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indicative of, not diagnostic for, AshY.

Fixed specimens were superior to fresh ones for the DAPI test, because DNA from nuclei was often smeared extensively in unfixed sections. This smearing sometimes made it difficult to ascertain the original location of fluorescent particles. Nuclei in fixed sections retained their integrity, and cell outlines were clearer than in unfixed sections. which facilitated the identification of cell

Comparison of DAPI test with Dienes' stain. The DAPI test gave more conservative and definitive results than did Dienes' stain. Of the 73 ash tested, 38 were declared positive and 20 negative for MLO infection in both tests. All of the remaining 15 ash were negative in the DAPI test, whereas five were declared positive (weak positive reaction) and 10 ambiguous with Dienes' stain. DAPI and Dienes' stain always gave the same result when the Dienes' stain reaction was strong, as in sections from witches'brooms. Weak Dienes' stain reactions could not be interpreted reliably, because they occurred not only in sections from diseased trees but sometimes in sections from trees known to be free from MLOs. Healthy-appearing trees that were growing rapidly were sometimes scored ambiguous with Dienes' stain but were always scored negative with DAPI. In sections scored ambiguous with Dienes' stain, diffuse light blue pigment often occurred throughout the phloem, dark blue color sometimes appeared in scattered parenchyma cells, and blue particles often occurred in sieve tubes. Immature tissues near meristems often stained light blue, whether or not a strong positive reaction developed in mature

sieve tubes. In sections treated with DAPI, fluorescent particles other than the organelles of parenchyma cells were usually seen only in phloem sieve tubes, and ambiguous results were rare.

Sampling scheme. Of the 117 trees from which twig and root specimens were tested with DAPI, 75 (64%) were initially scored positive for MLO infection in sieve tubes of the root or the twig, or both. Thirty-one trees were scored negative, and 11 were undetermined because of unsatisfactory specimens. The 37 trees that were negative or undetermined on first examination were resampled (one twig and one root, as before) during April-May 1987. MLOs were detected in one tree that had initially been scored negative and in five that had been undetermined. The proportion of trees scored as MLO-infected was therefore 69% in the final data set (Table 1). Thus, repeated sampling of trees initially scored negative or undetermined resulted in only a 5% improvement in diagnostic accuracy. Considering only the trees initially scored negative, resampling resulted in only a 1% increase in diagnostic accuracy.

MLOs were detected more than twice as often in root samples as in twigs from the same trees (Table 1). The DAPI test was positive for both twigs and roots of 22 trees, for twigs only of 5 trees, and for roots only of 54 trees. In work not reported here, we noted that the incidence and intensity of DAPI fluorescence in twigs of diseased trees diminished during the winter, although autofluorescence of sieve tubes persisted.

Our findings for MLO detection are in accord with those of Schaper and Seemüller (11,12) and Seemüller et al

(13,14) for apple proliferation and pear decline. They used graft transmission as well as the DAPI test to show that MLOs in the aboveground parts of trees degenerated and became increasingly difficult to detect during late winter, whereas MLOs in roots were readily detectable at any time. Apparently the roots of apple, pear, and ash infected with MLOs are the principal site of overwintering of the MLOs, and these parasites spread up into branches and twigs during the growing season, as was suggested for MLOs in elm by Braun and Sinclair (1). In ash, some twigs may be missed during the annual recolonization of the aboveground parts. Incomplete recolonization or low titer of MLOs in twigs could explain the lower incidence of detection of MLOs in twigs than in

Frequency of MLO detection in individual trees in relation to sampling intensity. For the 15 trees known to be infected with MLOs, 9.8 of 10 root samples per tree were positive, on average, when tested with DAPI. No infected tree had fewer than nine roots positive. All of the 15 slowly growing but previously DAPI-negative trees remained negative when 10 root specimens per tree were tested. Within the limits of the DAPI technique, therefore, testing one root per tree would give a false-negative result for the tree as a whole in fewer than 10% of cases. If two roots from a given tree were tested, and the associated probabilities of false results were independent, the tree would erroneously be scored negative in fewer than 1% of cases.

