

A. Klinke · J. Müller · G. Wricke

## Characterization of nematode resistance genes in the section Procumbentes genus *Beta*: response to two populations of *Heterodera schachtii*

Received: 25 February 1996 Accepted: 8 March 1996

**Abstract** Three species of the section Procumbentes genus *Beta*, nine monosomic additions, and five translocation lines were tested for resistance to two *Heterodera schachtii* populations. Nematode population 129-v (129-virulent) was selected for virulence to resistance gene(s) transferred from chromosome 1 of *Beta procumbens* to the diploid resistant sugar beet KWS-NR 1. This population is considered to be a pathotype. The unselected sib population 129-av (129-avirulent) was reared continuously on fodder rape, *Brassica napus* cv Velox. Monosomic additions with chromosome 1 from the three species of the section Procumbentes were susceptible to population 129-v, regardless of the origin of the alien chromosome. Translocations with a gene(s) for resistance from chromosome 7 of *B. procumbens* and *B. webbiana* were also susceptible to the pathotype. However, a monosomic addition with chromosome 7 of *B. webbiana* was resistant to population 129-v. The three wild beets of the section Procumbentes, *Beta procumbens*, *Beta webbiana* and *Beta patellaris*, also were highly resistant to the two populations. The results indicate the existence of just two different major genes for resistance to *H. schachtii* in the entire Procumbentes section.

**Key words** Resistance · Sugar beet · Procumbentes · Virulence · *Heterodera schachtii*

### Introduction

High levels of resistance to the beet cyst nematode (*Heterodera schachtii* Schm.) have never been observed

in cultivated beet (*Beta vulgaris* L. ssp. *vulgaris* var. *altissima* Döll). Within the genus *Beta*, complete resistance is found exclusively in the three species of the section Procumbentes, *B. procumbens* Chr. Sm., *B. webbiana* Moq., and *B. patellaris* Moq. (Hijner 1952; Shepherd 1959). Some resistance to *H. schachtii* occurs in the sea beet (*B. vulgaris* ssp. *maritima* L.), but it is not complete and appears to be controlled by a polygenic and recessive genetic system (Heijbroek 1977; Mesken and Lekkerkerker 1988). Therefore, most attempts were made to transfer genes for resistance from wild species of the section Procumbentes to *B. vulgaris*. Savitsky (1975) was the first to produce monosomic additions, i.e. with an extra chromosome of *B. procumbens*, that were resistant to the beet cyst nematode. This material was used to transfer nematode resistance into the genome of cultivated beet (Savitsky 1975, 1978). The selected diploids (translocations) were highly resistant to *H. schachtii*; thus, Savitsky supposed a single dominant gene to be responsible for full nematode resistance. Further research programmes, especially in Europe, followed this approach to produce nematode-resistant beets (see also review by Lange et al. 1990), resulting in different resistant monosomic additions, fragment additions and translocations, from all the three species of the section Procumbentes (Speckmann and De Bock 1982; Heijbroek et al. 1983; Löptien 1984a; De Jong et al. 1986; Jung and Wricke 1987). Later approaches to transfer the alien genes for resistance to cultivated beet used molecular techniques (Jung et al. 1990, 1992; Salentijn et al. 1992; Klein-Lankhorst et al. 1994).

Morphological studies and isozyme analyses proved the existence of at least five different chromosomes with major resistance genes in the section Procumbentes: chromosome 1 of all three wild beets (pro-1, web-1, pat-1) and chromosome 7 of *B. procumbens* (pro-7) and *B. webbiana* (web-7) (Löptien 1984b; Lange et al. 1988; Van Geyt et al. 1988; Reamon-Ramos and Wricke 1992; Reamon-Büttner 1994). Another monosomic addition showing altered plant morphology but incomplete resistance has been described as 'Type c' (Jung et al. 1986;

Communicated by G. Wenzel

A. Klinke (✉) · J. Müller  
Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Nematologie und Wirbeltierkunde, Toppeideweg 88, 48161 Münster, Germany

G. Wricke  
Institut für Angewandte Genetik, Universität Hannover, Herrenhäuser Strasse 2, 30419 Hannover, Germany

Jung and Wricke 1987). The added chromosome was identified as chromosome 8 of *B. webbiana* (Reamon-Ramos and Wricke 1992; Reamon-Büttner 1994).

