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Wild hops – New genetic resources for resistance to hop powdery mildew *(Podosphaera macularis ssp. humuli)*

Hop powdery mildew is a serious disease of hop causing a dramatic drop of yield and quality on susceptible hop varieties. The most effective and economic way of controlling powdery mildew on hop can be achieved by using resistant varieties in commercial hop production. Just from the beginning of all breeding efforts at the Hop Research Center Hüll, emphasis has been put on the development of hop cultivars with a broad range of resistance to all major diseases. Over the last 15 years the main focus in breeding has been to improve resistance to hop powdery mildew (PM) in Hüll breeding lines and new cultivars. Extensive studies on the virulence spectrum of powdery mildew populations had revealed that all hop resistance genes currently known were overcome by virulent strains of PM occurring in the hop growing regions of the Hallertau, England, France, and the USA. Thus, for hop breeding it was urgently needed to look for new sources of resistance which were expected to be found in wild hops. Since 2001 more than 15,000 wild hops from throughout the world have been screened in the greenhouse for PM resistance. Subsequently, resistant individuals were retested in the laboratory using the detached leaf assay and afterwards in the fields under natural infection conditions. In this way 54 very promising wild hops were identified showing resistance to all virulent PM strains currently known. Resistant individuals will be used as crossing partners in our breeding programs to broaden the genetic basis for PM resistance in the Hüll hop germplasm.

Descriptors: *Humulus lupulus*, hop powdery mildew, wild hop germplasm, resistance

1 Introduction

Powdery mildew of hop which is caused by *Podosphaera macularis ssp. humuli* [Braun] (formerly called *Sphaerotheca humuli* [DC.] Burrill) affects hop production in Europe and also in the USA (7). Infections on susceptible varieties cause severe loss of yield and quality (Fig. 1). Thus, especially in years with highly conducive conditions for powdery mildew (PM) infections intensive fungicide programs assisted by specific labor-intensive cultural practices are necessary. In 2002 the costs for fungicides to control this disease amounted to 4.9 million Euro alone in the Hallertau growing region. Facing increasing competition on the international market, even in years with severe PM infestation pressure hop growers are striving to reduce their costs for fungicide treatments while maintaining or even improving hop quality. On the other hand also the brewing industry is demanding superior brewing quality with a maximum of food safety which means that under no circumstances they would accept hops with harmful residues of pesticides. Thus, genetically fixed disease resistance is of utmost importance for commercially grown hop cultivars.

Since 1926, when all breeding efforts have been started at Hüll, step by step a broad range of resistance or tolerance to *Verticillium* wilt (*V. albo-atrum* or *dahliae*) and downy mildew (*Pseudoperonospora humuli*) has been built up in the Hüll hop germplasm and in Hüll cultivars. Only recently also powdery mildew resistance could be achieved in two new varieties. 'Hallertauer Merkur' and 'Herkules', the two powdery mildew resistant high alpha varieties were released in 2001 and 2006, respectively. Resistance in both varieties is based on the *R2* gene deriving from the English cultivar 'Wye Target'.

Extensive information on the effectiveness of currently known sources of PM resistance in hop was obtained when the virulence spectrum of powdery mildew populations deriving from the Hallertau region, from France, England, and the USA was investigated (5). Using nine hop varieties as "differential set" with seven different major resistance genes (Table 1) the spectrum of virulence genes present in 189 single spore PM isolates from the various hop growing regions mentioned above was examined. These studies, funded by the Wissenschaftsförderung der Deutschen Brauwirtschaft (Scientific Fund of the German Brewing Industry), revealed that all seven major genes (*R* genes) conferring race-specific resistance were already overcome by corresponding virulence genes (*v1-v6*, and *vB*) occurring in the PM populations collected from the major hop growing regions. Only in specific regions single *R* genes were still effective to ward off PM infections. In Germany the *R2* resistance gene deriving from the English cultivar 'Wye Target' is the only one which is still effective. Based on these results it could be concluded that 'Hallertauer Merkur' and 'Herkules' carrying the monogenic *R2* based resistance were still protected from PM infections in Germany. On the other side it became quite obvious that virulent pathotypes of *Podosphaera macularis ssp. humuli* which are able to overcome the resistance of 'Wye Target' could evolve at any time in Germany or might be spread from England, Belgium or the USA where PM strains of the *v2*-pathotype already occurred (P. Darby and C.M. Ocamb, pers. commun.).

