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FULL RESEARCH PAPER

Response of UK winter wheat cultivars to *Soil-borne cereal mosaic* and *Wheat spindle streak mosaic viruses* across Europe

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Abstract Twenty-one UK winter wheat cultivars were grown over three seasons at sites with natural inoculum sources of *Soil-borne cereal mosaic virus* (SBCMV) and *Wheat spindle streak mosaic virus* (WSSMV) located in France, Italy and the UK. Plants were assessed visually for virus symptoms and leaf extracts were tested for the presence of each virus using enzyme-linked immunosorbent assays (ELISA). Cultivars showing little or no foliar symptoms and low levels of virus in leaf tissue were classified as resistant to each virus. All the trials were taken to harvest and agronomic data collected. At the most heavily infected sites, severe symptoms of SBCMV were observed in all UK cultivars except Aardvark, Charger, Claire, Cockpit, Hereward and Xi 19. The latter cultivars exhibited either light or no symptoms and little or no SBCMV infection in leaves. In fields with WSSMV, the virus failed to develop in Italy, but was detected in the leaves of all the susceptible control cultivars at a site in France. However, no UK cultivar tested positive for WSSMV. Multi-site analysis indicated that the presence of WSSMV did not increase the impact of SBCMV on the height, thousand-grain weight or yield of UK cultivars. The wheat cultivars on test gave a similar response to SBCMV across three European countries. Possible sources of SBCMV resistance are discussed.

Keywords SBCMV · WSSMV · *Triticum aestivum* · Winter wheat cultivar · Resistance · SBWMV · Multi-site trials · REML

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Introduction

Soil-borne cereal mosaic virus (SBCMV) and *Wheat spindle streak mosaic virus* (WSSMV) are viral species from different families. Both are soil-borne and cause serious diseases of winter wheat (*Triticum aestivum*). SBCMV is a member of the genus *Furovirus* and is widely distributed across Europe (France, Germany, Italy, Denmark and Poland; Canova and Qualglia 1960; Koenig and Huth 2000). The virus was detected in the UK for the first time in 1999 on a farm in Wiltshire (Clover et al. 1999). SBCMV has been found subsequently at 12 further sites in the UK, including the Isle of Wight, Kent and Northampton. In Europe, WSSMV was first detected in France in 1977 (Signoret et al. 1977), and is now known to occur throughout Belgium, France, Germany and Italy (Gitton et al. 1999; Huth 2000; Rubies Autonell and Vallega 1987; Vaianopoulos et al. 2006). WSSMV is often found infecting wheat in combination with SBCMV, but this virus has not yet been reported in the UK.

Both SBCMV and WSSMV induce mottle and mosaic leaf symptoms and can cause plant stunting, reduced tillering and reduced grain yield. Symptom severity and titre for both viruses is dependent on temperature and can fluctuate during the season. The strongest visual symptoms of both diseases generally occur in the spring (February to April in Europe) and tend to disappear as temperatures rise. Small-scale trials in the UK have shown that SBCMV can reduce grain yield in susceptible UK cultivars of winter wheat by up to 50% (Clover et al. 1999). In Italy, yield losses of up to 70% have been recorded in cases of mixed infections of SBCMV and WSSMV in durum wheat (Vallega and Rubies-Autonell 1985).

Both SBCMV and WSSMV are vectored by *Polymyxa graminis* (Ledingham 1939), a soil dwelling protist able to survive and remain infective in soil for over a decade (Kendall and Lommel 1988). Cultivars vary in susceptibility to each virus; some cultivars have been shown to have low virus titre in leaf material, mild or no symptoms, and little or no yield penalty when grown on virus-infected land, and therefore offer a practical method for disease management. Profiling the resistance of wheat cultivars to soil-borne viruses has been conducted for many years by evaluating agronomic performance on infected land and correlating results with viral concentration in plant tissues and symptom development (Hunger et al. 1991; Vallega et al. 1999; Rubies-Autonell et al. 2003). Such trials have been useful in determining the economic viability of growing individual cultivars and identifying useful germplasm for resistance breeding.

This study was undertaken to determine the field reactions and agronomic performance of modern UK winter wheat cultivars on land with natural inoculum sources of SBCMV and/or WSSMV at various sites across Europe.

Materials and methods

Crop and site details

Fifteen winter wheat cultivars (Aardvark, Buster, Charger, Claire, Consort, Equinox, Hereward, Madrigal, Malacca, Napier, Reaper, Rialto, Riband, Savannah and Shamrock) were selected from the UK recommended and provisionally recommended national lists to represent bread-making, cake/biscuit-making and feed wheat. Poor performing or obsolete cultivars (Buster, Reaper and Riband in 2001 and Cockpit, Eclipse and Buchan in 2002) were substituted with new cultivars (Buchan, Cockpit and Eclipse in 2001 and Biscay, Deben and Xi19 in 2002). Local cultivars with known reactions to both viruses were also planted at each site to act as controls. In France, these were Aztec (susceptible to SBCMV but resistant to WSSMV), Cezanne (susceptible to both viruses) and Tremie (resistant to both viruses). In Italy, cvs Grazia and Valnova (susceptible to both viruses) were used. No additional cultivars were planted at the site in the UK.

Trial sites with a history of viral infection were selected in France, Italy and the UK over three seasons (2000, 2001 and 2002). In total, 11 trials were conducted with an incomplete replication of all sites in each season. Infected fields were identified with either a single virus or a combination of both viruses by prior testing with susceptible cultivars. The presence of SBCMV was confirmed by testing leaf material from susceptible controls using SBCMV-specific real-time RT-PCR (Ratti et al. 2004) and WSSMV by diagnosis with species-specific polyclonal antibodies.

Chosen sites were: Minerbio, Italy, SBCMV (2001, 2002); Ozzano, Italy, SBCMV (2000, 2002); Rome, Italy, SBCMV and WSSMV (2002); Chambon sur Cisse, France, SBCMV and WSSMV (2000, 2001, 2002); Landes Le Gaulois, France, WSSMV (2000,

2002) and Wiltshire, UK, SBCMV (2002). Resident farmers managed general crop husbandry according to local good farm practice. Fungicides and insecticides were applied to each trial as required to minimise the impact of other diseases and pest infestation. Seed batches of each cultivar were identical across all sites.

Field assessments

Both SBCMV and WSSMV induce pale green or yellow mottling on the leaves as well as plant stunting and reduced tillering. WSSMV can be distinguished from SBCMV only by the transient appearance of spindle-shaped dashes in early spring. On sites where both SBCMV and WSSMV were present (Chambon sur Cisse and Rome), no attempt was made to distinguish between symptoms of each virus. On such sites, ELISA tests were employed to confirm the presence of each virus. Plots were assessed for viral symptoms on three occasions through the growing season. In Italy symptom severity was scored according to a disease index where 0.0–1.0=slight or no symptoms; 1.1–2.0=mild mottling and stunting; 2.1–3.0=moderate mottling and stunting; 3.1–4.0=severe mottling and stunting with some virus-killed plants (Vallega and Rubies Autonell 1985). Symptoms in France and the UK were scored using a scale of 0–5 where 0=no disease symptoms; 1=slight symptoms; 2=mild mottling and stunting; 3=moderate mottling and stunting; 4=severe mottling and stunting; 5=severe mottle progressed to yellow streaking. To facilitate across site symptom data collected on different scales, symptom severity scores were transformed to a S0–S2 scale where S0=no definite viral symptoms (0–0.49); S1=mild to moderate mottling and stunting (0.5–2.99); and S2=severe mottling and stunting (3.0–5.0).

