

Breeding for resistance to whitefly-transmitted geminiviruses

Francisco J. Morales

Virologist, International Center for Tropical Agriculture (CIAT), AA 6713, Cali, Colombia. Tel.

57-2-4450000, Fax 57-2-450073, E.mail: f.morales@cgiar.org

Introduction

The whitefly *Bemisia tabaci* Genn. (Homoptera:Aleyrodidae) has caused millions of dollars worth of crop losses in tropical and subtropical agricultural regions in the five continents of the world (Brown, 1994). Besides the direct damage caused by *B. tabaci* (plant nutrient loss; physiological disorders; honey dew excretions, etc), the sweet potato or cotton whitefly is an efficient vector of numerous geminiviruses (plant viruses consisting of two 'twined' or 'geminate' particles, encapsidating one or two single-stranded DNA genomes). The geminiviruses transmitted by *B. tabaci* belong to the genus *Begomovirus* (sigla for the type species, *Bean golden mosaic virus*), according to current taxonomic classification (Regenmortel *et al.*, 2000). These viruses infect a large number of cultivated plant species, following their transmission by *B. tabaci* from wild or other cultivated hosts (Padidam *et al.*, 1999). Currently, over 100 begomoviruses are transmitted by at least two biotypes of the whitefly *B. tabaci*, to more than 20 different cultivated species of socioeconomic importance. The main food crops affected by whitefly-transmitted geminiviruses are: common bean, mung bean, blackgram, lima bean, soybean, cowpea, tomato, potato, eggplant, pepper, chili peppers, melon, watermelon, squash, okra and cassava (Muniyapa, 1980; Brown, 1994).

The extreme pathogenicity and severe yield losses induced by begomoviruses, and absence of immune genotypes in most of the plant species attacked, has led to considerable pesticide abuse in order to control the whitefly vector. As a result, *B. tabaci* has developed resistance to most of the insecticides used in the past.

Breeding for begomovirus resistance

Despite the lack of immune cultivars recorded for the majority of the crops affected by *B. tabaci*-transmitted geminiviruses, breeding for disease resistance has proven to be the most successful and sustainable of the integrated whitefly/begomovirus control methods implemented to date. A comparative analysis of the three main cases of important food crops improved for begomovirus resistance, is presented here.

Breeding for resistance to African cassava mosaic virus

The case of cassava (*Manihot esculenta* Crantz) represents one of the earliest attempts at breeding for resistance to an important group of geminiviruses, collectively known as *African cassava mosaic virus* (ACMV). ACMV is transmitted by *Bemisia tabaci*, but the main method of dissemination is through the vegetative propagation of ACMV-infected cuttings (Swanson and Harrison, 1994). Currently, ACMV spreads in East and West Africa (Hong *et al.*, 1993).

The search for resistance to African cassava mosaic viruses began in East Africa in the 1920s. Initially, several ACMV-tolerant cultivars were identified in large cassava germplasm collections evaluated in Madagascar and Tanzania (Jennings, 1994). Despite the initial successes in achieving notable levels of ACMV resistance following intraspecific crosses (Cours, 1951), cassava breeders resorted to interspecific crosses, using *Manihot glaziovii*, *M. dichotoma*, *M. catingae*, and a genotype called "tree cassava" (probably a natural *M. esculenta* X *M. glaziovii* hybrid), seeking higher levels of cassava mosaic resistance (Jennings, 1957). The first generation of *M. glaziovii* X *M. esculenta* produced in 1937, had non-tuberous roots and became infected by ACMV under field conditions. Backcrossing was necessary to restore root quality. Resistance to

ACMV seemed to have improved slightly following three generations of backcrosses, probably due to the use of *M. esculenta* parents with intermediate levels of ACMV resistance.

