Euphytica **139:** 105–121, 2004.

Sources of resistance to diseases of sugar beet in related *Beta* germplasm: I. Foliar diseases

M.C. Luterbacher[1], M.J.C. Asher[1,*], E. DeAmbrogio[2], E. Biancardi[3], P. Stevenato[3] & L. Frese[4]
[1]*Broom's Barn Research Station, Higham, Bury St Edmunds, Suffolk, IP28 6NP, U.K.;* [2]*Società Produttori Sementi S.p.a. (SPSB), Galleria del Reno 3, 40122 Bologna, Italy;* [3]*Istituto Sperimentale per le Colture Industriali (ISCI), Viale Amendola 82, 45100 Rovigo, Italy;* [4]*Bundesanstalt für Züchtungsforschung an Kulturpflanzen (BAZ) Gene Bank, Bundesallee 50, 38116 Braunschweig, Germany; (*author for correspondence; e-mail: mike.asher@bbsrc.ac.uk)*

Received 13 January 2004; accepted 24 August 2004

Key words: beet mild yellowing virus (BMYV), beet yellows virus (BYV), *Beta* species, *Cercospora beticola, Erysiphe betae,* resistance, sugar beet

Summary

Resistance to four foliar diseases of sugar beet (*Beta vulgaris* ssp. *vulgaris*), virus yellows caused by Beet mild yellowing virus (BMYV) and Beet yellows virus (BYV), powdery mildew (*Erysiphe betae*) and Cercospora leaf spot (*Cercospora beticola*), was assessed in up to 600 accessions of closely related wild and cultivated *Beta* species. Most accessions were from the Section *Beta*, a taxon containing types most closely related to, and sexually compatible with, sugar beet and therefore most valuable for use in crop improvement. Between 1–12% of accessions were highly resistant (resistance scores of $\leq$2 on an international standardised resistance scale of 1–9) to these diseases. These levels, however, underestimate the potential number of resistant sources available from this section as some accessions with intermediate mean resistance scores contained a significant proportion of highly resistant plants within segregating populations. Variation in resistance to all diseases except BYV was observed within the Section *Beta*. Much higher levels of resistance were observed, and more frequently, in more distantly related sections of the genus *Beta*. Accessions of the Section *Corollinae* were highly resistant to both viruses (>62% of accessions tested), but less so to Cercospora (15%) and they were very susceptible to powdery mildew. Section *Procumbentes* accessions were highly resistant to BMYV and Cercospora (100%) but less so to powdery mildew (50%) and BYV (20%). However, sexual incompatibility between these sections and sugar beet make utilisation of these sources impractical using conventional breeding methods.

Introduction

Sugar beet (*Beta vulgaris* ssp. *vulgaris*) is an economically important crop grown throughout the non-tropical world and produces about 30% of the world's sugar (Cooke & Scott, 1993). It is a host to several foliar and soil-borne diseases, some of which have a significant impact on yields, and intervention is often required to maintain production. Control of many of these diseases is achieved by pesticides, applied either directly against the pathogens responsible or against their vectors.

Genetic resistance to several pathogens has been identified, e.g. the agents of downy mildew and rhizomania (Bosemark, 1993; Scholten & Lange, 2000), but for some this is only partial and pesticides are still needed, e.g. powdery mildew and Cercospora leaf spot; for others resistance is currently not available, e.g. virus yellows (Luterbacher et al., 1998; Panella & Frese, 2000). The lack of resistance to some diseases reflects the success of pesticides in their control and plant breeder's priorities, e.g. higher yields and quality. However, pesticides are coming under greater scrutiny

in relation to safety, cost, environmental impact and the development of resistance in the target organisms. For other diseases, particularly those that are soil-borne such as rhizomania, resistance offers the only practical solution for control.

Several potential sources of resistance genes are available. Sugar beet germplasm held by breeders are the most obvious, but the gene pool from which most modern cultivars are derived is relatively small and has been made narrower by breeding for specific agronomic traits (Doney, 1993). Alternatively, related *Beta* species can be used as resistance sources (Heijbroek et al., 1988; Van Geyt et al., 1990). The genus *Beta* is composed of a diverse range of highly variable wild and cultivated species with a number of useful traits including disease resistance (Buttler, 1977; Letschert, 1993; Lange et al., 1999). The genus is subdivided into four sections (Figure 1), each having varying potential as a source of resistance genes. A detailed account of the importance of each *Beta* section as a resistance source is given in Frese & Desprez (1999).

With a view to exploring a wider gene-pool than that normally used by breeders the project 'Evaluation and enhancement of *Beta* collections for the extensification of agricultural production' (GENRES – CT95 – 42) was established, managed by several European agricultural research institutes and sugar beet breeding companies. It was led by the BAZ Gene Bank in Germany, and co-funded by the European Union and several national funding bodies. Among the traits being evaluated were resistance to several foliar diseases of sugar beet, including virus yellows, powdery mildew and Cercospora leaf spot.

Virus yellows are a group of aphid-transmitted diseases found on sugar beet throughout the world (Duffus & Ruppel, 1993). Several viruses are involved but among the most important are Beet mild yellowing virus (BMYV, family *Luteoviridae*) and Beet yellows

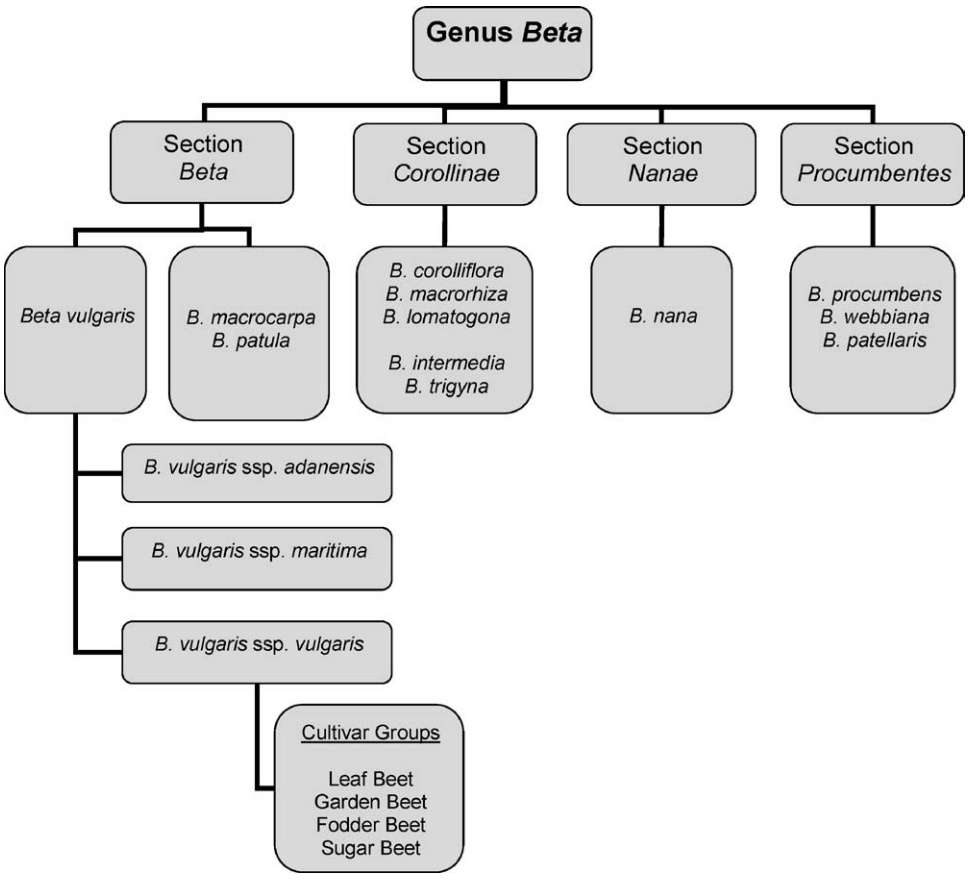


Figure 1. The taxonomy of the genus *Beta*.

virus (BYV, family *Closteroviridae*). BMYV is found throughout the Eurasian region but predominates in northern areas e.g. the U.K., whilst BYV has a wider, worldwide distribution and is important in southern Europe (Cariolle, 1990). A third virus, *Beet chlorosis* virus (BChV), has recently been identified on the basis of different biological, serological and molecular characters (Hauser et al., 2000).

BMYV and BYV cause yellowing of leaves, which reduces photosynthetic activity and yield. Maximum losses arise when infection *via* aphids (primarily *Myzus persicae*) occurs early in the growing season and in the absence of control measures. Yield reductions can be as high as 30% and 50% for BMYV and BYV respectively and sugar impurities increase significantly (Smith & Hallsworth, 1990). Currently, virus yellows is controlled by using insecticides directed at the aphid vectors, applied as a seed treatment, e.g. imidacloprid, or as foliar sprays, e.g. pirimicarb (Dewar et al., 1996).

