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Viruses Infecting Peanuts *(Arachis hypogaea)*: Taxonomy, Identification, and Disease Management

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Conversion Table

U.S. Abbr.	Unit	Approximate Metric Equivalent
	Length	
mi	mile	1.609 kilometers
yd	yard	0.9144 meters
ft or '	foot	30.48 centimeters
in or "	inch	2.54 centimeters
	Area	
sq mi or mi^2	square mile	2.59 square kilometers
acre	acre	0.405 hectares *or* 4047 square meters
sq ft or ft^2	square foot	0.093 square meters
	Volume/Capacity	
gal	gallon	3.785 liters
qt	quart	0.946 liters
pt	pint	0.473 liters
fl oz	fluid ounce	29.573 milliliters or 28.416 cubic centimeters
bu	bushel	35.238 liters
cu ft or ft^3	cubic foot	0.028 cubic meters
	Mass/Weight	
ton	ton	0.907 metric ton
lb	pound	0.453 kilogram
oz	ounce	28.349 grams

Metric Abbr.	Unit	Approximate U.S. Equivalent
	Length	
km	kilometer	0.62 mile
m	meter	39.37 inches *or* 1.09 yards
cm	centimeter	0.39 inch
mm	millimeter	0.04 inch
	Area	
ha	hectare	2.47 acres
	Volume/Capacity	
liter	liter	61.02 cubic inches *or* 1.057 quarts
ml	milliliter	0.06 cubic inch *or* 0.034 fluid ounce
cc	cubic centimeter	0.061 cubic inch *or* 0.035 fluid ounce
	Mass/Weight	
MT	metric ton	1.1 tons
kg	kilogram	2.205 pounds
g	gram	0.035 ounce
mg	milligram	3.5×10^{-5} ounce

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Contents

Abbreviations of Naturally Occurring Peanut Viruses

APCV	African peanut clump virus
BYMV	Bean yellow mosaic virus
CCMV	Cowpea chlorotic mottle virus
CMMV	Cowpea mild mottle virus
CMV	Cucumber mosaic virus
GCSV	Groundnut chlorotic spotting virus
GCV	Groundnut crinkle virus
GEV	Groundnut eyespot virus
GRAV	Groundnut rosette assistor virus
GRV	Groundnut rosette virus
GVCV	Groundnut veinal chlorosis virus
GYMV	Groundnut yellow mosaic virus
GYMtV	Groundnut yellow mottle virus
IPCV	Indian peanut clump virus
PCLSV	Peanut chlorotic leaf streak virus
PFWV	Passionfruit woodiness virus
PGMV	Peanut green mosaic virus
PMV	Peanut mottle virus
PStV	Peanut stripe virus
PSV	Peanut stunt virus
PYSV	Peanut yellow spot virus
SYBV	Sunflower yellow blotch virus
TSV	Tobacco streak virus
TSWV	Tomato spotted wilt virus

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Introduction

The peanut (*Arachis hypogaea* L.), also called groundnut, is grown extensively in tropical and subtropical parts of the world as an oil seed crop or a grain legume (Porter et al. 1982, 1984). The crop is subject to the attack of numerous pests and pathogens. Diseases caused by viruses are known to be constraints to production in all peanut-growing areas of the world (Feakin 1973; Porter et al. 1984; Kolte 1985; Reddy 1988). Peanut viruses also are important because they infect other major legumes such as beans, clover, peas, and soybeans as well as some nonlegume crops. Some viruses, first isolated naturally from other plant species, also infect peanuts both under natural and laboratory conditions. Various crops, particularly the legumes, frequently are grown in peanut production areas, and insect vectors can move viruses from one crop to another (Reddy et al. 1983a; Kuhn and Demski 1984; Tolin 1984). Thus, epidemiological considerations and methods of control for a single virus may be complex.

In this paper we review the viruses which have been reported to infect peanuts either naturally or under experimental conditions. Analysis of the literature on peanut viruses has been complicated by the fact that a certain number of these viruses have not been characterized sufficiently and sometimes the same causal agent probably is described by different names. The viruses are broadly divided into taxonomically characterized (tables 1 and 2) and uncharacterized (table 3) categories. The characterized viruses are further divided into taxonomic groups based mainly on particle morphology, physicochemical and genomic properties, and transmission characteristics. Abbreviations for viruses which are used throughout the text are given at the beginning of the bulletin.

This paper is intended to be useful for researchers of virus diseases of peanuts and other legumes; for those involved in breeding, quarantine, and extension; and for those who teach virus diseases of legumes.

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Table 1. Taxonomically Characterized Viruses Naturally Infecting Peanuts

Virus group	Virus	Geographical distribution	Reference
Bromovirus	Cowpea chlorotic mottle	USA	Kuhn and Demski 1987
Carlavirus	Cowpea mild mottle	Ghana, India, Indonesia Ivory Coast, Nigeria	Iizuka et al. 1984
	Groundnut crinkle	Ivory Coast	Duberr and Dollet 1981
Caulimovirus	Peanut chlorotic leaf streak	India	Iizuka and Reddy 1986
Cucumovirus	Cucumber mosaic	China	Xu and Barnett 1984
	Peanut stunt	USA	Miller and Troutman 1966; Fisher and Lockhart 1978
Furovirus	African peanut clump[a]	Burkino Faso, Ivory Coast, Senegal	Thouvenel et al. 1976
	Indian peanut clump	India	Reddy et al. 1983b; Nolt et al. 1988
Geminivirus	Groundnut yellow mosaic	India	Sudhakar Rao et al. 1980
Ilarvirus	Tobacco streak	Brazil	Costa and Carvalho 1961; Sdoodee and Teakle 1987
Luteovirus	Groundnut rosette assistor[a]	Africa	Hull and Adams 1968; Reddy et al. 1985a; Rajeshwari and Murant 1988
	Sunflower yellow blotch	Malawi	Theuri et al. 1987
Plant rhabdovirus	Groundnut veinal chlorosis	India	Naidu et al. 1989
Potexvirus	Groundnut chlorotic spotting	Ivory Coast	Fauquet et al. 1985; Dollet et al. 1987
Potyvirus	Bean yellow mosaic	USA	Bays and Demski 1986
	Groundnut eyespot	Ivory Coast	Dubern and Dollet 1980
	Passion fruit woodiness	Australia	Boswell and Gibbs 1983
	Peanut green mosaic	India	Sreenivasulu et al. 1981
	Peanut mottle[a]	Worldwide	Kuhn 1965; Behncken 1980; Bock 1973; Paguio and Kuhn 1973; Rajeshwari et al. 1983; Reddy et al. 1978
	Peanut stripe[a]	China, India, Indonesia, Japan, Philippines, Thailand, USA	Demski et al. 1984, 1988; Xu et al. 1983
Tomato spotted wilt virus	Peanut yellow spot	India, Thailand	Wongkaew 1986
	Tomato spotted wilt[a]	Worldwide	Ghanekar et al. 1979; Francki and Hatta 1981; Reddy et al. 1983a
Tymovirus	Groundnut yellow mottle	Nigeria	Lana 1980

a. Viruses believed to be of the greatest economic importance.

Table 2. Taxonomically Characterized Viruses Known Experimentally to Infect Peanuts

Virus group	Virus	Reference
Alfalfa mosaic virus	Alfalfa mosaic	Hull 1969; Staikov et al. 1979; Boswell and Gibbs 1983
Carlavirus	Potato virus M	Staikov et al. 1979
	Potato virus S	Staikov et al. 1979
Cauliomovirus	Cauliflower mosaic	Hull and Davies 1983
Cucumovirus	Black locust true mosaic	Boswell and Gibbs 1983
Dianthovirus	Red clover necrotic mosaic	Hollings 1977; Boswell and Gibbs 1983
Geminivirus	Abutilon mosaic	Costa 1955
Luteovirus	Bean leaf roll	Boswell and Gibbs 1983
	Beet western yellows	Boswell and Gibbs 1983
	Legume yellows	Boswell and Gibbs 1983
	Michigan alfalfa	Boswell and Gibbs 1983
	Milk vetch dwarf	Boswell and Gibbs 1983
	Pea leaf roll	Boswell and Gibbs 1983
	Soybean dwarf	Boswell and Gibbs 1983
	Subterranean clover stunt	Grylls and Butler 1959
Necrovirus	Tobacco necrosis	Boswell and Gibbs 1983
Nepovirus	Strawberry latent ringspot	Schmelzer 1969; Murant 1974
	Tobacco ringspot	Chohan and Troxel 1963
	Tomato black ring	Kaiser et al. 1978
	Tomato ringspot	McLean 1962
Plant rhabdovirus	Lucerne enation	Boswell and Gibbs 1983
Potexvirus	Clover yellow mosaic	Boswell and Gibbs 1983
	Potato acuba mosaic	Staikov et al. 1979
	Potato virus X	Staikov et al. 1979
	White clover mosaic	Quantz 1968
Potyvirus	Bean common mosaic	Iizuka and Yunoki 1975
	Clover yellow vein	Boswell and Gibbs 1983
	Cowpea aphid-borne mosaic	Iwaki et al. 1975
	Pea mosaic	Edwardson 1974
	Potato virus A	Staikov et al. 1979
	Potato virus Y	Staikov et al. 1979
	Soybean mosaic	Iizuka and Yunoki 1975
	Turnip mosaic	Inouye and Inouye 1964
Sobemovirus	Southern bean mosaic	Boswell and Gibbs 1983
Tobamovirus	Tobacco mosaic	Niazi et al. 1973
Tobravirus	Pea early browning	Bos and Van der Want 1961
	Tobacco rattle	Staikov et al. 1981
Tymovirus	Clitoria yellow vein	Bock and Guthrie 1977; Lana 1980
	Okra mosaic	Givord and Koenig 1974

Taxonomically Characterized Viruses

Sixty-two taxonomically characterized viruses infecting peanuts have been reported. Twenty-three viruses occur naturally in field-grown peanuts (table 1), 15 of which were isolated and identified initially from peanuts and eight from other plant species before being found in

peanuts. The names "peanut mild mottle virus" and "peanut chlorotic ring mottle virus" have been used in the literature several times. They are now believed to be symptom variants of peanut stripe virus (PStV) (Demski et al. 1988; McKern et al. 1989). The other 39 viruses have been shown to infect peanuts by mechanical or vector inoculation under experimental conditions (table 2). They have the potential to occur naturally in field-grown peanuts and therefore may be of economic importance.

