superimposed on another."

One reason for confusion about mechanisms for resistance is that two fundamentally different and independent types of mechanisms for nonfunctioning of intimate relationships are either not distinguished or are inconsistently treated. This distinction of types of mechanisms has now been made for the pistil-pollen relationship and has improved understanding of crossing barriers in higher plants (12–14, and references cited there). It is important to apply this improved understanding to the field of host-parasite relationships. This process has already been initiated (3,4,12–14) and should continue.

The Pistil-Pollen Relationship, Functioning and Nonfunctioning

In fertilization, the pollen grain germinates and forms a tube that penetrates the pistil tissues, grows to the ovule and into the embryo sac, and releases its contents for fusion with the egg. Fusion of the two partner genomes starts the diplophase of the life cycle. This chain of events depends upon accurate coordination of a series of processes in the pollen tube with those in the pistil to produce a functional interaction.

The pistil may be regarded as a complex of barriers and promoters, and the pollen may be regarded as an organism carrying all the genetic information necessary to penetrate all barriers and to react to all promoters. Each pistil and pollen tube character is governed by one or more genes. Normal functioning of the relationship requires matching genetic systems in pistil and pollen, so that for each barrier gene or gene complex in the pistil, there is a corresponding penetration gene or gene complex in the pollen; for each promotion gene or gene complex in the pistil, there is a corresponding reaction gene or gene complex in the pollen. Each gene (or gene complex) couple governs one step in the chain of processes and interactions necessary for normal functioning of the relationship.

Such a balanced relationship results from coevolution of the partners. The matching genetic systems of the partners may include one gene-to-one gene correspondences, but may also include correspondences of more genes-to-one gene, one gene-to-more genes, and more genes-to-more genes. A consequence of a prolonged coevolution is that more and more processes in one partner become accurately coordinated to those in the other, so

that the relationship becomes increasingly specialized.

At least two types of mechanisms can impede the normal functioning of an intimate partner relationship. First, one partner may *lack genetic information* about some relevant character of the other. This phenomenon of incomplete matching of genetic systems is called *incongruity* (12,13). Secondly, *incompatibility* may *prevent or disturb the functioning of the relationship* even though each partner contains the genetic potential for functioning. The inhibition results from the interaction of complementary products of incompatibility genes (*S*-genes) in pistil and pollen having the same specificity (1,11,15,16,18,20).

These two types of mechanisms differ fundamentally in their evolution (incompatibility protects against inbreeding, incongruity results from evolutionary divergence), genetics (incompatibility is generally simple and based on multiple allelic genes, incongruity may range from simple to complicated), and nature (incompatibility results from a very specific interaction, incongruity has a variable nature) (13,14). There are good reasons to suppose that the distinction between incongruity and incompatibility as causes of nonfunctioning is valid in every intimate relationship between biological partners.

The Host-Parasite Relationship, Functioning and Nonfunctioning

The above description of the pistil-pollen relationship can, after a modification of some terms, be applied to the host-parasite relationship. The normal functioning of the latter requires accurate coordination of a chain of events in the parasite with an interrelated chain of events in the host. The parasite carries all the genetic information for adequate action or reaction. As a counterpart of each barrier and promotion process in the host, the potential for the corresponding penetration and reaction process must be present in the parasite and each process must be sequentially coordinated. This requires matching genetic systems in host and parasite in which a series of barrier genes or gene complexes in the host correspond to penetration genes or gene complexes in the parasite, and a series of promotion genes or gene complexes in the host correspond to reaction genes or gene complexes in the parasite. Each step in a functioning host-parasite relationship is governed by a one gene-to-one gene correspondence, or a correspondence of one gene-to-more genes, more genes-to-one gene, or more genes-to-more genes. This concerns all aspects of the relationship, including those that are impossible to distinguish now because of inadequate detection methods.

Such a balanced relationship results from coevolution of host and parasite, comparable to that of pistil and pollen. It is important to note that host characters relevant to the relationship with the parasite may result from *two categories of selective forces*. First, selection may be based on environmental stress without influence of the parasite. Secondly, stress may result from damage caused by the parasite, which gives a selective advantage to host characters that provide defense against the parasite. These two types of selective forces may reinforce or counteract each other. Characters from the first category may be favorable, neutral, or unfavorable to the parasite; those from the second category will be unfavorable to the parasite genotype concerned. Similar reasoning can be followed with regard to these two categories of selective forces acting on parasite characters relevant to the relationship with the host.

Just as in the pistil-pollen relationship, two basically different principles can impede the normal functioning in the host-parasite relationship. The first is *a lack of genetic information* in one partner about some relevant character of the other. *The relationship* is then *incomplete*. An evolutionary change of the host may, for instance, result in an extra character that strongly influences the host-parasite relationship and for which the parasite lacks the corresponding information. This implies that at some moment after contact the relationship is frustrated or fails. Such a situation of evolutionary divergence may be permanent or temporary, depending on the genetic potential and flexibility of the parasite and on the nature and strength of the selective forces. When the parasite acquires the corresponding genetic information, the relationship is restored, partners are again fully matching. This is equivalent to the concept of "basic compatibility" (7; see also ref. 3). In general, the incompleteness of a relationship will be greater as the degree of coevolution is lower.

The second principle, *disturbance*, is relevant when the relationship between partners is complete. Then the only margin for regulation to protect the host is to *prevent or disturb the functioning of the relationship*. Just as in pistil-pollen relationships, this inhibiting principle may simply result from a reaction between very specific products of host and parasite genes in a kind of signal-sensor interaction. The specificity of the interaction would require *recognition* between partners, based on the *interaction of complementary molecules*. The product of this interaction may induce a host response that prevents functioning of the relationship. In that case, if the parasite changed the specificity of its signal, the disturbing principle would not arise and the relationship would be rendered functional. The host could restore the inhibiting principle by acquiring the sensor specificity corresponding to that of the altered signal.

