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THE NATURE OF SELF-INCOMPATIBILITY

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RESUMEN

La presente revisión resume los más importantes hechos del fenómeno de la incompatibilidad en plantas superiores. Describe algunos sistemas y algunas formas de anular su efecto. Analiza las reacciones del fenómeno tanto en los órganos femeninos como masculinos y sus consecuencias. Describe los tipos de incompatibilidad y finalmente analiza algunas de las implicaciones y usos más importantes del fenómeno dentro.del mejoramiento de plantas cultivadas.

SUMMARY

The present review summarizes the most important facts on incompatibility in higher plants. It describes some of the most important systems and discusses some attempts to bypass the incompatibility reaction. It analizes the reaction in the male and female and the consequences. The different types of incompatibility and the implications related to plant breeding are discussed.

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CONTENT

THE NATURE OF SELF-INCOMPATIBILITY*

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INTRODUCTION

Among the various systems of pollination control in plants, incompatibility plays a very important role in preventing inbreeding and promoting outcrossing. It can be as efficient as strict dioecy in enforcing cross pollination and has the advantage that every plant bears seed and thereby contributes directly to the propagation of the species.

There are several similar definitions of incompatibility. Crane and Lawrence (12) indicate that incompatibility is the failure of plants with normal pollen and ovules to set seed due to some physiological hindrance which prevents fertilization. Williams (58) in a more detailed definition describes incompatibility as the failure of pollen tubes to penetrate the full length of the style and to effect fertilization. Arasu (3) holds that incompatibility may be defined as the inability of a plant producing functional gametes to set seed

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when self-pollinated. These definitions show that incompatibility may operate at any stage from pollination to maturation of the ovules.

Incompatibility is widely spread in the plant kingdom. Families of flowering plants which are useful for man including Leguminosae, Rosaceae, Solanaceae, Sterculiaceae, Compositae, Cruciferae and the Gramineae exhibit this characteristic. In 1940, East (16) estimated that it occurs in more than 3000 species among 20 families of flowering plants, but subsequently many additional cases have been reported (58). Lewis (37) pointed out that East's estimate was very low, since it was based on few breeding tests.

This paper presents a general review and a short discussion of the most important aspects related to the nature of incompatibility and its implications in plant breeding. Cytological and developmental observations with respect to the site of inhibition of pollen tube germination and growth are included, as well as some features of the biochemical nature of its mechanism. It is important to point out that the incompatibility reaction appears to be a biochemical process under rather simple genetic control. It is not the purpose of this paper to discuss the genetic analysis of incompatibility. The information has been obtained mainly from the available literature of the last ten years; however, some comments make reference to older papers, in which many of the principles of incompatibility have been settled.

SYSTEMS OF INCOMPATIBILITY

There are three main systems of incompatibility: 1) gametophytic, 2) sporophytic, 3) heteromorphic and/or homomorphic (35).

Gametophytic incompatibility was originally called the oppositional factor system by Preel (49) and was further characterized by East and Mangelsforf (17). It is featured by the independent action in both pollen and style of the two alleles of the incompatibility locus (S) present in any one diploid individual. This system is controlled by a single gene which exists in a very large number of allelic forms. The pollen-tube growth is very slow in a style that contains the same S allele. This incompatibility reaction in gametophytic species invariable takes place in the styles. In the past decade, some evidence has shown that gametophytic incompatibility can also operate at the two-locus level. Also, most of the species reported to have a two-locus system of incompatibility belong to the Gramineae family (58).

Sporophytic incompatibility is very similar to gametophytic incompatibility because it is controlled by a single gene with multiple alleles but it differs, as the same implies, in the fact that it is determined by the diploid nucleus of the sporophyte. In other words, the incompatibility reaction is given to the pollen grain by the plant upon which the pollen is produced. Arasu (3) has indicated that this type of incompatibility is very complex because the S - alleles may show dominance, individual action or competitive action and dominance in either pollen or styles according to the allelic combination involved.

