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Viral diseases of cowpea and their control by resistance-conferring genes

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Abstract

Cowpea crops are susceptible to more than 20 viral diseases. Some of the most destructive viral pathogens are transmitted from one plant generation to the next through the seed, and thus are generally disseminated to most cowpea-producing regions of the world. Seedborne cowpea viruses, after establishment in plantings as seedborne inoculum, are typically spread within fields by insect vectors (either aphid or beetle species). The most effective control of cowpea viral diseases, universally, has been the development of improved genotypes with resistance to viral infection. The historic productiveness of cowpea breeder-geneticists, describing genes/ resistance to almost every major virus, now provides opportunities to develop multiple resistance to diseases, insect pests, *Striga* spp., and drought. Although cowpea may lag behind other major food plants in the availability of superior new cultivars with multiple-disease/pest resistance, an extremely valuable base of germplasm exists for much greater development and utilization in the future.

Introduction

Far-reaching developments have occurred in plant virology since the First World Cowpea Research Conference in November 1984 (Thottappilly and Rossel 1985). Since that time, researchers have sequenced and mapped the genomes of many viruses, determining the genetic structure/function of important viral pathogens, and have established a meaningful taxonomic system for virus families and genera. In this system, molecular-genetic information developed for *one member* of a viral family provides essential clues to the nature of lesser-known members of that family. Indeed, strategic molecular biology research has facilitated logarithmic increases in our knowledge of the properties of viruses since 1984.

There have also been many surprises along the way, particularly in the genetic engineering of viral genes into crop species, producing transgenic plants. Whereas viral gene transfers were initially carried out somewhat simplistically, they are now viewed with increased understanding and maturity. We are now learning that very small changes in viral gene sequences (Lindbo et al. 1993b) and the points of insertion into host chromosomes

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have significant consequences for viral-gene expression and in the trans-gene antiviral function. Accordingly, successes from "viral coat protein-mediated resistance" have ranged from mediocre to superb, usually with little understanding of the disparity (Lindbo et al. 1993a). Mixed results from this approach have prompted scientists (1) to transform plants with mutant (defective) viral coat-protein genes and/or investigate the mechanisms yielding successes; (2) to explore/implement viral genes other than the coat protein gene (native or mutant); or (3) to transform plants with nonviral genes/sequences that logically might interfere with one or more steps of viral genome translation, transcription, or genome/virion movement. These and other newer lines of research promise improved understanding of viral structure and function, as well as clearer insights into mechanisms of natural resistance to viral infection.

General knowledge pertaining to *Vigna unguiculata* genetics and germplasm has also expanded. Numerous sources of disease/pest resistance have been reported during the past decade. Implementation of these resources has resulted in new, improved cowpea cultivars with multiple disease resistance, pioneered by Lima et al. (1979), Mali et al. (1981), Patel et al. (1982), and Price and Cishahayo (1986). A new cowpea cultivar, recently developed for Senegal, possesses combined resistance to two cowpea aphid-borne mosaic virus pathotypes, bacterial blight, storage weevil, *Striga*, and drought (Ndiaye et al. 1993; Cisse et al. 1995). Cultivars with multiple virus resistance were also developed in Nigeria (Singh et al. 1987) and Brazil (Santos et al. 1987, 1990). Other reported virus-resistant cowpea genotypes include 'Seoweondongbu', Korea (Kim et al. 1986), and 'Bettersnap', USA (Fery and Dukes 1995). Neither breeding approaches nor germplasm resources are any longer factors limiting such advancements. The future holds further promise in this regard, with new insights expected from biotechnology. But in 1996, conventional resistance breeding remains the most practicable measure for controlling cowpea viral diseases.

