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TRANSFER OF RESISTANCE TO BEET CYST NEMATODE FROM *BETA PATELLARIS* TO SUGAR BEET

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SUMMARY

The chromosome bearing the gene(s) for resistance to the beet cyst nematode (*Heterodera schachtii* SCHM.), could be transferred from *Beta patellaris* to *B. vulgaris* by interspecific hybridization and repeated backcrossing. A tetraploidized *B. vulgaris* originating from Anatolia (Turkey) was used as an intermediate. After several backcrosses with a number of different tetraploid and diploid beet cultivars, monosomic additions could be obtained which had the resistance bearing chromosome of *B. patellaris*. Cytological techniques were used for the study of this chromosome in resistant hybrids and monosomic additions. The analysis of pairing behaviour of the *B. patellaris* chromosome was hampered by the occurrence of non-specific stickiness of the chromosomes in meiocytes at pachytene and diakinesis.

Moreover, the nature of resistance in monosomic additions was studied in growth cabinet experiments, revealing that the penetration rates of the larvae into the root system did not differ from the susceptible control plants.

Among the F_1B_6 and F_1B_7 backcross derivatives, no plants with intermediate levels of resistance were found.

INTRODUCTION

Infestation of sugar beet with cyst nematodes (*Heterodera schachtii* SCHM.) has become rather widespread in most European countries and a number of sugar beet growing areas in the USA. Crop rotation adapted to the degree of infestation and based on regular soil sample analyses cannot be applied everywhere since alternative crops are few. Application of nematicides may alleviate infestations but is expensive; it cannot completely prevent crop losses and has no significant influence on the population development in the long term (STEUDEL & THIELEMAN, 1967; HEIJBROEK, 1973). This gap in the control of beet cyst nematode might be filled by tolerant and/or resistant varieties.

Partial resistance was found among *Beta vulgaris* and *B. maritima* origins and could be raised to a limited extent by selection. This type of resistance proved to be polygenic,

to inherit recessively and to disappear after two backcrosses to sugar beet varieties (HEIJBROEK, 1977).

Complete resistance or 'immunity' occurs only in the wild species belonging to the section *Patellares* and is based on a hypersensitivity reaction of the host tissue preventing the parasite to multiply. The resistance is based on simple dominant inheritance, segregates disomically in both *B. procumbens* (SAVITSKY, 1975) and *B. patellaris* (DE BOCK, pers. comm.) and can be transmitted to next generations. Hence, resistant sugar beet can be obtained by adding the wild beet chromosome bearing the gene(s) for nematode resistance to the sugar beet genome through interspecific hybridization and subsequently, by incorporating the gene(s) concerned into one of the sugar beet chromosomes by means of crossing-over.

Until now, numerous attempts have been made to hybridize sugar beet with one of the species of the section *Patellares*. Although hybrids are fairly easy to produce (SAVITSKY, 1960; FILUTOWICZ, 1961), most of them generally fail to grow: they die at the seedling stage or are completely sterile.

SAVITSKY (1973) was the first to transfer the *B. procumbens* chromosome with the gene(s) for nematode resistance to sugar beet. She was able to select four resistant monosomic additions from 6750 backcross derivatives obtained from 60000 seeds. Analysis of microsporocytes at diakinesis revealed that pairing associations between the alien chromosome and its homoeologous counterparts were very rare and incorporation of the chromosome segment with the gene for resistance into one of the sugar beet chromosomes succeeded only twice in the total progeny of trisomic generations (8834 plants). Recently also SPECKMANN & DE BOCK (1982) studied the production of alien monosomic additions as a source for the transfer to sugar beet of gene(s) for cyst nematode resistance from species of the section *Patellares*.

In this paper the transfer of one of the resistance bearing chromosomes from *B. patellaris* to sugar beet is described. *B. patellaris*, a tetraploid member of the section *Patellares*, has been used as the donor and the production of resistant monosomic additions at the diploid level was achieved by repeated backcrossing, first with tetraploid and later with diploid *B. vulgaris*. Cytological techniques have been used to study the behaviour of the *B. patellaris* chromosomes in mitosis and meiosis of resistant monosomic additions. Finally, the alien chromosome is compared to that in similar monosomic additions obtained from *B. vulgaris* × *B. procumbens* hybrids.

