Seed Transmission of Indian Peanut Clump Virus (IPCV) in Peanut and Millets

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ABSTRACT

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An enzyme-linked immunosorbent assay (ELISA) procedure was developed to test peanut seed for Indian peanut clump virus (IPCV). A double antibody sandwich form of ELISA detected the Hyderabad isolate (IPCV-H) in seed of peanut. Correlation was established between the results from ELISA performed on cotyledons of peanut seed and grow-out tests. Seed transmission in the field-infected peanut plants ranged from 3.5 to 17%, depending on the genotype. The transmission frequency was 48 to 55% in seed collected from plants infected through seed. Because testae of all seed contained viral antigen, their removal was essential for the determination of frequency of seed transmission. Apparently the virus present only in cotyledons and embryo contributed to the seed transmission. For the first time, IPCV-H was shown to be seed transmitted in finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), and pearl millet (*Pennisetum glaucum*) at frequencies of 5.2, 9.7, and 0.9%, respectively. Seed transmission was not observed in sorghum (*Sorghum bicolor*). Significance of seed transmission in millet crops is discussed.

Peanut clump disease caused by Indian peanut clump virus (IPCV) is an economically important disease in the Indian subcontinent (16). It is transmitted to peanut (*Arachis hypogaea* L.) through seed (16) and by a plasmodiophoraceous fungus, *Polymyxa graminis* Ledingham (14). A similar disease was reported from West Africa (19) but the causal virus, peanut-clump virus (PCV), even though sharing similarities with IPCV, is serologically and genomically distinct from the Indian isolates (11–13,22).

IPCV and PCV are seed-transmitted at a high frequency (16,21) and therefore are regarded as high-risk pathogens for germ plasm exchange. IPCV infects grains such as sorghum and millets that are either grown as intercrops or rotated with peanut, without exhibiting any overt symptoms. It is essential to determine whether IPCV can be transmitted through seed of preferred grain hosts of the vector (9), *Polymyxa* sp., because seed-infected plants may contribute to the establishment of the disease. An isolate of PCV from Senegal was transmitted in peanut at a rate of 24 and 14% in seeds from artificially and naturally infected plants, respectively (21). Although PCV was detected in peanut seeds by enzyme-linked immunosorbent assay (ELISA; 8), the authors did not observe a good correlation between the results from ELISA and grow-out tests. In preliminary tests conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Asia Center (IAC) on transmission through peanut seed, correlation between IPCV presence in seed and grow-out tests could not be established. In those tests, cotyledons and testae were used in preparing the extracts for ELISA, and all the seed from infected plants showed the presence of viral antigen. However, in grow-out tests less than 15% of the plants became infected (D. V. R. Reddy, *unpublished data*). Therefore, this study was undertaken to develop an ELISA procedure for determining precisely the frequency of seed transmission in peanut and some of the cereal hosts.

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MATERIALS AND METHODS

Demarcation of IPCV-infested soils and seed collection. Areas that showed more than 70% of IPCV-H-infected (13) peanut plants from observations during the rainy season were demarcated in field RCW17A of the IAC farm. Various peanut genotypes, randomly selected from ICRISAT germ plasm, as well as millets and sorghum, were grown in different infested areas of this field. Peanut, millets, and sorghum seeds were collected from plants that tested positive by ELISA and dried under natural conditions. To confirm the presence of intact virus particles, especially in grain hosts, ELISA-positive plants were also tested by immunosorbent electron microscopy (ISEM).

ELISA. The double antibody sandwich form of ELISA employed is similar to that reported by Hobbs et al. (6) with minor modifications. Immunoglobulin (IgG) concentration was 1 µg/ml for coating the plates (Greiner GmbH, Germany); tissues were ground in a mortar and pestle at a ratio of 1:20 (wt/vol) in antigen extraction buffer. IgGs conjugated with penicillinase enzyme (18) were used at a dilution of 1:2000. Results were recorded after 30 min of substrate reaction time. Readings were considered positive if the difference in the absorbance value at 620 nm between infected and control sample exceeded 1 optical density (OD) unit.

Infectivity assay. Plant extracts were prepared in 0.05 M potassium phosphate buffer, pH 7.0, containing 0.075% thioglycerol. Leaves of *Phaseolus vulgaris* L. were inoculated manually with plant extracts. IPCV-H causes veinal necrosis on inoculated and systemically infected leaves.