Cowpea viruses

This review complements and/or updates previous reviews by Allen (1983), Mali and Thottappilly (1986), Shoyinka et al. (1988), and Thottappilly and Rossel (1985, 1992). Of the viruses occurring in cowpea crops around the world (Table 1; the viral terms and acronyms used are consistent with those of Hull et al. [1991], wherever possible), the seedborne viruses considered most insidious and damaging include: blackeye cowpea mosaic potyvirus (BlCMV), cowpea aphid-borne mosaic potyvirus (CABMV), cucumber mosaic cucumovirus (CMV), cowpea mosaic (CPMV) and cowpea severe mosaic (CPSMV) comoviruses, southern bean mosaic sobemovirus (SBMV), and cowpea mottle carmovirus (CPMoV). Some combinations (e.g., BlCMV + CMV; BlCMV + CPSMV; and CMV + CPSMV + SBMV) can cause drastically worsened disease symptoms and crop losses (Kuhn 1990; Anderson et al. 1994). Other detected cowpea mixed-infections include CMV + CPSMV and CPSMV + SBMV (R.O. Hampton et al. 1992, unpublished results). These viruses have been disseminated to, and established in, most cowpea-producing areas of the world as infected commercial seedlots, variety trials, or germplasm.

Important nonseedborne viruses include cowpea golden mosaic geminivirus, which causes one of the most destructive cowpea diseases in the world, and cowpea chlorotic mottle bromovirus, which causes disease losses either alone or in combination with other viruses (reviewed by Kuhn 1990).

Table 1. Some properties of viruses causing principal diseases of cowpea†.

Virus	Transmission			Particle	Coat protein Mol Wt x 10^4	Genome		Key references
	Mech.	Vector	Seed (%)			Parts	Nucleotides x 10^3	
Blackeye cowpea mosaic potyvirus (BlCMV)	Yes	Aphid	3–55	Filament	3.4	One	9.5	Purcifull and Gonsalves 1985; Taiwo et al. 1982a
Cowpea aphid-borne mosaic potyvirus (CABMV)	Yes	Aphid	0–40	Filament	3.4	One	9.5	Bock and Conti 1974; Taiwo et al. 1982a
Cowpea chlorotic mottle bromovirus (CCMV)	Yes	Beetle	0	Icosahedron	2.0	Three	8.2	Kuhn 1964; Allison et al. 1989
Cowpea golden mosaic geminivirus (CGMV)	No	Whitefly	0	Duplex	31	ssDNA§ Two	5.0	Thottappilly and Rossel 1992; Bashir and Bashir 1988
Cowpea mosaic comovirus (CPMV)	Yes	Beetle	0–5	Icosahedron	2.3, 3.7	Two	9.4	Agrawal 1964; van Kammen and de Jager 1978; Lomonossoff and Shanks 1983
Cowpea mottle carmovirus (CPMoV)	Yes	Beetle	0–10	Icosahedron	4.4	One	4.4	Bozarth and Shoyinka1979; Thouvenel et al.1990
Cowpea severe mosaic comovirus (CPSMV)	Yes	Beetle	3–10	Icosahedron	2.3, 3.7	Two	9.4	de Jager 1979; Chen and Bruening 1992a,b
Cucumber mosaic cucumovirus (CMV)	Yes	Aphid	4–26	Icosahedron	2.4	Three	8.3	Francki et al. 1979; Rezaian et al. 1984
Southern bean mosaic sobemovirus (SBMV)	Yes	Beetle	4–4	Icosahedron	3.1	One	4.2	Shepherd and Fulton 1962; Wu et al. 1987

† Other viruses reported to infect cowpea include alfalfa mosaic virus (ilar-like), cowpea mild mottle carlavirus, peanut mottle potyvirus (PMV), peanut stunt cucumovirus, sunnhemp mosaic tobamovirus, tobacco ringspot nepovirus (TRSV), and tobacco streak ilarvirus. Tomato spotted wilt tospovirus is thrip-transmissible and, since 1984, has assumed almost worldwide distribution in both temperate and semitropical regions, and can potentially cause damage to food legume crops, including cowpea.

§ All other viruses listed have genomes comprising ssRNA.

Blackeye cowpea mosaic potyvirus (BlCMV). BlCMV occurs more or less worldwide and is transmitted nonpersistently by several aphid species, including *Aphis craccivora* (Purcifull and Gonsalves 1985). Particularly in combination with other viruses (Pio-Ribeiro et al. 1980; Collins et al. 1985; Kuhn 1990), it can inflict severe losses on cowpea crops. Distinct BlCMV strains exist (Bashir 1992; Bashir and Hampton 1992), but strain variants may be less decisive in BlCMV disease epidemics than is notable for CABMV.

