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The effect of different levels of beet cyst nematodes (*Heterodera schachtii*) and beet necrotic yellow vein virus (BNYVV) on single and double resistant sugar beet cultivars

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Abstract

Beet cyst nematode-resistant cultivars, which were introduced recently, originated from the homozygous inbred line B883. This translocation product was unstable and the transmission of resistance when crossed with a susceptible cultivar did not exceed 94%. Tests with the resistant cultivars in climate cabinets showed a wide variety of resistance against *Heterodera schachtii* and beet necrotic yellow vein virus (BNYVV), expressed as average numbers of infective units per plant and percentages of resistant plants. In a series of field trials at different levels of infection of *H. schachtii*, their multiplication rates on all resistant cultivars depended on the initial density, which was caused by the presence of small numbers of susceptible plants. Since tolerance to wilting was also incorporated in B883, reasonable yields were obtained in the presence of *H. schachtii*. However, at increasing initial densities of *H. schachtii*, yields decreased considerably, since penetrating juveniles cause a hypersensitivity reaction in resistant plants. Based upon the results of three series of field trials, it was concluded that resistant cultivars should preferably be applied at population densities between 500 and 2000 eggs and juveniles of *H. schachtii* per 100 ml of soil. Cultivars with double resistance against *H. schachtii* and BNYVV behaved like those with *H. schachtii* resistance in soils infected with beet cyst nematodes, but not with BNYVV. In soils with a combined infection of *H. schachtii* and BNYVV double resistant cultivars were far superior to single resistant ones, since damage caused by BNYVV was far more serious than damage caused by *H. schachtii*. No substantial interaction between soil pathogens nor types of resistance could be detected.

Introduction

The three wild *Beta* species of the section Procumbentes possess major genes for resistance against the beet cyst nematode *Heterodera schachtii*. Hybrids between these wild beet species and *Beta vulgaris* were produced by De Jong et al. (1985), Heijbroek et al. (1983), Lange et al. (1990), Savitsky (1973) and Speckmann et al. (1985). This resulted in several monosomic addition lines with different genes for resistance originating from *B. webbiana*, *B. patellaris* and *B. procumbens*. Savitsky (1975) obtained the first translocation product with a chromosome fragment originating from *B. procumbens*. This translocation product was unstable, but after recurrent selection a homozygous inbred line was obtained (Yu, 1984). However, this inbred line showed an extensive hypersensitivity reaction, which prevented the formation of a good tap root on soils infected by *H. schachtii*. As a result, the material released by McFarlane in 1981, was suitable only as a trap crop.

To avoid this problem, a Dutch research group (Lange et al., 1990) used pollinators selected for wilting tolerance and a vigorous root growth (Heijbroek et al., 1977) and screened for tolerance to the hypersensitivity reaction in the translocation product. Among

the many diploid nematode-resistant introgression products only a few were sufficiently stable and viable (Jung and Wricke, 1987).

All beet cyst nematode-resistant sugar beet cultivars, produced by the breeding companies and already registered in several countries, originated from the homozygous sugar beet B883, released in 1986 (Heijbroek et al., 1988). This material had a fragment of chromosome 1 for beet cyst nematode resistance from *B. procumbens* incorporated distally (De Jong et al., 1981). Although this introgression product was homozygous for resistance, the transmission was not more than about 94%, since in a small part of the plants the resistance gene was lost during irregular meiosis. This means nematode multiplication rates (P_f/P_i) were higher than in a completely resistant population and depended on the initial population density (P_i) of *H. schachtii*.

Genes for tolerance to wilting and to the hypersensitivity reaction were incorporated in the homozygous B883. The progeny showed improved root growth and less damage caused by invading juveniles. This is the reason why the offspring, after back-crossing with different commercial inbred lines, showed a good root-production capacity (Heijbroek, 1991).