Heteromorphic and homomorphic systems are characterized by differences in the morphology of the flowers of different plants and differences in such other characteristics as relative size of pollen and stigma cells. Allard (2) has pointed out that heteromorphic systems are unimportant among crop plants. Again, these systems are governed

by a single locus or gene with two alleles and the incompatibility reaction of the pollen is impressed on them by the genotype of the parent plant, that is, by the previous sporophytic generation (37).

SOME ATTEMPTS TO BYPASS THE INCOMPATIBILITY REACTION

The process of the fertilization of plants involves the germination of the pollen and the growth of the tube into the stigma and through the style into the ovary and ovule. Under normal conditions pollen grows rapidly. Rosen (53) has pointed out that pollen tubes are perhaps the most rapidly growing cells in the plant world having rates of several millimeters per hour in vitro. Pollen grows in a highly polar fashion with growth restricted to a small and clearly defined apical region.

The degree of inhibition of the growth of the pollen tubes varies between species and genotypes and it is also affected by some environmental conditions at the time of pollination.

The growth of incompatible tubes in detached styles is found also to be a function of the physiological age of the pistil. Ascher and Peloquin (5) working with Lilium longiflorum found that the growth of both compatible and incompatible tubes was restricted when pistils were excised and pollinated before anthesis. In pistils excised during the first four days following anthesis, incompatible tubes grew only about half the length achieved by compatible tubes in the first 48 hours after pollination. When pollination was delayed until six to nine days after anthesis, the growth of incompatible tubes more nearly approximated that the compatible tubes. Later pollinations of intact flowers with incompatible pollen led to seed set.

Lewis (34) demonstrated in Linum grandiflorum (pin x thrum and thrum x pin crosses) that the pollen tube growth was more rapid at 30°C than at 20°C, indicating that these were typical compatible pollen tubes since their growth increased at higher temperatures. He also studied illegitimate pollinations in selfs and crosses between plants of the same type; the styles were examined for pollen tube growth at four hours and 24 hours after pollination. In all pin (long-style) pollinations the pollen did not germinate; in thrum (short-style) pollinations the pollen grains germinated and four hours after pollination the tubes were three times the diameter of the pollen grain but the tips had swelled and burst. In other self-incompatible species, at low temperatures (10 -15°C), incompatible was well as compatible pollen tubes grew faster; however, the rate of growth of incompatible pollen tubes is decreased at higher temperatures. The results indicate that different physiological factors affect the rate of growth of compatible and incompatible tubes. One might postulate that incompatibility is gametophytically determined in cases in which the incompatible pollen is able to germinate and grow part of the way through the style.

Depending on the species, incompatibility can be reduced or entirely onvercome by subjecting the pistil to a different temperature before or after pollination. Bali and Hecht (6) working with species of Oenothera have reported that immersing the pistil in warm water (50°C) for five minutes followed by immediate pollination permitted incompatible pollen to germinate and grow through the stigmas and into the styles. In experiments where pollination is delayed after the warm water treatment, the effect of the warm water is still evident after 24 hours.

In Lycopersicon peruvianum self-incompatibility appears to be broken in 3 ways: 1) spontaneous mutations that occur with a frequency of 0-1 per million, 2) by the combination of genes outside the S - locus that are already present, 3) a high-temperature sensitivity of the incompatibility reaction after inbreeding (20). This sensitivity of the incompatibility reaction to high temperature (about 40°C) seems to be governed by one recessive gene in this species.

In Brussels sprouts and Savoy cabbage, the sporophytic incompatibility barrier can be broken by applying a direct electric potential difference of 100 v. between pollen and stigma during pollination (51). The authors explain that due to electrical attraction forces, pollen grains come in very close contact with the papillae, thus inducing the sticking reaction for the pollen grain to germinate. The wax layer can be damaged or its (crystalline) structure changed in this way to facilitate the sticking reaction. The electric potential difference, which exists in cell walls (including the cuticular layer), may be disturbed and as a result its permeability is changed.