Table 3. Peanut Virus and Virus-like Diseases Caused by Taxonomically Uncharacterized Viruses, Other Pathogens, or Nonpathogenic Conditions

Disease	Geographical distribution	Virus particle	Transmission[a] Sap	Seed	Vector	Reference
Bunchytop	India		-	+	-	Sharma 1966
Chlorosis	India		+	+	Aphids	Sharma 1966
Chlorotic ringspot	U.S.A.		+			Wagih and Melouk 1987
Chlorotic spot	India		+			Haragopal and Nayudu 1971
Dwarf	U.S.S.R.					Kushnirenko et al. 1980
Flecking	Ivory Coast		-		-	Dubern 1979
Golden	Ivory Coast		-		-	Dubern 1979
Latent	Africa		+			Bock et al. 1968
Marginal chlorosis	New Guinea			+		Van Velson 1961
Mild mosaic	U.S.A.		+			Cooper 1950
Severe mosaic	U.S.A.		+		Aphids	Cooper 1950
Mosaic	China	Flexuous rods (725nm)	+		Aphids	Shih and Hsu 1979
	Java		-		Leafhopper	Bergeman 1956
	India		-			Nariani and Dhingra 1963
	Indonesia					Iwaki 1979
	Ivory Coast		+		Aphids	Dubern 1979
	West Malaysia		+		Aphids	Poh et al. 1972; Geh and Ting 1973
Ring mosaic	India		+			Narayanasamy et al. 1975
Ring mottle	India		-	+	-	Sharma 1966
Ringspot	U.S.A.		-	+		Kuhn et al. 1964
	South Africa		+			Klesser 1966
Rugose leaf curl	Australia		-		Leafhopper	Grylls and Day 1966
	Ivory Coast		-			Monsarrat 1977
Rosette[b]	Philippines	Spherical (28-30nm)	+	+	Not *Aphis craccivora*	Benigno and Favali-Hedayat 1977
Streak	Ivory Coast		+		Aphids	Dubern 1979; Fauquet and Thouvenel 1987
Top paralysis	U.S.A.	Flexuous rods	+			Wagih et al. 1988
Vein banding	South Africa		+		Aphids	Klesser 1967

a. - = negative, + = positive. If blank, no test.
b. This disease appears to be distinct from the ground rosette disease that occurs in Africa.

These 62 viruses can be placed in 20 of about 35 official taxonomic virus groups (International Committee on Taxonomy of Viruses) (Brown 1989; Matthews 1982) (tables 1 and 2). Twenty-eight of the viruses have elongated particles, 30 have isometric particles (including alfalfa mosaic virus), two have geminate particles, and two have bacilliform particles.

One very important peanut virus, groundnut rosette virus (GRV), is not grouped taxonomically. No virus-like particles have been found in plants infected with GRV; however, the infective entity was tentatively identified as a single-stranded ribonucleic acid (ssRNA), typical in size of many viruses (Reddy et al. 1985b). All 62 viruses have ssRNA with the exception of the two in the geminivirus group (ss deoxyribonucleic acid [DNA]) and the two in the caulimovirus group (double-stranded [ds] DNA). Forty-two of the viruses have a monopartite genomic organization, 11 are bipartite, six are tripartite, and two have four RNA segments in each particle. Four of the viruses with envelopes (lipid membranes) are included in either the plant rhabdovirus or the tomato spotted wilt virus groups.

Elongated Particles

Viruses with elongated particles infecting peanuts occur in six taxonomic virus groups (tables 1, 2, and 4). Fourteen of the 28 elongated viruses belong to a single virus group, the potyviruses, and all are in potyvirus sub-group 1 (aphid-transmitted) (Murant and Harrison 1970). The elongated monopartite virus groups include the potyviruses which have elongated flexuous rod particles (680-900 × 11 nm) and are transmitted by aphids in a nonpersistent manner (some potyviruses which do not infect peanuts are transmitted by fungi, mites, and whiteflies); the carlaviruses which have flexuous rod particles (620-700 × 13 nm) and are transmitted by whiteflies or aphids in a nonpersistent manner; the potexviruses which have flexuous rod particles (470-580 × 13 nm) are transmitted through vegetative plant parts and by contact and aphids; and a tobamovirus which has rigid rod particles (300 × 18 nm) is transmitted by contact and in the soil. Two bipartite virus groups include the tobraviruses, which have rigid rod particles (180-215 and 46-114 × 22 nm) and are transmitted by nematodes, and the furoviruses, which have straight rods (250-300 and 100-195 × 22 nm) and are transmitted by fungi.

Spherical Particles

Spherical viruses infecting peanuts are placed in 12 taxonomic virus groups (tables 1, 2, and 4). Particles (80-90 nm in diameter) of the tomato spotted wilt virus group are enveloped by a membrane. Members of the caulimovirus group have 50-60 nm diameter particles. Viruses in nine groups have particles ranging in diameter from 25-35 nm and can be distinguished by size from the tomato spotted wilt virus and caulimovirus groups but not from each other. However, genomic organization, mode of transmission, and serology can be used to identify them.

The spherical viruses are divided broadly into three categories depending on the number of pieces of genomic RNA (tables 1, 2, and 4). The monopartite virus groups include the luteoviruses which are aphid-transmitted in a persistent manner and not mechanically transmitted; a necrovirus which is soilborne and fungus-transmitted; and the tymoviruses and a sobemovirus which are beetle-transmitted but differ in host range, serology, and other properties. The five viruses with a bipartite genome reported to infect peanuts belong to the dianthovirus and nepovirus groups. Strawberry latent ringspot virus, tomato black ring virus, tomato ringspot virus, and tobacco ringspot virus are transmitted by nematodes and through seed of at least one host, whereas red clover necrotic mosaic virus (RCNMV) is transmitted by a fungus (MacFarlane

Table 4. Certain Physicochemical Properties of Taxonomically Characterized Viruses Naturally Infecting Peanuts[a]

Virus	Particle morphology[b] (size in nm)	Virus polypeptides No.	Virus polypeptides Mol. wt. (Kd)	Virus nucleic acid Type[c]	Virus nucleic acid No. of genomic segments	Virus nucleic acid Mol. wt. (Kd)
African peanut clump	ER (245, 160-190 x 24)	1	23	ssRNA	2	2.1, 1.7
Bean yellow mosaic	ER	1	-[d]	ssRNA	-	-
Cowpea chlorotic mottle	S (26)	1	19.6	ssRNA	3[e]	1.1, 1.0, 0.73
Cucumber mosaic	S (29)	1	26	ssRNA	3[e]	1.27, 1.13, 0.82
Cowpea mild mottle	ER (610-650)	1	33	ssRNA	1	2.6
Groundnut chlorotic spotting	ER (456 x 13)	-	-	ssRNA	-	-
Groundnut crinkle	ER (650 x 15)	1	34	ssRNA	-	-
Groundnut eyespot	ER (755 x 15)	1	32.5	ssRNA	-	-
Groundnut rosette assistor	S (28)	1	24	ssRNA	1	2.09
Groundnut veinal chlorosis	B (E)	-	-	ssRNA	-	-
Groundnut yellow mosaic	G	-	-	ssDNA	-	-
Groundnut yellow mottle	S (29)	-	-	ssRNA	-	-
Indian peanut clump	ER (249, 184 x 24)	1	24	ssRNA	2	1.9, 1.7
Peanut chlorotic leaf streak	S (45-50)	-	-	dsDNA	-	-
Passionfruit woodiness	ER (745)	1	33	ssRNA	-	-
Peanut green mosaic	ER (750)	1	34.5	ssRNA	1	3.25
Peanut mottle	ER (740-750)	1	35	ssRNA	1	3.0
Peanut stripe	ER (752 x 13)	1	33.5	ssRNA	1	3.1
Peanut stunt	S (30)	1	26	ssRNA	3[e]	1.19, 1.02, 0.75
Peanut yellow spot	S (E) (70-90)	-	-	ssRNA	-	-
Sunflower yellow blotch	S (26)	-	-	ssRNA	-	-
Tobacco streak	S (26-35)	1	28.5	ssRNA	3[e]	1.35, 1.10, 0.85
Tomato spotted wilt	S (E) (85-95)	4	78.0, 58.0, 52.0, 27.0	ssRNA	4	2.7, 1.9, 1.7, 1.3

a. References for the respective viruses are the same as given in table 1.
b. ER = elongated rods, S = spherical, G = geminate, B = bacilliform or bullet-shaped, (E) enveloped.
c. ss = single stranded, ds = double stranded.
d. - = data not available.
e. = Virions contain a fourth small subgenomic ssRNA of about 0.35 Kd.