MATERIALS AND METHODS

Diploid *Beta vulgaris* (2n = 18), originating from Anatolia (Turkey), was supplied by the US Department of Agriculture (P.I. 176422) and tetraploidized by colchicine treatment. Viable interspecific hybrids were obtained by crossing the tetraploid beet with *B. patellaris* (2n = 36). In the consecutive backcross generations the following sugar beet varieties or inbred lines were used: Kuhn Elite (Kuhn); KW 5282, Kawemono, Kawemegamono (Kleinwanzlebener Saatzucht); 546 H3 (USDA); Muf 207 (van der Have) and Hill 81503 (Hilleshög). Tolerance to beet cyst nematode damage was incorporated by pollinating resistant hybrids with the diploid selections RW 660 and RW 880 (HEIJBROEK et al., 1977). In the later part of the breeding programme, a number of mangold varieties was used: Flandria, Stompvoet DePe, Civarres. Seeds

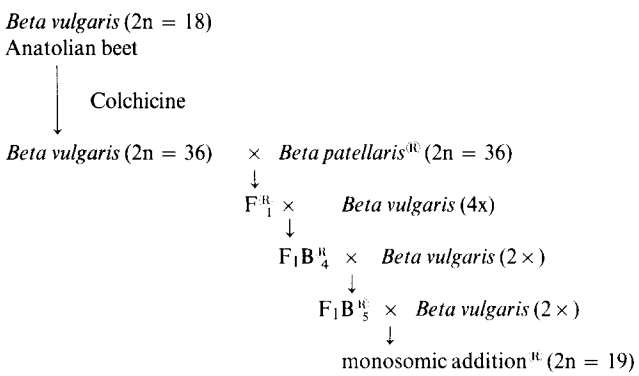

Fig. 1 Schematic course of the interspecific hybridization between *Beta vulgaris* and *B. patellaris* and the backross programme revealing beet cyst resistent monosomic additions at the diploid level.

of this material were kindly supplied by Mr Th. S. M. de Bock of the Foundation for Agricultural Plant Breeding, Wageningen. A schematic representation of the breeding programme is given in Fig. 1. The consecutive backcrosses were numbered F_1B_1, F_1B_2, etc., irrespective of the fact that first tetraploid and later diploid *B. vulgaris* was used as recurrent parent.

Nematode selection tests were carried out as described earlier (HEIJBROEK, 1977). During the last few years the first part of the screening method has been altered. This resulted in the following procedure. In each unit filled with quartzsand hundred seeds were sown to which hatched larvae or filled cysts were added. Seedlings were grown in the greenhouse at 20–25°C and were supplied with nutrient solution according to STEINER (1968). Five to six weeks later white immature cysts had developed and could easily be detected. All plants which had in one out of three consecutive tests more than two cysts on the root system were considered to be susceptible and consequently discarded.

Investigations into the nature of resistance in hybrids and monosomic additions were performed in plant growth cabinets (Conviron) at 15° and 25°C, 80% humidity and 16 hours of photoperiod. Seedlings were planted in small pots containing gravel and Steiner nutrient solution to which a standardized inoculum of larvae was added. The different stages of larvae and adult beet cyst nematodes were determined from root tissues after homogenizing and staining with lactophenol acid-fuchsin, as described earlier (HEIJBROEK, 1977).

At first all crosses were performed in isolated cabinets in greenhouses, but after the fourth backcross generation all selections were vernalized for four to six months during winter and were open- or cross-pollinated in cabinets or isolated field plots.

Chromosome numbers were determined in squashed root tips which were stained in lacto-propionic orcein according to DE JONG & DE BOCK (1978). Meiosis was studied in microsporocytes of young anthers which were stained in carmine-Giemsa (DE JONG, 1978).