Thus, our objective was to identify new sources of PM resistance to be utilized in hop breeding and following this intention wild

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Tables and Figures see Appendix

hops were expected to be a promising, so far unexploited source for these genes.

Since 1999 a large collection of wild hop germplasm has been built up at the Hop Research Center Hüll. Due to its broad geographic origin encompassing wild hops from more than 155 locations throughout Europe, Asia, Australia, and North America, a very promising genetic resource is now accessible.

Wild hops were pre-tested for powdery mildew resistance in the greenhouse in 2001 and 2002. Systematic screening based on artificial inoculation with PM spores with characterized virulence genes has been started in the greenhouse and in the laboratory in 2003 within a project funded by the Wissenschaftliche Station für Brauerei in München e.V. (Scientific Station for Breweries in Munich).

2 Material and Methods

2.1 Plant Material

In spring plants were raised from seeds of wild hops or rootstocks in the greenhouse at the Hop Research Center Hüll, Germany. Seeded cones and in few cases also rootstocks were collected from Germany, Austria, Belgium, China, Finland, Hungary, Italy, Japan, New Zealand, Norway, Russia, Slovakia, Sweden, Turkey, Ukraine, and the USA.

2.2 Assays for PM resistance

2.2.1 Powdery mildew isolates

Monosporic isolates of *P. macularis ssp. humuli* were produced in 1999 and 2000 from leaves of infected plants collected from the Hallertau, England, France, and the USA. Using a set of nine differential hop genotypes carrying seven different resistance genes the spectrum of virulence genes of 189 fungal isolates was determined in 2000 (5). At current, a collection of fifteen PM isolates is being maintained on leaves of 'Northern Brewer', 'Hallertauer Magnum' and in some cases of 'Wye Target' as inoculation material for all PM infection assays. Virulence reactions of all isolates are being re-checked every year in order to monitor possible genetic changes affecting the virulence genes. Eight isolates (Table 2) encompassing all virulence genes known and characterized so far were used in this screening of the wild hop germplasm.

2.2.2 Greenhouse Testing

Three to four-week-old plantlets raised from seeds or root stocks were transferred into the greenhouse for testing their reaction toward PM. While seedlings derived from seeds were tested in germination trays, plants raised from rootstocks were screened in single pots. Heavily infected spreader plants ('Hallertauer Magnum' or 'Northern Brewer') were placed between the wild hops as a permanent source of PM spores for artificial inoculation. For initial infection of the spreader plants specific PM strains (BU10, BU13, ES1, HU9; see Table 2) representing the prevalent virulence spectrum in the Hallertau hop growing region were provided by EpiLogic, Freising, Germany. In order to favor germination and sporulation of PM in the greenhouse temperature was kept at 22–24 °C during daylight (16 hours) and reduced to 12 °C during darkness. At night the relative humidity was kept at 80 %, while at daylight humidity could fall down to 30–40 %. Ten to fourteen days after plants were brought into the inoculation chamber of the greenhouse seedlings or young plants were scored for PM symptoms using a disease severity scale from 0 to 9 as described in Table 3. Individuals with score 0 and 1 (no infection or small spots of slight decoloration on the leaves as sign for a defense response) were considered as being resistant.

Plantlets rated as resistant remained in the greenhouse for up to three months while being assessed for their reaction towards PM every four weeks.

