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Investigation of the Danish *Bremia lactucae* (lettuce downy mildew) population in the period 1979–1984

Undersøgelse af den danske Bremia lactucae *(salatskimmel) population i perioden 1979–1984*

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Summary
An investigation of the Danish *Bremia lactucae* (lettuce downy mildew) population was carried out between 1979 and 1984. The virulence phenotype of 75 isolates was determined and 46 different virulence phenotypes (physiological races), possessing from 2 to 12 virulence factors (v-factors), were found. The frequencies in the homozygote state of the 12 known v-factors in the isolates were calculated. Virulence factor 7 was present in all isolates, virulence factor 12 in 97% of the isolates, while virulence factor 11 occurred with the lowest frequency, 16%. Virulence factor 11, however, became more frequent during the course of the investigation period, thus corresponding to the increased use from the middle of the seventies, of cultivars with the matching resistance factor 11. Complex isolates with many »unnecessary« virulence factors were common. By alternating between suitable cultivars with different resistances, disease losses can be reduced. Lastly, there is a need for alternative lettuce cultivars with new and effective resistance towards the Danish lettuce downy mildew population. To fulfill this aim will require the instigation of a special breeding programme.

Key words: *Bremia lactucae,* lettuce downy mildew, *Lactuca sativa,* lettuce, virulence phenotype, physiological race, virulence, resistance.

Resumé
En undersøgelse af den danske salatskimmel *(Bremia lactucae)* population blev foretaget fra 1979 til 1984. 75 svampeisolaters virulensspektrum (angrebsevne) over for salat *(Lactuca sativa)* blev bestemt, og der blev fundet i alt 46 smitteracer af svampen (virulens fænotyper), som besad fra 2 til 12 virulensfaktorer. En test, som kunne bestemme tilstedeværelsen af de 12 kendte virulensfaktorer v1 – v12 viste, at alle 12 virulensfaktorer var til stede, men med varierende frekvens. Salatskimmelsvampen er meget variabel med hensyn til angrebsevne. Frekvenserne i det homozygote stadium af de 12 undersøgte virulensfaktorer i svampeisolaterne blev beregnet. Virulensfaktor 7 fandtes i alle testede isolater, virulensfaktor 12 i 97% af isolaterne, mens virulensfaktor 11 optrådte mindst hyppigt, nemlig kun i 16%

af isolaterne. Dette betyder, at den modsvarende resistens i salaten, resistensfaktor 11, vil give den bedste beskyttelse mod angreb, idet kun 12 af de 75 testede isolater kan angribe salatsorter med resistensfaktor 11. Imidlertid er virulensfaktor 11 øget betydeligt i løbet af undersøgelsesperioden, og dette er sket i takt med den øgede dyrkning af sorter med resistensfaktor 11 fra midten af 70'erne. Karakteristisk for svampeisolaterne er, at de indeholder mange virulensfaktorer. Salatskimmelangreb kan forebygges ved at veksle mellem salatsorter med resistens, som vides at kunne give effektiv beskyttelse, samt ved at benytte sorter med egnede resistensfaktorer i kombination. Endelig er det nødvendigt at fremskaffe salatsorter med ny og effektiv resistens over for den danske salatskimmelpopulation, hvilket kræver, at et forædlingsprogram med dette specielle formål igangsættes.

Nøgleord: *Bremia lactucae,* salatskimmel, *Lactuca sativa,* salat, virulens fænotype, smitterace, virulens, resistens.

Introduction

Lettuce downy mildew, caused by the parasitic fungus, *Bremia lactucae* Regel, is the most destructive pathogen of the Danish lettuce crop both under glass and in the field.

In order to improve the control of this pathogen, an investigation of the *Bremia lactucae* population was started in 1979.

The interaction between many different hostpathogen pairs has been described by the gene-for-gene hypothesis (6,16). A similar model for *Lactuca-Bremia,* based partly on the gene-for-gene-hypothesis, was proposed by *Crute* and *Johnson* (3). The model has since been modified and extended by a number of investigators (9, 10, 13) and the work has not yet been completed with respect to establishing the number of resistance genes and their mode of action (14). It has become apparent that the system originally proposed for *Lactuca-Bremia* is more complex than earlier thought to be the case (14).

