

A New Gene for Resistance to *Bremia lactucae*

J. E. Yuen and J. W. Lorbeer

Graduate research assistant and professor, respectively, Department of Plant Pathology, New York State College of Agriculture and Life Sciences, Cornell University, Ithaca 14853.

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ABSTRACT

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The lettuce cultivar Vanguard 75 was free of downy mildew caused by *Bremia lactucae* in a lettuce cultivar evaluation trial during 1980 in Oswego County, NY, while other cultivars of lettuce in the trial had various amounts of mildew. Vanguard and Vanguard 75 were resistant when inoculated with a number of isolates of *B. lactucae*, but they were completely susceptible when inoculated with other isolates, indicating that the resistance in these

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cultivars is race specific. Analysis of resistance and susceptibility patterns indicates that this is a new resistance factor, different from the 12 previously described. By testing F_1 , F_2 , and testcross families from crosses of Vanguard 75 and susceptible cultivars, it was determined that the resistance factor in Vanguard 75 is conditioned by a single dominant gene.

There are a number of genes in lettuce (*Lactuca sativa* L.) for resistance to *Bremia lactucae* Regel, although these genes impart immunity against only some populations of *B. lactucae*. In the United States, only four genes have been intentionally used in lettuce breeding programs. Two genes from the cultivar Romaine blonde lente a monter were used in the breeding of the Imperial cultivars (8). A single gene from plant introduction (P.I.) 167150 was used in the breeding of Valmaine (12) and a single gene from P.I. 91532 was used in the breeding of Valverde (11). Calmar contains the two resistance genes from Romaine blonde lente a monter and the single resistance gene from P.I. 91532 (21).

A total of 13 different resistance genes in lettuce have been described (1,4). Crute and Johnson (4) analyzed the relationship of *B. lactucae* and lettuce with a "gene-for-gene" scheme, where factors for resistance in lettuce are correlated with factors for virulence in *B. lactucae*. If an isolate of *B. lactucae* can overcome the resistance in a specific lettuce cultivar, it is assigned the virulence factor corresponding to that resistance. A list of lettuce cultivars and their genes for resistance has been published by Crute (2). Bannerot (1) reported an additional resistance gene from *Lactuca serriola* L.

When we observed that the lettuce cultivars Vanguard 75 and Commander were free of downy mildew in a lettuce cultivar evaluation trial conducted by the Joseph Harris Company during 1980 in Oswego County, NY, we suspected that this might be due to race-specific resistance. This type of resistance was suspected, since other cultivars of lettuce in the trial had downy mildew and Vanguard 75 had been susceptible to *B. lactucae* in other parts of the United States. Vanguard 75 was chosen for further study since it currently was being used in the New York State lettuce breeding program conducted by R. W. Robinson at the New York State Agricultural Experiment Station, Geneva, NY. Vanguard 75 was not bred to be downy mildew resistant, and there was no reason to suspect its resistance to *B. lactucae* until it was observed to be free of downy mildew in the lettuce cultivar evaluation trial.

MATERIALS AND METHODS

The lettuce cultivar evaluation trial planted by the Joseph Harris Company, Rochester, NY 14624, was rated for downy mildew on 15 July 1980. The trial was of a randomized complete block design.

with 28 cultivars each planted in a double 6.1-m (20-ft) row. Routine application of pesticides, along with thinning and weeding, had been performed by the grower. The incidence of downy mildew was estimated by counting the total number of plants and the number of plants showing any downy mildew symptoms for each plot.

Lettuce seed of the cultivars Ithaca and Vanguard 75 were obtained from the Joseph Harris Company. Seed of the cultivars Vanguard and Vanguard 75 were obtained from R. W. Robinson. Vanguard 75 seed was obtained from William Waycott, Vegetable Production Research Unit, USDA, Salinas, CA 93915. Lettuce seed of the differential cultivars used to determine virulence factors of *B. lactucae* were obtained from the same seed companies as those used in a previous study (22).

The isolates of *B. lactucae* used in this study were grown from single sporangiospores taken from cultures that had been established and maintained in the laboratory. M-7-SS1 was isolated in 1978, 1-80-SS1 was isolated in 1980, and the remainder of the isolates were isolated in 1981. The virulence phenotype of each of these isolates was determined as in a previous study (22). These isolates were maintained on detached lettuce cotyledons of plants of cultivar Ithaca on moist filter paper in petri dishes kept in an illuminated incubator (14 C, 12-hr photoperiod, 3,000 lux) through weekly transfer of sporangia. During routine maintenance, the cotyledons were shaken in distilled water and the resulting suspension was used directly, but for resistance and susceptibility studies the sporangia were pelleted in a centrifuge at 10,500 g and resuspended in distilled water to obtain a concentration of 10^5 sporangia per milliliter. This pelleting and resuspending was performed to remove a water-soluble germination inhibitor that reduces germination in high concentrations of sporangia (14).

