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Resistance of wild lettuce to lettuce infectious yellows virus

Haley, Valerie Jean, M.A.

San Jose State University, 1990

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RESISTANCE OF WILD LETTUCE TO LETTUCE INFECTIOUS YELLOWS VIRUS

A Thesis

Presented to

The Faculty of the Department of Biological Science

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

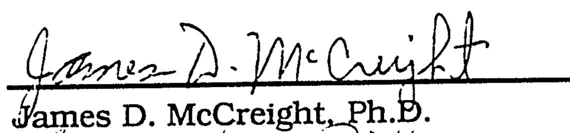
Master of Arts

By

Valerie Haley

May 1990

APPROVED FOR THE
DEPARTMENT OF
BIOLOGICAL SCIENCES



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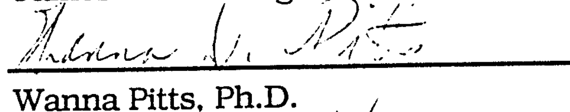

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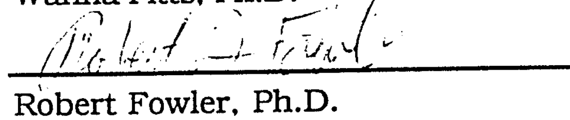

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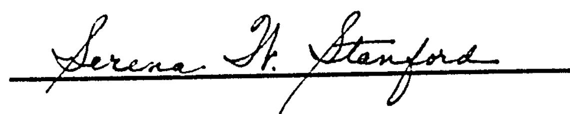

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RESISTANCE OF WILD LETTUCE TO LETTUCE INFECTIOUS YELLOWS VIRUS

ABSTRACT

Lettuce Infectious Yellows Virus (LIYV) is a serious problem in the southwest United States. LIYV infects important crops including lettuce, beets, cantaloupe, and squash. LIYV infects 45 plant species in 15 families. The virus is transmitted by the tobacco whitefly, *Bemisia tabaci.*

The present study investigated the genetics of resistance to LIYV observed in wild lettuce, *Lactuca saligna.* Cross-pollinations were made between susceptible and resistant accessions of *L. saligna.* Observed F_2 segregation ratios did not conform to any known simple pattern of inheritance. Instead the F_2 families showed a continuous range of disease severity, which implies that *L. saligna* has polygenically controlled resistance to LIYV.

Analysis of variance showed a significant difference among the parents and their F_2 families for mean number of infected leaves per plant. Means comparisons showed that reciprocal F_2 families were not significantly different. This indicates that cytoplasmic inheritance is not involved.

INTRODUCTION

Lettuce infectious yellows (LIY) is a recently recognized virus disease of the desert southwest United States. The disease became apparent during the 1981-1982 winter production season when it reached epidemic proportions in southern California and Arizona (McCreight *et al.*, 1986; Duffus and Flock, 1982; Duffus *et al.*, 1986). LIYV (lettuce infectious yellows virus) is one of five viruses transmitted by the sweet potato whitefly, *Bemisia tabaci* Genn. (Hoefert *et al.*,1988).

The LIY epidemic damaged many important crops in California and Arizona desert production areas, including lettuce (*Lactuca sativa* L.), cantaloupe (*Cucumis melo* L.), squash (*Cucurbita* spp.), and sugar beets (*Beta vulgaris* L.) (Duffus and Flock, 1982). The economic losses were severe, amounting to a reported $100 million to growers and consumers. Crop yields were down. Lettuce yield was 50-75% lower than expected. Squash and melon growers suffered an $8 million crop loss (Duffus *et al.*,1986).

Crop loss due to LIY continues to be a problem in the desert southwest (Duffus *et al.*, 1986). In fall 1988, the Arizona lettuce crop was severely infected, resulting in growers recovering only about half their production costs (Shannon, 1988). In addition to the impact of the disease, unseasonably high temperatures contributed to lower quality and yield of lettuce.

LIYV has a wide host range, 45 plant species in 15 families (Duffus *et al.*, 1986). A dozen of these species are weeds. Because both crops and weeds can be hosts, it is difficult to eradicate diseased

plants. The weeds act as virus reservoirs from which whiteflies can infect nearby crops.

LIY is a yellowing-type disease characterized by the following symptoms: stunting of infected plants, rolling, yellowing, reddening, vein-clearing and brittleness of infected leaves (Duffus and Flock, 1982; Duffus *et al.*, 1986; McCreight *et al.*, 1986). Plants that normally have high levels of anthocyanin show interveinal reddening instead of yellowing (McCreight, 1987). Infected plants may also have necrotic lesions at or near leaf margins (McCreight *et al.*, 1986). Symptoms appear on the lowest leaves first in cultivated lettuce about two to three weeks after inoculation (Hoefert *et al.*, 1988; McCreight, 1987). LIY symptoms are similar to those caused by the aphid-transmitted beet western yellows virus (Duffus *et al.*, 1986; McCreight *et al.*, 1986). Symptoms result in reduced marketable yield and reduced quality and shelf-life (McCreight, personal communication).

Duffus and his colleagues at the U.S.D.A., Agricultural Research Service discovered and named LIYV in 1982 (Wood, 1988). Duffus *et al.* (1986) purified the virus and determined its ultrastructure. The virus particles are flexuous filaments approximately 13-14 nm wide and 2000 nm long (Duffus *et al.*, 1986; Hoefert *et al.*, 1988). The virus is found in the host's phloem tissue and is composed of RNA and protein (Hoefert *et al.*, 1988).

LIYV is thought to have a possible relationship to the closterovirus group (Hoefert *et al.*, 1988). Although there is no direct evidence that LIYV is a closterovirus, its size and flexibility are like that of closteroviruses (Duffus *et al.*, 1986). Hoefert and McCreight

(personal communication) performed light microscope studies of LIYV inclusion bodies in infected lettuce. Inclusion bodies were phloem-limited as are those described by Christie and Edwardson (1987) for the closterovirus group. LIYV is atypical of the group because it is neither aphid-transmitted nor mechanically transmissible (Christie and Edwardson, 1987; Duffus *et al.*, 1986).

One way of controlling the spread of LIY is to reduce whitefly populations. Use of insecticides has not proved effective. It is difficult to spray the undersides of leaves where the whiteflies live and the whiteflies' waxy coating easily sheds the spray (Duffus *et al.*, 1986). Whiteflies have become resistant to the insecticides permethrin and cypermethrin that have been heavily used in the Imperial Valley (Toscano, 1987). Natural insect predators of whiteflies such as mirids, chalcidids, and *Chrysopa* spp. may provide some disease control (El-Helaly *et al.*, 1971).

Crop and weed management can also be used to control LIY. Duffus stressed the importance of destroying weeds that the whiteflies prefer, especially wild morning glory (*Convolvulus sepium* L.), sunflower (*Helianthus* spp.), ground cherry (*Physalis* spp.), and wild lettuce (*Lactuca* spp.) (see Wood, 1988). Crops should be rotated so that there are host-free periods between crops. A two to three week period free of cucurbits in July or August would reduce the LIY infection rate (Duffus *et al.*, 1986; Hassan and Duffus, 1990).

Another way to achieve disease control is breeding for resistant plants. McCreight *et al.* (1986) screened lettuce cultivars for resistance to LIY. They found a range of tolerances in the cultivars.

'Climax' showed the mildest symptoms, whereas 'El Toro', 'Minetto', and 'Emperor' had the most severe symptoms. Their findings suggested that there was a relationship between the inherent vigor of a cultivar and LIYV symptom severity. The most vigorous cultivar had the mildest symptoms.

Because cultivated lettuce did not appear to have useful resistance to LIY, McCreight (1987) began investigating wild lettuce as a potential source for breeding resistance into cultivated lettuce. He screened wild accessions of *L. serriola* L., *L. virosa* L., and *L. saligna* L. All of the accessions of *L. serriola* and *L. virosa* showed disease symptoms after inoculation with LIYV. Fifteen of 25 *L. saligna* accessions were found resistant to the virus. McCreight (1987) concluded that *L. saligna* is a good source of resistance to LIY and has promise in breeding programs. Past research found *L. saligna* to be a source of insect and disease resistance. Plant introduction (PI) 261653, an accession of *L. saligna* from Portugal, was found by Whitaker *et al.* (1974a) to be resistant to cabbage looper, *Trichoplusia ni* (Hubner). Whitaker *et al.* (1974a) found that the larval stages of the cabbage looper were retarded by feeding on leaves of PI 261653 and that 26% of the larvae died before the second instar stage.

Provvidenti *et al.* (1980) found PI 261653 to be resistant to a strain of cucumber mosaic virus (CMV). Their tests also indicated that *L. saligna* is resistant to turnip mosaic virus. Netzer *et al.* (1976) assayed *L. saligna* accessions collected in Israel for resistance to local races of downy mildew (*Bremia lactucae* Reg). They found six accessions to be resistant. Michelmore (1986) screened a line of *L.*

saligna with isolates of lettuce anthracnose (*Marssonina panattoniana* (Berl.) Magn.). He found *L. saligna* resistant to all the isolates tested.

The natural insect and disease resistance found in *L. saligna* can be a source of genes for lettuce improvement. *L. saligna* is a wild relative of cultivated lettuce, *L. sativa*. Both species are in the Cichoreae tribe of the Asteraceae (Compositae) (Ryder, 1986). *Lactuca saligna* and *L. sativa* are cross-fertile but their hybrids have low fertility (Provvidenti *et al.*, 1980; Ryder, 1979).

The objective of the present study was to investigate the genetic nature of the resistance to LIYV observed in *L. saligna*. My hypothesis was that from crosses between susceptible and resistant accessions of *L. saligna* I could determine how many genes control resistance by examining F_2 phenotypic ratios. This information may facilitate breeding programs for LIYV resistant lettuce cultivars. The present study also documents selected *L. saligna* characteristics.

MATERIALS AND METHODS

PARENTAL LINES

Seeds of 18 PIs of wild lettuce, *L. saligna*, were planted in June 1987 (Table 1). Three of these accessions were susceptible to LIYV and the other 15 resistant (McCreight, 1987). Twenty-five seeds of each accession were sown in 10-cm plastic pots containing 20 mesh sand and a square of Mirafi cloth that covered the drain holes. Pots were placed in a Conviron growth chamber at 18 C with a 16 hr photoperiod (1/2 incandescent and 1/2 flourescent lighting). Light intensity, measured with a LICOR photometer, model LI-185, was 250 microeinsteins/m^2/sec at the center of the chamber. For each accession, germination records were kept for first emergence, 50% emergence, and total emergence. After the seedlings emerged, the growth chamber temperature was raised to 22 C and the seedlings were watered with 0.33% modified Wards solution (Ward, 1973). Ten seedlings of each accession were transplanted into 10-cm pots (one seedling per pot) at the first true leaf stage of growth. On June 16,1987, half of the seedlings of each accession were placed in a greenhouse with a natural photoperiod. The other half of the seedlings remained in the growth chamber as specified above to hasten flowering. After 45 days (July 31,1987), all plants were transported to the U.S.D.A. research station in Salinas, California where they were transplanted to 24-cm plastic pots containing sand and placed on automatic irrigation. The emitter system supplied 0.33% modified Wards solution four times a day for two minutes

Table 1. Accessions of wild lettuce, *Lactuca saligna* , their reaction to inoculation with lettuce infectious yellows virus and native origin (R = resistant; S = susceptible). Reactions are those reported by McCreight, 1987.

Accession	Reaction	Origin
PI 261653	R	Portugal
PI 490999	S	Turkey
PI 491000	S	Turkey
PI 491001	S	Greece
PI 491204	R	Greece
PI 491205	R	Greece
PI 491206	R	Greece
PI 491207	R	Greece
PI 491208	R	Greece
PI 509519	R	Greece
PI 509521	R	Greece
PI 509522	R	Greece
PI 509523	R	Greece
PI 509524	R	Greece
WP 246A	R	Greece
PI 509525	R	Greece
U 5	R	Israel
UC83US1	R	California

each time. Plants were grown until maturity without supplemental light. Data on the following characteristics were recorded: location of spines and anthocyanin, first flower date, flower diameter, total plant height (crown to stem apex) at maturity, and seed color.

CROSS-POLLINATIONS

Cross-pollinations were made between the 15 resistant and three susceptible PIs (Table 1). Each resistant line was cross-pollinated with each of the following susceptible lines: PI 491000, PI 491001, and PI 490999. Reciprocal crosses were also made. The number of crosses for each set of parents ranged from 10 to 15, including reciprocals. Because many of the lines bloomed at different times of the morning, the desired parents were often held at different temperatures to delay or advance anthesis.