All other interspecific crosses were discarded due to various agronomic problems. Unfortunately, the high expectations for the *M. glaziovii* X *M. esculenta* hybrids, were realized in some but not all regions of East Africa. A high proportion of the hybrid cassava lines selected, succumbed to ACMV in the coastal areas of Kenya. However, we now know that there are different ACMV strains and, more important, distinct species in what was originally considered as African cassava mosaic (Hong *et al.*, 1993), which may explain the differential reaction exhibited by the improved cassava genotypes in different locations of eastern Africa. On the other hand, the average proportion of *M. glaziovii* genes in the hybrid progenies had been reduced to 1/16 in the backcrossing process, and resistance to ACMV appeared to be multigenic and recessive. Thus, the expression of *M. glaziovii* genes was probably low, and the resistance achieved was the result of the accumulation of genes from moderately resistant *M. esculenta* parents used for backcrossing. Later on, some of the most resistant backcross hybrids were intercrossed to concentrate genes for resistance, which may have become dispersed among the various breeding lines, as well as to increase the levels of homozygosity of recessive resistant genes.

Breeding for resistance to begomoviruses infecting common bean

Four main begomoviruses transmitted by *B. tabaci* have been reported to attack common bean (*Phaseolus vulgaris* L.) in the Americas (Morales, 2000). *Bean golden mosaic virus* (BGMV) in Brazil, Argentina and Bolivia; *Bean golden yellow mosaic virus* (BGYMV), in southern Mexico, Central America and the Caribbean region; *Bean dwarf mosaic virus* (BDMV) in northwestern Argentina, and *Bean calico mosaic virus* (BCaMV) in northwestern Mexico.

The first attempts at breeding for BGMV resistance were made in Brazil. Pompeu and Krantz (1977) initially selected symptomless individual plants within field populations of three BGMV-susceptible common bean cultivars. These selections were shown to be susceptible to the virus in subsequent evaluations (Costa, 1987). Another plant improvement strategy pursued in Brazil, was the use of radiation to create genotypic mutants possessing resistance to BGMV (Tulman-Neto, 1979). One of these common bean mutants, TMD-1, showed resistance to the virus but its yielding ability was poor, and its use in conventional breeding programs did not produce any outstanding progenies.

A parallel breeding project was initiated in Guatemala, in 1974, to solve the bean golden yellow mosaic problem in Central America, Mexico and the Caribbean. Approximately, 7,000 germplasm bank accessions of common bean were evaluated under natural disease pressure in southeastern Guatemala, but no immune genotypes were observed. Among these accessions, a group of black-seeded genotypes, namely Turrialba 1, Porrillo 70, Porrillo Sintetico, ICA-Pijao and ICA-Tui, was selected for their better performance under natural BGYMV pressure. Due to their tolerance (acceptable yielding ability despite expressing noticeable foliar yellowing), Porrillo Sintetico, Turrialba 1 and ICA-Pijao were ultimately selected as potential parental materials (Yoshii *et al.*, 1979). The best lines derived from different crosses between the selected parental genotypes, were soon released in Guatemala as cultivars ICTA-Quetzal, ICTA-Jutiapan and ICTA-Tamazulapa (Yoshii *et al.*, 1980). In the absence of pesticide applications, ICTA-Jutiapán, ICA-Pijao and the local black-seeded cultivar 'Rabia de Gato', sustained yield losses of 38%, 53% and 86%, respectively.

However, yield losses for the DOR lines fluctuated proportionally with viruliferous *B. tabaci* populations, and no progress was made in breeding for BGYMV resistance in the red-seeded common bean cultivars preferred in Costa Rica, Nicaragua, Honduras and El Salvador (Morales, 2000). Fortunately, a serendipitous event took place in the mid 1980s. A common bean line improved for its upright architecture (A 429), showed a high level of BGYMV resistance under field conditions in Guatemala. A progeny test revealed the existence of a common bean

genotype belonging to the Mexican Durango race, which does not react with the characteristic yellowing when inoculated with BGYMV, despite being systemically affected by plant malformation and flower abortion by the virus. This Mexican common bean genotype, called 'Garrapato', combined with the Mesoamerican black-seeded source of BGYMV resistance, Porrillo Sintetico (also a parent of A 429), was associated with the high level of BGYMV resistance found in A 429 (Morales and Niessen, 1988). A 429 soon became one of the most widely used sources of begomovirus resistance in common bean breeding programs in Latin America (Singh *et al.*, 2000). Subsequent research identified the gene *bgm-1*, responsible for conditioning mosaic resistance in Garrapato (Morales and Niessen, 1988; Blair and Beaver, 1993a).