Grow-out test. Peanut seeds were grown in a glasshouse at 25 to 30°C in wooden trays containing approximately 25 liters of soil. The plants were watered with tap water. Each tray contained a maximum of 100 seeds. The soil was collected from a disease-free field and autoclaved twice at 1-day intervals. Millet and sorghum seeds were grown under the same conditions in 40-cm pots, utilizing a maximum of 30 seeds per pot. Peanut plants were scored for symptoms such as reduced growth and chlorotic mottling on young leaves 3 weeks after emergence. All the plants, including millets and sorghum, were initially tested in groups of 5 (peanut) or 10 (millets and sorghum) by ELISA. Individual seedlings were tested from the groups that gave positive ELISA results. Peanut, millet, and sorghum seed derived from healthy plants were raised in the same soil sample to ascertain that the soil used was free of IPCV-H inoculum.

Detection of IPCV-H in peanut seed by ELISA. A procedure which does not affect the viability of seed was used (1), therefore permitting ELISA-tested seed to be used in grow-out tests. A small portion of cotyledons (2 to 3 mm) from the end opposite the embryo was tested for 465 seeds of field-infected TMV 2 cultivar. Embryos of those seeds which contained viral antigens in their cotyledons were also tested. Testae were tested separately and were avoided when preparing extracts from cotyledons or embryos. Seeds with cotyle-

dons which tested negative by ELISA were also included in grow-out tests.

Immunosorbent electron microscopy (ISEM). The grids were coated with a 1:1000 dilution of IPCV-H antiserum. Leaf and seed extracts were prepared in 0.01 M phosphate buffer, pH 6.5. Other details were as reported (17).

Correlation between ELISA, grow-out test, infectivity assay, and ISEM. The seeds from six peanut genotypes, ICG 221, ICG 1697, ICG 2106, ICG 3704, ICG 4790, and ICGV 86708, were investigated. A portion of the cotyledons was used for the ELISA test and rest of the seeds were used in grow-out tests. Additionally, 5 ELISA-positive seedlings from each genotype were tested by infectivity assay and ISEM to confirm virus presence.

In experiments aimed at testing a range of genotypes for determining seed transmission frequency, only cotyledons from seed of 22 peanut genotypes were tested by ELISA. Initially, cotyledons from 5 seeds were included for each well of the ELISA plate. Individual seeds were tested from the lots that gave a positive reaction.

Frequency of transmission in peanut seed derived from plants infected through seed-borne inoculum. Three genotypes, ICG 156 (cv. M-13), ICG 221 (cv. TMV 2), and ICG 4749 (PI337394F), were chosen. All ELISA-positive seed were sown individually in 40-cm pots in sterile soil and maintained in a glasshouse at 25 to 30°C until maturity. All plants were ELISA-tested. Seed were tested individually by ELISA and subsequently in grow-out tests.

Frequency of seed transmission in millets and sorghum. Grow-out tests were done with seed collected from finger millet (*Eleusine coracana* (L.) Gaertn.), foxtail or Italian millet (*Setaria italica* Beauv.), pearl millet (*Pennisetum glaucum* (L.) R. Br.), and sorghum (*Sorghum bicolor* (L.) Moench) plants grown in IPCV-H-infested areas that gave positive results in ELISA and ISEM.

RESULTS

Detection of IPCV-H in various parts of peanut seeds. The testae from all 465 seeds of field-infected ICG 221 (cv. TMV 2) plants gave a positive ELISA reaction. However, none of the extracts from testae produced symptoms on *P. vulgaris* and no virus was observed in ISEM. Only 49 of 465 cotyledons (10.5%) gave positive results in ELISA and corresponding positive results in infectivity assays. Embryos of these 49 seeds also tested positively in ELISA and infectivity assays. All the seeds

Table 1. Correlation between enzyme-linked immunosorbent assay (ELISA) and grow-out tests for determining Indian peanut clump virus, Hyderabad isolate, seed transmission frequency among six peanut genotypes

Identity: ICRISAT accession code (other)	Botanical type	No. of seed tested by ELISA	No. of seed positive by ELISA[b]	Grow-out tests[a]	
				No. of seed germinated	No. of seedlings positive by ELISA[c]
ICG 221 (TMV 2)	Spanish	186	20 (10.7%)	179	20
ICG 1697 (NCAc 17090)	Valencia	93	12 (12.9%)	89[d]	11
ICG 2106 (Small Japan)	Spanish	93	13 (14.0%)	80[e]	11
ICG 3704 (EC 21024)	Valencia	282	29 (10.3%)	275[d]	28
ICG 4790 (KU No. 24)	Valencia	173	6 (3.5%)	170	6
ICGV 86708 (JH 60 x PI259747)	Valencia	228	20 (8.8%)	211[e]	18

[a] Each of the 3-week-old seedlings tested by ELISA.
[b] A small portion of the cotyledons was tested retaining the embryo. The percentage of seed positive by ELISA is indicated in parentheses
[c] Five seedlings at random from each genotype were also tested by infectivity assays and immunosorbent electron microscopy to confirm ELISA results. Perfect correlation was observed between virus presence in cotyledons and grow-out test for the seed that germinated.
[d] One ELISA-positive seed did not germinate.
[e] Two ELISA-positive seeds did not germinate.