Although breeding for virus yellows resistance has been attempted, success remains elusive. Some tolerant cultivars were bred in the 1960s but these suffered from a yield penalty when grown in years of low disease incidence and fell out of favour with growers (Bosemark, 1993). However, some moderate resistance to the related virus, Beet western yellows virus (BWYV), has been exploited in the US (Duffus & Ruppel, 1993). Although virus yellows resistance has been reported in *Beta vulgaris* ssp. *maritima* (*B. v. maritima*, sea beet) and species of the sections *Corollinae* and *Procumbentes* (Van Geyt et al., 1990), none has been fully exploited in sugar beet.

Two important fungal diseases affecting sugar beet foliage are powdery mildew (*Erysiphe betae* (Vanha) Weltz) and Cercospora leaf spot (*Cercospora beticola* Sacc). Both are common throughout the world but powdery mildew is particularly damaging in areas with relatively mild winters that allow overwintering survival of the inoculum, e.g. southern and maritime Europe, the Middle-East and California, whilst Cercospora development is greatest in warm humid regions (Ruppel, 1995) such as the Mediterranean region, mid-Europe, and parts of the U.S.A. (Holtschulte, 2000).

Powdery mildew causes chlorosis of the host tissue, reduces photosynthesis, accelerates leaf senescence and can reduce sugar yield by 25% (Anon, 1982; Byford, 1996). Cercospora leaf spot causes progressive destruction of leaves, which induces the plant to continually replace leaves at the expense of sugar production, leading to yield losses of up to 50% and an increase in impurities (Holtschulte, 2000). The effects on yield are aggravated when sugar beet is attacked simultaneously by both diseases (Ayala & Gordo, 1998).

Currently, there are some partially resistant cultivars available to both diseases (Bosemark, 1993; Panella & Frese, 2000). The development of partially resistant cultivars for powdery mildew has occurred by selecting for high yielding cultivars in areas where the disease is prevalent (Francis, 2002). Resistance to powdery mildew has been identified in *B.v. maritima* (Whitney, 1989) and within the Section *Procumbentes* (Ruppel & Tomasovic, 1997). Several sugar beet breeding lines have been developed from *B.v. maritima* in the U.S.A. (Lewellen & Schrandt, 2001). Most *Cercospora* resistant material presently available is derived from breeding programmes started in Italy in the 1930s; resistance genes in *B.v. maritima* were introgressed into sugar beet by Munerati (1932). Since then, there has been little effort to identify novel sources of *Cercospora* resistance (Panella & Frese, 2000)

Despite the availability of cultivars moderately resistant to both diseases, fungicides are still required to maintain high yields, in particular to Cercospora leaf spot (Panella & Frese, 2000). However, the recent discovery of *C. beticola* strains resistant to fungicides, e.g. DMI fungicides in Greece (Ioannidis & Karaoglandis, 2000), has prompted renewed interest in developing new resistant lines.

In this paper, we describe the outcome of evaluating *Beta* germplasm for BMYV, BYV, powdery mildew and Cercospora leaf spot resistance and consider its potential in future breeding programmes. In this context, we also consider the possibility of identifying *Beta* accessions that show 'multiple' resistance to several foliar diseases. We explore the merits of the evaluation procedures and how they can be improved. Finally, we examine how this material is being utilised in the development of new resistant sugar beet cultivars and in improving our understanding of the genetic mechanisms that control resistance to these pathogens.

Materials and methods

The evaluation of resistance to virus yellows and powdery mildew was conducted at Broom's Barn Research Station, U.K., whilst Cercospora resistance was evaluated jointly by the Società Produttori Sementi (SPSB) and the Istituto Sperimentale per le Colture Industriali

(ISCI) in Italy. Up to 600 accessions were provided by the BAZ Gene Bank, Germany to be evaluated for each resistance trait. Most were cultivated beets (50%) or wild species (40%) of the Section *Beta.* The rest were from the Sections *Corollinae* (8%) and *Procumbentes* (2%). Accessions were provided as seed which was stored at 8 °C until use. Seed of accessions from the sections *Corollinae* and *Procumbentes* were scarified to facilitate germination.

Virus yellows

All virus yellows screening tests were conducted in a temperature-controlled glasshouse maintained at ca. 22 °C with a 16/8 h light/dark regime, during the years 1997–2000. In total, 16 and 14 tests were conducted for BMYV and BYV resistance respectively. In each test, depending on seed viability, 18 to 24 seedlings per accession were grown (except in the sections *Corollinae* and *Procumbentes*, where 10–24 seedlings were grown) to the two true-leaf stage and inoculated with aphids (*Myzus persicae*) carrying BMYV or BYV. Viruliferous aphids were raised on either BMYV infected *Capsella bursa pastoris* or BYV infected *Tetragonia expansa*. After four days, inoculated plants were fumigated using nicotine (Dow Agrosciences, U.K.) to remove aphids and grown on for four weeks under high light intensity (supplementary light of ca. 300 μmol m^{-2} for 16 h per day).

Sap was extracted from 15 mm discs cut from the two first true leaves of each plant and the virus content was quantified by an ELISA test specific for each virus. BMYV resistance was assessed with a triple-antibody sandwich (TAS) ELISA test using a BMYV specific monoclonal antibody (MAFF 24) according to the method of Smith et al. (1996). BYV resistance was assessed with a double-antibody sandwich (DAS) ELISA test and a BYV polyclonal antibody produced at Rothamsted Research, using the method of Stevens et al. (1994). In all ELISA tests, the mean % virus content of each accession was estimated using a standard curve derived from the serially diluted sap of a highly infected plant of the susceptible U.K. sugar beet cultivar 'Saxon'.

Tests were conducted over a period of four years and, to improve the comparability of results between tests for each trait, it was necessary to minimise any inter-experimental variation. Therefore, the % virus content of each accession was expressed relative to that of the susceptible standard sugar beet cv. Saxon included as a control in each test, thus:

$$\text{Relative level of infection of accession (RLI)} = \frac{\%\text{ virus content of test accession}}{\%\text{ virus content of susceptible standard}}$$

Subsequently, the RLI values were used to adjust % virus content values of each accession relative to the mean % virus content of the susceptible standard across all tests, thus:

$$\text{Adjusted \% virus content} = \text{RLI of accession} \times \text{mean \% virus content of standard}$$

These 'adjusted' % virus content values of each accession were transformed to a simplified international standard 1–9 resistance scale, where a resistance score (RS) of 1 indicated no or extremely low symptom expression (equivalent to 0–11% 'adjusted' mean % virus content) and an RS of 9 signified extremely high symptom expression (equivalent to >88% 'adjusted' mean % virus content).

In total, 595 and 597 accessions were evaluated for BMYV and BYV resistance respectively. Most were from the Section *Beta* (96%) but species of the Sections *Corollinae*, (*B. corolliflora*, *B. intermedia*, *B. lomatogona*, *B. macrorhiza* and *B. trigyna*) and *Procumbentes* (*B. patellaris*, *B. procumbens* and *B. webbiana*) were also evaluated.

Powdery mildew

Field evaluation

Four years of evaluations were conducted (1997–2000) and, because of the vulnerability of accessions of the Sections *Corollinae* and *Procumbentes* to the U.K. climate, field testing was limited to Section *Beta* accessions. Evaluations were made in nurseries constructed to maximise infection from naturally occurring powdery mildew epiphytotics. Accessions were sown in single plots, each containing 20–30 plants, depending on seed viability, (except in 1997 when 10 plants per plot were sown) divided equally in three rows. Plots were sown in May to avoid frosts. Every fourth plot and the space between parallel rows of plots were sown with the susceptible U.K. sugar beet cultivar 'Sandra' to encourage uniform infection. Bolting and senescing plants were cut back to encourage re-growth and thus lengthen the growing period. A single disease assessment on up to 25 plants (10 in 1997) was made in late

Table 1. Powdery mildew disease assessment scale

Score	Description
0	No obvious infection.
1	Very few colonies present on some leaves; colonies discrete.
2	Increasing number of discrete colonies, occasionally coalescing, on many older leaves (<50% of surface area). Young leaves not affected.
3	Many older leaves extensively infected (>50% of leaf area).
	No or very little infection of younger leaves.
4	Profuse growth and sporulation. All older leaves extensively infected; many younger leaves also infected.
5	Almost total infection of all leaves.

August/September using a 0–5 infection scale (Table 1) and a mean resistance value for each accession was obtained. Mean resistance values were adjusted in relation to the standard sugar beet cultivar Sandra using the method described for virus yellows and transformed to the standard 1–9 resistance scale (a RS of 1 was equivalent to a mean resistance value of $\leq$0.55 and a RS of 9 $\geq$ 4.45).