The aim of this investigation is to establish which virulence factors are present in the Danish lettuce downy mildew population and to what extent they occur. Furthermore, an evaluation of the variation of the virulence factors in the isolates for the period 1979–1984 is undertaken. The results could form the basis for the choice of lettuce cultivars containing resistance useful under Danish conditions (18, 19). The results will give information to the plant breeders about the future needs for new resistance in lettuce. This is the first study of the *Bremia lactucae* population undertaken in Denmark.

The term virulence phenotype is used instead of physiological race. The latter term is inadequate and impractical, when the number of existing virulence phenotypes is as large as it is in the case with *Bremia lactucae* (11, 13).

As the gene-for-gene system is only partly understood for the *Lactuca-Bremia* system, the term factor is used instead of gene in connection with both virulence and resistance (14).

Materials and methods

Isolates of Bremia lactucae

75 samples of lettuce downy mildew from 43 holdings – 38 glasshouse nurseries and 5 market gardens – were investigated in the period 1979–1984. Each sample consisted of diseased lettuce leaves taken from one or several lettuce plants. The samples were collected and sent from all parts of Denmark and the geographic distribution of the holdings was as follows: 20 in Zealand, 18 in Funen and 5 in Jutland.

Differential cultivars

The determination of virulence phenotype was carried out using a differential series consisting of lettuce cultivars with known resistance factors (1,3,15). The differential series used in 1979–1984 is listed in Table 1. In 1979 a series of 12 cultivars, enabling 8 of the 12 v-factors to be identified, was used. However, when possible, tests were carried out the following year, enabling all 12 v-factors to be identified. The cultivar Cobham Green is assumed to be fully susceptible, (R0). Cv Hilde, earlier believed to be susceptible, is now known to possess resistance because isolates of the fungus not virulent on Cv Hilde, have been found. But such isolates are rare, and it is debatable, whether this resistance should have been included in test system (4) as was the case in this investigation. The resistance factor in Cv Hilde is termed R12 (8).

Table 1. Differential series to determine virulence phenotypes of *Bremia lactucae* from 1979–1984.

Lettuce cultivar	Resistance factors	1979	1980	1981-84
Cobham Green	0			+
Blondine	1	+	+	+
Mildura	3			+
Valmaine	5		+	+
Sabine	6			+
Great Lakes 659.	7	+	+	+
Bourguignonne	9		+	+
Sucrine	10		+	+
Capitan	11		+	+
Hilde × Lactuca serriola	11	+		
Hilde	12	+	+	+
Bremex	1+7		+	+
Noran	2+4	+	+	+
Ancora	2+4	+		
Portato	2+7+(1)	+	+	+
Brioso	2+7+(1)	+		
Kordaat	3+4	+	+	+
Solito	3+7	+	+	+
Avondefiance	6+8		+	+
Calmar	7+8	+	+	+
Ardente	1+6+7		+	+
Edgar	2+3+7		+	+
Pallas	2+3+7	+		

+ = cultivar included in the differential series

In 1979 and 1980 50 seedlings of each of the differential cultivars were grown on moist filter-paper in 18 cm plastic dishes and covered with transparent plastic. After 1980 transparent plastic boxes (29×26×6 cm), divided into 20 compartments, were used. Each compartment contained 25 seedlings of a differential cultivar.

Inoculation

By rinsing diseased lettuce leaves, spores of *Bremia lactucae* were released and inoculum containing $10^4 - 10^6$ spores/ml was prepared, as described by *Crute* and *Dickinson* (2). Seedlings of the differential cultivars were spray inoculated, when they were 7–9 days old. Incubation was at 15°C under a photoperiod of 16 hrs. Samples of downy mildew on leaves not tested immediately, were frozen and stored at –20°C in plastic boxes.

Determination of virulence phenotypes

Following incubation for 7–10 days, the number of infected plants was counted. A second count on the 12–15th day and yet a third count on day 16–20 was made. Differential cultivars were scored resistant when none or less than 2.5% were infected, and susceptible when more than 2.5% were infeced.