Because lettuce, including *L. saligna*, has perfect flowers and is obligately self-pollinating, the following method of cross-pollination was used. The flower head consists of 10-15 florets. Each floret has an anther sheath through which the stigma elongates (Fig.1). The flower of the female parent must have its pollen removed before cross-pollination. This is done by washing the pollen from the emerging stigma with a fine stream of water and blowing dry. Washing and blowing is repeated successively three times. Then a large drop of water is left on the head. This serves to keep foreign pollen away and to displace any remaining pollen of the female parent. At this point, the flower head is tagged with the parents' identifications and date.

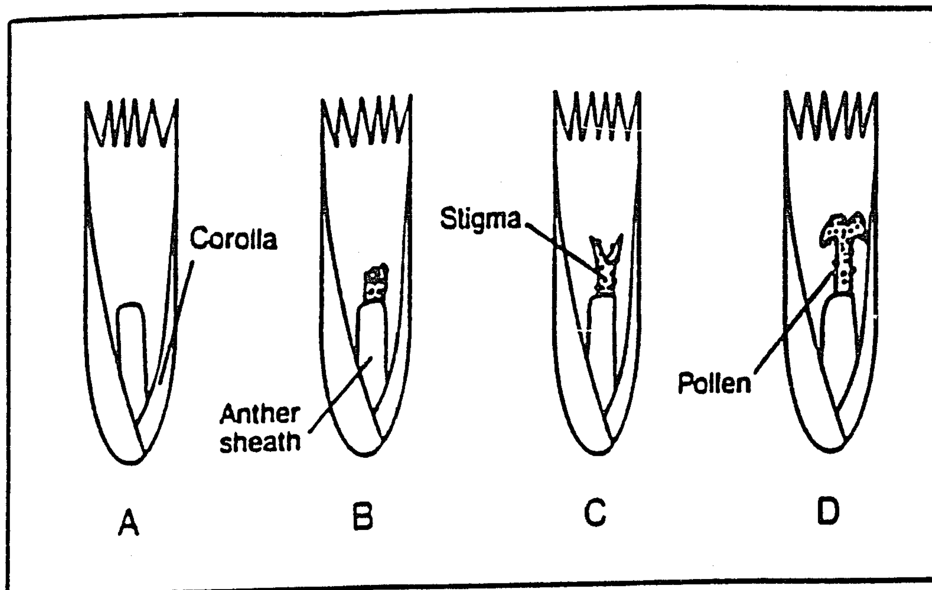

Figure 1. Structure and stages of anthesis of a lettuce floret.

(A) Early, stigma not emerged from anther sheath.

(B) Stigma emerging, covered with pollen.

(C) Ideal stage for pollen removal.

(D) Too late for crossing; selfing has occurred.

(From Ryder, 1986)

The flower is receptive to cross-pollination when its stigma splits open (Ryder, 1986) (Fig. 1). Mature pollen from the male parent is applied by gently pressing the two flower heads together. Throughout the above procedure, a hand lens is used to monitor floral structures and pollen maturation. About six hundred cross-pollinations were done over a four month period beginning in September, 1987.

DETERMINATION OF F_1 HYBRIDS

About 12-14 days after cross-pollination, the F_1 seeds were ready to harvest. Tagged seed heads were individually collected. Each seed head was placed in a separate envelope and assigned a unique pedigree number.

F_1 families and their respective parents were sown in 10 cm plastic pots containing sand. Twenty seeds from each hybrid combination and 10 seeds of each parent were sown. Families from crosses of a resistant female with a susceptible male were sown first. For example, the combination 261653-5 female x 491000-2 male sowing consisted of seeds from three seed heads: 34722 (six seeds), 34723 (seven seeds), 34724 (seven seeds). Later, lines from crosses of a susceptible female with a resistant male were sown.

Because self-pollination and seed contamination can occur during crossing and harvesting, respectively, it was necessary to examine every putative F_1 plant to verify that it was in fact an F_1 individual. Hybrids were determined either by morphological comparison of a putative F_1 with its parents or by the results of inoculation with LIYV. True hybrids have morphological characteristics of both parents. Disease resistance is also useful for

identification of F_1 plants. Preliminary observations indicated that LIYV resistance was conditioned by recessive genes (McCreight, personal communication). In a cross of a resistant female with a susceptible male, the hybrids will have symptoms after inoculation with LIYV, whereas plants from self-pollination will be resistant. Availability of a sufficient number of whiteflies for LIYV inoculation was the main reason for successive sowings.

Because only two to three F_1 families were inoculated at a time, inoculations were done over a six month period beginning in January, 1988. Subject to whitefly availability, the inoculation format was as shown in Table 2. The lettuce cultivar 'El Toro' was included in each test as a susceptible control to indicate that the whiteflies were viruliferous. Random spot-checks using enzyme-linked immunosorbent assay (ELISA) were done to verify LIYV infection. ELISA procedures were done according to those of Duffus *et al.* (1986).

LIYV INOCULATION PROCEDURE

Plants were inoculated with LIYV at three to four weeks of age using *B. tabaci* as the vector. The LIYV isolate was obtained from infected lettuce plants maintained at the U.S.D.A. Salinas greenhouse. The isolate used had been collected in Imperial Valley. Whiteflies from an insectary greenhouse were transferred from aviruliferous sweet potato, *Ipomoea batatas* (L.), plants to detached LIYV-infected lettuce leaves. The leaves were placed in a vial of water to maintain

Table 2. LIYV inoculation format.

Entry	Inoculated	Control
Parent 1	2	2
Parent 2	2	2
P_1 x P_2	10	5
P_2 x P_1	10	5
'El Toro'	4	2

turgor and permit whitefly feeding. The whiteflies fed for 24 hrs. to acquire the virus. Fifty whiteflies were transferred via pipette tubing to each test plant. Test plants were covered with a clear plastic sleeve cage (105 mm x 50 mm diameter) capped with nylon fabric. After a 48 hr. feeding period, the sleeve cages were removed and the plants were sprayed with Resmethrin three times at 45 min. intervals to kill the whiteflies and stop the inoculation. Control plants were not inoculated, but were also kept in sleeve cages and sprayed as above.

REARING *BEMISIA TABACI*

The whiteflies used in the inoculation procedure were reared in an insectary greenhouse on aviruliferous sweet potato plants. Because *B. tabaci* is of tropical origin, it is essential to maintain the greenhouse temperature in a warm range (25-45 C). To insure this, the greenhouse was monitored with a PTC model No. 615 thermograph. Within the greenhouse were four insect "hotels," each containing three sweet potato plants. Whiteflies were removed from the "hotels" through portholes lined with fabric sleeves by a modified cordless, rechargeable vacuum cleaner (Dustbuster Plus, Black and Decker, Inc.) (Fig. 2). To establish a whitefly colony, 1000 whiteflies were placed in a "hotel" containing two insect-free sweet potato plants. Two weeks later a third plant was added. Every three to four weeks a new plant was exchanged for a declining one. To support this cycling of plants, a second greenhouse was used for propagating sweet potato plants. To avoid root rot, cuttings were rooted in a medium of 1 part sand to 2 parts (V:V) potting soil. Plants were fertilized weekly with

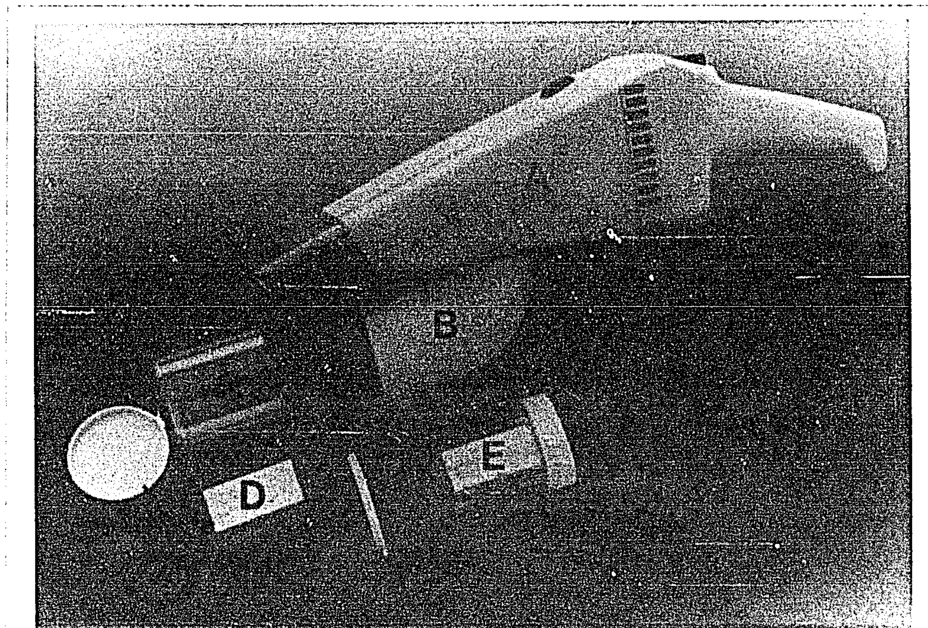

Figure 2. Whitefly collection system, modified rechargeable vacuum.

(A) Cordless rechargeable auto vacuum cleaner.

(B) Cylinder adaptor.

(C) Clear plastic cylinder sleeve cage.

(D) Lettuce test plant.

(E) Inoculation chamber.

(From Cohen et al., 1989)

concentrated 20-20-20 fertilizer. Care was taken to keep plants as insect-free as possible, using frequent insect surveys and spraying of insecticides. Because whiteflies are sensitive to insecticides, sprayed plants had to be held three to four days after spraying before they could be placed in a "hotel."

PRODUCTION OF F_2 SEED

F_1 hybrids were grown to maturity and allowed to self-pollinate to produce F_2 seed. To speed maturation, greenhouse lights were put on a timer to provide a supplemental photoperiod from 7:00 pm to 3:00 am every night from May 20, 1988 through August 30, 1988. After the plants had self-fertilized, seed was harvested from F_2 plants separately and assigned a unique F_2 pedigree number. F_2 seed was cut with dead lettuce seed at a rate of 1/8 teaspoon live seed to 1/2 teaspoon dead seed to reduce thinning of plants during the F_2 field trials. The dead seed was prepared by oven drying at 200 C for eight hours.

FINDINGS FROM GREENHOUSE AND FIELD TESTS CHANGE PROJECT DESIGN

Unexpected results from U.S.D.A., Imperial Valley field tests in early spring, 1988 showed many of the accessions that had been previously determined resistant by McCreight (1987) were displaying LIY symptoms. Results from the field were confirmed by greenhouse inoculation tests that same spring.

To explore the possibility of new LIYV strains, two different types of inoculation tests were performed. A transmission test varied the number of whiteflies used per plant to transmit LIYV. The results

were compared to past findings to see if there were any indications that the virulence of the virus had changed. A LIYV isolate test used four isolates provided by J. E. Duffus that came from three different species (*L. sativa, Cucumis melo,* and *Beta vulgaris*). The isolates were collected in Yuma, Arizona. Both tests compared symptom expression on PI 261653 and cultivar 'Summer Bibb'.

F_2 FIELD TEST FOR NATURAL INOCULATION

Due to the 1988 results, it was decided that the remainder of the project would concentrate on F_2 individuals that resulted from crosses between PI 261653 as the resistant parent and PI 490999, PI 491000, or PI 491001 as the susceptible parent. PI 261653 was chosen because of its resistance to an array of insects and diseases. The susceptible PIs were chosen because they were the first ones found susceptible by McCreight (1987).

The field test was planted at the U.S.D.A., Irrigated Desert Research Station, Brawley, Calif. during the 1988-1989 winter production season. The F_2 and parental generations were planted in a field trial with three replications subjected to natural infection. Each replication consisted of 10 randomized plots of F_2 plants from PI 261653 X PI 490999, PI 261653 X PI 491000, PI 261653 X PI 491001, their reciprocals, and the four parents (Fig.3). Each plot was 15.25 meters long and consisted of two rows of approximately 45-50 plants per row (90-100 per plot).