1982). Three groups with tripartite genomes whose members infect peanuts are the bromovirus, cucumovirus, and ilarvirus groups. The bromoviruses are beetle-transmitted, whereas the cucumoviruses are aphid-transmitted in a nonpersistent manner. The ilarviruses are recently reported to be transmitted by thrips (Sdoodee and Teakle 1987).

The twelfth spherical taxonomic group is the alfalfa mosaic virus group which has small bacilliform and spherical particles ranging in size from 18-58 x 18 nm. Also, it is a fourth group with a tripartite genome. Although alfalfa mosaic virus has mostly small bacilliform particles, it probably should be considered closely related to the bromovirus, cucumovirus, and ilarvirus groups (van Vloten-Doting et al. 1981; Francki 1985). Viruses in all four groups have genomes consisting of three, positive-sense ssRNA molecules and at least one subgenomic ssRNA which is encapsidated in particles with one type of protein. Alfalfa mosaic virus is transmitted by aphids.

Geminate Particles

Two viruses with geminate particles are known to infect peanuts (tables 1, 2, and 4). These geminiviruses, abutilon mosaic virus and groundnut yellow mosaic virus (GYMV), have 18-20 nm isometric particles in pairs and an ssDNA as their genome. They are transmitted either by whiteflies or leafhoppers and sometimes by mechanical inoculation. They are found predominantly in tropical climates where they cause rugose, yellow vein, or yellow mosaic diseases in plants.

Bacilliform Particles

Viruses infecting peanuts having bacilliform particles are in the plant rhabdovirus group. Particles (160-380 x 50-90 nm) are enclosed within an envelope and are transmitted by a variety of plant-sucking arthropods (aphids and leafhoppers).

Partially Characterized Virus

Groundnut rosette is a destructive peanut disease (up to 100% yield loss) that is widespread in Africa (Zimmerman 1907; Feakin 1973; Yayock et al. 1976; Gibbons 1977; Reddy 1984a; Dollet et al. 1987). Rosetted plants contain a complex of two viruses and a viral satellite RNA. The single-stranded RNA of GRV can be transmitted mechanically (Reddy et al. 1985b), but no particles have been associated with its infection in any host (Casper et al. 1983; Reddy et al. 1985a, 1985b). Groundnut rosette assistor virus (GRAV), a luteovirus, causes no overt symptoms but is essential for aphid transmission (in a persistent manner) of GRV (Storey and Bottomley 1925; Hull and Adams 1968). (It is theorized that GRV-RNA is encapsidated in GRAV coat protein when mixed infections occur [Casper et al. 1983; Murant and Kumar 1989].) A GRV satellite RNA is required for both rosette symptom production (Murant et al. 1988) and aphid transmission (Murant 1990). Variants of the satellite RNA are responsible for two forms of the disease: chlorotic rosette and green rosette (Murant and Kumar 1989). The most severe disease occurs when peanut plants are infected with all three causal agents (Murant et al. 1988; Ansa et al. 1990).

To the best of our knowledge, groundnut rosette is unique to the African continent. A rosette disease of peanuts has been reported in the Philippines (Benigno and Favali-Hedayat 1977). However, the following properties indicate that the African (AGR) and Philippine (PGR) diseases are probably caused by different viruses: (i) PGR virus is seed-borne—AGR virus is not; (ii) PGR virus is readily transmitted by sap—AGR virus requires special attention (Olorunju et al. 1990); (iii) AGR virus is transmitted by *Aphis craccivora* Koch.—PGR virus is not; and (iv) PGR virus is stable in crude extracts from infected plants—AGR virus is not.

Taxonomically Uncharacterized Viruses

Numerous diseases of peanuts with virus-like symptoms have been reported and, frequently, viruses have been isolated from the plants (table 3). In some cases, distinct virus-like particles have been observed and some viral taxonomic properties have been determined, but critical comparisons with known viruses with similar types of particles and properties have not been made. Therefore, it is not clear whether they are unique viruses, strains, or even identical to known viruses. In other cases, taxonomic criteria are deficient and only an informed guess as to taxonomy can be made.

The name peanut or groundnut mosaic virus has been associated with diseases in seven countries (table 3) (Demski et al. 1988). Based on the limited information available, it is probable that the viruses in these reports are related to peanut mottle virus (PMV), PStV, or tomato spotted wilt virus (TSWV).

Several peanut diseases have been described as bud blight, bud necrosis, chlorosis, ringspot, ring mosaic, ring mottle, stunting, bushy, bunchy top, or a combination of these symptoms

(Nariani and Dhingra 1963; Kuhn et al. 1964; Chohan 1974; Narayanasamy et al. 1975; Ghanekar and Nene 1976) (table 3). After considerable research experience with TSWV, Ghanekar et al. (1979) and Reddy (1988) suggested that some of these diseases and others, including chlorotic ringspot and chlorotic spot, could be caused by TSWV.

Groundnut streak (table 3) reported in the Ivory Coast (Fauquet and Thouvenel 1980) is caused by a potyvirus, but critical comparisons with potyviruses PMV and groundnut eyespot virus (GEV), also reported in Africa, are necessary to confirm whether it is a distinct virus.

Top paralysis (Wagih et al. 1988) and chlorotic ring spot (Wagih and Melouk 1987) diseases observed on wild peanuts in a greenhouse at Oklahoma State University, USA, could be isolates or strains of PMV, since the virus from these diseased plants produced necrotic local lesions on Topcrop beans (*Phaseolus vulgaris* L.) and *Chenopodium amaranticolor* L., and reacted weakly with PMV antiserum (table 3).

The etiology of flecking, golden, latent, and vein banding peanut diseases reported in African countries (Bock et al. 1968; Dubern 1979) and the dwarf disease observed in the USSR (Kushnirenko et al. 1980) is obscure because of too little information (table 3).

Black gram leaf crinkle virus (Narayanasamy and Jaganathan 1974) is known experimentally to infect peanuts and certain other legumes (cluster beans, cowpeas, green grams, and pigeon peas). However, the virus has not been characterized.

Virus-Like Diseases

The symptoms of the marginal chlorosis disease (Van Velsen 1961) resemble mineral deficiency. The viral nature of this disease requires confirmation. In a 1984 survey conducted in Papua, New Guinea, from where this disease was reported, no peanut plants with marginal chlorosis were observed (D. V. R. Reddy, personal observation).

Groundnut witches' broom, caused by a mycoplasma-like organism (MLO), is reported from India, Indonesia, Japan, People's Republic of China, Taiwan, and Thailand (Reddy 1984b). The symptoms of the disease are the proliferation of auxiliary shoots leading to bushy plants, small pale yellow leaves, apogeotropically growing pegs, and inhibition of development of pods. The causal agent is transmitted by grafting and by the leafhopper, *Orosius argentatus* Evans (Bergman 1956). Recently, Hobbs et al. (1987b) partially purified the MLO and produced an antiserum; this work should facilitate the determination of serological relationships among the MLOs of groundnut witches' broom reported from Asian countries.

Rugose leaf curl reported in Australia is known to be caused by a rickettsia-like organism (Reddy 1984a). Rugose leaf curl reported in the Ivory Coast is probably caused by groundnut crinkle virus, which was reported later in the same country (Dubern and Dollet 1981). The primary symptoms (leaf curl and crinkle) of the two diseases are apparently very similar (table 3).

Identification of Peanut Viruses

Taxonomy of viruses is primarily dependent on the intrinsic or physicochemical properties of virus particles. These properties include particle morphology and size, number and size of viral polypeptides, number and size of viral nucleic acids, and the genomic biochemical

mechanism related to virus replication. Much of this information is available for the viruses we have labeled taxonomically characterized (tables 1 and 2). Guidelines and experimental procedures for the characterization and identification of plant viruses in general are available in the literature (Hamilton et al. 1981; Bock 1982; Bos 1983; Boswell and Gibbs 1983; Hill 1984; Hull 1985; Brown 1989). Unfortunately, the scientific expertise and the laboratory facilities are minimal or lacking in many peanut production areas of the world. Therefore, it is frequently necessary to rely on a combination of biological, chemical, and serological properties (described in the following sections) for the detection and identification of peanut viruses.

Symptomatology and Host Range

Symptoms in peanut plants, especially a single plant, should not be used alone for the identification of a virus. The type and intensity of symptoms can be influenced by variable nutritional and environmental conditions. Strains of a virus frequently cause different symptoms in the same host, and specific strains of different viruses may cause similar symptoms in the same host, at least at some stages of disease development. For example, symptoms in peanuts caused by the chlorosis and necrosis strains of PMV are similar to those caused by TSWV (Sreenivasulu et al. 1988), and TSWV and African peanut clump virus (APCV) mimic GRV in producing rosette-type symptoms. Furthermore, cowpea chlorotic mottle virus (CCMV) causes no symptoms in peanuts (Kuhn and Demski 1987), and GRAV causes no symptoms in peanuts or in any other of the 11 hosts it is known to infect (Adams 1967; Hull and Adams 1968; Rajeshwari and Murant 1988).