It was not known in how far sugar yield and quality parameters of this combined beet cyst nematode resistance and wilting tolerance responded to different initial population densities (P_i). Therefore trials had to be laid on fields with a range of different *H. schachtii* infection levels. Since combined infections of beet cyst nematodes (*H. schachtii*) and beet necrotic yellow vein virus (BNYVV) occur frequently in all major sugar beet growing areas in Europe, double resistant varieties were developed. Resistance against BNYVV is not completely stable, since low numbers of susceptible plants occur, but can be managed more easily than *H. schachtii* resistance. The proportion of partially susceptible plants in the population is restricted to a maximum of 2% under field conditions (Bürcky and Büttner, 1991) and these plants showed a delayed replication of BNYVV, which did not seriously affect sugar production. The most important risk is the loss of beet cyst nematode resistance during large-scale seed production and recurrent selection for resistance has to be carried out for every generation.

The major questions to be solved are:

- how will beet cyst nematode-resistant sugar beet cultivars behave in fields with different degrees of initial infections (P_i) and to what extent will the multiplication rates of *H. schachtii* be reduced?
- what will be the response of double resistant cultivars to mixed infections of *H. schachtii* and BNYVV?

Materials and methods

Testing single and combined resistance against H. schachtii *and BNYVV in the climate cabinet*

Cysts of *H. schachtii* were collected and hatched in root diffusate of oil seed rape (Maas and Heijbroek, 1982). The second stage juveniles were suspended in water and about 500 were inoculated in 50 ml units with sugar beet plants at the two-leaf stage, grown in silver sand and a nutrient solution (Yu et al., 1999). Seeds were drilled in 120 units per container and two containers were randomly placed in the climate cabinet at 22/15 °C and light of 20,000 lux for 16 h per day. After six weeks the plants were harvested and the newly formed cysts on the root system were counted.

For the characterisation of BNYVV resistance, the cultivars were planted in sand and transplanted during the two-leaf stage in soil originating from Nagele (A type; mpn = circa 60 i.u. BNYVV/100 g of soil). 96 plants were grown in four replicates of 24 soil filled pipes (Heijbroek et al., 1999). After six weeks, the plants were harvested and the fresh weight of the roots and their BNYVV content were determined. By running a dilution series of purified BNYVV the actual virus content could be calculated (Alderlieste and Van Eeuwijk, 1992). The average number of cysts and the content of BNYVV per plant were expressed as percentages of the susceptible standard.

Two series of trials were conducted with three cultivars with a single *H. schachtii* resistance (N), four with a double resistance (RN) and four with a single BNYVV resistance (R). The cultivars with a single *H. schachtii* resistance were not put in the BNYVV test and vice versa.

The following sugar beet cultivars or experimental lines were used:

- susceptible standard A001.
- beet cyst nematode-resistant cultivars E001, E002 and E003.
- rhizomania-resistant cultivars B006, B008, B012 and B015.
- beet cyst nematode- and rhizomania-resistant cultivars M002, M004, M008 and M009.

The samples originated from seed lots of cultivars put forward for the official variety trials and selected to represent a wide range of resistance levels.

Trial fields with different initial densities of H. schachtii

From fields infected with *H. schachtii* soil samples were taken in blocks of circa 0.3 ha. The samples consisting of 20 cores were dried and sub-samples of 2×100 ml were extracted by the centrifugation method (Coolen, 1979). All cyst forming nematodes were identified and after crushing the cysts, eggs and juveniles were counted in a potter homogeniser.

According to the results of the soil sample analyses, fields were selected with *H. schachtii* densities ranging from *circa* 500–10,000 eggs and juveniles per 100 ml of soil. The minimal range of densities per field was 2000 eggs and larvae. The plot size was 3×15 m^2 and depending from the distribution pattern of the nematodes 16–24 plots were laid per cultivar in a random block design. Soil samples of 20 cores were taken and analysed from all plots before and after cropping. P_f / P_i ratios from all trial fields in the same year were plotted against P_i. This could be done because physical soil conditions do not have a substantial influence on multiplication rates (Heijbroek, 1996), as weather conditions during spring and early summer are highly determining (Heijbroek and Withagen, 1997).