Plot	REP 1	Plot	REP 2	Plot	REP 3
10	F_2 11434	20	F_2 11423	30	F_2 11409
11	F_2 11401	21	PI 491000	31	F_2 11400
12	F_2 11430	22	PI 261653	32	F_2 11433
13	F_2 11394	23	F_2 11404	33	PI 491000
14	PI 490999	24	F_2 11399	34	PI 491001
15	F_2 11422	25	F_2 11435	35	PI 261653
16	PI 261653	26	PI 491001	36	F_2 11420
17	PI 491000	27	F_2 11431	37	F_2 11438
18	PI 491001	28	PI 490999	38	PI 490999
19	F_2 11415	29	F_2 11417	39	F_2 11428

Figure 3. Schematic of the replicated field test at the Irrigated Desert Research Station, Imperial Valley, California. *Lactuca saligna* parent and F_2 generations subjected to natural infection with Lettuce Infectious Yellows Virus. Plot dimensions 15.3 x 1.0 m. PI = Plant Introduction

Fertilization and irrigation were done according to standard cultural operations common to lettuce production in the southwest United States (Whitaker *et al.*, 1974b). Prior to the sowing of the seed, the field was fertilized with 120 lbs/acre of 11-52-0 (monobasic ammonium phosphate) and 159 lbs/acre of 46-0-0 (urea).

The initial irrigation was applied Sept. 20, 1988 with sprinklers for 36 hrs. For the remainder of the growing season, the field was furrow irrigated at three to four week intervals, depending on weather conditions. The seedlings were thinned to 35 cm apart. This thinning resulted in a sample size of about 2300 plants for the three replications.

The *L. saligna* seedlings were exposed to natural field inoculation by whiteflies transmitting LIYV. On March 20, 21, and 22 each plant in the three replications was evaluated for symptom severity by counting the number of infected leaves.

The field data were analyzed statistically as a randomized complete block using the Least Squares analysis of the SAS General Linear Model Procedure (SAS, 1985a) because the experimental design was unbalanced (i.e., each plot had a unique sample size, n). Homogeneity of plot variances of was tested using the Burr-Foster Q-test (Anderson and McLean, 1974). Skewness was tested using the SAS Univariate Procedure (SAS, 1985b). Because these data were counts, the data were transformed prior to analysis using the $\sqrt{x+0.5}$ transformation (Sokal and Rohlf, 1981). Mean number of infected leaves per plant were calculated using the LSMEANS option of the Least Squares analysis. Means comparisons (untransformed data) were

done using *t*-tests calculated by the PDIFF option of the Least Squares analysis. Frequency distributions (untransformed data) were plotted by pedigree.

RESULTS

PARENTAL LINES

The germination record varied with each *L. saligna* accession (Table 3). First emergence ranged from three to seven days after planting. Accessions PI 509519 and PI 491207 were the fastest, whereas PI 261653 was the slowest. Fifty percent emergence ranged from four to ten days after sowing. Total emergence ranged six to eleven days. Overall, germination was slower in accessions UC83US1, U 5, and PI 261653. The number of seedlings germinated per 25 seeds ranged from 10 to 24. Accession UC83US1 had the lowest proportion germinated.

Selected *L. saligna* characteristics were recorded when the accessions reached maturity (Table 4). There were two experimental groups. One group had plants grown in the greenhouse after the first true leaf stage. The other group had plants grown for 45 days in a growth chamber with a daily photoperiod of 16 hours and then grown in the greenhouse. Days to flowering and plant height varied between the two groups, whereas flower diameter, anthocyanin location, and spine location did not differ between treatments.

Most plants grown in the growth chamber treatment (16 hour photoperiod) reached first flowering earlier than those grown with a natural, summer photoperiod. Notable differences in first flowering were seen in accessions PI 491001, PI 491206, and PI 491207. PI 491001 plants in the growth chamber treatment flowered 68.2 days earlier than those grown in the greenhouse. PI 491206 and

Table 3. Days from sowing to first, 50% and total emergence of *Lactuca saligna* accessions in a growth chamber , 16 hr. photoperiod 18 C. Percent represents the number germinated per 25 seeds.

Accession	1st	50%	Total	%
PI 261653	7.0	9.0	10.0	64.0
PI 490999	5.0	7.0	8.0	76.0
PI 491000	5.0	6.0	8.0	80.0
PI 491001	5.0	5.0	7.0	68.0
PI 491204	5.0	7.0	8.0	88.0
PI 491205	5.0	7.0	9.0	88.0
PI 491206	5.0	7.0	8.0	84.0
PI 491207	3.0	4.0	6.0	88.0
PI 491208	5.0	6.0	7.0	96.0
PI 509519	3.0	4.0	8.0	76.0
PI 509521	5.0	7.0	7.0	72.0
PI 509522	6.0	7.0	8.0	76.0
PI 509523	5.0	7.0	7.0	76.0
PI 509524	5.0	7.0	8.0	92.0
WP 246A	5.0	7.0	8.0	72.0
WP 247	5.0	7.0	8.0	96.0
U 5	5.0	10.0	10.0	52.0
UC83US1	6.0	10.0	11.0	40.0

Table 4. Characteristics of *Lactuca saligna* accessions recorded at maturity. Plants grown under two treatments, greenhouse and growth chamber. Data on flowering and plant height are means of five plants.

		Days to	Flower diameter	Plant height	Location of	
Accession	Treatment	flower	(cm)	(cm)	Anthocyanin	Spines
PI 261653	GH*	192.6	1.5	148 .0	leaf margin	midribs
					stem	lobe tips
	GC**	187.2	1.4	166.0	same	same
PI 490999	GH	118.2	1.3	155.0	stem	midribs
						serrations
						lobe tips
	GC	96.6	1.3	141.0	same	same
PI 491000	GH	130.0	1.3	120.0	leaf margin	midribs
					stem	lobe tips
	GC	100.7	1.3	94.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of	
					Anthocyanin	Spines
PI 491001	GH	163.0	1.5	160.0	stem	midribs
						lobe margins
	GC	94.8	1.5	142.0	same	same
PI 491204	GH	189.4	1.5	202.0	leaf margin	midribs
						lobes
						serrations
	GC	199.6	1.6	200.0	same	same
PI 491205	GH	119.4	1.3	162.0	leaf margin	midribs
					new growth	lobe tips
					stem	serrations
	GC	109.4	1.3	135.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of	
					Anthocyanin	Spines
PI 491206	GH	195.4	1.4	177.0	leaf margin	midribs
					new growth	lobe tips
					stem	serrations
	GC	142.8	1.3	166.0	same	same
PI 491207	GC	105.4	1.4	178.0	same	same
	GH	156.6	1.4	194.0	leaf margin	midribs
						lobe tips
PI 491208	GH	157.0	1.4	204.0	leaf margin	midribs
					stem	lobe tips
	GC	112.8	1.4	180.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of	
					Anthocyanin	Spines
PI 509519	GH	133.6	1.4	194.0	leaf margin	midribs
					stem, blade	lobe tips
	GC	117.8	1.4	187.0	same	same
PI 509521	GH	148.8	1.4	194.0	leaf margin	midribs
					stem	lobe tips
	GC	111.4	1.4	164.0	same	same
PI 509522	GH	140.4	1.5	197.0	leaf margin	midribs
					new growth	lobe tips
					stem	
	GC	105.0	1.5	169.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of	
					Anthocyanin	Spines
PI 509523	GH	182.8	1.4	178.0	leaf margin	midribs
					stem	lobe tips
						serrations
	GC	145.2	1.4	169.0	same	same
PI 509524	GH	165.2	1.3	199.0	leaf margin	midribs
					stem	lobe tips
	GC	132.0	1.3	203.0	same	same
WP 246A	GH	116.8	1.4	167.0	leaf margin	midribs
					stem	lobe tips
						serrations
	GC	102.6	1.4	139.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of	
					Anthocyanin	Spines
PI 509525	GH	137.8	1.3	169.0	leaf margin	midribs
					new growth	lobe tips
					stem	
	GC	99.4	1.3	161.0	same	same
UC83US1	GH	168.6	1.5	174.0	leaf margin	midribs
					stem spines	lobe tips
	GC	184.0	1.5	198.0	same	same

Table 4. (continued)

Accession	Treatment	Days to flower	Flower diameter (cm)	Plant height (cm)	Location of Anthocyanin	Location of Spines
U 5	GH	151.0	1.5	184.0 5	leaf margin	midribs
					leaf blades	lobe tips
					new growth	serrations
	GC	123.0	1.5	173.0	same	same

* Plants grown in the greenhouse after first true leaf stage.

**Plants grown in growth chamber with a 16 hr. photoperiod for 45 days and then grown in the greenhouse until maturity.

PI 491207 in the growth chamber treatment flowered 52.6 and 51.2 days earlier, respectively, compared with siblings grown in the greenhouse treatment. There were two exceptions to the above trend. PI 491204 and UC83US1 plants in the greenhouse treatment flowered about 10 and 15 days earlier than those in the growth chamber treatment. Most plants in the greenhouse treatment were on the average taller than their counterparts in the growth chamber treatment. The differences in height ranged from 2.0 to 30.0 cm. Accession PI 261653 was an exception because growth chamber plants were 18.0 cm taller on the average than greenhouse plants.

Locations of anthocyanin and spines were the same for a given accession, regardless of growing conditions. Anthocyanin was found in the stems and leaf margins of most accessions. A few accessions had anthocyanin associated with new growth and spines. All plants of all accessions had spines located on their leaf midribs. The second most common location of spines was on leaf lobes and serrations.

CROSS-POLLINATIONS

Because all of the accessions received the greenhouse and growth chamber treatments, the span of flowering was increased for each accession. This provided parent flower material for cross-pollinations over a four month period. Most of the accessions bloomed early in the morning from about 7:00 to 8:00 am. In a few cases, desired parents did not bloom at the same time of the morning. Accessions U 5 and UC83US1 tended to bloom half an hour later than the other accessions. This problem was solved by holding the earlier flowering parent at cooler temperatures outside the greenhouse to

delay anthesis or by placing U 5 and UC83US1 under a lamp for two to three hours to hasten anthesis before cross-pollinations. The majority of the cross-pollinations yielded fertile seed. There were no apparent differences between reciprocal crosses. Either parent could serve as the male or female. Seed matured 12 to 14 days after cross-pollination.

F_1 HYBRID DETERMINATION

The proportion of true F_1 hybrids per parental combination ranged from 19.0 to 80.0 %. Low percentages were due to self-pollination or seed contamination. The majority of hybrids having a resistant female parent showed symptoms as predicted by the idea of resistance being conditioned by recessive genes. Morphologically, some plants appeared to be true hybrids, but they were symptomless after inoculation. Morphological comparisons of a putative F_1 with its parents were more reliable than inoculation results for determination because of the possibility of ineffective inoculation, i. e. no infection. Leaf morphology, leaf color, and spines were the most useful characteristics for hybrid determination.

GREENHOUSE INOCULATIONS

Parents and F_1 families were inoculated with the LIYV isolate used by McCreight (1987). Symptom expression was evaluated weekly starting three weeks after inoculation. Records were kept for four to six weeks, depending upon when symptom expression stabilized. Most of the *L. saligna* plants had symptoms four to five weeks after inoculation, whereas 'El Toro' showed symptoms at about three weeks. Percent infection varied in both parents and F_1 families (Table 5). Of

the parents, PI 490999 had the highest percent infection, 85.7%. F_1 families from PI 490999 x PI 261653 (including reciprocals) had 100.0% infection. F_1 families from PI 491000 x PI 261653 tended to outgrow symptoms by shedding older diseased leaves before symptoms appeared in younger leaves. The majority of uninoculated controls showed no LIY symptoms. A few controls showed symptoms on later evaluations, indicating that contamination occurred in the greenhouse. All of the inoculated 'El Toro' plants (susceptible) developed LIY symptoms. PI 261653 had 73.3% of the plants infected, which conflicts with the level of resistance found by McCreight (1987). He found no plants of PI 261653 to be susceptible.

TRANSMISSION TESTS

Different numbers of whiteflies were used to transmit LIYV to PI 261653 and cultivar 'Summer Bibb'. For PI 261653, the transmission rates established by 5, 10, 20, or 40 whiteflies per plant were: 60.0, 80.0, 100, and 100%, respectively (Table 6). For 'Summer Bibb', the transmission rates were: 40.0, 50.0, 80.0, and 80.0% respectively. In all of the whitefly numbers tested, PI 262653 had higher transmission rates than 'Summer Bibb'. Five whiteflies per plant proved to be a sufficient number to transmit LIYV. Overall, the transmission rates were consistent with those found by Duffus *et al.* (1986), indicating that the pathogenicity of this LIYV isolate had not changed.

