

Field Resistance of Crisphead Lettuce to *Bremia lactucae*

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ABSTRACT

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Field resistance to *Bremia lactucae* (causal agent of downy mildew of lettuce) was observed in several crisphead lettuce cultivars in experimental plantings within commercial lettuce fields in Oswego County, New York, during 1980 and 1981. In 1980 three crisphead lettuce cultivars (Ithaca, Mesa 659, and Iceberg) were measured for severity of downy mildew with a key specifically designed for this purpose. Plants of Ithaca and Mesa 659 were more susceptible to mildew than Iceberg, but Ithaca was more susceptible than Mesa 659. In 1981, plants of Florida breeding line FL 49015 were the most resistant; these data were obtained with a graphics digitizer used to measure leaf and lesion area of leaf images in a similar

experiment with six cultivars of lettuce (none with any known specific resistance factors). Similar readings of disease severity resulted from using either total lesion area or the percent area infected. Among the remaining cultivars, the average severity of disease developed on leaves of the New York State cultivars (Ithaca and Minetto) and the Wisconsin cultivars (Greenlakes and Montello) were almost the same. Minetto was much more resistant to downy mildew than was Ithaca. Plants of cultivar Ithaca from Foundation stock seed were more susceptible and developed larger lesions than those of cultivar Ithaca grown from commercial seed.

Additional key words: *Lactuca sativa*

Bremia lactucae Regel, the causal agent of downy mildew of lettuce (*Lactuca sativa* L.), is a serious problem of lettuce grown on organic soil in New York. Although specific resistance (race specific resistance) to this pathogen is available in a number of cultivars of lettuce, none of these cultivars are horticulturally suitable for growing in New York. Furthermore, more virulent races of *B. lactucae* are known to be present in New York that can overcome most if not all of the resistance factors responsible for this specific resistance (11). We considered a number of control measures other than the use of specific resistance after discovering the presence of these more virulent races. Among these control strategies was the use of field resistance.

Field resistance was first noticed in Oswego County, New York,

when a planting of different lettuce cultivars (including Mesa 659) was planted next to a field planted with the cultivar Ithaca. These different lettuce cultivars had been planted to trap more virulent races of *B. lactucae*, and most of them are not suitable horticulturally for growing outdoors in Oswego County during the summer. One exception was the cultivar Mesa 659; although virtually all the plants of this cultivar (which has specific resistance factor R-7) and the adjoining plants of the cultivar Ithaca were infected with *B. lactucae*, the severity of downy mildew on the plants of Ithaca was much greater than on the plants of Mesa 659. Plants of cultivar Ithaca had numerous downy mildew lesions on the frame and cap leaves, whereas the plants of Mesa 659 appeared much healthier, having only a few downy mildew lesions restricted to the lower frame leaves of the plants.

This study was initiated to investigate the phenomenon of field resistance to *B. lactucae* in selected crisphead lettuce cultivars, and to characterize and quantify the degree of resistance in several cultivars grown in New York.

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MATERIALS AND METHODS

For the trial in 1980, seed of lettuce cultivars Ithaca and Mesa 659 were obtained from the Joseph Harris Company (Harris), Moreton Farm, Rochester, NY 14624. Seed of cultivar Iceberg was obtained from I. R. Crute at the National Vegetable Research Station, Wellesbourne, Warwick, England. In this experimental planting, plants of these cultivars of lettuce were each planted in single 12-m rows in the field of a grower cooperater on 31 July 1980 (four reps). The adjoining lettuce was also planted on this date. The lettuce was thinned on 18 August 1980, and routine application of insecticides and herbicides was conducted by the grower cooperater. Indigenous inoculum of *B. lactucae* infected plants in the trial. On 16 September 1980, when the surrounding lettuce planted at the same time was maturing, 20 randomly selected frame leaves from each of the three cultivars were removed from the plants, placed in plastic bags, and transported to the laboratory. With the aid of a disease assessment key for downy mildew of lettuce (5), the percent area infected with *B. lactucae* was estimated for each leaf. These data were analyzed by analysis of variance and the means of infected leaf area for each of the three cultivars were compared by orthogonal contrast analyses.