Virulence is defined as the ability of a particular genotype within a nematode species to multiply on certain plant cultivars (Müller 1989). Müller (1990) was the first to report virulence genes in *H. schachtii* populations breaking the resistance originating from *B. procumbens*. He was able to increase the low level of virulence genes occurring in common *H. schachtii* populations by continuous multiplication on a homozygous resistant diploid sugar beet. The selected nematode populations were virulent against a major resistance gene and, consequently, were considered to be a pathotype (Müller 1992). Using this pathotype, Lange et al. (1993) and Klinke (1995b) found differences between some sources of nematode resistance in the section Procumbentes.

The present study was aimed at characterizing genes in the section Procumbentes giving complete resistance to *H. schachtii*. In the sense of the definition given by Vanderplank (1984, 1986), plants carrying the resistance gene from chromosome pro-1 have a specific susceptibility to the pathotype. The results of Lange et al. (1993) and Klinke (1995a) presume more specific susceptibilities, or unspecific resistances, between plants with different resistance genes and the pathotype. Their occurrence would probably allow a judgement on the quality and specificity of the resistance genes of the section Procumbentes.

## Materials and methods

### Plant material

The plant material consisted of: (1) the three wild species of the section Procumbentes, *Beta procumbens* Chr. Sm. ( $2n = 18$ ), *Beta webbiana* Moq. ( $2n = 18$ ) and *Beta patellaris* Moq. ( $2n = 36$ ), (2) monosomic additions ( $2n = 19$ ) of beet, carrying different wild beet chromosomes with the gene(s) for resistance to the beet cyst nematode *Heterodera schachtii* (Table 1); and (3) diploid nematode-resistant lines. Table 2 presents the origin of the gene(s) for resistance in the diploid breeding stocks. The resistant plant materials were obtained from the Institute of Applied Genetics, University of Hannover, except for KWS-NR 1

**Table 1** Monosomic additions from wild beets of the section Procumbentes used in this study

Monosomic addition ( $2n = 19$ )	Added chromosome	Wild beet
12566 12644 12626	Chromosome 1	<i>Beta procumbens</i>
11191 11192	Chromosome 1	<i>Beta webbiana</i>
6019 14026	Chromosome 7	<i>Beta webbiana</i>
13033 13038	Chromosome 1	<i>Beta patellaris</i>

**Table 2** Diploid nematode-resistant beets used in this study

Diploid resistant beet ( $2n = 18$ )	Origin of the translocated gene(s)	Wild beet
KWS-NR 1 PRO 3	Chromosome 1 Chromosome 7	<i>Beta procumbens</i>
WEB 8 WEB 11	Chromosome 1 Chromosome 7	<i>Beta webbiana</i>

which was produced by KWS, Einbeck, Germany. Due to incomplete transmission of the extra chromosome carrying the gene(s) for resistance, the monosomic additions segregate into plants with or without the alien chromosome. The transmission rate of the chromosome has been reported to be 10–20% (Speckmann et al. 1985; Lange et al. 1990). Of the diploid resistant beets, only KWS-NR 1 is homozygous for resistance. The remaining diploids segregated for resistant and susceptible plants when pollinated with diploid susceptible sugar beets. The sugar beet variety 'Désirée' (A. Dieckmann-Heimburg, Nienstädt, Germany) and KWS-NR 1 served as susceptible and resistant controls, respectively.

### Nematode populations

The two nematode populations (129-av and 129-v) originated from population 129, which was collected and described by Müller (1992). Population 129-v (129-virulent) was selected for virulence by six multiplications on the diploid resistant sugar beet KWS-NR 1. The unselected sib population 129-av (129-avirulent) was reared on fodder rape, *Brassica napus* L. cv. Velox.

### Resistance tests

Test for resistance were done in a modified version of the method described by Toxopeus and Lubberts (1979). Young seedlings were transplanted into PVC tubes containing 96 ml of quartz sand, which was moistened with a nutrient solution. After 1 week each plant was inoculated with a suspension containing about 600 juveniles of *H. schachtii*. The plants were cultivated in a greenhouse at about 22°C. The first experiments with the accessions PRO 3 and WEB 11 were evaluated 4 weeks later by counting white females on the root surface. In subsequent experiments, the cysts were separated from the roots and sand by the centrifugation technique (Müller 1980), and the brown cysts were counted under a stereoscopic microscope at 10x magnification. Each experiment included the two nematode populations, as well as the susceptible control 'Désirée' and the resistant control KWS-NR 1.

The plant material was segregating, except for the breeding line KWS-NR 1 and the susceptible control. The data are presented as frequency distributions of cyst numbers per plant with a class width of ten cysts (see Fig. 1). Plants were considered resistant when they could clearly be differentiated from susceptible plants on the basis of the frequency distribution. In case of overlapping distributions only plants which were equal to, or had less than, the maximum cyst number found on the resistant control were considered to be resistant.