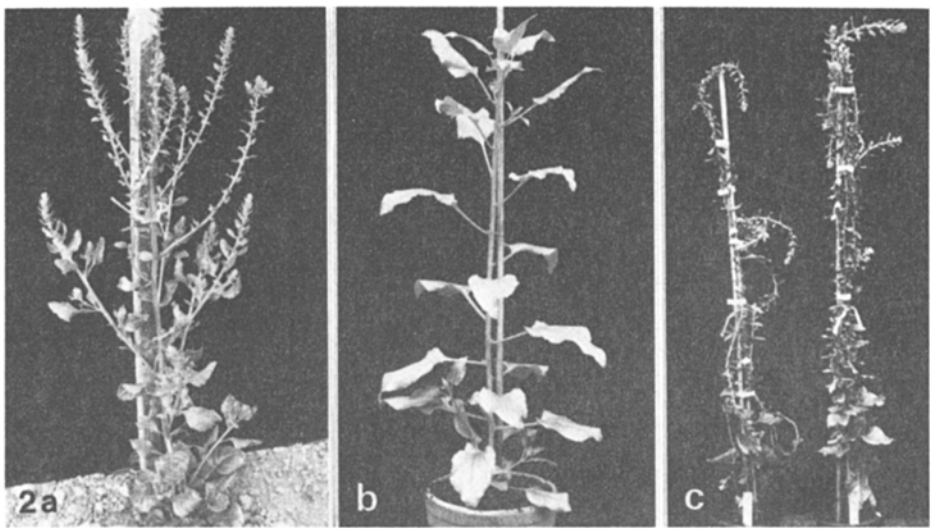

Fig. 2. The wild type origins and beet cyst nematode resistant F_1-hybrids. a) The tetraploidized *B. vulgaris* from Anatolia (Turkey). b) *B. patellaris*. c) Tetraploid resistant hybrids *B. vulgaris* × *B. patellaris*.

RESULTS

The Anatolian diploid *B. vulgaris* (2n = 18) was found to be completely male sterile but appeared to hybridize rather well with the beet cyst nematode resistant species of the section *Patellares*. At first in 1960, some of these Anatolian beets were pollinated with *B. procumbens* and *B. webbiana* producing a number of viable, but completely sterile hybrids. All of them were resistant to beet cyst nematode. Pollination with other *B. vulgaris* (commercial) varieties, *B. maritima* and *B. atriplicifolia* did not yield any viable seed.

For the production of viable and fertile *Beta vulgaris* × *B. patellaris* hybrids, tetraploid *B. vulgaris* lines appeared to be necessary. Therefore, seeds of the Anatolian beet were treated with colchicine for chromosome doubling. Tetraploid plantlets could be distinguished morphologically and were raised to the flowering stage. An example of a tetraploid Anatolian beet is shown in Fig. 2a. Out of four plants that were pollinated with *B. patellaris* (Fig. 2b), one produced seeds with viable embryos. Sixteen percent of the seeds developed into healthy hybrids, which were all male sterile and resistant to beet cyst nematode. These F_1-hybrids (Fig. 2c) were pollinated with the Anatolian beet, giving one resistant F_1B_1 plant. This plant was backcrossed with a tetraploid sugar beet (commercial variety) and among the 120 descendants, six plants were resistant. The hybrids showed many heterogenous morphological characters and were mainly annual. Most of them possessed obvious tumors on the roots. The chromosome numbers ranged from 34 to 37.

In the next backcross generation 80 plants were obtained, of which only one was resistant and biennial and had 36 chromosomes. To expand the breeding programme this plant was multiplied by cloning. After vernalization some of these clones produced

Fig. 3. The first biennial tetraploid hybrids occurring in the F_1B_4 backcross generation of *Beta vulgaris* × *B. patellaris*, with *B. vulgaris* as the recurrent parent.
Fig. 4. Differences in morphological characters between plants of the F_1B_5 and F_1B_6 backcross generations of *Beta vulgaris* × *B. patellaris*, with *B. vulgaris* as the recurrent parent.

small amounts of pollen. In the next generation plants were obtained with improved seed setting, viability and pollen fertility (Fig. 3). Annuality decreased, but tumors on roots and leaves still occurred regularly. At the same time a large variation in plant morphology among families of this and the two consecutive backcross generations could be established (Fig. 4). The somatic chromosome number of the resistant plants varied from 34 to 38, but proved to be 36 in the majority of the material. In all these plants, microsporocytes at diakinesis – metaphase I showed univalents and bivalents and, to a lesser extent, also quadrivalents. Trivalents occurred only rarely and were detected in a few hybrids only.