Ockendon (45) found 17°C to be the temperature at which there was full pollen tube growth in a compatible cross between lines of Brussels sprouts, but little or no tube growth in an incompatible cross or self-pollination. Studying the number of pollen tubes, he found that there was a sharp increase in the number of tubes between 23°C and 26°C following self-pollination. Although a considerable number of tubes were also found at 30°C, most of them were short, swollen or distorted, suggesting that there is partial inhibition of pollen tube growth at this temperature. He observed an intrinsic variation between flowers which was previously attributed to physiological differences.

Nettancourt et al. (42), using leaf irradiation and the adventitious bud technique, derived self-compatible clones of Nicotiana alata from self-incompatible mother plants. In some cases the plants maintained in the style of the original S_2 and S_3 specificities but produced self-compatible pollen. The self-compatible factor in these plants was always associated with tetraploidy and all tetraploid plants were self-compatible. In the control diploid population some self-compatible plants were detected but in the plants irradiated only the pollen was self-compatible.

CYTOCHEMICAL OBSERVATIONS OF THE INCOMPATIBILITY REACTION

The self-incompatibility reaction can occur at several points: 1) on the surface of the stigma, 2) during the growth of the pollen tube through the style (39), 3) beyond the style (4, 11, 25). This phenomenon may indicate little affinity between the male and female gametes.

Correlations between pollen cytology (microsporogenesis) and the site of inhibition have been observed in homomorphic flowering plants for these two types of incompatibility systems (7). Sporophytic incompatibility (reaction Type 1) is observed primarily in species with trinucleate pollen iwth inhibition of germination on the stigma surface. Binucleate grains and inhibition during pollen tube growth have been found in species with gamethophytic (reaction Type 2) incompatibility. However, this relationship fails to hold in the heteromorphic species which possess the sporophytic type of incompatibility and which have either binucleate pollen as in Primula or Lythrum or trinucleate grains as in Linum or Fagopyrum.

Sucrose appears to be a key to successful germination and growth of pollen in vivo. Brewbaker (7) has postulated that the physiological action of the incompatibility alleles may be mediated via the control of sucrose uptake by the pollen grain or pollen tube. It appears that trinucleate pollen grains might be relatively sucrose-deficient at maturity due to the occurrence of the second mitotic division and the late stage of development. In contrast, binucleate grains might be relatively rich in sucrose or starch.

Although a number of differences have been reported between compatible and incompatible pollinations with regard to nuclear behavior in the pollen, pollen cytology, and pistil respiration, it is generally thought that the primary expression of the incompatibility reaction is to be found in protein metabolism (53). On the basis of this concept, the remaining discussion presented in this paper will be cytochemically oriented.

Incompatibility reaction type 1

Observations more recent than Brewbaker's have indicated that the cuticle of the stigma is the incompatibility barrier (9, 39). This material can be broken down enzymatically by a cutin-breaking enzyme called cutinase. Experiments with Brassica oleracea have shown that the pollen is able to penetrate the self stigma if it is first placed for a short period on the surface of a foreign stigma. This indicates that cutinase is irreversibly activated during the contact between pollen and stigma surface.

Much effort has been devoted during the last ten years to understanding the nature of incompatibility through the knowledge of pollen

wall structure, the presence of enzymes and substances with antigenic characteristics as well as the site of the pollen wall in which these substances are found.

The inner stratum of the pollen grain wall, the cellulosic intine, contains substantial amounts of protein including various hydrolytic enzymes which are probably involved in germination, early pollen-tube nutrition and penetration of the stigma (29).

Cytochemical methods have been used to follow the incorporation of enzymes and antigens in the cellulosic intine of pollen grains. Knox (27) has found that acid phosphatase, esterase and ribonuclease are first detected in the developing intine of the pollen grain of Gladiolus gandarensis. Enzyme activity is also noted in the peripheral region of the protoplast during the period of intine growth. Also, the appearance of antigens is traced during pollen development. Antigens were first detected in the early vacuolate period. In slurry preparations using maturing pollen, enzymes and antigen are found to diffuse into the medium within 30 seconds. These observations indicate that vacuolate and tubular cavities in the intine are the probable sites of the enzymes and antigens.