The work of Taiwo et al. (1982a) partitioned potyviruses seedborne in cowpea into two distinct kinds. With differing results and interpretations, Dijkstra et al. (1987) distinguished two potyviruses, but recommended that both be called BlCMV. The relationship between BlCMV and CABMV was discussed at a potyvirus taxonomy workshop (Barnett 1992), with clear indications that BlCMV and CABMV were distinct potyviruses and that separate nomenclature be maintained.

Bashir (1992) biologically and serologically characterized some 140 cowpea potyvirus isolates seedborne in cowpea seedlots from various countries (Bashir 1992; Bashir and Hampton 1992, 1993), in comparison with type isolates BlCMV-Georgia (BlCMV-GA) and CABMV-Morocco (CABMV-Mor). This work clearly partitioned the two viruses, determined that CABMV-Kenya (Bock 1973; Dijkstra et al. 1987) was instead BlCMV, and verified much of the work of Taiwo et al. (1982a). Key isolates characterized by Bashir (1992) were also instrumental in definitive monoclonal antibody distinctions of the two viruses by Huguenot et al. (1993, 1994). The Florida isolate of BlCMV was considered by McKern et al. (1992) to be a strain of bean common mosaic virus.

Genetic resistance to BlCMV and CABMV in cowpea is distinct (Bashir 1992) and independently inherited (Taiwo et al. 1982b). The nucleotide sequence of the BlCMV genome has not yet been published.

Cowpea aphid-borne mosaic potyvirus (CABMV). First described by Lovisolo and Conti (1966), CABMV is endemic in Africa. It is now widely disseminated in the world through infected cowpea seedlots, and causes severe crop damage either alone (Ndiaye et al. 1993) or in combination with other viruses. Like BlCMV, it is transmitted nonpersistently by several aphid species, including *Aphis craccivora*. The virus comprises numerous distinct strains (Fischer and Lockhart 1976; Bashir 1992; Ndiaye et al. 1993), with separate cowpea genes conferring resistance to each (Bashir 1992; Ndiaye et al. 1993).

CABMV and BlCMV produce indistinguishable symptoms on cowpea genotypes susceptible to them, typically consisting of veinal chlorosis, interveinal chlorosis, or dark-green vein banding (Bock and Conti 1974; Purcifull and Gonsalves 1985). The Morocco isolate (Fischer and Lockart 1976), CABMV-Mor, has been widely used as a quasi type isolate, but it is extremely virulent and poorly representative of 80 separate seedborne CABMV isolates that were evaluated at Corvallis, Oregon, USA (Bashir 1992; Ndiaye et al. 1993).

The potyvirus designated PTY+ by Ndiaye et al. (1993) was later determined to be a distinct, virulent strain of CABMV (R.O. Hampton, unpublished results). This CABMV pathotype clearly differs from CABMV-Mor, and sources of cowpea genetic resistance were identified (Ndiaye et al. 1993). A sizeable but unknown number of pathogenic variants exist in nature, some of them responding to separate cowpea genes/alleles for resistance. The nucleotide sequences of the CABMV genome have not yet been published.

Cowpea chlorotic mottle bromovirus (CCMV). CCMV was not accepted as a distinct virus until the definitive work of Kuhn (1964a) and Bancroft et al. (1968). Kuhn (1964b) also developed differential hosts for distinguishing CCMV, SBMV, CMV, and BYMV (actually BlCMV). In susceptible cowpea cultivars, CCMV can cause severe crop damage, alone or in mixed infections. Uniquely severe disease is caused by CCMV in mixed infections with SBMV (Kuhn and Dawson 1973). Once assumed to be confined to North and South America, CCMV was more recently isolated from *Desmodium heterocarpon* and *Clitoria ternatea* in Nigeria (Thottappilly et al. 1993). The occurrence of CCMV in natural hosts outside of the Americas suggests that it may persist in native legumes of other cowpea producing regions of the world. The genomic RNA of CCMV was sequenced and compared to that of other bromoviruses by Allison et al. (1988, 1989).