In 1981, a study was conducted in conjunction with the Department of Vegetable Crops at Cornell University, Ithaca, New York. While that department was interested in the overall performance of 24 lettuce cultivars, we were primarily interested in only six of these cultivars. Thus, although a total of 24 cultivars were planted, samples from only six were taken for our study. These six cultivars of lettuce were Ithaca, Minetto, Greenlakes, and Montello from Harris; Ithaca (Foundation seed [some of the original Ithaca foundation seedstocks from L. A. Ellerbrock, Department of Vegetable Crops, Cornell University, Ithaca, NY 14853]); and FL 49015 (from V. L. Guzman, Agricultural Research and Education Center, P.O. Drawer A, Belle Glade, FL 33430). The planting was established in a randomized complete block design with two replicate blocks and was planted on the same day as the adjoining lettuce. Routine application of fungicides and insecticides, along with weeding and thinning the lettuce, was performed by the grower cooperater. As in the 1980 trial, infection was by means of indigenous inoculum of *B. lactucae*. The lettuce was planted on 10 July 1981 and evaluated on 4 September 1981 when the commercial lettuce in the field was harvested.

Evaluation was performed by randomly removing 10 leaves from plants representing each of the six cultivars (five from each replicate), placing them in plastic bags, and transporting them to the laboratory. Photographs of the leaves were made with a photocopy machine. In most cases, the downy mildew lesions were usually quite evident. However, to ensure that there would be no question at a later date, the leaf copies were compared with the original leaves and the lesions were outlined with a pencil line and lightly shaded. By using a computer-assisted graphics pad (Micro Digi-Pad Tablet Digitizer, GTCO Corporation, Rockville, MD 20850), the total leaf area and total lesion area were measured and

the number of lesions was recorded for each of the 10 leaf images of each of the cultivars. These figures were used to calculate the percent area of each of the leaves covered with lesions and the mean lesion size for each of the cultivars. These data were analyzed according to a standard analysis of variance and the resulting means were compared with orthogonal contrast analyses.

Since six cultivars were measured, a set of five orthogonal contrasts were analyzed. These were based on relationships among the different cultivars of lettuce, and represent preplanned comparisons among cultivar means. The first contrast compared the northern cultivars (Ithaca, Minetto, Montello, and Greenlakes) with the one breeding line from Florida. The second contrast compared the New York cultivars (Ithaca and Minetto) with the Wisconsin cultivars (Greenlakes and Montello). The third contrast compared the two Wisconsin cultivars (Greenlakes and Montello) with each other. The fourth contrast compared the average of the two sources of cultivar Ithaca seed (Foundation seed and Joseph Harris Company seed) with Minetto. The fifth contrast compared the two sources of cultivar Ithaca with each other.

While it was known that neither Ithaca nor Minetto contain specific resistance factors (I. R. Crute, *personal communication*), the presence of specific resistance in Montello, Greenlakes, and FL 49015 was not known. Two different seed lots of Montello and Greenlakes (from R. W. Robinson, New York State Agricultural Experiment Station, Geneva 14456 and the Joseph Harris Company) and the lot of FL 49015 used in the trial planting (obtained from V. L. Guzman via the Department of Vegetable Crops, Cornell University, Ithaca) were tested for specific resistance to *B. lactucae*. Seedlings were grown on moist Cornell potting mix, and the excised cotyledons were inoculated with *B. lactucae* as previously described (12). The isolates of *B. lactucae* used were 12-81-SS1 (V-7), 22-81-SS1 (V-7 and V-13), and 1-80-SS1 (V-5, V-6, V-7, and V-8).

RESULTS

In 1980, the means of percent area infected for each of the three lettuce cultivars were significantly different from each other. Ithaca had the highest mean area infected (31%), followed by Mesa 659 (20%), and Iceberg (9%). When orthogonal contrasts were made between these three means, two contrasts resulted. The first contrast examined the difference between the average of Ithaca and Mesa 659 (cultivars that were grown in Oswego County) and Iceberg (a cultivar not presently grown commercially in Oswego County). Iceberg had much less mildew (as measured by percent area infected) than the average of Mesa 659 and Ithaca. This difference in percent area infected was 17% with a *t* value of 6.5 (significant at *P* = 0.01). The second contrast examined the difference between Ithaca and Mesa 659. In this case, Mesa 659 had less mildew (as measured by percent area infected) than Ithaca. This difference in percent area infected was 11% with a *t* value of 3.6 (significant at *P* = 0.01).