Table 5. Percent infection of *Lactuca saligna* accessions and their F_1 and F_2 families inoculated with LIYV in greenhouse and field tests.

Pedigree	Greenhouse		Field	
PI 261653	73.3	11/15	82.0	173/211
PI 490999	85.7	12/14	83.1	192/231
PI 491000	7.7	1/13	68.6	144/210
PI 491001	62.5	10/16	39.4	93/236
	F_1		F_2	
PI 261653 x PI 490999	100	9/9	75.3	174/231
PI 490999 x PI 261653	100	8/8	71.1	177/249
PI 261653 x PI 491000	33.3	2/6	66.7	154/231
PI 491000 x PI 261653	100	3/3	73.4	174/237
PI 261653 x PI 491001	87.5	7/8	61.2	134/219
PI 491001 x PI 261653	50.0	4/8	64.4	150/233

Table 6. Transmission rates (measured as percent infection) of LIYV to PI 261653 and 'Summer Bibb' using 5, 10, 20, or 40 viruliferous whiteflies per plant.

	Number of whiteflies							
Entry	5		10		20		40	
PI 261653	60	6/10	80	8/10	100	10/10	100	10/10
Summer Bibb	40	4/10	50	5/10	80	8/10	80	8/10

LIYV ISOLATES TEST

The infection rates were consistent among the four isolates tested, falling in a high range, 80.0 - 100% (Table 7). Both melon isolates had 100% infection in PI 261653 and 'Summer Bibb'. This preliminary study did not find significant differences between the isolates tested. More work is needed in this area to substantiate whether new strains of LIYV now exist.

FIELD TEST

The level of natural inoculum was high as shown by 90.0 - 100% infection on the border rows of cultivated lettuce. Many whiteflies were present on the *L. saligna* seedlings, insuring transmission of LIYV. When data were combined across replications, PI 491001 had the lowest percent of infected plants (39.4) and the mean number of infected leaves per plant was 3.2 (Tables 5 and 8). PI 490999 had the highest percent of infected plants (83.1) and its mean number of infected leaves per plant was 13.6. The present field study noted a new type of LIY symptom expression. In addition to the yellowing and reddening already described, some diseased leaves had a metallic sheen that gave a bronzing effect. ELISA verified such leaves to be infected with LIYV.

Findings on the percent of infected plants showed similar trends in greenhouse and field tests (Table 5). Of the parents, PI 261653 and PI 490999 had the higher percentages of infected plants in both the greenhouse and the field. The F_1 families,

Table 7. Frequency of infection (percent and number per inoculation) with four isolates of LIYV from different host plants collected in Yuma, Arizona.

	Isolate (host)							
	28A		34A		50A		50B	
Entry	(sugar beet)		(lettuce)		(melon)		(melon)	
PI 261653	80	4/5	100	5/5	100	12/12	100	5/5
Summer Bibb	100	8/8	80	4/5	100	15/15	100	8/8

Table 8. Range and mean number of infected leaves per plant of four *Lactuca saligna* accessions and their F_2 families in a field test, Brawley, California. Untransformed data.

Pedigree	n	Range	Mean ± SE[z]
Parents			
PI 261653	211	0 - 20	5.4 ± 1.1
PI 490999	231	0 - 50	13.6 ± 1.0
PI 491000	210	0 - 30	7.7 ± 1.1
PI 491001	236	0 - 35	3.2 ± 1.0
F_2 families			
PI 261653 x PI 490999	231	0 - 35	8.2 ± 1.0
PI 490999 x PI 261653	249	0 - 30	7.6 ± 1.0
PI 261653 x PI 491000	231	0 - 40	6.8 ± 1.0
PI 491000 x PI 261653	237	0 - 35	7.6 ± 1.0
PI 261653 x PI 491001	219	0 - 30	5.6 ± 1.1
PI 491001 x PI 261653	233	0 - 30	6.7 ± 1.0

[z] standard error of the mean

PI 261653 x PI 490999, PI 490999 x PI 261653, and PI 491000 x PI 261653 had high percentages of infected plants in the greenhouse. PI 491000 responded differently, 7.7% in the greenhouse and 68.6% in the field test.

Although PI 261653 had 82.0% percent infected plants in the field, it had a low mean number of infected leaves per plant (5.4). Of all the pedigrees tested, PI 261653 had the lowest maximum number of infected leaves per plant (20.0).

Analysis of variance of the transformed data showed a significant difference between replications for the mean number of infected leaves per plant (Table 9). There were significant differences among pedigrees. Table 10 shows the probability values for means comparisons of number of infected leaves per plant. Most parental means differed significantly. There were no significant differences among F_2 families. Reciprocal F_2 families did not differ significantly from each other. Comparisons of F_2 means with parental means were mixed. For example, the PI 491000 mean was not significantly different from its F_2 means, whereas PI 491001 and PI 490999 means were significantly different from their F_2 means. PI 261653 did not differ significantly from any of its F_2 families.

FREQUENCY DISTRIBUTIONS

The untransformed field data were combined from the three replications to graph the frequency distributions of the number of infected leaves per plant for the parents and F_2 families. Among the parents (Figs. 4-7), the frequency distribution for PI 491001 has the least number of infected leaves and is skewed to the right (Fig.7).

Table 9. Analysis of variance for number of LIYV infected leaves per plant in four *L. saligna* accessions and their F_2 families in a replicated field test, Brawley, California, 1988-89. Transformed $(\sqrt{x+0.5})$ data.

Source	df	Mean Square	F[z]
Rep	2	6.41	3.35 *
Pedigree	9	48.75	6.19 **
Experimental error	18	7.88	4.12 **
Sampling error	2257	1.91	

z Pedigree effect tested with Rep x Pedigree effect; Rep and Experimental error effects tested with Sampling error.

* Significant at $P = 0.05$

** Significant at $P = 0.01$.

Table 10. Probabilities for means comparisons among PI 261653, PI 490999, PI 491000, PI 491001, and their F_2 families using t-tests ($P > |t|$ H0: mean(i)=mean(j)).

					261653 x 490999	490999 x 261653	261653 x 491000	491000 x 261653	261653 x 491001	491000 x 261653
	261653	490999	491000	491001						
i/j	1	2	3	4	5	6	7	8	9	10
1										
2	0.0004									
3	0.5167	0.0017								
4	0.0207	0.0001	0.0049							
5	0.1478	0.0095	0.4148	0.0006						
6	0.3375	0.0024	0.7714	0.0018	0.5758					
7	0.7543	0.0006	0.7240	0.0091	0.2373	0.5068				
8	0.3362	0.0027	0.7633	0.0019	0.5902	0.9883	0.5029			
9	0.6929	0.0001	0.3003	0.0461	0.0692	0.1754	0.4746	0.1762		
10	0.7578	0.0006	0.7194	0.0091	0.2342	0.5022	0.9956	0.4984	0.4768	

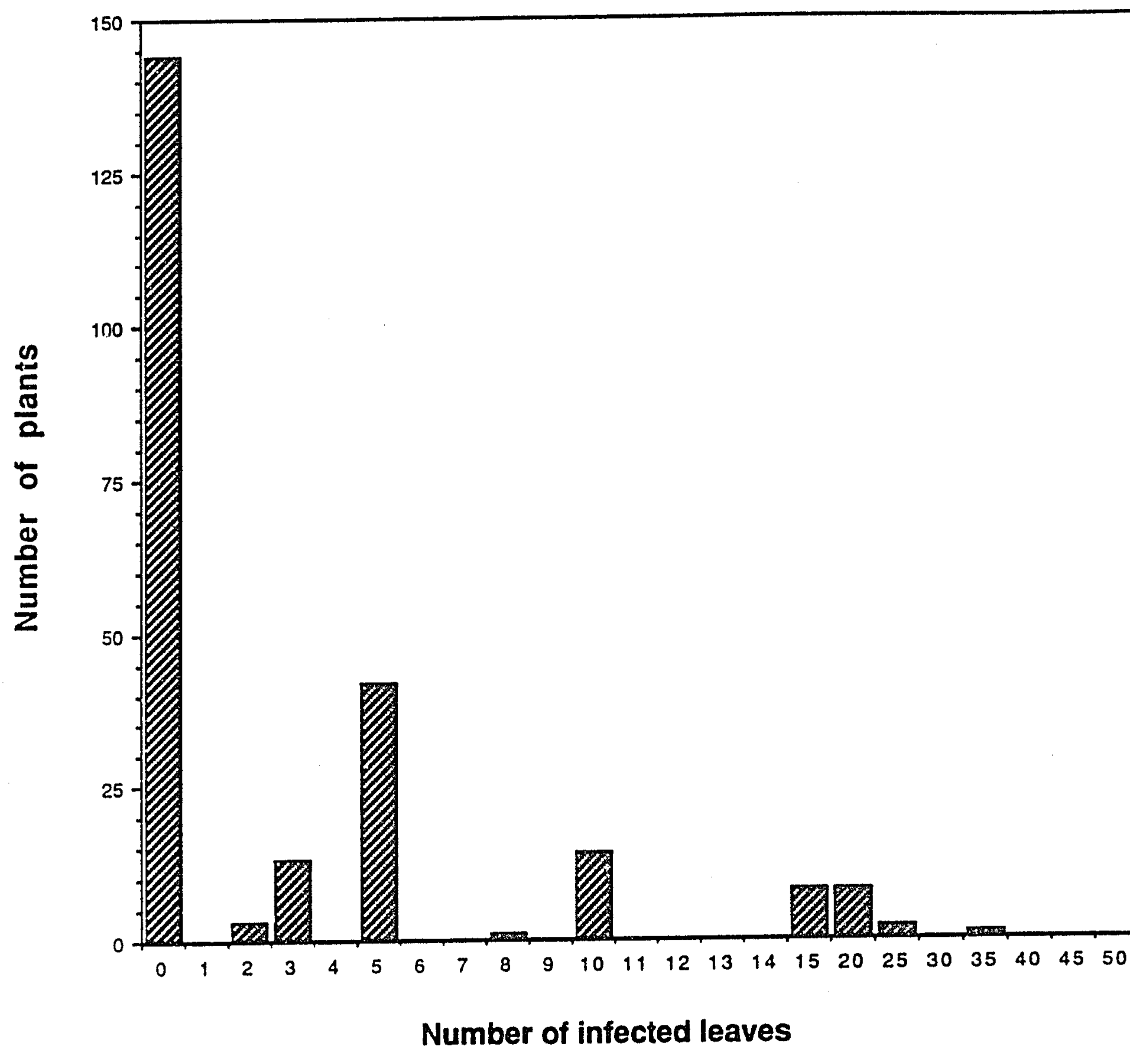

Figure 7. Frequency distribution of the number of infected leaves per plant. PI 491001 untransformed data combined across three replications.