DAPI reaction as related to symptoms. Positive DAPI reactions occurred in the root phloem of 88% of the 105 trees with deliquescent branching, 82% of the 38 trees with dieback but lacking deliquescent branches, and 61% of the 70 slowly growing trees showing neither of the above symptoms. Four of 14 normal-

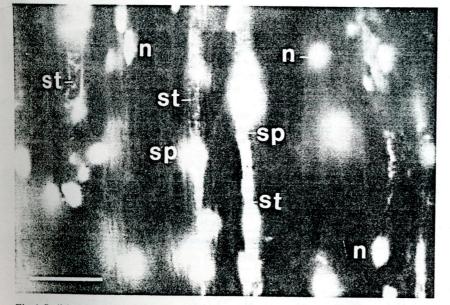


Fig. 1. Radial section of secondary phloem of an MLO-infected ash root about 4 mm in diameter, treated with DAPI and observed with an epifluorescence microscope. Fluorescent particles assumed to be MLOs are visible in sieve tubes (st) and have aggregated at some sieve plates (sp). Nuclei (n) of phloem parenchyma cells appear as elliptical fluorescent spots above and below the plane of focus. Bar =  $50 \mu m$ .

Table 1. Detection of MLOs in roots and twigs of white ash trees in three health classes by means of the DAPI test

Health class <sup>a</sup>	Total trees	Trees with MLOs detected in:			
		Root	Twig	Root or twig	
Normal	9	2	2	3 (33%)	
Slow	54	33 <sup>b</sup>	9	34 (63%)	
Dieback	54	41 <sup>b</sup>	18	44 (81%)	
All	117	76 <sup>b</sup>	29	81 (69%)	

<sup>a</sup> Normal = apical twigs growing at least 25 cm per year, no dieback of twigs in middle or upper crown; slow = apical twigs growing less than 25 cm per year, no dieback of twigs in middle or upper crown; dieback = dieback in addition to normal death of shaded branches. <sup>b</sup>Difference in frequency of MLO detection between roots and twigs significant at

P = 0.01 by chi-square analysis.

appearing trees were also scored positive. These findings are similar to those of Matteoni and Sinclair (8), who used a combination of direct testing and symptom interpretation to estimate that 57% of the ash they studied on plots in central and southeastern New York were infected with MLOs. MLOs in phloem of normal-appearing white ash may represent strains of low virulence, early stages of colonization by strains of normal virulence, or strains infecting tolerant

Contrary to the suggestion of Matteoni and Sinclair (8), deliquescent branching is not definitively diagnostic for ash yellows, because 12% of the trees in the deliquescent category tested negative for MLO infection. As shown earlier in this paper, it is unlikely that more than one of the deliquescent trees would have tested positive if resampled. In survey work to be reported elsewhere, we have noted deliquescent branching, dieback, and slow growth in ash on various sites where no witches'-brooms or histological evidence of MLO infection was found. Apparently, deliquescent branching may be induced by various factors that damage apical buds or suppress growth for several years.

Recommendations for sampling for diagnosis of AshY. When the DAPI test is used to detect MLO infection in ash, a given tree may be accurately assessed (<1% chance of false-negative result) by collecting and examining two small roots from different parts of the root system. If the frequency of infection in an array of trees is to be assessed to less than 5% error, only one small root per tree need be examined.

## ACKNOWLEDGMENTS

We thank C. R. Hibben, G. W. Hudler, and anonymous reviewers for helpful suggestions for the presentation of this report.

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## Inheritance of Resistance to Tomato Yellow Leaf Curl Virus (TYLCV) in Lycopersicon pimpinellifolium

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## ABSTRACT

Kasrawi, M. A. 1989. Inheritance of resistance to tomato yellow leaf curl virus (TYLCV) in Lycopersicon pimpinellifolium. Plant Disease 73:435-437.

The inheritance of resistance in Lycopersicon pimpinellifolium to tomato yellow leaf curl virus (TYLCV) was studied in progenies derived from crosses between the resistant parents L. pimpinellifolium Hirsute-INRA and LA 1478 and the susceptible parent L. esculentum Special Back'. Resistance appeared to be stable in these parents. Field-grown seedlings were subjected to natural infection with the tomato yellow leaf curl virus. Analysis of F1, F2, and backcross populations from crosses of L. pimpinellifolium with the susceptible cultivar revealed that resistance is controlled by a single dominant gene. It is suggested that the symbol Tylc be assigned for this gene in L. pimpinellifolium.

Additional keywords: disease resistance

Tomato yellow leaf curl virus (TYLCV), transmitted by the whitefly Bemisia

This study was part of project No. 4-6-86 of the Department of Plant Production, Faculty of Agriculture, University of Jordan, and was supported by the Deanship of Academic Research, University of Jordan, Amman.