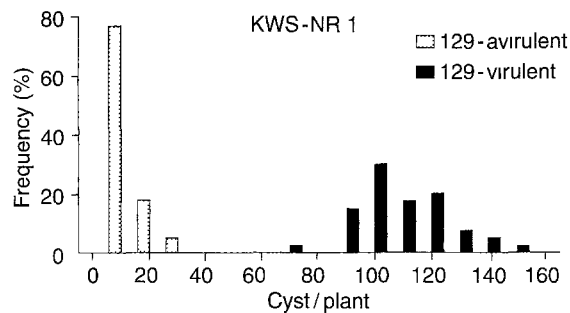
## Results

### Wild beet species

A total of 240 plants of the wild beet species *B. procumbens*, *B. webbiana* and *B. patellaris* were tested with the two nematode populations. Only six cysts were found

**Table 3** Mean ( $\bar{x}$ ), lowest (min), highest (max) numbers of cysts of *H. schachtii* and numbers of plants (*n*) in three wild beets, cv Désirée, and resistant sugar beet KWS-NR 1 tested with two nematode populations (129-avirulent, 129-virulent)

Plant material	129-avirulent				129-virulent			
	$\bar{x}$	Min	Max	<i>n</i>	$\bar{x}$	Min	Max	<i>n</i>
<i>Beta procumbens</i>	0.025	0	1	40	0.025	0	1	40
<i>Beta webbiana</i>	0.025	0	1	40	0.025	0	1	40
<i>Beta patellaris</i>	0.050	0	1	40	0.0	0	0	40
Désirée	108.3	67	159	40	115.7	58	148	40
KWS-NR 1	8.5	1	25	39	140.5	68	143	40

**Fig. 1** Frequency distributions of cysts per plant (class width = 10 cysts) on resistant KWS-NR 1 tested with two nematode populations

on six plants (Table 3), confirming the high resistance of these *Beta* species to the *H. schachtii* populations used.

#### Homozygous resistant line KWS-NR 1

On the homozygous resistant sugar beet KWS-NR 1, carrying the gene(s) for nematode resistance originating from chromosome 1 of *B. procumbens*, the two nematode populations could clearly be distinguished by two separate frequency distributions (Fig. 1). Average cyst numbers were low with population 129-av, whereas population 129-v gave a normal distribution with a minimum of 68 cysts per plant, and a mean similar to that of 'Désirée' (Table 3). The virulent *H. schachtii* population

was able to break the resistance from chromosome 1 of *B. procumbens*.

#### Resistance from chromosome 1

In Table 4 and Fig. 2 the results of three monosomic additions, 12626, 11191 and 13038, each carrying chromosome 1 of *B. procumbens*, *B. webbiana* and *B. patellaris*, respectively, are presented. Clear segregation in resistant and susceptible individuals was found in all monosomic additions when infected with nematode population 129-av. The frequencies of resistant plants were 20% for 12626, 14% for 11191 and 26% for 13038. When the virulent nematode population 129-v was used, no segregation could be observed in the monosomic additions 12626 and 13038. Although plants with the alien chromosome, carrying the gene(s) for resistance, must have been present, a clear distinction from susceptible plants was not possible. The resistance of plants with the chromosome 1 of *B. procumbens* and *B. patellaris* had been overcome by the virulent *H. schachtii* population.

The monosomic addition 11191 carrying chromosome web-1 gave a deviating result with population 129-v. About 15% of the plants produced cyst numbers which indicate neither resistance nor full susceptibility (Fig. 2). The virulent *H. schachtii* population only partially broke the resistance from chromosome web-1.

**Table 4** Mean ( $\bar{x}$ ), lowest (min), highest (max) numbers of cysts of *H. schachtii* and numbers of plants (*n*) of resistant and susceptible fractions in offspring of four monosomic additions in *Beta vulgaris*

Plant material		129-avirulent				129-virulent			
		$\bar{x}$	Min	Max	<i>n</i>	$\bar{x}$	Min	Max	<i>n</i>
12626	Resistant	14.3	5	21	16	—	—	—	—
	Susceptible	92.9	31	144	64	127.3	42	194	77
11191	Resistant	5.0	1	9	9	31.5	13	52	11
	Susceptible	113.1	78	181	54	123.7	89	185	60
13038	Resistant	10.3	0	23	21	—	—	—	—
	Susceptible	122.4	77	167	59	137.7	51	328	80
14026	Resistant	6.0	2	12	9	7.0	0	18	7
	Susceptible	129.9	27	183	62	162.6	106	235	62
PRO 3	Resistant	3.2	0	11	56	—	—	—	—
	Susceptible	52.3	26	97	54	34.3	8	71	110
WEB 11	Resistant	9.4	1	20	53	—	—	—	—
	Susceptible	63.9	23	107	57	36.0	11	62	110

and two diploid sugar beets, tested with two nematode populations (129-avirulent, 129-virulent)