In 1998, an experiment examining different disease assessment dates was conducted within the main trial. Sixteen accessions, previously tested in 1997 and representing all resistance levels, were resown and assessed using the standard infection assessment scale at two-weekly intervals from the first appearance of powdery mildew (late July). Data were analysed using Spearman's Rank Correlation test to see if the relative resistance of accessions in earlier assessments correlated with those in the final assessment. Additionally, the single point assessment data were combined to produce a value for the Area Under the Disease Progress Curve (AUDPC - Campbell & Madden, 1990) to represent the continuous development of powdery mildew on each accession, thus:

$$\text{AUDPC} = \sum_{i}^{n-1} ((y_i + y_{i+1})/2)(t_{i+1} - t_i)$$

where y = disease intensity (expressed as a mean plant score of each test accession) at intervals i and $i + 1$ separated between times t and $t + 1$.

During each year's trial, data were collected on the extent of bolting exhibited by each accession in order to assess the influence that the annual growth habit had on resistance. Accessions were classified as annual (>90% plants bolted), biennial (<10% bolted) or mixed (10–90% bolted). These were collated with the powdery mildew RS values obtained for each accession. Analysis was confined to *Beta* species where relative resistance exhibited by annual and biennial accessions was measured by counting the number of accessions of each with RS values above and below the mean RS for all accessions.

Additionally, the geographical distribution of powdery mildew resistance in *B.v. maritima* was examined; this sub-species was used because sufficient accessions had been evaluated and accurate information on their geographical origin was available on the IDBB database (IDBB, 2003). Analysis was restricted to accessions from Europe and North Africa (98% of total). This area was divided into two zones, north and south of 46°N; the southern zone was further subdivided, east and west of 15°E. Effectively, this delineated three geographical zones: NW Europe, the Western Mediterranean (centred on Spain) and the Eastern Mediterranean (centred on Greece). The level of powdery mildew resistance observed in each zone was measured in the same manner used for testing the effects of annuality on resistance.

Glasshouse evaluation

A single glasshouse experiment was conducted to compare the relative resistance of the sections *Corollinae* and *Procumbentes*, both considered too vulnerable to test in the U.K. climate, with selected Section *Beta* accessions representing a range of resistance levels. Comparisons of the resistance levels expressed by Section *Beta* accessions in the glasshouse and field were also made to see if glasshouse evaluation might be a feasible alternative to field testing.

Thirty-two accessions of the Sections *Beta*, *Corollinae* and *Procumbentes* were evaluated. Thirty seeds were sown per accession; emerged seedlings were transplanted to 6.5 cm pots, and maintained in a glasshouse at ca. 25 °C with 16 h supplementary light. Seedlings were infected with naturally occurring powdery mildew inoculum present in the glasshouse. All emerged plants (Section *Beta* >20 plants; sections *Corollinae* and *Procumbentes* 6–20) were assessed for infection using the field assessment scale (Table 1) after 10 weeks from sowing and a mean infection score calculated for each accession. Results for Section *Beta* accessions were compared with the equivalent field results collected in 1998.

Table 2. Location of Cercospora trials in Italy

Year	Trial Organisers[1]	Location in Italy
1997	SPSB	Bentivoglio, Bologna (Azienda Olmo Donzelli)
1998	SPSB	Budrio, Bologna (Azienda Riccardina)
1998–2000	ISCI	Rovigo (Azienda di Consorzio Agrario Provinciale)
2001	ISCI	Rovigo (Azienda Saccomani)

[1]SPSB = Società Produttori Sementi S.p.a, Italy; ISCI = Istituto Sperimentale per le Colture Industriali, Italy.

Table 3. Cercospora leaf spot assessment scale

Score	Description
1	Very low susceptibility; no or very few discrete lesions observed on outer leaves.
3	Low susceptibility; few, evenly distributed discrete lesions found on outer leaves.
5	Intermediate susceptibility; lesions beginning to coalesce forming small areas of necrotic tissue (about 25% of total leaf area).
7	High susceptibility; lesions coalescing to form large areas of necrotic tissue (about 75% of total leaf area).
9	Very high susceptibility; diseased leaves and petioles completely necrotic and dry.

Cercospora leaf spot

The Cercospora evaluation programme was conducted by SPSB (1997–1998) and ISCI (1998–2001) at several sites in Italy (Table 2). Changes in location and management were required as the SPSB sites were located in Emilia-Romagna, a region where growing annual *Beta* species is prohibited to protect locally grown sugar beet seed crops from pollen contamination; this prevented annual accessions from being tested in this region.

A similar protocol was used at all sites. Section *Beta* accessions were sown directly in the field in March-April. Section *Corollinae* and *Procumbentes* accessions were initially propagated in glasshouses; seed was sown in pots containing a soil/sand mixture, left to grow to the 6–8 leaf stage in a controlled environment (20–25 °C and a natural photoperiod) and subsequently transplanted in May into the same trial used for evaluating Section *Beta* accessions. Plants were distributed in 1–3 rows, each row containing 20–45 plants, depending on seed viability. Uniform infection was achieved by artificially inoculating accessions with *C. beticola* spores, prepared by grinding severely infected sugar beet leaves collected in the previous year, suspending the inoculum in water and spraying it onto plants in the first week of June (to coincide with the first natural infections). Infection assessment was made in late July-August (except in 1997, when a hailstorm, which destroyed many original leaves, forced the assessment to take place in September on newly emerged leaves). The leaf symptoms on each row per accession were assessed using a 1–9 Cercospora leaf-spot assessment scale (Table 3) and a mean score derived. The Cercospora data collected in each region were adjusted using the standard susceptible sugar beet cultivar 'Gilamon' (1997–1998) or 'Gabriela' (1999–2001); both cultivars exhibited similar levels of susceptibility. Subsequently, results were transformed to the standard RS 1–9 resistance scale.

Data interpretation and analysis

Analyses were conducted hierarchically. In the first place, the distribution of RS (resistance score) values of all accessions, regardless of identity, was measured and an overall mean estimated. Subsequently, comparisons were made between the three *Beta* sections (*Beta*, *Corollinae*, *and Procumbentes*). Next, contrasts were made between species within the Section *Beta* (not repeated with other sections as relatively few accessions were assessed) by counting the number of accessions within each species above and below the overall mean response, and comparing distributions. Finally, the number of very highly resistant accessions (RS $\leq$2) within each species is reported.

Assessments of multiple resistance were limited to the 428 accessions tested against all four diseases. Each accession was assigned an RS value equivalent to the worst score observed for any of the resistance traits under consideration. Data were then investigated in the same hierarchical manner used for single resistance traits.

Results

Virus yellows resistance

Overall, a wide range of resistance was observed; the distribution of all results was near-normal (Figure 2a) with a mean RS of 4.4 and 4.6 recorded for BMYV and BYV respectively. The mean resistance and the range

