Literature Cited

1. Aquino, D. I., and J. P. Mamisao. 1938. Soil survey of the Maquiling area. *Phil. Agr.* 27:647-665.
2. Cockshull, K. E., and A. P. Hughes. 1968. Accumulation of dry matter by *Chrysanthemum morifolium* after flower removal. *Nature* 217:979-980.
3. Coyne, D. P. 1966. The genetics of photoperiodism and the effect of temperature on the photoperiodic response for time of flowering in *Phaseolus vulgaris* L. varieties. *Proc. Amer. Soc. Hort. Sci.* 89:350-360.
4. Francis, C. A. 1970. Modification of the ozalid paper technique for measuring integrated light transmission values in the field. *Crop Sci.* 10:321-322.
5. Friend, D. T. C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42:577-580.
6. Gunkel, W. W., and C. W. Mulligan. 1953. Leaf punch for foliage samples. *Farm Res.* 19(1):3.
7. Hartman, L. L., and W. A. Brun. 1971. Effect of atmospheric carbon dioxide enrichment at different developmental stages on growth and yield components of soybeans. *Crop Sci.* 11:886-888.
8. Jones, L. H. 1967. Factors affecting the productivity of dwarf French beans. *Agr. Progress* 42:32-52.
9. Leopold, A. C., E. Niedergang-Kamien, and J. Janick. 1959. Experimental modification of plant senescence. *Plant Physiol.* 34:570-573.
10. Loach, K. 1970. Analysis of differences in yield between six sugarbeet varieties. *Ann. Appl. Bio.* 66:217-223.
11. Lyons, T. 1968. Control of tomato fruitset to concentrate yield for mechanical harvest. Ph.D. Thesis, Cornell University, 128 p. Univ. Microfilms, Ann Arbor, Mich. *Diss. Abstr.* 29:1895B.
12. Meadley, J. T., and G. M. Milbourn. 1971. The growth of vining peas. III. The effect of shading on abscission of flowers and pods. *J. Agr. Sci.* 77:103-108.
13. Molisch, H. 1929. Die Lebensdauer der Pflanze. Gustav Fischer, Jena. 168 p.
14. Nosberger, J., and E. C. Humphries. 1965. The influence of removing tubers on dry matter production and net assimilation rate of potato plants. *Ann. Bot. N.S.* 29:579-588.
15. ______, and G. N. Thorne. 1965. The effect of removing florets or shading the ear of barley on production and distribution of dry matter. *Ann. Bot. N.S.* 29:635-644.
16. Ojehomon, O. O. 1970. Effect of continuous removal of open flowers on the seed yield of two varieties of cowpea, *Vigna unguiculata* (L). Walp. *J. Agr. Sci.* 74:375-381.
17. Smith, Francis L., and Richard H. Prior. 1962. Effects of maximum temperature and age of flowering and seed production in three bean varieties. *Hilgardia* 33:669-688.
18. Thorne, G. N. 1966. Physiological aspects of grain yield in cereals. p. 88-105. The growth of cereals and grasses. ed. by F. L. Milthorpe and J. D. Ivins. Butterworths, London.

Inheritance and Linkage of Turnip Mosaic Virus and Downy Mildew (*Bremia lactucae*) Reaction in *Lactuca serriola*[1]

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Abstract. Data for resistance in *Lactuca serriola* L. to turnip mosaic virus (TuMV) and downy mildew were obtained from 5 F_2 progenies of crosses between TuMV-susceptible, mildew-resistant, and TuMV-resistant, mildew-susceptible parents. The F_1 progeny were TuMV and mildew-resistant. Of 1,103 F_2 plants assayed 823 were TuMV-resistant and 280 TuMV-susceptible. A total of 834 mildew-resistant plants were observed, and 269 mildew-susceptible. Resistance to TuMV and mildew are each controlled by a single dominant allele, designated *Tu* and *Dm*, respectively. The TuMV gene, *Tu tu*, is linked with the mildew gene, *Dm dm*. In the repulsion phase, the crossover value was 12.0% ± 2.9. F_2 progenies of crosses between TuMV-susceptible, mildew-resistant *L. serriola* and TuMV-susceptible, mildew-resistant *L. sativa* cv. 'Calmar' or 'Imperial 410', and crosses among cv. 'Calmar', 'Imperial 410', and 'E-4', indicated they possessed the same dominant allele for mildew-resistance, and the same recessive allele for TuMV-susceptibility.