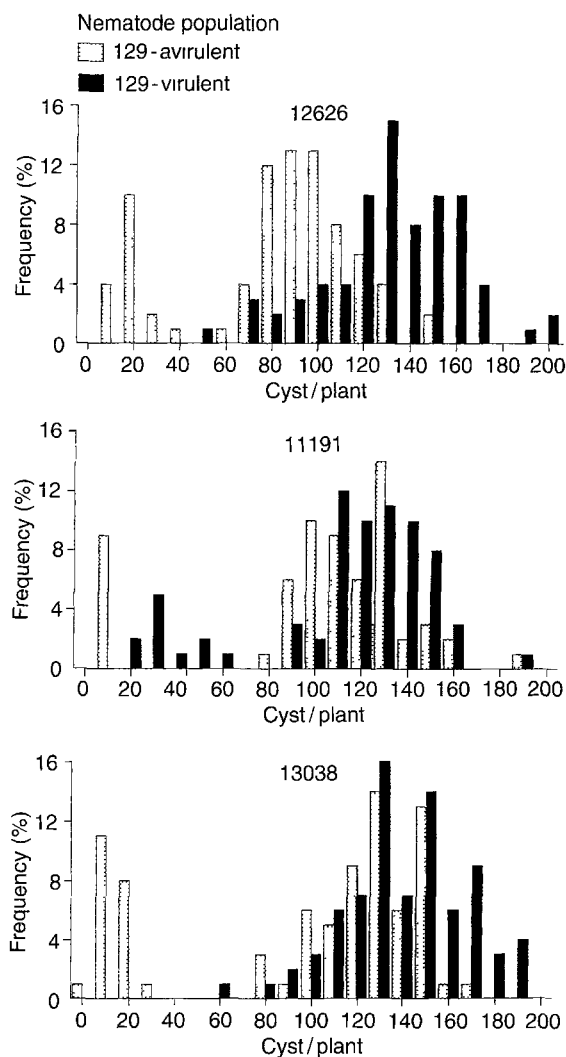


Fig. 2 Frequency distributions of cysts per plant (class width = 10 cysts) on three monosomic additions tested with two nematode populations

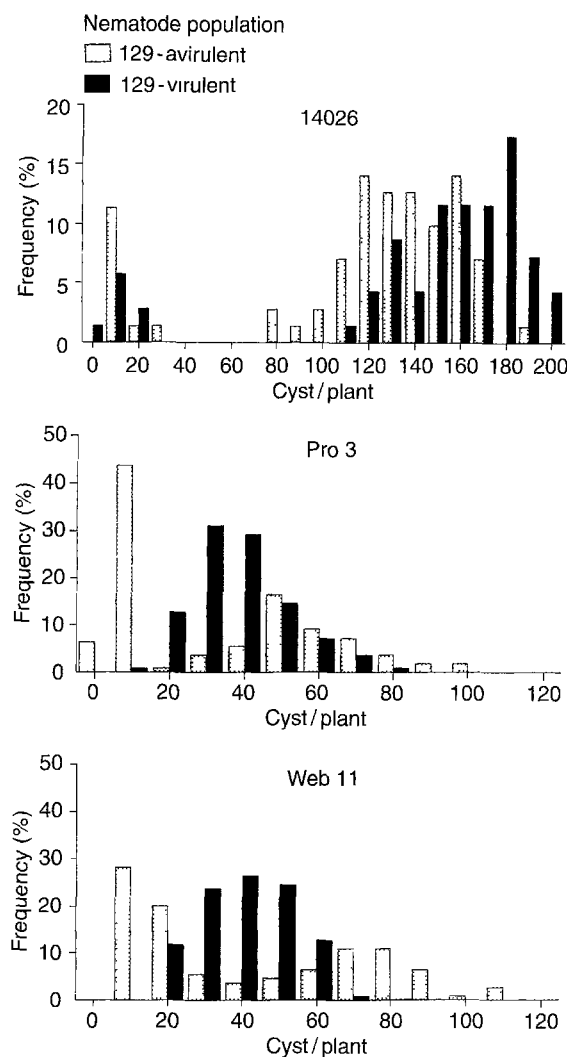


Fig. 3 Frequency distributions of cysts per plant (class width = 10 cysts) on monosomic addition 14026 and diploid resistant lines tested with two nematode populations