Knox and Heslop-Harrison (29) observed the early events following the arrival of pollen on the stigmas of a grass, Phalaris tuberosa, in compatible and incompatible matings. An immunofluorescence technique indicated that the main source of the antigens released by the pollen grains on leaching is the intine. They found that the intine-held antigens leave the pollen grains and spread out on the stigma surface very soon after contact is made. They suggested that there is no difference between compatible and incompatible pollinations with respect

to the behavior of the discharged material. The enzymes from the wall sites may be among the antigens but most may be recognition substances. The authors postulated that incompatible pollen from the same or different species may borrow recognition-material from the compatible, which would allow selfing or interspecific hybridization. This fact has been confirmed as is shown later in this paper.

There are several proteins diffusing from moistened pollen and some of them are potent allergens. Of the protein fractions actually detected, antigens E and K have been purified and their activity is greater than that of the total remaining pollen extract. For example, antigen E represents at least 90% of the allergenic activity in ragweed (Ambrosia tenuifolia) (26). Knox and Heslop-Harrison (29, 31) have detected cytochemically pollen wall enzymes of ten species of flowering plants. The site of deposition of the hydrolytic enzymes is the cellulosic intine. On the basis of this evidence, it seems that the enzymes released from moistened pollen are derived from extracellular sites. They are rapidly diffused and easily leached, so they have some function in pollen germination and hence in the penetration of the stignma.

Knox (28) has followed the release of wall held materials from the pollen of ragweed and Cosmos bipinnatus onto the stigma surface. He has seen a fluid substance coating pollen grains, pollen tubes and adjacent stigmatic papillae. The fluid contains proteins, carbohydrates, lipids and the allergen antigen E. In both compatible and incompatible (selfed) pollinations, the pollen wall antigens are released rapidly onto the stigma surface before pollen germination. The stigmatic papillae near the grains become invested with antigens and control

is exerted to determine whether germination will occur and whether the pollen tube will penetrate the tissues.

Roggen (50) using a Jeol JSM-U3 scanning microscope described the following steps for a compatible reaction in Brassica: 1) the initial recognition resulting in the "sticking" of the pollen grain to the wax of the papilla; 2) a change in the properties of the papillar cuticle, resulting in wax removal and interconnections of the pollen exine with the papillar cuticle; 3) the beginning of pollen germination if the sticking coincides with the germ furrow, the site at which the wax layer must be pierced; 4) pollen tube penetration into the papillar wall.

It has been mentioned that one of the most potent allergens released from moistened pollen is antigen E. Cytochemical staining methods and immunofluorescence techniques have been extensively used by botanists to study the diffusion of this antigen from pollen grains. The most recent investigation, to the authors' knowledge, has been conducted by Howlett, Knox and Heslop-Harrison (22) with pollen of ragweed and C. bipinnatus. In mature pollen of these two species antigenic proteins are present at two distinct sites in the pollen wall: in the inner cellulosic intine layer and in the intervacuolar cavities and the caves exine. It is now evident that the pollen grain wall plays many roles in the life of the male gametophyte: the apertures have other functions than to provide a path of the exit for the pollen tube. They are important as sites for the storage and release of gametophytic proteins including the intine-held enzymes and probably recognition substances.

Similar results have been reported by Heslop-Harrison et al (18) in studies of pollen-wall proteins of the Malvaceae. It is suggested

that the intine-held proteins of angiosperm pollen grains are always produced by the male gametophyte, while those held in the exime cavities are of sporophytic origin, being derived from the tapetum.

While the wall-borne enzymes may be among the antigens released, much of the protein is non-enzymatic and it has been suggested that some of the materials may act as recognition substances in the control of the incompatibility reaction. They constitute a large part of the protein located in the inner cellulose layer of the pollen grain wall. The proteins with both enzymatic antigenic and allergenic properties are in the intine (inner cellulosic layer) of the pollen wall. They are readily released on moistening and diffuse out through the exine, particularly at the germination apertures. The enzymatic substances constitute only a fraction of the total substances released. These proteins are the so called recognition substances, since they function in the control of pollen germination and tube growth in both inter and intraspecific crosses (27, 29, 30, 31).