Seedlings of cultivars Ithaca, Vanguard, and Vanguard 75 were grown by placing seed on moist Cornell potting mix (a mixture of peat moss and perlite) in 104-mm (4-in.)-diameter plastic pots and then covering the seeds with a thin layer of vermiculite. These pots were then kept in a greenhouse (18–24 C) for 7–10 days. Seedlings were removed from the pot by severing them at the soil line with a razor blade, and the two cotyledons were removed with a scalpel. These plant parts were placed, abaxial side upward, on moist filter paper in ordinary glass petri dishes (10 cotyledons per dish) or on moist paper towels in plastic sandwich boxes (50 cotyledons per box) and kept at room temperature and lighting for 1 day prior to inoculation.

Lettuce cultivars were tested for resistance or susceptibility by inoculating the detached cotyledons with single 10- μ l droplets of a suspension of *B. lactucae* at 10^5 sporangia per milliliter and

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incubating them in the illuminated incubator (14 C; 12-hr photoperiod, 3,000 lux). After 10 days, cotyledons were rated for susceptibility (as evidenced by sporulation of *B. lactucae*) or resistance (as evidenced by lack of sporulation). Cotyledons of Vanguard or Vanguard 75 showing an apparent resistant reaction were observed microscopically by first vacuum infiltrating them with water (as described by Micheltore and Ingram [15]) and observing them with a light microscope. At each of 25 penetration points showing the hypersensitive reaction described by Crute and Johnson (4), the number of melanized epidermal cells was counted. If this hypersensitive reaction was not evident, the interior of the cotyledon was searched for mycelia of *B. lactucae*. If neither the hypersensitive reaction nor mycelium was observed, then the cotyledon was considered uninfected and was not included in the analysis.

Single leaves from the progeny of a number of crosses of cultivars Vanguard 75 and either Ithaca or Minetto were obtained from R. W. Robinson. These consisted of an F₁ of a cross of Vanguard 75 ×

Ithaca; F₂'s of Vanguard 75 × Minetto, Minetto × Vanguard 75, and Vanguard 75 × Ithaca; and a test cross of [(Vanguard 75 × Ithaca) F₁ × Ithaca] BC₁. In addition, a small set of F₂ plants was grown from an Ithaca × Vanguard 75 cross. The individual leaves of the first set of crosses were inoculated with 10-μl drops of a suspension of isolate 1-80-SS1 and their resistance (no sporulation) or susceptibility (sporulation) was noted 10 days later. Leaf disks were taken from the F₂ plants and similarly tested with the same isolate.

RESULTS

In the lettuce cultivar field trial, the only cultivars of lettuce that were completely free of downy mildew were Vanguard 75 and Commander. The others (Ithaca, FL 1265, A-8, A-1, Minetto, FL 9042, FL 1365, Greenlakes, Montello, Mesa 659, Empire, Fairton, Coolguard, Crispy, and Empress) had amounts of mildew varying from 2 to 74% (Table 1).

When inoculated with isolates M-7-SS1, 18-81-SS1, 20-81-SS1, and 22-81-SS1 under laboratory conditions, Vanguard and Vanguard 75 were susceptible (Table 2). The virulence phenotype of these isolates as determined by the set of differential cultivars with known resistance factors is also in Table 2. When inoculated with the isolates 1-80-SS1, 5-81-SS1, 12-81-SS1, 23-81-SS1, 28-81-SS1, and 29-81-SS1, no sporulation was seen on the cotyledons of either Vanguard or Vanguard 75 after 14 days (Table 2). The virulence phenotype of these isolates is also presented in Table 2. When cotyledons of Vanguard and Vanguard 75 inoculated with the nonvirulent isolates of *B. lactucae* were examined under the microscope, the hypersensitive response was seen in all cotyledons. In this hypersensitive reaction, only one (very rarely two) epidermal cells were melanized. A microphotograph of this hypersensitive response is presented in Fig. 1.