During the summer, wilting symptoms were recorded. At harvest, root yield and contents of sucrose Na, K and α-amino N were determined according to standard procedures (de Bruijn and Vermeulen, 2001). The results in terms of multiplication rates (P_f / P_i) and sugar yields were plotted against P_i. Regression analysis was carried out using the general linear models directive in Genstat.

The following sugar beet cultivars or experimental lines were used:

- susceptible standard A001.
- beet cyst nematode-resistant cultivars E001, E002 and E003.
- beet cyst nematode- and rhizomania-resistant cultivars M002 and M009.

Trial fields with different combinations of single initial infections of H. schachtii *and BNYVV in one field*

In the same period, trials were laid in fields with single moderate to very severe infections of *H. schachtii*, combined with BNYVV infections. The latter were estimated by applying a bio-assay on two dilutions of soil samples (10× and 100×) in ten replicates and determining the percentages of BNYVV positive plants after six weeks growth in a greenhouse (Tuitert, 1990). The trial fields had a plot size of 3×15 m^2 and were laid in 6 replicates per cultivar in a random block design. The degree of infestation was judged by observing symptoms in the field on the susceptible standard (A001) and the level of Na and sucrose content at harvest. The categories light, moderate and severe were distinguished. During spring and summer symptoms of BNYVV and wilting caused by beet cyst nematodes were recorded. At harvest, root yield and contents of sucrose, Na, K and α-amino N were determined according to standard procedures (de Bruijn and Vermeulen, 2001).

The following sugar beet cultivars or experimental lines were used:

- susceptible standard A001.
- beet cyst nematode-resistant cultivars E001, E002, E003 and E004.
- BNYVV-resistant cultivars B001, B003, B005, B008 and B012.
- beet cyst nematode- and rhizomania-resistant cultivars M002, M003, M004, M005 and M009.

Results

Determining characteristics of resistance in climate cabinet trials

From two series of trials a compilation is made in Table 1.

In all beet cyst nematode-resistant (N and RN) cultivars except one (M009), an inverse correlation was observed between the relative number of newly formed cysts on the roots and the percentage of resistant plants. The cultivar M009, however, had a low number of newly formed cysts combined with a relatively low percentage of resistant plants.

An inverse correlation was also observed between relative BNYVV content and the percentage of BNYVV-resistant plants in rhizomania-resistant cultivars (R and RN) with the same exception. The average relative virus content of M009 was somewhat higher and the percentage of resistant plants was lower than that of the other BNYVV-resistant cultivars.

Two double resistant cultivars, M002 and M004, had not lost any *H. schachtii* or BNYVV resistance as compared to the best cultivars with single resistance. On the contrary, M008 showed less resistance to both *H. schachtii* and BNYVV.

Table 1. Characteristics of cultivars with resistance against *H. schachtii* (N type) and/or BNYVV (R type) in a climate cabinet test, as compared to the susceptible standard A001

Cultivar	Type of resistance	*H. schachtii*		BNYVV	
		Relative number of cysts/plant[a]	Percentage resistant plants[b]	Relative virus content[c]	Percentage resistant plants[d]
A001		100 d*	0 a	100 a	0 a
E003	N	25 bc	56 c	—	—
E001	N	15 ab	69 cd	—	—
E002	N	8 a	73 d	—	—
B006	R	—	—	32 b	43 c
B008	R	—	—	24 bd	47 c
B012	R	—	—	8 c	70 d
B015	R	—	—	12 c	68 d
M002	R N	14 ab	70 cd	8 c	74 d
M004	R N	7 a	73 d	10 c	65 d
M008	R N	35 c	19 b	44 e	2 a
M009	R N	9 a	57 c	18 bd	27 b

[a]100 = 69; [b]less than 3 cysts/root; [c]100 = 456 ng/ml; [d]less than 0.56 ng/plant.
*Figures in a column followed by the same letter do not differ significantly at $P = 0.05$.