In 1981, the total leaf area, the total lesion area, the percent area infected, the number of lesions, or the average lesion size were used as the dependent variable in an analysis of variance. Differences among each of these parameters were evident (as indicated by the *F*-value) except in the case of average lesion size (Table 1). The orthogonal contrasts were used to compare the means and identify the source of differences among the cultivars of lettuce.

Plants of Florida cultivar FL 49015 were more resistant than were the northern cultivars. This was evident from its smaller lesion area, less percent area infected, and fewer lesions. When examined as groups, New York cultivars and Wisconsin cultivars were equally resistant. Of the Wisconsin cultivars, there was no difference between Greenlakes and Montello. Within the group of New York cultivars, Minetto was more resistant than Ithaca. This was evident from a smaller lesion area, less percent area infected, and fewer lesions. Ithaca (from Foundation seeds) was more resistant than Ithaca (Joseph Harris Company) based on reduced lesion area, less percent area infected, and smaller lesions.

When tested in the laboratory with all three isolates of *B. lactucae*, abundant sporulation occurred 1 wk after they were

TABLE 1. Mean downy mildew ratings of six lettuce cultivars infected with *Bremia lactucae* in 1981

Cultivar	Total area (mm ²)	Lesion area (mm ²)	Percent of area infected	Lesions per leaf (no.)	Average lesion size (mm ²)
Ithaca ^a	25,812	2,617	10	9.5	237
Ithaca ^b	25,898	5,463	22	13.6	694
Minetto	23,176	541	2	5.3	81
Greenlakes	28,692	2,263	8	15.9	141
Montello	33,202	2,096	7	12.0	160
FL 49015	30,165	264	1	2.3	47
<i>F</i> -value ^c	13.2	6.9	7.3	8.1	2.3

^a Foundation seed.

^b Joseph Harris Seed Company, Rochester, NY.

^c With 5 and 54 degrees of freedom.

inoculated on all cotyledons of both seed lots of Greenlakes, both seed lots of Montello, and FL 49015. This indicates that the only specific resistance factor that these cultivars could possess is R-7.

DISCUSSION

The cultivars of crisphead lettuce investigated in this study differ in susceptibility to *B. lactucae* under field conditions in Oswego County. This difference in susceptibility is not due to presently known race-specific resistance factors. The laboratory testing of cultivars Montello, Greenlakes, and FL 49015 indicates that the only resistance factor that these cultivars could possess is R-7, which is matched by V-7 in the New York population of *B. lactucae* (11). Detection of R-7 is impossible with the isolates of *B. lactucae* present in New York since all isolates have V-7. Ithaca and Minetto have been tested in England and contain no specific resistance factors (I. R. Crute, *personal communication*). Resistant plants in the field are not immune to *B. lactucae* and develop lesions but have less diseased leaf area. Furthermore, this phenomenon of field resistance is additive to the effects of metalaxyl (13).

A number of terms have been used to describe this type of resistance in other plant diseases (horizontal resistance, polygenic resistance) but because this phenomenon was first noticed in lettuce cultivars grown in the field and has not yet been demonstrated in the laboratory, it is called field resistance in this study. Whether this type of resistance is uniform for all isolates of *B. lactucae* and how it is inherited in lettuce is not known, which also makes the term field resistance much more appropriate than horizontal resistance or polygenic resistance.

The field resistance we have observed is characterized by a smaller total lesion area in resistant plants. If the total lesion area is adjusted with the total leaf area of each cultivar to yield percent area diseased, the differences between cultivars remain. This reduced lesion area is due in part to a reduction in the number of lesions in resistant cultivars, and also partly due (in the two sources of the cultivar Ithaca) to a reduced lesion size. In a study investigating the interaction of metalaxyl and this field resistance (13), the field resistance also appeared in the form of a lower incidence of downy mildew in the more resistant cultivars.