Later on, a red kidney line, DOR 303, was also selected for its apparent high level of BGYMV resistance under field conditions. An evaluation of the parental materials selected to produce this line, revealed the presence of a red kidney genotype of Andean (race Nueva Granada) origin (Singh *et al.*, 1991), besides the traditional black-seeded source of resistance, Porrillo Sintetico. In subsequent tests, this genotype was shown to behave as a tolerant genotype, producing flowers and pods despite its striking mosaic/yellowing foliar symptoms (Morales and Niessen, 1988). Porrillo Sintetico has considerable vigor, which often allows plants to escape infection, particularly in cases where the virus is inoculated after the first 2-3 weeks after emergence of the plants (Morales and Niessen, 1988). Thus, a second favorable interracial recombination of Mesoamerican and Andean genes had occurred, to produce a red-seeded common bean genotype possessing high levels of BGYMV resistance. The BGYMV-resistance gene in DOR 303 was later identified as *bgm-2* (Velez *et al.*, 1998).

A selection of diverse grain types was evaluated in different countries of Latin America, from Argentina to northern Mexico, in order to identify different mechanisms of virus resistance and sources of resistance to the different begomoviruses present in these regions. At least 10 new sources of begomovirus resistance were identified in the *P. vulgaris* accessions evaluated (grain colors different than black), as well as different mechanisms of resistance. Among the most interesting bean begomovirus-resistance mechanisms identified, were: disease escape, low mosaic expression, virus localization, low flower abortion, and low pod malformation (Morales and Niessen, 1988). The mean squares of the general combining ability of these traits was highly significant ($P < 0.01$) and larger than values for specific combining abilities, which indicates that selection for the various traits evaluated was possible in true breeding lines, due to the existence of significant additive genetic variance (Morales and Singh, 1991). In subsequent studies, 83 recombinant inbred lines (RIL) selected from a population generated from the cross between a Mexican (Pinto UI 114) and a Mesoamerican (ICA-Pijao) common bean genotypes, were evaluated for their reaction to BGYMV. Of these lines, 11 did not show symptoms, 24 lines had mean disease incidence of 8%, 28 lines had a disease incidence of 26.6% and developed intermediate mosaic symptoms, and 20 lines were more susceptible than either of the parents. Thus, values for the 83 RILs transgressed the values of the two parents at both extremes (resistance and susceptibility) for both disease incidence and mosaic expression. These results show that the BGYMV-resistance genes present in the two parental materials (common bean races) are different and complementary to each other, and, consequently, that gene pyramiding could be attempted. Subsequent interracial crosses have generated highly resistant lines adopted as bean cultivars in different countries of Central America. Begomovirus multiplication in these improved genotypes is highly restricted according to molecular tests performed on these line (Morales, 2000), and this type of resistance has also been associated to quantitative traits (QTLs), which reduce symptom expression (Miklas *et al.*, 1996). On the contrary, common bean genotypes derived from intraracial populations, usually behave as moderately resistant under severe whitefly/virus pressure (Singh *et al.*, 2000).

Breeding for resistance to tomato begomoviruses

A major boom of non-traditional export crops has taken place in most of the agricultural regions affected by whitefly-transmitted geminiviruses around the world. One of the predominant plant species found in these new cropping systems, is tomato (*Lycopersicon esculentum* Mill.). This is a highly profitable but costly crop, due to the amount of chemical inputs usually required to protect tomato from the various pests and diseases that attack this crop. The well documented pesticide abuse associated with tomato production has greatly contributed to the development of pesticide-resistant *B. tabaci* populations. This whitefly species is capable of vectoring over 20 different begomoviruses that attack tomato in tropical and subtropical regions of the world (Polston and Anderson, 1997; Zeidan *et al.*, 1999).