Multiplication rates (P_f/P_i) of H. schachtii *in field trials*

Average values of P_f/P_i and P_i ranges were plotted against each other as shown in the Figures 1a–c. A logarithmic model best fits the data for the susceptible standard cultivars and the *H. schachtii* resistant cultivars with a high multiplication rate at low P_i. In 1998, all resistant cultivars behaved similarly (Figure 1a). The most striking differences were observed between resistant and susceptible cultivars at low P_i.

In 1999, the multiplication rates were much higher (Figure 1b) and significant differences could be detected between some resistant cultivars. Again the differences between resistant and susceptible cultivars were maximal at low P_i.

In 2000, no soil samples could be taken from the original field with a range of *H. schachtii* densities at St. Philipsland because of extreme weather conditions. Therefore, data from five other field trials with single initial densities of *H. schachtii*, ranging from 900–41,000 eggs and juveniles per 100 ml of soil, were used. As can be seen in Figure 1c the multiplication rate of the susceptible standard was considerably less than in the preceeding years and in the two resistant cultivars E001 and E002 P_f/P_i did not exceed 0.5. The results for M002 were variable, because this cultivar was significantly less resistant in most trials.

In all three years, the differences in multiplication rates between the resistant varieties and susceptible standard decreased at increasing P_i. Incidentally, differences between the resistant cultivars were detected.

The effect of initial infection on sugar yield

In one field trial at Achthuizen 1998, the sugar yield at harvest was plotted against initial infections with *H. schachtii* for the different cultivars (Figure 2a). In this field, the range of P_i was relatively narrow and small numbers of plots were situated at low P_i.

For all three cultivars, the sugar yield decreased linearly with an increasing logarithmically transformed P_i and no statistical differences in the slopes of the lines was detected. The data of a field trial at St. Philipsland in 1999 (Figure 2b) showed a similar correlation, but here the slope of the line for the susceptible cultivar A001 deviated significantly from E001, but not from the other two. This time, the range of P_i values was wider (from *circa* 100–3000 eggs and juveniles per 100 ml of soil) with a sufficient number of plots at low P_i. In one part of the trial field, a few isolated plants showed symptoms of BNYVV during August, but they did not affect sugar yield, as could be deduced from the sucrose and Na content.

In 2000 (St. Philipsland) the range of initial populations (P_i) was smaller, which resulted in lower correlation coefficients. Similar to 1998, no differences between the slopes of all varieties were detected. For the first time in soil samples of this trial field a