The transmission rates of resistance were up to ten percent during the backcross generations F_1B_3 to F_1B_6 and could not be raised by selectively crossing the progenies showing high transmission rates. The average transmission values of the backcrosses

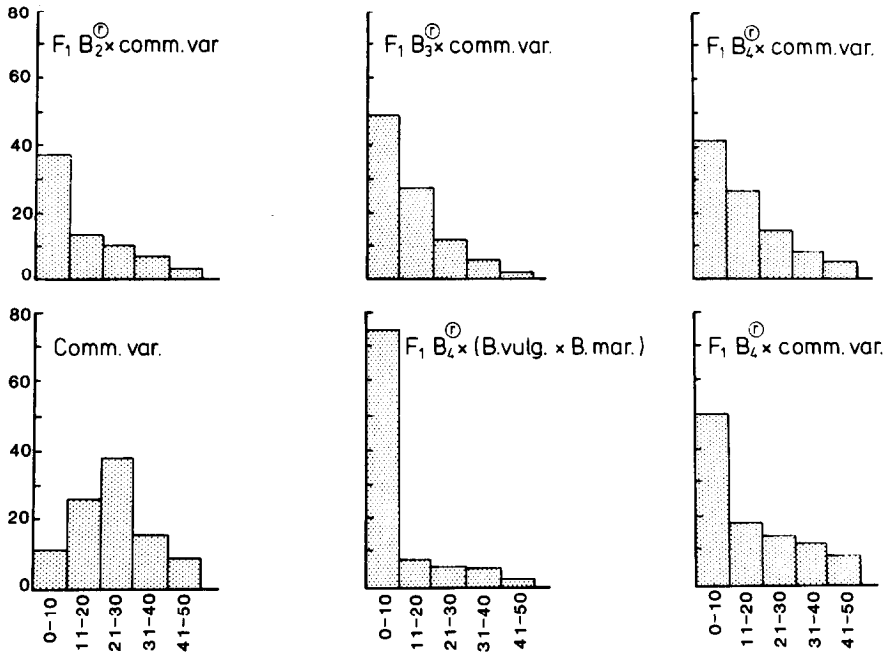

Fig. 5. Frequency diagrams of cyst number groups on the root systems of different backcross generations as compared to *B. vulgaris*. Vertical axis: Percentage of plants within one group. Horizontal axis: Classified cyst number groups. The lower middle diagram represents a backcross generation in which a partial resistant *B. vulgaris* × *B. maritima* hybrid is used as a pollinator.

with different commercial varieties remained low (Table 1) and showed considerable variation from plant to plant. On the other hand, successive backcrossings with tetraploid pollinators derived from commercial varieties, did not lower the level of transmission. This phenomenon is demonstrated in Fig. 5. In this figure, respresenting the diagrams of different backcrosses with the plants classified according to cyst number groups and expressed as percentage of all tested plants, no obvious differences in the distributions can be observed. Only in the diagram presenting the backcross with a partially resistant *Beta vulgaris* × *B. maritima* hybrid used as pollinator, some further increase of the low cyst number group can be observed. This effect could not be detected in the transmission rates (Table 1), since these values only reflect complete resistance, i.e. 0–3 cysts on the roots, after three consecutive tests.

To simplify the study of chromosome behaviour and to obtain disomic segregation of the resistance, the breeding programme was gradually brought from the F_1B_4 generation onwards to the diploid level, using diploid *B. vulgaris* selections as pollinators. Apart from some inbred lines of commercial varieties, also selections were applied that were tolerant to beet cyst nematode damage.

In the next backcross generation, resistant hybrids with chromosome numbers of 27 and 28 have been found. These plants showed high vigour and good fertility, while the average transmission rates of the resistance did not decrease (Table 1). By backcrossing again with diploid beets, small numbers of monosomic additions could be

Table 1. Transmission of resistance after three consecutive nematode tests and the occurrence of monosomic additions in a series of backcrosses, starting with the F_1B_3 *B. patellaris* × *B. vulgaris* hybrids.

