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New sources of major gene resistance in *Lactuca* to *Bremia lactucae*

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Summary

A total of 1789 accessions of several lettuce collections was screened to find new major gene resistance to the downy mildew fungus *Bremia lactucae* Regel. The accessions belonged to the species *Lactuca sativa* (N = 1288), *L. serriola* (N = 399), *L. saligna* (N = 52) and *L. virosa* (N = 50). A total of 20 races of *B. lactucae* were used, 14 of which were NL-races, isolated from cultivated lettuce in the Netherlands. The other six races were isolated from wild *L. serriola* in Czechoslovakia. The accessions were initially screened with two races: NL1 and NL3. Accessions with resistance to one or both of these races were tested with the other races. Phenotypes with new resistance were found in accessions of all four *Lactuca* species. Of *L. sativa,* four accessions were found with resistance phenotypes that could not be explained by combinations of known major genes. Many accessions of *L. serriola* had resistance phenotypes that indicated the presence of unknown resistance genes. All interactions between accessions of *L. saligna* and races of *B. lactucae* were incompatible in leaf disc tests, except for four accessions, which showed some sporulation with race NL6. Several accessions of *L. virosa* were resistant to all races used. Other accessions of *L. virosa* gave a race-specific interaction with *B. lactucae.*

Introduction

The downy mildew fungus *Bremia lactucae* Regel causes an important disease of lettuce (*Lactuca sativa* L.) worldwide. Introductions of cultivars with new resistance genes or new combinations of resistance genes have quickly been followed by the appearance of new races which can overcome that resistance (Johnson & Crute, 1975; Blok, 1989).

The genetic interaction between *B. lactucae* and lettuce has been defined as a gene-for-gene system (Crute & Johnson, 1976). Dominant resistance genes (Dm genes) correspond with dominant avirulence genes. The combination of a Dm gene and a corresponding avirulence gene results in an incompatible interaction, based on hypersensitivity of the host. In genetic analysis, the conclusive proof for a new Dm gene is the segregation of one matching resistance gene in the host with one avirulence gene in the pathogen (Farrara et al., 1987). For *B. lactucae* the convention is that as long as a resistance factor has not been proved to be a single Dm gene, it should be indicated with an R (Johnson et al., 1978). Nowadays 22 R-factors have been named (Farrara et al., 1987). The Dm genes corresponding with these R-factors have been determined for all these R-factors, except for R12, R18 and R21, resulting in thirteen Dm genes and corresponding avirulence genes (Farrara et al., 1987).

The low durability of resistance based on Dm genes means that a more durable form of resistance would be desirable. However, attempts to obtain a high level of partial resistance in butterhead lettuce (Eenink, 1981; Eenink et al., 1982; Eenink & De Jong, 1982; Eenink et al., 1983) were not successful. In crisphead lettuce the prospects of partial resistance look more promising (Crute & Norwood, 1981; Norwood et al., 1985; Pink & Crute, 1989), although no commercial cultivars have yet been produced. This means that using resistance based on Dm genes will remain the most important strategy in breeding lettuce with resistance to *B. lactucae*. The occurrence of new races of *B. lactucae* in the Netherlands in the 1980's (especially NL12, NL15 and NL16) severely reduced the number of Dm genes effective in the field situation. Therefore a large collection of *Lactuca* accessions was screened to find new resistance genes providing complete resistance to *B. lactucae.*

Materials and methods

Races

Table 1 shows the virulence phenotypes of the races used for testing. The NL-races were supplied by Mrs. I. Blok (IPO, Wageningen, The Netherlands). Maintenance and multiplication of the NL-races was carried out on seedlings of different cultivars resistant to most of the other races. The races 26/81, 27/81, 1/82, 2/82, 3/82 and 4/82 were isolated from *L. serriola* (Lebeda, 1984b) and maintained on the *L. serriola* genotype PI 273617. A stock of each race was kept at a temperature of – 20° C. A differential series of lettuce genotypes (Table 2) was used to check the virulence phenotypes of the races. 'Cobham Green' was used as a susceptible genotype to the NL-races. It has resistance to the races 26/81, 27/81, 2/82 and 3/82 caused by an unknown R-factor (Lebeda, 1990a).