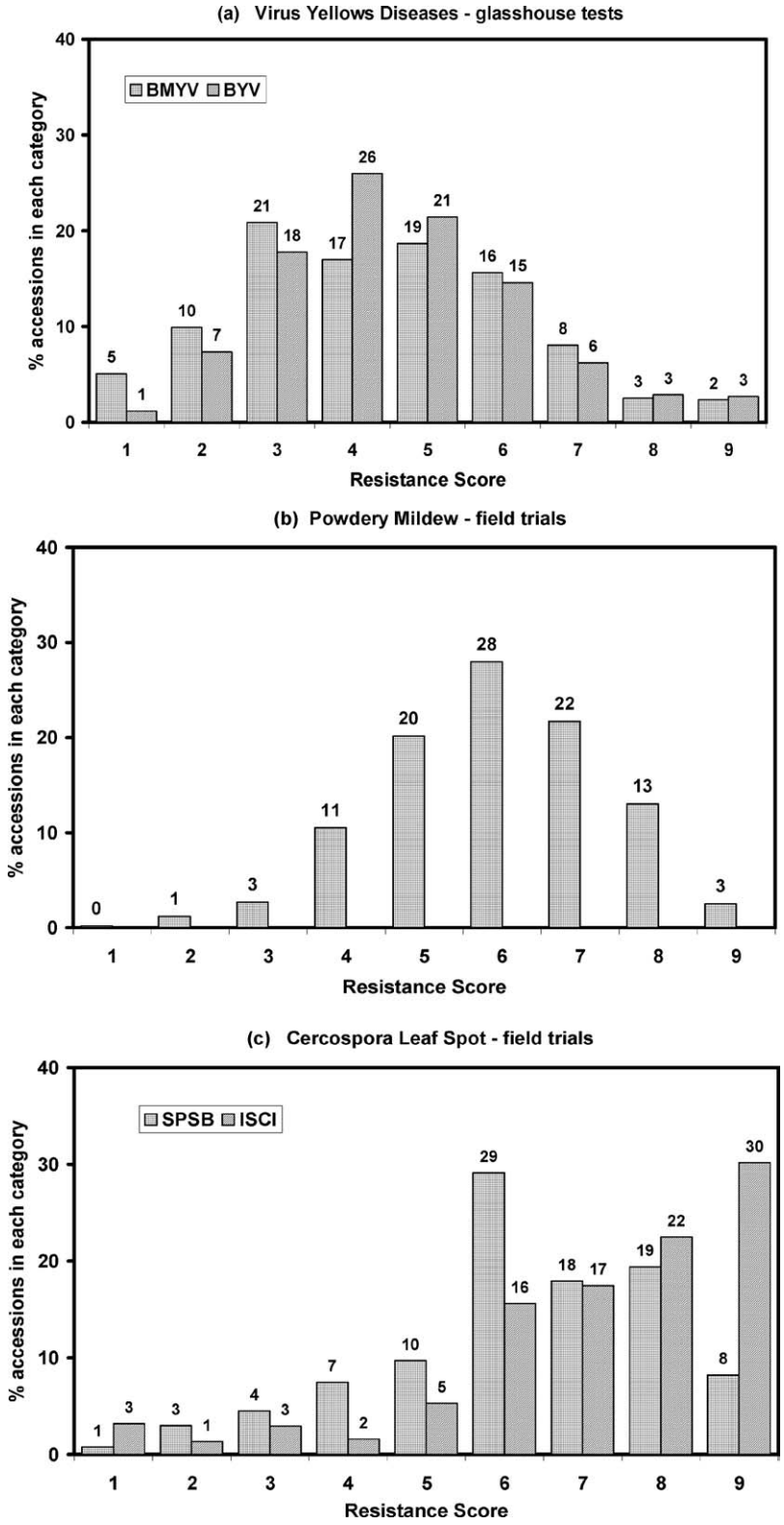


Figure 2. Frequency distribution of resistance in genus *Beta* accessions to four foliar diseases in glasshouse and field tests.

Table 4. Summary of resistance to virus diseases within the genus *Beta*

Disease	BMYV				BYV			
Test Centre/Method[1]	BB – GLASS				BB – GLASS			
Beta section/species	n[2]	Mean RS[3]	Range RS	nRS 1–2[4]	n	Mean RS	Range RS	nRS 1–2
Sections of the genus *Beta*								
Corollinae	12	1.0	1	12	13	2.3	1–4	8
Procumbentes	10	1.1	1–2	10	10	3.9	1–9	2
Beta	573	4.5	1–9	69	574	4.6	1–9	40
Species/sub-species/cultivars of the Section *Beta*								
Wild types								
B. macrocarpa	13	4.5	3–6	0	13	5.2	3–8	0
B. patula	1	1.0	1	1	1	7.0	7	0
B. vulgaris spp.	52	4.4	2–8	9	52	4.5	1–7	4
B.v. adanensis	13	5.8	4–9	0	13	5.7	3–9	0
B.v. maritima	158	4.8	2–9	10	159	4.7	2–9	11
Cultivated types								
Fodder beet	61	4.2	1–9	6	61	4.5	2–8	6
Garden beet	121	3.5	1–9	35	121	4.6	1–9	9
Leaf beet	123	5.4	1–9	5	123	4.7	2–9	11
Sugar beet	31	4.4	2–9	2	31	4.7	1–9	1
χ^2 value[5]	56.5 ($p < 0.001$)				8.5 (ns)			

[1]BB = Broom's Barn; GLASS = evaluations conducted in glasshouse.
[2]n = number of accessions tested.
[3]RS = mean and range of resistance scores (1–9 scale: 1 = very resistant and 9 = very susceptible).
[4]nRS 1–2 = number of very highly resistant accessions within section/species/subspecies/cultivar of *Beta* with RS 1–2.
[5]χ^2 value and probability for comparisons between Section *Beta* types (not including *B. patula*).

of responses for each section, and within the Section *Beta*, are given in Table 4. The mean RS of the standard sugar beet cultivar (cv. Saxon) in each virus yellows test was 6.

BMYV

All species evaluated in Sections *Corollinae* and *Procumbentes* were very highly resistant (RS $\leq$2) to BMYV with mean RS of 1.0 and 1.1 respectively; some had no detectable virus (Table 4). Section *Beta* species exhibited a more diverse range of resistance, which was reflected in a mean RS of 4.5. Significant differences ($p < 0.001$) in the relative resistance of Section *Beta* species to BMYV were observed; collectively, garden beets were the most resistant (mean RS 3.5) and leaf beets the most susceptible (mean RS 5.4) cultivated beets. Amongst wild types, *B. vulgaris* species (mean RS 4.4) were generally the more resistant and *B.v. adanensis* (mean RS 5.8) the more susceptible although a single accessions of *B. patula* had a RS of 1. These observations corresponded with the percentage of highly resistant accessions (RS $\leq$2); garden beets (29%) and *B. vulgaris* species (17%) accessions had the most, whilst none were observed amongst *B.v. adanensis* and *B. macrocarpa* accessions. Although leaf beets were generally susceptible, a single accession had a RS of 1.

BYV

Section *Corollinae* and *Procumbentes* accessions were also the most resistant to BYV, although mean RS levels were lower (2.3 and 3.9 respectively) and the infection range greater than for BMYV (Table 4). Consequently, there were fewer accessions with high resistance. Nevertheless, single *B. intermedia*, *B. lomatogona*, *B. macrorhiza* and *B. patellaris* accessions with a RS of 1 were identified. Section *Beta* species were the least resistant (RS 4.6), but the differential with other sections was lower. Collectively, there

were no significant differences within the Section *Beta* (Table 4). The frequency of highly resistant (RS $\leq$2) accessions was low among most types. The lone *B. patula* accession was highly susceptible (RS 7). Nevertheless, there were garden and sugar beet, and wild *B. vulgaris* spp. accessions, which had RS values of 1.

Powdery mildew resistance

Field evaluation

The overall distribution of responses in the 575 Section *Beta* accessions tested was skewed towards susceptibility (Figure 2b) with a mean RS of 6.0. Powdery mildew epiphytotics were consistent throughout testing with symptoms on the standard sugar beet cultivar 'Sandra' scoring 2.8–3.1 on the infection scale used (equivalent to a mean RS of 6). Significant differences in resistance were observed within the Section *Beta* ($p < 0.05$) (Table 5). The most resistant cultivated and wild types were garden beets and *B. vulgaris* spp. (both mean RS 5.7), whilst sugar beet (mean RS 6.1) and *B. macrocarpa* (mean RS 7.5) were the most susceptible. Only three garden and leaf beet accessions had very high levels of resistance (RS $\leq$2).

Disease evaluation dates had no effect on the relative resistance of individual accessions. Results from evaluations 6, 4 and 2 weeks prior to the final assessment on 7 September were highly correlated ($p < 0.001$) with the final assessment itself (Table 6). Nor were there any differences between single point and continuous (AUDPC) assessments.

Annuality levels varied in the powdery mildew trials. Wild *B. vulgaris* spp. and cultivated garden and leaf beets had a significant number of both annual and biennial accessions (Table 7). When the resistance of annual and biennial types was compared, only those within *B.v. maritima* were significantly different ($p < 0.001$), with biennial accessions being the most resistant. Subsequent analysis (data not shown) showed that all but one biennial *B.v. maritima* accession were from northern Europe and resistance levels in this region were significantly higher than in the south ($p < 0.001$). There were no differences in annuality and resistance between the areas of southern Europe. A sub-analysis of *B. v. maritima* accessions in northern Europe indicated that resistance levels in annual types were not significantly different from those in biennial types ($p = 0.12$).

Glasshouse screening

Section *Procumbentes* accessions were the most resistant (mean RS 3.0) in the glasshouse test; the most resistant species was *B. patellaris* (Table 5). Section *Beta* accessions were intermediate in resistance (mean RS 6.3), whilst all Section *Corollinae* accessions were highly susceptible (mean RS 8.5). There was a significant correlation between glasshouse and field results of the Section *Beta* accessions tested in both environments (Spearmans rank correlation $R = 0.64$; $p < 0.01$) (Figure 3). However, relative differences in the glasshouse were smaller as accessions exhibiting resistance in the field were prone to higher infection under the more severe disease pressure generated in the glasshouse.