2.2.3 Testing in the laboratory

Using the detached leaf assay the first pair of fully expanded leaves on the first or second node from the wild hop seedlings were collected in spring. Leaves were placed on water-agar plates, adaxial side uppermost, and inoculated with conidia of specific PM isolates (HU62; E8, E9 or E10; see Table 2) by using a settling tower. Eight days after incubation at 22 °C under a 12h-photoperiod regime, leaves were assessed (Table 4) and rated as resistant or susceptible to the PM strain employed. Seedlings were classed as resistant when scored as either 0, 0.1 or 0.2 on a scale from 0 to 1. Each test was replicated with new leaves 2-3 times.

2.2.4 Testing in the field

Female wild hops were screened for PM resistance in a hop yard near Schrittenlohe in the vicinity of Hüll, Germany, while male hops were tested in a specific hop yard near Freising, Germany. In both fields there was no chemical control for PM and hop aphids and the application of pesticides to fight downy mildew was reduced to the minimum. Leaves were assessed for PM infections twice during the season in the field, whereas cones were examined once in the field and later after harvest as dried cones. Resistance of cones was judged on a scale of 0 to 9. Following the scale of PM development on leaves (Table 3) here a score of 0 meant no infection on cones, while 9 stood for very heavy infection and malformation of the cones associated with a total loss of yield and quality.

Since here all wild hops were already prescreened for PM resistance in the greenhouse and laboratory, only plants showing no infection on cones (score 0) were classed as resistant.

3 Results and Discussion

3.1 Powdery mildew isolates used for screening of wild hop germplasm

Out of a collection of fifteen single spore isolates of *P. macularis* available eight isolates (Table 2) were used for the resistance tests in the greenhouse and the laboratory. With this set of PM strains encompassing seven different virulence genes it is possible to test for all seven complementary *R* genes currently known and characterized in hops (1, 2). According to the gene-for-gene-hypothesis for host-pathogen interactions, which also applies to hop and its pathogen *Podosphaera macularis ssp. humuli,* for each resistance gene *R* in hop there is a corresponding virulence gene *v* occurring in the pathogen which is necessary that the fungal strain can overcome the *R* gene based resistance and infect its host (see Table 1). Employing PM strains in our resistance tests, which cover all currently known virulence genes (Table 2), all corresponding resistance genes known so far in hop can be overcome. Only wild hops with new, so far not characterized resistance genes cannot be infected by the PM isolates used.

3.2 Testing for powdery mildew resistance in the greenhouse

First tests for PM resistance in wild hops were conducted in the greenhouse in 2001 and 2002. In 2003 this screening of native hop germplasm could be continued systematically within this project

funded by the Wissenschaftliche Station für Brauerei in München e.V.. In the meantime infection conditions were optimized significantly which improved the reliability and reproducibility of the resistance data obtained in the greenhouse: Each season starting in February specific powdery mildew strains (HU9, BU10, BU13, ES 1 see Table 2) with characterized virulences of the *v3*, *v4*, *v6* and *vB* type were provided as inoculation material by our project partner EpiLogic, Freising. In this way resistance tests could be conducted with those PM strains which are representing the virulence spectrum of the PM population of the Hallertau growing region. In addition, by starting the infection on the leaves of highly susceptible hop varieties ('Northern Brewer' and 'Hallertauer Magnum' were used as "spreader plants") with freshly sporulating inoculation material provided by EpiLogic the PM infection pressure could be increased significantly in the greenhouse.

Up to June 2006 approximately 15,000 wild hops collected from Europe, Australia, Asia, and North America were screened for PM resistance in the greenhouse. Seeds from wild hops were germinated in trays and three to four weeks later seedlings raised from these seeds were transferred into the greenhouse between heavily infected plants of cv. 'Northern Brewer' and 'Hallertauer Magnum' (Fig. 2). Each day the "PM spreader plants" were shaken and in this way the young seedlings were inoculated artificially with PM spores. Two to three weeks after their transfer into the greenhouse, the leaves of the hop plants were checked for blisters or PM pustules and classed as resistant or susceptible (Table 3). After this mass screening of seedlings in trays, plants which were classes as resistant after this first screening step were transferred into single pots and remained under greenhouse infection conditions for up to three months. During this period of time they were assessed for PM resistance every two or three weeks (Fig. 3). Thus, for each wild hop screened in the greenhouse four to five resistance ratings were obtained during the screening season. Plants with scores of 0 to 1 were judged as being resistant and these wild hops were re-tested the following year together with seedlings which were tested for the first time.