Detached leaves from all 27 plants of the (Vanguard 75 × Minetto) F₁ were resistant when inoculated with 1-80-SS1 (Table 3). From the four F₂ families, a total of 123 susceptible plants were found among the 374 plants tested for resistance to isolate 1-80-SS1 (Table 3) with a calculated chi-square of 0.41 ($P = 0.48$). The observed and expected number of susceptible plants from each of

TABLE 1. Incidence of downy mildew (caused by *Bremia lactucae*) in a cultivar evaluation trial planted by the Joseph Harris Company^a in 1980

Cultivar ^b	Mildew ^c (%)	Cultivar ^b	Mildew ^c (%)
Ithaca	34	Montello	64
Ithaca	38	Montello	71
Ithaca	35	Ithaca	74
FL 1265	24	Ithaca	64
A 8-1-13	16	Vanguard 75	0
A 1	22	Mesa 659	62
Minetto	40	Empire	8
Minetto	24	Fairton	2
FL 9042	20	Coolguard	25
FL 1365	36	Crispy	16
Greenlakes	28	Empress	20
Greenlakes	72	Commander	0

^aJoseph Harris Company, Rochester, NY 14624.

^bMore than one seed lot of some cultivars was planted.

^cLSD ($P = 0.05$) for percent mildew is 27%.

TABLE 2. Reaction of 10 single-spore isolates of *Bremia lactucae* with 21 differential cultivars of lettuce, and cultivars Vanguard, Vanguard 75, and Ithaca^a

Lettuce cultivar	Resistance factor	1-80	M-7	5-81	12-81	18-81	20-81	22-81	23-81	28-81	29-81
Hilde	0	+	+	+	+	+	+	+	+	+	+
Premier	1	-	+	-	-	-	-	-	-	-	-
Mildura	3	-	-	-	-	-	-	-	-	-	-
Valmaine	5	+	-	+	-	-	-	-	-	-	-
Mesa 659	7	+	+	+	+	+	+	+	+	+	+
Valverde	8	+	-	+	-	-	-	-	-	-	-
GBH ^b	9	-	-	-	-	-	+	-	-	-	-
Sucrine	10	-	-	-	-	+	-	-	-	-	-
Capitan	11	-	-	-	-	-	-	-	-	-	-
Amanda Plus	2,4	-	-	-	-	-	-	-	+	-	-
Kordaat	3,4	-	-	-	-	-	-	-	-	-	-
Bremex	1,7	-	+	-	-	-	-	-	-	-	-
Larganda	2,7	-	-	-	-	-	-	-	+	-	-
Solito	3,7	-	-	-	-	-	-	-	-	-	-
Fila	2,11	-	-	-	-	-	-	-	-	-	-
Avondefiance	6,8	+	-	+	-	-	-	-	-	-	-
Calmar	7,8	+	-	+	-	-	-	-	-	-	-
Ardente	1,6,7	-	+	-	-	-	-	-	-	-	-
Edgar	2,3,7	-	-	-	-	-	-	-	-	-	-
Avoncrisp	6,7,8	+	-	+	-	-	-	-	-	-	-
Diana	3,7,8	-	-	-	-	-	-	-	-	-	-
Vanguard	13 ^c	-	+	-	-	+	+	+	-	-	-
Vanguard 75	13 ^c	-	+	-	-	+	+	+	-	-	-
Ithaca	0	+	+	+	+	+	+	+	+	+	+
V.P. ^d		5,6,7,8	1,6,7,13	5,6,7,8	7	7,10,13	7,9,13	7,13	2,4,7	7	7

^aIsolate numbers are abbreviations: eg, 1-80 = 1-80-SS1; M-7 = M-7-SS1; etc.

^bGBH = cultivar Grosse blonde d'hiver.

^cResistance factor 13 is used since Bannerot (1) reported R-12 from *Lactuca serriola*.

^dV. P. = virulence phenotype of each isolate (1-80 to 29-81).

^e+ = susceptible; - = resistant.

the F₂ families, along with the calculated chi-square and probability, are listed for each family in Table 3. The test cross of [(Vanguard 75 × Ithaca) F₁ × Ithaca] BC₁ yielded 72 plants, 36 of which were susceptible (Table 3).