Cowpea golden mosaic geminivirus (CGMV). CGMV, as a singular causal agent, has not yet been isolated, purified, and identified. Thottappilly (1992) and Thottappilly and Rossel (1992) reported the occurrence of CGMV-like diseases in at least seven countries of Africa. The agent may be similar to pathogens partially characterized as "cowpea yellow fleck" from India (Sharma and Varma 1976), as "cowpea bright yellow mosaic" from Pakistan (Ahmed 1978), and as "mungbean yellow mosaic virus" from Pakistan (Bashir and Bashir 1988). Cowpea samples from Nigeria with CGM symptoms produced weak reactions with monoclonal antibodies specific to whitefly-transmitted geminiviruses (Thottappilly and Rossel 1992), suggesting that CGM is a geminivirus.

The CGM disease, as currently recognized in Pakistan (M. Bashir, personal communication), has caused increasingly severe damage to cowpea plantings in that country since 1988. No sources of genetic resistance to CGM were identifiable in recent evaluations in Pakistan of *V. unguiculata* germplasm. According to Anno-Nyako (1980), many cowpea cultivars tested at IITA in Nigeria were resistant to CGMV, and attempts to retrieve the virus from inoculated plants were unsuccessful. The identification of resistance sources, however, is expected to depend on controlled inoculations of plant genotypes with defined virus isolates capable of reproducing typical golden mosaic symptoms in standardized cowpea genotypes. If the disease is caused by a complex of distinct viruses, cowpea resistance must then be independently tested for each component pathogen of the complex.

Cowpea mosaic comovirus (cowpea yellow mosaic) (CPMV). CPMV, originally described as cowpea yellow mosaic virus (Chant 1959), reportedly occurred in the Americas before 1964, since an isolate from Suriname was identified as CPMV (Agrawal 1964). It has since been reported from several African countries (Thottappilly and Rossel 1985). Though its identity and existence in older cowpea landraces/varieties in both West Africa (Chant 1959; Patel and Kuwite 1982) and India (Hampton et al. 1992) are generally accepted, CPMV was not detected recently in either Senegal (Ndiaye et al. 1993) or Pakistan (Bashir and Hampton 1993). Some CPMV isolates appear to be marginally seed transmissible (Gilmer et al. 1974 suspected 1–5%), but this could not be confirmed in other cowpea genotypes (Thottappilly and Rossel 1988a).

Owing to its common occurrence, epidemic potential, and pathogenicity, CPMV is one of the most important cowpea viruses in Africa. Most locally grown varieties (large, white, rough-seeded) appear highly sensitive and susceptible. The virus also occurs in pigeonpea

(Bock 1971), soybean (Thottappilly and Rossel 1992), and bambara groundnut (Thottappilly and Rossel 1997). The best and most practical method of control may be the use of resistant cultivars (Robertson 1965; Williams 1975, 1977; Singh et al. 1987).

The RNA genome of CPMV, type member of the comovirus group, has been sequenced and defined in a classic series of investigations by van Kammen and colleagues, as reviewed by Matthews (1991).

Cowpea mottle carmovirus (CPMoV). Originally isolated in Nigeria (Shoyinka et al. 1978; Bozarth and Shoyinka 1979), CPMoV readily cross-reacts with antiserum to bean mild mosaic carmovirus (Gillaspie et al. 1994) and is probably abiotically transmitted in soil for > 2 months after infected plants are removed (R.O. Hampton, unpublished results). An Ivory Coast isolate of CPMoV was characterized by Thouvenel et al. (1990), who also considered it a significant disease, since it caused a 65% reduction in yield there. In addition, the virus has been reported from the Republic of Benin (Thottappilly and Rossel 1988b), Togo (Gumedzoe et al. 1990), and Pakistan (Bashir and Hampton 1993). It has also been detected in seedlots from Botswana and Senegal (R.O. Hampton, unpublished).

The capsid protein gene of CPMoV was sequenced by Kim and Bozarth (1992), and the sequencing of the whole CPMoV genome was recently completed by You (1995) and You et al. (1995). The genomes of four other carmoviruses have been sequenced, as reviewed by Hacker et al. (1992) and Skotnicki et al. (1993), further promoting the possibility of developing viral-gene-mediated resistance to CPMoV in cowpea.