Regardless of their problems, symptoms are extremely important in detecting the presence of virus infections and identification of strains of specific viruses. When coupled with host range studies, symptoms can serve as an indication of virus identity, particularly when diagnostic hosts have been ascertained. For viruses naturally infecting peanuts, symptoms have been observed on many plant species (table 5 and table 8). When preliminary identification studies of unknown peanut viruses are being conducted, it should be useful to select a host range of eight to 12 plant species that frequently become infected with known viruses (table 5 and table 8).

Table 5. Plant Species Commonly Infected by Viruses Which Naturally Infect Peanuts

No. of viruses that can infect	Plant species
10 or more	*Arachis hypogaea, Chenopodium amaranticolor, Chenopodium quinoa, Phaseolus vulgaris, Vigna unguiculata*
5 to 9	*Canavalia ensiformis, Gomphrena globosa, Glycine max, Lycopersicon esculentum, Nicotiana clevelandii, Pisum sativum*
3 or 4	*Cucumis sativum, Cyamopsis tetragonoloba, Datura stramonium, Nicotiana benthamiana, Nicotiana glutinosa, Nicotiana rustica, Nicotiana tabacum, Petunia hybrida*
1 or 2	Note table 8

Table 6. Certain Biological Properties of Taxonomically Characterized Viruses Naturally Infecting Peanuts[a]

Virus	Symptoms on peanut[b]	Virus stability in sap[c]			Transmission		
		TIP	LIV	DEP	Sap	Seed	Vector[d]
African peanut clump	MT, CRS, ST	64	28 d	4	+	+	F: *Polymyxa graminis*
Bean yellow mosaic	CRS	50-55	4 d	4	+		Ap: *Aphis craccivora*
Cowpea chlorotic mottle	SI	67-76	1-44 d	3-5	+	-	CL: *Ceratoma ruficornis* *C. trifurcata* *Diabrotica balteata* *D. undecimpuncta*
Cucumber mosaic	CS, LR, M, MT, VCH, ST	55-60	5-7 d	2-3	+	+	Ap: *Macrosiphum euphorbiae*
Cowpea mild mottle	LNL, LCRS, LP, CHL, LR, VN, ST	65-80	8 d	3-4	+	-	Al: *Bemisia tabaci*
Groundnut chlorotic spotting	CS	55-60	5-14 h	5-6	+		Ap: *A. craccivora* *A. spiraecola*
Groundnut crinkle	CR	65-70	6h-5 d	3-4	+	-	Al: *B. tabaci*
Groundnut eyespot	CS, CRS, LP	42-44	3 h	3-4	+	-	Ap: *A. citricola* *A. craccivora*
Groundnut rosette assistor	SI				-		Ap: *A. craccivora* *Myzus persicae*
Groundnut veinal chlorosis	VCH, DF, LR, ST				-	-	
Groundnut yellow mosaic	YM, DF				-		Al: *B. tabaci*
Groundnut yellow mottle	YMT	70	23 d	7	+		CL: *Podagrica* and *Syagrus* sp
Indian peanut clump	M, MT, CRS, ST	60-65	20 d	3-4	+	+	F: *P. graminis*
Peanut chlorotic leaf streak	CS, CST, DF, ST	80-85	3 d	4	+		
Passionfruit woodiness	Not described	55-60	3-4 d	4-5	+		Ap: *A. gossypii* *M. persicae*
Peanut green mosaic	MT, M, VCL RS, ST	55-60	3-4 d	3-4	+	-	Ap: *A gossypii* *M. persicae*
Peanut mottle	Strain dependent MT, LR, IVD, M, SN, LP, ST	55-65	0-7 d	4-6	+	+	Ap: *A. craccivora* *A. gossypii* *M. persicae* *Rhopalosiphum padi*
Peanut stripe	Strain dependent M, STP, ST, B	55-60	3 d	3-4	+	+	Ap: *A. craccivora* *M. persicae*
Peanut stunt	Strain dependent CHL, MT, GVB, LR, DF, ST	50-55	1 d	3-4	+	+	Ap: *A. craccivora* *A. spiraecola* *M. persicae*
Peanut yellow spot	LCRS, YS	45			+		Th: *Scirtothrips dorsalis*
Sunflower yellow blotch	SK, SN				-	-	Ap: *A. gossypii*
Tobacco streak	Not described	55-60	1-9 h	3-5	+	-	Th: *Frankliniella* sp *Thrips tabaci*
Tomato spotted wilt	CRS, SN, DF, LP, PR, DF, RO, MT, M, ST	45	5h	3	+	-	Th: *F. fusca* *F. schultzei* *S. dorsalis* *T. tabaci*

a. References for the respective viruses are the same as given in table 1.

b. B = blotches, BL = black lesions, CHL = chlorosis, CL = chlorotic lesions, CR = crinkling, (L)CRS = (local) chlorotic ring spots, CS = chlorotic spotting, CST = chlorotic streaks, DF = systemic leaf deformation, GVB = green vein banding, IVD = interveinal depression, LI = latent infection, LP = line pattern, LR = leaf rolling, M = mosaic, MT = mottle, (L)NL = (local) necrotic lesions, NRS = necrotic ring spots, PR = proliferation, RO = rosette, RS = ringspots, S = systemic, SI = symptomless infection, SK = streaking, SN = systemic necrosis/severe necrosis, SNS = systemic necrotic spotting, ST = stunting, STP = stripes, VB = vein banding, VCH = vein chlorosis, VCL = vein clearing, VN = veinal necrosis, YM = yellow mosaic, YMT = yellow mottle and YS = yellow spot.

c. TIP = thermal inactivation point (10 min), LIV = longevity in vitro (h = hours, d = days), DEP = dilution end point at 10^{-1}, 10^{-2}, etc.

d. F = fungus, Ap = Aphididae, CL = Coleoptera, Al = Aleyrodidae, Th = Thysanoptera, - = negative, + = positive.

Table 7. Serological Relationships of Taxonomically Characterized Viruses Naturally Infecting Peanuts

Virus	Serological test used[a]	Positive to antisera of	Negative to antisera of	Reference
African peanut clump	Microprecipitin	--	Barley stripe mosaic, beet necrotic yellow vein, Indian peanut clump, Nicotiana velutina mosaic, pea early browning, potato moptop, soil-borne wheat mosaic, tobacco mosaic and tobacco rattle viruses	Thouvenel and Fauquet 1981a, 1981b
Bean yellow mosaic	ELISA	Bean yellow mosaic and clover yellow vein viruses	Blackeye cowpea mosaic, pepper veinal mottle, potato Y, soybean mosaic, tobacco etch and watermelon mosaic viruses	Bays and Demski 1986
Cowpea chlorotic mottle	AGDD	--	Broadbean mottle, brome mosaic, cowpea mosaic and southern bean mosaic (cowpea strain) viruses	Bancroft 1971
Cucumber mosaic-CA	AGDD, ELISA	CMV strains D, S, CI and Bt and tomato asperm[illegible] virus	Peanut stunt virus strains E, W, T	Xu and Barnett 1984
Cowpea mild mottle	ELISA, precipitin tube	Cowpea mild mottle (West Africa), groundnut crinkle, and carnation latent viruses	Cactus 2, chrysanthemum B, narcissus latent, passiflora latent, pea streak, potato M, potato S and red clover vein viruses	Brunt and Kenten 1973, 1974; Iizuka et al. 1984
Groundnut chlorotic spotting	Microprecipitin	--	Cactus virus X, clover yellow mosaic, cymbidium mosaic, groundnut eyespot, narcissus mosaic, papaya mosaic, peanut green mosaic, peanut mottle, pepper veinal mottle, potato X and white clover mosaic viruses	Fauquet et al. 1985

Table 7 (continued)

Virus	Serological test used[a]	Positive to antisera of	Negative to antisera of	Reference
Groundnut crinkle	Microprecipitin	Carnation latent, passiflora latent, potato M and potato S viruses	Groundnut chlorotic rosette, groundnut eyespot, okra mosaic, peanut clump, peanut mottle, peanut stunt and tobacco mosaic viruses	Dubern and Dollet 1981
Groundnut eyespot	Microprecipitin	Guinea-grass mosaic, iris fulva mosaic, passion fruit ringspot, pepper veinal mottle, soybean mosaic and wisteria vein viruses	Arizona pepper virus, bean common mosaic, bean yellow mosaic, bidens mottle, clover yellow vein, Columbian datura, cowpea aphid-borne mosaic, henbane mosaic, hippeastrum mosaic, lettuce mosaic, parsnip mosaic, peanut clump, peanut mottle, pea seed-borne mosaic, potato A, potato Y, ryegrass mosaic, sugarcane mosaic, tobacco etch, tobacco mosaic, turnip mosaic and yam mosaic viruses	Dubern and Dollet 1978, 1980
Groundnut rosette assistor	ISEM, ELISA	Bean leaf roll, beet western yellow and potato leaf roll viruses	Carrot red leaf, subterranean red leaf and tobacco necrotic dwarf viruses	Casper et al. 1983; Reddy et al. 1985a; Rajeshwari et al. 1987
Groundnut yellow mottle	AGDD, microprecipitin	Cocoa yellow mosaic, desmodium yellow mottle, Kennedya yellow mosaic, okra mosaic and turnip yellow mosaic viruses	Belladona mottle, cowpea mosaic, eggplant mosaic (Abelia strain) and hibiscus ringspot viruses	Lana 1980
Indian peanut clump	PRIT, ELISA, ISEM	--	African peanut clump, pea early browning and tobacco rattle viruses	Reddy et al. 1983b
Passionfruit woodiness		--	Bean yellow mosaic and pea mosaic viruses	Taylor and Greber 1973