Of the three cultivars grown in 1980, Iceberg was the most resistant to *B. lactucae*. This crisphead lettuce cultivar does not grow well under the conditions in Oswego County. Mesa 659 is grown in Oswego County and is more resistant than Ithaca, but it also is not well suited to Oswego County conditions and thus has not received widespread grower acceptance, partly due to the requirement of a longer growing period before reaching maturity.

In 1981, the most resistant cultivar was FL 49015. We initially suspected that this was due to a combination of specific resistance in FL 49015 and heterogenous inoculum in the field simulating field resistance. Laboratory studies indicated that FL 49015 contains no specific resistance factor that could not be matched by virulence in

the *B. lactucae* inoculum. FL 49015, a breeding line from Florida, is not a named cultivar and its suitability for commercial use on organic soil in New York State is still uncertain. Of the remaining northern cultivars, there were no significant differences between the Wisconsin and the New York cultivars either in percent area infected or total lesion area. The Wisconsin cultivars developed more severe disease symptoms (measured by either total lesion area or percent area infected) than Minetto, but less than Ithaca.

Of the New York cultivars, Minetto was the most resistant to *B. lactucae*. This resistance was evident through smaller lesions, smaller total lesion area, and a smaller percent area infected. It is surprising that Ithaca and Minetto are so different in susceptibility to *B. lactucae* because neither carries any specific resistance factors. However, their pedigrees are different (1,10). Ithaca was a result of a cross of Calmar and Fulton, while Minetto resulted from a cross of Imperial 456 and Empire.

Plants of Ithaca from two different sources produced different results. Both total lesion area and percent area infected were greater for plants of Ithaca from Harris than for plants grown from Foundation seed due to the larger lesions which developed on the former. This disparity may be due to inadvertent selection during commercial seed production that has taken place in the cultivar Ithaca since its release in 1969. This cultivar was released as an F₅ and, therefore, was not completely homozygous. Subsequent selfing of the plants during seed production could have produced a population of plants of Ithaca that vary in resistance to *B. lactucae*. Then selection could have taken place to select more susceptible members of the population. If this is the reason for increased susceptibility of the cultivar Ithaca from Harris, then it might be worthwhile to self the original Ithaca seedstocks several times without selection and then to select for more resistant plants. Another possible explanation of the apparent resistance in the cultivar Ithaca foundation seedstock is that this particular lot of seed, having been stored for a long time, was not as vigorous as those grown from the seed from Harris and, therefore, grew more slowly, producing plants that were physiologically younger than the plants from the seed from Harris, and this age difference was responsible for the differences in mildew susceptibility. However, since the two seed sources produced leaves that were the same size, this is not likely.

When several lettuce cultivars were examined for field resistance in a naturally infected trial in England, differences among the cultivars in the percent leaf area infected or percent basal area infected were detected by Dixon et al (6). Of the cultivars tested in that study, the only one examined in the present study was Mesa 659. The infected leaf area of Mesa 659 obtained in the present study was 26%, which is surprisingly close to the 25.3% infected basal area reported by Dixon et al (6). Crute (2) reported that some cultivars appear to be more resistant than others when grown in the field, but did not discuss particular cultivars in detail. In a Finnish study examining European butterhead lettuce cultivars, substantial

TABLE 2. Downy mildew development on head lettuce. Values of contrasts of cultivar means and their *t* value^a for various parameters of downy mildew development in 1981

Contrast of cultivar means ^a	Total lesion area (mm ²)		Percent area infected		Number of lesions		Mean lesion size (mm ²)		Total leaf area (mm ²)	
	value	<i>t</i>	value	<i>t</i>	value	<i>t</i>	value	<i>t</i>	value	<i>t</i>
Northern vs southern cultivars	2,332	3.00 ^b	8.4	2.86 ^b	9.0	4.52 ^b	215	1.24	-2809	-2.06 ^c
New York vs Wisconsin cultivars	695	1.07	4.1	1.57	-4.8	-2.71 ^b	186	1.29	-5985	-6.65 ^b
Cultivar Greenlakes vs cultivar Montello	167	0.17	1.6	0.40	3.9	1.51	-19	-0.09	-4511	-3.24 ^b
Cultivar Ithaca vs cultivar Minetto	3,499	4.03 ^b	13.8	3.95 ^b	6.2	2.82 ^b	384	1.99	2679	2.22 ^c
Cultivar Ithaca (Harris) vs cultivar Ithaca (Foundation)	2,845	2.84 ^b	12.8	3.18 ^b	4.1	1.60	457	2.05 ^c	86	0.06

^aThe *t* value is calculated by dividing the value by its standard deviation.