DISCUSSION

Lettuce plants grown from three seed lots of Vanguard 75 and one lot of Vanguard were completely resistant to a number of single sporangial isolates of *B. lactucae*, but were completely susceptible when inoculated with a number of other isolates. This indicates that the resistance found in Vanguard and Vanguard 75 must be race specific, since it does not confer resistance equally to all isolates of *B. lactucae*. The patterns of resistance and susceptibility detected indicate that this is a previously undescribed resistance factor. This conclusion is based on the following logic. If the resistance factor in Vanguard 75 was the same as one of those previously described, virulence of isolate 22-81-SS1 (which was virulence factor 7) on Vanguard 75 indicates that this resistance factor must be R-7. However, other isolates with V-7 (such as 12-81-SS1) are not virulent on Vanguard 75, indicating that the presence of V-7 alone does not guarantee virulence on Vanguard 75. We have tentatively named this resistance factor R-13, since Bannerot (1) discovered resistance in a collection of *L. serriola*, and named it R-12.

Resistance factor R-13 will prevent development of downy mildew on Vanguard 75 even under field conditions, as long as the corresponding virulence factor is not present in the *B. lactucae* inoculum, since Vanguard 75 was resistant in the cultivar evaluation trial. The cultivar Commander also was resistant in the cultivar evaluation trial, but this was due to the presence of a different resistance factor, R-8, which was incorporated from cultivar Calmar during the breeding of cultivar Commander (R. W. Robinson, *personal communication*). Virulence factor 8 is known to be present in Oswego County (22), although it obviously was not present in the cultivar evaluation trial. Other cultivars of lettuce in the trial had varying amounts of mildew (2–74%). However, due to the large number of cultivars planted, the high variance in combination with limited replication, and the fact that the trial and evaluation procedure were not arranged to facilitate further analysis, no further comparisons were made. It is possible that some of the differences observed were due to field resistance (from 34 to 74% mildew on cultivar Ithaca, depending on seed lot, and from 28 to 72% for different seed lots of Greenlakes), but since this phenomenon has been the subject of an investigation involving specifically designed field experiments that we have not yet reported, no further discussion is included in this paper.

In one study (4), different classes of lettuce resistance responses to *B. lactucae* have been distinguished on the basis of the number of host cells that became necrotic. In another study (13), the different classes of resistance responses were distinguished not only on the basis of the number of host cells that became necrotic, but by utilizing several other chemical and cytological tests as well. According to the classification of Crute and Johnson (4), the reaction here is a type 1, since only a single host cell was killed. According to the classification of Maclean and Tommerup (13), this same resistance reaction would appear to be a type 1, although

the elaborate chemical and cytological tests used in their study were not performed and this conclusion is based only on the number of host cells that were killed during infection.

The observation that all plants in the (Vanguard 75 × Minetto) F₁ were resistant indicates that the resistance in Vanguard 75 is completely dominant. The segregation of the F₂ families into the 3 resistant:1 susceptible ratio, and the segregation of the testcross into a 1 resistant:1 susceptible ratio indicates that a single dominant gene is responsible for the downy mildew resistance in Vanguard 75. None of the families departed significantly from the expected 3:1 ratio, except the (Vanguard 75 × Ithaca) F₁ ($P = 0.96$). However, a chi-square value this large would be observed approximately 4% of the time, and in light of the other genetic data, it was decided that this was not significant. Other genetic studies on race-specific resistance to downy mildew in lettuce (6–10, 18, 20, 23) indicate that single dominant genes are responsible for the resistance factors 2, 3, 5, 6, 8, and 10, and that two complementary genes govern resistance factor R-7.

Vanguard and Vanguard 75 were not bred for resistance to downy mildew. However, the plant breeder, in producing resistant cultivars of lettuce, also provides the means for distinguishing different races of *B. lactucae*. If all known races of *B. lactucae* happen to be pathogenic on Vanguard and Vanguard 75, those cultivars would be classified as "susceptible" until a race incapable of overcoming the resistance was used as inoculum. Only then would the resistance in the lettuce become known. This was the case with Vanguard and Vanguard 75 in California, where they are classified as susceptible (24). Osara and Crute (16) theorized that a number of European cultivars of lettuce also have either R-1 or an undescribed resistance factor in addition to their known resistance factors, but that this has not been detected due to the widespread occurrence of V-1 in the European population of *B. lactucae*. Crute and Lebeda (5) have presented evidence that a heretofore