Results

Determination of virulence phenotypes

The virulence phenotype of 75 isolates was determined, and in Table 2 they are ranked according to the observed frequency. Host source, the year(s) of collection and expected host plant resistance factors are listed as well. The number of isolates investigated in the years 1979–1984 was as follows: 17 isolates in 1979, 28 in 1980, 14 in 1981, 2 in 1982, 10 in 1983 and 4 in 1984. A total of 46 virulence phenotypes were determined. Of these, 36 occurred only once, 6 occurred twice, 2 occurred three times and 1 occurred four times. The most common virulence phenotype was registered 17 times and 12 of these finds occurred in 1980 on Funen where all the material had originated from the same source of infected seedlings in the spring of 1980.

Frequency of virulence factor v1 to v12 in the isolates

All 12 tested v-factors were present in the Danish population.

B. lactucae is diploid in its vegetative phase (20) and heterothallic (12). Assuming that the investigated population is in balance, i.e. that the population is panmictic, and behaving according to Hardy-Weinberg Law (17), then a virulent isolate must be homozygous for the recessive v-factors. The observed frequency of the homozygotes

Table 2. Virulence phenotype (physiological race) of 75 isolates of *Bremia lactucae* (1979–84).

Virulence phenotype												Host source/year	Host resistance	No. of time recorded
1	2	3	4	x	6	7	x	x	x	x	12	Salina/80,81 Ostinata/80 Plus/80,81 Alicia/80 Winalda/80	R0, R3, R2+4, R?	17
1	x	3	x	5	x	7	8	x	x	x	12	Ostinata/80 Vasco/80	R3, R?	4
1	2	3	x	x	x	7	x	x	x	x	12	Salina/81 Ostinata/79 Great L. 659/80	R0, R3, R7	3
1	2	3	4	5	6	7	8	9	10	x	12	Ostinata/81 Nicole/79	R3, R?	3
x	x	x	x	x	x	7	8	x	x	x	12	Great L. III/80 Iceberg/81	R7, R?	2
1	x	3	x	x	x	7	x	x	x	11	12	Parmanta/83 Leona/83	R2+11, R?	2
1	2	3	x	x	x	7	x	x	x	11	12	Panvit/79	R2+11	2
1	x	3	4	.	.	7	8	.	.	x	12	Salina/79 Ostinata/79	R0, R3	2
1	x	3	x	5	x	7	8	9	10	x	12	Salina/80 Ostinata/79	R0, R3	2
1	x	3	x	5	6	7	8	x	10	x	12	Salinas/82 ?/84	R7+8, R?	2
x	x	x	x	x	x	7	x	x	x	x	12	?/83	R?	1
1	x	3	x	x	x	7	x	x	x	x	x	Ostinata/81	R3	1
x	x	x	x	5	x	7	x	x	x	11	12	Nanda/84	R?	1
x	x	x	.	x	.	7	x	9	x	11	12	Bellona/79	R0	1
x	x	x	.	5	.	7	x	x	10	x	12	Bellona/80	R0	1
1	2	3	x	.	.	7	x	.	.	x	12	Ostinata/79	R3	1
1	x	3	x	.	.	7	8	.	.	x	12	Great L. 659/79	R7	1
1	x	3	x	.	.	7	x	.	.	11	12	Salina/79	R0	1
1	x	3	x	x	6	7	x	x	x	x	12	Ostinata/79	R3	1
1	x	3	x	x	.	7	x	x	10	x	12	Ostinata/80	R3	1
1	x	3	4	x	x	7	x	x	x	x	12	Nanda/83	R?	1
x	x	x	x	5	x	7	8	x	10	x	12	Wintercut/82	R?	1
1	2	3	4	.	.	7	x	.	.	x	12	Ostinata/79	R3	1
1	x	x	x	.	.	7	8	9	10	x	12	Great L. 659/79	R7	1
1	x	3	x	5	.	7	8	.	.	x	12	Ostinata/79	R3	1
1	2	3	4	x	x	7	x	x	x	x	12	Ostinata/80	R3	1
1	x	3	x	x	x	7	x	9	10	x	12	Iceberg/83	R?	1
x	x	x	x	5	6	7	8	x	10	x	12	Iceberg/81	R?	1
1	2	3	x	x	.	7	x	9	10	x	12	Ostinata/79	R3	1
1	x	3	x	5	x	7	8	.	10	x	12	Ostinata/79	R3	1
1	x	3	x	5	x	7	8	x	10	x	12	Salina/80	R0	1
1	x	x	x	5	6	7	8	9	x	x	12	Iceberg/83	R?	1
1	2	3	4	x	6	7	x	9	x	x	12	Salina/80	R0	1
1	2	3	4	x	6	7	x	x	x	11	12	Plus/80	R2+4	1
1	2	3	4	5	6	7	x	x	x	x	12	Salina/81	R0	1
1	2	3	4	x	6	7	x	9	10	x	12	Ostinata/80	R3	1
1	2	3	x	5	x	7	8	9	10	x	12	Ostinata/80	R3	1
1	2	3	4	5	6	7	8	x	x	x	12	Salina/81	R0	1
1	x	3	4	5	x	7	8	9	10	x	12	Ostinata/83	R3	1
1	x	3	4	5	x	7	8	9	10	11	x	No. 2535RZ/83	R?	1
1	2	3	4	5	x	7	x	9	x	11	12	Montana/84	R?	1
1	2	x	4	5	6	7	8	9	10	x	12	Leona/81	R?	1
1	2	3	4	5	x	7	8	9	10	x	12	Ostinata/81	R3	1
1	x	3	4	5	6	7	8	9	10	x	12	Salina/84	R0	1
1	2	3	4	5	6	7	8	x	10	11	12	Nanda/83	R?	1
1	2	3	4	5	6	7	8	9	10	11	12	Arda/81	R?	1

