A new look at incompatibility relationships in higher plants

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Summary. Pollen tube growth was evaluated using an 18-step scale after both intra- and interspecific pollinations of genotypically widely differing diploid potato species and potato dihaploids expressing monofactorial gametophytic incompatibility. The results obtained account for a wide array of types of pollen tube growth resulting from crossing partners with distinct incompatibility behavior. Based on the assumption that inhibition of pollen tubes is the rule and solely prevented by the pollen itself, a model proposing one common cause underlying different mechanisms for both intraspecific self-incompatibility and interspecific incompatibility in diploid is put forward. Data supporting the model are presented from the experimental results of this study and from the literature. The strength of pollen-style interaction depends on particular S-alleles in combination with recognition and activity properties of the basic S-genotypes. The model is suitable to explain all former observations on incompatibility in diploids with a gametophytic system of incompatibility and, with modifications of the manner of phenotypic expression, also in plants with sporophytic incompatibility. The proposed scheme of pollen tube growth phenotypes permits prediction of pollen tube growth behavior in an intended cross combination. The model is based on both classical Mendelian genetics and recent molecular genetic insight.

Key words: Gametophytic incompatibility - Self-incompatibility - Unilateral interspecific incompatibility - Potato (Solanum) species

Introduction

Incompatibility mechanisms are known from 70 families of angiosperms representing 250 genera with more than 3000 species (Gastel 1976). Families of most crop plants harbor gametophytically or sporophytically determined incompatibility mechanisms which are thought to be regulated by the action of one or more loci (Lundqvist 1965; Nettancourt 1977; Richards 1986). For both gametophytic and sporophytic types of incompatibility, intra- and interspecific relationships can be distinguished. Various theories have been developed to describe the general terms of incompatibility relationships, considering either only pre-zygotic or both pre- and post-zygotic barriers to progeny formation. The experimental and theoretical work of Lewis and Crowe (1958) summarizes pre-zygotically determined incompatibility relationships in both intra- and interspecific hybridizations, assuming one common basic cause for both gametophytic and sporophytic incompatibility systems. They distinguish between self-incompatible (SI) and self-compatible (SC) species. The latter are unilaterally incompatible as males in crosses with SI pistillate partners. SC species, when used as males, are also unilaterally incompatible with the Sc class of self-compatible species, since Sc styles inhibit SC pollen, as it is inhibited in SI styles. The same basic mechanism to bring about both self- and interspecific incompatibility in diploid tomato was also postulated by Martin (1963). A balanced relationship between pollen tube growth-promoting and stylar inhibiting substances, both determined polygenically, was thought to control incompatibility. A change from incompatibility to compatibility would supposedly not require to be preceded by any changes in the properties of the S gene itself. It was concluded that an excess of pollen tube growth substance would cause both self- and interspecific compatibility.

Grun and Radlow (1961) and Grun and Aubertin (1966) assumed the existence of an independent locus responsible for interspecific incompatibility relationships not related to the S-locus that determines self-incompatibility. Pandey (1969) found stepwise incompatibility in interspecific crosses involving self-incompatible and self-compatible Nicotiana species. His interpretation of these findings is that two genomic sites, causing intra- and interspecific incompatibility, respectively, coexist. Ab-
dalla (1970) and Abdalla and Hermsen (1972), working with potato, proposed an additional system of dominant (UI) genes independent of the S-locus causing unilateral sterility in crosses of the type SI female × SC male. Following this concept, an SI progeny resulting from intercrossing SC plants and expressing unilateral incompatibility in interspecific crosses, as observed by Rick and Chetelat (cited in Chetelat and DeVerna 1991), is difficult to explain.

The concept of one common cause for both intra- and interspecific incompatibilities was reviewed theoretically by Pandey (1964, 1968). Nettancourt et al. (1974) and Nettancourt (1977) also suggested that the two mechanisms were related. Recently, on the basis of findings in tomato crosses, Chetelat and DeVerna (1991) have again expressed the suspicion of biochemical and physiological linkage between self-incompatibility and unilateral interspecific incompatibility.