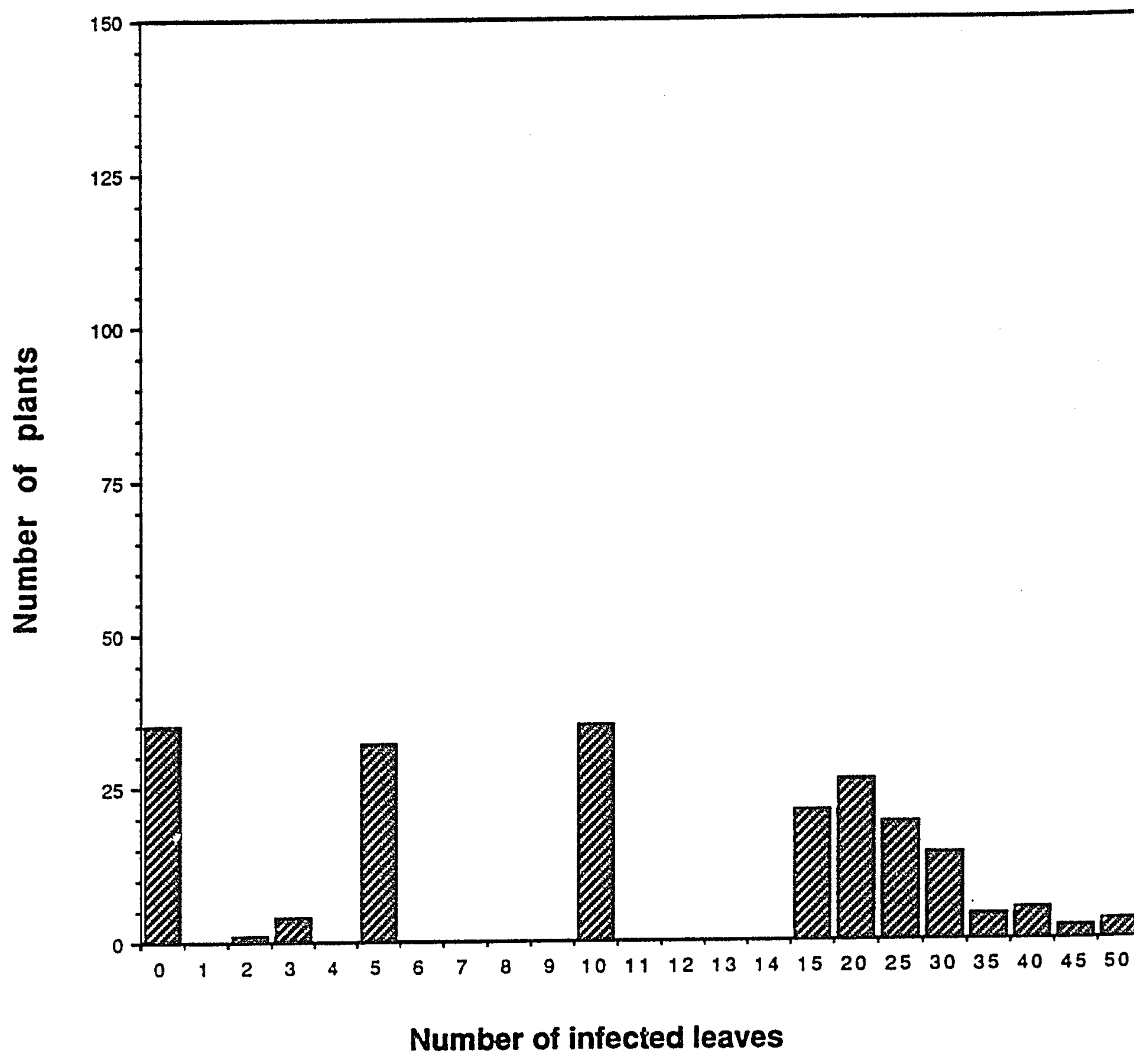

Figure 5. Frequency distribution of the number of infected leaves per plant. PI 490999 untransformed data combined across three replications.

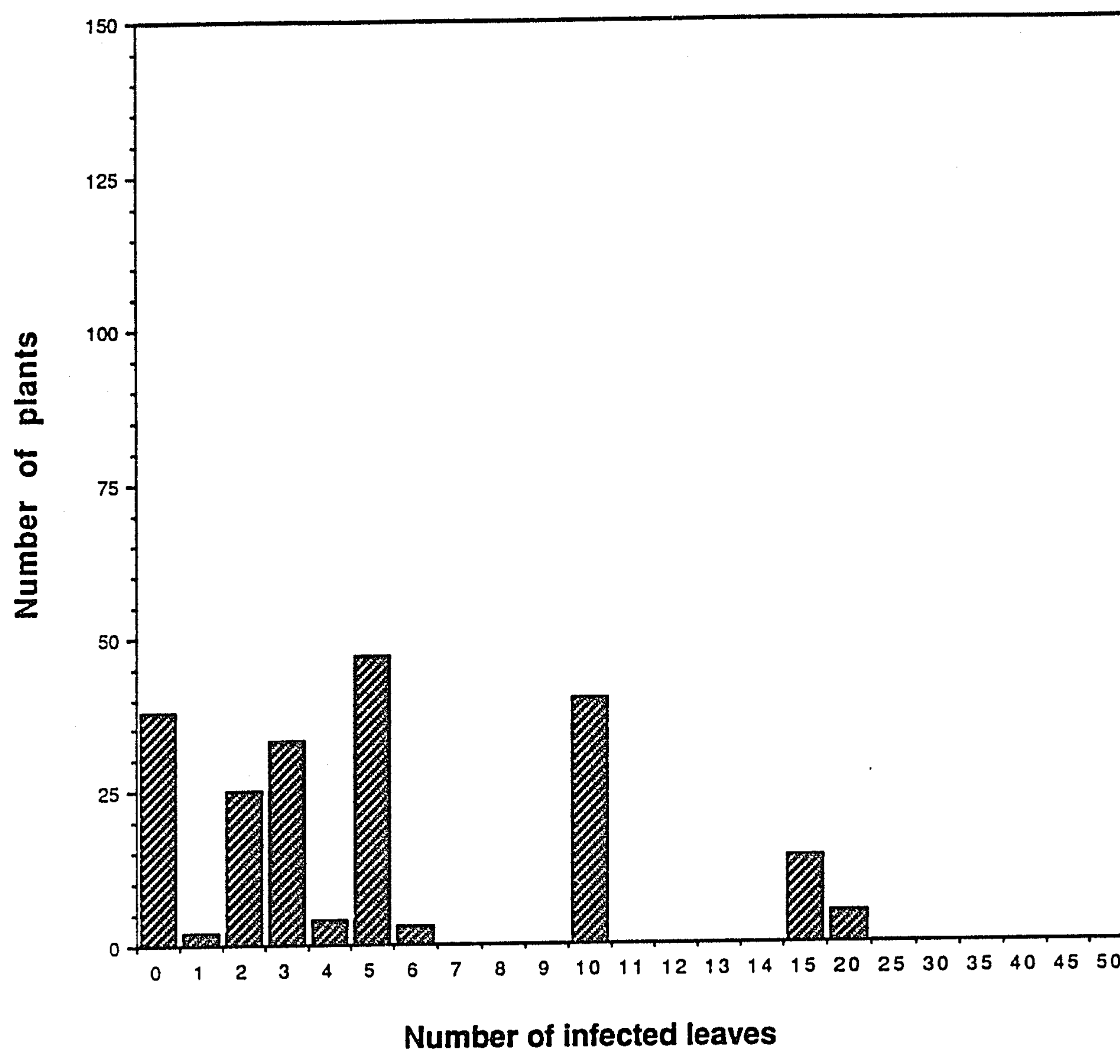

Figure 4. Frequency distribution of the number of infected leaves per plant. PI 261653 untransformed data combined across three replications.

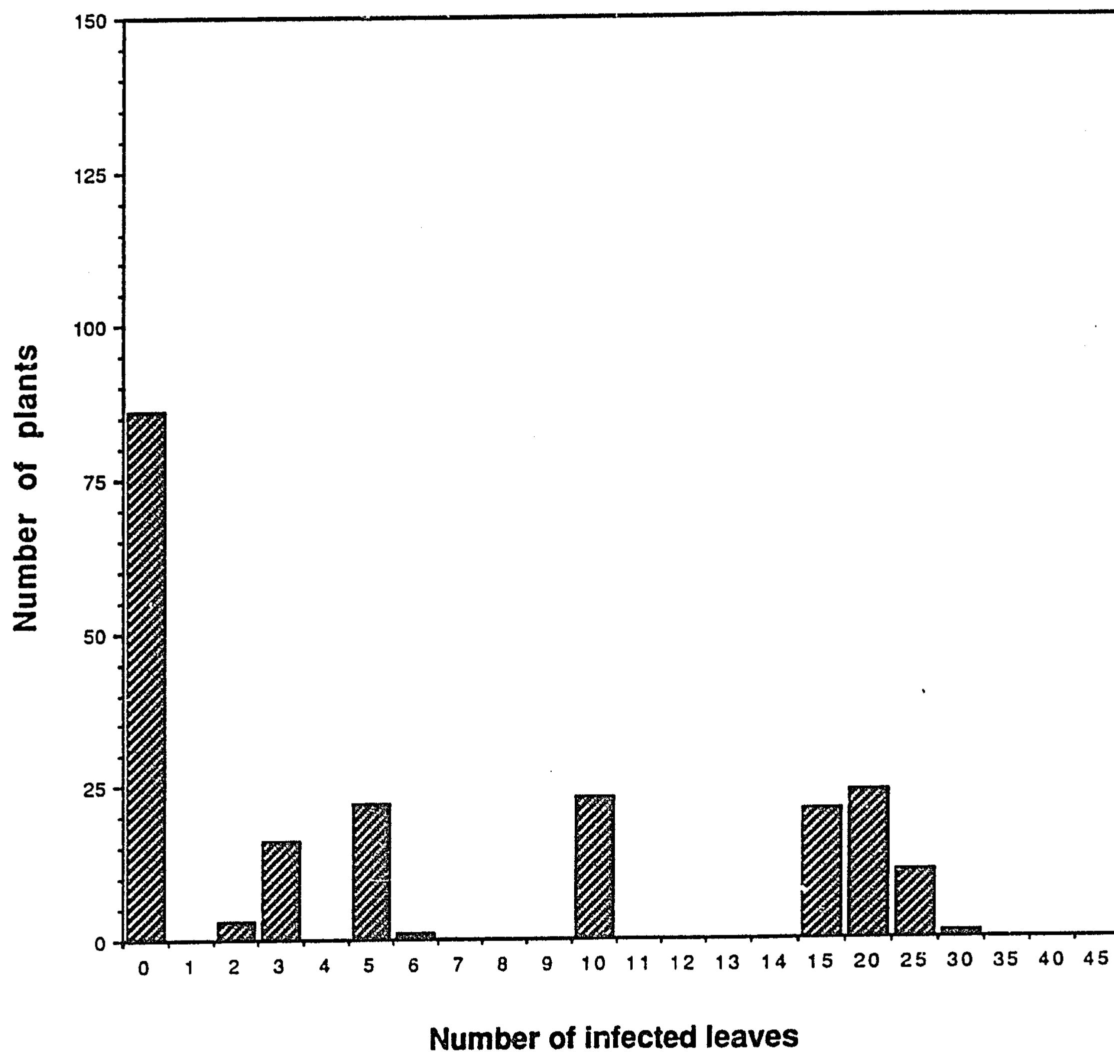

Figure 6. Frequency distribution of the number of infected leaves per plant. PI 491000 untransformed data combined across three replications.

About 150 plants in the three PI 491001 plots had zero number of infected leaves. The graph also shows low variability for the number of infected leaves. Of the parents, the frequency distribution for PI 490999 has the highest number of infected leaves and is skewed toward higher categories (Fig.5). PI 490999 was the only parent to have plants with 50 infected leaves. Its frequency distribution (Fig. 5) also shows high variability.

The F_2 frequency distributions show similar patterns when the data for a given pedigree are combined (Figs. 8-13). All F_2 families are skewed to the right (higher number of infected leaves). The F_2 families show a high degree variability and a wide range for the number of infected leaves. The frequency distributions of the three different F_2 pedigrees (reciprocal families combined) are remarkably alike (Figs. 14-16).