Table 2. Frequency of Indian peanut clump virus, Hyderabad isolate, seed transmission in 22 peanut genotypes

Identity: ICRISAT accession code (other)	Botanical type	Number of seed tested	Seed positive by ELISA[a]	
			Number	Percentage
ICG 173 (Happasari)	Spanish	217	24	11.1
ICG 221 (TMV 2)	Spanish	1302	125	9.6
ICG 799 (Robut 33-1)	Virginia	352	41	11.6
ICG 1326 (J 11)	Spanish	658	69	10.5
ICG 2738 (Gangapuri)	Valencia	168	25	14.9
ICG 3323 (Issue de-Cuba)	Spanish	133	17	12.8
ICG 3145 (AK 811)	Runner	132	16	12.1
ICG 4507 (S-7-2-13)	Virginia	68	8	11.8
ICG 4747 (PI259747)	Valencia	101	14	13.8
ICG 4749 (PI337394F)	Valencia	415	39	9.4
ICG 7827 (JL 24)	Spanish	264	27	10.2
ICG 3120 (Ah 7223)	Runner	157	19	12.1
ICG 1697 (NCAc 17090)	Valencia	93	12	12.9
ICG 3704 (EC 21024)	Valencia	282	29	10.3
ICG 87358 (OG 69-6-1 × NCAc 17090)	Spanish	211	21	9.9
ICG 7633 (UF 71513)	Valencia	908	107	11.8
ICG 2716 (EC 76446 [292])	Valencia	59	10	16.9
ICG 86708 (JH 60 × PI259747)	Valencia	228	20	8.8
ICG 86644 (HG 1 × NCAc 17090)	Spanish	84	8	9.5
ICG 86707 (G 37 × NCAc 17090)	Virginia	77	8	10.4
ICG 86635 (NCAc 2768 × NCAc 17090)	Valencia	124	13	10.5
ICG 86745 (Commet × EC 76446 [292])	Spanish	551	61	11.1
Total		6,584	713	10.8

[a] Since there was 100% correlation (with the exception of a few seeds that did not germinate) between enzyme-linked immunosorbent assay (ELISA) and seed transmission among 6 cultivars (Table 1), it is assumed that the percentage of seed positive by ELISA on the basis of tests conducted on cotyledons is also equal to the percentage of seed transmission among these 22 cultivars.

that gave negative results in ELISA on the basis of tests on cotyledons were negative in grow-out tests.

Frequency of seed transmission in peanut. In tests with six peanut genotypes, with the exception of a few seeds that did not germinate, each seed that contained virus in its cotyledons also gave positive results in grow-out tests, as confirmed by the presence of symptoms and ELISA (Table 1). A perfect correlation was observed between symptoms and the ELISA tests on the seedlings. Virus presence in grow-out tests was confirmed for the 5 seedlings of each genotype tested by ISEM and infectivity assays. For the rest of the genotypes, frequency of seed transmission was determined on the basis of positive reaction in ELISA tests conducted on a portion of cotyledon (Table 2). Genotype ICG 4790 (KU No. 24) showed the lowest frequency, 3.5% (Table 1).

In tests for ascertaining seed transmission frequency from plants infected through seed-borne inoculum, ICG 156 (cv. M 13), ICG 221 (cv. TMV 2), and ICG 4749 (PI337394F) showed 55.5% (71/128), 48.4% (45/93), and 50% (18/36) seed transmission, respectively.

Frequency of seed transmission in millets and sorghum. IPCV-H was seed-transmitted in finger millet (5.2%), foxtail millet (9.7%), and pearl millet (0.90%) but not in sorghum (Table 3).