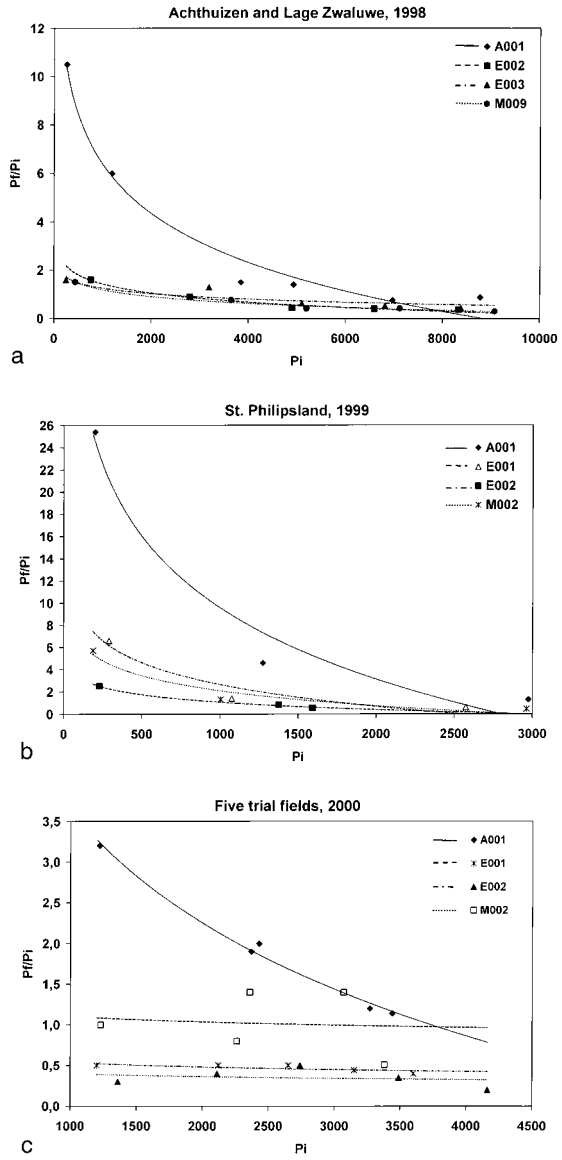

Figure 1. Initial infection (P_i) and multiplication rate (P_f/P_i) of *H. schachtii* on resistant sugar beet cultivars in field trials. (a) Achthuizen and Lage Zwaluwe, 1998. A001 (susceptible standard), E002, E003 and M009. (b) St. Philipsland, 1999. A001 (susceptible standard), E001, E002 and M002. (c) Achthuizen, Oud Beijerland, Lage Zwaluwe, St. Maartensdijk and St. Philipsland, 2000. A001 (susceptible standard), E001, E002 and M002.

considerable quantity of BNYVV was detected, which caused disease symptoms in plants from the end of June onwards. For E001, this resulted in a considerable loss of root yield and sucrose content, even when compared to the susceptible standard A001. No interaction

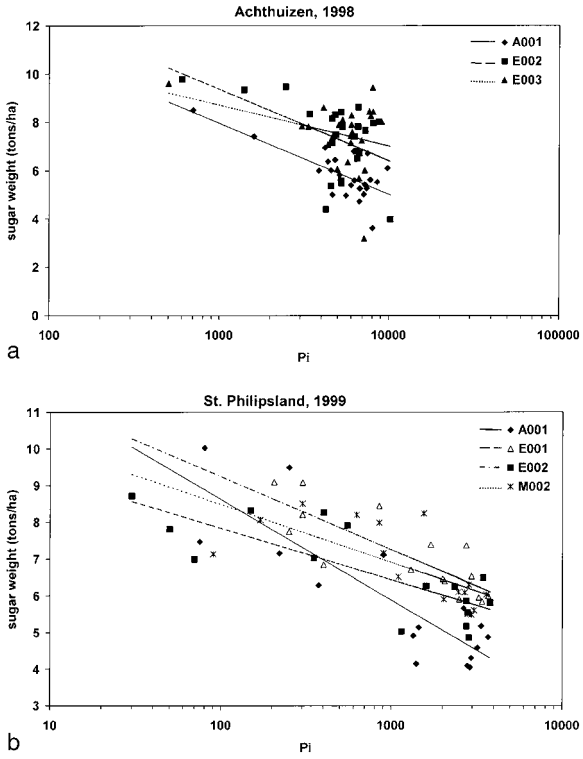

Figure 2. The correlation between initial infection (P_i) of *H. schachtii* and sugar yields of resistant sugar beet cultivars in field trials. P_i is logarithmically transformed. (a) Achthuizen 1998. A001 (susceptible standard), E002 and E003. (b) St. Philipsland 1999. A001 (susceptible standard), E001, E002 and M002.

between P_i of *H. schachtii* and BNYVV was detected, since the slopes of double resistant cultivars did not differ significantly from those of the others.

Trials on fields with one population level of H. schachtii *or BNYVV alone or in different combinations*

In a series of field trials, cultivars were compared at one level of infection with *H. schachtii* per field alone or in combination with different degrees of rhizomania infection.