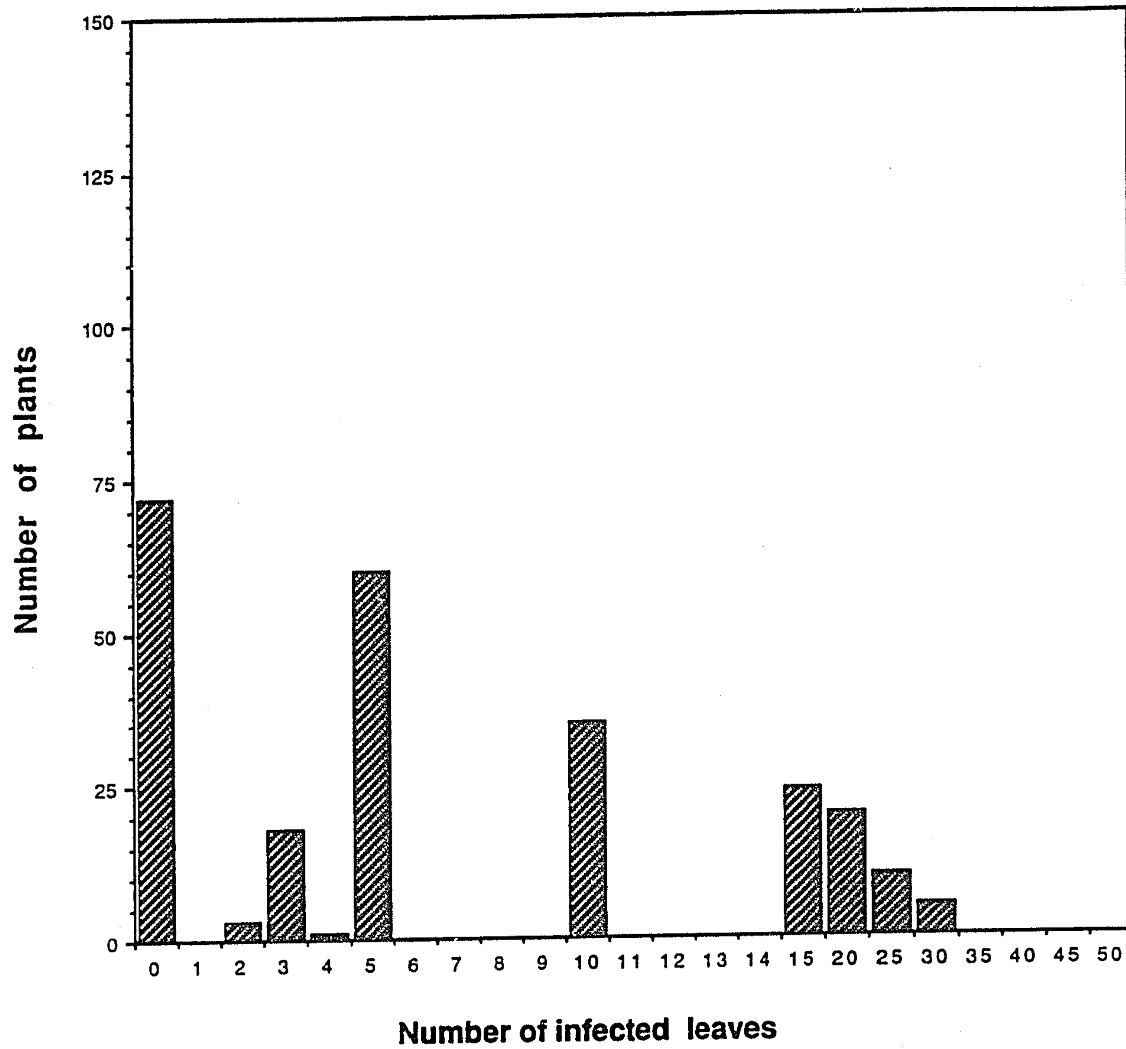

Figure 9. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 490999 x PI 261653, untransformed data combined across three replications.

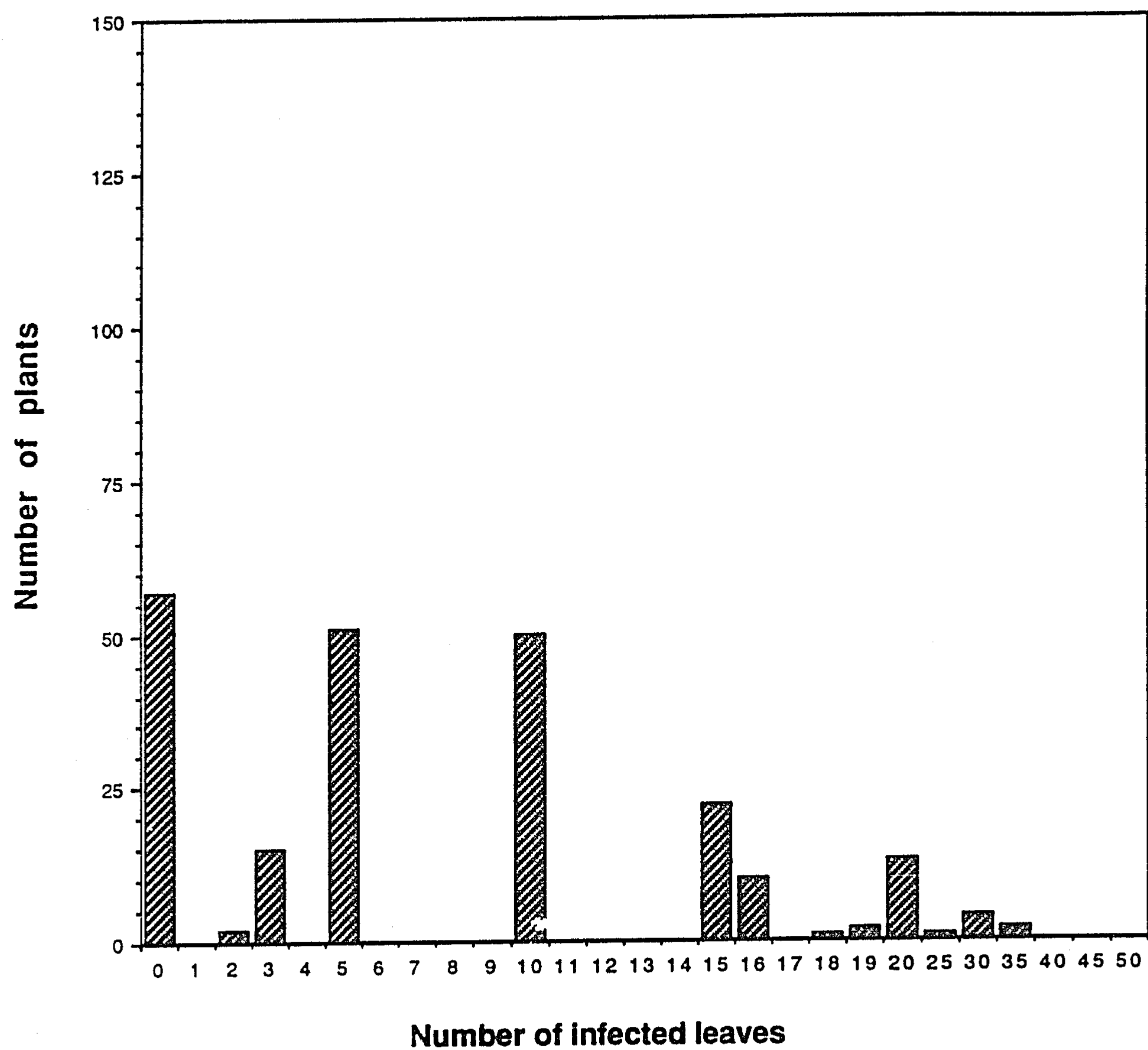

Figure 8. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 490999, untransformed data combined across three replications.

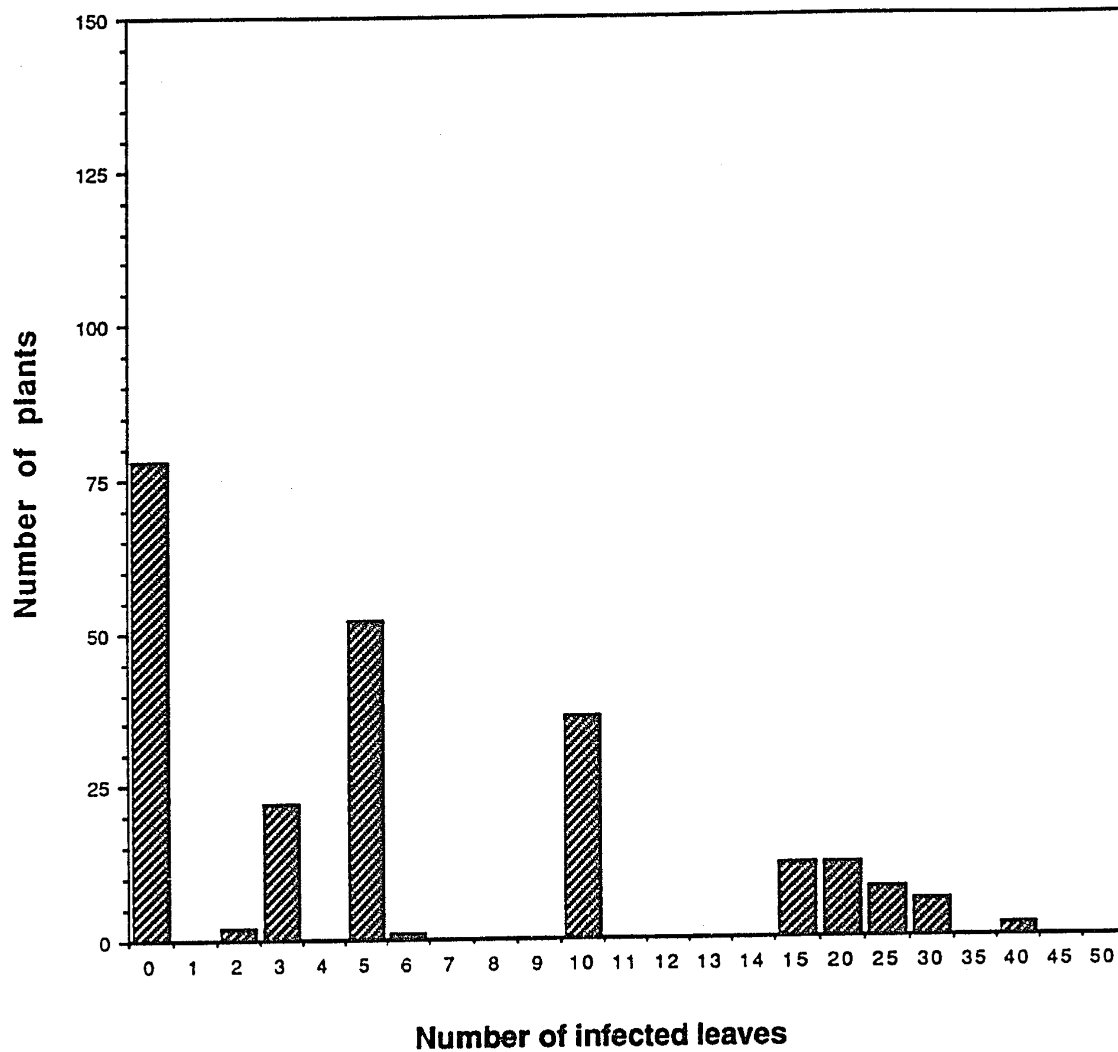

Figure 10. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 491000, untransformed data combined across three replications.

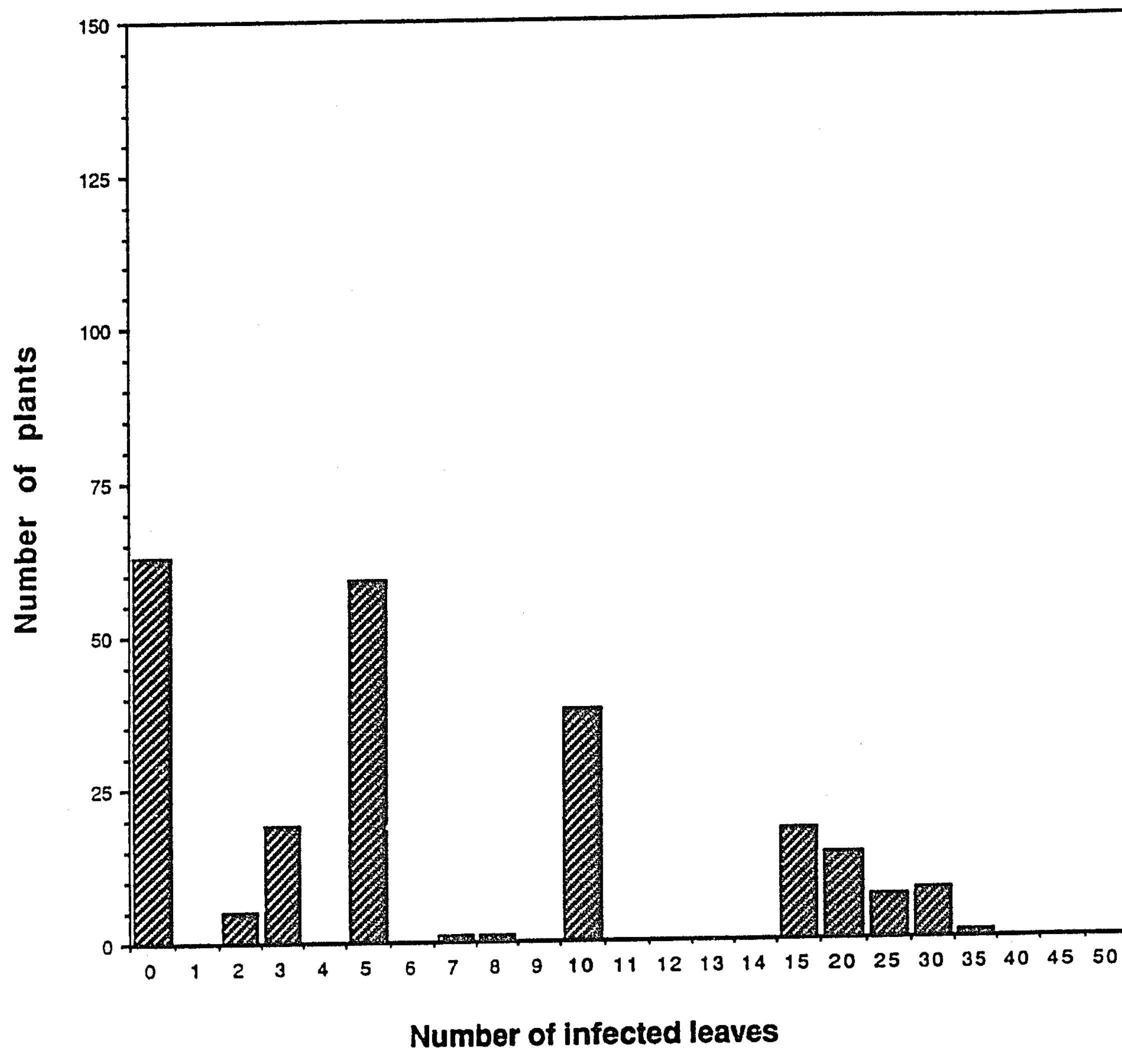

Figure 11. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 491000 x PI 261653, untransformed data combined across three replications.