Downy mildew-resistant *Lactuca sativa* L. crisphead cultivars currently grown in the United States are turnip mosaic virus (TuMV)-susceptible (9, 11). Zink and Duffus (9, 10) have reported circumstantial evidence which indicates that TuMV-susceptibility in *L. sativa* cvs. Calicel, Calmar, Imperial 410, Valrio, Valtemp, and Valverde is associated with mildew-resistant progenies derived from a *Lactuca serriola* L. collection (P.I. 91532)[4] from Russia (5, 8). In a survey of *L. serriola* growing in noncultivated areas in the Santa Clara and Salinas Valleys of California the populations fell into 3 classes: a) TuMV-resistant, mildew-resistant; b) TuMV-resistant, mildew-susceptible, and c) TuMV-susceptible, mildew-resistant (9). From this collection several lines were selected which were homozygous TuMV-susceptible, mildew-resistant.

The purpose of this paper is to report: a) the nature of inheritance of TuMV-susceptibility and mildew-resistance in *L. serriola;* b) the linkage relation of TuMV and mildew reaction; and c) new information concerning the inheritance of mildew-resistance in *L. sativa.*

Materials and Methods

Crosses were made between the homozygous TuMV-resistant, mildew-susceptible 'Great Lakes 118' and the homozygous TuMV-susceptible, mildew-resistant *L. serriola* lines to study the inheritance of TuMV-susceptibility, mildew-resistance, and the linkage of the TuMV gene with the mildew gene. In each cross, the *L. serriola* line was used as the pollen parent.

A second series of crosses were made between homozygous TuMV-susceptible, mildew-resistant *L. serriola* lines and homozygous TuMV-susceptible, mildew-resistant cvs. Calmar, and Imperial 410 to determine if the genes for mildew and TuMV reaction are the same in *L. serriola* lines and *L. sativa* cultivars. In each cross, *L. serriola* was used as the pollen parent. Crosses were also made among the homozygous TuMV-susceptible, mildew-resistant cvs. Calmar, Imperial 410, and E-4, to test for identity of the alleles for resistance to mildew and susceptibility to TuMV.

Seed for plants to be assayed for disease reaction was

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germinated on moist filter paper in petri dishes at temp in the range of 20 to 22°C under continuous light. The young seedlings (cotyledon stage) were transplanted into flats.

Downy mildew inoculum was collected from commercial lettuce fields in the central coastal districts of California. Test of the mildew inoculum indicated that race 5 was present, since cultivars resistant to race 4 were susceptible (4, 5). To maintain an available supply of mildew for inoculation, cultures of mildew were maintained continuously on 'Great Lakes 118'. For the assay test in the linkage study, young seedlings with 5 to 7 true leaves were inoculated with a water suspension of spores of the fungus 6 to 7 days after TuMV inoculation, and tested by methods described by Rodenburg (6). In the mildew allelism tests, young seedlings with expanded cotyledons were inoculated with a water suspension of spores in a growth chamber similar to that described by Huyskes (3).

Nonviruliferous green peach aphids, *Myzus persicae* (Sulz.), were reared on radish, *Raphanus sativus* L. The nonviruliferous aphids were transferred to TuMV-infected turnip plants, *Brassica campestris* L. (Rapifera group), for 24 hr; then approx 10 to 20 individuals were transferred to each of the F_2 lettuce seedlings for an infection feeding period of 24 hr. After inoculation with aphids, all plants were sprayed with nicotine sulfate and placed in greenhouses which were fumigated at weekly intervals with nicotine sulfate. The F_1 plants were inoculated with TuMV after they had produced seed. In the TuMV allelism tests seedlings with 2 to 3 true leaves were inoculated with TuMV. Two independent F_2 populations from each cross were assayed for mildew or TuMV reaction in the allelism tests.

Table 1. F_2 of parental combinations, showing single factor mode of inheritance to turnip mosaic virus resistance.[z]

Family	Parentage	Observed Res.	Observed Suscp.	X^2	P
5	GL 118 X *L. serriola*-8	178	53	0.521	0.50-0.30
7	GL 118 X *L. serriola*-8	141	52	0.389	0.70-0.50
8	GL 118 X *L. serriola*-14	161	58	0.257	0.70-0.30
15	GL 118 X *L. serriola*-20	179	53	0.575	0.50-0.30
26	GL 118 X *L. serriola*-20	164	64	1.146	0.30-0.20
Total		823	280	0.015	0.95-0.70

[z]Homogeneity of families = 2.873, P = 0.70-0.50.

The seedlings of 5 crosses involving 4 parents in the linkage study were classified with respect to disease reaction in 4 categories: 1) TuMV-resistant, mildew-resistant; 2) TuMV-resistant, mildew-susceptible; 3) TuMV-susceptible, mildew-resistant; and 4) TuMV-susceptible, mildew-susceptible.

Linkage values were determined from repulsion F_2 progenies by using the product moment method and deriving values from Fisher and Balmukands tables (2).

Results

Inheritance of TuMV susceptibility. TuMV-resistant F_1 plants were obtained from the crosses between the TuMV-resistant 'Great Lakes 118' and the susceptible *L. serriola* lines. The data obtained for segregation of TuMV-resistance in the F_2 progenies from crosses are presented in Table 1. The data indicate that a recessive gene confers susceptibility to TuMV in *L. serriola*.