Plots were taken to harvest and the agronomic performance was evaluated by measuring stem height at harvest, grain yield (measured at 15% moisture) and thousand grain weight (TGW) (g). Additional fertile tiller assessments were conducted at the trials in France and the UK by assessing the number of plants in 6×0.5 m of row.

Experimental design and statistical analysis

Each trial consisted of a randomised block design with three (France and the UK) or four (Italy) replicate plots of each cultivar. Plot size varied between countries; 8 m^2 in France, 10 m^2 in Italy and 24 m^2 in the UK. Planting density was 250 seeds m^{-2} in France, 400 seeds m^{-2} in Italy and 375 seeds m^{-2} in the UK. Plots were planted each season between the 13th and 28th October. Analyses were performed using Genstat version 8. Data from individual sites were analysed using ANOVA and means separated using the Bonferroni correction (Bonferroni 1936). Data were correlated as required using Pearson's or Spearman's rank correlation as appropriate (Siegel and Castellan 1988; Rice 1995). A residual maximum likelihood (REML) analysis was conducted to investigate varietal performance whilst allowing for data variability due to site and year (Patterson and Thompson 1971). The REML analysis was performed using yield, TGW and height as response variables, and cultivar and virus (either SBCMV, WSSMV or SBCMV with WSSMV) as fixed effects, with year and site inserted as random effects. Using this analysis, the additive effect of WSSMV in the presence of SBCMV was compared to the presence of SBCMV alone for height, TGW and grain yield. Due to the unbalanced nature of this analysis, it was not possible to derive a least significant difference of means (LSD). For each pair of cultivars, differences more than twice the corresponding standard error for the difference of the means were deemed significant (Parker et al. 2004).

To compare severity scores between cultivars across all sites a multinomial analysis with a generalized linear model and a logit link function (McCullagh and Nelder 1983) was applied using symptom severity scores transformed to the S0–S2 scale. Due to a low number of replicates per site and the unbalanced nature of the analysis, an overall effect of cultivars was investigated with no account of years or sites. The multinomial analysis assumes proportionality of the odds (two odds in the case of three categories as used in this analysis: $\frac{P_1}{P_2+P_3}$ and $\frac{P_1+P_2}{P_3}$ where p_1, p_2 and p_3 are the estimated probability of being in categories 1, 2 and 3, respectively). The analysis assumes the same distribution of cut-points as defined by the natural logarithm of the odds throughout all levels of the factor of interest. Therefore the output shows a displacement, with accompanying standard error, for all cultivars compared to an arbitrary reference cultivar, Xi 19.

Negative estimates for any given cultivar show a displacement of the fitted distribution of the scores towards the lowest scores (i.e. least diseased plants) compared to Xi 19 and vice versa.

To investigate whether the symptoms recorded were due to the virus and not to some abiotic factor, a regression analysis was completed between raw absorbance data from the ELISA and symptom severity scores for each plot at the sites in Italy and the UK (Genstat version 8).

Virus testing

In Italy and the UK, five random leaf samples were bulked from each plot during the time of peak symptom expression. In France, leaves from five to ten random plants were tested for each cultivar. Each sample was tested for the presence of SBCMV and WSSMV using enzyme-linked immunosorbent assay (ELISA) techniques as described, respectively, by Ratti et al. (2004) and Vallega et al. (2003). For both viruses, absorbance$_{405\ nm}$ values greater than three times the mean negative control (healthy wheat material) were considered positive (Hugo et al. 1996; Ratti et al. 2004).

Results

SBCMV

Symptom severity scores and ELISA results from leaf material confirmed that susceptible local control cultivars became infected with SBCMV at all sites; however, the severity of infection varied across sites and years (Table 1). SBCMV infection at Ozzano in 2000 and Rome 2002 was mild and patchy across both sites with no cultivar consistently testing positive for the virus. Severe, patchy infection at the site in Ozzano in 2002, reduced plant density and prevented the collection of any post-harvest data. Despite good infection and symptom expression in control cultivars, disease developed inconsistently in UK cultivars for both years at the site in Minerbio (Table 1). With the exception of Consort and Shamrock, grain yield for the UK cultivars grown at Minerbio was not badly affected by this low level of virus infection (Table 2).

All sites remained relatively free from fungal pathogens and pest damage by the routine application of pesticides. A significant linear relationship (P= <0.001) was observed between raw absorbance data from the ELISA and symptom severity scores for each plot at the sites in Italy and the UK. However, due to the large leverage of the high symptom severity scores from the Wiltshire site, this result can be used merely as an indication that the symptom severity recorded was due to the presence of SBCMV (Fig. 1).

The most severe symptoms of SBCMV were evident at the sites in Chambon sur Cisse in 2000 and Wiltshire in 2002 (Table 1). Strong foliar symptoms were accompanied by plant dwarfing and yield reductions in the majority of cultivars on these sites (Tables 1, 2 and 3). TGW was not consistently reduced in any individual cultivar; however a significant reduction was frequently detected in cultivars showing strong foliar symptoms (Table 4). Cultivars Charger, Claire, Cockpit and Hereward showed little or no foliar symptoms on land containing natural inoculum sources of SBCMV (Table 1). Triple antibody sandwich (TAS) ELISA confirmed SBCMV levels were below detectable limits in the leaves of all of these cultivars and so they were deemed to be resistant to SBCMV. Despite showing sporadic symptom expression, cultivars Aardvark and Xi19 were also deemed resistant due to consistently low levels of virus in leaf tissue (Table 1).

Yield, TGW, and plant height at harvest all exhibited a significant negative correlation with symptom severity for Chambon sur Cisse in 2001 and 2002 and in Wiltshire in 2002 (Table 5). No relationship was observed between disease severity and TGW at Chambon sur Cisse in 2000; however a significant negative correlation was observed between disease severity and plant emergence at this site (Table 5).