To overcome this obstacle, incompatible pollen has been mixed with compatible (mentor) pollen which has been killed by gamma radiation (54). The function of the compatible pollen is to provide the necessary stimulus for germination and tube growth in the form of the recognition substances mentioned above. Using killed recognition pollen and its extracts, Knox, Willing and Ashford (32) were able to produce over 500 hybrids between Poplar deltoides and P. alba although the cross between these species had always failed to yield progeny in control pollinations. When P. deltoides was pollinated with a mixture of viable P. alba and inviable, irradiated P. deltoides pollen, a seed set of 5 seeds/capsule was obtained. When recognition pollen

of P. deltoides killed with methanol was used, 4.5 seeds/capsule resulted. Eleven seeds/capsule were produced when the P. deltoides pollen had been killed by repeated freezing and thawing. This is an excellent test of the hypothesis that the wall-held proteins are the recognition factors concerned.

Incompatibility reaction type 2

The second type of incompatibility barrier in flowering plants is associated with the gametophytic system and binucleate pollen and results in the inhibition of pollen tube growth within the style before reaching the embryo sac.

In a few species incompatible tubes grow as rapidly as compatibel tubes and reach the ovary. Theobroma cacao L. is exceptional in that the incompatibility mechanism expresses itself after the release of the male nuclei into the embryo sac, resulting in the failure of embryo formation and the collapse of the ovular apparatus. Cope (11) observed that the tubes reached the female nuclei and released the sperm nuclei but in 25%, 50% or 100% of the ovules of each flower the gametes did not fuse (15, 40, 57). Brewbaker (7) pointed out that the several species in which incompatible tubes reach the ovary have hollow styles; he suggested that intimate contact between pollen tubes and stylar tissue is necessary for inhibition to occur in the style.

Modlibowska in 1945 cited by Arasu (4) found that in apples tube growth varied with variety and temperature. Arasu (4) found that in cross-pollinated flowers (for seven species and different cultivars) the pollen tubes entered the ovary freely and many tubes could be seen deep inside the ovary. Three days after pollination, the extent

to which self-pollen tubes penetrated into the ovary varied with species. Some rarely reached the top of the ovary, others reached the top of few ovules, and others penetrated fairly deeply. In almost all cases fertilization did not occur in selfed flowers. The numbers of instances where self-pollen tubes entered ovules varied with species and season.

Kho and Baer (25), crossing two species of Rhododendron, observed tubes which entered the embryo sac and grew out again without effecting fertilization, but they could not find a satisfactory explanation for this. Because they found temperature to be an important factor in pollen tube growth and fertilization, they considered the phenomenon physiological as well as genetical.

Various interpretations have been postulated for gametophytic incompatibility, the second type of incompatibility barrier. Two possible mechanisms have been proposed to explain the reaction: 1) complementary stimulation and 2) inhibition.

The first mechanism has been suggested on the basis of a particular substance in the style which is complementary to the substances carried in the pollen and stimulates fast growth of the tubes. When tubes grow at a very slow rate, either the promoting substances are absent or they are not complementary to the compounds present in the style. In vitro studies conducted by Pfahler (48), Brewbaker and Kwalk (8), Rosen (52), Cook and Nalden (10) with respect to germination and growth of pollen tubes under different treatments, indicate the absence of a specific stimulating substance due to the ease with which pollen-tube growth can be accomplished.

The second and most important mechanism is an inhibitory reaction

which implies the action of an inhibitor acting only against pollen tubes having the same alleles as those present in the style.

As has been mentioned, protein metabolism is the primary expression of the incompatibility reaction. Lewis (36) and Rosen (53) found that antisera induced in rabbits by pollen grain extracts give precipitation reactions to diffusates of germinating pollen, with higher titer values resulting from homologous cominations than from semi-homologous or heterogenous ones. This experiment indicates that an inhibiting system, very similar to the antigen-antibody reaction of animals, is the cause of the second type of incompatibility reaction. Rosen (52) postulated that although immune type reactions has not been demonstrated in the pistil, the incompatibility reaction is basically an immune reaction; he proposed that the pollen antigen may be an enzyme, many of which are reported to be released by germinating pollen.