Two extreme effects of single *H. schachtii* infections are presented. At Achthuizen 1998 (Figure 3a) the initial population (P_i) of *H. schachtii* was 6100–8500 eggs and juveniles per 100 ml of soil. In spite of this very high P_i the maximum difference in sugar weight between the susceptible standard A001 and the nematode resistant cultivars was less than 15%; in this field incidentally wilting symptoms occurred.

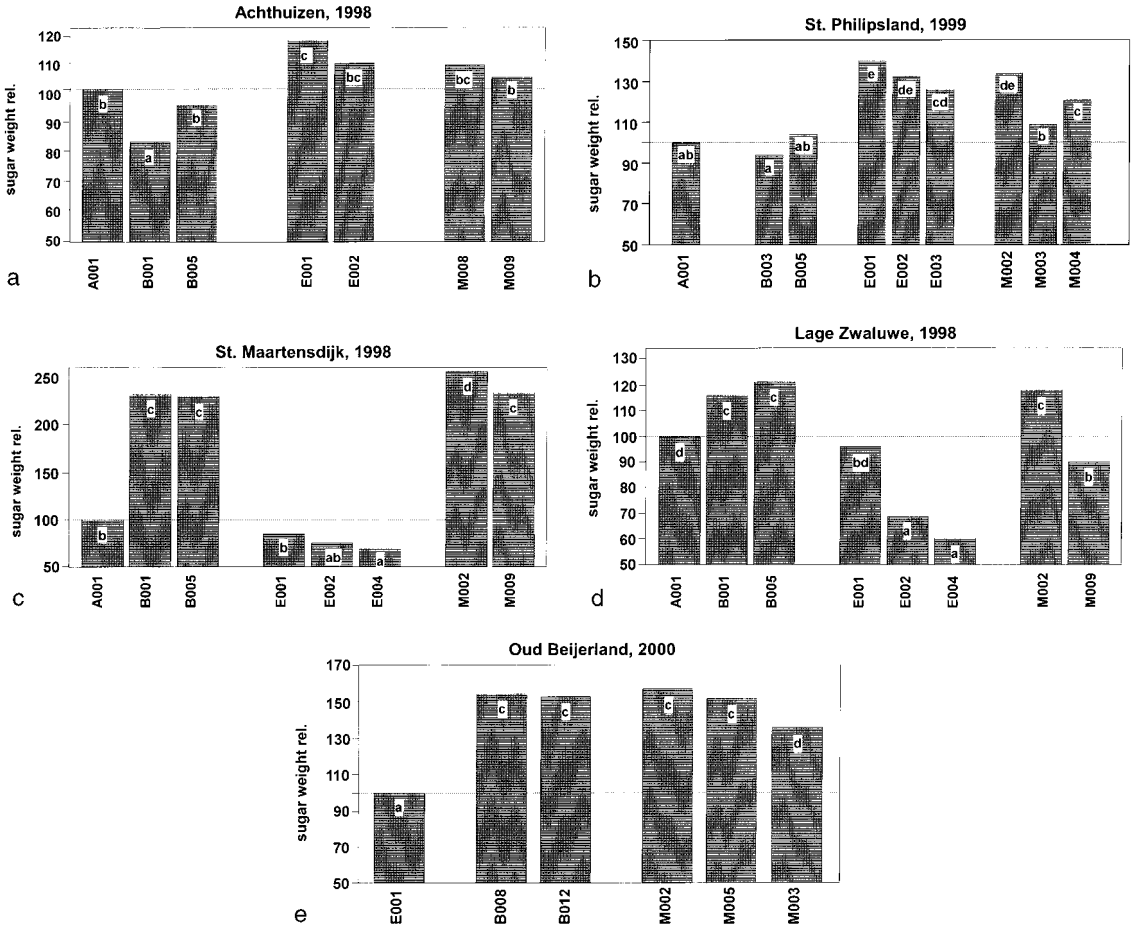

Figure 3. Sugar yields of resistant sugar beet cultivars on field trials with one level of *H. schachtii* or rhizomania (BNYVV) infection and different combinations of both diseases. Bars with the same letter are not significantly different. (a) Achthuizen 1998; P_i of 6100–8500 eggs and juveniles of *H. schachtii* per 100 ml of soil. (b) St. Philipsland 1999; P_i of 1000–1600 eggs and juveniles of *H. schachtii* per 100 ml of soil. (c) St Maartensdijk 1998; severe infection with BNYVV and *circa* 150 eggs and juveniles of *H. schachtii* per 100 ml of soil (far below the tolerance limit). (d) Lage Zwaluwe 1998; moderate infection with BNYVV and 250–550 eggs and juveniles of *H. schachtii* per 100 ml of soil. (e) Oud Beijerland 2000; moderate infection with BNYVV and 2200–2700 eggs and juveniles of *H. schachtii* per 100 ml of soil.

At St. Philipsland 1999 (Figure 3b) the Pi was only 1000–1600 eggs and juveniles per 100 ml of soil, but larger differences in sugar weight to a maximum of 40% could be established. The year to year differences in the degree of infestation occurred regularly, but were rarely as large as between 1998 and 1999.

Among the double resistant cultivars, M002 was the most productive and did not deviate from the single resistant cultivar E001. However, M003 was not very resistant ($P_f/P_i = 3.8$) and frequently showed nearly as many wilting symptoms caused by beet cyst nematodes during dry periods as the susceptible standard A001. This resulted in low sugar production. Most *H. schachtii*-resistant cultivars showed a low wilting rate early in the season, but later on, the differences with the susceptible standard were not significant. A particularly high wilting tolerance was found in the BNYVV-resistant cultivar (B003), although this did not result in an increased yield.