Cowpea severe mosaic comovirus (CPSMV). CPSMV was characterized by Shepherd (1964) as "Arkansas cowpea mosaic virus". Its host range was very extensive, compared to the narrow host range of cowpea mosaic, and isolates of this type, transmitted by Chrysomelid beetles, were separated from CPMV by Agrawal (1964) and named CPSMV (de Jager 1979). CPSMV-induced symptoms in some cowpea genotypes are similar to those of CPMV. Contrary to the term "severe", these symptoms may or may not be more severe than those of CPMV. Certainly, the CPSMV isolate of de Jager (1979) induced very severe symptoms on well-known cowpea cultivars. Crop losses inflicted by CPSMV can be severe (50–80%, Debrot and De Rojas 1967; Valverde et al. 1982); however, losses depend largely on specific interactions between CPSMV strains and cowpea genotypes. CPSMV is seed transmissible and also efficiently transmitted by several beetle species, including *Cerotoma ruficornis* and *C. trifurcata* (Walters and Barnett 1964; Debrot and De Rojas 1967), which can retain the infective virus for more than 7 days.

The virus may have assumed worldwide distribution via movement of infected seedlots and appears to be more common than CPMV in the cowpea cultivars of southern Europe and the Americas and less common in old world cowpea-growing regions (Bashir and Hampton 1993; Ndiaye et al. 1993).

CPSMV comprises at least nine serotypes (J.H. Hill, isolate donations to The American Type Culture Collection; Di et al. 1993) and an unknown number of pathogenic variants. No sources of CPSMV resistance are known among US cowpea cultivars, as reviewed by Kuhn (1990); however, four IITA TVu lines (612, 1460–2, 1948, and 2480) were highly resistant to all tested CPSMV variants (Fulton and Allen 1982). The nucleotide sequence of CPSMV genomic RNA was published by Chen and Bruening (1992a,b).

Cucumber mosaic cucumovirus (CMV). CMV is one of the most broadly adapted of all plant viruses (Francki et al. 1979), and is also commonly seedborne in cowpea seedlots. Despite its common and widespread occurrence, through both seed- and aphid-transmission, CMV is considered a mild cowpea pathogen, except in infection-sensitive genotypes and/or when combined with BlCMV (Pio-Ribeiro et al. 1980; Anderson et al. 1994) or with other viruses (Collins et al. 1984; Kuhn 1990). The epidemiology of CMV in *Vigna* spp. has been documented by Lakshman et al. (1985).

Although the term "cowpea strain" (CMV-CP) is used in the literature, it was not included among recognized CMV strains by Gibbs and Harrison (1970) or Francki et al. (1979). The extent to which cowpea isolates differ from other legume-infecting forms is not well defined. Legume-infecting isolates CMV-Pg and CMV-Le (Hampton and Francki 1992) are distinguishable from CMV-CP biologically but have antigenic determinants in common with CMV-CP. Antisera/IgG to either CMV-Pg or CMV-Le react with, but also differentiate, CMV-CP (R.O. Hampton, unpublished results).

The tripartite RNA genome of CMV was sequenced and defined by Symons and colleagues (Gould and Symons 1982; Rezaian et al. 1984, 1985) and cloned, transcribed, and tested for infectivity by Hayes and Buck (1990). Several pathological traits have been ascribed to genomic RNA-1, 2, and 3 (Rao and Francki 1982; Edwards et al. 1983; Lakshman et al. 1985). Because of our present knowledge of the CMV genome, CMV-mediated transgenic resistance appears plausible as a CMV control measure, particularly if no natural resistance to CMV were available in *V. unguiculata.*

Southern bean mosaic sobemovirus (SBMV). The cowpea strain of SBMV (SBMV-C) was discovered as a seedborne isolate in a seedlot of 'Wilt Resistant Early Ramshorn' cowpea (Shepherd and Fulton 1962). It often occurs in mixtures with other beetle-transmissible viruses, including CCMV (Kuhn 1990) and CPSMV (R.O. Hampton, unpublished results). Like other seedborne cowpea viruses, SBMV-C is becoming distributed to most cowpea-producing regions of the world. Reports of SBMV from India and many locations in Africa since 1974 were reviewed by Thottappilly and Rossel (1992).