Table 7 (continued)

Virus	Serological test used[a]	Positive to antisera of	Negative to antisera of	Reference
Peanut green mosaic	AGDD, hemagglutination, ELISA	Adzuki bean mosaic, blackeye cowpea mosaic, groundnut eyespot, peanut stripe, potato Y and soybean mosaic viruses	Bean common mosaic, bean yellow mosaic, clover yellow vein, peanut mottle, sugarcane mosaic and turnip mosaic viruses	Sreenivasula et al. 1981
Peanut mottle (S-strain)	AGDD, Microprecipitin, ELISA	Peanut mosaic and peanut mottle viruses	Bean common mosaic, bean yellow mosaic, celery mosaic, clover yellow vein, cowpea aphid-borne mosaic, iris mosaic, peanut stripe, potato Y, soybean mosaic, sugarcane mosaic and tobacco etch viruses	Bock and Kuhn 1975; Bijaisorodat and Kuhn 1988
Peanut mottle	AGDD, microprecipitin, ELISA	--	Bean yellow mosaic, clover yellow vein and soybean mosaic viruses	Tolin and Ford 1983
Peanut mottle (Indian)	ISEM	Columbia datura, potato Y and tobacco etch viruses	Barley yellow mosaic, bean common mosaic, beet mosaic, carnation mottle, celery mosaic, fressia mosaic, henbane mosaic, hippeastrum mosaic, onion yellow dwarf, pea seed-borne mosaic, pepper mottle, plum pox, potato A viruses, rice necrosis mosaic, sugarcane mosaic, tulip breaking, turnip mosaic, watermelon virus, wheat yellow mosaic and wild potato mosaic viruses	Meyer 1982
Peanut mottle (Indian)	PRIT, ELISA, ISEM	Adzuki bean mosaic, amaranthus leaf mottle, clover yellow vein, Colombian datura virus, potato Y, soybean mosaic and tobacco etch viruses	Groundnut eyespot, peanut green mosaic, pepper veinal mottle, potato virus Y, sugarcane mosaic and turnip mosaic viruses	Rajeshwari et al. 1983

Table 7 (continued)

Virus	Serological test used[a]	Positive to antisera of	Negative to antisera of	Reference
Peanut stripe	ELISA	Blackeye cowpea mosaic, clover yellow vein, pepper veinal mottle and soybean mosaic viruses	Bean yellow mosaic, peanut mottle, potato Y and tobacco etch viruses	Demski et al. 1984
Peanut stunt	AGDD	Cucumber mosaic and tomato aspermy viruses (strain dependent)	Western strain of PSV to cucumber mosaic virus	Mink 1972; Xu et al. 1986
Peanut yellow spot		PYSV	Tomato spotted wilt virus	Wongkaew and Sae-Wein 1984; Wongkaew 1986
Tobacco streak	AGDD	Bean red node and black raspberry latent viruses	Alfalfa mosaic, black raspberry latent, citrus leaf rugose, citrus variegation, lilac ring mottle, spinach latent and tulare apple mosaic viruses	Jones and Mayo 1975; Scott et al. 1961; Van der Meer and Huttinga 1979; Bos et al. 1980; Fulton 1967
Tomato spotted wilt	Haemagglutination	Tomato spotted wilt virus	--	Ghanekar et al. 1979

a. AGDD = agar gel double diffusion, ELISA = enzyme-linked immunosorbent assay, ISEM = immunospecific electron microscopy, and PRIT = precipitin ring interface test.

Table 8. Host Range Key for the Tentative Diagnosis of Certain Viruses Naturally Infecting Peanuts

A_1 Viruses infecting *Chenopodium amaranticolor* ---- African peanut clump virus (APCV), bean yellow mosaic virus (BYMV), cowpea chlorotic mottle virus (CCMV), cucumber mosaic virus (CMV), cowpea mild mottle virus (CMMV), groundnut chlorotic spotting virus (GCSV), groundnut rosette virus (GRV), groundnut yellow mottle virus (GYMtV), passionfruit woodiness virus (PFWV), peanut green mosaic virus (PGMV), peanut mottle virus (PMV) (most strains), peanut stripe virus (PStV), peanut stunt virus (PSV), tobacco streak virus (TSV), tomato spotted wilt virus (TSWV).

- B_1 Viruses infecting either *Cucumis sativus* or *Cucurbita pepo* ---- APCV, CMV, CCMV, GYMtV, PFWV, PSV, TSV, TSWV.
  - C_1 Hosts infected = *Gomphrena globosa, Glycine max, Nicotiana glutinosa, Phaseolus vulgaris, Triticum aestivum Vigna unguiculata,* ---- APCV.
  - C_2 Hosts infected = *Canavalia ensiformis, Datura stramonium, G. globosa, Lycopersicon esculentum, Nicotiana clevelandii, N. glutinosa, Nicotiana tabacum, P. vulgaris, Pisum sativum, V. unguiculata, Zinnia elegans*; hosts not infected = *G. max* ---- CMV.
  - C_3 Hosts infected = *G. globosa, G. max, P. vulgaris, V. unguiculata*; hosts not infected = *L. esculentum, N. glutinosa, Z. elegans* ---- CCMV.
  - C_4 Hosts infected = *Cajanus cajan, C. ensiformis, G. globosa, Hibiscus esculentus, V. unguiculata*; hosts not infected = *G. max, N. glutinosa, Nicotiana rustica, Z. elegans* ---- GYMtV.
  - C_5 Hosts infected = *C. cajan, C. ensiformis. G. globosa, H. esculentus, V. unguiculata* ---- PFWV.
  - C_6 Hosts infected = *C. ensiformis, D. stramonium, G. globosa, G. max, L. esculentum, P. vulgaris, P. sativum, V. unguiculata, Z. elegans* ---- PSV.
  - C_7 Hosts infected = *Cyamopsis tetragonoloba, G. max, L. esculentum, N. glutinosa, N. tabacum, P. vulgaris, Phaseolus aureus, Phaseolus mungo, P. sativum, Sesamum indicum, Solanum melongena, V. unguiculata, Vinca rosea, Z. elegans* ---- TSV.
  - C_8 Hosts infected = *C. ensiformis, D. stramonium, G. max, G. globosa, L. esculentum, N. clevelandii, N. glutinosa, N. tabacum, Petunia hybrida, P. vulgaris, P. sativum, V. unguiculata, V. rosea, Z. elegans* ---- TSWV.
- B_2 Viruses not infecting either *C. sativus* or *C. pepo* ---- BYMV, CMMV, GCSV, GRV, PCLSV, PGMV, PMV (most strains), PStV.
  - C_1 Hosts infected = *P. vulgaris, P. sativum, V. unguiculata*; hosts not infected = *G. max* ---- BYMV.
  - C_2 Hosts infected = *C. cajan, C. tetragonoloba, G. max, P. vulgaris* (cv Topcrop), *V. unguiculata*; hosts not infected = *D. stramonium, L. esculentum, P. hybrida, P. sativum, V. rosea* ---- CMMV.
  - C_3 Hosts infected = *Physalis floridana, Nicotiana benthamiana*; hosts not infected; *C. tetragonoloba, G. max, P. vulgaris, V. unguiculata* ---- GCSV.
  - C_4 Hosts infected = *G. max, P. vulgaris*; hosts not infected = *C. tetragonoloba, V. unguiculata* ---- GRV.
  - C_5 Hosts infected = *C. ensiformis, C. tetragonoloba, D. stramonium, G. max, N. glutinosa, N. rustica, P. sativum, P. vulgaris* (local, cv Topcrop), *V. unguiculata*; hosts not infected = *C. cajan, Cassia obtusifolia* ---- PCLSV.
  - C_6 Hosts infected = *G. max*; hosts not infected = *P. vulgaris* (cv Topcrop), *P. sativum* ---- PStV.
  - C_7 Hosts infected = *C. tetragonoloba, P. vulgaris* (cv local), *S. indicum, Tetragonia expansa*; hosts not infected = *C. ensiformis, G. max, P. sativum, P. vulgaris* (cv Topcrop), ---- PGMV.
  - C_8 Hosts infected = *C. tetragonoloba, G. max, P. vulgaris, P. sativum, V. unguiculata*; hosts not infected = *Beta vulgaris, C. cajan,* ---- PMV (most strains).

A_2 Viruses not infecting *C. amaranticolor* ---- Groundnut crinkle virus (GCV), groundnut eyespot virus (GEV), Indian peanut clump virus (IPCV), peanut mottle virus (PMV) (mild strain).

- B_1 Hosts infected = *C. ensiformis, P. sativum, P. vulgaris, V. unguiculata*; hosts not infected = *L. esculentum, N. clevelandii* ---- GCV.
- B_2 Hosts infected = *C. ensiformis, L. esculentum, N. clevelandii, P. sativum, V. unguiculata*; hosts not infected = *C. cajan, P. vulgaris.* ---- GEV.
- B_3 Hosts infected = *C. ensiformis, C. tetragonoloba, N. clevelandii, P. vulgaris, V. unguiculata*; hosts not infected = *G. max, P. sativum.* ---- IPCV.
- B_4 Hosts infected = *C. ensiformis, C. tetragonoloba, G. max, N. clevelandii, P. sativum, P. vulgaris* (cv Topcrop), *V. unguiculata*; hosts not infected = *B. vulgaris, C. cajan, L. esculentum* ---- PMV (mild strain).