Cercospora resistance

512 accessions were tested for Cercospora resistance (134 by SPSB in Emilia-Romagna and 378 by ISCI in Veneto). Accessions of all *Beta* sections were tested in Veneto, including a high proportion of Section *Corollinae* (7.8%), but the SPSB evaluation was confined to predominately biennial accessions of the Section *Beta* (Table 5). The frequency distribution of resistance was skewed towards susceptibility in both regions, more so in the ISCI (mean RS 7.7) than in SPSB trial (mean RS 6.3). The two distribution patterns were significantly different (for analysis, data were divided into accessions that had high (RS 1–3), intermediate (RS 4–6) and low (RS 7–9) resistance regardless of whether all accessions were included in the analysis (Figure 2c; χ^2 37.4; $p < 0.001$) or Section *Beta* species alone (χ^2 48.8; $p < 0.001$). Consequently, the data from each region were considered independently.

SPSB

Cercospora infection was consistent in 1997 and 1998; the standard sugar beet cultivar 'Gilamon' had a RS of 9 in both years. Significant differences ($p < 0.001$) in the relative resistance of Section *Beta* species were observed (Table 5); *B.v. maritima* accessions were the most resistant (mean RS of 4.5), whereas fodder (mean RS 7.3) and sugar beets (mean RS 7.5) performed poorly. Correspondingly, *B.v. maritima* had most resistant accessions (RS $\leq$2), with three in total. A single garden and sugar beet accession had a RS of 2. A resistant sugar beet cultivar 'Jollysaros' had an RS of 3–4.

ISCI

Cercospora infection in Veneto was more variable (RS of 7–9 on the susceptible sugar beet cv. 'Gabriela'). Collectively, Section *Procumbentes* accessions were

Table 5. Summary of resistance to fungal diseases within the genus *Beta*

Disease	Powdery mildew								Cercospora leaf spot							
Test centre/method[1]	BB – FIELD				BB – GLASSHOUSE				SPSB – FIELD				ISCI – FIELD			
Beta section/species	*n*[2]	Mean[3] RS	Range RS	*n*RS[4] 1–2	*n*	Mean RS	Range RS	*n*RS 1–2	*n*	Mean RS	Range RS	*n*RS 1–2	*n*	Mean RS	Range RS	*n*RS 1–2
Sections of the genus *Beta*																
Corollinae	nt[5]	–	–	–	11	8.5	8–9	0	nt	–	–	–	40	4.0	1–7	6
Procumbentes	nt	–	–	–	4	3.0	2–4	2	nt	–	–	–	11	1.1	1–2	11
Beta	575	6.0	1–9	6	17	6.3	5–9	0	134	6.3	1–9	5	327	7.7	3–9	0
Species/sub-species/cultivars of the Section *Beta*																
Wild types																
B. macrocarpa	13	7.5	6–8	0	nt	–	–	–	nt	–	–	–	1	7.0	7	0
B. patula	1	5.0	5	0	nt	–	–	–	nt	–	–	–	nt	–	–	–
B. vulgaris spp.	53	5.7	3–9	0	1	6.0	6	0	2	7.0	7	0	65	8.5	6–9	0
B.v. adanensis	13	6.7	5–8	0	nt	–	–	–	nt	–	–	–	5	8.0	8	0
B.v. maritima	159	6.1	3–9	0	3	6.0	5–7	0	28	4.5	1–7	3	57	7.3	3–9	0
Cultivated types																
Fodder beet	61	6.3	4–8	0	2	6.0	5–7	0	31	7.3	6–9	0	31	7.8	5–9	0
Garden beet	121	5.7	2–8	4	6	6.4	5–8	0	23	6.2	2–9	1	86	7.9	5–9	0
Leaf beet	123	5.9	1–9	3	4	6.2	4–9	0	35	6.3	4–9	0	65	7.1	4–9	0
Sugar beet	31	6.1	4–9	0	1	6.0	6	0	15	7.5	2–9	1	17	7.5	4–9	0
χ^2 value[6]			15.8 ($p < 0.05$)				nt				38.9 ($p < 0.001$)				27.2 ($p < 0.001$)	

[1]BB = Broom's Barn, U.K.; SPSB = Società Produttori Sementi S.p.a, Italy; ISCI = Istituto Sperimentale per le Colture Industriali, Italy; GLASS = evaluations conducted in glasshouse; FIELD = evaluations conducted in the field.
[2]*n* = number of accessions tested.
[3]RS = mean and range of resistance scores (1–9 scale: 1 = highly resistant and 9 = highly susceptible).
[4]*n*RS 1–2 = number of very highly resistant accessions within section/species/subspecies/cultivar of *Beta* with RS 1–2.
[5]nt = not tested.
[6]χ^2 value and probability for comparisons between Section *Beta* types (not including *B. patula*).

Table 6. Comparison of single point and continuous assessment of powdery mildew infection levels on selected accessions within the Section *Beta*

Accession		Powdery mildew infection levels (0–5)[1]				
IDBB No[3]	Identity	Final result[4]	6 weeks earlier	4 weeks earlier	2 weeks earlier	AUDPC[2]
1098	Leaf beet	0.48	0.00	0.00	0.00	2.41
3408	Garden beet	0.52	0.00	0.18	0.33	2.70
6223	Garden beet	0.56	0.00	0.00	0.18	2.69
3963	Garden beet	1.04	0.18	0.37	0.78	5.33
6453	Garden beet	1.33	0.22	0.37	0.93	6.98
3863	*B.v. maritima*	1.81	0.26	0.41	0.74	9.57
2193	*B.v. maritima*	1.85	0.07	0.33	1.48	9.09
2671	*B.v. maritima*	2.81	0.96	1.55	2.44	16.15
6281	Garden beet	3.11	1.01	1.67	2.67	17.74
8540	Garden beet	3.42	1.56	2.16	3.04	20.39
7104	*B.v. maritima*	3.56	0.47	0.86	2.67	18.21
6327	Fodder beet	3.62	1.36	1.79	2.91	20.68
8643	Leaf beet	4.21	1.24	1.85	3.28	23.42
9080	Leaf beet	4.22	1.44	2.15	3.34	23.66
9058	Leaf beet	4.31	1.19	2.12	3.48	24.25
			Sugar beet cultivars			
Roberta	Sugar beet	2.96	0.22	0.85	1.93	15.35
Saxon	Sugar beet	3.19	1.44	1.74	2.63	18.67
Sandra	Sugar beet	3.33	1.18	1.63	2.59	19.00
Mean[5]		2.57	0.71	1.11	1.97	14.24
Spearman's *R* value			0.84	0.91	0.97	0.98
P			<0.001	<0.001	<0.001	<0.001

[1]Powdery mildew infection levels assessed using 0–5 assessment scale where 0 = no infection and 5 = almost total infection of leaves (see Table 1).
[2]AUDPC = Area Under the Disease Progress Curve (Campbell & Madden 1990).
[3]IDBB = International Data Base for *Beta*.
[4]Final powdery mildew infection results (7 September) were compared with results taken 6, 4 and 2 weeks earlier.
[5]Mean of powdery mildew infection levels of all accessions tested.

most resistant (mean RS 1.1); all but one accession had RS of 1 and several had no symptoms at all. Overall, Section *Corollinae* accessions were moderately resistant (mean RS of 4.0) but individual species showed high resistance, e.g. *B. trigyna* (mean RS of 2.8). Despite significant differences being observed within the Section *Beta* ($p < 0.001$), these reflected varying degrees of susceptibility rather than any one type exhibiting high levels of resistance; in general, leaf beets (mean RS 7.1) and *B.v. maritima* (mean RS 7.3) were not as susceptible as *B. vulgaris* spp. (mean RS 8.5). However, no Section *Beta* accessions had very high resistance (RS < 2); the best were three *B.v. maritima* accessions with RS of 3.

Multiple resistance

The frequency of occurrence of resistance to more than one disease within an accession was highest in the Section *Procumbentes*, despite the low numbers tested (Figure 4). Twenty-five percent of all Section *Procumbentes* accessions tested (all *B. patellaris*) were resistant to the four foliar diseases at RS ≤2, and 50% at RS ≤4.

