Reaction of Downy Mildew-Resistant Lettuce Cultivars to Infection by Turnip Mosaic Virus

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Accepted for publication 16 September 1974.

ABSTRACT

Lettuce cultivars resistant to one or more *Bremia lactucae* races in Israel or The Netherlands were assayed for reaction to the California race of *B. lactucae* and to turnip mosaic virus (TuMV). Forty-three cultivars resistant to one or more Israeli or Netherlands races were resistant to U.S. race 5 which is prevalent in California. By using the world lettuce cultivar differentials for identifying races of *B. lactucae,* we found U.S. race 5 to be different from British races W1, W2, and W3; Israeli races 1, 2, and 4; and Netherlands races 1, 2, 3, and 4. Israeli race 3 and U.S. race 5 appear to be similar. Downy mildew-resistant, TuMV-susceptible cultivars were restricted to the crisphead type. Cultivars Calicel, Calmar, Calmaria, E-4, Imperial 410, Imperial Triumph, Montemar, Monterey, Valrio, Valtemp, and Valverde were mildew-resistant and TuMV-susceptible. The crisphead cultivar Avoncrisp was resistant to both mildew and TuMV. Twenty-seven butterhead type cultivars, two leaf types, one cos type, and one Latin type were resistant, both to U.S. race 5 of *B. lactucae* and to TuMV. The genetic relationships of mildew-resistant and TuMV-susceptible cultivars are discussed.

Phytopathology 65:243-245

Additional key words: races, linkage.

Downy mildew (incited by *Bremia lactucae* Reg.)-resistant crisphead lettuce cultivars *Lactuca sativa* L. grown in the United States are susceptible to turnip mosaic virus (TuMV) (16, 17, 18, 19). These cultivars are derived from crosses of Imperial D × *Lactucae serriola* L. (P.I. 91532), reported in the early literature as P.I. 104854 (8, 14). Resistance to *B. lactucae,* U.S. race 5, is conferred by a single dominant allele, designated *Dm,* in cultivars with the *L. serriola* (P.I. 91532) source of resistance (8, 17). Susceptibility to TuMV is conferred by a recessive allele, designated *tu*; the TuMV allele, *Tu tu*, is linked with the mildew allele, *Dm dm* (17, 18).

Cultivars with P.I. 91532 source of resistance to *B. lactucae* are susceptible to U.S. race 6 in Texas, a new race in California, British race W3, Israeli races 1 and 4, and Netherlands races 3 and 4 (3, 4, 9, 10). There is need, therefore, for additional mildew resistant alleles, free of the linkage to the TuMV-susceptible allele, to broaden the genetic base for resistance to races of *B. lactucae*.

The purposes of this article are: (i) to report the identity of the prevalent race of *B. lactucae* in California, and to compare its identity with races in England, The Netherlands, and Israel; (ii) to list cultivars resistant to U.S. race 5 of *B. lactucae*; (iii) to list cultivars that are TuMV resistant and carry allele(s) that confer resistance to one or more British, Israeli, The Netherlands, and U.S. races of *B. lactucae*; and (iv) to report information concerning the inheritance of resistance to races of *B. lactucae* in relationship to TuMV susceptibility.

MATERIALS AND METHODS.—Forty-three lettuce cultivars resistant to one or more *B. lactucae* races in Israel or The Netherlands were assayed for reaction to U.S. race 5 of *B. lactucae* and to TuMV. Approximately 70 seedlings of each cultivar were assayed for mildew reaction, and about 40 for TuMV reaction.

Downy mildew inoculum was collected from commercial lettuce fields in the central coastal districts of California. Cultures of mildew were maintained continuously on Great Lakes 118 to provide a readily available supply of inoculum. The mildew race or races prevalent in this area were determined by use of the world lettuce cultivar differentials for identifying races of *B. lactucae* (11).