Diagnostic hosts are reliable for quick identification of some peanut viruses (Xu et al. 1986; Nolt et al. 1988). For example, PMV and most of its reported strains can be differentiated easily from many other viruses naturally infecting peanuts, as they produce characteristic local necrotic lesions that spread along veins on *Phaseolus vulgaris* cv Topcrop. Thus, Topcrop bean is used frequently to distinguish PMV strains from other potyviruses that infect peanuts (Demski et al. 1988). TSWV can be differentiated from other viruses based on its diagnostic symptoms on a set of host plants such as *Lycopersicon esculentum* Mill., *Nicotiana glutinosa* L.,

Petunia hybrida, Tropaeolum majus, Vigna unguiculata cv 152, and *Vinca rosea* (Reddy and Wightman 1988). A host range key useful for the tentative diagnosis of certain viruses naturally infecting peanuts is given in table 8.

Stability of Virus in Sap

The stability in sap of viruses naturally infecting peanuts is sometimes useful as a diagnostic tool (table 6). For example, GEV, peanut yellow spot virus (PYSV), and TSWV are unstable at low temperatures (thermal inactivation point), and peanut chlorotic leafspot virus (PCLSV) is highly stable. While most viruses have dilution end points between 10^{-3} and 10^{-5}, groundnut yellow mottle virus (GYMtV) is still infective at a dilution of 10^{-7}. Longevity in vitro is less than 24 hr for groundnut chlorotic spotting virus (GCSV), GEV, and TSWV. Unfortunately, the potyviruses, the taxonomic group with about one-third of the naturally occurring peanut viruses, cannot be distinguished by stability in sap properties. Francki (1980) has discussed the limitations of relying on these properties for virus identification.

Transmission

GRAV, groundnut veinal chlorosis virus (GVCV), GYMV, and sunflower yellow blotch virus (SYBV) are not sap transmissible (table 6). TSWV and PYSV are sap transmissible only under special conditions (inoculum from early infection of young source plants, cold 0.02 M potassium phosphate buffer [pH 7.0] containing either 2-mercaptoethanol or sodium sulphite, and a cold mortar and pestle). Furthermore, to achieve a high percentage of infected peanut plants, GRV requires stringent inoculation conditions (including the use of bentonite and latex gloves) to protect its RNA from ribonuclease (Olorunju et al. 1990). The remaining viruses given in table 6 are known to be sap-transmitted easily.

Beetles are the vectors of CCMV and GYMtV (table 6). Cowpea mild mottle virus (CMMV), groundnut crinkle virus (GCV), and GYMV are transmitted by *Bemisia tabaci*. APCV and Indian peanut clump virus (IPCV) are soilborne viruses transmitted by *Polymyxa graminis*. Thrips are vectors of PYSV and TSWV; they have been shown to transmit tobacco streak virus (TSV) under experimental conditions. Bean yellow mosaic virus (BYMV), cucumber mosaic virus (CMV), GCSV, GEV, passionfruit woodiness virus (PFWV), peanut green mosaic virus (PGMV), PMV, PStV, and peanut stunt virus (PSV) are nonpersistently transmitted by various aphid species. GRAV and SYBV are known to be transmitted by aphids in a circulative, persistent manner. GRV is transmitted (persistent) by aphids only when it occurs in a mixed infection with GRAV. The probable insect vectors for the remaining viruses are aphids for PCLSV and leafhoppers for GVCV.

Of the characterized viruses naturally infecting peanuts (table 1), PMV, PStV, IPCV, APCV, CMV, and PSV are known to be transmitted through peanut seeds (table 6). Recently, a carlavirus, distinct from the reported CMMV and GCV, causing severe mottle on commercial peanut plants in India, also was shown to be transmitted through peanut seeds (Sivaprasad et al. 1990).

Serology

Serology has been the premier tool for the diagnosis of virus diseases and identification of viruses. Polyclonal antibodies for most of the viruses that infect peanuts naturally have been produced and used worldwide to identify peanut viruses (table 7). Polyclonal antisera are

available from two sources: (i) Dr. D. V. R. Reddy, ICRISAT, Patacheru—502 324, Andhra Pradesh, India, and (ii) Dr. J. W. Demski, Department of Plant Pathology, Georgia Station, Griffin, GA 30223, USA. Monoclonal antibodies have been produced and used for identification of APCV, GRAV, PMV, and TSWV (Rajeshwari et al. 1987; Sherwood et al. 1987, 1989; Huguenot et al. 1989, 1990).

A wide variety of serological tests has been used to detect viruses in leaf tissue and seeds and to determine serological relationships among peanut and various characterized viruses. These include agar gel double diffusion, electroblot immunoassay, enzyme-linked immunosorbent assay (ELISA), hemagglutination, immunospecific electron microscopy, and precipitation ring test (table 7) (Ghanekar et al. 1979; Dubern and Dollet 1981; Sreenivasulu et al. 1981, 1991; Meyer 1982; Rajeshwari et al. 1983, 1987; Iizuka et al. 1984; Reddy et al. 1985a; Fukumoto et al. 1987; Hobbs et al. 1987a).

Serology also has been used to test peanut seed for PMV (Bharathan et al. 1984) and PStV (Demski and Warwick 1986). This nondestructive test employs the removal of 0.02 to 0.5 g of cotyledonary tissue from the end of the peanut seed distal to the radicle. The seed piece is triturated in antigen buffer and tested by the ELISA system as described by Rajeshwari et al. (1983). Furthermore, the procedure is sensitive enough to allow detection of one infected seed in a sample containing between 15 and 30 seeds (Bharathan et al. 1984).

Virus Protein and Nucleic Acid

For identification of viruses to the taxonomic group level, sodium dodecyl sulphate-polyacrylamide gel electrophoresis can be used to determine the number of virus polypeptide species and their molecular weights. Similarly, virus nucleic acid species and their molecular weights are determined by acrylamide, agarose, or agarose-acrylamide gel electrophoresis (Hull 1985). Table 4 gives information on the proteins and nucleic acids of peanut viruses.

Radioactive nucleic acid probes were first used to determine the nucleotide sequence homologies of PMV and PStV (Sukorndhaman 1987; Bijaisoradat and Kuhn 1988). Eight strains of PMV have similar nucleotide sequence homologies. On the other hand, PStV showed an average of 55% homology with several strains of PMV. Partly as a result of these studies, scientists from Southeast Asia and the United States agreed to consider peanut mild mottle virus and peanut chlorotic ring mottle virus as symptom variants of PStV (Demski et al. 1988).

Dot blot hybridization, using complementary (c)DNA probes, has been used for the detection of PMV and PStV in peanut seeds (Bijaisoradat and Kuhn 1988). Both viruses can be detected readily in 1 mg of infected seed tissue and in extracts from seeds that have been diluted 1/62,500 with buffer. A virus in one part (1 mg) of an infected seed can be detected reliably when it is mixed with 99 parts (99 mg) of healthy seeds. cDNA probes also have been used for detection of IPCV and TSWV in peanut tissue (Cho et al. 1989; Roneo et al. 1989; D. V. R. Reddy, unpublished).

Since no particles (or coat protein) have been associated with single infections of GRV, the 900 base pair double-stranded RNA (satellite RNA) has been used effectively as a diagnostic tool (Breyel et al. 1988; Olorunju 1990; Olorunju et al. 1991; Olorunju et al. 1992). The method is simple. sensitive, and rapid. Small quantities (one leaflet or about 0.1 g) of leaf tissue are ground in water, centrifuged at low speed, incubated at 37°C, and electrophoresed on agarose. The entire procedure is complete within 4-6 hr.

High performance liquid chromatographic (HPLC) peptide profiling of potyvirus coat protein digests has been shown recently to be very useful for differentiating potyviruses and their strains (Shukla et al. 1988; McKern et al. 1989). This procedure compares the entire protein and reflects the extent of amino acid sequence identities between two proteins. Results demonstrate that different strains of individual potyviruses have very similar HPLC peptide profiles, whereas the peptide profiles from distinct potyviruses are very different. Use of this procedure with PStV isolates showed that the coat protein of PStV and its variants (blotch, stripe, chlorotic ring mottle, mild mottle) have peptide profiles that are very similar to each other and to those obtained from the coat proteins of blackeye cowpea mosaic virus and azuki bean mosaic virus. In contrast, profiles of the above viruses differ significantly from those of BYMV, clitoria yellow vein virus, PMV, and soybean mosaic virus. The results suggest that PStV, blackeye cowpea mosaic virus, and azuki bean mosaic virus may be strains of the same potyvirus (McKern et al. 1992).

Management of Peanut Virus Diseases

Although all 23 viruses naturally infecting peanuts probably cause economic losses, we believe the five diseases of greatest economic importance, on the basis of general surveys, disease incidence, and disease severity, are groundnut rosette, peanut clump, peanut mottle, peanut stripe, and the disease caused by tomato spotted wilt virus. Integrated management practices, which include growing resistant or tolerant cultivars and adoption of cultural strategies which restrict virus spread in order to control these diseases, are discussed below.