DISCUSSION

The ELISA procedure described is reliable to detect seed transmission frequency of IPCV-H in peanut seed. Unlike peanut mottle (PMV; 1) and peanut stripe viruses (PStV; 5), IPCV-H antigens were detected in testae of all the seed collected from infected peanut plants. This result is similar to the findings of Iizuka (7) and Bowers and Goodman (2) for soybean mosaic potyvirus (SMV) in soybean, and Maury et al. (10) for pea seedborne mosaic potyvirus (PSbMV) in peas. Although infectious SMV and PSbMV were recovered from the testae of immature seed, both the viruses were inactivated during the seed maturation, even though viral antigens were detected in testae of mature seed by ELISA. In this study, infectivity tests were conducted on extracts from testae of all mature peanut seed which transmitted IPCV-H, with negative results. IPCV-H presence only in cotyledons was correlated with transmission to seedlings in six peanut genotypes, including Spanish and Valencia types. Therefore, ELISA tests on a portion of cotyledons will be adequate to identify the seed with potential to transmit the virus. Consequently, tests on dry seed lots will facilitate conservation of virus-free seed. Although a frequency ranging from 3.5 to 14.0% transmission was observed with a range of genotypes (Table 1), the majority of the genotypes had about 10% IPCV-H seed-transmission (Table 2). Reddy et al. (16) reported a similar rate (11%) of seed transmission for two isolates of IPCV by grow-out tests. Frequency of seed transmission for IPCV is higher than any of the currently known seed-transmitted peanut viruses (15), thus posing serious problems in seed exchange. Interestingly, plants infected through seed-borne inoculum showed over 50% seed transmission. These plants showed less stunting and produced more pods compared to plants infected at an early stage from soil-borne inoculum (*results not shown*). The higher rate of seed transmission in the second generation of embryonically infected plants than in the first generation emphasizes the risk of virus propagation through seed. This aspect was also highlighted by Thouvenel and Fauquet in the case of PCV (19).

An isolate of PCV from Senegal was 14% seed-transmitted as determined by grow-out tests (21). Although ELISA tests were used to determine seed transmission frequency for an isolate of PCV from Burkina Faso, testae of seed from infected plants were not individually tested (8). Interestingly, 16.5% seed were positive by ELISA and less than half (7.5%) transmitted the virus in grow-out tests. The authors de-hulled the seeds but did not mention if testae were carefully excluded for preparing ELISA extracts. Therefore, the discrepancy may have arisen due to retention of enough testae in some of the seed while preparing extracts to give a positive ELISA reaction. It is also likely, as discussed by the authors, that some infected seeds may not have germinated in grow-out tests conducted under field conditions. In our experiments, seeds were tested under glasshouse conditions and care was taken to avoid exposure to soil pathogens. In 200 dissected seeds, PCV was detected in both cotyledons and embryos of 32 seeds (8), as observed in the case of IPCV-H.

Transmission of IPCV in the seed of millets and sorghum, which are often grown in rotation or as intercrops with peanut, was studied because of the potential of seed-transmitted virus to establish clump disease in soils infested with the fungal vector *Polymyxa* sp. This aspect also has significance to plant quarantine. A PCV isolate from Senegal was not seed-transmitted in *S. arundinaceum* (Desv.) Stapf (19). *S. arundinaceum* was not included in our study. The only host in which IPCV-H was not seed-transmitted was *S. bicolor*. Millets in which IPCV-H is seed-transmitted are hosts of the vector *Polymyxa* (9,14). Additionally, the vector is widely distributed in the majority of sandy soils in India (4) and West Africa (19). Experiments conducted at IAC have shown that virus-containing peanut seed could not serve as a source of inoculum to the vector, whereas virus-infected rhizomes of *Cynodon dactylon* (L.) Pers. led to disease establishment (3). *Polymyxa* resting spores are seldom observed in peanut roots, and it does not reproduce in peanut, reducing the risk for seed-borne virus to establish as soil-borne inoculum in new sites. In contrast, monocotyledonous hosts such as millets and *C. dactylon* which do not show overt symptoms are a great threat, since they support *Polymyxa* multiplication and thus may promote virus acquisition. Although, in West Africa, pearl millet was regarded as a non-host for *Polymyxa* and PCV (20), recent observations (4) show that pearl millet is indeed a host of several *Polymyxa* isolates from Senegal. These findings have important implications for the epidemiology of PCV and IPCV. Therefore, to avoid dissemination of IPCV, care should be taken to avoid movement of germ plasm of monocotyledonous crops raised on infested soils to prevent virus spread and disease establishment in new areas. We are currently evaluating additional monocotyledonous crops for seed transmission frequency and for their potential to serve as a source of inoculum for the dissemination and establishment of IPCV.

Table 3. Frequency of seed transmission of Indian peanut clump virus, Hyderabad isolate, in millets and sorghum

Name of the crop	Cultivar	No. of seedlings Tested	No. of seedlings Positive by ELISA[a]	Percent seed transmission
Finger millet (*Eleusine coracana*)	Arjuna	1276	66	5.2
Foxtail millet (*Setaria italica*)	ISE 147	1722	167	9.7
Pearl millet (*Pennisetum glaucum*)	WCC 75	213	2	0.9
Sorghum (*Sorghum bicolor*)	ICSV 1	1114	0	0

[a] Enzyme-linked immunosorbent assay.

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