Seeds for plants to be assayed for mildew reaction were placed on moist blotter paper in 11.5 × 10.5 × 3 cm plastic "sandwich boxes," 35 seeds per box. The boxes were placed on slant trays at a 45-degree angle, and a well of one-quarter strength Hoagland's solution (5) was maintained at the base of each box during germination and incubation. The seeds were germinated at 20-22 C under continuous light. On the seventh day, the young seedlings with expanded cotyledons were inoculated with a water suspension of spores. The plastic boxes containing the seedlings were then placed in a growth chamber similar to that described by Huyskes (6). A second inoculation of mildew was made two days after the first inoculation. A photoperiod of 14 hours of light and 10 hours dark was used. During the 'day' the temp was 15 C, with a relative air humidity of 95%, while at 'night' it was 5 C, with 100% relative humidity. An incubation period of 14 days after the second inoculation was allowed before the seedlings were scored for mildew reaction. By misting the seedlings, and then placing lids on the "sandwich boxes" for 10 hours in the dark, conidiophores and conidia were formed on the surfaces of the cotyledons of susceptible cultivars. A cultivar was susceptible if 100% of the plants became infected, and resistant if none were attacked. In each test, mildew-resistant Calmar and mildew-susceptible Great Lakes 118 were included.

The TuMV isolate was obtained from a commercial planting of Calmar in the Salinas Valley of California. All isolates of TuMV thus far collected are capable of infecting susceptible lettuce cultivars (16). To provide a readily available supply of inoculum, the virus was maintained continuously in turnip plants, *Brassica campestris* L. (Rapifera group).

Nonviruliferous green peach aphids, *Myzus persicae* (Sulz.), were reared on radish, *Raphanus sativus* L. The nonviruliferous aphids were transferred to TuMV-

infected turnip plants for about 24 hours; then approximately 20 aphids were transferred to each lettuce seedling for an infection feeding period of about 24 hours. After inoculation with aphids, all plants were sprayed with nicotine sulfate and placed in greenhouses, which were fumigated at weekly intervals with nicotine sulfate. An incubation period of 21 days after inoculation was allowed before the seedlings were scored for TuMV reaction. A clear distinction between susceptible and resistant cultivars was observed. A cultivar was susceptible if 100% of the plants became infected, and resistant if none were infected. Resistant cultivars have extremely high resistance ("immunity") to TuMV (16).

RESULTS.—*Identification of mildew race.*—The following cultivars were susceptible to the mildew collection from the central coast of California; Caravan, Climax, Delta, Francisco, Grand Rapids, Great Lakes 65, Great Lakes 118, Groso, Hilde, Imperial D, Imperial F, Imperial 615, Resistant, Suzan, and Wonder van Voorburg. The cultivar Bourguignonne from the world collection was susceptible, but our stock of Bourguignonne was resistant to the California race.

Cultivars resistant to the prevalent race in California are as follows: *Crisphead type* – Avoncrisp, Calicel, Calmar, Calmaria, E-4, Imperial 410, Imperial Triumph, Montemar, Monterey, Valrio, Valtemp, Valverde. *Butterhead type* – Agilo, Amplus, Arlon, Avondefiance, Brioso, Bourguignonne, Interrex, Kloek, Knap, Kordaat, Korrekt, Kwiek, Larganda, Liba, Magiola, Meikoningin, Noran, Proeftuin's Blackpool, Portato, Rapide, Regina, Secura, Solito, Tinto, Tonika, Valore, Ventura. *Leaf type* – Red Salad Bowl, Salad Trim. *Cos type* – Valmaine. *Latin type* – Sucrine. The reaction of these cultivars indicates that U.S. race 5 was present since cultivars Imperial F, Imperial D, and Imperial 615 resistant to U.S. race 4 were susceptible (7, 8). The cultivars Calmar, Valverde, and Valmaine were resistant; therefore, U.S. race 6 was not present (10). With the use of the system suggested by Tjallingii and Rodenburg (11), we determined that U.S. race 5, the prevalent race in California, is different from Netherlands (NL) races 1, 2, 3, and 4. Based on the results of Netzer (9) on the reaction of cultivars to four Israeli races, it is apparent that U.S. race 5 is different from Israeli races 1, 2, and 4. Forty-eight cultivars, used for identifying races, inoculated with U.S. race 5 gave identical reactions as those reported by Globerson et al. (4) for Israeli race 3. United States race 5 and Israeli race 3 appear to be similar. The reaction of test cultivars indicates that the British races W1, W2, and W3 differ from U.S. race 5 (2).

Resistance to TuMV and Bremia lactucae.—To determine how widespread susceptibility to TuMV is in mildew-resistant cultivars of *L. sativa,* the world cultivar differentials for identifying races of *B. lactucae* also were surveyed for TuMV resistance.