Although most of the begomoviruses that attack tomato are found in the New World, very little breeding work has been done to minimize the severe damage that these viruses cause to tomato plantings in this region. Moreover, despite its tropical American origin, most of the tomato breeding work has been conducted in temperate countries. Hence, tomato growers in tropical and subtropical America have relied almost exclusively on pesticides to control *B. tabaci* and the geminiviruses this vector transmits.

The situation in the Old World is similar, due to the severe damage caused by a group of geminiviruses transmitted by *B. tabaci* in tomato plantings throughout the Mediterranean region, the Middle East, north Africa, central Africa and southeast Asia (Czosnek and Laterrot, 1997). These related although distinct geminivirus species, are collectively referred to as *Tomato yellow leaf curl virus* (TYLCV). This geminivirus was accidentally introduced in the last decade into the Americas in the early 1990s (Nakhla *et al.*, 1994), where it has already caused millions of dollars worth of industrial and fresh tomato production losses.

Early efforts to identify sources of resistance to TYLCV within *L. esculentum*, only revealed the existence of some moderately resistant or tolerant genotypes (Cohen and Harpaz, 1964; Nitzany, 1975; Abu-Gharbieh *et al.*, 1978). However, Cohen and Nitzany (1966) observed that some wild relatives of tomato, namely *L. pimpinellifolium* and *L. peruvianum*, possessed a higher level of resistance to TYLCV, although they were not immune. Crosses between *L. esculentum* and *L. pimpinellifolium* (currant tomato/accession LA 121) and genetic analyses of F₁₋₃ and backcross generations, indicated the existence of incomplete dominance of resistance over susceptibility, suggesting a monogenic control of resistance (Pilowski and Cohen, 1974). A dominant gene (*Tylc*) was later proposed for the resistance gene in *L. pimpinellifolium* (Kasrawi, 1989). The progenies derived from this cross showed only moderate symptoms, but their yield was markedly reduced. Nevertheless, among the *Lycopersicon* species, *L. pimpinellifolium* is one of the most compatible for crossing with *L. esculentum* (Picó *et al.*, 1996).

In contrast, the inheritance of tolerance to TYLCV in *L. peruvianum* (PI 126935) is controlled by five recessive factors, according to Pilowski and Cohen (1990). This breeding program initiated in 1977, resulted in the release of the commercial hybrid TY-20, in 1988. This hybrid delays symptom expression and viral DNA accumulation in infected plants, resulting in acceptable yields (Pilowski and Cohen, 1990). Other tolerant/resistant TY-lines generated by this breeding program are: TY172, TY197, TY198, and TY536 (Lapidot *et al.*, 1997; Friedmann *et al.*, 1998).

In 1991, other wild tomato species: *L. chilense* and *L. hirsutum*, besides *L. peruvianum* and *L. pimpinellifolium*, were examined for the presence of viral DNA and symptom expression following their inoculation with whiteflies removed from TYLCV-infected tomato plants. Approximately 85 days after inoculation, all of the above species had infected plants with detectable levels of viral DNA, but *L. chilense* and *L. hirsutum* were the most resistant species, with the majority of the inoculated plants remaining symptomless, and only few containing viral DNA (Zakay *et al.*, 1991). The TYLCV resistance gene in *L. chilense* was identified as *Ty-I* (Michelson *et al.*, 1994). The resistance to this virus in *L. hirsutum*, on the other hand, seems to be dominant and controlled by more than one gene (Mazyad *et al.*, 1982). *L. hirsutum* has been

crossed with *L. esculentum*, yielding tolerant and immune lines. One of the immune lines was crossed with *L. esculentum*, to produce the hybrid FAVI-9 or Line F1-901. The immune reaction was associated with 2-3 additive genes (Vidavski and Czosnek, 1998). Another promising species evaluated for TYLCV resistance, *L. cheesmanii*, possesses recessive resistance to TYLCV. Breeding projects in the Mediterranean region have also used *L. cheesmani*, *L. peruvianum* and *L. pimpinellifolium* to control TYLCV in this region (Laterrot, 1990, 1992, Laterrot and Moretti, 1996). Some of the TYLCV-resistant lines obtained from this project are: Pimpertylc-J-13 and Chepertylc-92.