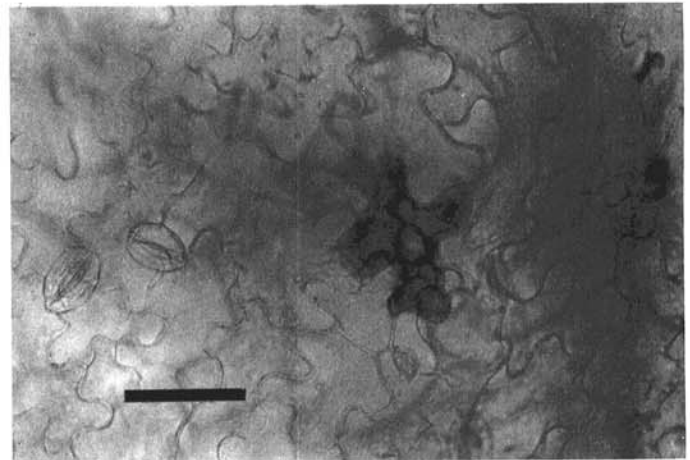


Fig. 1. Surface view of the hypersensitive reaction of Vanguard 75 lettuce when inoculated with isolate 1-80-SS1 of *Bremia lactucae*. Scale bar equals 20 μ m.

TABLE 3. Genetic analysis of crosses of Vanguard 75 with susceptible lettuce cultivars inoculated with isolate 1-80-SS1 of *Bremia lactucae* (virulence factors V-5, 6, 7, and 8)

Family of lettuce plants	Number of plants	Expected segregation	Expected susceptible	Observed susceptible	Chi-square	Probability
(Vanguard 75 × Minetto) F ₁	27	0:1	0.00	0	... ^a	... ^a
(Vanguard 75 × Minetto) F ₂	87	1:3	21.75	19	0.30	0.42
(Minetto × Vanguard 75) F ₂	165	1:3	41.25	45	0.34	0.44
(Vanguard 75 × Ithaca) F ₂	75	1:3	18.75	27	4.26	0.96
(Ithaca × Vanguard 75) F ₂	47	1:3	11.75	14	0.57	0.55
Total all F ₂ families	374	1:3	93.50	123	0.41	0.48
[(Vanguard 75 × Ithaca) F ₁ × Ithaca] BC ₁	72	1:1	36.00	36	... ^a	... ^a

^aChi-square was not calculated because data did not deviate from expected ratio.

undescribed resistance factor is very widespread in the European lettuce population, but neither Vanguard nor Vanguard 75 were among the cultivars that they tested. Preliminary genetic experiments by Crute and Lebeda (5) indicated that this new resistance factor was not simply inherited. It is entirely possible that there are other undiscovered genes for resistance in lettuce, and they have not yet been discovered because all the races of *B. lactucae* that have been used as inoculum also have the corresponding (but possibly as yet unknown) virulence factors.

Vanguard was released for commercial use in 1958 (19), but there was no mention of resistance to *B. lactucae*. It has a diverse background, including three different plant introductions of *L. serriola* (P.I. 114512, P.I. 114535, and P.I. 125819), and one of *Lactuca virosa* L. (P.I. 125819) (19). Unfortunately, these plant introductions are no longer available from the regional plant introduction station in Pullman, WA, and cannot be tested. Crute and Davis (3) and Bannerot (1) also have discovered downy mildew resistance in several other accessions of *L. serriola* and *L. virosa*, though the ones in Vanguard's progeny were not among those tested. *L. serriola* is the source of resistance factors R-5, -6, -7, -8, -11, and -12. Thus, it is entirely possible that at least one of the plant introductions was responsible for the resistance in Vanguard. Vanguard 75 was produced by backcrossing a gene for lettuce mosaic virus resistance into Vanguard (17). Thus, the two cultivars are nearly isogenic for lettuce mosaic resistance, and probably both contain the same gene for resistance to downy mildew.

Although employment of the resistance gene to *B. lactucae* in Vanguard 75 may not prove to be useful in New York State (since the corresponding virulence factor is known to be present in the *B. lactucae* population in New York) it may prove to be useful elsewhere. The presence of race-specific resistance in Vanguard and Vanguard 75 also may help explain anomalous reactions of differential cultivars of lettuce and *B. lactucae* isolates. Vanguard 75 may be susceptible to *B. lactucae* in California (17) due to the presence of the matching virulence factor in the pathogen population there, which may or may not be present elsewhere. In the absence of this virulence factor, a single dominant gene in Vanguard 75 detected in the present study will render it resistant to *B. lactucae*.