Host-parasite interactions involving specific recognition may also protect the parasite as in the example where the interaction prevents the functioning of a host resistance principle such as a hypersensitive reaction. The signal-sensor interaction permits the functioning relationship to develop, so the protection of the host would be restored by changing its sensor specificity to differ from that of the parasite. Thus, the specificity interaction may lead to resistance in certain cases and to susceptibility in others (Models I and II in reference 19).

Both of the principles described above—incomplete relationship and disturbance—may be the basis of resistance. In the literature on the host-parasite relationship the only term used for mechanisms for nonfunctioning of the relationship is "incompatibility." Based on the distinction of two basically different principles described above and on the analogy of the pistil-pollen relationship, I propose the use of two separate terms: *incongruity* representing the case of resistance due to an incompleteness of the relationship, and *incompatibility* representing the case of resistance due to disturbance in functioning caused by a specific recognition reaction between the partners.

Incongruity is nonfunctioning due to any *missing link* in the genetic *correspondence* or adaptation of each partner to the other. It results from incomplete convergence to, or from evolutionary divergence from, that which Ellingboe terms the "basic compatibility." *Incompatibility* occurs when the basic genetic correspondence between partners is complete, but *specificity gene products interact* complementarily and form a *disturbing principle*.

As stated for the pistil-pollen relationship, incongruity and incompatibility differ essentially with regard to their evolution, genetics, and nature. For instance, evolution of the incompatibility system requires mutual influences of host and parasite and contact is needed for its development, whereas incongruity may result from selective forces due to environmental stresses on either partner as well as to interactions between them and contact between partners is not needed. The genetics of incompatibility is generally simple; that of incongruity may range from simple to complex. The nature of incompatibility will generally be less variable than that of incongruity.

Impact of Distinguishing Between Incongruity and Incompatibility for Resistance Breeding

It follows from the above reasoning on (co)evolution that both incongruity and incompatibility can be used in breeding for resistance. Durability of resistance is important in agriculture, but in many cases it is a matter of wait and see. How can the above distinction of resistance principles help in predicting durability.

Incompatibility is based on a very *specific interaction* of host and parasite genes comparable to that of S-alleles in higher plants. It is genetically simple and probably often based on a one gene-to-one gene interaction. Incompatibility regulates race-specific resistances and will often, but not necessarily, be expressed in "yes" or "no" reactions. Different incompatibility systems may occur as in higher plants.

Incompatibility generally results in unstable resistance, because a change from one specificity to another is genetically a minor step; only a change in the specificity cistron is required.

Incongruity is variable in nature. Each step in the evolution of the host that renders the relationship incomplete can be the source of incongruity and thus may concern *any character* that is relevant to the host-parasite relationship. It means that incongruity may have an immense diversity of forms (the inability to suppress defense reactions [4] is just an example). Incongruity may be the basis of race-specific resistance as well as of nonspecific resistance or even of what is called nonhost resistance. Resistance resulting from incongruity may have any level. Its durability is also variable and depends, among other things, on the number of parasite genes that correspond to the host character concerned. It is obvious that exploiting incongruity improves the chance of finding more durable resistance.

How can resistance based on incongruity be distinguished from that based on incompatibility? This important, challenging subject of research can be approached through genetics, biochemistry, and physiology. The patterns of relationship between host and parasite genotypes for the two categories of resistance should be distinguishable, because incompatibility results from an *interaction of specificity genes* and incongruity from *missing links in the genetic correspondence*. Analysis of these patterns, combined with analysis of F_2 progeny from crosses between genotypes could indicate which category of resistance is functioning. The ploidy level of host and parasite and possible interactions between incompatibility genes should be taken into account, because uncertainty about these aspects as well as lack of knowledge on the parasite genetics may hinder the distinction.

Important contributions toward distinguishing incongruity from incompatibility may come from biochemists who develop methods to identify the specific interactions of the signal-sensor type. The knowledge of the incompatibility systems in higher plants will be useful in their research.

Another approach to this distinction is to study physical influences, eg, temperature effects. Many examples of temperature-sensitive resistance are known (17,25). From the analogy of incompatibility and incongruity research in higher plants, we may expect resistance based on incompatibility to be temperature sensitive. High temperatures could induce either lower or higher levels of resistance. Resistance based on incongruity may prove less likely to be temperature sensitive.

A very interesting possibility for distinguishing incongruity from incompatibility is illustrated in the mentor pollen technique applied in research on pistil-pollen relationships. Necessary genetic information that is lacking in alien pollen can be provided by mixing it with the pollinated plant's own pollen (22). In host-parasite relationships, preinoculation with a functioning pathogen sometimes enables another pathogen to function (17). The results of such experiments may indicate the mechanism of resistance.

In general, durability is improved as the number of genes that need to be changed in the parasite for overcoming the new host character is increased. To achieve this, the breeder now aims at introducing complexes of characters; these are often difficult to handle in breeding programs. The ideal introduction of a host gene that cannot be overcome by the parasite and by which disease

development is prevented, is sometimes reached (examples cited in reference 6). With the totally new techniques now being developed for recombination of genetic information, chances for introduction of host characters that are beyond the genetic potential of the parasite may greatly improve. The ways in which incongruity could be manipulated to discern such host characters that are beyond the adaptive capacity of the parasite are still unknown. Concerted discussions among specialists in the fields of phytopathology, flower biology, biochemistry, and plant breeding should contribute to the solution to this problem and would be of interest for all research fields concerned with intimate relationships.

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