WSSMV

WSSMV susceptible control cultivars (Cezanne, Valnova or Grazia) showed strong foliar symptoms for both years at Landes Le Gaulois, which contained a natural inoculum source of WSSMV; however only moderate symptoms were recorded at the site in Rome. Double antibody sandwich (DAS) ELISA testing of leaf material confirmed the presence of WSSMV from the WSSMV susceptible control cv. Cezanne for both years at Landes Le Gaulois. The

Table 1 Frequency distribution of virus symptom severity scores as recorded at the time of peak symptom expression for each site

Site	Chambon sur Cisse (F)			Landes Le Gaulois (F)		Ozzano (I)	Minerbio (I)		Rome (I)	Wiltshire[a] (U)
Year	2000	2001	2002	2000	2002	2000	2001	2002	2002	2002
Assessment date	03 May	22 May	11 April	09 March	17 April	18 April	05 March	03 April	19 March	24 April
Aztec (L)	0,0,3 (+)[−]	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	–	–	–	–	–
Cezanne (L)	0,0,3 (+)[+]	0,0,3 (+)[+]	0,0,3 (+)[+]	0,0,3 (nt)[+]	0,0,3 (nt)[+]	–	–	–	–	–
Tremie (L)	3,0,0 (−)[−]	3,0,0 (−)[−]	–	3,0,0 (nt)[−]	–	–	–	–	–	–
Grazia (L)	–	–	–	–	–	0,4,0 (+)[−]	0,2,2 (+)[−]	0,0,4 (+)[−]	0,4,0	–
Valnova (L)	–	–	–	–	–	0,4,0 (+)[−]	0,1,3 (+)[−]	0,0,4 (+)[−]	1,3,0	–
Aardvaark (R)	0,3,0 (+)[−]	2,1,0 (−)[−]	1,2,0 (−)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	2,2,0 (−)[nt]	2,2,0 (+)[nt]	3,1,0 (−)[nt]	1,3,0	0,2,1 (+)[nt]
Charger (R)	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	3,1,0 (−)[nt]	4,0,0 (−)[nt]	0,4,0 (−)[nt]	3,1,0	2,1,0 (−)[nt]
Claire (R)	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	2,2,0 (−)[nt]	4,0,0 (−)[nt]	3,1,0 (−)[nt]	4,0,0	3,0,0 (−)[nt]
Cockpit (R)	–	0,3,0 (−)[−]	–	–	–	–	4,0,0 (−)[nt]	–	–	–
Hereward (R)	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (−)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	4,0,0 (−)[nt]	3,1,0 (−)[nt]	2,2,0 (−)[nt]	2,2,0	3,0,0 (−)[nt]
Xi 19 (R)	–	–	2,1,0 (−)[−]	–	3,0,0 (nt)[−]	–	–	0,4,0 (−)[nt]	0,4,0	0,1,2 (+)[nt]
Biscay	–	–	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	–	0,4,0 (−)[nt]	1,3,0	0,0,3 (+)[nt]
Buchan	–	0,0,3 (+)[−]	–	–	–	–	0,4,0 (+)[nt]	–	–	–
Buster	0,0,3 (+)[−]	–	–	3,0,0 (nt)[−]	–	3,1,0 (+)[nt]	–	–	–	–
Consort	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	1,3,0 (−)[nt]	0,4,0 (+)[nt]	2,2,0 (−)[nt]	0,4,0	0,0,3 (+)[nt]
Deben	–	–	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	–	0,4,0 (+)[nt]	4,0,0	0,0,3 (+)[nt]
Eclipse	–	0,0,3 (+)[−]	–	–	–	–	0,4,0 (+)[nt]	–	–	–
Equinox	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	3,1,0 (−)[nt]	0,4,0 (+)[nt]	1,3,0 (−)[nt]	4,0,0	0,0,3 (+)[nt]
Madrigal	0,0,3 (+)[−]	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	2,2,0 (+)[nt]	2,2,0 (+)[nt]	–	–	–
Malacca	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	3,1,0 (−)[nt]	2,2,0 (+)[nt]	3,1,0 (−)[nt]	2,2,0	0,0,3 (+)[nt]
Napier	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	3,1,0 (+)[nt]	1,3,0 (+)[nt]	0,4,0 (−)[nt]	4,0,0	0,0,3 (+)[nt]
Option	–	–	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	–	1,3,0 (−)[nt]	3,1,0	0,0,3 (+)[nt]
Reaper	0,0,3 (+)[−]	–	–	3,0,0 (nt)[−]	–	3,1,0 (−)[nt]	–	–	–	–
Rialto	0,0,3 (+)[−]	0,0,3 (+)[−]	–	2,1,0 (nt)[−]	–	3,1,0 (+)[nt]	1,3,0 (+)[nt]	–	–	–
Riband	0,0,3 (+)[−]	–	–	3,0,0 (nt)[−]	–	0,4,0 (+)[nt]	–	–	–	–
Savannah	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	1,3,0 (−)[nt]	0,4,0 (+)[nt]	4,0,0 (−)[nt]	2,2,0	0,0,3 (+)[nt]
Shamrock	0,0,3 (+)[−]	0,0,3 (+)[−]	0,0,3 (+)[−]	3,0,0 (nt)[−]	3,0,0 (nt)[−]	4,0,0 (−)[nt]	4,0,0 (+)[nt]	3,1,0 (−)[nt]	3,1,0	0,0,3 (+)[nt]
Tanker	–	–	0,0,3 (+)[−]	–	3,0,0 (nt)[−]	–	–	0,4,0 (−)[nt]	1,3,0	0,0,3 (+)[nt]

Frequency classes are calculated from three replicate plots on trials conducted in France (*F*) and the UK (*U*) and four replicate plots on trials conducted in Italy (*I*). Frequency classes are presented as the number of plots containing plants showing either no definite virus symptoms, disease index 0–0.49 (Left); mild virus symptoms including mild foliar mottling and/or stunting, disease index 0.5–2.99 (centre); or severe virus symptoms including severe mottling and/or severe stunting, disease index 3.0–5.0 (right). The results of testing leaf material for the presence of SBCMV ( ) or WSSMV [ ] using ELISA from the corresponding plots are also presented. Sap extracts from plots were considered positive + if the absorbance$_{405\ nm}$ exceeded three times that measured in the negative control, otherwise the extract was deemed negative – for SBCMV; nt indicates samples not tested.

R indicates cultivar deemed resistant to SBCMV based on low symptom severity and negative ELISA results. *L* indicates a local control cultivar.

[a] WSSMV confirmed absent from field using ELISA (Clover et al. 1999).

Table 2 Mean grain yield (t ha^{-1}) from all sites calculated from three (France (F) and the UK(U)) or four (Italy (I)) replicate plots