Accessions

A total of 1783 *Lactuca* accessions from several genebanks were screened: almost the complete lettuce collection of the Centre for Genetic Resources, The Netherlands (CGN, Boukema et al., 1990); the lettuce collection of the Vegetable Genebank (VGB) of Horticultural Research International, Wellesbourne, U.K. as far as it did not duplicate the CGN collection, provided by Dr. D. Astley; 102 accessions of the PI lines collection

Table 1. Virulence phenotypes (–: no virulence; (–): incomplete avirulence; (+): incomplete virulence; +: virulence) of the races of *Bremia lactucae* used for testing

R-factor/ Dm gene	NL-races														Races from *L. serriola*					
	1	2	3	4	5	6	7	10	11	12	13	14	15	16	26/81	27/82	1/82	2/82	3/82	4/82
1	+	+	–	+	+	+	+	+	+	+	+	+	+	+	–	–	+	–	–	–
2	+	+	–	+	–	+	+	+	–	–	–	(+)	+	+	–	–	+	–	–	+
3	–	+	–	–	+	–	+	+	–	–	+	+	+	+	–	–	–	–	–	–
4	+	+	+	+	+	+	+	+	+	+	–	+	+	+	–	–	+	–	–	+
5	–	+	+	+	–	+	–	+	+	+	+	+	+	+	–	–	–	–	–	–
6	–	+	+	+	(–)	(+)	+	+	+	+	+	+	–	+	–	–	–	–	–	–
7 + 13	–	–	+	+	+	–	+	+	+	+	+	–	+	+	+	+	–	+	(+)	–
10	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–
11	–	–	–	–	–	+	(–)	(–)	–	+	+	+	+	+	(+)	(–)	–	–	–	+
R12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	(–)	–	+
13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	(–)	–	–
14	+	+	+	+	–	+	+	+	+	+	+	+	–	–	(+)	+	–	–	–	–
15	(–)	–	+	–	+	(–)	(–)	(+)	+	+	+	–	–	–	+	+	–	+	+	–
16	–	–	–	–	–	–	–	–	+	+	–	–	–	+	+	+	+	+	+	+
R18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

(Agricultural Research Station, Salinas, California, USA) provided by Dr. E. Ryder; 39 lettuce accessions provided by Dr. A. Lebeda (Czechoslovakia); four accessions provided by Dr. Nagy (Hungary); four lettuce accessions provided by Dr. Stoyanov (Bulgaria) and 58 samples of *L. serriola* collected in Hungary in 1988 by K. Reinink.

Test methods

Tests were performed in plastic boxes of 31 × 46 × 8 cm. The boxes were closed by bright plastic covers. Growth conditions were: a photo active period of 12 h and a constant temperature inside the boxes of 15° C. Two tests were used: a seedling test and a leaf disc test. In the seedling test twenty seeds of each accession were carefully placed on filterpaper, moistened with a nutrition solution. Each box contained 12 accessions plus one susceptible and one resistant control. One box per inoculation contained the differential series of lettuce genotypes (Table 2) to check the purity of the race used. After sowing, the boxes were closed and put at 2° C for one to three days to break possible dormancy. Afterwards, the boxes were transported to 15° C and seven days later the seedlings were inoculated by spraying a spore suspension upon the fully expanded cotyledons until run off. Inoculum was prepared by washing sporulating seedlings in fresh water. The spore concentration was adjusted to 5×10^4 spores·ml^{-1}. After inoculation a dark period of at least 12 h was given. Eight to 12 days after inoculation the seedlings were assessed for sporulation.

In the leaf disc test, leaf discs of 1.7 cm diameter were cut from fully expanded healthy leaves and laid upside down on filterpaper moistened with water. Each accession was tested using five plants, taking one leaf disc from each plant. When less than five plants were available, more than one leaf disc was taken from a plant. Each box contained 24 accessions plus a susceptible and a resistant control genotype. To check the race one box per inoculation contained the genotypes of the differential series (Table 2). The leaf discs were inoculated directly after cutting. The rest of the testing was performed as described for the seedling test.