Inheritance of mildew resistance. Crosses between the mildew-resistant *L. serriola* lines and susceptible 'Great Lakes 118' produced F_1 plants that were mildew-resistant. The parental combinations, the observed number of F_2 plants resistant and susceptible to downy mildew, are presented in Table 2. These data indicate that the F_2 progenies of the several crosses segregated closely to a ratio of 3 resistant to 1 susceptible to the physiologic race or races of *Bremia lactucae* prevalent in the central coastal districts of California.

Linkage relation. The observed segregation of the F_2 population, Chi square, probability values, and cross-over values of crosses between TuMV-resistant, mildew-susceptible ('Great Lakes 118') *Tu Tu dm dm* and TuMV-susceptible mildew-resistant lines of *(L. serriola) tu tu Dm Dm* are presented in Table 3. The frequencies obtained in the F_2 population clearly deviate from a 9:3:3:1 ratio. The deviation resulted from an excess in the parental classes and a deficiency in the recombination classes. Linkage is indicated.

Mildew allelism tests. Crosses between the mildew-resistant *L. serriola* lines and mildew-resistant cvs. Calmar, or Imperial 410, and crosses among the mildew-resistant cvs. Calmar, Imperial 410, and E-4, produced F_1's that were mildew-resistant. Approximately 197 plants were assayed for disease reaction from each of 12 F_2 families and found mildew-resistant. The same single dominant allele is indicated for mildew-resistance in *L. serriola* lines and *L. sativa* cvs. Calmar, Imperial 410, and E-4.

Table 2. F_2 of parental combinations, showing single factor mode of inheritance of downy mildew resistance.[z]

Family	Parentage	Observed Res.	Observed Suscp.	X^2	P
5	GL 118 X *L. serriola*-8	172	59	0.036	0.95-0.70
7	GL 118 X *L. serriola*-8	150	43	0.761	0.50-0.30
8	GL 118 X *L. serriola*-14	162	57	0.123	0.95-0.70
15	GL 118 X *L. serriola*-20	171	61	0.207	0.70-0.30
26	GL 118 X *L. serriola*-20	179	49	1.497	0.30-0.20
Total		834	269	0.220	0.70-0.50

[z]Homogeneity of families = 0.240, P = 0.70-0.50.

TuMV allelism tests. The same crosses as in the mildew allelism tests were assayed for TuMV reaction. The F_1's were TuMV-susceptible. A total of 1120 plants were tested from the

Table 3. F_2 of parental combinations, showing linkage of turnip mosaic-reaction gene with downy mildew-reaction gene.

Family	Parentage	Observed segregation TuMV-res. mildew-res.	TuMV-res. mildew-suscp.	TuMV-suscp. mildew-res.	TuMV-suscp. mildew-suscp.	Total	X^2 for 9:3:3:1	P	Linkage value %
5	GL 118 X *L. serriola*-8	120	58	52	1	231	20	<0.01	13.5 ± 4.2
7	GL 118 X *L. serriola*-8	98	43	52	0	193	--		--
8	GL 118 X *L. serriola*-14	105	56	57	1	219	26	<0.01	12.5 ± 6.6
15	GL 118 X *L. serriola*-20	119	60	52	1	232	21	<0.01	13.5 ± 6.4
26	GL 118 X *L. serriola*-20	116	48	63	1	228	23	<0.01	13.5 ± 6.5
Total observed		558	265	276	4	1103	106.9	<0.01	12.0 ± 2.9
Total expected 9-3-3-1		620	207	207	69	1103			

12 F_2 families and found TuMV-susceptible. The evidence in the crosses indicates the same single recessive allele for susceptibility in *L. serriola* lines and *L. sativa* cvs. Calmar, Imperial 410, and E-4.

Discussion

Zink and Duffus (10) reported linkage of the mildew reaction gene, *Dm dm* with the TuMV reaction gene, *Tu tu*, with a cross-over value of 12.5% ± 1.6 in *L. sativa*. In the present study we found a similar genetic relationship in the 3 *L. serriola* lines that were TuMV-susceptible and mildew-resistant. The cross-over value for the *L. serriola* crosses was 12.0% ± 2.9. These 2 linkage values are probably estimates of the same value. Also the same allele for mildew-resistance and the same allele for TuMV-susceptibility was demonstrated in cvs. Calmar, Imperial 410, and E-4, and in the 3 *L. serriola* lines. These genetic relationships are additional strong circumstantial evidence that TuMV susceptibility in *L. sativa* is associated with mildew-resistant progenies derived from *L. serriola* (P.I. 91532).