### Resistance from chromosome 7

The results for monosomic addition 14026, carrying chromosome 7 of *B. webbiana*, and the two diploid accessions, WEB 11 and PRO 3, carrying the gene(s) for resistance from chromosome 7 of *B. webbiana* and *B. procumbens*, respectively, are presented in Table 4 and Fig. 3. Plants with the added chromosome web-7 segregated into resistant and susceptible individuals when tested with the two nematode populations 129-av and 129-v. The proportions of resistant plants of breeding line 14026 were 12.7% and 10.1%, respectively. The virulent *H. schachtii* population did not break resistance from chromosome web-7.

The diploid accessions WEB 11 and PRO 3 were offspring of heterozygous resistant plants pollinated with susceptible sugar beets. They both segregated into resistant and susceptible plants when tested with the

nematode population 129-av (Fig. 3). In the case of WEB 11, plants with up to 20 cysts were considered resistant on the basis of the frequency distribution and consistency, with the expected segregation of 1:1 resistant to susceptible plants. Thus, the resistant plants of WEB 11 had a slightly lower degree of resistance than the resistant plants of PRO 3 (Table 4). No segregation could be observed when the diploid accessions were tested with 129-v. The plants carrying the gene(s) for resistance could not be distinguished from the susceptible ones, both in WEB 11 and PRO 3. Resistance from chromosome 7 of *B. procumbens* and *B. webbiana*, introgressed in the diploid accessions PRO 3 and WEB 11, respectively, had been overcome by the virulent *H. schachtii* population.

The resistance to the nematode population 129-v of the monosomic additions and the diploid accessions presented in Tables 1 and 2 is summarized in Table 5.

**Table 5** Susceptibility of monosomic additions and diploid beets with genes for resistance from wild beets of the section Procumbentes to the virulent nematode population. (X = susceptible; (X) = slightly susceptible; O = resistant; I = not available)

Source of resistance		Monosomic addition	Diploid beet
<i>Beta procumbens</i>	Chromosome 1	X	X
	Chromosome 7	O <sup>a</sup>	X
<i>Beta webbiana</i>	Chromosome 1	(X)	X
	Chromosome 7	O	X
<i>Beta patellaris</i>	Chromosome 1	X	I

<sup>a</sup> Results of Lange et al. (1993)

## Discussion

In the three species of the section Procumbentes there are six chromosomes known to carry genes for resistance to *H. schachtii* (Löptien 1984b; Jung and Wricke 1987; Van Geyt et al. 1988; Reamon-Ramos and Wricke 1992). The different genomes of the wild beets, specifically those of *B. procumbens* and *B. webbiana*, are supposed to be the same and consequently the different genes for resistance might be identical (Curtis 1968; Kishima et al. 1987; Fritsche et al. 1987; Mita et al. 1991; Wagner et al. 1989; Jung et al. 1992), but very little is known about the quality and specificity of these genes. In the present study, we were able to differentiate the sources of resistance through a pathotype (nematode population 129-virulent) of *H. schachtii*. Population 129-v was selected for virulence to a gene(s) for resistance from chromosome pro-1 on the diploid genotype KWS-NR 1. The pathotype was able to break the resistance on KWS-NR 1 and the resistance of all monosomic additions carrying chromosome 1, regardless of the origin of the chromosome. This is a strong indication of an identical, or a very similar, gene for resistance on chromosome 1 of all three wild beets of the section Procumbentes. There are probably no other resistance genes on chromosome 1 except in *B. webbiana*.

Similarities between *B. procumbens* to *B. webbiana* have been reported: Curtis (1968) suggested that *B. procumbens* and *B. webbiana* are two extremes of a single ecospecies, because of comparable morphological and physiological characters. The isozyme patterns do not show any differences between the two species (Wagner et al. 1989). The nine monosomic additions with chromosomes of *B. procumbens* and *B. webbiana*, respectively, can be characterized by nearly the same isozyme markers (Van Geyt et al. 1988; Reamon-Ramos and Wricke 1992; Reamon-Büttner 1994). Further similarities have also been described for the resistance of chromosome 1 from *B. procumbens* and *B. patellaris*. On the basis of molecular markers linked to the gene(s) for resistance, they appear to be identical (Jung et al. 1992;

Salentijn et al. 1992). The results of the resistance tests of Lange et al. (1993) support this assumption. Reamon-Ramos and Wricke (1992) suggest that earlier in evolution the three species of the section Procumbentes had the same basic complement, but that *B. patellaris* had undergone further polyploidization. The results of the present investigation confirm the idea of a common phylogenetic basis.