In potato, it has been demonstrated that post-zygotic barriers to embryo development and seed set occur and that they function independently of pre-zygotic barriers (Johnston and Hanneman 1980). Hogenboom's theory of incongruity relationships (1973) considers both pre- and post-zygotic barriers as the same mechanism; it serves well to interpret observed phenomena, but is less effective for making predictions of crossability. Studies on the biochemical nature of self-incompatibility have revealed that stylar products, related to S-genotypes causing self-incompatibility, are glycoproteins in both types of plants expressing gametophytic or sporophytic incompatibility relationships (reviewed by Nasrallah et al. 1991). S-Glycoproteins are expressed independently of pollination, and they are controlled by the style genotype alone (Xu et al. 1990). It has also been shown for some solanaceous plants that stylar S-glycoproteins have ribonuclease (RNase) activity (McCure et al. 1989, 1990; Broothaerts et al. 1991). In particular cases, almost all stylar RNase activity is related to the S-glycoproteins (Broothaerts et al. 1991). Interestingly, however, styles of SC Nicotiana tabacum, investigated by McCure et al. (1989), have only low RNase activity. However, Franklin-Tong and Franklin (1992) report from styles of Papaver rhoeas L. no RNase activity at all.

In selflings, inhibition of pollen tube growth depends on highly specific interactions; inhibition only occurs when one or both S-phenotypes of the diploid style match the S-phenotype of the pollen. In contrast, unilateral incompatibility in interspecific crosses cannot be highly specific, because of the sometimes extremely remote relationship of the crossing partners. But Lewis and Crowe (1958), Pandey (1969), Hermansen and Taylor (1979) and Novy and Hanneman (1991) have clearly shown that the universal principle of unilateral inhibition of SC pollen in SI styles functions precisely.

Pollen-specific products related to incompatibility have not been found yet, although recent findings on co-segregation of genetic markers with interspecific incompatibility of intergeneric hybrids (Chetelat and DeVerna 1991) account for their existence. They could possibly represent a physical barrier to stylar products related to incompatibility, preventing them from reaching the site of interaction or inactivating them. Franklin-Tong and Franklin (1992) reported pollen-expressed genes that are up- and down-regulated in response to incompatible pollination in Papaver rhoeas L. They propose a model of self-incompatibility in which inhibition of pollen tubes is caused by signal transduction through the pollen tube membrane. A gene, discovered by Goring and Rothstein (1992), that encodes a receptor kinase in one part and in the other part an amino acid sequence homologous to the corresponding S-glycoprotein, accounts for the same model of pollen-pistil interaction. This gene is expressed in both pistil and anthers in Brassica and it segregates with the S-genotype.

Thus, basic interaction between pollen and style would consist in a steady resistance of the developing pollen tube against stylar products related to incompatibility. Two types of interruption of such a relationship resulting in inhibition of the pollen tube could be envisaged: (1) the pollen S-allele matches one of the style’s S-alleles; and (2) pollen products fail to cause resistance against stylar products, or stylar products lose their hostility to pollen tubes. Based on these assumptions, a model of pollen-pistil interactions is developed that explains the functioning of stylar incompatibility in both intra- and interspecific incompatibility relationships. Experimental results from investigations of pollen tube growth in interspecific crosses of wild diploid potato species which support this model are presented.

**Materials and methods**

Plants of diploid (2n = 2x = 24) wild potato species accessions and parthenogenetically induced (Hougas and Peloquin 1958) potato dihaploids (2n = 2x = 24), presented in Table 1, were grown under standard conditions in plant beds and in a greenhouse at CIP, Lima, Peru, during 1991. Plants of the long-day-adapted species brd, etb, and frn and all potato dihaploids were kept under additional light to promote flowering. Silver thiosulfate (STS) was sprayed on some plants of the dihaploids to promote flower longevity (Rahimi and Carter 1989). STS does not influence pollen tube growth (Trognitz 1990).

Seedlings of the species were clonally propagated by cuttings. Depending on flowering intensity, 5–25 plants per clone were used for pollen collection and crosses. Mature anthers were collected from the flowers and air dried for 2 days before pollen was extracted. Pollen samples used for all pollinations were stored in gelatin capsules at −24°C over silica gel. Viability of stored pollen was assessed using carmino acetic acid staining and the more reliable X-Gal assay detecting β-galactosidase activity as described in Trognitz (1991).

Crossings were performed in Lima during July–November on plants at optimal flowering stages.

To investigate pollen tube growth, pollinations were made on emasculated flowers. Two to ten carpels per replication were excised 48 h after pollination and frozen immediately. Clearing, macerating and callose staining with modified Schreiter’s solution and evaluation of pollen tube growth were performed as described earlier (Trognitz 1991). Of each sample, the pistil with the most advanced tube development was taken as standard. The phenotype of pollen tube growth in a certain cross combination was highly similar in all pistils of the same sample.

All genotypes that were available and flowered, were subsequently included in the crosses ranging from one cross combination