Backcross generation and applied pollinator		Number of plants tested	Transmission of resistance in %	% of monosomic additions in resistant population
Tetraploid level:				
F_1B_3 × BV comm. var.		478	2.5	–
F_1B_4 × BV comm. var.		327	3.1	–
F_1B_5 × BV comm. var.		1574	2.2	–
F_1B_5 × BV tol. RW660		918	3.6	–
F_1B_5 × F_1B_5		23	4.3	–
Triploid level:				
F_1B_4 × BV comm. var.		1120	5.5	0
F_1B_5 × BV comm. var. I		1249	1.0	0
F_1B_5 × BV comm. var. II		1779	3.4	11
Diploid level:				
F_1B_5 × BV comm. var. I		352	4.7	80
F_1B_5 × BV comm. var. II		145	2.8	100
F_1B_5 × *B. maritima*		673	1.6	100
F_1B_5 × BV × BM tol. RW 880		769	1.6	100
F_1B_5 × BV tol. RW 660	plant 1	2285	5.4	21
	plant 2	881	3.7	27
	plant 3	360	3.6	100
	plant 4	891	2.7	63
	plant 5	218	10.1	100

obtained. These resistant plants, with 2n = 19 chromosomes, proved to be very weak and most of them did not survive the three consecutive nematode tests or died shortly after flowering. The first plants obtained were annual and showed green or red tumors on the leaves and the flowers. Seeds were monocarp and often tended to shed quite early. After two backcrosses with diploid *B. vulgaris*, resistant monosomic additions could be isolated that resembled the sugar beet in several respects and exhibited improved vigour and fertility. An example is given in Fig. 6a. All plants showed small fleshy roots and needed two months of cold induction for bolting. One of the hybrids, which was repeatedly backcrossed with the variety Civarres, showed a transmission rate stabilizing at about 8 percent as germination of the seeds improved (Table 2). Plants of this selection showed remarkable better vigour and most of them survived the three nematode selection tests.

The study of somatic chromosomes in root tip meristems revealed little or no deviations. Well-spread metaphase plates contained two or less chromosomes with satellites. The remaining chromosomes in the karyogram could not be identified because of their morphological similarity (De Jong & De Bock, 1978). Mitotic anaphase bridges occur seldom, whereas chimaeras with 19 and 38 chromosome sectors have never been observed. Pairing behaviour of the *B. patellaris* chromosome and the transmission of this chromosome through gametogenesis have been studied at microsporocytes in young anthers. The general description of meiosis in *Beta* has been reported elsewhere (De Jong & Oud, 1979). Because of poor vitality and relative low number of flower

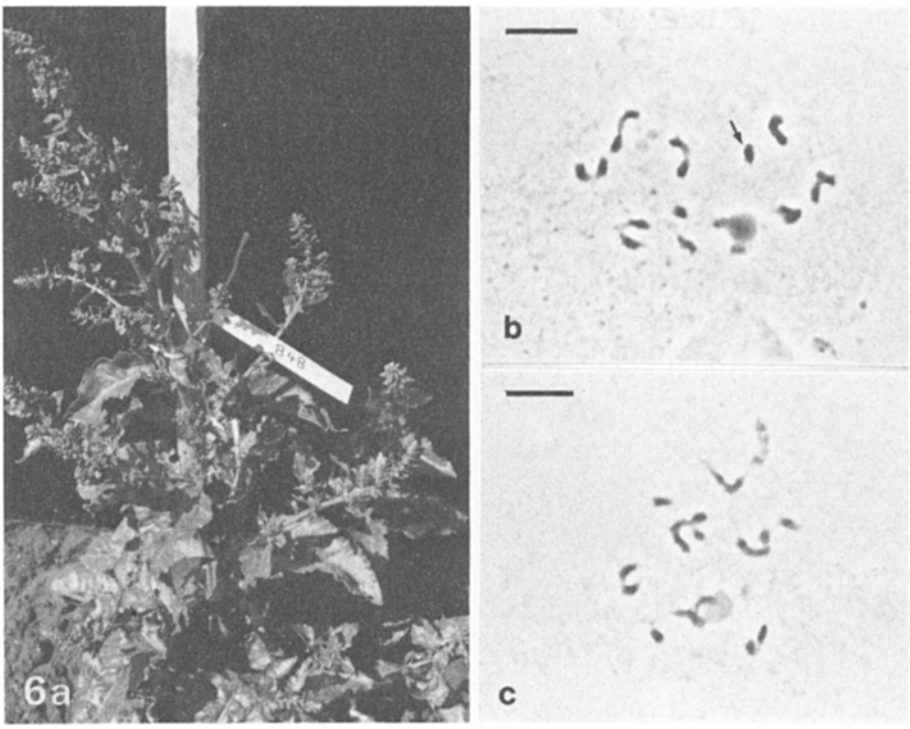

Fig. 6. Beet cyst nematode resistant *B. vulgaris* × *B. patellaris* monosomic addition. a) Plant shape. b) Pollen mother cell at diakinesis. The univalent is indicated by arrow. c) Nucleus at the same stage showing the occurrence of nonspecific stickiness of homologues. Bar equals 10 μm in both figures.