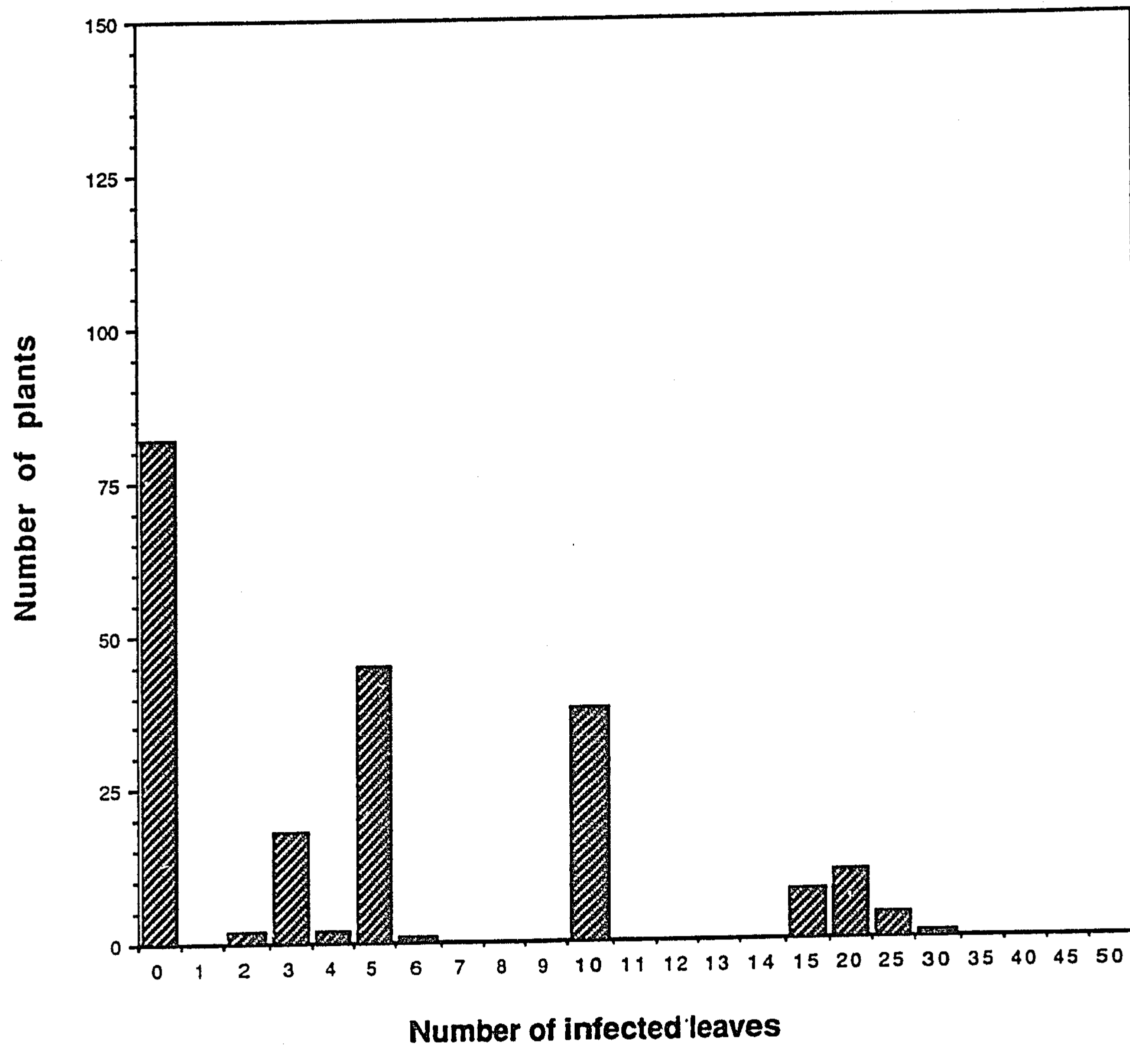

Figure 12. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 491001, untransformed data combined across three replications.

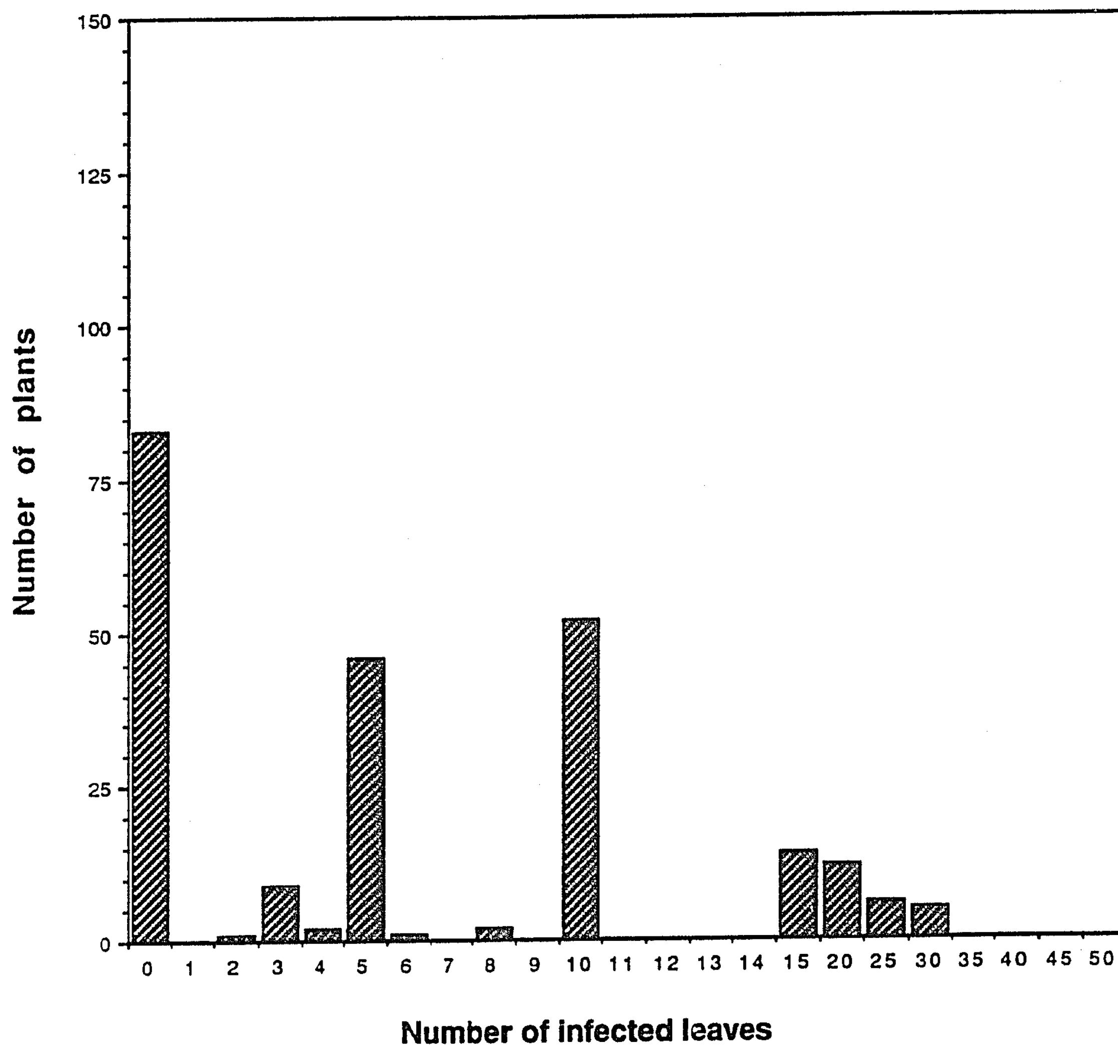

Figure 13. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 491001 x PI 261653, untransformed data combined across three replications.

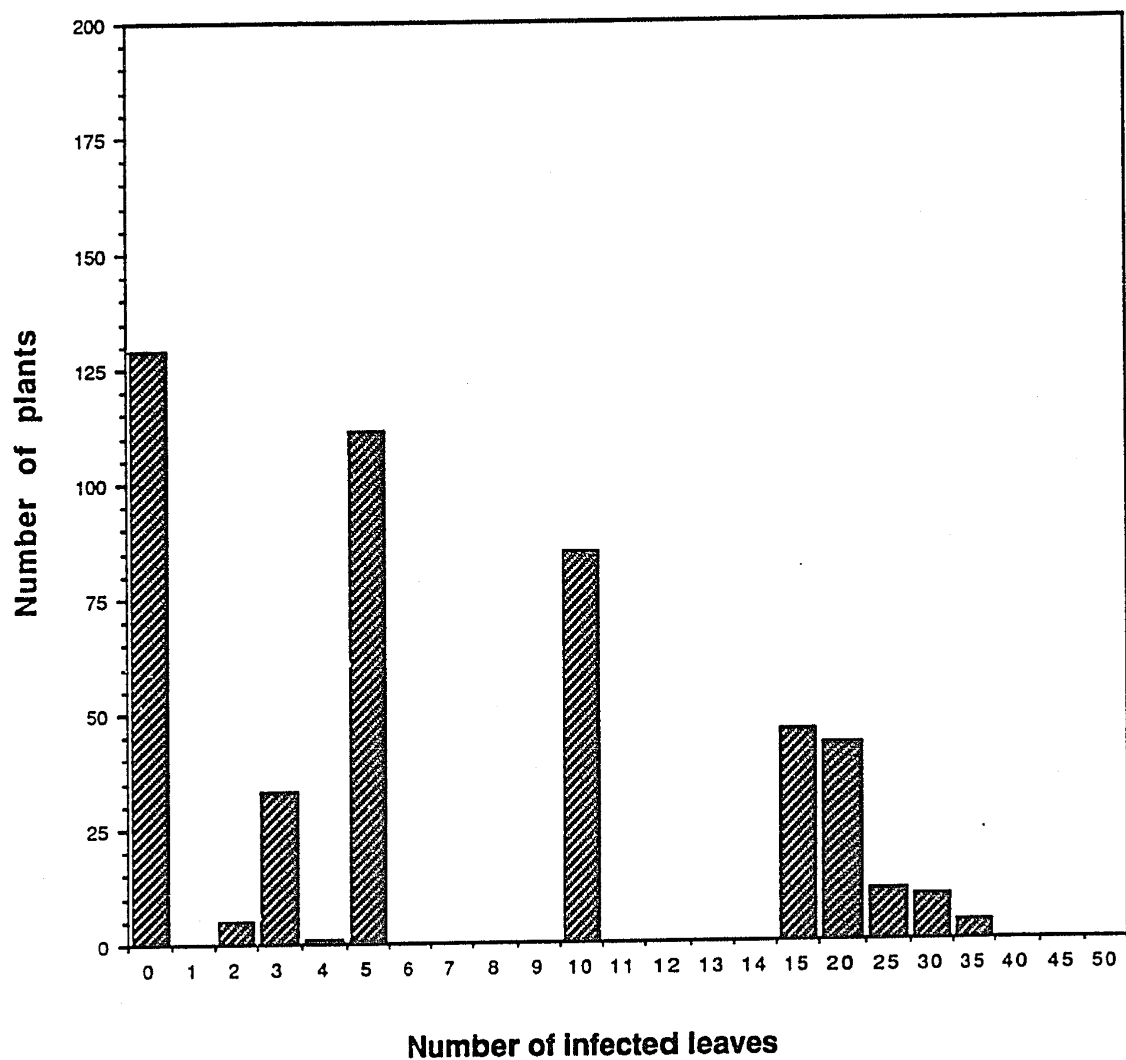

Figure 14. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 490999 and reciprocals, untransformed data combined across three replications.