Number 1 to 12 = virulence factor present
x = virulence factor absent
. = virulence factor not determined or not tested.

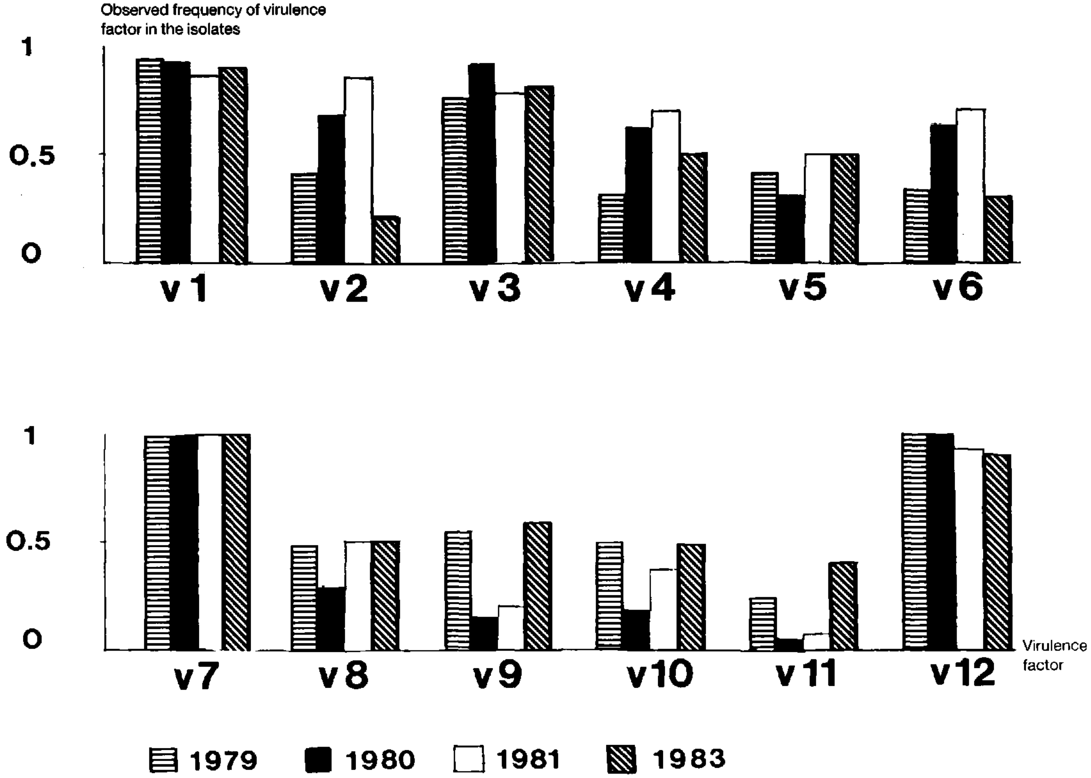

Fig. 1. The observed frequency of isolates (q^2) homozygous for virulence factor 1 to 12 in Denmark in the years 1979, 1980, 1981 and 1983 including 69 isolates.