In Figure 3c, the resulting yields are shown of a trial field where, in soil samples according to the mpn bio-assay, a severe infection with BNYVV and only 150 eggs and juveniles per 100 ml of soil of *H. schachtii* (far below the tolerance level) were detected. The sugar yields of the single rhizomania-resistant cultivars only slightly differed from the ones

Figure 4. Leaf and root tumours and multiple crowns occurring incidentally in *H. schachtti*-resistant cultivars. (a) Severe tumour formation on the outer leaves and trap root. (b) Distorted hart leaves by excessive galling. (c) A sugar beet plant with a multiple crown in a trial field. (d) A dissection through the stems showing a multiple crown of the first B883 back-cross generation.

with combined resistance. As a consequence of differences in production capacity the nematode-resistant cultivars yielded 8–31% less sugar per hectare than the susceptible standard.

At Lage Zwaluwe, the Pi of *H. schachtii* varied from 250–550 eggs and juveniles per 100 ml of soil and, according to the mpn bio-assay and symptom development in the field, a moderate initial infection with BNYVV was present. In this field, no effect of the low *H. schachtii* infection on sugar yield was found (Figure 3d) and the single nematode-resistant cultivars produced less.

In a field with 2200–2700 eggs and juveniles of *H. schachtii* and a moderate infection of BNYVV at Oud Beijerland 2000 (Figure 3e), the effect of the latter was far more drastic than that of *H. schachtii*. During the whole season no wilting occurred, since this was suppressed by symptoms of BNYVV appearing mid-July and sufficient water supply. In this trial, no susceptible standard was incorporated, but the absence of differences in yield between the single rhizomania and the double beet cyst nematode/rhizomania-resistant cultivars suggested very little impact of beet cyst nematodes.