^bNorthern cultivars are Ithaca, Minetto, Greenlakes, and Montello; the southern cultivar is FL 49015. New York cultivars are Ithaca and Minetto; Wisconsin cultivars are Greenlakes and Montello.

^cSignificant at *P* = 0.01.

^dSignificant at *P* = 0.05.

variation in relative susceptibility and resistance was present under field conditions (9). None of the cultivars they tested were utilized in the present study.

The characteristics of the field resistance reported by Crute et al (3) in several lettuce cultivars resemble those of the characteristics of the field resistance detected in the present study. Crute et al (3) found that field resistance was characterized by a lower disease incidence, restriction of infection to the outermost leaves, fewer leaves infected per plant, fewer and smaller lesions, and a slower rate of disease progress. In their study, detailed comparisons were made initially among a large number of cultivars, but later comparisons were made between Hilde (a butterhead cultivar) and Iceberg (a crisphead type). They pointed out that the resistance they reported may result from morphological or physiological differences between the two types of lettuce. No comparisons were made among crisphead lettuce types. Crute et al (4) also were able to correlate occurrence and intensity of sporulation on artificially inoculated seedlings with disease severity in the field, and have data from F₂ and F₃ populations from crosses of susceptible and resistant plants indicating that the resistance is polygenic.

Eenink (7) detected "partial resistance" in a number of lettuce cultivars. He found no clear interaction between environment and genotype, and no clear correlation between resistance and lettuce type, erectness, or plant size. Eenink et al (8) subsequently reported that genotype-fungus interactions were small and possibly due to residual R-genes or environmental factors. They also reported that a correlation existed between partial resistance and latent period, infection frequency, and number of infected leaves.

In all studies to date, disease severity on the individual lettuce plants has been measured with the aid of a key for lettuce downy mildew (5). Accurate measurement of disease is important in the study of field resistance, since the mere presence or absence of downy mildew should no longer suffice as a measure of resistance or susceptibility. While arbitrary disease-rating scales may impart some information concerning disease severity, they are by nature subjective and often nonadditive and, therefore, fail to meet the basic assumptions in an analysis of variance. The use of a key is helpful in standardizing measurements, and may prove to be the most useful method of measuring disease severity. However, the key employed in the above studies (and in the initial study reported here) was designed specifically for butterhead lettuce and may not be the most suitable one for crisphead lettuce cultivars. The use of a graphics digitizer for measuring disease severity eliminates most of the problems associated with either rating scales or a key. The possible error involved in making the measurement is very small, and there is little room for subjective measurements. Furthermore, comparisons can easily be made even if different people have measured the leaves. However, it is time consuming and requires a minimum amount of equipment. With further developments in image analysis, absolute measures of disease severity of foliar diseases may become trivial in the near future.

Repeated attempts to verify field resistance on intact plants or detached plant parts under controlled conditions were not successful in the present study. Further studies are required to determine if the field resistance reported herein is the same

resistance as that reported by other workers (3,7,8). In addition, the inheritance of this type of resistance must be determined before it can be effectively used in a breeding program. The lack of durability in race-specific resistance used in lettuce breeding has led to greater emphasis on "field" (3) or "partial" (7,8) resistance in the hopes that it will not be overcome by increased virulence or aggressiveness in the pathogen.

Although more research is required to discover the exact mechanism of resistance, and how it is inherited, the lettuce growers of Oswego County (New York State) who have severe downy mildew problems presently have available cultivar Minetto which has excellent field resistance. This cultivar was bred specifically for growing conditions in Oswego County, so there is no question of its suitability for growth under those conditions. While further studies on the nature of this resistance are required, it is already present in a well-adapted cultivar and no further breeding will be required to introduce it into a commercial lettuce cultivar.

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