After three years of continuous testing in the greenhouse during the growing season and based on 3,600 rating scores obtained from 830 single plants which were tested as single plants 75 wild hops could be selected which did not show any infection or only few spots of slight leaf decoloration as sign of a defense reaction. Thus it could be concluded that these plants are resistant to virulent powdery mildew races occurring in the Hallertau region.

3.3 Testing for powdery mildew resistance in the laboratory

Wild hops which had been assessed as being resistant in the greenhouse towards PM strains occurring in the Hallertau region (*v3, v4, v6*, and *vB* virulence spectrum) were re-screened in the laboratory for their reaction towards non-indigenous PM strains of the *v1, v2,* and *v5* virulence type which already evolved in England or the USA. Using the detached leaf assay (Fig. 4) in this screening step it was possible to employ PM strains that do not occur in the Hallertau growing region. With this testing system any risk of an escape of dangerous PM strains into the hop growing region could be prevented. For example, fungal strains from England possess the virulence gene *v2* which can overcome resistance based on the *R2* gene deriving from English cv 'Wye Target' which is still effective in Germany. Since this resistance was mainly used in the Hüll breeding programs, these virulent strains would be highly dangerous to the Hallertau region and in particular to the Hüll cultivars 'Hallertauer Merkur' and 'Herkules' carrying PM resistance based on the 'Wye Target'.

In Petri dishes young leaves of wild hops were inoculated with PM strains of the *v1*, *vB*, *v3* type (E8 from England and HU62 from the Hallertau region) and the *v1*, *v2*, *v3*, *vB* virulence type (E10 from England), respectively. However, in 2004 isolate E10 lost its *v2* virulence. After three failed attempts to produce a new isolate carrying the *v2* virulence, finally in spring 2005 from infected leaves of 'Wye Target' from England we succeeded in producing an isolate expressing the *v1, v2, v3, v5, vB* virulence type. Employing this isolate E 11 we could test for *R2* and furthermore for *R5* based resistance for the first time.

In principle, only wild hops which had proven as being resistant in the greenhouse towards PM strains occurring in the Hallertau were re-tested for their reaction towards foreign PM virulences, but a lot more than the above mentioned 75 hops, which showed no symptoms of PM infection in the greenhouse, were tested. The reason for this was that in many cases the resistance screening in the greenhouse for a specific wild hop was not finished when leaves were taken for the detached leaf assay. Since former tests had confirmed the comparability of the reactions of plant leaves in the greenhouse or field tests to the results obtained by the detached leaf assay in the laboratory (5), PM strains predominant in the Hallertau, which had already been tested in the greenhouse, were not used once more for the screening in the laboratory.

In this way the costs of our resistance surveys could be kept at a reasonable level.

The reaction of young leaves of wild hops was assessed eight to ten days after inoculation with a specific PM strain. Wild hops with leaves showing no or very slight sporulation (no or 10–20 % of sporulation of the susceptible reference variety – see Table 4) were classed as resistant toward the PM strain used. Following this procedure, the leaves of approximately 645 individuals were tested in petri dishes from 2003 onwards. Each plant was tested at least twice before resistance or susceptibility was confirmed. Leaves of resistant wild hops were re-tested the following years.