will equal the frequency in the virulence phenotype (q^2). In Fig. 1 the frequencies of virulence phenotypes homozygous for v1 to v12 observed in Denmark in the years 1979, 1980, 1981 and 1983 are shown including 69 isolates. V-factor 7 was found in all isolates ($q^2=1$), while v-factor 12 was in 67 of the isolates ($q^2=0.97$). Least common was v-factor 11, which only occurred in 10 of the 69 isolates ($q^2=0.15$). V-factor 11 had the lowest frequency until 1983, when it increased: from 0.07 in 1981 to 0.40 in 1983 (Fig. 1). However, as v-factors also occurs hidden in the heterozygote state, it is necessary to combine both the homozygous and heterozygous state together (q^2+2pq), to get the total frequency of isolates carrying a particular v-factor.

This has been done and the result can be seen in Fig. 2 for the years 1979, 1980, 1981 and 1983. From the figure it can be seen that the frequencies of isolates possessing v-factor 1, 3 and 7 is approximately 1.0 for all years. The frequencies of isolates with v-factor 2 and 6 increased during the first years, after which they declined to such an extent, that v-factor 2, occurred with the lowest frequency in 1983, namely 0.70. Frequencies of isolates with v-factor 11 increased from 0.46 in 1981 to 0.87 in 1983.

Virulence phenotype complexity

In Fig. 3, the virulence phenotype complexity, calculated from Table 2, is presented in terms of number of virulence phenotypes in the homozygous state with two to twelve v-factors. The most simple type with only one v-factor was not observed and only one isolate with two v-factors was found. Most common isolates had five and six v-

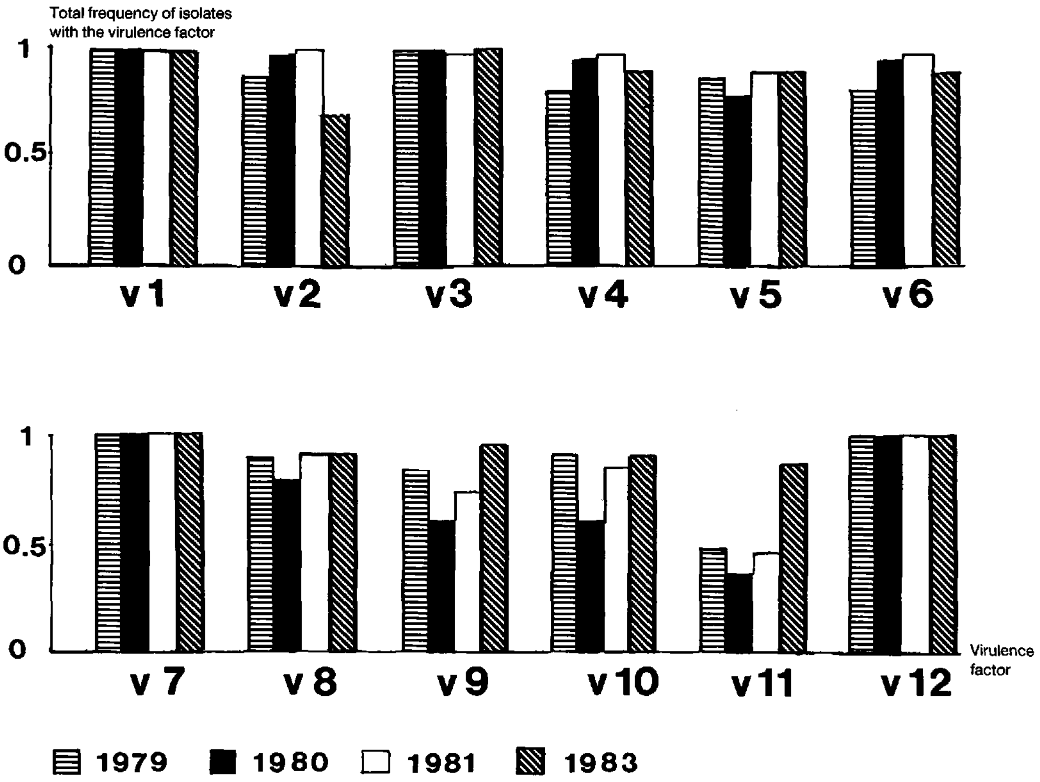

Fig 2. The calculated frequency of isolates carrying virulence factor 1 to 12 either in the homozygous state (q^2) or the heterozygous state (2pq) performed in the years 1979, 1980, 1981 and 1983 in Denmark, including 69 isolates.

factors and these made up 1/4 of the isolates. Highly complex phenotypes were determined, i.e. isolates with ten, eleven or twelve v-factors and these were observed on 4, 2 and 1 occasions respectively.