The cultivars tested were either susceptible or resistant to TuMV, with no segregation within the population of a given cultivar. TuMV-susceptible, downy mildew-resistant cultivars were all of the crisphead type: Calicel, Calmar, Calmaria, E-4, Imperial 410, Imperial Triumph, Montemar, Monterey, Valrio, Valtemp, and Valverde. Cultivars resistant to TuMV and to U.S. race 5 as well as to one or more Israeli and Netherlands races of *B. lactucae* are as follows: *Crisphead type* – Avoncrisp. *Butterhead type* – Agilo, Amplus, Arlon, Avondefiance, Brioso, Bourguignonne, Interrex, Kloek, Knap, Kordaat, Korrekt, Kwiek, Larganda, Liba, Magiola, Meikoningin, Noran, Proeftuin's Blackpool, Portato, Rapide, Regina, Secura, Solito, Tinto, Tonika, Valore, Ventura. *Leaf type* – Red Salad Bowl, Salad Trim. *Cos type* – Valmaine. *Latin type* – Sucrine. The crisphead cultivars Caravan, Francisco, and Great Lakes 65 are TuMV-resistant, and resistant to British races W1 and W2, but susceptible to U.S. race 5 of *B. lactucae*. Caravan is also resistant to Netherlands races 1 and 2.

DISCUSSION.—Zink and Duffus (16, 17, 18) reported strong circumstantial evidence that TuMV susceptibility was introduced into the pedigrees of mildew resistant crisphead cultivars by P.I. 91532. The pedigrees of all lettuce cultivars known to be susceptible to TuMV apparently contain this *L. serriola* collection from Russia (1, 8, 14, 16, 17, 18). The mildew-resistant, TuMV-resistant crisphead cultivar Avoncrisp released by the National Vegetable Research Station, Wellesbourne, England, is a selection from USDA breeding line 45634M (12). Avoncrisp's pedigree includes P.I. 91532, Imperial D, Imperial F, and Imperial 152 (14). The fact that Avoncrisp is TuMV-resistant does not necessarily disagree with this hypothesis. Avoncrisp has a different pedigree than the TuMV-susceptible cultivars (14). Probably, the linkage between the mildew-resistant allele and the TuMV-susceptible allele was broken in one of the crosses in the pedigree of Avoncrisp, and by chance, a double-resistant progeny was selected.

Globerson et al. (4), in their study on the inheritance of resistance to races in Israel (IL) and The Netherlands (NL), concluded that resistance to races IL2, IL3, IL4, NL1, NL3, and NL4 is conferred, in each instance, by a different dominant allele, and that resistance to NL2 is conferred by two dominant complementary alleles.

Zink (15) reported there are at least three dominant alleles that confer resistance to U.S. race 5. Thus, the implication is that more than one dominant allele may confer resistance to a given race.

Reaction of the world lettuce cultivar differentials indicated that there are three races of *B. lactucae* in Israel and four in The Netherlands, and that at least seven distinct races exist in these two countries (4). In contrast, no separation of races was found in California surveys during the period 1967 through 1972.

Direct and indirect evidence has suggested that races in *B. lactucae* originated through mutation, rather than through adaptation, hybridization, or heterocaryosis (3, 8). Many new races have been reported from Britain, The Netherlands, and Israel. In contrast, there has been only one new race, U.S. race 5, reported in California in 41 years, 1932-1973. Significant acreages of Calmar have been planted in California since 1963, and the resistance continues to be effective, through 1973 (13). A possible explanation for this phenomenon is that Calmar has more alleles for resistance than the single dominant allele that confers resistance to U.S. race 5. These other alleles may have blocked the establishment of a new mutant race. This hypothesis is supported by the resistance of Calmar to seven races: U.S. 5, IL2, and IL3, NL1, and NL2, and British race W1, and W2 (2, 4, 8). Globerson et al. (4) reported that Calmar has two dominant alleles, one of which confers resistance to IL2, and the other to IL3.

Calmar also carries two dominant complementary alleles, which confer resistance to NL2 and NL1 (4). The inheritance of resistance to the British races has not been reported. It is not known whether the single dominant allele that confers resistance to U.S. race 5 is the same as one of the alleles that confers resistance to one or more of the Israeli, Netherlands, or British races. The similarity of U.S. race 5 and IL3 suggest that the single dominant allele which confers resistance to U.S. 5 is the same allele which confers resistance to IL3.