Discussion and conclusions

After three years of field trials, the first conclusions about the influence of different initial densities (P_i) on the *H. schachtii*-resistant cultivars were drawn and the first reactions of cultivars with a combined resistance against *H. schachtii* and BNYVV on different disease situations were established. From the climate cabinet experiments, it can be concluded that there are differences in the degree of *H. schachtii* resistance between the cultivars, mainly caused by lower transmission rates of resistance genes (Heijbroek et al., 1988). This is expressed as a decreased percentage of resistant plants and an increased average number of newly formed cysts on the roots. In only one cultivar (M009) was the percentage of resistant plants low, as the average number of newly formed cysts remained the same. In this case, one can assume that a partial resistance was expressed with a relatively high number of susceptible plants showing somewhat more than three cysts on the roots. In this cultivar, the percentage of BNYVV-resistant plants was also very low compared to the other rhizomania-resistant cultivars. This was expressed also as a lower sugar yield in trials on fields with a high *H. schachtii* as well as BNYVV infestation compared to the single nematode- and rhizomania-resistant standards respectively.

The cultivars M002 and M004 with a combined *H. schachtii* and BNYVV resistance performed, in the resistance tests, just as well as cultivars with a single resistance. M008 proved to be less resistant against both *H. schachtii* and BNYVV in all aspects. Significant correlations between the log P_i and the multiplication factor P_f/P_i were demonstrated not only for the susceptible, but also for the *H. schachtii*-resistant cultivars. These correlations corresponded with the ones found the past five years for other fields at different locations.

The effect of beet cyst nematode-resistant cultivars on the *H. schachtii* population differed in the three years, and was related to the multiplication rate on the susceptible standard. Prolonged rainfall during the summer of 1998 as compared to the relative dryness of 1999 caused differences between the years in wilting rates and multiplication of *H. schachtii* (Figure 1a,b). In 2000, the multiplication was very low. This corresponded with relatively low temperatures during spring and summer. As compared to the susceptible standard, the tested cultivars showed a resistance, which was most pronounced at low initial densities (P_i) of *H. schachtii*. At a Pi of more than 6000 eggs and juveniles per 100 ml of soil, multiplication rates on the susceptible standard were less than 1, which was not deviating significantly from the resistant cultivars. A significant difference between the resistant cultivars E001 and E002 at low to moderate P_i was detected in 1999 only, but was not repeated in other years. Tolerance to beet cyst nematode damage (Heijbroek et al., 1977) will never be 100%, because invading juveniles cause considerable damage to resistant hybrids due to the hypersensitivity reaction. This is the reason why yields of resistant cultivars are always affected by increasing populations of beet cyst nematodes. Apart from that, in some of the nematode-resistant cultivars tumours on roots and leaves and multiple crowns (see Figure 4) were found on a small part of the plant population (Savitsky, 1978).

The results from three years clearly show that the nematode-resistant cultivars decrease in yield substantially at increasing initial densities (P_i) of beet cyst nematodes. This means that these cultivars, if applied at high initial population densities, will show considerable losses.

Consistent differences in yield response to the P_i between the resistant cultivars could not be detected, partially because resistant genetic sources supplied

differed from year to year. They all seem to react similarly and do not deviate in slope from the susceptible standard, but the production levels were sometimes statistically different, for instance between E001 and M002 at St. Philipsland in 2000. However, these differences could be explained by considerable damage caused by BNYVV. Since at increasing infections the effect of a *H. schachtii*-resistant variety on the multiplication is less and the yield is considerably reduced, beet cyst nematode-resistant cultivars can not be applied economically at high initial densities. Apart from that, the risk of rapidly emerging resistance-breaking pathotypes (Müller, 1992) will be higher with increasing frequency of growing *H. schachtii*-resistant cultivars (Müller and Klinke, 1996).

Cultivars with a combined beet cyst nematode/rhizomania resistance seem to behave similarly towards *H. schachtii* as compared to single beet cyst nematode-resistant ones. However, the number of trials was still too low to detect differences. Moderate to severe infections with BNYVV were proved to cause far more serious crop losses than in the case of similar infections with *H. schachtii*. Therefore, in case of BNYVV suspicion, the advice will be to grow a double resistant, or if not available a single BNYVV-resistant cultivar. Even severe infections with *H. schachtii* will only cause damage if weather conditions allow an early nematode attack of the young beet seedlings.

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