Resistance of lettuce cultivars

Distributions of resistance factors present in the lettuce cultivars from which *B. lactucae* was isolated show (Fig. 4) that resistance factor 3, present in Cv Ostinata, was the most common factor and present in 37% of the samples. Cultivars without resistance (R0), represented by Salina and Bellona were present in 21% of the samples. Only 4% of the samples came from newly introducted cultivars with R-factor 11 e.g. cultivars Parmanta and Panvit. These cultivars are commonly grown in the winter season.

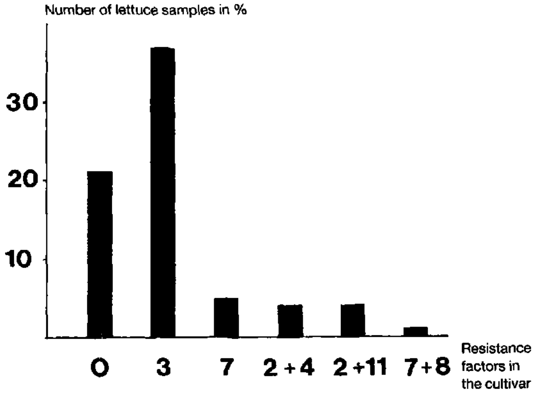

Fig. 4. Distribution in % of resistance factors in the lettuce samples in the period 1979–1984.

Discussion

The investigation shows, that the Danish *B. lactucae* population possesses great genetic variation

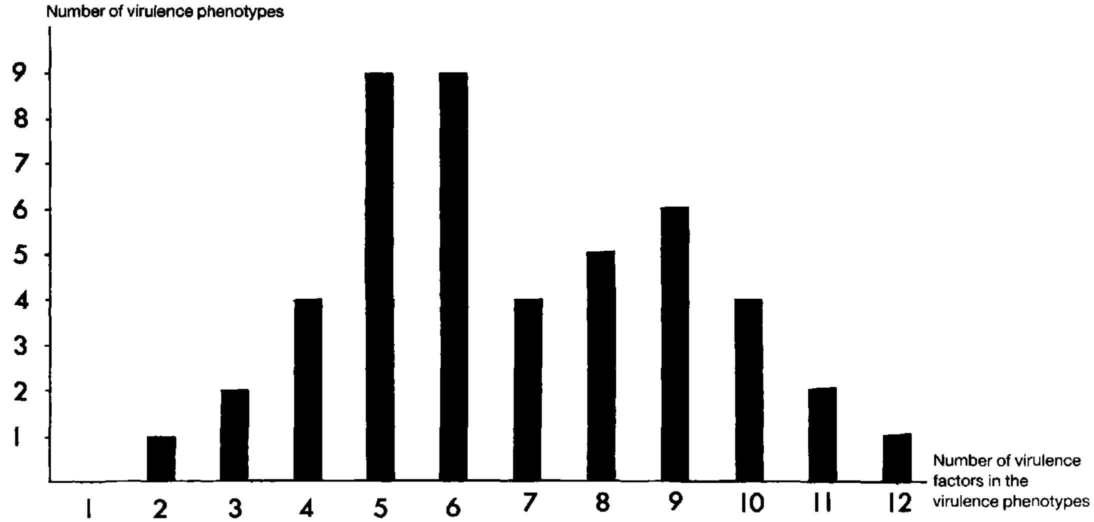

Fig. 3. The complexity of the 46 different virulence phenotypes in the homozygous state in the period 1979–1984.

with regard to virulence. This is illustrated by the number of different phenotypes found, namely 46 different phenotypes out of a total of 75 isolates (Table 2). Similar results have been obtained from England (5), Finland (15), Czechoslovakia (11) and Sweden (8).

The pathogen content of v-factors reflects not only the resistance, that is present in the particular lettuce cultivar under attack, but also the total resistance present in the lettuce cultivars which have been grown in Denmark many years before this investigation.