SBMV-C-induced symptoms are exceptionally variable among cowpea genotypes (Kuhn 1990), ranging from symptomless infection to severe mottle/mosaic with leaf deformity. Kuhn (1990) reviewed several forms of SBMV resistance in cowpea, including infection localization and inhibition of virus synthesis. Another resistance mechanism in 'Bountiful' bean, associated with the formation of abnormal SBMV-C virions, apparently prevented systemic spread of the virus to noninoculated trifoliolate leaves (Fuentes and Hamilton 1993). However, resistance to intercellular SBMV-C movement in inoculated primary bean leaves was overcome by co-infection with sunnhemp mosaic tobamovirus (Fuentes and Hamilton 1991). The molecular structure of the SBMV virion was determined by Rossman and colleagues (e.g., Silva and Rossman 1987) and has perhaps received more attention than any other plant virus, relative to virion fine-structure. Antigenic determinants of the SBMV capsid were defined with monoclonal antibodies by Tremaine et al. (1985). The SBMV RNA genome was sequenced and defined by Wu et al. (1987).

Other viruses. Viruses isolated from cowpea but of undetermined or minor significance include alfalfa mosaic virus (Jaspers and Bos 1980), cowpea mild mottle carlavirus (Brunt and Kenton 1973; Anno-Nyako 1980), peanut mottle potyvirus (Demski et al. 1983), peanut stunt cucumovirus (Abdelbagi and Ahmed 1990), sunnhemp mosaic tobamovirus (Chant and Gbaja 1987), and tobacco ringspot nepovirus (de Zeeuw and Ballard 1959; Mali and Ganacharya 1984). Beet curly top geminivirus (Matthews 1991) has been observed and identified in cowpea, in California (R.O. Hampton and A. Hall 1990, unpublished). Tomato spotted wilt tospovirus is infectious to cowpea, has caused increasing damage to susceptible crops in temperate and semitropical regions (Brunt et al. 1996), and could become a threat to cowpea crops.

Genetics of cowpea viruses

A significant and expanding base of information on nucleotide sequences and junctions of viral genes is now available for genetic engineering. This database provides unprecedented opportunities to increase our understanding of viral gene structure and function, facilitating effective choices and applications of viral-sequences and mutant viral-sequences as transgenes. In the past, sequences from the viral coat-protein gene were used almost exclusively to produce transgenic plants. However, all viral genes are now being viewed as potential and manipulable inhibitors of virus synthesis and/or movement. This subject was reviewed expertly by Buck (1991) and, notwithstanding some confusion in resistance terminology, by Fraser (1990a,b).

Genes conferring resistance to cowpea viruses

Until genetic engineering is further refined, breeding for virus resistance remains the most practical approach for controlling viral diseases of cowpea (e.g., Rossel and Thottappilly 1988). Current concepts relating to virus-resistance breeding were thoroughly reviewed recently from three perspectives (Kyle and Provvidenti 1993; Provvidenti 1993; Scully and Federer 1993). Resistance- or tolerance-conferring cowpea genes or genetic resources were reported between 1955 and 1992 for ten viruses pathogenic to cowpea crops (Table 2). Of the resistance-conferring cowpea genes that have been reported (whether or not named), ten are recessive and eight are dominant.

It is noteworthy that resistance to BlCMV was determined to be recessive in three cases (Reeder et al. 1972; Walker and Chambliss 1981; Taiwo et al. 1982b) and dominant in two (Strniste 1987; Ouattara and Chambliss 1991). The recessive-gene sources were, respectively, PI 297562, TVu 2480, and cultivar Worthmore. The dominant-gene sources were cultivars Pinkeye Purple Hull BVR and White Acre BVR. These two genes were compared by Strniste (1987) and shown, by demonstration of independent inheritance, to be distinct. Two independent genes governing resistance were also demonstrated for a Tanzanian isolate of CABMV, one recessive and one "partially dominant" (Patel et al. 1982). Partial dominance in this case was probably attributable to lower-than-normal virulence of the virus isolate, which may have been modified (partially attenuated) after successive local-lesion passage through *Chenopodium amaranticolor*. This virus isolate was later reported to be BlCMV, rather than CABMV (Bashir 1992; P.N. Patel, personal communication, 1992). Likewise, both dominant and recessive genes govern cowpea resistance to CPMV (Patel 1982a) and SBMV (Brantley and Kuhn 1970; Hobbs et al. 1987).