Jung et al. (1992) observed different arrangements of repetitive elements on resistance-bearing segments from chromosome 1 of *B. procumbens* and *B. webbiana*, present in two translocation lines. This might explain the slightly lower susceptibility of monosomic additions carrying chromosome web-1 to the pathotype, caused by mutations of the resistance gene on chromosome 1 of *B. webbiana*. The existence of a second resistance gene might be an alternative explanation.

Chromosome 7 is another chromosome in *B. procumbens* and *B. webbiana* carrying a gene(s) for resistance (Van Geyt et al. 1988; Reamon-Ramos and Wricke 1992). Monosomic additions with chromosome 7 are phenotypically described as b-type (Löptien 1984b). Müller et al. (1992) and Lange et al. (1993) had already demonstrated in resistance tests that chromosome pro-7 carries at least one gene for resistance which is different from that on chromosome pro-1. The results obtained with monosomic addition 14026 indicate the same situation in *B. webbiana*. In addition to the morphological similarity of monosomic additions carrying chromosome 7 from *B. procumbens* and *B. webbiana* (Löptien 1984b; Speckmann et al. 1985), they both show a coincidentally high resistance to the pathotype. This is another indication of homology between chromosome 7 from the two wild beets.

The susceptibility of translocation lines PRO 3 and WEB 11 to the population 129-v provides evidence that these lines carry the same, or a very similar, resistance gene as KWS-NR 1. The gene for resistance of PRO 3 and WEB 11 originated from chromosome 7 of *B. procumbens* and *B. webbiana*, respectively, and monosomic additions with the complete alien chromosome are resistant to the pathotype. This leads to the conclusion that chromosome 7 carries more than one gene for resistance. Lange et al. (1993) postulated the existence of one gene for resistance on chromosome pro-7 different from that on chromosome pro-1. There is now strong evidence that there is a resistance factor on chromosome 7, in addition to a major gene which occurs identically on chromosome 1 and on chromosome 7. Nakamura et al. (1991) proposed the existence of a minor gene(s) conferring weak resistance or a gene(s) modifying the level of expression of the major resistance genes in wild beets of the section Procumbentes. At this stage of analysis, it is not possible to decide whether there are two independent genes providing strong resistance, or if there is a minor gene modifying one major gene on chromosome 7.

The observed differences in the level of resistance to the unselected population 129-av between PRO 3 and

WEB 11, as well as between the monosomic additions, might be due to the different genetical background of the plant material. However, the high level of resistance of the three wild species of the section Procumbentes is in agreement with the results of previous studies (e.g. Hijner 1952; Golden 1958, 1959). Even the pathotype produces only very few cysts on *B. procumbens* and *B. patellaris*, which is presumably due to the combined action of different genes in one plant (Lange et al. 1993). Due to the low level of cyst formation on *B. webbiana*, this assumption can be applied to all three species of the section Procumbentes.

The results of the resistance tests indicate an identical, or very similar, gene for resistance to *H. schachtii* on five different chromosomes in the section Procumbentes. Chromosomes 7 of *B. procumbens* and *B. webbiana* carry more resistance genes, but they might be identical because of the homology of the two chromosomes. Further resistance information can be expected in *B. patellaris*, but it also might be analogous to the gene(s) on chromosome 7 of *B. procumbens*, and *B. webbiana*, because of the demonstrated similarity of chromosome 1 of the three wild beets. The additional information on chromosome 1 of *B. webbiana* does not provide evidence of a strong resistance. Presumably, in the section Procumbentes there occur only two different genes giving strong resistance to *H. schachtii*.

**Acknowledgements** Thanks are due to the KWS, Kleinwanzlebener Saatzucht, Einbeck, Germany and the Dieckmann-Heimburg Saatzucht, Nienstadt, Germany for providing the seed. The authors are grateful to Dr. S. M. Reamon-Büttner for her comments and critical reading the manuscript. The financial support of the Gemeinschaft zur Förderung der privaten deutschen landwirtschaftlichen Pflanzenzüchtung e.V. (GFP), is gratefully acknowledged.