LITERATURE CITED

- Bannerot, H. 1980. Screening wild lettuce for *Bremia* resistance. Pages 104-106 in: Proceedings Eucarpia Meeting on Leafy Vegetables. J. W. M. Smith, and F. A. Langton, eds. 11-14 March 1980. Littlehampton, England. Glasshouse Crops Research Institute, Littlehampton, UK. 137 pp.
- Crute, I. R. 1979. Lettuce mildew—Destroyer of quality. Agric. Res. Council. (G.B.) Res. Rev. 5(1):9-12.
- Crute, I. R., and Davis, A. A. 1977. Specificity of *Bremia lactucae* from *Lactuca sativa*. Trans. Br. Mycol. Soc. 69:405-410.
- Crute, I. R., and Johnson, A. G. 1976. The genetic relationship between races of *Bremia lactucae* and cultivars of *Lactuca sativa*. Ann. Appl. Biol. 83:125-137.
- Crute, I. R., and Lebeda, A. 1981. Evidence for a race-specific resistance factor in some lettuce (*Lactuca sativa* L.) cultivars previously considered to be universally susceptible to *Bremia lactucae* Regel. Theoret. Appl. Genet. 60:185-189.
- Globerson, D., Netzer, D., and Tjallingii, F. 1974. Mode of inheritance of resistance in lettuce (*Lactuca sativa* L.) to three Israeli and four Dutch races of downy mildew (*Bremia lactucae* Reg.). Euphytica 23:54-60.
- Jagger, I. C. 1924. Immunity to mildew (*Bremia lactucae* Regel) and its inheritance in lettuce. (Abstr.) Phytopathology 14:122.
- Jagger, I. C., and Whitaker, T. W. 1940. The inheritance of immunity from mildew (*Bremia lactucae*) in lettuce. Phytopathology 30:427-433.
- Johnson, A. G., Crute, I. R., and Gordon, P. L. 1977. The genetics of race specific resistance in lettuce (*Lactuca sativa*) to downy mildew (*Bremia lactucae*). Ann. Appl. Biol. 86:87-103.
- Johnson, A. G., Laxton, S. A., Crute, I. R., Gordon, P. L., and Norwood, J. M. 1978. Further work on the genetics of race specific resistance in lettuce (*Lactuca sativa*) to downy mildew (*Bremia lactucae*). Ann. Appl. Biol. 89:257-264.
- Leeper, P. W., Whitaker, T. W., and Bohn, G. W. 1959. Lettuce—mildew resistant variety. Am. Veg. Grower 7(9):18.
- Leeper, P. W., Whitaker, T. W., and Bohn, G. W. 1963. Valmaine—a new cos type lettuce variety. Am. Veg. Grower 11(9):7, 16.
- Maclean, D. J., and Tommerup, I. C. 1979. Histology and physiology of compatibility and incompatibility between lettuce and downy mildew fungus, *Bremia lactucae* Regel. Physiol. Plant Pathol. 14:291-312.
- Mason, P. A. 1973. Studies on the biology of *Bremia lactucae* Regel. Ph.D. thesis. University of Cambridge, Cambridge, England.
- Michelmore, R. W., and Ingram, D. S. 1980. Heterothallism in *Bremia lactucae*. Trans. Br. Mycol. Soc. 75:47-56.
- Osara, K., and Crute, I. R. 1981. Variation for specific virulence in the Finnish *Bremia lactucae* population. Ann. Agric. Fenn. 20:198-209.
- Ryder, E. J. 1979. 'Vanguard 75' lettuce. Hortscience 14:284-286.
- Sequeira, L., and Raffray, J. B. 1971. Inheritance of downy mildew resistance in two plant introductions of *Lactuca sativa*. Phytopathology 61:578-579.
- Thompson, R. C., and Ryder, E. J. 1961. Description and pedigrees of nine varieties of lettuce. U.S. Dep. Agric. Tech. Bull. 1244. 19 pp.
- Ventura, J., Netzer, D., and Globerson, D. 1971. Inheritance of resistance in lettuce to race 3 of downy mildew (*Bremia lactucae* Reg.). J. Am. Soc. Hortic. Sci. 96:103-104.
- Welch, J. E., Grogan, R. G., Zink, F. W., Kihara, G. M., and Kimble, K. A. 1965. Calmar—A new lettuce variety resistant to downy mildew. California Agriculture 19(8):3-4.
- Yuen, J. E., and Lorbeer, J. W. 1982. Virulence factors of *Bremia lactucae* in New York. Phytopathology 72:1363-1367.
- Zink, F. W. 1973. Inheritance of resistance to downy mildew (*Bremia lactucae* Regel) in lettuce. J. Am. Soc. Horticultural Science 98:293-296.
- Zink, F. W., and Duffus, J. E. 1969. Relationship of turnip mosaic virus susceptibility and downy mildew (*Bremia lactucae*) resistance in lettuce. J. Am. Soc. Hortic. Sci. 94:403-407.