Certain combinations of v-factor pairs were not observed in the population of the fungus. In 1979, 1980 and 1981 3 combinations were not detected namely: v5 & v11, v8 & v11 and v10 &v11. However in 1983 also these combinations were registered (Table 2), and this may be ascribed to the increase in the frequency of v-factor 11. Being aware of the small number of samples, v-factor pairs v2 & v5, v2 & v8 and v6 &v8 occurred with a significantly lower frequency than expected, in the period 1979–1981. A real analysis and comparison of the observed and expected frequencies of combinations of v-factor pairs was not carried out for the reasons described by *Wolfe* and *Knott* (21).

Because *B. lactucae* is diploid, it is necessary, when choosing cultivars with resistance suitable for use in Denmark, to take into account the total frequency of the individual v-factors in the isolates. Frequency under 0.5 were only observed for isolates carrying v-factor 11 (period 1979–1981), which can be seen in Fig. 2. The equivalent resistance factor R11 originates from *Lactuca serriola* L., and it has been incorporated into a great number of cultivars of *L. sativa.* In Denmark cultivars with R-factor 11 were introduced in the middle of the 70's (eg. cvs Capitan, Panvit and Parmanta). This is reflected in the frequency of isolates with v-factor 11, which increased from 1979 to 1983 (Fig. 1 and 2). Whether the Danish lettuce downy mildew population contained v-factor 11 before cultivars with R-factor 11 were brought into cultivation, is not known. R-factor 2 is known to be present in some of the new cultivars with R-factor 11. V-factor 7 occurs in all the isolates determined, and v-factor 12 in 73 of the 75 investigated isolates. It is in agreement with the widespread use over many years of cultivars with R-factor 7 (eg. Great Lakes) and R-factor 12 (eg. Hilde).

No great differences could be found in the geographic distribution of the 12 known v-factors frequencies in Denmark. Comparing the Danish *B. lactucae* population with that of the rest of Europe, variations from country to country have been found. However, it is characteristic, that v-factor 11 had the lowest frequency in all populations investigated in Europe about 1980. A comparison between the populations in Denmark and our neighbouring country, Sweden, carried out in 1980, and involving 28 and 25 isolates respectively (7), showed great differences in the frequencies of v-factor 1, 2, 3, 5, 8, 9, 10 and 11. For v-factor 4, 6 and 7, however, the frequencies were almost identical.

The number of v-factors in the 46 virulence phenotypes was large (Fig. 3), and 85% contained more than 4 v-factors and 38% contained 8 or more v-factors. This was the case irrespective of whether the host contained none, 1 or 2 resistance factors. Several of the isolates contained as many as 10 »unnecessary« v-factors, i.e. v-factors not corresponding to R-factors in the host. Because of its great capacity for virulence, the pathogen is able to infect a large number of cultivars with different R-factors. This means it is very difficult to replace susceptible cultivars with alternative ones containing usable resistance. Cultivars with effective resistance, which has no known matching virulence is not accessible. Complex virulence phenotypes with a large content of »unnecessary« v-factors are widespread and common (5,8,11). This may be due to combined effect of the diploidy of the fungus, frequent occurence of sex recombination and presence of linkage between the loci controlling virulence (14).

Very few cultivars with suitable R-factors are grown in Denmark, namely only cultivars with R-factor 2 and 11 (Fig. 4). Particulary summer season cultivars of lettuce resistant to *B. lactucae* are lacking. Therefore, better information on the R-factors of cultivars from seed firms, who carry out the breeding work, is necessary. Such information, together with a consideration of the v-factor situation in the country or locality, would provide a much better basis for the choice of cultivars with useful resistance. By means of plant breeding, attempts should be made to incorporate new resistance to *B. lactucae* into lettuce cultivars that are suitable for use under Danish conditions.

Conclusion

On the basis of this investigation into the Danish *B. lactucae* population it can be concluded that:

1. The population is very heterogenous. 46 different virulence phenotypes were determined from 75 isolates of the pathogens.
2. All 12 known virulence factors were present.
3. V-factor 7 was present in all isolates, v-factor 12 in 97% of the isolates. Least common was v-factor 11, which was only found in 16% of the isolates.
4. The occurrence of »unnecessary« v-factors was very common.
5. The frequency of the occurrence of v-factor 11 increased concurrently with the increase in the use of cultivars with R-factor 11.
6. By means of plant breeding, attempts should be made to incorporate new resistance to *B. lactucae* into lettuce cultivars suitable for use under Danish conditions.
7. By alternating between cultivars with one or more suitable R-factors, disease losses could probably be reduced.