3.4 Testing for powdery mildew resistance in the field

Later on, wild hops which had shown resistance in the greenhouse and in the laboratory were re-screened in specific hop yards under natural infection conditions with no chemical control of PM and Damson hop aphids and a minimum of pesticide control for downy mildew. Male hops were planted in a hop yard near Freising, while female individuals were grown near Hüll. Only in 2002 a sufficiently high PM infection pressure was observed in these fields and in the whole hop growing region. From 2003 till 2005 only very slight infections, even on susceptible cultivars, could be seen. Thus, reliable data for PM resistance in the field could only be obtained for 21 wild hops in the season 2002, when leaves and also cones could be scored for resistance to *P. macularis*. For other wild hops being collected and screened for resistance later than 2002 no field data under a sufficiently high infection pressure are available. Although there are only few field data available, so far resistance data obtained from leaves tested in the greenhouse could be confirmed for leaves and cones of wild hops grown in the hop yards in showing no infections on leaves and cones as well. In this way the reliability of resistance data collected under artificial infection conditions could be verified, at least for the reaction towards indigenous PM strains in the Hallertau area with their respective spectrum of virulence genes.

Resistance tests in the greenhouse and in the laboratory cannot replace field tests, especially when cone resistance should be che-

cked. But on the other side in years with low infection pressure the great benefits of the above mentioned resistance tests based on artificial inoculation of leaves in the greenhouse and in Petri dishes under standardized infection conditions are quite obvious.

3.5 New sources of resistance and their utilization

From 2003 onwards, 830 wild hops, which turned out to be resistant after the mass screening in germination trays, were tested in the greenhouse as single plants. In this way more than 3,600 resistance ratings could be obtained. In addition, around 2,500 ratings could be gained from 645 plants using the detached leaf assays in the laboratory of EpiLogic. Based on these data sets including the field data obtained from leaves and cones of 21 individuals, finally 54 wild hops could be identified as being resistant to all races of *P. macularis* characterized and available so far. Since these wild hops survived these screening procedures without any signs of PM infection or with only small spots of leaf decoloration as sign of defense it could be concluded that they possess new, so far not characterized resistance genes. Table 4 gives an overview of the various locations where resistant wild hops derived from. Based on the assumption that hop germplasm from regions which were unexploited in European or US breeding programs so far offer a greater chance of detecting new resistance genes, it was not astonishing that wild hops from Turkey, China and Japan proved to provide new sources of resistance. Even in Germany promising wild hops could be found. From more than 250 North American native hops tested between 2003 and 2005, the majority turned out to be resistant to the English strains of the *v1* and *v2* pathotype used in the detached leaf assays, while being susceptible to the Hallertau PM strains. Also among more than 300 Italian and 80 Austrian wild hops not a single plant could be identified which remained free of any infection in the greenhouse and in the laboratory.

All testing for PM resistance in wild hop germplasm will be continued. In the new screening season which started in February 2006 promising results could be obtained in detecting 21 recently collected wild hops from the USA and 16 from Germany which showed resistance to PM strains after several tests run in the greenhouse and the laboratory (Table 5).

In particular resistant wild hops from the USA collected by Anheuser-Busch, USA, from Missouri and native American hops provided by Dr. Kim Hummer, National Clonal Germplasm Repository, Oregon, USA, and the Japanese and Chinese germplasm sent by Dr. Murakami, Kirin, Japan, as well significantly increase our genetic resources in introducing new subvarieties of *Humulus lupulus* (3, 6). So far our Hüll breeding material was predominated by the European hop *Humulus lupulus* var. *lupulus* and by *H. lupulus* var. *lupuloides* (4) which is the native hop form of the eastern part of the USA, whereas the newly collected wild hops from the USA and Japan represent the other three subvarieties of hop: *H. lupulus* var. *neomexicanus* and var. *pubescens* from the western North America and the American Midwest, respectively, and *H. lupulus* var. *cordifolius* from Japan. Thus, it can be expected that these newly imported native hop germplasm reveals new promising traits and resistances besides PM resistance and in this way significantly broaden the genetic basis for our various breeding programs.

Those individuals showing resistance in all tests for several years are or will be used as crossing partners in our breeding programs to enlarge the genetic basis of PM resistance in our Hüll genetic resources. Certainly other selection criteria such as good agronomic characteristics, promising chemical data of the lupulin glands or broader resistance to other diseases increase the chance of a specific PM resistant wild hop for being used as a crossing partner.