Five classes were distinguished to score the resistance of the accessions tested: 1) complete resistance: no sporulation; 2) incomplete resistance: only a few sporangia; 3) incomplete susceptibility: reduced sporulation on at least 80% of the seedlings or 100% of the leaf discs; 4) susceptibility: profuse sporulation on at least 80% of the seedlings or 100% of the leaf discs and 5) a heterogenous reaction: profuse sporulation on less than 80% of the seedlings or on less than 100% of the leaf discs. The accessions were prescreened using the seedling test with the races NL1 and NL3, to reduce the number of accessions that had to be tested with 20 races of *B. lactucae*. NL1 and NL3 were used in prescreening for two reasons. Firstly, these races have relative little virulence (Table 1), so a genotype with resistance factors is likely to be detected. Secondly, the virulence genotypes of these races are complementary for six of the Dm genes (Table 1), so susceptibility to one or both races gives information about Dm genes that cannot be present in a genotype. Only four known resistance genes

Table 2. Differential series of lettuce genotypes resistant to *Bremia lactucae*

Cultivar/line	Dm gene/R-factor	Cultivar/line	Dm gene/R-factor
'Cobham Green'	?	'Capitan'	11
'Lednicky'	1	'Hilde'	R12
UCDM2	2	'Pennlake'	13
'Dandy'	3	UCDM14	14
Line 4/57/D	4	PIVT 1309	15
'Valmaine'	5/8	LSE/18	16
'Sabine'	6	'Mariska'	R18
UCDM10	10	'Mesa 659'	7 + 13

give resistance to both NL1 and NL3 (Table 1). Therefore, there is a good chance that a genotype with resistance to both NL1 and NL3 contains new major gene resistance.

Accessions with resistance to at least one of these two races were retested with the leaf disc test for resistance to NL1 and NL3, to improve the reliability of the results and to make it possible to select resistant plants in accessions reacting heterogeneously. After this second test, plants with resistance to NL1 or NL3 were tested for resistance to the races NL12, NL15 and NL16 using the leaf disc test. NL12, NL15 and NL16 are currently the most important races in The Netherlands. By using the leaf disc test, the same plants could be evaluated in all tests. Of the accessions resistant to NL1 or NL3, a subset was tested for resistance to all 20 races using the leaf disc test. This subset contained all accessions with resistance to both NL1 and NL3 and the accessions of *L. sativa* and *L. serriola* that had shown to be resistant to both NL12 and NL15 or NL16. The first accessions were chosen, because there was a good chance they contained new major gene resistance (see before). The latter were chosen because of their importance for Dutch lettuce breeders.

Results

Table 3 shows the percentages of the accessions scored resistant, heterogeneous or susceptible to the races NL1 and NL3. In this table and in the following frequency tables (Tables 4 and 5) accessions scored as incompletely resistant were regarded as resistant and accessions scored as incompletely susceptible were regarded as susceptible. Resistance to NL1 and NL3 was found in all species tested. Accessions of *L. saligna* often showed a heterogeneous reaction when tested on seedlings. However, in leaf disc tests all accessions of *L. saligna* were resistant to NL1 and NL3.

Table 4 shows the results of tests with races NL12, NL15 and NL16. This table contains accessions selected for resistance to NL1, NL3 or both. Accessions of *L. sativa* showed more resistance to NL12 than to NL15 or NL16. This could be expected, because NL15 and NL16 occurred later and overcame resistance in lettuce cultivars that were bred for resistance to older races. In contrast, within the species *L. virosa* the frequency of resistance to NL15 and NL16 was higher than to NL12. Again, all accessions of *L. saligna* were scored resistant.