Groundnut Rosette

Groundnut rosette was first reported in Africa (Zimmerman 1907) and is recognized as the most important virus disease of peanuts in Africa (South of the Sahara). Subsequently, peanut diseases referred to as rosette have been reported in Argentina, India, Indonesia, the Philippines, and Russia. However, no direct comparisons of the latter diseases have been made with the African disease. In some cases, certain characteristics (transmission, viral-like particles, and *in vitro* sap properties) are quite different from the more thoroughly studied African disease, suggesting the diseases are different. Rosette disease reported in India is believed to be bud necrosis caused by TSWV (Reddy 1988).

The etiology was discussed previously in this publication. Two rosette diseases, green rosette and chlorotic rosette, are induced by specific GRV satellite RNAs (Murant and Kumar 1990). The causal viruses GRV and GRAV are transmitted in a persistent manner by *Aphis craccivora*, and no transmission has been demonstrated through peanut seeds.

Sauger and Catherinet (1954a, 1954b) and de Berchoux (1958) reported resistance in peanuts to rosette disease, but the cultivars found in Cote de Ivorie and Burkina Faso require a long season for maturation and are small-seeded and low-yielding. Resistance to both green and chlorotic rosette is controlled by two recessive genes (de Berchoux 1960; Nigam and Bock 1990; Olorunju 1990; Olorunju et al. 1992). Subsequently, long-season rosette-resistant cultivars have been bred and released in Cote de Ivorie, Malawi, and Nigeria (Gibbons 1977). Some of these cultivars, listed by Reddy (1984a), are 'RG 1', 'RMP 12', 'RMP 91', 'KH 14-9A', '55-437', '55-127', '69-101', and 'M-25-68'. Recent studies in Malawi (Bock et al. 1990) and Nigeria (Olorunju 1990; Olorunju et al. 1992) on the virus status of resistant and susceptible

cultivars indicated that the genes govern resistance to GRV but not to GRAV. Despite the release of several rosette-resistant cultivars, they are not grown widely because of a long maturation period and lack of acceptable confectionary characteristics. Ongoing breeding programs for resistance to rosette are underway in Malawi and Nigeria in conjunction with the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the Peanut Collaborative Research Support Program (United States Agency for International Development, Department of State).

Rosette disease can be controlled to some extent by adopting suitable cultural practices and by spraying with aphicides. A'Brook (1964, 1968) conclusively demonstrated lower incidence of rosette and higher yields in early planted peanuts at high plant densities. Rosette incidence was greatest in plants grown with wide spacings between plants and rows and was associated with higher aphid populations on these peanut plants. Secondary spread of the disease is also slower in densely planted fields than in sparsely planted ones. Thus, careful adjustment of sowing dates (in relation to vector migration) and planting at high densities to cover the ground without affecting the yield due to plant competition are desirable cultural practices.

Phytosanitary methods, such as the destruction of infected volunteer peanut plants during the dry season and plants with primary infections in a current crop, will reduce the spread of rosette disease. Reports from African countries have shown that *Euphorbia hirta*, a host of the aphid vector, is not a source of virus during the dry season. If alternative hosts of GRV, and possibly GRAV, could be identified, their eradication might reduce disease incidence. However, the persistent nature of the virus(es)/vector relationship probably allows long-distance spread of the virus, at least partly negating the importance of eradication of local hosts.

Aphis craccivora is the principle field vector of the rosette disease viruses. Davies (1975) reported effective insecticide control of aphids in Uganda. He tested several insecticides over a period of five years (1965-1970) and suggested menazon as the most efficient in decreasing the incidence of rosette disease and in improving the yield and quality of peanuts. The insecticides endosulfan, dimethoate, phosphamidon, and dicrotophos were less effective than menazon. Natural predators of *A. craccivora* have been reported (Brooker 1963), so insecticidal sprays should not be used indiscriminately.

The long-term remedy to the rosette disease depends on the development of agronomically and commercially acceptable peanut cultivars resistant to the disease pathogens. Meanwhile, selective cultural practices and the timely use of insecticides may minimize losses caused by rosette disease in Africa (Misari 1987).

Peanut Clump

Two furoviruses, similar in physicochemical properties but different serologically, cause similar diseases, both called peanut clump. In Africa, the virus is named African peanut clump virus, and in India the virus is Indian peanut clump virus. In India, soil biocides, such as dibromochloropropane, carbofuran, and aldicarb, effectively control the peanut clump disease. However, yield increase did not cover the cost of the pesticides (Reddy 1988). ICRISAT screened 6,500 peanut germplasm lines on two agricultural university farms (Ludhiana, Punjab; Bapatla, Andhra Pradesh), and none of them was found to be either immune or resistant to clump. APCV and IPCV are seed-borne; therefore, seed for planting should not be used from clump-infested areas. In India, peanuts escape the disease when they are sown after the rainy season in November and December.

In West Africa, soil treatment with fungicides and the use of healthy seed are suggested for the field control of peanut clump (Fauquet and Thouvenel 1987).

Peanut Mottle

PMV is seed-transmitted (0 to 8.5%, depending on virus strain, peanut cultivar, and environment) and nonpersistently transmitted by aphids, including *Myzus persicae, Aphis craccivora, A. gossypii,* and *Rhopalosiphum padi* (Paguio and Kuhn 1973; Highland et al. 1981). In the United States, peanut seeds provide the source of primary inoculum for peanuts and other important legume crops: clover, cowpeas, lupines, navy beans, peas, and soybeans (Demski 1975; Kuhn and Demski 1984). Since resistance to PMV has not been found in commercial peanuts, use of virus-free seeds produced under rigorous seed certification programs is extremely important (Kuhn and Demski 1975). Recently identified at ICRISAT are peanut genotypes in which seed transmission of PMV does not occur (Bharathan et al. 1984; D. V. R. Reddy, unpublished data). For example, there was no evidence of seed transmission in 12,800 seeds produced on plants of NcAc 17/33 (RF) infected with the Indian isolate. However, PMV was transmitted through five of 297 and four of 232 seeds of NcAc 17/33 (RF) using U.S.A. isolates from clover and lima bean, respectively. The mild isolate from the USA, which is the most common PMV strain, was not transmitted through 314 seeds of this genotype in comparison tests. Genes for this nonseed-transmission characteristic can be transferred by conventional breeding methods.

Several other cultural practices are noteworthy: removal of volunteer peanut plants, removal of susceptible perennial weeds such as *Desmodium* species in which PMV may survive in roots, growing peanuts at least 100 m from crop hosts susceptible to PMV, and separating peanuts from other crops with hedge/barrier crops such as maize (Demski 1975; Demski and Kuhn 1977).

Kuhn et al. (1978) identified two peanut genotypes (PI 261945, PI 261946) that are tolerant (minimal yield loss even though virus replication and movement within plants is relatively unrestricted) to PMV infection. Furthermore, tolerance to PMV has been observed recently in NC Ac 2240 and ICG genotypes in India. Currently, several crosses of these genotypes are being made at ICRISAT. Resistance to PMV has been found in some wild species of *Arachis* (Demski and Sowell 1981; Melouk et al. 1984) and in other legume species (Bijaisoradat et al. 1988). Attempts should be made to transfer this resistance into *A. hypogaea,* the commercial cultivated species.

Peanut Stripe

Similar to PMV, PStV is transmitted through peanut seeds and is nonpersistently transmitted by aphids (Demski et al. 1984). Detailed studies on the epidemiology and control of peanut stripe have not been conducted. In Thailand, however, Wongkaew (1986) has identified, in addition to peanut seeds, several hosts as sources of primary inoculum for young peanut seedlings. They include *Calopogonium caeruleum, Centrocema* sp., *Crotalaria striata, Desmodium siligudum, Pueraria phaseoloides,* and *Vigna unguiculata.* Culver et al. (1987) have recently identified some wild species of *Arachis* as resistant to PStV. Over 5,400 germplasm lines were screened for resistance to PStV in Indonesia and none was found to be resistant (Saleh et al. 1989). Efforts are under way to screen additional germplasm lines in Indonesia. Additionally, two genotypes in which PMV is not seed-borne showed negligible seed transmission of PStV (D. V. R. Reddy, unpublished data).

On the basis of experience in the United States, it seems likely that control practices recommended for peanut mottle will be useful for peanut stripe. The major emphasis should be on the avoidance of sources of primary inoculum, either peanut seeds or weeds and other natural reservoirs.

PStV was first discovered in research and institutional test plots in the USA in 1982 (Demski et al. 1984). Subsequent studies established that the virus had been introduced through peanut seeds from the People's Republic of China. FStV has not been detected in commercial peanut cultivars in Georgia, indicating that the virus has not entered the chain of seed production, beginning with breeder's seed and progressing to certified seed. Guidelines for controlling and/or eliminating PStV from scientifically important groundnut seed lots were developed (Demski and Lovell 1985). These guidelines also should be highly useful in situations and localities where peanut stripe is endemic and an economic problem. Two main features of the guidelines are the use of virus-free seeds and of serological testing procedures to analyze individual seeds while maintaining their viability.

Tomato Spotted Wilt Virus (Bud Necrosis)

The infection of peanuts by TSWV can induce a variety of symptoms, presumably because of virus strain, host genotype, age of plant when infected, and environmental influences. In India, the predominant symptom caused by TSWV in peanuts is necrosis of the terminal bud. In the USA, other symptoms, such as leaf chlorosis and necrosis and general stunting of plants, are more prominent than bud necrosis. TSWV has a wide host range, including several crops such as black grams (*V. mungo* L.), cowpeas, eggplants (*Solanum melongena* L.), green grams (*Vigna radiata* L.), lettuce, peas, peppers, sunflowers, tobacco, tomatos, and many ornamental plants. Reddy and Wightman (1988) have recently listed over 250 plant species, including many weeds, as hosts of TSWV. The thrips vector also has a wide host range. TSWV is not known to be seed-transmitted in peanuts or other crop plants (Reddy and Wightman 1988).