Until the singularity or diversity of CGMV is clearly defined, cowpea resistance to the CGM disease cannot be expected.

Table 2. Genes or genetic sources reported for resistance to viral diseases of cowpea.

Virus†	Gene(s)	Source§	Reference
BYMV (BlCMV)¶	*By*‡	PI 297562	Reeder et al. 1972
BlCMV	*bcm*	TVu 2480	Taiwo et al.1982b
	blc	Worthmore	Walker and Chambliss 1981
	–	PEPH-BVR, WA-BVR, Corona	Kuhn et al. 1984
	1-r††	Mississippi Silver	Melton et al. 1987
	1-D§§	PEPH-BVR	Strniste 1987
	1-D§§	WA-BVR	Ouattara and Chambliss 1991
	–	TVu 2657 and 3433, Big Boy, Brown Sugar Crowder, Corona, Texas Cream #8, Serido	Bashir 1992
CABMV (BlCMV)¶¶	1-r††	TVu 612, TVu 1948	
	1-Dp§§	Tvu 408-P, TVu 410 (many others also)	Patel et al. 1982
CABMV	–	(sources unknown)‡‡	Ladipo and Allen 1979
	–	TVu 401, TVu 1582	Bashir 1992
CMV	*cc*‡	PI 255811	Rogers et al. 1973
CMV	1-D§§	'Black', Dixie Queen	Sinclair and Walker 1955
	1-D§§	Selection from 'Black'	de Zeeuw and Crum 1963
	1-D§§	'Fetriat' (tolerance)	Khalf-Allah et al. 1973
CPMV	–	Arlington, Blackeye, others	Robertson 1965
	mvs	TVu 227, TVu 345, TVu 612, and TVu 2331	Patel 1982a
	–	Arlington	Eastwell et al. 1983
	1-D§§	Arlington	Ponz et al. 1988a
CPMoV	–	TVu 3901 (tolerant)	Allen et al. 1982
CPSMV	–	TVu 612, TVu 1460-2, TVu 1948, TVu 2480, Macaido	Fulton and Allen 1982
PMV	–	Corona, Early Pinkeye, Iron, Worthmore	Bijaisoradat et al. 1988
SBMV	–	Iron, Clay, others	Kuhn and Brantley 1963
	Sbm‡	Clay	Brantley and Kuhn 1970
SBMV	–	PI 147562, PI 186465	Kuhn et al. 1986
SBMV	*sbc-l, sbc-2*	Mississippi Silver	Melton et al. 1987
	sbm-2	(PI 186465)	Hobbs et al. 1987
TRSV	*Tr*‡	California Blackeye #5	de Zeeuw and Ballard 1959
	–	(sources unknown)‡‡	Mali et al. 1981
	1-D§§	Arlington	Ponz et al. 1988a

† See Table 1 for virus names.
§ BVR = BlCMV-resistant; PEPH = Pink Eye Purple Hull; WA = White Acre.
¶ Reported as BYMV; actually BlCMV (O.L. Chambliss, personal communication).
‡ Term assigned by Fery; previously reviewed (Fery 1985).
†† Resistance apparently conferred by a single recessive gene; no term assigned.
§§ Resistance apparently conferred by a single dominant gene; no term assigned.1-Dp = partial dominance reported.
¶¶ Reported as CABMV; actually BlCMV (P.N. Patel, personal communication).
‡‡ Published resistance sources not accessible to authors.