Table 3. Percentages of the accessions of four *Lactuca* species showing a resistant (−), heterogeneous (*) or susceptible (+) reaction to the races NL1 and NL3 of *B. lactucae*

Species	Reaction type	Races	
		NL1	NL3
L. sativa	−	23	31
(N = 1288)	*	3	3
	+	74	65
L. serriola	−	14	16
(N = 399)	*	5	5
	+	80	79
L. saligna	−	92	75
(N = 52)	*	8	25
	+	0	0
L. virosa	−	26	26
(N = 50)	*	12	4
	+	62	70

Table 4. Percentages of the accessions of four *Lactuca* species showing a resistant (−), heterogeneous (*) or susceptible (+) reaction to the races NL12, NL15 and NL16 of *B. lactucae*

Species	Reaction type	Races		
		NL12	NL15	NL16
L. sativa	−	52	7	3
(N = 619)	*	3	1	0
	+	45	92	97
L. serriola	−	38	44	33
(N = 132)	*	3	2	1
	+	59	54	66
L. saligna	−	100	100	100
(N = 51)	*	0	0	0
	+	0	0	0
L. virosa	−	37	50	77
(N = 30)	*	0	3	0
	+	63	47	23

Table 5 shows the results with the other 15 races of *B. lactucae*. This Table contains 294 accessions selected for resistance to both NL1 and NL3. Among the accessions of *L. sativa*, resistance to the races NL4, NL6, NL11 and the races isolated from *L. serriola* was relatively frequent. This could be expected, because like NL1 and NL3, NL4, NL6 and NL11 are avirulent on Dm3 and the races isolated from *L. serriola* were already shown to have little virulence on lettuce cultivars (Lebeda, 1984b). Among the accessions of *L. serriola* resistance to the NL-races and the races 1/82 and 4/82 was relatively frequent, but there was very little resistance to the races 26/81, 27/81, 2/82 and 3/82. Four accessions of *L. saligna* (CGN 5305, CGN 5319, CGN 5320 and CGN 9312) were scored incompletely susceptible to NL6. All other interactions between accessions of *L. saligna* and races of *B. lactucae* were scored incompatible.

Most of the accessions of *L. virosa* with resistance to both NL1 and NL3 were also resistant to all other races. Accessions showing race-specific resistance indicate the presence of Dm genes in this species.

Sources of new resistance

Table 6 contains all genotypes of *L. sativa* and *L. serriola* showing new major gene resistance. Four *L. sativa* accessions were found with resistance phenotypes that could not be explained by combinations of known Dm genes. CGN 5170 (cv. 'Batavia la Brillante') was resistant to NL11 and susceptible to NL12 (Table 6). The only known difference in virulence phenotype between NL11 and NL12 is, that NL11 is avirulent on DM11 and NL12 virulent (Table 1). However, CGN 5170 cannot have Dm11, since it then would also have been resistant to NL2, NL5, NL7 and NL10. PI 379354 was already identified as a genotype with new resistance by Farrara and Michelmore (1987). Possibly PI 379354 contains Dm2 and Dm14 (Table 6, Table 1), but its resistance to NL7, NL10 and NL14, cannot be explained by these genes, nor by any other combination of known Dm genes. To a large extent, Dm3 and Dm14 could explain the resistance phenotypes of VGB 4925 ('Amasyh Wo 5') and selected plants from PI 169501 (Table 6). However, these genes cannot explain incomplete susceptibility of VGB 4925 to NL1, NL6 and NL12, nor of PI 169501 to NL6 and NL12 (Table 6). Possibly the

Table 5. Percentages of the accessions of four *Lactuca* species showing a resistant (−), heterogeneous (*) or susceptible (+) reaction to the races NL2, NL4, NL5, NL6, NL7, NL10, NL11, NL13, NL14, 26/81, 27/81, 1/82, 2/82, 3/82 and 4/82 of *B. lactucae*