Currently, research has been started to develop molecular markers for various resistance genes deriving from wild hops to increase the efficiency and reliability of testing for PM resistance in the Hüll germplasm. DNA markers will prove their special benefits when several resistance genes should be pyramided in one individual. Double or multiple resistance cannot be recognized on the phenotype, but can be proven by identifying several resistance markers within the genetic fingerprint of one plant. Resistance based on several genes is expected to confer a more durable protection against fungal infections.

4 Summary

Over the last years we succeeded in identifying resistance genes in wild hop germplasm which are conferring resistance to all virulent PM strains currently known and available. Approximately 15,000 wild hops collected from Europe, Asia, Australia, and North America were screened after artificial inoculation in the greenhouse for their reaction toward various PM isolates occurring in the Hallertau region. Subsequently, resistant hops were also tested for their reaction towards PM pathotypes non-indigenous in Germany by using the detached leaf assay in the laboratory. Field tests were also conducted, but the assessment of resistance under natural infection conditions in the fields was limited due to low infection pressure in the years from 2003 onwards. Nevertheless, reliable resistance data could be obtained by exploiting the two different screening systems in the greenhouse and the petri dish and by employing PM strains which encompass the whole spectrum of virulence genes known so far. Thus, after three years of comprehensive testing 54 wild hops could be identified which possess new, so far not characterized resistance genes. Screening for resistance in the wild hop germplasm will be continued in the greenhouse, laboratory and in the field. Those individuals showing resistance in all tests for several years will be used as crossing partners in our breeding programs to broaden the genetic basis of PM resistance in our Hüll genetic resources.

5 Acknowledgements

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Appendix

Table 1 **List of resistance genes in hop varieties and their corresponding virulence genes in PM strains which can overcome the action of the R genes**

differential hop variety	origin	hop resistance gene*	corresponding virulence gene in PM pathotypes	occurrence of PM pathotypes in Germany
Zenith	England	*R1, RB*	*v1, vB, v3*	low frequency
Wye Target	England	*R2*	*v2*	–
Wye Challenger	England	*R3, RB*	*v3, vB*	high frequency
Serebrianker	Russia	*R4*	*v4*	high frequency
Early Choice	England	*R5*	*v5*	low – medium high frequency
Nugget	USA	*R6*	*v6*	high frequency
Yeoman	England	*RB*	*vB*	high frequency

* designation according to Neve (3) and Darby (1, 2)

Table 2 **Virulence reaction of powdery mildew isolates on leaves of differential hop varieties carrying the hop resistance genes *R1 –R6*, and *RB;* R0 = no resistance gene; v = virulent**

PM isolate	virulence type	NB (R0)	Ze (R1,RB)	WT (R2)	WCh (R3, RB)	Se (R4)	EC (R5)	Nu (R6)	Yeo (RB)
HU9	v3,vB	v			v				v
BU10	v3,v4,v6,vB	v			v	v		v	v
BU13	v3,v4,v6,vB	v			v	v		v	v
ES1	v3,v4,v6,vB	v			v	v		v	v
HU62	v1,v3,vB	v	v		v				v
E8	v1,v3,vB	v	v		v				v
E10*	v1,v2,v3,vB	v	v	v*	v				v
E11	v1,v2,v3,v5,vB	v	v	v	v		v		v

Differential hop varieties: NB = 'Northern Brewer'; Ze = 'Zenith'; WT = 'Wye Target', WCh = 'Wye Challenger'; Se= 'Serebrianker'; EC = 'Early Choice'; Nu = 'Nugget'; Yeo = 'Yeoman';
In 2004 the English PM isolate E10* lost its effectiveness to infect hops with *R2* based resistance.