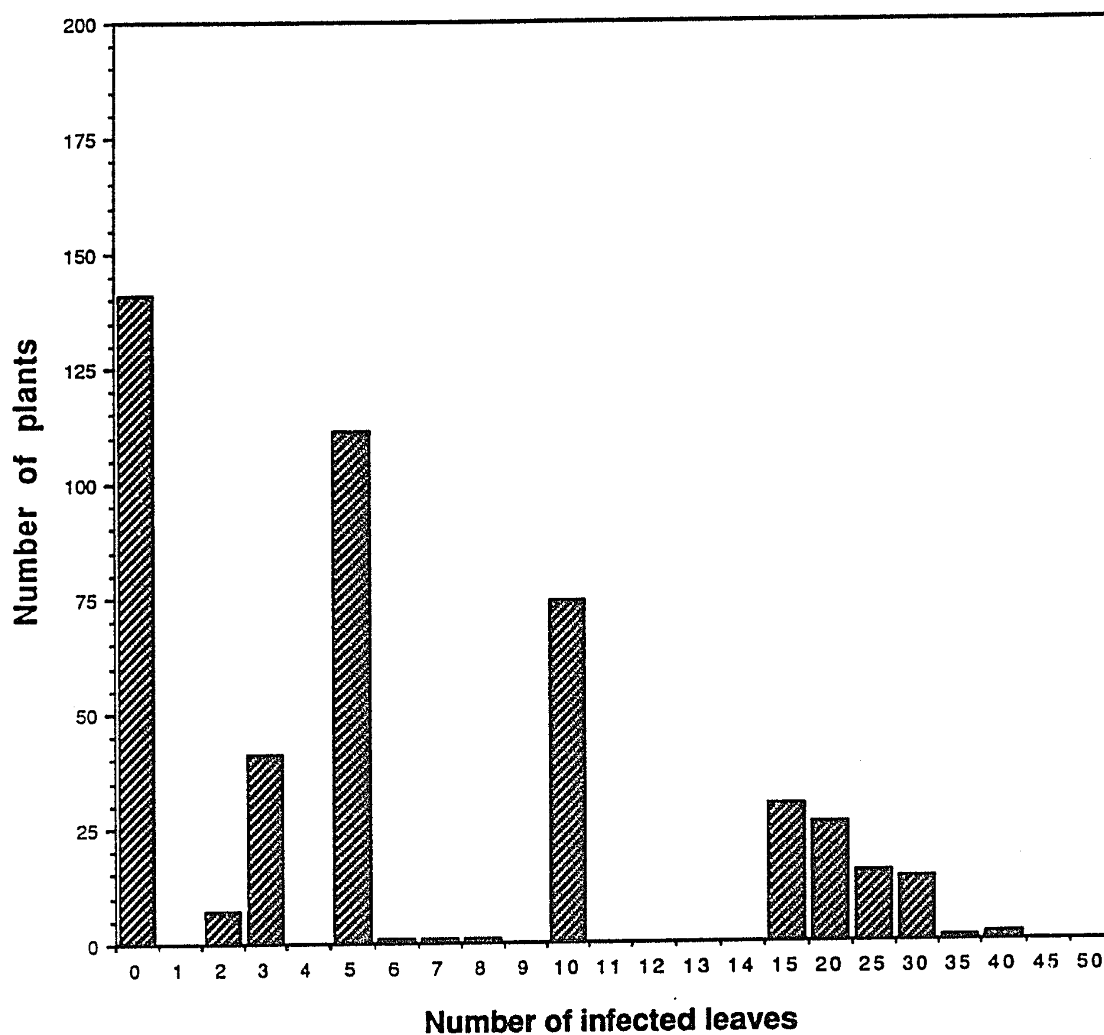

Figure 15. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 491000 and reciprocals, untransformed data combined across three replications.

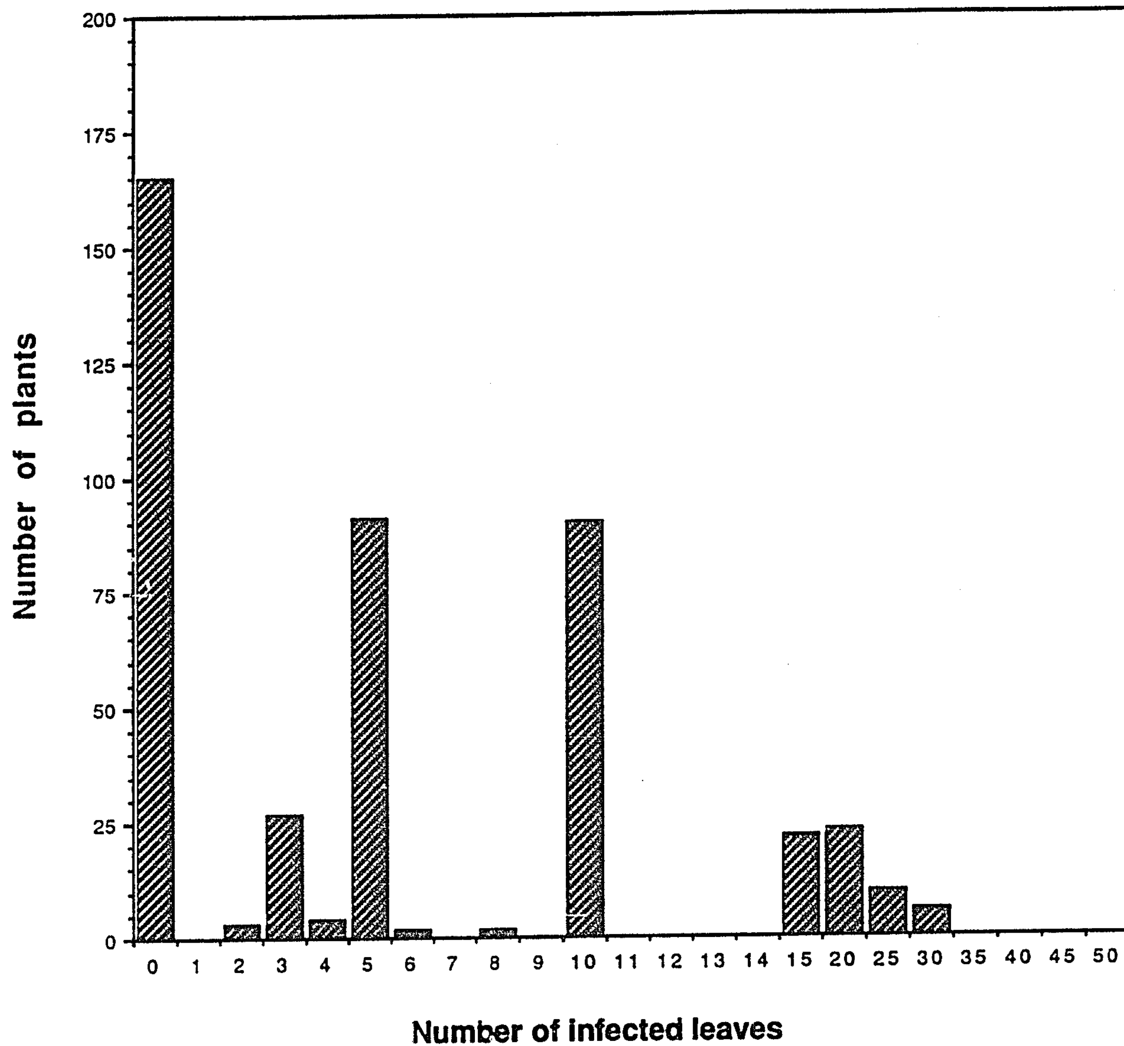

Figure 16. Frequency distribution of the number of infected leaves per plant. F_2 family, PI 261653 x PI 491001 and reciprocals, untransformed data combined across three replications.

DISCUSSION

The main purpose of this study was to observe F_2 segregation ratios (resistant versus susceptible) in hopes of determining the number of genes in *L. saligna* that condition resistance to LIYV. The observed F_2 segregation ratios did not conform to any known simple pattern of inheritance. Instead, the F_2 families showed a continuous range of disease severity as indicated by the number of infected leaves. The number of infected leaves per plant was highly variable. This continuous variation implies polygenically controlled horizontal resistance (Fraser, 1986). Horizontal resistance, if inherited polygenically, can be lost when breeding for crop characters determined by major genes (Fraser, 1985). To restore this kind of resistance is difficult in breeding programs (Robinson, 1969). Wild host species such as *L. saligna* may contain polygenes useful for breeding disease-resistant plants. Although polygenes are difficult to manipulate, they confer longer lasting resistance compared with vertical resistance, which is controlled by a few major genes (Robinson, 1969; Simons, 1972). Vertical resistance is subject to resistance breakdown and often operates completely or not at all (Robinson, 1969). The varied range of disease severity found in this field test indicates that vertical resistance to LIYV is not operating in *L. saligna*. Polygenic inheritance offers the most plausible explanation.

Reciprocal F_2 families did not have significant differences between their mean number of infected leaves per plant. This homogeneity indicates that in *L. saligna* resistance to LIY is not due to cytoplasmic inheritance.

Most perplexing is the discrepancy between the high resistance to LIYV in PI 261653 reported by McCreight (1987) and the susceptibility of PI 261653 found in the present study. The findings of this field inoculation vary from those found by McCreight (1987). He tested the same four parental accessions in the same field. He did not find any susceptible plants of accession PI 261653. Yet this study found 82.0% of PI 261653 to be infected. In general, parental infection was higher during this field test compared with McCreight's earlier study. A possible explanation is the occurrence of a new pathotype of LIYV or a more virulent form. This requires a change in the RNA of the virus. RNA genomes tend to have a high mutation frequency (Fraser, 1986). If the resistance observed in *L. saligna* is polygenically controlled, it is highly unlikely that the many needed mutations have occurred to increase virulence. It is difficult for resistance breakdown to occur when many genes are involved. The preliminary test comparing different host isolates did not find significant differences in the percent of infected plants (Table 7). At present, there is no evidence that a new strain of LIYV has developed.

A tentative explanation held by McCreight and Ryder of the U.S.D.A. (personal communication) is that the resistance to LIY in *L. saligna* may not be as strong as once thought. Their field observations indicate that environmental factors can modify symptom expression. Environmental factors include photoperiod, temperature, and mineral nutrition. Perhaps the environmental conditions present during McCreight's earlier study favored disease resistance. Disease tolerance versus resistance does not seem likely. Strictly speaking, when a

plant tolerates a disease, there is little or no loss in vigor or yield (Cooper and Jones,1982; Simons, 1972). Yet, LIY infected *L. saligna* plants have reduced vigor and yield (McCreight, personal communication).

LIY symptoms also vary depending on the host's stage of growth. When cultivated lettuce is in the heading process, the wrapper leaves show severe symptoms. The heading process requires nutrients. Diseased lettuce plants have stunted root systems that are unable to supply the needed nutrients. Therefore, diseased plants develop yellowing symptoms due to mineral deficiencies. This positively correlates with the findings of McCreight *et al.* (1986), who found that the most vigorous cultivar, 'Climax', which has a large root system, had the mildest symptoms.

In conclusion, the present study indicated the following about the genetic nature of resistance to LIYV found in *L. saligna* : it appears to governed by polygenes; these genes are most likely found in the nuclear DNA; and the gene expression is modified by environmental factors which can alter the level of resistance operating in *L. saligna.*

The *L. saligna* accessions tested easily cross-fertilized and were amenable to extended photoperiods for shortening generation time. *L. saligna* continues to be less symptomatic in the field compared with LIYV susceptible lettuce cultivars. The natural resistance to disease and insects found in *L. saligna* has evolved in rugged native habitats. The high variability found in the parents and their F_2 families may reflect the inherent genetic variation found in *L. saligna.* This

heterogeneity will provide valuable germplasm for lettuce breeding programs.

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