Species	Reaction type	NL-races									Races from *L. serriola*					
		2	4	5	6	7	10	11	13	14	26/81	27/81	1/82	2/82	3/82	4/82
L. sativa	−	51	83	39	88	14	11	93	54	43	91	97	99	90	99	94
(N = 149)	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	+	49	17	61	12	86	89	7	46	57	9	3	1	10	1	6
L. serriola	−	55	87	70	63	70	68	64	56	59	5	16	74	7	7	62
(N = 78)	*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	+	45	13	30	37	30	32	35	44	41	95	84	26	93	93	38
L. saligna	−	100	100	100	92	100	100	100	100	100	100	100	100	100	100	100
(N = 51)	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	+	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
L. virosa	−	69	69	75	63	100	69	94	63	81	75	69	69	81	69	69
(N = 16)	*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	+	31	31	25	38	0	31	6	38	19	25	31	31	19	31	31

Table 6. Accessions of *L. sativa* and *L. serriola* with resistance phenotypes[a] that could not be explained by known Dm genes

Accession[b]	NL-races														Races from *L. serriola*					
	1	2	3	4	5	6	7	10	11	12	13	14	15	16	26/81	27/81	1/82	2/82	3/82	4/82
L. sativa																				
CGN 5170	−	+	−	−	+	+	+	+	−	+	+	+	+	+	−	−	+	−	−	+
VGB 4925	(+)	+	−	*	−	*	+	+	(−)	(+)	+	+	−	−	−	−	−	−	−	−[c]
PI 169501[f]	−	+	−	(−)	−	(+)	+	+	(−)	(+)	+	+	−	−	−	−	−	−	−	−[c]
PI 379354	+	+	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	·	·	+[d]
L. serriola																				
Several[g]	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−
CGN 4673[f]	−	−	−	−	−	−	−	−	−	(−)	−	−	−	(+)	+	+	−	+	+	−
CGN 5009	−	−	−	−	(+)	−	−	−	−	−	−	−	(−)	(−)	(+)	+	−	(+)	(+)	−
CGN 5091	(−)	−	−	(−)	−	−	−	−	−	−	−	−	−	−	+	+	−	·	·	−
CGN 5096	(−)	(−)	−	(−)	−	−	−	−	−	−	−	−	−	−	+	+	−	·	·	−
CGN 5106[f]	*	−	−	(−)	−	−	−	−	−	−	−	−	(−)	(−)	+	+	·	·	·	−
CGN 5110[f]	−	−	−	−	−	(−)	−	−	−	−	−	−	−	−	+	+	−	·	·	−
CGN 10938	*	−	*	−	−	−	−	−	−	−	−	−	−	−	(+)	(−)	−	(+)	(+)	−
CGN 10939	*	−	−	−	−	−	−	−	−	−	−	−	(+)	(−)	+	+	−	+	+	−
CGN 14258	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	(+)	+	−
CGN 14267[f]	−	−	−	−	−	−	−	−	−	−	−	−	−	(−)	+	+	−	+	+	−
CGN 14268	(−)	−	−	−	−	−	−	−	−	−	−	−	(+)	(+)	+	+	−	+	+	−
CGN 14269[f]	−	−	−	−	−	−	−	−	−	(−)	−	−	−	(−)	+	+	−	+	+	−
CGN 14280	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	(+)	−	(+)	+	−
CGN 14283	−	−	−	−	(−)	−	−	−	−	−	−	−	(+)	(+)	+	+	−	+	+	−
Several[h]	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−
CGN 14239	−	(+)	−	−	−	(−)	−	(−)	−	−	−	−	−	−	(+)	+	−	(+)	+	−
CGN 14254[f]	−	+	−	−	−	−	−	−	*	−	−	−	−	−	+	+	−	+	+	−
CGN 14270[f]	−	(+)	−	−	−	−	−	−	−	−	−	−	−	−	+	+	−	+	+	−
CGN 5100	+	+	+	+	−	(−)	−	−	−	+	−	+	(−)	−	+	−	+	·	·	−
CGN 5110[f]	+	+	+	+	+	(−)	+	+	+	+	+	+	+	+	+	+	+	·	·	+
CGN 5153[f]	−	−	−	−	(+)	−	+	+	+	+	(+)	−	−	−	+	+	−	+	+	−[e]
CGN 5784	*	*	+	(−)	−	−	(−)	(−)	(−)	(−)	(−)	−	−	−	+	+	*	·	·	−
CGN 5916	−	−	−	−	−	−	−	−	−	−	−	−	−	−	(+)	−	(−)	·	·	−
CGN 10879	−	−	−	(+)	+	−	(−)	−	(−)	−	(−)	−	−	−	+	+	−	·	·	−
CGN 14269[f]	−	+	−	−	+	(−)	−	(+)	−	(−)	−	−	−	(−)	+	+	−	+	+	−
CGN 14270[f]	−	(+)	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−
VGB 6187	+	−	*	−	−	−	−	−	(+)	+	−	−	−	−	+	(+)	−	*	−	−
PI 491229	+	(−)	+	(−)	(+)	+	−	(+)	+	+	+	(−)	+	−	+	+	+	+	+	+