The probability of multiple resistance occurring in sections *Corollinae* (9 accessions tested) and *Beta* (415 accessions tested) were progressively lower; neither had accessions resistant to more than two diseases at RS ≤2. However, both showed greater potential at

Table 7. Resistance to powdery mildew exhibited by annual and biennial accessions of the Section *Beta* in field trials

Section *Beta* type	Annuality[1]	Number tested	% Above average resistance accessions[2]	Probability[3]
Garden beet	Annual	10	50	0.86
	Biennial	66	47	
Leaf beet	Annual	33	46	0.16
	Biennial	35	29	
B. vulgaris spp.	Annual	31	33	0.34
	Biennial	10	50	
B.v. maritima	Annual	129	29	<0.001
	Biennial	14	86	

[1] Annual accessions >90% bolting in field; biennial accessions <10% bolting in field.
[2] Percentage of accessions scoring above the mean resistance score of all Section *Beta* accessions (RS ≤5).
[3] Probability of difference following analysis using Fisher exact test on numbers of 'above' and 'below' mean resistance score.

a lower level of resistance (RS ≤4), depending on the combination of diseases involved. *B. corolliflora* and *B. macrorhiza* were the most promising within the Section *Corollinae*, whilst in the Section *Beta*,*B.v. maritima* had the greatest potential with three accessions exhibiting resistance to four diseases at RS ≤4. The only cultivated beet displaying the same potential was a single garden beet accession. The least likely sources for multiple resistance were *B.v. adanensis* and *B. macrocarpa*.

Discussion

The evaluation programmes have demonstrated the potential of *Beta* germplasm as a source of resistance to four important foliar diseases of sugar beet. For several traits, there is a significant pool of resistance genes already available in gene banks that can be utilised immediately. However, the value of these sources will differ. The most important criterion for selection will be the ease with which novel resistance genes can be introgressed into sugar beet. *Beta* species differ in their sexual compatibility with sugar beet and therefore in their use as parents in conventional breeding programmes. To reflect this, the genus has been divided into three gene pools – primary, secondary and tertiary – each containing species with differing compatibility status with sugar beet. (Frese et al., 2001).

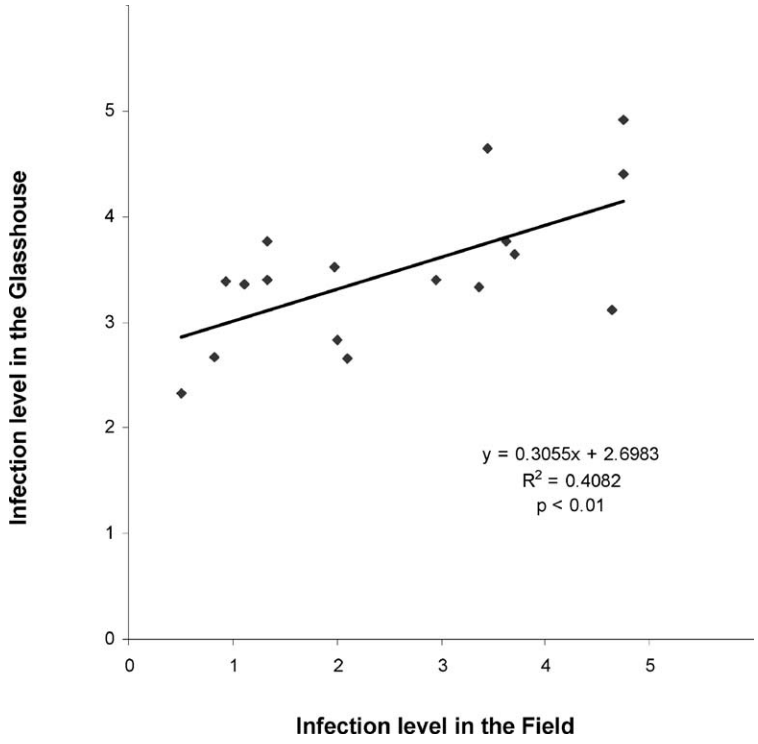
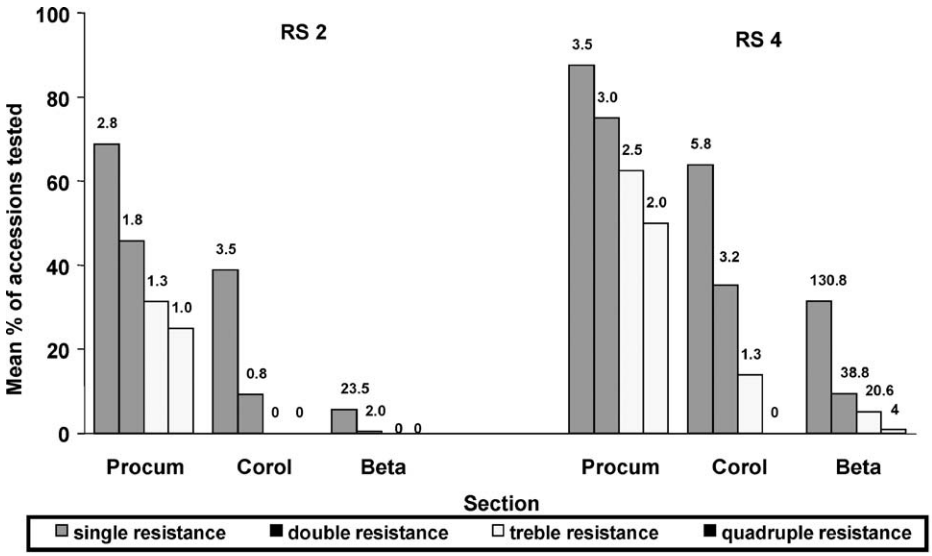


Figure 3. Comparisons of powdery mildew infection levels in field and glasshouse tests of 17 Section *Beta* accessions.



RS 2 = mean % of accessions scoring RS≤2; RS 4 = mean % of accessions scoring RS≤4.

Procum = Section *Procumbentes* accessions; Corol = Section *Corollinae* accessions; Beta = Section *Beta* accessions.

Numbers heading each column are the actual number of accessions in that category

Figure 4. Multiple resistances within the genus *Beta* to powdery mildew, Cercospora leaf spot and the yellowing viruses (BMYV and BYV).

The primary gene pool, consisting of Section *Beta* types, including cultivated beets, is highly compatible with sugar beet; some species such as *B.v. maritima* form natural hybrids with sugar beet (Van Geyt et al., 1990). The cross-compatibility seen within the Section *Beta* reflects their common heritage; *B.v. maritima* is believed to be the progenitor of all cultivated beets, including sugar beet, as it shares many genotypic and phenotypic characters in common (Poehlman, 1987). Consequently, these species can be used readily in conventional breeding programmes. However, collectively they have the lowest potential as resistance sources; mean RS values ranged from 4.5 to 7.7. Despite this, high levels of heterogeneity in resistance were observed, perhaps as a result of the species' relatively widespread distribution and geographical variation in the prevalence of diseases (Francis & Luterbacher, 2003), and high resistance (RS $\leq$ 2) was detected, albeit at a low frequency (1–12%).

Species of sections *Corollinae* and *Procumbentes* (secondary and tertiary gene pools respectively) are progressively more incompatible with sugar beet. Indeed, genomic differences between sugar beet and Section *Procumbentes* species suggest that the latter should be considered as a separate genus (Jung et al., 1993). Consequently, these sections are regarded less favourably by breeders. However, they could be invaluable as resistance sources; with one exception, species of these sections were more resistant to the four foliar diseases than those of the Section *Beta*, some exhibiting apparent immunity.

The superiority of sections *Corollinae* and *Procumbentes* was demonstrated in the virus yellows evaluation tests, particularly against BMYV, where the high resistance observed confirmed earlier observations (Van Geyt et al., 1990). Of more immediate practical use was the relatively high frequency of virus yellows resistance found within the Section *Beta*. Here, garden beets were more resistant collectively and individually, with more highly resistant accessions (RS $\leq$2) than in other cultivated types. Conversely, no differences were observed in the frequency of BYV resistance among Section *Beta* species; the numbers of highly resistant accessions were evenly distributed. How resistance to these virus yellows diseases

functions – against the virus or the aphid vector – is unknown. However, resistance to BMYV does not confer resistance to *Beet chlorosis* virus; accessions identified as resistant to the former were susceptible to the latter (unpublished data).

Results from the powdery mildew and Cercospora field trials indicated that most accessions were susceptible to these diseases, giving skewed frequency distributions. Although there were significant differences within the Section *Beta*, there was little to distinguish the major types; all were variable, most were generally susceptible, and there were few highly resistant (RS $\leq$2) accessions. *B.v. maritima* has been considered an important source of resistance to powdery mildew (Whitney, 1989), but here its performance was moderate and similar to other Section *Beta* species. The difference may result from using different accessions of the species or testing at widely separated locations, each of which may have its own spectrum of pathogenicity or exert different disease pressure. Other annual species (*B. macrocarpa* and *B.v. adanensis*) performed relatively poorly in our trials. However, glasshouse evaluation indicated that Section *Procumbentes* species were highly resistant, as observed by Ruppel & Tomasovic (1997), but Section *Corollinae* species were susceptible.