At ICRISAT, in-depth studies have been made on bud necrosis. Reddy et al. (1983a) and Reddy and Wightman (1988) have suggested integrated management practices to control this important disease of peanuts in India, and these practices are likely to be useful elsewhere.

The incidence of bud necrosis largely depends on migrant thrips infesting the crop (Reddy et al. 1983a; Reddy and Wightman 1988). In India, peanut seeds sown early in the rainy and post-rainy seasons are infected less and yield more than peanuts sown later in each season. Disease incidence is less in dense than in sparse stands, indicating that close plant spacing helps reduce disease incidence.

In India, the primary source of the virus is not peanuts (Reddy et al. 1983a). Many crop plants (*Canavalia gladiata, Crotalaria juncea, Glycine max, Lycopersicon esculentum, Pisum sativum, Solanum melongena* and *S. tuberosum, Vicia faba, Vigna mungo, V. radiata, V. unguiculata*), ornamentals (*Cosmos bipinntatus* and *Zinnia elegans*), and weeds (*Acanthospermum hispidum, Ageratum conyzoides, Calotropis gigantica, Cassia tora, C. obtusifolia, Desmodium triflorum, Lagascea mollis*, and *Xanthium strumarium*) were identified as hosts of the virus (Reddy et al. 1983a). Many of the above plants are also reported to harbor thrips. Some of the above weeds, common in and around peanut fields, are usually abundant soon after monsoon showers and are likely to be sources of inoculum. Thus, it may not be feasible to eliminate these sources. Secondary spread of the virus within the crop has not been demonstrated; there-

fore, roguing of initially infected peanut plants is unlikely to be effective in preventing the spread of the virus.

In India, the practice of inter-cropping peanuts with black grams, cowpeas, and green grams is discouraged because these species serve as sources both of vector and of virus. However, inter-cropping peanuts with a fast-growing cereal, such as pearl millet, is encouraged because this practice minimizes vector movement and consequently decreases disease incidence.

Use of insecticides (carbofuran and dimethioate) for the control of thrips was studied at ICRISAT. Weekly sprays decreased disease incidence, but the marginal increase in seed yield did not cover the cost of insecticide applications. Furthermore, in a three-year study in the USA, weekly applications had no effect on the incidence of TSWV (J. W. Todd, A. K. Culbreath, and J. W. Demski, unpublished).

Arachis hypogaea cultivars resistant to TSWV and to thrips have been identified (Amin and Singh, unpublished data; Scholbery et al., unpublished data). Genotype NC Ac 2575 has some resistance to thrips and cultivar Robut-33-1 has shown a field type of resistance which appears to be due to nonpreference by thrips (Amin 1985). At ICRISAT in India, a number of genotypes with field resistance to TSWV have been identified, and they are being evaluated at different locations (ICRISAT 1988). Field tests in Georgia in 1990 confirmed earlier studies that the cultivar 'Southern Runner' exhibits field resistance to infection with TSWV. In insecticide-treated plots, incidence of TSWV-infected plants was 26.8% in 'Florunner' and 13.2% in 'Southern Runner'; in untreated plots, incidence was 27.2% in 'Florunner' and 8.1% in 'Southern Runner' (Todd, Culbreath, and Demski, unpublished).

Arachis chacoense and *A. pusilla* have not been infected by TSWV after repeated sap inoculations in the laboratory (Reddy et al. 1983a).

Summary

Sixty-two taxonomically characterized viruses are known to infect peanuts either naturally or under experimental conditions: one alfalfa mosaic virus, one bromovirus, two caulimoviruses, four carlaviruses, three cucumoviruses, one dianthovirus, two furoviruses, two geminiviruses, one ilarvirus, 10 luteoviruses, one necrovirus, four nepoviruses, two plant rhabdoviruses, five potexviruses, 14 potyviruses, one sobemovirus, one tobamovirus, two tobraviruses, two tomato spotted wilt viruses, and three tymoviruses. GRV (ssRNA, mol.wt. 1.55×10^6d) has not been assigned to any virus group because no particles have been associated with infections. The physicochemical, biological, and serological properties essential for identification and taxonomic classification to the virus group level are presented and discussed.

At least 26 virus and virus-like peanut diseases have been reported for which the causal agent has not been critically identified and classified. In most cases, the causal agents are probably viruses; however, they may be the same as, or strains of, existing viruses. A few properties of the causal agents are presented.

Disease management and control strategies are discussed for the five most economically important virus diseases of peanuts: groundnut rosette, peanut clump, peanut mottle, peanut stripe, and TSWV disease (sometimes called bud necrosis). A high level of resistance in cultivars of *Arachis hypogaea* is available only for groundnut rosette. A moderate level of resistance to TSWV has been found in the USA (*A. hypogaea* cv Southern Runner). Tolerance to PMV in *A.*

hypogaea may be useful. Extreme resistance (no infection detectable) to PMV, PStV, and TSWV has been reported in wild species of *Arachis*. IPCV, PMV, and PStV are seed-borne; thus, the use of virus-free seeds for annual planting is recommended for the diseases they cause, particularly if local susceptible alternative hosts (weeds, other crops) are not present. Pesticides can effectively control the aphid vector of the viruses (GRV and GRAV) which cause rosette and the fungal vector of IPCV. For all five diseases, a variety of cultural practices can be useful in suppressing disease incidence.

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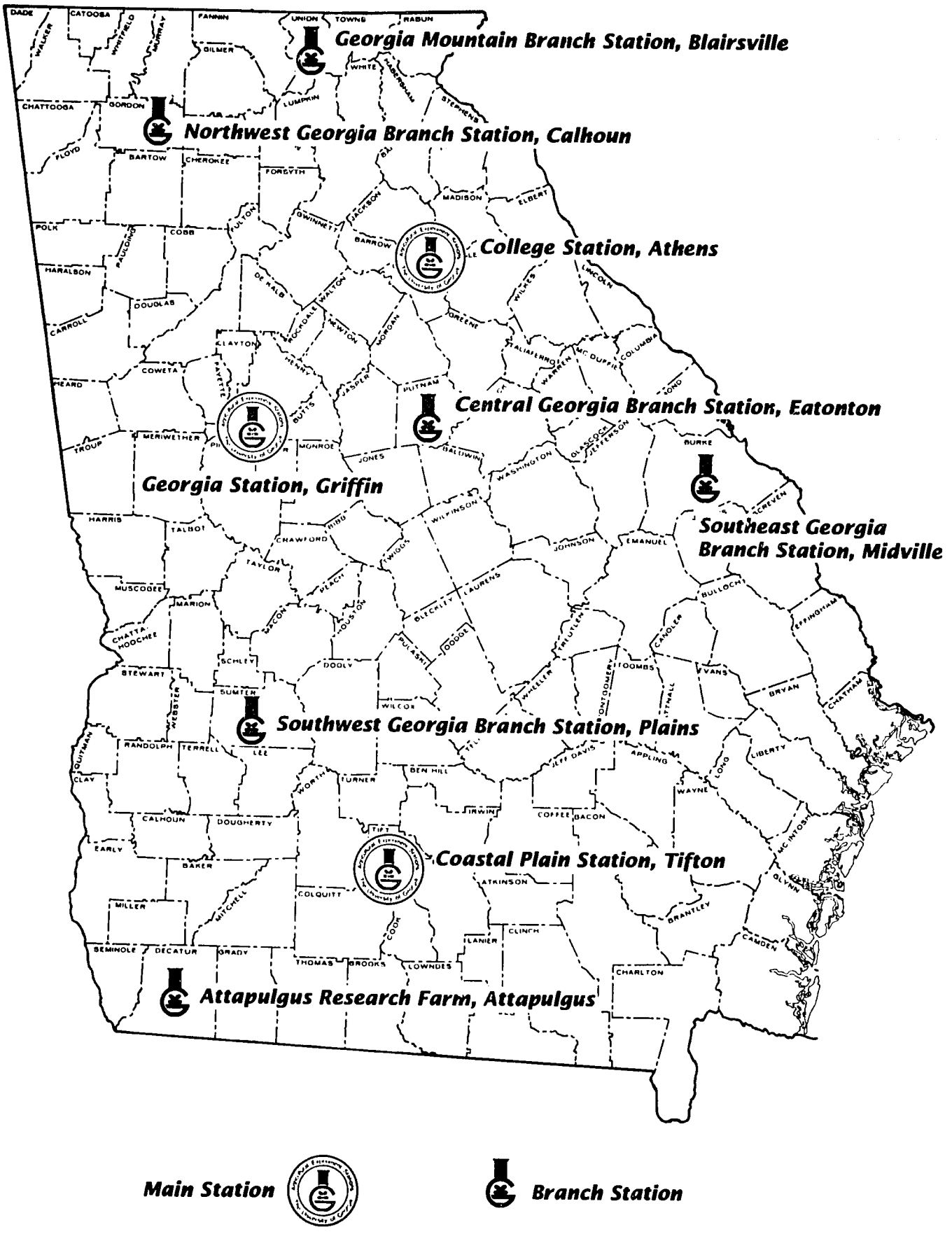
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