After the evaluation of cowpea genotypes for possible resistance to CMV by Brantley et al. (1965), most cowpea researchers concluded that resistance to CMV in *Vigna unguiculata* was rare or nonexistent, despite reports to the contrary by Sinclair and Walker (1955), de Zeeuw and Crum (1963), and Khalf-Allah et al. (1973). Unfortunately, identities of the 476 cowpea genotypes tested by Brantley et al. (1965) were not published for future reference. In Kuhn's review (1990), however, it was concluded that most cowpea cultivars were tolerant to CMV, and that CMV resistance in *V. unguiculata* was unlikely. More recently, cowpea cultivar 'Pampo' has been reported as highly resistant to CMV (Da Ponte and Alves 1994). Such conflicting reports of cowpea resistance to CMV could suggest intraline heterogeneity, differences among CMV strains, and/or different inoculation methods used for resistance screening. Further investigation is still needed to determine whether resistance to CMV exists in established cowpea cultivars or in international collections of *V. unguiculata* germplasm.

Resistance to CPMV is commonplace among *V. unguiculata* cultivars. Wilson (1977) and Patel (1982b) each found a broad assortment of CPMV-tolerant and resistant cowpea genotypes, and many new cowpea lines and cultivars are CPMV-resistant (e.g., Ndiaye et al. 1993). Epistatic/hypostatic relationships among dominant genes conferring resistance to CPMV (Patel 1982a) were reviewed by Fery (1985).

Numerous pathogenic variants of some viruses, particularly CABMV and CPSMV, constrain breeding programs which attempt to incorporate genes conferring resistance either to all known pathotypes or to locally predominant pathotypes. The effects of coexisting pathogenic variants were exemplified in the work of Ndiaye et al. (1993), in which new cowpea lines bred specifically for CABMV resistance were severely attacked by a distinct indigenous strain of CABMV, and that too in the same region. Resistance breeding to the corporate indigenous strains of CPSMV has been successful in boosting cowpea production in South America (Rios and Neves 1982; Mendoza et al. 1990; and Santos et al. 1987, 1990). Fortunately, Fulton and Allen (1982) used several available CPSMV strains in screening cowpea for CPSMV resistance. By this process, three TVu lines (612, 1460–2, 1948) were determined to be uniformly resistant/immune to all tested isolates of the virus (i.e., these genotypes possessed genes/alleles conferring resistance to all available pathogenic variants). As indicated previously (see CPSMV), the pathogenic variation among CPSMV isolates is extensive and, to date, remains only meagerly defined. The genes conferring resistance to CABMV had not previously been named (Fery and Singh 1997), and additional work is required to define genes conferring tolerance to CPMoV and resistance to CPSMV.

Bruening and associates effectively integrated the knowledge of plant genetics (Eastwell et al. 1983; Sanderson et al. 1985; Bruening et al. 1987) with viral molecular genetics (Kiefer et al. 1984) and molecular mechanisms of virus resistance (Ponz et al. 1988a,b). In this classical effort, an inhibitor of CPMV polyprotein processing was found to be coinherited with immunity to CPMV in cowpea cultivar Arlington. The data showed that immunity to CPMV was conferred by a specific *V. unguiculata* proteinase inhibitor in this cultivar. Without cleavage by a CPMV-encoded proteinase, the polyprotein product CPMV RNA translation was rendered functionless and virus synthesis was thus precluded.

The large range of genotypes identified as resistance sources for BlCMV, CPMV, and SBMV particularly, allows breeders to more readily develop new virus-resistant cultivars of different maturities, classes of plant and seed type, and market requirements. Similarly, multiple sources of virus resistance provide a broader genetic background, probably providing more stable resistance for new cultivars than could be expected from single resistance sources. The total genetic resources available to cowpea breeders compare favorably with those of other world crops, and warrant greater utilization by breeding programs of both developing and developed countries (Fery 1985).

Beyond the purposes of this chapter, a condensation and synthesis of worldwide virus-resistance sources would be beneficial to cowpea breeding programs. Otherwise, valuable bits of information tend to lie hidden for decades.

An updated, corrected list of genes described for *Vigna unguiculata* is included in another chapter of this book (Fery and Singh 1997). It should help fill the information gap, and thus pave the way for effective utilization by crop improvement scientists of the available sources of resistance.

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