Tupy (56) studied the changes in the amino acid pools of styles of incompatible plants after pollination. He showed that this pool is diminished in a characteristically different manner after self and cross pollinations. Linskens (39) has accepted the immunological theory of incompatibility as the most acceptable explanation. He has pointed out that a re-interpretation in terms of current biochemical concepts involving enzyme induction, feed-back and end-product inhibition, is necessary to explain the immunological theory. He has proposed a model to show that antibody production by nucleic acid templates and they synthesis of these templates is inhibited by the product of an enzyme almost identical in configuration with the antibody. On the other hand, the antigen (pollen) by combining with the enzyme, prevents the production of the antibody (Figure 1).

INCOMPATIBILITY

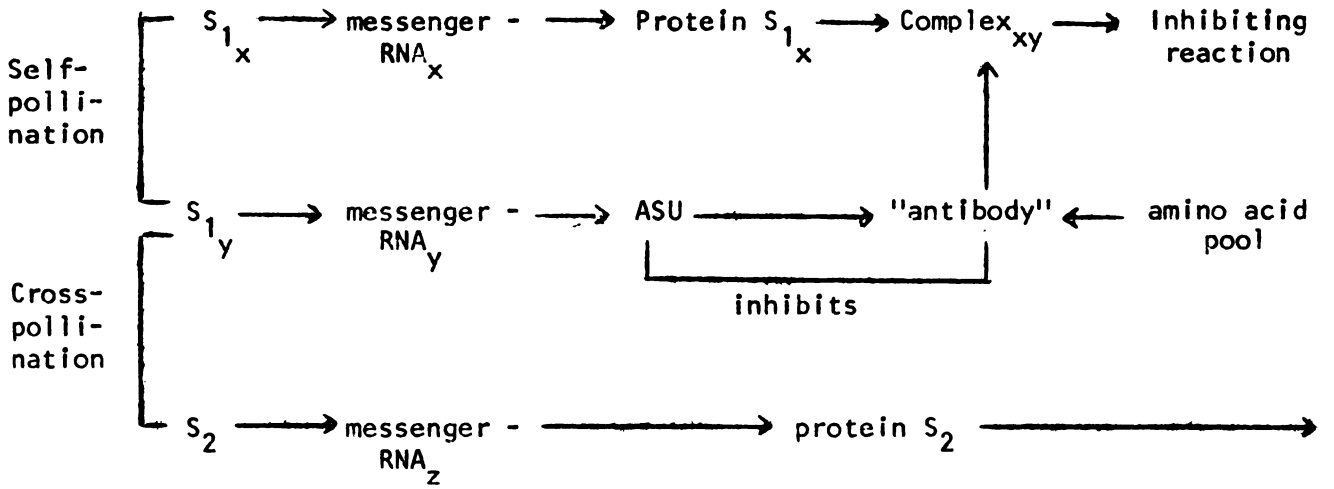

Figure 1

Genetical aspects: The existence of an antibody is not implied. The S gene consists of two cistrons. One of them controls the specific grouping of the protein that is active in the incompatibility reaction. The other controls the carrier responsible for the activity of this protein in the pollen and style. The active protein causing the S incompatibility in plants is called an antigen because enzymes and antigen are similar.

Biochemical aspect: Antibody formation is implied. It is in the synthesis of a new protein in which a transfer of information is necessary in the form of nucleic acid molecules. There are also an antibody synthesizing unit (ASU) and an aminoacid pool leading to the formation of antibody molecules. This reaction is inhibited when antibody concentration is sufficiently high but it continues when antigen combines with and removes the antibody.