Cultivar	Chambon sur Cisse (F)			Landes Le Gaulois (F)		Ozzano (I)	Minerbio (I)		Rome (I)	Wiltshire (U)
Year	2000	2001	2002	2000	2002	2000	2001	2002	2002	2002
Aztec (L)	4.64	3.35		6.30						
Cezanne (L)	3.46	2.72	5.28	5.03	10.65					
Tremie (L)	8.23	5.96		6.45						
Grazia (L)						3.76	3.89	3.32	3.82	
Valnova (L)						4.55	2.07	2.49	3.41	
Aardvaark (R)	7.43cd	5.14cdef	9.91e	4.20a	10.22bcd	5.11bc	8.38gh	5.42bc	5.36ab	8.26c
Charger (R)	8.88d	5.77ef	9.83e	5.76a	10.00abcd	5.48c	7.01efgh	6.06c	6.19b	7.33bc
Claire (R)	8.34d	5.88ef	10.00e	4.21a	10.93cd	4.71abc	8.48h	4.95abc	6.24b	8.82c
Cockpit (R)		6.02f					6.62cdef			
Hereward (R)	8.19d	5.59def	9.62e	5.23a	9.07ab	4.82abc	6.39cde	5.00bc	5.37ab	8.31c
Xi 19 (R)			9.28de		11.18d			4.81abc	5.52ab	8.01c
Biscay			8.98cde		11.10cd			6.17c	6.40b	4.90a
Buchan		2.86a					7.51efgh			
Buster	5.38b			5.30a		4.76abc				
Consort	4.83b	3.52ab	6.59b	4.93a	10.02abcd	5.03abc	3.99ab	3.20a	4.02a	3.77a
Deben			7.13bcd		10.64cd			5.57bc	5.10ab	5.00cab
Eclipse		3.86abcd					7.44efgh			
Equinox	2.24a	3.48abc	4.26a	3.87a	10.33bcd	5.27bc	7.96fgh	4.55abc	4.71ab	2.74a
Madrigal	4.28b	3.67abc		3.60a		4.65abc	6.87defg			
Malacca	5.82bc	4.56bcdef	6.62b	5.06a	10.09abcd	4.81abc	5.41bcd	4.02ab	5.20ab	4.00a
Napier	4.95b	4.62abcde	6.89bc	5.73a	10.31bcd	5.15bc	7.20efgh	5.24bc	5.47ab	3.50a
Option			5.44ab		10.24bcd			5.14bc	5.39ab	3.71a
Reaper	4.71b			3.81a		5.00abc				
Rialto	4.93b	3.93abcd		5.16a		4.92abc	6.35cde			
Riband	4.54b			4.87a		4.04a				
Savannah	5.33b	4.20abcd	5.83ab	5.11a	10.60cd	4.39ab	5.11bc	4.28bc	5.12ab	3.43a
Shamrock	5.35b	4.83bcdef	6.87bc	5.38a	8.78a	5.23b	2.62a	4.16bc	5.19ab	4.33a
Tanker			6.76b		9.71bcd			4.43bcd	4.44ab	3.14a
P value	<0.001	<0.001	<0.001	0.015	<0.001	<0.001	<0.001	<0.001	0.005	<0.001
SED	0.47	0.41	0.55	0.61	0.36	0.26	0.40	0.45	0.50	0.59

Data from each individual site were analysed using ANOVA with blocking included. Means were separated using the Bonferroni correction; means with a common letter do not differ significantly from one another testing at 95% confidence limits.

L indicates local control cultivars, which were not included in the analysis. *R* indicates cultivar deemed resistant to SBCMV based on symptom severity and ELISA scores. *SED* is the standard error of the difference between a pair of means.

levels of WSSMV in Valnova and Grazia from Rome remained low and therefore no ELISA data are presented from this trial. At Landes Le Gaulois, where SBCMV was not present, no definite symptoms of WSSMV were observed on any UK cultivars despite strong symptoms in the WSSMV susceptible control cv. Cezanne. DAS ELISA testing confirmed the absence of WSSMV in all leaf material from UK cultivars from this site in both years. These results are summarised in Table 1.

Multi-site analysis

Agronomic data for grain yield, TGW and plant height were collated from all five SBCMV with WSSMV and SBCMV only sites over three years. Ozzano, 2002 was excluded due to the lack of harvest data. An REML analysis was conducted to investigate differences in varietal performance whilst allowing for data variability due to site and year. For the REML analysis, site and year were taken as random

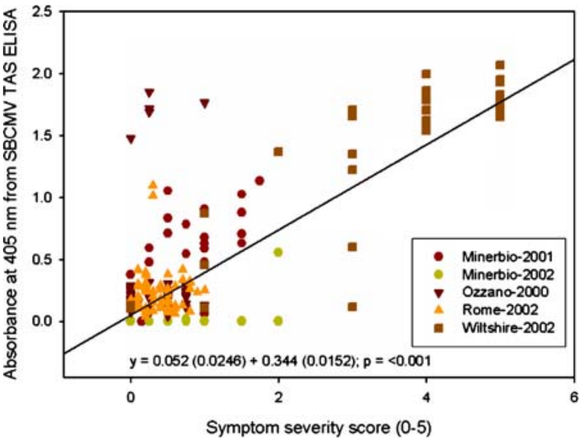


Fig. 1 Regression plot of raw absorbance data from the SBCMV ELISA and symptom severity scores for each plot from four trials in Italy and one in the UK

effects while wheat cultivar and virus types were analysed as fixed effects. No interaction between cultivar and virus type was included due to lack of observations.

REML analysis suggested no significant overall additive effect of WSSMV on SBCMV for grain yield (χ^2=0.57; *df*=1; *P*=0.45), TGW (χ^2=2.23; *df*=1; *P*=0.14) or height (χ^2=0.12; *df*=1; *P*=0.73). However, significant effects of wheat cultivar were found for grain yield (χ^2=175.4; *df*=22; *P*<0.001), TGW (χ^2=222.2; *df*=22; *P*<0.001) and height (χ^2=385.0; *df*=22; *P*<0.001). Due to a low number of observations for Buchan, Buster, Cockpit, Eclipse, Reaper and Riband, conclusions regarding these cultivars should be made with caution. For each variable, the cultivar with the highest and lowest value was compared with each other cultivar in a series of pairwise comparisons (Table 6). Using pairwise testing of the multinomial analysis the cultivars could be grouped into four categories (Fig. 2). However it should be noted that not all the odds were proportional for these data, and therefore the results from the multinomial analysis should only be taken as an indication of overall cultivar performance.

Discussion

The majority of UK cultivars tested (15/21) exhibited severe symptoms of SBCMV at infected sites across Europe. ELISA tests revealed high levels of virus in leaf material, confirming susceptibility. Conversely, cvs Aardvark, Charger, Claire, Cockpit, Hereward and Xi19 showed little symptom development coupled with low levels of virus in the majority of foliar tissues when grown on land with natural inoculum sources of SBCMV, suggesting these cultivars can be recommended for use on such land. Results for Cockpit were based on only two trials in 2000; however, this cultivar was also found to be resistant when grown in small tussock plots in Wiltshire (Bayles and Napier 2002).

Of the six cultivars identified as resistant, Claire, Hereward and Xi 19 are on the current winter wheat 2007/08 recommended list (http://www.hgca.com) and are therefore available for immediate use by UK farmers. Currently, commercially viable resistant cultivars of winter wheat have been developed by chance, as breeders do not actively select for SBCMV resistance. In order to secure the future of growing winter wheat on infected land, resistance to SBCWV should be incorporated into the current breeding strategy. Several European groups are in the process of investigating resistance to SBCMV using mapping or transcriptional profiling (Maccaferri et al. 2005; Perovic et al. 2005). A brief study of the parentage of the resistant cultivars indicated four possibly distinct sources of resistance (Fig. 3). Bayles and Napier (2002) tested cvs Moulin and Cadenza as possible resistance sources and both were found to be resistant. Cadenza is the common resistant parent for Aardvark and Xi 19, both of which showed foliar symptoms and sporadic ELISA positives in leaf material with little apparent loss of yield. In the case of cvs Charger and Claire, both derived from Moulin, no ELISA positives were detected. These differences in resistance were highlighted in the multinomial GLM analysis, which suggested Moulin-derived lines showed significantly lower symptom expression across all SBCMV infected sites than Cadenza-derived resistance. Each of these potential sources should be included in future studies on SBCMV resistance.