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[a] Resistance scores: ·: not determined; −: complete resistance; (−): incomplete resistance; (+): incomplete susceptibility; +: susceptibility; *: heterogeneous

[b] CGN: Centre for Genetic Resources, The Netherlands, Wageningen, The Netherlands; VGB: Vegetable Genebank of Horticultural Research International, Wellesbourne, U.K.; PI: PI lines collection: Agricultural Research Station, Salinas, California, USA.

[c] Potentially carrying Dm14.

[d] Potentially carrying Dm2 and Dm14.

[e] Potentially carrying Dm1 and Dm7.

[f] Selected plants from the named accession.

[g] Resistance phenotype of accessions CGN 10886, CGN 14255, CGN 14257, CGN 14263, CGN 14271, CGN 14275 and CGN 14278.

[h] Resistance phenotype of accessions CGN 14251, CGN 14256, CGN 14260, CGN 14261, CGN 14272, CGN 14277, PI 491178 and PI 491231[f]

expression of Dm3 is not complete in these genotypes. Incomplete expression of Dm genes was reported before by Crute and Norwood (1978).

Many *L. serriola* genotypes showed resistance phenotypes that could not be explained by known Dm genes (Table 6). Some similarities could be discerned in the resistance phenotypes of these *L. serriola* accessions. One group had resistance to all NL-races and the races 1/82 and 4/82, but was susceptible to the races 26/81, 27/81, 2/82 and 3/82. This resistance phenotype was shown by seven accessions. Another 14 accessions probably have the same resistance, but showed minor deviations such as incomplete resistance, incomplete susceptibility or a heterogeneous reaction for a few races. A second group only differed in resistance phenotype from the previous group by being susceptible to NL2. Eight accessions showed this phenotype, while another three accessions showed only minor deviations from this phenotype. Apart from these two resistance phenotypes, a group of 10 other *L. serriola* accessions was found, with a range of different resistance phenotypes indicating new resistance factors. Probably the genotypes of this group carry several new resistance factors.

Discussion

Previous screens of *Lactuca* collections have identified several sources of resistance (Eenink, 1979; Farrara & Michelmore, 1987; Lebeda, 1984a; Norwood et al., 1981). In this screen 1789 accessions were tested with 20 races of *B. lactucae.* A total of four accessions of *L. sativa* and 42 of *L. serriola* with resistance not attributable to previously known resistance genes was detected. The accessions PI 491231 and PI 491178 were also identified by Farrara and Michelmore (1987) as genotypes with unknown resistance to downy mildew. The results in this paper confirm their results. Four accessions of *L. saligna* (CGN 5305, CGN 5319, CGN 5320 and CGN 9312) showed incomplete susceptibility to NL6. As all other interactions between accessions of *L. saligna* and races of *B. lactucae* were incompatible, the results still support the belief that *L. saligna* is a nonhost for *B. lactucae* (Gustafsson, 1989; Lebeda, 1986; Lebeda & Boukema, 1991; Norwood et al., 1981). This could mean that resistance in *L. saligna* is not race-specific and consequently not determined by Dm genes. A new resistance mechanism providing high levels of resistance to *B. lactucae* would be very useful for lettuce breeding and the mechanism and genetics of resistance in *L. saligna* to *B. lactucae* should be studied more closely. A total of 13 accessions of *L. virosa* were resistant to all 20 races of *B. lactucae:* VGB 6168, VGB 6661, CGN 4683, CGN 5077, CGN 5145, CGN 5148, CGN 5332, CGN 5333, CGN 5793, CGN 5794, CGN 9316 and selected plants from the accessions CGN 9364 and CGN 9365. Although *L. virosa* is difficult to cross with *L. sativa* (De Vries, 1990), Smith and Langton (1989) succeeded in transporting a usable resistance to *B. lactucae* from *L. virosa* to *L. sativa.* The resistance encountered in the 13 *L. virosa* accessions is very interesting to breeders. Since resistance in *L. virosa* shows race-specificity, it is expected that resistance in *L. virosa* is determined by Dm genes as was stated before (Lebeda & Boukema, 1991).