Lewis (38) in suggesting his dimer hypothesis of gametophytic incompatibility stated that: "1) the S gene complex produced a polypeptide whose specificity, determined by the primary structure- is different for each allele. Each allelic polypeptide is an identical molecule in pollen and style. 2) the polypeptide polymerizes into a dimer in both pollen and style. 3) the first step in the incompatible reaction is that the same dimers in pollen and style, and only the same combine to form a tetramer with the aid of an allosteric molecule which may be glucose, a protein or one of many small molecules. 4) the second step in the incompatible reaction is that the tetramer acts as a genic regulator either to induce the synthesis of an inhibitor or to repress the synthesis of an auxin of pollen tube growth." The monogenic system of this hypothesis explains the consistent individual action of S alleles in the style. In the haploid pollen grain, however, there is normally no possibility of hybrid dimer formation and therefore no local conditions have been maintained by selection to prevent hybrid dimerization between different allelic forms. Lewis's physiological and biochemical observations lead to the conclusion that at the second step of the reaction, the induction of an inhibitor rather than the repression of an auxin is operating in the incompatibility reaction.

Pandey (47) describes two hypotheses relating to the time of S-gene action. The first hypothesis proposes re- or early-meiotic S-gene action in the sporophytic system and late- or post-meiotic action in gametophytic species. The S-gene is thought to produce allele-specific precursos which are converted into incompatibility substances after the second mitotic division when the male gametophyte is presumably deficient in metabolites. In the trinucleate pollen of

sporophytic species, inhibition occurs in the stigma. In the case of trinucleate pollen in gametophytic species, inhibition is delayed until the second mitotic division and thus occurs in the style.

The second hypotheses holds that S-gene action is directly associated with the second mitotic division and therefore occurs in the trinucleate pollen grains of sporophytic species and in the pollen tubes of gametophytic species which have binucleate pollen.

Both hypothesis hold that the actual production of the incompatibility substances is dependent on the second mitotic division in the male gametophyte.

Other substances have been suggested to account for the inhibition of pollen tube growth within the style. Peroxidase isozymes, characteristic of the S allele or genotype have been postulated to be equivalent to Lewis's dimers in incompatible pollination. The activated tetramer peroxidase causes inhibition of the pollen tube growth by its action on indoleacetic acid (IAA); the isozyme may destroy IAA present in the pollen tubes (46).

Information concerned with the physiology and ultrastructure of compatible pollen tubes in angiosperms is abundant in the literature. Jensen and Fisher (23) reported on the entrance and discharge of the compatible pollen tube in the embryo sac. Rosen (53), Larson (33) and many others describe the bipartite structure of the tube wall and the growth of the pollen tube through the style until it breaks down in the mycropilar region of the embryo sac and releases the mass of granular particles in the synergid.

Nettancourt et al (43) have studied the mechanism of pollen tube rejection after incompatible pollinations in the wild tomato species

L. peruvianum Mill. They compared the growth and anatomy of compatible and incompatible tubes. The results obtained indicate that the tip of the incompatible pollen tube bursts open after the outer wall has considerably expanded in the intercellular spaces of the conducting tissue. At this time, numerous granular particles have congregated in the tube cytoplasm and the inner wall has disappeared. These particles look different from the particles observed in compatible tubes; they appear to resemble the spheres which are discharged by compatible pollen tubes and may consist of a mixture of incompatibility proteins and basic tube wall constituents. They also confirm the theory that the tube wall is the site of action for the incompatibility proteins.

Self-compatibility in L. peruvianum may have various genetical bases: 1) a recessive gene for high temperature sensitivity of the incompatibility reaction, 2) mutation of the S-allele, that is, of the pollen and stylar regulatory cistron or the specificity cistron, or of the pollen-regulatory cistron only, 3) the addition of an S-allele-bearing chromosome fragment and competitive interaction between different S-alleles in the pollen, 4) genes weakening the self-incompatible reaction (21).