Accepted for publication 20 October 1988 (submitted for electronic processing).

tabaci Gennadius, is responsible for serious losses of tomato production in many countries of the Middle East. Although all tested tomato lines and cultivars were highly susceptible to TYLCV, resistance has been reported in Lycopersicon pimpinellifolium (L.) Mill., L. hirsutum Humb. and Bonpl., and L. peruvianum (L.) Mill. (3,5,6,8).

Studies on the inheritance of resistance of L. pimpinellifolium to TYLCV in different areas of the Middle East have produced variable results. Pilowsky and Cohen (6) reported that resistance derived from LA 121 is controlled by a single gene with incomplete dominance, whereas Hassan et al (4) showed that resistance derived from LA 121 or LA 373 is quantitatively inherited with partially recessive gene action. Yassin (7) indicated that resistance in LA 1582 is conditioned by a single dominant gene.

The objective of this work was to determine the inheritance of resistance of L. pimpinellifolium Hirsute-INRA and LA 1478 to TYLCV in crosses with the susceptible commercial tomato cultivar Special Back.

## MATERIALS AND METHODS

Plants that showed resistance (symptomless carriers) to TYLCV in a previous study (5), belonging to L. pimpinellifolium Hirsute-INRA and LA 1478, were used as resistant parents. The susceptible parent is a commercial tomato cultivar, Special Back. Seeds of L. pimpinellifolium Hirsute-INRA and LA 1478 were obtained from H. Laterrot (France) and from C. M. Rick (United States), respectively. Parents were selfed for two generations and tested for TYLCV resistance before being used in crosses.

Interspecific crosses were made between susceptible and resistant parents to produce  $F_1$  populations.  $F_1$  hybrids ere selfed and backcrossed to the susceptible parent to produce  $F_2$  and  $BC_1$  populations, respectively. In all crosses, resistant parents were used as the pollen parent. Plants of parents  $F_1$ ,  $F_2$ , and  $BC_1$  generations (Table 1) were evaluated for TYLCV resistance under field conditions at the Jordan University Experiment Station in the Jordan Valley.

In early September of 1987, 4-wk-old seedlings were transplanted to the field in rows 16 m long with between-row spacings of 75 cm and in-row spacings of 40 cm. All plants were subjected to natural infection. An ample supply of viruliferous whiteflies was ensured by growing two rows of tested tomato plants between two single rows of previously established TYLCV-infected plants of the susceptible parent. The number of tested plants in each generation is listed in Table 1.

A disease rating scale (0 = symptomlessto 3 = severe symptoms) was used for evaluating TYLCV resistance. All plants rated "0" were considered equivalent to the resistant parent and were classified as resistant. Plants in the remaining ratings (1-3) were classed as susceptible. Individual seedlings were inspected for TYLCV resistance 3 wk after transplanting and were rated for the development of symptoms throughout the 20-wk growing season. Seven to 10 symptomless plants of each generation were back-indexed. Scions from symptomless plants were grafted onto healthy seedlings of the susceptible cultivar Special Back that were raised in insect-proof cages. Grafts were observed over a period of 5 wk for the development of TYLCV symptoms.

The chi-square test for goodness-of-fit was used to test hypothetical ratios for the inheritance of TYLCV resistance.

## RESULTS AND DISCUSSION

The number of resistant and susceptible plants in parents  $F_1$ ,  $F_2$ , and  $BC_1$  of

different crosses is given in Table 1. Over a 2-wk period of field tests, all plants of TYLCV-resistant parents remained symptomless, whereas plants of the susceptible parent developed persistent, severe symptoms. These results are similar to those reported by Kasrawi et al (5), who screened the same material under plastic house conditions, indicating that resistance in these parents is stable.

All F<sub>1</sub> plants of the two crosses were resistant, and their performance in the field was similar to the resistant parent, indicating that inheritance of resistance in these parents is dominant. However, some F1 plants developed very slight symptoms on some leaves at the seedling stage (5 wk after transplanting), giving the appearance of an intermediate resistance. These slight symptoms did not continue on younger leaves, and plants were completely symptomless at later stages (6-8 wk after transplanting). F1 plants were vigorous, large, extremely floriferous, and had a high fruit set and yield. Check plants were stunted with yellow growing points, had curled leaflets, and were generally barren. Fruits of  $F_1$  plants were round and similar to those of the resistant parents, but a little bigger. The observed transitory symptoms differ from those obtained by Pilowsky and Cohen (6), who reported that 8 wk after inoculation all F1 plants were infected and were smaller in size with permanently downward-cupped leaflets that developed interveinal chlorosis. They did not report on the flowering and fruiting of these