## References

- Curtis GJ (1968) Observation of fruit shape and other characters in the species of the section *Patellares*, genus *Beta*. *Euphytica* 17: 485–491
- De Jong JH, Speckmann GJ, De Bock ThSM, Lange W, Van Voorst A (1986) Alien chromosome fragments conditioning resistance to beet cyst nematode in diploid descendants from monosomic additions of *Beta procumbens* to *Beta vulgaris*. *Can J Genet Cytol* 28: 439–443
- Fritsche K, Metzlaß M, Melzer R, Hagemann R (1987) Comparative restriction endonuclease analysis and molecular cloning of plastid DNAs from wild species and cultivated varieties of the genus *Beta*(L.). *Theor Appl Genet* 74: 589–594
- Golden AM (1958) Interrelationships of certain *Beta* species and *Heterodera schachtii*, the sugar-beet nematode. *Plant Dis Rep* 42: 1157–1162
- Golden AM (1959) Susceptibility of several *Beta* species to the sugar-beet nematode (*Heterodera schachtii*) and root-knot nematodes (*Meloidogyne* spp.) *J Am Soc Sugar Beet Technol* 10: 444–447
- Heijbroek W (1977) Partial resistance of sugarbeet to beet cyst eelworm (*Heterodera schachtii* Schm.). *Euphytica* 26: 257–262
- Heijbroek W, Roelands AJ, De Jong JH (1983) Transfer of resistance to beet cyst nematode from *Beta patellaris* to sugar beet *Euphytica* 32: 287–298
- Hijner JA (1952) De gevoeligheid van wilde bieten voor het bietencystenaaltje (*Heterodera schachtii*). *Meded Inst v Rationele Suikerproductie* 21: 1–13
- Jung C, Wricke G (1987) Selection of diploid nematode-resistant sugar beet from monosomic addition lines. *Plant Breed* 98: 205–214
- Jung C, Wehling P, Löptien H (1986) Electrophoretic investigations on nematode-resistant sugar beets. *Plant Breed* 97: 39–45
- Jung C, Kleine M, Fischer F, Herrmann RG (1990) Analysis of DNA from a *Beta procumbens* chromosome fragment in sugar beet carrying a gene for nematode resistance. *Theor Appl Genet* 79: 663–672
- Jung C, Koch R, Fischer F, Brandes A, Wricke G, Herrmann RG (1992) DNA markers closely linked to nematode resistance genes in sugar beet (*Beta vulgaris* L.) mapped using chromosome additions and translocations originating from wild beets of the Procumbentes section. *Mol Gen Genet* 232: 271–278
- Kishima Y, Mikami A, Hirai A, Sugiura M, Kinoshita T (1987) Beta chloroplast genomes: analysis of fraction-I protein and chloroplast DNA variation. *Theor Appl Genet* 73: 330–336
- Klein-Lankhorst RM, Salentijn EMJ, Dirkse WG, Arens-de Reuver M, Stiekema WJ (1994) Construction of a YAC library from a *Beta vulgaris* fragment addition and isolation of a major satellite DNA cluster linked to the beet cyst nematode resistance locus *Hs1<sup>pat-1</sup>*. *Theor Appl Genet* 89: 426–434
- Klinke A (1995a) Characterization of resistance genes in the genus *Beta* with a virulent *Heterodera schachtii* population. *Nematologica* 41: 317
- Klinke A (1995b) Untersuchungen zur Resistenz gegen *Heterodera schachtii* in der Sektion Procumbentes der Gattung *Beta* sowie zur Virulenz des Nematoden. Dissertation Universität Hannover
- Lange W, De Bock ThS, Van Geyt JPC, Oléo M (1988) Monosomic additions in beet (*Beta vulgaris*) carrying extra chromosomes of *B. procumbens*. II. Effects of the alien chromosomes on in vivo and in vitro plant development. *Theor Appl Genet* 76: 656–664
- Lange W, Jung C, Heijbroek W (1990) Transfer of beet cyst nematode resistance from *Beta* species of the section *Patellares* to cultivated beet. *Proc 53rd Winter Congr Int Inst Sugar Beet Res, Brussel*. pp 89–102
- Lange W, Müller J, De Bock ThSM (1993) Virulence in the beet cyst nematode (*Heterodera schachtii*) versus some alien genes for resistance in beet. *Fundam Appl Nematol* 16: 447–454
- Löptien H (1984a) Breeding nematode-resistant beets. I. Development of resistant alien additions by crosses between *Beta vulgaris* and wild species of the section *Patellares*. *Z Pflanzenzücht* 92: 208–220
- Löptien H (1984b) Breeding nematode-resistant beets. II. Investigations into the inheritance to *Heterodera schachtii* Schm. in wild species of the section *Patellares*. *Z Pflanzenzücht* 93: 237–245
- Mesken M, Lekkerkerker B (1988) Selectie op partiele resistentie tegen het bietencystenaaltje in kruisingen van suiker- en voederbieten met *B. maritima* Prophyta (bijlage januari). 68–71
- Mita G, Dam M, Casciari P, Pasquali A, Selva E, Minganti C, Piccardi P (1991) Assessment of the degree of genetic variation in beet based on RFLP analysis and the taxonomy of *Beta*. *Euphytica* 55: 1–6
- Müller J (1980) Ein verbessertes Extraktionsverfahren für *Heterodera schachtii* Nachrichtenbl Deut Pflanzenschutz 32: 21–24
- Müller J (1989) Zur Definition von Resistenz und anderer Fachbegriffe in der Nematologie. *Nachrichtenbl Deut Pflanzenschutz* 41: 137–139
- Müller J (1990) Virulenzunterschiede bei *Heterodera schachtii* gegenüber resistenten *Beta*-Rüben- und -Zuckerrüben. *Mitt a d Biol Bundesanst.* Heft 266: 455
- Müller J (1992) Detection of pathotypes by assessing the virulence of *Heterodera schachtii* populations. *Nematologica* 38: 50–64
- Müller J, De Bock ThSM, Lange W (1992) Virulenz von *Heterodera schachtii*-Populationen gegenüber verschiedenen Resistenzgenen in der Gattung *Beta*. *Mitt a d Biol Bundesanst.* Heft 283: 285
- Nakamura C, Skaracis GN, Romagosa I (1991) Cytogenetics and breeding in sugar beet. In: Tsuchiya T, Gupta PK (eds) *Chromosome engineering in plants: genetics, breeding, evolution*, Elsevier Science Publishers, Amsterdam, pp 295–314