The resistant and susceptible varietal designations in this study were assigned due to consistent reactions on land infected with SBCMV from France, Italy and the UK. Previous studies, based on similarities in nucleic acid sequence, identified *European wheat mosaic virus* (France) and the European strain of

Table 3 Mean plant height (cm) of plants from all sites calculated from three [France (F) and the UK(U)] or four [Italy (I)] replicate plots

Cultivar	Chambon sur Cisse (F)			Landes Le Gaulois (F)		Ozzano (I)	Minerbio (I)		Rome (I)	Wiltshire (U)
Year	2000	2001	2002	2000	2002	2000	2001	2002	2002	2002
Aztec (L)	49.6	50.9		77.3						
Cezanne (L)	48.3	41.8	75.0	82.3	95.7					
Tremie (L)	80.0	78.3		77.7						
Grazia (L)						83.5	72.5	74.3	83.8	
Valnova (L)						82.3	71.8	70.8	81.3	
Aardvaark (R)	77.0cd	65.0cd	80.0de	73.0ab	84.7bcde	70.5bcd	85.0abc	80.0bcd	75.0ab	78de
Charger (R)	75.6bcd	70.0de	75.0cd	74.0ab	78.7abc	69.0abcd	83.8ab	78.8abc	73.8ab	73d
Claire (R)	79.7d	70.0de	79.0de	81.7abc	85.7de	72.5cde	92.5cd	84.8def	80.0abc	81de
Cockpit (R)		80.0e					112.5e			
Hereward (R)	80.3d	70.0de	80.0de	79.3abc	86.7def	70.5bcd	86.3bc	80.0bcd	75.0ab	82de
Xi 19 (R)			90.0e		96.3g			88.8fg	82.5bc	83e
Biscay			71.0bcd		90.7efg			87.5efg	80.0abc	59bc
Buchan		40.2a					79.0ab			
Buster	53.4a			75.3abc		65.3abc				
Consort	51.3a	54.7bc	66.7abc	77.0a	85.0cde	66.3abcd	79.5ab	78.0abc	75.0ab	55abc
Deben			79.7de		93.0fg			91.0g	85.0c	61c
Eclipse		45.7ab					86.3bc			
Equinox	49.7a	51.8abc	56.7a	72.0a	78.3ab	67.3abcd	76.3a	73.8a	73.8ab	51ab
Madrigal	49.0a	43.9ab		72.3a		63.3ab	78.6ab			
Malacca	51.8a	50.4ab	59.3ab	78.3abc	85.0cde	75.0de	85.0abc	83.3cde	77.5abc	51ab
Napier	51.6a	52.8abc	66.0abc	74.7abc	83.7bcd	70.5bcd	81.0ab	78.0abc	73.8ab	50ab
Option			59.3ab		88.0def			83.3cde	77.5abc	51ab
Reaper	57.6abc			83.0bc		74.8de				
Rialto	65.5abcd	41.2ab		84.7c		80.8e	96.3d			
Riband	55.0a			82.0abc		72.5cde				
Savannah	56.4ab	53.0abc	63.3abc	80.0abc	85.7de	61.0a	82.0ab	77.3ab	75.0ab	58abc
Shamrock	48.3a	51.9abc	58.7a	76.3abc	82.0abcd	71.0bcd	79.3ab	78.3abc	71.3a	54abc
Tanker			58.3a		76.3a			76.5ab	72.5bc	49a
P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SED	6.0	3.5	3.1	2.7	1.7	2.4	2.3	1.4	2.5	2.4

Data from each individual site were analysed using ANOVA with blocking included. Means were separated using the Bonferroni correction; means with a common letter do not differ significantly from one another testing at 95% confidence limits.

L indicates local control cultivars, which were not included in the analysis. *R* indicates cultivar deemed resistant to SBCMV based on symptom severity and ELISA scores. *SED* is the standard error of the difference between a pair of means

Soil-borne wheat mosaic virus (Italy and the UK) as SBCMV (Clover et al. 2001; Yang et al. 2001). However, no data have been presented to show similarities in the field pathology of SBCMV from these areas. This study presents the first data suggesting the pathogenicity of SBCMV from France, Italy and the UK is similar when tested against a panel of winter wheat cultivars.

An REML analysis was used to allow for the variation in data across sites and years. In this analysis, data for both trials at Landes Le Gaulois, the WSSMV only site, were excluded due to lack of visual symptoms and absence of virus in plant tissue. The results indicate cvs Aardvark, Biscay, Charger, Cockpit, Hereward and Xi19 produced grain yields that were not significantly different from the highest yielding cv. Claire. All these cultivars were identified as resistant based on viral titre in leaf material and low symptom expression, except Biscay. The high overall grain yield seen for Biscay was surprising considering consistent symptom expression and detection of virus in leaf material. However, this cultivar

Table 4 Mean thousand grain weight (TGW) in g at 15% humidity from all sites calculated from three [France (F) and the UK(U)] or four [Italy (I)] replicate plots

Cultivar	Chambon sur Cisse (F)			Landes Le Gaulois (F)		Ozzano (I)	Minerbio (I)		Rome (I)	Wiltshire (U)
Year	2000	2001	2002	2000	2002	2000	2001	2002	2002	2002
Aztec (L)	37.23	36.38		34.78						
Cezanne (L)	39.83	44.69	42.19	37.11	53.38					
Tremie (L)	49.42	49.90		39.11						
Grazia (L)						50.65	41.71	36.10	43.32	
Valnova (L)						60.38	26.05	40.84	49.54	
Aardvaark (R)	49.42b	48.69gh	50.87e	40.67bc	53.00ef	37.94abc	40.55ef	31.45b	44.24efg	51.11d
Charger (R)	40.38a	46.49efg	47.80cde	33.95ab	46.20ab	36.44abc	29.73abc	29.99ab	43.96defg	47.72cd
Claire (R)	45.36ab	45.16defg	45.80bcde	35.38ab	45.77ab	31.50a	33.83bcd	26.56ab	42.01bcde	46.41bcd
Cockpit (R)		47.59fgh					33.11bcd			
Hereward (R)	43.28ab	45.79efg	46.03bcde	37.03abc	45.93ab	33.90abc	30.61bc	27.69ab	39.94ab	47.83cd
Xi 19 (R)			57.97f		52.70def			28.78ab	46.95g	47.60cd
Biscay			48.70de		50.33cd			31.73b	44.70efg	41.16abc
Buchan		37.55a					35.46cde			
Buster	43.05ab			40.23bc		37.15abc				
Consort	41.57ab	43.20cdef	41.67abc	36.23abc	46.63ab	31.98ab	27.94ab	22.93a	40.22abc	39.13abc
Deben			44.83bcde		51.13def			27.65ab	43.62def	40.57abc
Eclipse		41.16abcd					35.39cde			
Equinox	45.65ab	51.86h	49.07de	38.43abc	53.47f	40.92c	44.09f	33.93b	45.34fg	39.43abc
Madrigal	40.19a	40.49abc		31.52a		35.24abc	34.05cd			
Malacca	42.90ab	42.53bcde	39.90ab	34.09ab	44.43a	35.55abc	31.57bcd	27.19ab	40.24abc	33.19a
Napier	44.28ab	44.18cdefg	46.23bcde	40.30bc	50.27cd	36.54abc	37.46def	31.17b	43.42cdef	35.56a
Option			36.13a		44.53a			29.78ab	37.61a	37.16a
Reaper	44.82ab			40.23bc		37.39abc				
Rialto	42.58ab	43.04bcdef		40.24bc		38.23bc	30.50bc			
Riband	44.86ab			36.11abc		34.34abc				
Savannah	46.50ab	46.65efg	44.33bcd	43.07c	50.87de	36.95abc	31.52bc	27.02ab	43.62def	39.72abc
Shamrock	37.86a	38.53ab	41.13ab	34.66ab	44.53a	34.75abc	23.90a	27.17ab	40.74abcd	38.73ab
Tanker			46.07bcde		48.27bc			29.99ab	40.86abcd	37.31a
P value	0.004	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
SED	2.23	1.16	1.61	1.85	0.64	1.80	1.65	1.99	0.86	2.22

Data from each individual site were analysed using ANOVA with blocking included. Means were separated using the Bonferroni correction; means with a common letter do not differ significantly from one another testing at 95% confidence limits.