Table 3 Evaluation of powdery mildew resistance in the greenhouse

Scale	Development of powdery mildew on hop leaves
0*	no symptoms
1*	few spots of slight leaf decoloration as sign for defense reactions
2	very few, clearly visible infection spots, without mycelium
3	more frequent infection spots, none or hardly any mycelium
4	few infections, white mycelium with slight sporulation
5	blisters and many infections with mycelium formation and sporulation
6	many pustules with strong mycelium formation and sporulation
7	very many pustules and strong sporulation
8	very many pustules and strong sporulation, stem infected
9	extremely infected, growth of the plant affected

* classified as powdery mildew resistant

Table 4 Evaluation of PM resistance in the laboratory (detached leaf assay)

Scale	PM development on detached hop leaves in Petri dishes
0*	No symptoms
0.1*- 0.2*	10 – 20 % of sporulation of susceptible reference variety
0.3 – 0.6	30 – 60 % of sporulation of susceptible reference variety
0.7 – 0.9	70 – 90 % of sporulation of susceptible reference variety
1	strong sporulation, like susceptible reference variety**

* classified as powdery mildew resistant
** reference varieties showing high susceptibility to PM: 'Northern Brewer' or 'Hallertauer Magnum'

Table 5 Sources of PM resistance in wild hop germplasm based on tests conducted in the greenhouse and the laboratory over several year. Field data are only available for 21 wild hops

wild hop origin		number	sex
	Harburg	1	male
	Brunning	1	female
	Staudach	2	female
	Schweinfurt	3	female
	Kleinmachnow	1	male
Germany	Pirna	1	male
		1	female
	Peninsula Zingst	2	male
	Berlin	3	female
	Eifel	4	female
		6	male
Turkey	Bursa	4	female
		3	male
China /Japan	progeny from 4 female wild hops open pollinated in a Japanese breeding yard	15	female
		5	male
Sweden	Julita	1	female
New Zealand	unknown	1	female
Germany*	Neumarkt	16	?
USA*	Missouri	19	?
	Nebraska	2	?

* promising resistant wild hops based on one year's screening in the greenhouse and laboratory

Fig. 1 Heavy infection of powdery mildew on hop cones resulting in a total loss of yield and quality

Fig. 2 Testing of wild hop seedlings for powdery mildew resistance in the greenhouse

Fig. 3 Different reactions of three wild hops to powdery mildew in the greenhouse: vigorous sporulation and many pustules on the leaves of a highly susceptible plant (left; score 8 see Table 3), blisters and many infections with mycelium formation (in the middle; score 5) and no infection on the leaves of a PM resistant wild hop (right; score 0)

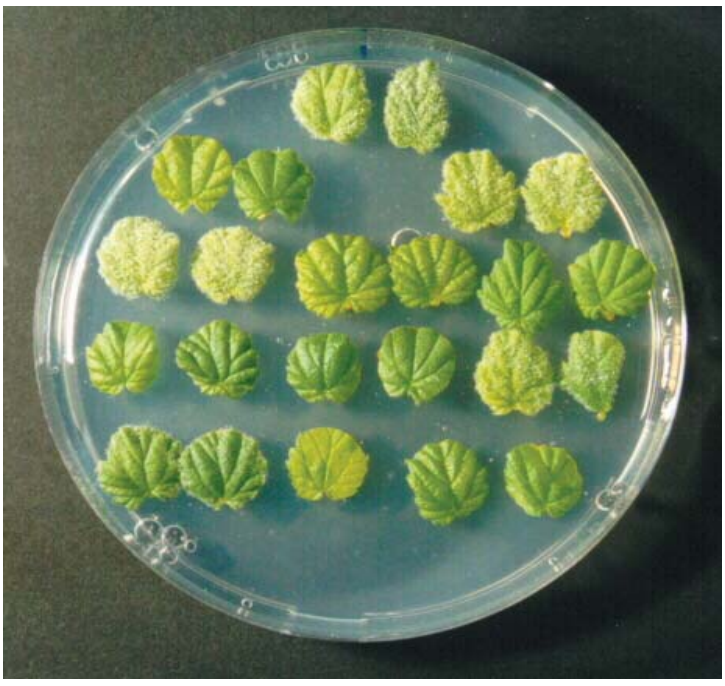

Fig. 4 Testing wild hops for their resistance to powdery mildew in the laboratory using the detached leaf assay