Tabel 2. Emergence and transmission of resistance from the triploid level to the monosomic addition at the diploid level in one breeding line, using the diploid mangold Civarres as pollinator.

	Emergence (%)	Number of plants tested	Rate of transmission (%)
F_1B_5 triploid	101	608	5.4
F_1B_6 monosomic add.	15	315	8.6
F_1B_7 monosomic add.	111	557	8.2

buds of most resistant monosomic additions, only few plants could successfully be used for the analysis of male meiosis. In the stages up to and including synizesis, striking irregularities have not been established. In *Beta,* chromosomes at pachytene are clearly observable enabling the study of pairing behaviour and morphological characters. Moreover, chromosomes at this stage can be karyotyped on the basis of length, centromere place and chromomere pattern (DE JONG, 1981). In the monosomic additions described in this report, chromosomes could not be studied accordingly because

of stickiness of the non-homologues at the centromere regions and despiralization or stretching of the distal achromatic parts. Neither univalents nor trivalents could be detected with certainty. In most nuclei at (post diffuse) diplotene and diakinesis, chromosomes are still clustered, apparently forming multivalent associations. The Figs. 6b and 6c present examples of microsporocytes at diakinesis. Comparison of both figures makes clear that the associations are based, at least partly, on non-specific stickiness, so that distinction between real trivalents and aspecific associations cannot be made. Univalents could be detected in over 98% of the nuclei.

At anaphase I – telophase I, the majority of the nuclei shows lagging chromosomes. In nuclei at interkinesis – telophase II, the percentage of laggards gradually decreases, though obvious differences in their number occur between different plants and between flowers of the same plant. Anaphase bridges, micronuclei and centric fragments have been found at very low frequencies.

The nature of resistance was studied in a growth cabinet at three different infection levels of 100, 500 and 1000 larvae per plant. The tests were performed at about 50 plants of which the root systems were analyzed every three days for the presence of the different stages of development of the nematodes during a period of 50 days.

The penetration rates of the larvae into the root system of the resistant monosomic additions were not different from those of the standard sugar beet variety Monohil; but the larvae did not develop into adults.

Among the hybrids no groups with intermediate resistant level, i.e. between completely resistant (0–3 cysts per plant) and susceptible plants could be detected. The average numbers of newly formed cysts on the roots of the non-resistant backcross material did not differ significantly ($p = 0.05$) from the numbers on the roots of the susceptible variety Monohil, at all infection levels.

DISCUSSION

The results shown here have demonstrated that viable and fertile interspecific hybrids of *Beta vulgaris* × *B. patellaris* and nematode resistant monosomic additions from these hybrids through repeated backcrossings and consecutive beet cyst nematode selection tests could be produced. Viable F_1-hybrids could be produced only with the male sterile *Beta vulgaris* landrace from Anatolia ($2n = 18$). Apparently, these beet plants contain a unique genetical background, which is indispensable for combining ability with *B. patellaris*. Since the latter species has $2n = 36$ chromsomes, the Anatolian beet had to be tetraploidized by colchicine treatment. All F_1-hybrids obtained accordingly had 36 chromosomes, were phenotypically rather uniform and showed in three consecutive nematode tests no cysts on the root system, indicating that the gene(s) for resistance are of dominant nature. After backcrossing with *B. vulgaris* or *B. maritima* origins, the average transmission rates varied from one to five percent. These low values can be explained assuming loss of the resistance bearing chromosomes during meiosis, weakness of the aneuploid gametes and premature death of the weak resistant plantlets.