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Literature

1. *Bannerot, H.* 1980. Screening wild lettuce for *Bremia* resistance. In Proc. Eucarpia Meeting Leafy Veg., 104–106. *(J. W. Maxon Smith & F. A. Langton* eds).
2. *Crute, I. R. & Dickinson, C. H.* 1976. The behavior of *Bremia lactucae* on cultivars of *Lactuca sativa* and other composites. Ann. appl. Biol. 82, 433–450.
3. *Crute, I. R. & Johnson, A. G.* 1976. The genetic re-

lationship between races of *Bremia lactucae* and cultivars of *Lactuca sativa*. Ann. appl. Biol. 83, 125–137.

4. *Crute, I. R. & 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. Theor. Appl. Genet. 60, 185–187.
5. *Dixon, G. R. & Wright, I. R.* 1978. Frequency and geographical distribution of specific virulence factors in *Bremia lactucae* populations in England 1973 to 1975. Ann. appl. Biol. 88, 287–294.
6. *Flor, H. H.* 1956. The complementary genic systems in flax and flax rust. Adv. Genet. 8, 29–54.
7. *Gustafsson, I.* 1983. Resistance studies of *Bremia lactucae* Regel. Växtskyddsnotiser 47, 61–67.
8. *Gustafsson, M., Arhammer, M. & Gustafsson, I.* 1983. Linkage between virulence genes, compatibility types and sexual recombination in the Swedish population of *Bremia lactucae*. Phytopath. Z. 108, 341–354.
9. *Johnson, A. G., Crute, I. R. & Norwood, J. K.* 1977. The genetics of race specific resistance in lettuce *(Lactuca sativa)* to downy mildew *(Bremia lactuca)*. Ann. appl. Biol. 86, 87–103.
10. *Johnson, A. G., Laxton, S. A., Crute, I. R. & Norwood, J. K.* 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.
11. *Lebeda, A.* 1982. Geographic distribution of virulence factors in the Czechoslovakian population of *Bremia lactucae* Regel. Acta Phytopath. Acad. Sci. Hung. 17, 65–79.
12. *Michelmore, R. W. & Ingram, D. S.* 1980. Heterothallism in *Bremia lactucae*. Trans. Br. mycol. Soc. 75, 47–56.
13. *Michelmore, R. W., Norwood, J. M., Ingram, D. S., Crute, I. R. & Nicholson, P.* 1984. The inheritance of virulence in *Bremia lactucae* to match resistance factors 3, 4, 5, 6, 8, 9, 10 and 11 in lettuce *(Lactuca sativa)*. Plant Pathology 33, 301–315.
14. *Norwood, J. M. & Crute, I. R.* 1984. The genetic control and expression of specificity in *Bremia lactucae* (lettuce downy mildew). Plant Pathology 33, 385–400.
15. *Osara, K. & Crute, I. R.* 1981. Variation for specific virulence in the Finnish *Bremia lactucae* population. Ann. Agric. Fenn. 20, 198–209.
16. *Person, C.* 1959. Gene-for-gene relationships in host-parasite systems. Can. J. Bot. 37, 1101–1130.
17. *Srb, A. M., Owen, R. D. & Edgar, R. S.* 1965. General Genetics. (2. ed.) W. H. Freeman and Company, San Francisco, 557 pp.
18. *Thinggaard, K.* 1980. Hvad sommeren afslørede om salatskimmel. Gartner Tidende 96, 720–723.
19. *Thinggaard, K.* 1981. Salatskimmel – en problematisk sygdom i salat. Månedsoversigt over plantesygdomme 529, 108–112.
20. *Tommerup, I. C.* 1981. Cytology and genetics of Downy Mildews. In: The Downy Mildews *D. M. Spencer* (ed.). Academic Press, London, 121–142.
21. *Wolfe, M. S. & Knott, D. R.* 1982. Populations of plant pathogens: Some constraints on analysis of variation in pathogenicity. Plant Pathology 31, 79–90.

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