Interspecific hybrids obtained from crosses between *L. pimpinellifolium*, *L. peruvianum*, and *L. hirsutum*, show transgressive segregation for their reaction to TYLCV, suggesting the existence of different, complementary genes (Kasrawi and Mansur, 1994).

In 1991, Muniyapa and coworkers reported that lines of *L. hirsutum* and *L. peruvianum* were resistant to another tomato geminivirus: *Tomato leaf curl virus* (ToLCV). The resistance mechanism in these wild species was subsequently associated with the presence of exudates from trichome glands on the leaf surface, in which whiteflies became entrapped (Channarayappa and Shivashankar, 1992). This is one of the few cases where genetic resistance to a viral disease has been achieved indirectly by incorporating genetic traits against *B. tabaci*. Nevertheless, there is sufficient evidence showing that different cultivars of plant species such as common bean and tomato, interact differentially with *B. tabaci*. For instance, In Sinaloa, northwestern Mexico, the common bean cultivar 'Azufrado Peruano-87', had 16% more nymphs/leaf than the geminivirus (BCaMV) resistant common bean cultivar 'Azufrado Higuera' (Lopez, 1996). Similar data has been obtained for tomato, although the preference shown by *B. tabaci* for some tomato cultivars, was not related to virus resistance/susceptibility traits in the tomato cultivars evaluated (Avilés, 1996).

Discussion

Many agricultural scientists have implied that there is no resistance to most whitefly-transmitted geminiviruses in cultivated species of cassava, common bean or tomato, probably confusing 'resistance' with 'immunity'. It is important to understand that 'resistance' is a relative term, which can span a range of disease reactions from a low to a high level. 'Tolerance' is another term which is often misused in reference to the degree of symptom expression (*e.g.* mild mosaic or plant malformation symptoms). The term 'tolerance' should be used in relation to the ability of a plant genotype to yield an acceptable or expected quantity or quality of product (*e.g.* seed, fruits, flowers, etc.) despite being affected by a biotic or abiotic factor. Both genetic resistance and tolerance can be found in most cultivated species attacked by whitefly-transmitted geminiviruses.

The strategy followed to incorporate high levels of begomovirus resistance in common bean, strictly through the intraspecific recombination and pyramiding of different resistance traits found in diverse gene pools of *Phaseolus vulgaris*, confirms the feasibility of this approach. Moreover, the underlying mechanism of resistance (*i.e.* restricted virus multiplication) is similar in the three crops discussed here (Zakay *et al.*, 1991; Lapidot *et al.*, 1997; Fargette *et al.*, 1996; Morales, 2000).

However, the important conclusion is that there is both direct and circumstantial evidence indicating the existence of adequate genetic variability in the primary and secondary gene pools of most cultivated species. This genetic variability can be exploited within and between cultivated species and their relatives. Interspecific hybridization in cassava, common bean and tomato, can be practiced not only in search of resistance to begomoviruses, but to other pathogens and pests as well (Nichols, 1947; Debouck, 1991). In the case of tomato, it is evident that the cultivars improved for TYLCV resistance, are also exhibiting acceptable levels of resistance to distinct New World begomoviruses attacking tomato in the Americas and Asia (Muniyapa *et al.*, 1991; Piven *et al.*, 1995). Another neglected but possible begomovirus control method is the

incorporation of genetic resistance to the whitefly vector, *Bemisia tabaci*, as it has been suggested by limited investigations in cassava (Fargette *et al.*, 1996), common bean (Blair and Beaver, 1993b), and tomato (Channarayappa *et al.*, 1992).

Undoubtedly, the utilization of all the genetic diversity present in the primary and secondary gene pools of these plant species, will require both conventional and advanced crop improvement techniques, such as molecular marker assisted selection (Chavarriga *et al.*, 1999; Singh *et al.*, 2000; Zamir *et al.*, 1994).

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