The results obtained should be interpreted with some care. The resistance of each accession to races other than NL1 and NL3 was usually tested on only five leaf discs. In few instances accessions that were incompletely susceptible or incompletely resistant did not react similarly in different tests with the same race. In these cases, the most susceptible score was noted. Therefore, the resistance phenotypes may contain anomalies.

Though recent work indicates the presence of a high level of partial resistance in some accessions of wild species (Lebeda, 1990b), lettuce cultivars with a commercially acceptable level of partial resistance are still not available (Eenink, 1981; Eenink et al., 1982; Eenink & De Jong, 1982; Eenink et al., 1983). Therefore new sources of major gene resistance remain of high value in breeding programs for resistance to *B. lactucae.* Since major gene resistance is not expected to be very durable, control strategies as mentioned by Zadoks and Schein (1979) should be used to increase the durability of resistance genes.

For several reasons, there are good chances of finding still more major genes for resistance to *B.*

lactucae in future screens. Firstly, it seems probable that additional major genes for resistance could be found in accessions of lettuce not tested in this study. Secondly, in this study only accessions with resistance to NL1 or NL3 were tested for new major gene resistance. Accessions susceptible to NL1 and NL3 may also carry new major gene resistance. Thirdly, many accessions with new major gene resistance were the result of a collection trip to a relatively small area in Hungary. There might be many other local populations of *Lactuca* that have not yet been sampled and collected in genebanks.

The virulence phenotypes of the NL-races (Table 1) were generally in agreement with results published by Lebeda & Blok (1991), except for some results with 'Sabine' (Dm6) and PIVT 1309. In contrast with Lebeda & Blok (1991) both genotypes were susceptible to NL13 and 'Sabine' was susceptible to NL4. In addition several results indicate that the virulence phenotypes of the races isolated from *L. serriola* given by Lebeda (1989, 1990a) (Table 1) need revision. The races 26/81, 27/81, 2/82 and 3/82 were virulent on Mesa 659, which carries Dm7 and Dm13 (Farrara et al., 1987). According to Lebeda (1989), none of these races is virulent on Mesa 659. In conflict with the results of Lebeda (1989, 1990a), 1/82 and 4/82 were avirulent on UCDM14 (Dm14). With the NL-races the accessions PI 491099 and PI 491110 showed the resistance pattern corresponding with Dm1. However, both were susceptible to all races isolated from *L. serriola*, while according to Lebeda (1989, 1990a) only 1/82 should be virulent on Dm1. With the NL-races the accessions CGN 4669 and PI 491128 showed the resistance pattern corresponding with Dm3. These accessions were scored susceptible to the races 26/81, 27/81, 2/82 and 3/82, which do not have virulence to Dm3 according to Lebeda (1989, 1990a). It is possible that some changes have occurred in the races isolated from *L. serriola*. However, it is more likely that these races carry unknown virulence and avirulence genes. This idea is supported by the presence of resistance to these races in cultivars hitherto considered to be susceptible to all races of *B. lactucae* (Lebeda, 1990a). Cultivars with well defined Dm genes, even those of the differential series (Table 2), may carry additional unknown Dm genes providing resistance to some of these races.

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