IMPLICATIONS IN PLANT BREEDING

The success of F_1 hybrids in naturally self-fertilized crops depends on a number of biological and economic factors which vary from species closely related to the economically important self-fertilized vegetable crop species is of great importance in the commercialization of hybrid seed (13). The potential value of self-incompatibility systems relative to male sterility is difficult to predict because of uncertainty

regarding the difficulty of sexually maintaining and increasing the self-incompatible lines. However, in insect pollinated crops lacking nectaries (e.g. tomatoes and lettuce) it appears essential to use self-incompatibility in order to obtain efficient pollination. In crops where the fruit is the marketable product it is desirable that the F_1 hybrids be self-compatible. This can be accomplished in both the gametophytic and sporophytic self-incompatibility systems by using an appropriate proportion of self-compatible pollen. Because of the effect of modifiers and the complex dominance relationships in the sporophytic systems, the breeder is advised to use a broad genetic base in attempting to transfer incompetibility to a self-fertilized species. This point is emphasized by the need also to transfer an efficient pollination system with the self-incompatibility. The greatest current problem in exploiting self-incompatibility is the need to temporarily overcome the self-incompatibility reaction. It is hoped that current research in the physiology of self-incompatibility reaction. It is hoped that current research in the physiology of self-incompatibility will lead to a simple chemical treatment for this purpose.

In Brussels sprouts (24 selection for strong and stable self-incompatibility behavior requires that tests be made under the conditions most conducive to self-compatibility in order that the selection pressure be as great as possible. Assessment of self-compatibility counts of pollen tubes ensures that selections are made on the basis of self-incompatibility and not self-infertility which is likely to be the case when making assessments on the basis of seed set.

Nievwholf (44) has proposed some procedures to obtain inbred lines heterozygous for the S-factor in inbreeding programs, their use and the way of maintaining incompletely sib-compatible parent lines of Brassica oleracea variety cole. Nasrallah and Wallace (41) have

considered the variation of self-compatibility and the sensitivity to environmental differences to be conditioned by genes which modify the incompatibility expression of the S-alleles. Thompson and Taylor (55) have recommended the use of self-incompatible parental inbreds. However, in the case of Kale their use is not so essential due to the extent of the environmental effect. From his work Ockendon (45) points out that self-compatibility in Brassica is not definitely genetically determined but it is not clear to what extent small differences in the degree of self-incompatibility are under precise genetic control In contrast to the lack of genetically controlled variation in self-compatibility between lines with high incompatibility and those with low incompatibility, the difference in self-compatibility at 17°C and at 26°C is very striking. It appears that some lines are segregating for genes controlling the strength of self-incompatibility. This possibility should not be ignored, but it is equally likely that the variation can be attributed partly, if not wholly, to environmental and intrinsic factors.

Incompatibility research on inbred material is hampered by inbreeding effects. There are not only effects of segregation of S-allele modifers, but particularly also effects of segregation of genes which influence fruit and seed setting generally (20).

Hogenboom (19) found genes for self-compatibility in L. peruvianum (L.) Mill. This character is of importance for genetic research on this species and opens up the possibility of a better exploitation of species hybrids with L. esculentum.

The possibility that in evolution both ways of development from

self- incompatible to self-compatible and from self-compatible to self-incompatible can occur is not ruled out (1). Both courses of development are even expected to occur. However, the probability of a self-compatible allele's surviving and increasing in a self-incompatible population is greater than the probability of a self-incompatible allele's building up a self-incompatible system in a self-compatible population. The important point in the case of self-compatibility being "older" is that self-incompatibility resulting from mutation of self-compatibility to self-incompatibility is the one which should be established before speciation can take place.

It has been shown in this review that the incompatibility reaction as it occurs in plants is a biochemical process controlled by genes and their alleles which are responsible for the production of different molecules, particularly enzymes and substances with antigenic characteristics. However, the complete or partial inhibition of the pollen tube growth and therefore its failure to carry out the process of fertilization, is not only a function of species and genotype, but also of the environmental conditions at the time of pollination and the physiological age of the female reproductive organs. Consequently, the gene-environment interaction responsible for the physiological expression of the incompatibility reaction is evidently operating in this phenomenon. In reference to this point, Dobzhansky and Holz (14) wisely stated more than 20 years ago the following: "genes produce not characters but physiological states which through interactions with the physiological states induced by all other genes of the organism and with the environmental influences, cause the development to assume a definite course and the individual to display certain characters at a given stage of the developmental process".

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