The value of *B.v. maritima* was more apparent in the Cercospora trials. Generally, it was the most resistant species of the Section *Beta* types with several highly resistant accessions identified. *B.v. maritima* has been, and remains, a valuable source in breeding for Cercospora resistance in sugar beet (Munerati, 1932, Panella & Frese, 2000; Skaracis & Biancardi, 2000). Usefully, high levels of resistance were also identified in several sugar and garden beet accessions. However, the highest level of resistance to Cercospora was observed in the Section *Procumbentes*; all the species tested (*B. patellaris*, *B. procumbens* and *B. webbiana*) exhibited high resistance, some were apparently immune. These observations agree with those of Coons (1954). Some highly resistant Section *Corollinae* accessions were also identified, but numbers were lower than in the Section *Procumbentes*; *B. trigyna* accessions were the most resistant.

There is some evidence to link levels of disease resistance to the annuality of accessions, as biennial *B.v. maritima* accessions were more resistant than annuals. However, whether these differences are related to physiological changes induced by bolting or some other mechanism is unclear. Most biennial *B.v. maritima* accessions originated from northern Europe, where powdery mildew is endemic. It is possible that natural selection in response to continuing infection pressure may account for the higher levels of resistance. Interestingly, analysis of the subset of annual and biennial *B.v. maritima* accessions from N. Europe revealed no differences, although the sample size was small. Alternatively, these differences may be an artefact of the methodology since annual accessions had much reduced leaf sizes and, in order to prolong their life-span to ensure infection, plants were repeatedly cut back to promote new growth.

The number of useful sources of resistance identified using mean RS values for each accession considerably underestimated the gene pool available for breeding, particularly within the Section *Beta* where significant heterogeneity within accessions was observed. This can be demonstrated from the BMYV resistance results from two garden beet accessions, both of which had a mean RS value of 5 (Figure 5). In accession #2582, 30% of the plants tested had RS scores of 1, making it a useful source of resistance genes for introgression into sugar beet. Therefore, both means and variation should be considered when making selections for further development otherwise useful material could be lost.

Accessions with potential as multiple sources of resistance were also identified. The numbers depended on the Section to which they belonged, the diseases of interest and the level of resistance sought. Multiple resistance to all four diseases at the highest level (RS $\leq$2) was common in the Section *Procumbentes*, largely within *B. patellaris*. Other sections did not contain accessions with resistance to more than two diseases. At resistance level RS $\leq$4, there were more candidates, although Section *Corollinae* accessions could not be a resistance source for more than three diseases because of their universal susceptibility to powdery mildew. Within the Section *Beta*, *B.v. maritima* and garden beets were most likely to exhibit multiple resistance at this level. RS values of 4 represent resistance levels higher than that achieved by many, currently available sugar beet cultivars. Details of the resistance observed (and other phenotypic traits) in each accession described here can be obtained from the International Database for Beta (IDBB) website: www.genres.de/idb/beta.

For resistant germplasm to be reliably identified, evaluation methods must be straightforward to implement, flexible enough to accommodate the diversity of material used, and sufficiently robust to provide consistent results. The glasshouse tests were simpler to

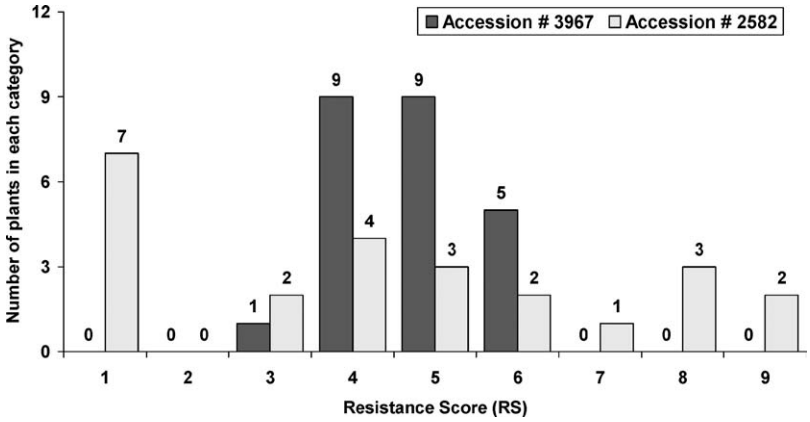


Figure 5. Distribution of BMYV resistance among plants of two garden beet (*Beta vulgaris*) accessions with mean RS values of 5 in glasshouse tests.

manage and under more precise environmental control than field trials, and were easier to evaluate. Virus yellows results were relatively consistent, particularly with BMYV, where a specific monoclonal antibody was used; resistant accessions were often tested twice to confirm results. The polyclonal antibody used for detecting BYV also proved adequate for discriminating between accessions. Another advantage of these tests was that they provided measures of resistance on a continuous scale, which could be manipulated more easily and were statistically more robust than those derived from the discontinuous scoring system used in field trials.

Field testing proved more challenging. Fortunately, powdery mildew and Cercospora epiphytotics, either naturally occurring or artificially created, were moderately severe at all sites, an important factor for the reliable identification of resistance (Panella & Frese, 2000). However, Cercospora evaluation results showed that disease intensity varied between and within regions, which may have influenced the results. The exact cause(s) of this variation can only be speculated at – levels of naturally occurring disease inoculum, the success of artificial inoculation, differences in annuality of accessions used at both sites, varying climatic conditions – but the outcome was to affect the distribution of resistance scores from the two Cercospora datasets. In the absence of susceptible and resistant standards common to both sets of evaluation data, it was difficult to combine the two and they were therefore reported separately.

Field assessments were left as late as necessary to ensure maximum infection, which may provide an apparent reason for the skewness in the distribution. However, the RS values in each trial were adjusted to reflect relative rather than absolute levels of disease infection and, as was shown in the 1998 powdery mildew trials, these do not appear to alter significantly during the course of infection. Logistically, it is much easier, and less prone to experimental variation, to assess large volumes of material when the disease is more readily observed.

During evaluation, a glasshouse test for assessing powdery mildew resistance was explored. Results indicated that field and glasshouse results were correlated, but that accessions considered resistant in the field developed higher levels of infection under glass. This effect may be due to plant age and its effect on the expression of resistance, the glasshouse environment, difficulties in assessing small plants using a scale developed for mature plants in the field, or a combination of all three. Nevertheless, the distinctions within the sections *Procumbentes* and *Corollinae* were sufficiently clear cut to warrant inclusion with results from field tested germplasm. Glasshouses could provide an environment in which to conduct a primary evaluation of *Beta* germplasm for resistance, to eliminate highly susceptible germplasm prior to field screening. This would reduce the size of field trials, which are more difficult to infect, relatively labour intensive and expensive. Attempts to develop a glasshouse test for Cercospora have met with limited success (Panella & Frese, 2000).

Exploitation of the resistant material so far identified has begun. Pre-breeding to introgress virus yellows and powdery mildew resistance genes into sugar beet breeding lines is being undertaken using Section

Beta accessions. The rate of progress will depend on the genetic complexity of the resistance but, even if successful, incorporating such resistance genes into a commercial sugar beet cultivar will be a lengthy process. At the same time, this large resource of disease resistant material offers the opportunity to increase our understanding of the genetic mechanisms of resistance and how they function, e.g. whether different sources have different genes, whether genes are allelic, closely linked or amenable to recombination to enhance resistance and whether they are associated with other traits. Many of these questions can be answered through the development of molecular markers linked to resistance genes, enabling the subsequent mapping of those genes. Some molecular markers have already been developed, for example to major genes for powdery mildew resistance and qualitative trait loci (QTL) controlling resistance to Cercospora (Nilsson et al., 1999; Schäfer-Pregl et al., 1999). Once identified, tightly linked molecular makers can be used to assist in the selection of resistant material, thus accelerating the breeding of new sugar beet cultivars.

Perhaps the biggest advance in breeding for resistance to virus yellows, powdery mildew and Cercospora in sugar beet would result from the utilisation of the highly effective resistance genes in the sections *Procumbentes* and *Corollinae*. However, because of sexual incompatibility, the utilisation of such genes (e.g. through the use of monosomic addition lines; Heijbroek et al., 1988) is difficult and can lead to genetic instability in succeeding generations. Alternatively, gene cloning and transformation of sugar beet with the target genes could be attempted. Such an approach has been used to isolate the gene in *B. procumbens* controlling resistance to the beet cyst nematode *Heterodera schachtii* (Cai et al., 1997). However, much research, breeding effort and public debate will have to be conducted before sugar beet cultivars containing such genes from these sources will be commercially available.

Acknowledgments

We wish to thank Jo Smith, Kathy Bean and Kevin Sawford for their technical assistance throughout the project. This work was supported by the Commission of the European Communities and funded through the Council Regulation (EC) No. 1467/94 on The Conservation, Characterisation, Collection and Utilisation of Genetic Resources in Agriculture. Additional funding in the U.K. was provided by the British Beet Research Organisation. Broom's Barn Research Station is a division of Rothamsted Research and receives grant-aided support from the Biotechnology and Biological Research Council, U.K.