L indicates local control cultivars, which were not included in the analysis. *R* indicates cultivar deemed resistant to SBCMV based on symptom severity and ELISA scores. *SED* is the standard error of the difference between a pair of means

performed poorly in Wiltshire, suggesting its field tolerance to SBCMV does not withstand the higher disease pressure encountered at the UK site.

REML analysis suggested resistant cultivars had the tallest plants (Cockpit) and the highest TGW (Xi 19). However, cultivars identified as resistant using ELISA and symptom data were not consistently taller nor did they have a consistently higher TGW than susceptible cultivars using the multi-site analysis. When sites were analysed individually, the significance of TGW reduction and plant dwarfing in susceptible cultivars was seen to vary between sites. At sites with low symptom expression (Rome and Minerbio), no significant reductions in TGW or height were recorded for susceptible cultivars. Contrastingly, sites with high symptom expression e.g. Chambon sur Cisse and Wiltshire showed significant reductions in height, TGW and even number of fertile tillers m^{-2},

Table 5 Pearson's correlation of grain yield (t ha^{-1}) and Spearman's rank correlation of symptom severity (0–5) vs. other crop characteristics at sites in Chambon sur Cisse (CSC) in France and Wiltshire in the UK

	Mean	Range	Yield (t ha^{-1})	Symptom severity (0–5)
CSC 2000				
Height at harvest (cm)	60	41–82	0.772***	−0.765***
TGW (g)	43.5	36–51	0.078	−0.136
Plant emergence (m^2)	254	202–323	0.251	−0.481***
Fertile tillers m^2	354	213–559	0.770***	−0.569***
Yield (t ha^{-1})	5.68	1.51–9.42	–	−0.694***
CSC 2001				
Height at harvest (cm)	56	33–85	0.799***	−0.748***
TGW (g)	44	37–53	0.318*	−0.494***
Plant emergence (m^2)	218	116–297	0.124	−0.024
Fertile tillers m^2	245	71–375	0.669***	−0.608***
Yield (t ha^{-1})	4.58	2.47–6.66	–	−0.788***
CSC 2002				
Height at harvest (cm)	69	53–90	0.737***	−0.714***
TGW (g)	45	35–59	0.523***	−0.494**
Plant emergence (m^2)	183	116–250	0.117	0.105
Fertile tillers per m^2	282	179–378	0.572***	−0.392**
Yield (t ha^{-1})	7.60	3.43–10.80	–	−0.857***
Wiltshire 2002				
Height at harvest (cm)	62	46–87	0.919***	−0.767***
TGW (g)	42	52–30	0.844***	−0.756***
Plant emergence (m^2)	224	178–274	−0.382**	0.256
Fertile tillers per m^2	386	194–538	0.658***	−0.511***
Yield (t ha^{-1})	5.28	2.10–9.71	–	−0.817***

All correlations calculated using data from 45 plots.

P=0.05

***P*=0.01

****P*=<0.001

(data not shown) in susceptible cultivars. Previous studies have implicated either a reduction in tillering or TGW as major causes of yield loss in SBWMV-infected wheat (Kucharek and Walker 1974; Campbell et al. 1975; Vallega and Rubies-Autonell 1985).

Interestingly, no additional effect of WSSMV on SBCMV was found using the multi-site analysis. Previous research has suggested WSSMV and SBWMV interact synergistically, leading to increased yield loss and symptom severity in cultivars of hard red winter wheat previously shown to be resistant to SBWMV (Lommel et al. 1986). It is reasonable to assume the interaction identified in hard red winter wheat could require a line to be susceptible to WSSMV in order for the virus to impact on SBCMV resistance. All the UK cultivars tested in the current study were found to be resistant to WSSMV when grown in France. The presence of cultivars susceptible to SBCMV but resistant to WSSMV, such as control cv. Aztec, indicates resistance to these viruses is conveyed by different genes.

Field trials were completed using different experimental designs across three countries with an incomplete replication of cultivars for each of 3 years. Using this approach, the cultivar list evolved through each year of the study, thereby allowing emerging cultivars to be included. However, this led to an unbalanced experimental design, whereby the estimates for some cultivars were based on a reduced number of observations, weakening any conclusions for these cultivars. By treating Site and Year as random factors, the REML analysis accounted for the

Table 6 Predicted means for yield, height and TGW (with standard errors) using REML analysis including data from all sites and years containing SBCMV

Cultivar	Yield (t ha^{-1})		Height (cm)		TGW (G)		Number of observations
	Mean	s.e.	Mean	s.e.	Mean	s.e.	
Consort	4.05 ^{l}	0.36	65.75	5.01	35.71*	2.64	28
Riband	4.12*	0.60	67.83	5.58	38.68	2.91	7
Equinox	4.30*	0.36	62.83*	5.01	43.52**	2.64	28
Tanker	4.40*	0.45	63.20*	5.22	38.26	2.74	14
Savannah	4.43*	0.36	65.61	5.01	39.12	2.65	28
Shamrock	4.50*	0.36	64.36*	5.01	35.19*	2.64	28
Option	4.70*	0.45	67.31	5.22	35.17 ^{l}	2.74	14
Madrigal	4.71*	0.45	60.32*	5.20	37.49*	2.73	14
Reaper	4.72*	0.60	70.25	5.58	40.33	2.91	7
Malacca	4.77*	0.36	67.34	5.01	36.51*	2.65	28
Rialto	4.84*	0.45	73.28	5.20	38.40	2.73	14
Buster	4.87*	0.60	62.99*	5.58	39.44	2.91	7
Buchan	5.06*	0.60	59.21 ^{l}	5.57	37.32*	2.90	7
Napier	5.09	0.36	65.67	5.01	39.69	2.64	28
Deben	5.37	0.45	77.98	5.22	38.81	2.74	14
Eclipse	5.48	0.60	65.71*	5.57	38.83	2.90	7
Cockpit (R)	5.96**	0.60	95.42 ^{h}	5.57	40.34	2.90	7
Hereward (R)	6.21**	0.36	76.72	5.01	38.80	2.64	28
Biscay	6.27**	0.45	73.29	5.22	41.17	2.74	14
Xi 19 (R)	6.38**	0.45	83.71	5.22	44.35 ^{h}	2.74	14
Aardvaark (R)	6.47**	0.36	75.19	5.01	43.65**	2.64	28
Charger (R)	6.65**	0.36	73.80	5.01	39.84	2.64	28
Claire (R)	6.73 ^{h}	0.36	78.98**	5.01	39.03	2.64	28

Cultivars are ordered by increasing yield. For each variable, the cultivar with the highest (^{h}) and lowest (^{l}) value was compared with each other cultivar in a series of pairwise comparisons. For each pairwise comparison, differences more than twice the corresponding standard error for the difference of the means were deemed significant.