Lettuce cultivars Calmar, Calmaria, and Montemar were found seriously affected with *B. lactucae* in commercial plantings in the Santa Maria Valley of California in the spring of 1974. This is the first observation of a race attacking cultivars with P.I. 91532 source of resistance in California. A new physiologic race is believed to be the cause of the recent outbreak of downy mildew in these previously resistant cultivars. At least it is a new race in California. It is not known if this is an introduced race, or one which developed as a mutant in California.

LITERATURE CITED

1. BOHN, G. W., and T. W. WHITAKER. 1951. Recently introduced varieties of head lettuce and methods used in their development. Pages 1-27 *in* U.S. Dep. Agric., Agric. Res. Serv. Circ. 881.
2. CHANNON, A. G., and Y. SMITH. 1970. Further studies on races of Bremia lactucae Regel. Hortic. Res. 10:14-19.
3. CHANNON, A. G., M. J. W. WEBB, and L. E. WATTS. 1965. Studies on two races of Bremia lactucae Regel. Ann. Appl. Biol. 56:389-397.
4. GLOBERSON, D., D. NETZER, and F. TJALLINGII. 1974. Mode of inheritance of resistance to three Israel and four Dutch races of downy mildew (Bremia lactucae Reg.). Euphytica 23:54-60.
5. HOAGLAND, D. R., and D. I. ARNON. 1960. The water-culture method for growing plants without soil. Calif. Agric. Expt. Stn. Circ. 347:1-31.
6. HUYSKES, J. E. 1971. Testing for resistance to fungal leaf disease in an inexpensive growth chamber. Euphytica 20:235-238.
7. JAGGER, I. C., and N. CHANDLER. 1933. Physiologic forms of Bremia lactucae on lettuce. Phytopathology 23:18-19.
8. JAGGER, I. C., and T. W. WHITAKER. 1940. The inheritance of immunity from mildew (Bremia lactucae) in lettuce. Phytopathology 30:427-433.
9. NETZER, D. 1973. Physiologic races of Bremia lactucae in Israel. Trans. Br. Mycol. Soc. 61:375-378.
10. SLEETH, B., and P. W. LEEPER. 1966. Mildew resistant lettuce susceptible to a new physiologic race of Bremia lactucae in south Texas. Plant Dis. Rep. 50:460.
11. TJALLINGII, F., and C. M. RODENBURG. 1969. Onderzoek van sharassen op vatbaarheid voor vier fysios van valse meeldauw (Bremia lactucae). Zaalbelangen 23:436-438.
12. WATTS, L. E., A. G. CHANNON, and M. J. W. WEBB. 1965. Breeding for downy mildew resistance. Grower 63:1114-1115.
13. WELCH, J. E., R. G. GROGAN, F. W. ZINK, G. M. KIHARA, and K. A. KIMBLE. 1965. Calmar, a new lettuce variety resistant to downy mildew. Calif. Agric. 19(8):3-4.
14. WHITAKER, T. W., G. W. BOHN, J. E. WELCH, and R. G. GROGAN. 1958. History and development of head lettuce resistant to downy mildew. Proc. Am. Soc. Hortic. Sci. 72:410-416.
15. ZINK, F. W. 1973. Inheritance of resistance to downy mildew (Bremia lactucae Reg.) in lettuce. J. Am. Soc. Hortic. Sci. 98:293-296.
16. ZINK, F. W., and J. E. DUFFUS. 1969. Relationship of turnip mosaic virus susceptibility and downy mildew (Bremia lactucae), resistance in lettuce. J. Am. Soc. Hortic. Sci. 94:403-407.
17. ZINK, F. W., and J. E. DUFFUS. 1970. Linkage of turnip mosaic virus susceptibility and downy mildew (Bremia lactucae), resistance in lettuce. J. Am. Soc. Hortic. Sci. 95:420-422.
18. ZINK, F. W., and J. E. DUFFUS. 1973. Inheritance and linkage of turnip mosaic virus and downy mildew (Bremia lactucae) reaction in Lactucae serriola. J. Am. Soc. Hortic. Sci. 98:49-51.
19. ZINK, F. W., J. E. DUFFUS, and K. A. KIMBLE. 1973. Relationship of a non-lethal reaction to a virulent isolate of lettuce mosaic virus and turnip mosaic susceptibility in lettuce. J. Am. Soc. Hortic. Sci. 98:41-45.