The two  $F_2$  populations segregated in a ratio of 3 resistant:1 susceptible ( $\chi^2 = 0.074$ , P = 0.79 for the INRA cross, and  $\chi^2 = 0.439$ , P = 0.51 for the LA 1478 cross). All the susceptible plants had TYLCV scores of 2 or 3; no plants scored 1. These data are consistent with the hypothesis that TYLCV resistance exhibited by *L. pimpinellifolium* Hirsute-INRA and by LA 1478 is conditioned by a single dominant gene. The segregation ratio of 1 resistant:1 susceptible ( $\chi^2 = 0.125$ , P = 0.73, and  $\chi^2 = 0.348$ , P = 0.57 for the INRA and LA 1478 backcrosses, respectively) obtained in plants of the

BC<sub>1</sub> generations further supports the hypothesis that resistance to TYLCV is governed by a single dominant gene.

Back-indexing results revealed that all tested symptomless plants are carriers of the virus. The possibility of escape was virtually excluded because of the presence of sufficient numbers of viruliferous vector whiteflies, complete infection of susceptible parents, and sample back-indexing of progeny.

Pilowsky and Cohen (6) indicated that resistance derived from L. pimpinellifolium LA 121 is controlled by a single gene with incomplete dominance. Although there is disagreement on the type of gene action involved, my conclusion is similar in that resistance is controlled by a single gene. Results obtained from greenhouse pot experiments by observing leaf symptoms of young plants and employing a known inoculum source of TYLCV-infected Datura stramonium L. plants (6) may not represent the field-grown plants subjected to natural infection. Therefore, my results may provide a better determination of the inheritance of resistance to any complex of TYLCV strains that might be found under the natural field conditions. In addition, mature plant expression of TYLCV reactions would allow careful plant classification among segregating populations. The data presented in this paper confirm the findings of Yassin (7), but do not agree with the observations of Hassan et al (4), who found that resistance derived from L. pimpinellifolium LA 121 or LA 373 is controlled quantitatively with partially recessive gene action. The discrepancies in the data obtained in the different countries of the Middle East may have resulted from the differences in the tested accessions, environmental conditions where studies were conducted, and/or the existence of different strains of TYLCV. The method of inoculation with the virus may also affect the inheritance of resistance. For example, Findley et al (1) concluded that resistance to maize dwarf mosaic virus in a maize inbred is controlled by two dominant genes when progenies are mechanically inoculated, but only one dominant gene conditions resistance when progenies are aphidinoculated.

The inheritance of TYLCV resistance should be useful in breeding programs attempting to transfer resistance from L. pimpinellifolium to adapted tomato cultivars. L. pimpinellifolium has a very close genetic relationship with cultivated L. esculentum Mill. and readily hybridizes with commercial cultivars. The only problem is the very small size of fruits of the wild type. However, Geneif (2) reported that gain in fruit size through backcrossing was rapid. It is suggested that the symbol Tylc (for tomato yellow leaf curl virus) be used for this single dominant gene in L. pimpinellifolium.

**Table 1.** Segregation of parents  $F_1$ ,  $F_2$ , and  $BC_1$  progenies for resistance to natural infection in the field in the Jordan Valley by tomato yellow leaf curl virus from crosses between *Lycopersicon esculentum* 'Special Back' ( $P_1$ ) and *L. pimpinellifolium* Hirsute-INRA ( $P_2$ ) and LA 1478 ( $P_3$ )

Generation	Parents or cross	Number of plants			Expected		
		Total	Resistant	Susceptible	ratio	$\chi^2$	P
Pı	Special Back	198		198			
P <sub>2</sub>	INRA	11	- 11	190			•••
F <sub>1</sub>	$P_1 \times P_2$	19	19				•••
F <sub>2</sub>	F <sub>1</sub> selfing	162	123	39	3:1	0.074	0.70
BC <sub>1</sub>	$P_1 \times F_1$	32	17	15	1:1	0.074 0.125	0.79
Pı	Special Back	198		198	1.1	0.123	0.73
P <sub>3</sub>	LA 1478	13	13			43	
Fı	$P_1 \times P_3$	21	21				
F <sub>2</sub>	F <sub>1</sub> selfing	246	189	57	3:1	0.439	0.51
BC <sub>1</sub>	$P_1 \times F_1$	46	25	21	1:1	0.439	0.51

## ACKNOWLEDGMENT

I am grateful to the Agricultural Material Co. (Miqdadi), Amman, Jordan, for reimbursing the expenses of manuscript publication.