R indicates cultivar deemed resistant to SBCMV based on symptom severity and ELISA scores.

Cultivars with means not significantly different from either the lowest (*) or highest (**) mean are indicated.

variation caused by these factors, allowing predictions for cultivars made for an average year and site from all years and sites present in the data. However, such an approach would not be suitable should comparisons of virus impact be required between years or sites, and in such cases, a balanced design ideally should be adopted.

The large seasonal fluctuations in the yield of susceptible cultivars observed at the site in Chambon sur Cisse demonstrate the importance of environmental conditions on SBCMV infection. Analysis of the meteorological data from this site (available from http://www.meteofrance.com) in 2000, when the yield loss was greatest, indicates autumn soil conditions were ideal for *P. graminis* infection. Daily average soil temperatures at 10 cm depth reached >12°C between 25 and 40 days post-planting and there were several cycles of short dry periods following short wet ones. In contrast, autumn planting conditions from the other 2 years were either far wetter (2001) or far drier (2002) than seen in 2000 (data not shown). Optimal activity of *P. graminis* from temperate locations has been shown to occur at or near 15°C (Legreve et al. 1998). Cycling wet and dry periods, as seen in 2000, have been shown to favour the growth of *P. graminis* (Adams et al. 1986), whereas prolonged periods of wetness have been shown to reduce spread (Ledingham 1939). In addition, Cadle-Davidson et al. (2003) have shown no significant transmission of *Soil-borne wheat mosaic virus* (SBWMV), a close relative of

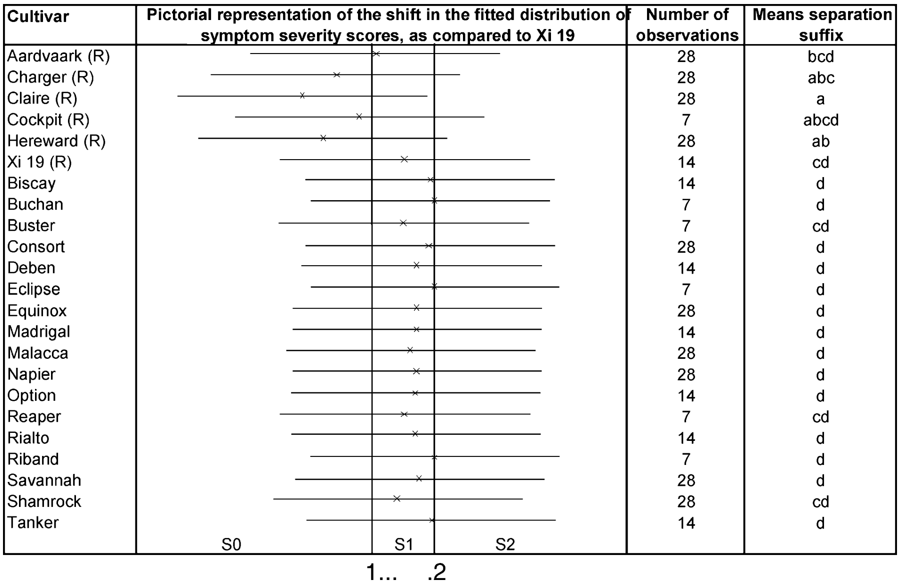
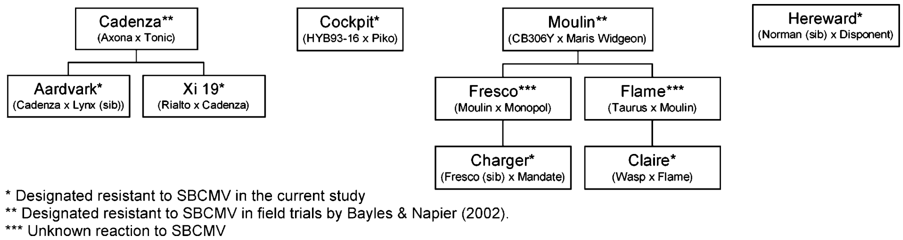


Fig. 2 Pictorial representation of the shift between cultivars (as compared to Xi 19) in the fitted distribution of symptom severity scores pooled from all sites and years as recorded at the time of peak symptom expression. The *horizontal bars* represent the 95% middle quartile of the fitted logistic distribution and the two vertical bars show the cut-points (the natural logarithm of the odds) showing (1) no definite symptoms (*S0*) vs. mild (*S1*) or severe symptoms (*S2*) and (2) no definite or mild vs. severe symptoms for cultivar Xi 19. Score data were analysed using a multinomial generalised linear model and pairwise means separation completed assuming a significance level of 95%. Different suffix represents significantly different symptom severity scores. *(R)* indicates cultivar deemed resistant to SBCMV based on symptom severity and ELISA scores. Local control cultivars were not included in the analysis. Note that the horizontal bars are not a representation of the errors associated with the shift in the fitted distribution for a given cultivar

SBCMV, at or below 6.5°C. Taken together, these data highlight the importance of autumn weather conditions in SBCMV epidemiology, as transmission is unlikely to occur through cold winter months.

The presence of WSSMV was confirmed in the leaf material of the susceptible control cultivars from each site containing a natural inoculum source of WSSMV. WSSMV was consistently below detectable limits in the leaf tissue of all UK cultivars tested in all six trials suggesting these cultivars show field resistance to WSSMV. This study demonstrates UK winter wheat cultivars represent a potentially valuable breeding resource for WSSMV and SBCMV resistance. Future work will concentrate on determining the effect of cultivar resistance on the build-up of soil inoculum and investigate possible resistance mechanisms.

Fig. 3 Trees showing four distinct lineages for winter wheat cultivars resistant to SBCMV. Two lineages trace back to back to cvs Moulin and Cadenza. Pedigrees for each cultivar are shown in parenthesis



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References

Adams, M. J., Swaby, A. G., & MacFarlane, I. (1986). The susceptibility of barley cultivars to *Barley yellow mosaic virus* (BaYMV) and its fungal vector *Polymyxa graminis*. *Annals of Applied Biology, 109*, 561–572.

Bayles, R. A., & Napier, B. (2002). Tolerance of wheat varieties to *Soil-borne wheat mosaic virus* (SBWMV). HGCA project report No. 278, London, UK: Home-Grown Cereals Authority.

Bonferroni, C. E. (1936). Teoria statistica delle classi e calcolo delle probabilità. *Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commerciali di Firenze, 8*, 3–62.