- Remon-Buttner SM (1994) Genomorganisation, verwandtschaftliche Beziehungen und genetische Diversität von Wildruben in den Sektionen Procumbentes, Corollinae und Nanae. Dissertation Universität Hannover
- Reamon-Ramos SM, Wricke G (1992) A full set of monosomic addition lines in *Beta vulgaris* from *Beta webbiana*. morphology and isozyme markers. Theor Appl Genet 84: 411–418
- Salentijn EMJ, Sandal NN, Lange W, De Bock ThSM, Krens FA, Marker KA, Stiekema WJ (1992) Isolation of DNA markers linked to a beet cyst nematode resistance locus in *Beta patellaris* and *Beta procumbens*. Mol Gen Genet 235: 342–440
- Savitsky H (1975) Hybridization between *Beta vulgaris* and *Beta procumbens* and transmission of nematode (*Heterodera schachtii*) resistance to sugar beet. Can J Genet Cytol 17: 197–209
- Savitsky H (1978) Nematode (*Heterodera schachtii*) resistance and meiosis in diploid plants from interspecific *Beta vulgaris* × *B. procumbens* hybrids. Can J Genet Cytol 20: 177–186
- Shepherd AM (1959) The invasion and development of some species of *Heterodera* in plants of different host status. Nematologica 4: 253–267
- Speckmann GJ, De Bock ThSM (1982) The production of alien monosomic additions in *Beta vulgaris* as a source for the introgression of resistance to beet root nematode (*Heterodera schachtii*) from *Beta* species of the section *Patellares*. Euphytica 31: 313–323
- Speckmann GJ, De Bock ThSM, De Jong JH (1985) Monosomic additions with resistance to beet cyst nematode obtained from hybrids of *Beta vulgaris* and wild *Beta* species of the section *Patellares*. I. Morphology, transmission and level of resistance. Z Pflanzenzücht 95: 74–83
- Toxopeus HJ, Lubberts JH (1979) Breeding for resistance to the sugar beet nematode (*Heterodera schachtii* Schm.) in cruciferous crops. Eucarpia "Cruciferae 1979" Conference, Wageningen, The Netherlands, p 151
- Van Geyt JPC, Oleo M, Lange W, De Bock ThSM (1988) Monosomic additions in beet (*Beta vulgaris*) carrying extra chromosomes of *Beta procumbens*. I. Identification of the alien chromosomes with the help of isozyme markers. Theor Appl Genet 76: 577–586
- Vanderplank JE (1984) Disease resistance in plants, 2nd edn. Academic Press, Orlando, Florida
- Vanderplank JE (1986) A reply to LE Browder and MG Eversmeyer. Phytopathology 76: 382
- Wagner H, Gimbel EM, Wricke G (1989) Are *Beta procumbens* Chr Sm and *Beta webbiana* Moq different species? Plant Breed 102: 17–21