Wide Hybridization and Cereal Improvement

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The potential of the phenomenal Green Revolution is enormous, and the rewards are just beginning. Continued success depends upon basic plant-science innovations to apply toward maintaining vitality in the new agricultural technology. One promising area for innovation is wide hybridization of cereals.

The wild relatives and progenitors of our major cereal crops have been tapped repeatedly for genes carrying special attributes not apparently present in the cultivated forms. Genes coding for rearranged protein synthesis priorities have been identified, resulting in nutritionally superior varieties (42, 47, 45, 44). As searches for desirable characteristics within species exhaust the known natural variability, attention will shift increasingly toward hybridizing widely diverse materials to develop entirely new species (78).

Relatively few viable wide interspecific and intergeneric hybrids have been obtained, largely because of gametic incompatibility and hybrid breakdown limitations. Most wide hybrids are virtually impossible without some biochemical modifications of the natural fertilization and differentiation mechanisms, yet such modifications should be minimized. Hence, new biochemical techniques must be developed to further control species barriers and to release the infinite potential for genetic recombinations in new species.

In this review and reinterpretation of the literature of wide hybridization, we suggest the existence of a new class of plant reaction — stereospecific inhibition reactions (SIR) analogous to immunochemical mechanisms in animals — may be a key to manipulating barriers to crossability between species and to synthesizing new cereal crops.

Intraspecific, Interspecific and Intergeneric Hybridizations

Crossability Barriers

Barriers to crossability exist without doubt. The wide diversity among plants alone attests to the fact, and the species concept — "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (68) — is based on that fundamental reality. Most of the isolating barriers, however, are only partial. They depend upon physical separations of time, distance, environment, or specific ecological niche, all of which can be manipulated during cultivar production. Only gametic incompatibility and hybrid breakdown, to date uncontrollable by man, have been considered absolute barriers (68). Many genetic, physiological, and cytological events concerning these phenomena have been described, yet our knowledge of the corresponding biochemical reactions is almost nonexistent.

Gametic Incompatibility

Gametic incompatibility, the more extensively studied of the two "absolute" barriers, is an incapacity of pollen to germinate on certain styles or to form a viable zygote with an egg of another species (68). Most research has centered on self-incompatibility, commonly believed to represent a primordial development to prevent inbreeding (68). Genetically, self-incompatibility usually is
determined by a complex multiple allelic system (S-genes) that prevents syngamy by sperm cells and eggs carrying identical S-alleles. When present within any particular taxonomic family, the type of incompatibility mechanism remains constant (76).

Attempts have been made to further classify self-incompatibility according to the time of gene action. S-alleles reportedly function in the diploid nucleus of the pollen mother cell in the sporophytic type of self-incompatibility (76). This type of system normally is associated with species producing trinucleate pollen grains and characterized by a range of interallelic interactions from no competition to complete dominance. The incompatibility substances thus are present in the cell walls. No pollen can germinate on styles of the same genotype because inhibiting substances would contact it immediately. In the gametophytic type of self-incompatibility, the S-alleles function within individual microspores. A single S-allele determines the incompatibility substance formed within each pollen grain. Pollen germination (or at least pollen swelling) is required to allow reactants to diffuse or inhibitors to interact.

The sites of self-incompatibility reactions also vary. Pandey suggests five general sites at or within which reactions may take place: (1) stigmas, (2) styles, (3) ovular tissues, (4) pre-fertilization embryo sacs, and (5) post-fertilization embryo sacs (51). The last-named site is not legitimately self-incompatibility, in that syngamy already has occurred. The stigma and style sites are most commonly recognized. The stigma reaction is restricted to the cutin-covered surface. Pollen germination and tube penetration occur when an active cutinase or an inactive precursor (subsequently activated by stigmatic exudates) solubilizes the cutin membrane. Self-incompatibility results when identical S-allele products are present in both pollen and stigma inactivating or inhibiting the cutinase reaction. This reaction has not been detected in vitro (7, 20, 35). In Cruciferae, pollen grains apparently react with the stigmatic surface, where they remain attached even after lactophenol reagent clearing for 24 hours (37). The stigma reaction in Gramineae has been described by Kato and Watanabe (26, 27).

Style type reactions, which occur when the pollen tube penetrates the stylar conducting or transmitting tissue, are believed to result from nutritional physiological factors. Pollen enzymes evidently are inhibited from utilizing stylar metabolites. Pollen grains having the most reserve substrates can penetrate incompatible sytles farthest (12). When pollen was grown through a compatible style into a graft-attached incompatible style, the pollen tube was stimulated to grow farther than if the compatible style metabolites had been absent (18). Stylar self-incompatibility inhibitors are quite heat labile. For example, a substance in Oenothera was inactivated by a five-minute, 50°C heat treatment; other vital enzymes apparently were not affected up to 70 to 100°C (19). A 48-hour treatment at 30°C destroyed Lilium inhibitors (3). Also it has been observed that in Lilium the self-incompatibility reaction is transient; the reaction, effective before anthesis, becomes less intense with floret aging and allows pollination by incompatible pollen six to nine days postanthesis (2).

Ovular or embryo sac-site reactions are less well understood but probably involve essential metabolites as do stylar-type reactions. The chemical nature of ovular or embryo sac reactions is unproven although Pandey has demonstrated that peroxidase isoenzymes may be the biochemical manifestations of multiple allelism. Specific isoenzymes are believed to react with indole acetic acid to effect self-incompatibility (52).

Other studies have shown that multiple S-alleles produce immunologically distinct proteins, which form “ward bodies” functioning possibly as intermediate enzyme-antienzyme products of the self-incompatibility reaction (32) or as components of an antigen-antibody type reaction system (33, 39). In some species the specific self-incompatibility proteins may even be synthesized during pollen