Cadle-Davidson, L., Schindelbeck, R. R., van Es, H. M., Gray, S. M., & Bergstrom G. C. (2003). Using air pressure cells to evaluate the effect of soil environment on the transmission of soilborne viruses of wheat. *Phytopathology, 93*, 1131–1136.

Campbell, L. G., Heyne, E. G., Gronau, D. M., & Niblett C. (1975). Effect of *Soilborne wheat mosaic virus* on wheat yield. *Plant Disease Reporter, 59*, 472–476.

Canova, A., & Qualglia, A. (1960). Il mosaico del frumento. *Informatore fitopatologico, 10*, 206–208.

Clover, G. R. G., Ratti, C., & Henry, C. M. (2001). Molecular characterization of European isolates of *Soil-borne wheat mosaic virus*. *Plant Pathology, 50*, 761–767.

Clover, G. R. G., Wright, D., & Henry, C. M. (1999). Occurrence of *Soil-borne wheat mosaic virus* in the UK. In *Proceedings of the Fourth Symposium of the International Working Group on Plant Viruses with Fungal Vectors* (pp. 105–108).

Gitton, F., Diao, A., Ducrot, O., Antoniw, J. F., Adams, M. J., & Maraite, H. (1999). A two-step multiplex RT-PCR method for simultaneous detection of soil-borne wheat mosaic virus and wheat spindle streak mosaic virus from France. *Plant Pathology, 48*, 635–641.

Hugo, S. A., Henry, C. M., & Harju, V. (1996). The role of alternative hosts of *Polymyxa betae* in transmission of beet necrotic yellow vein virus (BNYVV) in England. *Plant Pathology, 45*, 662–666.

Hunger, R. M., Sherwood, J. L., Smith, E. L., & Armitage, C. R. (1991). Symptomatology and Enzyme-Linked-Immunosorbant-Assay used to facilitate breeding for resistance to wheat soil-borne mosaic virus. *Crop Science, 31*, 900–905.

Huth, W. (2000). Viruses of Gramineae in Germany – a short overview. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz – Journal of Plant Diseases and Protection, 107*, 406–414.

Kendall, T. L., & Lommel, S. A. (1988). Fungus-vectored viruses of wheat in Kansas. In J. I. Cooper, & M. J. C. Asher (Eds.), *Developments in applied virology: Viruses with fungal vectors* (2nd ed, pp. 37–60). Association of Applied Biologists, Wellesbourne, England.

Koenig, R., & Huth, W. (2000). Soil-borne rye mosaic and European wheat mosaic virus: Two names for a *Furovirus* with variable genome properties which is widely distributed in several cereal crops in Europe. *Archives of Virology, 145*, 689–697.

Kucharek, T. A., & Walker, J. H. (1974). The presence of and damage caused by soil-borne wheat mosaic virus in Florida. *Plant Disease Reporter, 58*, 763–765.

Ledingham, G. A. (1939). Studies on *Polymyxa graminis*, n. General n.sp., a plasmodiophoracaeous root parasite of wheat. *Canadian Journal of Research, series C, 17*, 38–51.

Legreve, A., Delfosse, P., Vanpee, B., Goffin, A., & Maraite, H. (1998). Differences in temperature requirements between polymyxa sp. of Indian origin and *Polymyxa graminis* and *Polymyxa betae* from temperate areas. *European Journal of Plant Pathology, 104*, 195–205.

Lommel, S. A., Willis, W. G., & Kendall, T. L. (1986). Identification of wheat spindle streak Mosaic-Virus and its role in a new disease of winter-wheat in Kansas. *Plant Disease, 70*, 964–968.

Maccaferri, M., Ratti, C., Rotondo, F., Rubies Autonell, C., Tuberosa, R., et al. (2005). A molecular survey of the durum wheat (*Triticum durum* Desf.) genome for chromosome regions harboring resistance to SBCMV. *The 6th Symposium of the International Working Group on Plant Viruses with Fungal Vectors (IWGPVFV)*, Bologna, Italy.

McCullagh, P., & Nelder, J. A. (1983). *Generalized linear models*. London: Chapman and Hall.

Parker, S. R., Welham, S., Paveley, N. D., Foulkes, J., & Scott R. K. (2004). Tolerance of septoria leaf blotch in winter wheat. *Plant Pathology, 53*, 1–10.

Patterson, H. D., & Thompson, R. (1971). Recovery of inter-block information when block sizes are unequal. *Biometrika, 58*, 545–554.

Perovic, D., Weyen, J., Schondelmaier, J., Förster, J., Devaux, P., Hariri, D., et al. (2005). Linkage mapping and transcriptional profiling of resistance to Soil-borne viruses in hexaploid wheat. *10th Conference on Viral Diseases of Gramineae in Europe*, Louvain-la-Neuve, Belgium.

Ratti, C., Budge, G., Ward, L., Clover, G., Rubies-Autonell, C., & Henry, C. (2004). Detection and relative quantitation of soil-borne cereal mosaic virus (SBCMV) and *Polymyxa graminis* in winter wheat using real-time PCR (TaqMan ®). *Journal of Virological Methods, 122*, 95–103.

Rice, J. A. (1995). *Mathematical statistics and data analysis*. Belmont, USA: Duxbury.

Rubies Autonell, C., & Vallega, V. (1987). Observations on a mixed soilborne wheat mosaic virus and spindle streak mosaic virus infection in durum wheat. *Journal of Phytopathology, 119*, 111–121.

Rubies-Autonell, C., Vallega, V., & Ratti, C. (2003). Reactions of cultivars of common wheat (*Triticum aestivum* L.) to soil-borne wheat mosaic virus in northern Italy. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz – Journal of Plant Diseases and Protection, 110*, 332–336.

Siegel, S., & Castellan Jr., N. J. (1988). *Non-parametric statistics for the behavioral sciences*. New York: McGraw-Hill.

Signoret, P. A., Alliot, B., & Poinso, B. (1977). Présence en France du wheat spindle streak mosaic virus. *Annales de Phytopathologie, 9*, 377–379.

Vaianopoulos, C., Legreve, A., Lorca, C., Moreau, V., Steyer, S., Maraite, H., et al. (2006). Widespread occurrence of wheat spindle streak mosaic virus in Belgium. *Plant Disease, 90*, 723–728.

Vallega, V., & Rubies-Autonell, C. (1985). Reactions of Italian triticum-durum cultivars to soil-borne wheat mosaic. *Plant Disease, 69*, 64–66.

Vallega, V., Rubies-Autonell, C., & Ratti, C. (2003). Reaction of durum wheat cultivars to mixed SBWMV and WSSMV infection in central Italy. *Phytopathologia Mediterranea, 42*, 177–182.

Vallega, V., Rubies-Autonell, C., Turina, M., Ratti, C., & Contoli, S. (1999). Reactions of durum wheat cultivars to infections by SBWMV grown in northern Italy during 1995–96. *Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz – Journal of Plant Diseases and Protection, 106*, 284–290.

Yang, J. P., Chen, J. P., Chen, J. O., Cheng, Y., & Adams M. J. (2001). Sequence analysis of a soil-borne wheat mosaic virus isolate from Italy shows that it is the same virus as European wheat mosaic virus and soil-borne rye mosaic virus. *Science in China Series C – Life Sciences, 44*, 216–224.