References

Anon, 1982. Pests, Diseases and Disorders of Sugar Beet. Deleplanque & Cie, Maisons Lafitte, France.

Ayala, J. & L. Gordo, 1998. Effets de l'Oïdium et de la cercosporiose sur le rendement et al qualité de la betterave sucrière dans les conditions espagnoles. Plenary meeting Mediterranean Section of Institut International de Recherches Betteravières, pp. 21–30. IIRB, Brussels.

Buttler, K.P., 1977. Revision von Beta Sektion Corollinae (Chenopodiacea). I. Selbsterile Basisarten. Mitt Bot Munich 13: 255–336.

Byford, W.J., 1996. A survey of foliar diseases of sugar beet and their control. In Proceedings of the 59th Congress of the Institut International de Recherches Betteravières, pp. 1–10. IIRB, Brussels.

Cai, D., M. Kleine, S. Kifle, H-J. Harloff, N.N. Sandel, K.A. Marcker, R.M. Klein-Lankhorst, E.M.J. Salentijn, W. Lange, W.J. Stiekema, U. Wyss, F.M.W. Grundler & C. Jung, 1997. Positional cloning of a gene for nematode resistance in sugar beet. Science 275: 832–834.

Campbell, C.L. & L.V. Madden, 1990. Introduction to Plant Disease Epidemiology. J.W. Wiley and Sons. New York.

Cariolle, M., 1990. La jaunisse virale en Europe: evolution récente, incidence données épidémiologiques et schema d'avertissements. In Proceedings of the 53rd Congress of the Institut International de Recherches Betteravières, pp. 307–322. IIRB, Brussels.

Cooke, D.A. & R.K. Scott, 1993. The Sugar Beet Crop. Chapman & Hall, London

Coons, G.H., 1954. The wild species of *Beta*. Proc Am Soc Sugar Beet Technologists 8: 142–147.

Dewar, A.M., L.A. Haylock & P.M.J. Ecclestone, 1996. Strategies for controlling aphids and virus yellows in sugar beet. Proc Brit Crop Prot Conf – Pest and Diseases 1: 185–190.

Doney, D.L., 1993. Broadening the Genetic Base of Sugarbeet. J Sugar Beet Res 30: 209–219.

Duffus, J.E. & E.G. Ruppel, 1993. Diseases. In: D.A. Cooke & R.K. Scott (Eds.), The Sugar Beet Crop, pp. 346–427. Chapman & Hall, London.

Francis, S.A., 2002. Sugar-beet powdery mildew (*Erysiphe betae*). Mol Plant Pathol 3: 119–124.

Francis, S.A. & M.C. Luterbacher, 2003. Identification and exploitation of novel disease resistance genes in sugar beet. Pest Manag Sci 59: 225–230.

Frese, L. & B. Desprez, 1999. Utilization of *Beta* genetic resources. In: T. Gass, L. Frese, F. Begemann & E. Lipman (Eds.), Implementation of the Global Plan of Action in Europe – Conversation and Sustainable Utilization of Plant Genetic Resources for Food and Agriculture, pp. 172–180. IPGRI, Rome.

Frese, L., B. Desprez & D. Ziegler, 2001. Potential of genetic resources and breeding strategies for base-broadening in *Beta*. In H.D. Cooper, C. Spillane & T. Hodgkin (Eds.), Broadening the Genetic Base of Crop Production, pp. 295–309. IPGRI/FAO, Rome.

Hauser, S., M. Stevens, C. Mougel, H.G. Smith, C. Fritsch, E. Herrbach & O. Lemaire, 2000. Biological, serological and molecular variability suggest three distinct polerovirus species infecting beet or rape. Phytopathol 90: 460–466.

Heijbroek, W., A.J. Roelands, J. H. De Jong, C. Van Hulst, A.H.L. Schoone & R.G. Munning, 1988. Sugar beets homozygous for resistance to beet cyst nematode (*Heterodera schachtii* Schm) developed from monosomic additions of *B.procumbens* to *B. vulgaris.* Euphytica 38: 121–131.

Holtschulte, B., 2000. *Cercospora beticola* – worldwide distribution and incidence. In: *Cercospora beticola* Sacc. Biology, agronomic influence and control measures in sugar beet; Advances in Sugar Beet Research, pp. 5–16. IIRB, Brussels.

Ioannidis, P.M. & G.S. Karaoglandis, 2000. Competition between DMI sensitive and resistant strains of *Cercospora beticola* on untreated sugar beet crops. In: Proceedings of the 63rd Congress of the Institut International de Recherches Betteravières pp. 489–497. IIRB, Brussels.

IDBB, 2003. International Database for Beta (IDBB). Website: www.genres.de/idb/beta.

Jung, C., K. Pillen, S. Fähr & A.E. Melchinger, 1993. Phylogenetic relationships between cultivated and wild species of the genus Beta revealed by DNA 'fingerprinting'. Theor Appl Genet 96: 449–457.

Lange, W., W.A. Brandenburg & Th. S.M. De Bock, 1999. Taxonomy and cultonomy of beet (*Beta vulgaris* L.). Bot J Linn Soc 130: 81–96.

Letschert, J.P.W., 1993. Beta section Beta: biogeographical patterns of variation and taxonomy. Wageningen Agricultural University Paper 93–1.

Lewellen, R.T. & J.K. Schrandt, 2001. Inheritance of powdery mildew resistance in sugar beet derived from *Beta vulgaris* subsp. *maritima*. Plant Dis 85: 627–631.

Luterbacher, M.C., J.M. Smith & M.J.C. Asher, 1998. Sources of disease resistance in wild *Beta* germplasm. Asp App Biol 52: 423–429.

Munerati, O., 1932. Sull'incrocio della barbabietola coltivata con la beta selvaggia della costa adriatica. L'Industria Saccarifera Italiana 25: 303–304.

Nilsson N-O, M. Hansen, A.H. Panagopolous, S. Tuvesson, M. Ehlde, M Christiansson, I.M. Rading, M. Rissler & T. Kraft, 1999. QTL analysis of Cercospora beticola leaf spot resistance. Plant Breeding 118: 327–334.

Panella, L. & L. Frese, 2000. Cercospora resistance in *Beta* species and the development of resistant sugar beet lines. In: *Cercospora beticola* Sacc. Biology, agronomic influence and control measures in sugar beet; Advances in Sugar Beet Research, pp. 163–176. IIRB, Brussels.

Poehlman, J.M., 1987. Breeding Field Crops, 3rd ed. Van Nostrand Reinhold, New York.

Ruppel, E.G., 1995. Cercospora leaf spot. In E.D. Whitney & J.E. Duffus (Eds.) Compendium of Beet Diseases and Insects, pp. 8–9. American Phytopathological Society, St. Pauls, Minnesota.

Ruppel, E.G. & B.J. Tomasovic, 1997. Epidemiological factors of sugar beet powdery mildew. Phytopathol 67: 619–621.

Schäfer-Pregl R, D.C. Borchardt, E. Barzen, C. Glass, W. Mechelke, J.F. Seitzer & F. Salamini, 1999. Localisation of QTLs for tolerance to *Cercospora beticola* on sugar beet linkage groups. Theor Appl Genet 99: 829–836.

Scholten, O.E. & W. Lange, 2000. Breeding for resistance to rhizomania in sugar beet: a review. Euphytica 112: 219–231.

Skaracis, G.N. & E. Biancardi, 2000. Breeding for Cercospora resistance in sugar beet. In: *Cercospora beticola* Sacc. Biology, agronomic influence and control measures in sugar beet; Advances in Sugar Beet Research, pp. 177 -195. IIRB, Brussels.

Smith, H.G. & P.B. Hallsworth, 1990. The effects of yellowing viruses on yield of sugar beet in field trials, 1985 and 1987. Ann Appl Biol 116: 503–511.

Smith, H.G., I. Barker, G. Brewer, M. Stevens & P.B. Hallsworth, 1996. Production and evaluation of monoclonal antibodies for the detection of beet mild yellowing luteovirus and related strains. Eur J Plant Pathol 102: 163–169.

Stevens, M. H.G. Smith & P.B. Hallsworth, 1994. The host range of beet yellowing viruses among arable weed species. Plant Pathol 43: 579–588.

Van Geyt, J.P.C, W. Lange, M. Oleo & T.S.M. De Bock, 1990. Natural variation within the genus *Beta* and its possible use for breeding sugar beet: a review. Euphytica 49: 57–76.

Whitney, E.D., 1989. *Beta maritima* as a source of powdery mildew resistance in sugar beet. Plant Disease 73: 487–489.