After three backcrosses the viability of the seed improved, which enabled us to carry out nematode selection tests on a larger scale and calculate transmission rates more precisely. In the successive backcross generations from F_1B_4 onwards, transmission

rates did not widely deviate from five percent. However, the average figures mentioned in Table 1, were often lower. This was brought about because a large part of the resistant hybrids, classified in the 0–10 cyst number group (Fig. 5), was very weak and died after the first nematode selection test, so that these plants could not be taken into account for determining the transmission rates. Therefore the values shown in the diagrams are too low and vary depending on the degree of viability of the offspring. No significant improvement of transmission could be achieved by applying different sugar or mangold varieties or *B. maritima* selections as pollinators, except for one partial resistant *Beta vulgaris* × *B. maritima* hybrid (HEIJBROEK, 1977), as can be seen in Fig. 5. However, by repeated backcrossing, this transmission rate decreased again, because of the recessive inheritance of this type of resistance. As the hypersensitivity reaction of the hostplant to eelworm infestation could cause considerable damage to the root system, we also incorporated tolerance to beet cyst nematode damage into a number of backcross selections. This tolerance was derived from *B. vulgaris* selections of *B. vulgaris* × *B. maritima* hybrids and inherited dominantly (HEIJBROEK et al., 1977).

From the fact that the larvae of *H. schachtii* penetrated into the roots of resistant plants at the same rate as in the susceptible standard (Monohil) it might be concluded that the hatching response is comparable to the one under a host crop. Most of the larvae in the roots died as a consequence of necrosis in the surrounding tissues, caused by the hypersensitivity reaction.

Particularly in the later backcross generations no intermediate type of resistant plants could be detected. If they were not completely resistant the numbers of cysts formed on the roots did not deviate from those on the roots of a susceptible variety. This suggests a type of resistance based on a low number of genes located on the same chromosome.

In the first few backcross generations at the diploid level, only small parts of the offsprings were resistant. All plants showing no cysts on the root system in three consecutive tests, proved to have $2n = 19$ chromosomes. Evidently, the extra chromosome represents the *B. patellaris* chromosome with the gene(s) for nematode resistance. Most of the monosomic additions were still very weak and exhibited many features of the wild beet. In the later generations, all plants became more vigorous and gradually resembled the *B. vulgaris* phenotype. The resistant individuals with high vitality and fertility are selected now for the production of translocation hybrids, containing all *B. vulgaris* chromosomes plus the segment of the *B. patellaris* chromosome with the gene(s) for resistance incorporated. This genome constitution can be achieved by recombination between the alien chromosome and one of its homoeologous *B. vulgaris* chromosomes. Main condition for this process is that pairing association between the chromosomes involved, takes place. SAVITSKY (1975) observed in the monosomic additions derived from *B. vulgaris* × *B. procumbens* hybrids several trivalents in microsporocytes at diakinesis. The number of trivalents varied in locules, in flowers of one plant and between plants. TSUCHIYA & NAKAMURA (pers. comm.) investigated offspring of Savitsky's resistant monosomic additions and found 1.7% trivalents, on the average, whereas DE JONG (1981) concluded that in material also derived from Savitsky's monosomic additions, real trivalents occur, only at very low frequencies (less than 0.1%).

Cytological study of the male meiotic prophase in the *B. patellaris* monosomic additions could not elucidate any information on trivalent association, since poor meiotic division activity and the occurrence of chromosomal disturbances prevent reliable data on pairing behaviour of the alien chromosome.

In our study of Savitsky's monosomic material, it has been shown that the resistance bearing chromosome also contains a nucleolar organizer region (NOR), which means that this *B. procumbens* chromosome is one of the satellite chromosomes. Arguments for this result are the occurrence of trivalents attached to the nucleolus in nuclei at diakinesis, the presence of three Ag-NORs in the nuclei of calyptra cells as revealed with the silver staining technique (DE JONG, 1981) and the maximum number of three nucleoli in resting nuclei (unpublished results, Foundation for Agricultural Plant Breeding, Wageningen). Comparable studies of the *B. patellaris* monosomic additions could not reveal any similar evidence for the presence of satellites on the *B. patellaris* chromosome, and arguments supporting the presence of more than two NORs could not be established. In addition, anaphase bridges and fragments as observed in microsporocytes of *B. procumbens* monosomic additions, have only been found seldom in the *B. patellaris* material.

In spite of insufficient cytological evidence, it is clear that the monosomic addition described in this report differs from the *B. procumbens* monosomic additions of Savitsky in several respect. Not only the wild beet species used as donor of resistance, but also the genetic background and plasmatypes of both sources are obviously different. This new source of nematode resistance may become of interest.

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