'Imperial 410' was derived from original crosses of 'Imperial D' and P.I. 91532, and 'Imperial D' crossed to a mildew-resistant strain of 'Chinese Stem' lettuce (1). *Lactuca serriola* (P.I. 91532) is the source of mildew resistance in 'Calmar' (7, 8), and crosses between 'Calmar' and 'Imperial 410' indicated the same allele for mildew-resistance and the same allele for TuMV-susceptibility. It is probable that resistance in 'Imperial 410' stems from P.I. 91532.

Cultivar E-4 was released in 1943 by the late Dr. LeRoy E. Weaver, Growers Ice and Development Company, Salinas, California. The source of resistance to mildew and susceptibility to TuMV is not known, as no pedigree record is available. Crosses between 'Calmar' and 'E-4', or 'E-4' and 'Imperial 410' indicated the same allele for mildew-resistance and the same allele for TuMV-susceptibility. It appears likely, based on the history of 'E-4', and the genetic relationships reported herein, that 'E-4' is a selection from one of the late Dr. I. C. Jagger's advanced breeding lines derived from a cross with P.I. 91532.

Literature Cited

1. Bohn, G. W., and Thomas W. Whitaker. 1951. Recently introduced varieties of head lettuce and methods used in their development. *USDA, ARS Circ.* 881:1-27.
2. Fisher, R. A., and Bhai Balmukand. 1928. The estimation of linkage from offspring of selfed heterozygotes. *J. Genet.* 20:79-92.
3. Huyskes, J. E. 1971. Testing for resistance to fungal leaf diseases in an inexpensive growth chamber. *Euphytica* 20:235-238.
4. Jagger, Ivan C., and Norman Chandler. 1933. Physiologic forms of *Bremia lactucae* on lettuce. *Phytopathology* 23:18-19 (Abstr).
5. ———, and Thomas W. Whitaker. 1940. The inheritance of immunity from mildew *(Bremia lactucae)* in lettuce. *Phytopathology* 30:427-433.
6. Rodenburg, C. M. 1966. Some testing procedures and research experiences on resistance to *Bremia lactucae* Regel. in lettuce. *Euphytica* 15:141-148.
7. 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. Agr.* 19(8):3-4.
8. Whitaker, Thomas W., G. W. Bohn, J. E. Welch, and R. G. Grogan. 1958. History and development of head lettuce resistant to downy mildew. *Proc. Amer. Soc. Hort. Sci.* 72:410-416.
9. Zink, F. W., and James E. Duffus. 1969. Relationship of turnip mosaic virus susceptibility and downy mildew, *(Bremia lactucae)*, resistance in lettuce. *J. Amer. Soc. Hort. Sci.* 94:403-407.
10. ———, and ———. 1970. Linkage of turnip mosaic virus susceptibility and downy mildew, *(Bremia lactucae)* resistance in lettuce. *J. Amer. Soc. Hort. Sci.* 95:420-422.
11. ———, ———, 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. Amer. Soc. Hort. Sci.* 98:41-45.

Fruit-set and Development in the Pear: Diffusible Growth Substances from Seeded and Seedless Fruits[1]

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Abstract. Seasonal changes in natural growth substances were studied by collecting the diffusate, via the pedicel, from intact seeded 'Winter Nelis', seeded 'Bartlett', and parthenocarpic 'Bartlett' pear fruits. The diffusate of 'Bartlett' fruits collected 10 to 25 days after full bloom (AFB) contained more auxin-like promoter than did that of 'Winter Nelis' fruits. With the exception of the 45-day sample, the diffusate from parthenocarpic 'Bartlett' fruits had more promoter from 25 to 70 days (AFB) than did either seeded pear. In contrast, more gibberellin (GA)-like materials diffused from 'Winter Nelis' fruits than from seeded or parthenocarpic 'Bartlett' fruits. With all types of pears the concentration of abscisic acid-like materials in the diffusate was similar until harvest when the concentration was greater for 'Winter Nelis' than for 'Bartlett'. The combined effect of relatively low amounts of auxin-like and greater amounts of GA-like materials may explain why the presence of seeded pears during the postbloom period has a greater inhibitory effect on flower bud formation in 'Winter Nelis' than in 'Bartlett'.

In most studies concerning concn of endogenous growth regulators in fruits, the substances have been extracted from intact fruits, using organic solvents. The extractable hormones in pear fruits have been investigated by Rudnicki et al. (15) and by Gil et al. (6). There was no evidence, however, that these substances were involved in processes outside the fruits. The seasonal variations of diffusible growth promoter(s) collected from intact 'Bartlett' pear fruits were reported recently (7). In that investigation most of the growth promoter diffused from seedless, rather than seeded, fruits and this was considered related to the ability of spurs carrying seedless fruits to differentiate flower buds.

The purpose of the present work was to investigate the seasonal changes of natural growth-promoting and growth-inhibiting compounds diffusing from intact seeded and seedless pear fruits.

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