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# Detection, Viability, and Possible Sources of Urediniospores of Puccinia recondita f. sp. tritici in Louisiana

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#### **ABSTRACT**

Subba Rao, K. V., Snow, J. P., and Berggren, G. T. 1989. Detection, viability, and possible sources of urediniospores of *Puccinia recondita* f. sp. tritici in Louisiana. Plant Disease 73: 437-442.

Kramer-Collins 7-day spore samplers were operated continuously at two locations, Baton Rouge (BR) and Bossier City (BC) in Louisiana, and daily urediniospore counts were taken. The number and viability of spores trapped was maximum during the active epidemic period between February and May and was least during the summer. Viability of the urediniospores was significantly inversely correlated with ambient maximum temperature (r = -0.81 at BR and -0.59 at BC). The highest consecutive number of days that no urediniospores were trapped was 6 in 1986 and 7 in 1987 at BR, and 31 in 1986 and 14 in 1987 at BC. Cultivar McNair 1003, susceptible to the prevalent leaf rust population, was planted at BR from I May through 18 September in 1986 and 1987, at 14-to 20-day intervals. Leaf rust appeared in many plantings and survived temperatures up to 36 C for 82 days in 1986 and 74 days in 1987. McNair 1003 plants, in pots exposed at 14-to 15-day intervals during summer for 2 days in a field at BR and then incubated in an air-conditioned greenhouse, developed leaf rust with an incidence of 12.5-100%. Rusts from Hordeum pusillum and Lolium multiflorum failed to infect wheat and vice versa. Surveys during mid-December 1986 and 1987, at Alexandria and Baton Rouge, showed uniform distribution of leaf rust over a large area, indicating the possibility of a major exodemic origin of inoculum for winter wheat in Louisiana for these vears.

Additional keyword: epidemiology

Soft red winter wheat (Triticum aestivum L.), harvested for grain in Louisiana, increased from approximately 27,000 hectares in 1980 to nearly 100,000 hectares in 1987 (2), owing to the popularity of wheat-soybean double-cropping. Leaf rust, caused by Puccinia recondita f. sp. tritici Rob. ex Desm., occurs more frequently in Louisiana than any other disease of wheat and causes yield losses of up to 50% (3). In Louisiana, winter wheat is normally planted in late October through late November and is harvested by mid-May.

Approved for publication by the director of the Louisiana Agricultural Experiment Station as manuscript 88-38-2502.

Accepted for publication 5 December 1988.

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The time of onset of leaf rust varies from early December to early February. Disease progress generally slows with the onset of cooler temperatures in early January and then progresses faster with the onset of warmer temperatures in early March. Similar observations have been made in Texas (17). The critical period in the disease cycle for the survival of the fungus is the interval between the time of harvest in May and the emergence of new wheat in early November. How the fungus survives during this period has remained undetermined. Thalictrum flavum L. is an alternate host for P. r. f. sp. tritici, but is extremely rare in the United States (15,28). Other grasses such as Aegilops spp. (1), Bromus spp. (4,31), Hordeum spp. (1,13), and Lolium spp. (27) are occasionally infected by P. r. f. sp. tritici. The fungus also thrives on volunteer wheat plants, usually as dormant mycelium and occasionally as

sporulating mycelium (5,29). Race determination studies have been used to demarcate distinct epidemiological zones, depending on the regularity and frequency of occurrence of certain races. Based on these results, oversummering and overwintering within each epidemiological zone was postulated (16), and circumstantial evidence obtained during an 8-yr leaf rust race survey in Pennsylvania supported this theory (23). Studies in the Great Plains in the United States have demonstrated the presence and local movement of viable inoculum throughout the year in locations where studies were conducted (10), and showed that one of the principle factors that determines the duration of urediniospore survival is temperature (8).

Sources of primary inoculum for leaf rust of wheat in Louisiana have not been determined. Conditions for the survival of P. r. f. sp. tritici (29) are marginal in Louisiana during the summer. Temperatures are usually in the range (33-37 C) that reduces the amount of sporulation (26) and longevity of spore viability (8). Longevity of spore viability at high temperatures is also known to be affected by the location of urediniospores on soil or on living tissue. Soilborne urediniospores survive a simulated temperature regime of 34 C day/22 C night for up to 22 days on moist soil, 13 days on dry soil, and 8 days on dry foliage (12). Urediniospores on dry wheat foliage are also known to survive for at least 9 days at near-optimal (20  $\pm$  1 C) temperatures

This study was undertaken to determine if any grasses in Louisiana support the growth and survival of the fungus, to determine the temporal availability of viable inoculum in the state and test its potential effectiveness, and finally to