Project Report

The importance of potato mop top virus (PMTV) in Scottish seed potatoes

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1. SUMMARY

Potato mop-top virus (PMTV) causes spraing, necrotic arcs or flecks in the flesh of tubers. Infection is invariably linked with transmission by *Spongospora subterranea*, the cause of powdery scab. At present, losses occur primarily through the rejection of ware potatoes by processors and packers. In future however, it is likely that the disease will impact on exporters of seed potatoes because an increasing number of seed importing countries are designating PMTV as a quarantine organism.

In order to assess the effectiveness of potential control measures and to aid growers with decisions on affected crops, the objectives of this project were to determine the extent of PMTV infection in Scottish seed potatoes, the effect on yield and quality, the transmission rate from seed to daughter tubers and the relative importance of seed and soil inoculum on disease development.

The transmission of PMTV from seed to daughter tubers in cvs Cara, Maris Piper, Nicola, Rooster, Slaney and Winston was assessed over two years at SASA's Gogarbank Farm. Transmission from seed to daughter tubers was found to be less efficient than for aphid-borne viruses, with less than half the daughter tubers derived from PMTV-infected seed being infected by PMTV. Infection in daughter tubers from PMTV-free seed was generally very low or absent. In 2005, yield of daughter tubers from PMTV-infected seed was reduced significantly compared with that from PMTV-free seed but no difference was found in 2004. The development of symptoms on the growing plant varied with cultivar and year, probably because of differences in the summer temperatures in the two years.

The importance of soil and seed inoculum on PMTV infection over two successive generations at over 25 sites was examined using cv. Cara as a model in which the initial seed came from a common source. The amount of PMTV infection in initial seed was very low, <1.0%, in both years. Powdery scab was present in the majority of daughter crops. A high incidence of powdery scab was not generally correlated with a high incidence of PMTV. However, when PMTV infection was found, it was rare for powdery scab to be absent. No correlation was observed between the amount of infection by PMTV or powdery scab on seed tubers and that on the daughter tubers. Soil would, therefore, appear to be the main source of infection of potato crops by PMTV and high amounts of tuber infection occurred after one growing season. In the 2006 Cara study, planting PMTV-free seed in PMTV infested soil resulted in 6 out of 7 crops having PMTV-infected daughter tubers. Planting infected seed tubers in soil free of PMTV resulted in 4 out of 6 crops producing PMTV-infected daughter tubers and in 3 out of 6 soils being infested by PMTV when sampled after harvest.

A random selection of crops from 4 widely grown cultivars (cvs Hermes, Maris Piper, Saturna and Nicola) known to be susceptible to PMTV were selected from four major regions of Scotland covering 16 counties. The majority of crops were free of PMTV infection and spraing. Incidence of crops infected by PMTV differed greatly amongst the regions, with more crops grown in Central Scotland being infected than elsewhere.

In a glasshouse experiment with five cultivars, the development of powdery scab was much greater at 12°C than at 19°C or 27°C, where it was rare/absent. The incidence of PMTV infection in tubers was, however, similar at 12°C and 19°C but spraing was virtually absent at 19°C, even although the same post harvest treatment had been applied to all tubers to enhance its development.

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In summary, PMTV occurs in all regions of Scotland but is not particularly prevalent, even on known susceptible cultivars. Although its occurrence is linked to the powdery scab organism, there is no correlation between the amount of tubers affected by powdery scab and that infected by PMTV. Soil is the principal source of infection and can infect a considerable amount of tubers potentially resulting in a crop being unmarketable because of spraing. Planting infected seed tubers in clean land also brings a risk of introducing PMTV into the soil.

Recommendations:

- Recommend that growers test field soils for the presence of PMTV prior to planting in order to have some information on the risk of PMTV infection in daughter crops.
- Further work is required to refine the PMTV-soil bioassay in order to quantify the severity of infection which might occur given favourable conditions.
- Advise growers not to plant potatoes or a susceptible variety, particularly one which produces spraing, when soils are infested with PMTV.
- Advise growers not to plant infected seed potatoes in an uninfested field, this can be achieved by testing seed potatoes of known susceptible varieties.
- Recommend that the susceptibility of new and existing varieties is determined, whilst recognising that such testing is complicated because the vector is an obligate parasite which cannot be conveniently cultured nor can samples of powdery scab be easily tested directly for the presence of PMTV.
- Further work is required to determine whether roguing would have a positive impact on disease management. Preliminary evidence suggests that for some varieties roguing may reduce the level of infection but this is not true for all varieties as symptoms may be difficult to identify or absent.

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2. EXPERIMENTAL SECTION

2.1 Introduction

Potato mop top virus (PMTV) was first detected in a crop of cv. Kerr's Pink grown in Northern Ireland (Harrison, unpublished data), but was not formally reported until nearly 10 years later (Calvert and Harrison, 1966). PMTV typically produces slightly raised lines and rings on the surface and/or brown arcs and lines (commonly described as spraing) in the flesh of tubers of sensitive cultivars (Calvert and Harrison, 1966; Harrison and Jones, 1970; Kurppa, 1989). Secondary infected plants, i.e., those infected from tubers, may also produce misshapen or cracked tubers, often with elephant hide blemishes on the skin. Diagnosis of PMTV infection is complicated because infection by tobacco rattle virus which is transmitted by free living nematodes causes similar symptoms on plant and tuber (Calvert and Harrison, 1966: Jones, 1988).

Plants grown from PMTV-infected tubers produce three types of foliar symptoms: yellow blotches and chevrons on the leaves, distortion of leaflets often accompanied by blotching and a shortening of the internodes resulting in a bunched appearance, i.e., mop-top. In many cases, only a proportion of the stems are affected (Torrance *et al.*, 1992). Some or all of these symptoms may also be caused by infection by tobacco rattle, potato aucuba mosaic, alfalfa mosaic or tomato black ring viruses (Jones, 1988). Harrison (1974) provided some evidence that haulm symptoms of PMTV infection occur only if the seed tuber was infected and that symptom expression differed amongst cultivars. For example, cv. Saturna, widely used in the Scandanavian potato-processing industry, seems to be very susceptible to spraing in these countries (Sandgren, 1995, Nielsen and Mølgaard, 1997) whereas cv. Desirée was more resistant (Germundsson *et al.*, 2002).

PMTV is a fragile, rod shaped virus. Its genome consists of three single-stranded, positive sense RNA molecules (Torrance *et al.*, 1999). RNA 1 encodes the replicase functions, RNA 2 encodes the triple gene block proteins (TGB) thought to be involved in virus movement and a cysteine rich protein of unknown function (Torrance *et al.*, 1999, McGeachy and Barker, 2000), and RNA 3 encodes the coat protein, along with a possible read through protein thought to be involved in transmission of PMTV by the vector (McGeachy and Barker, 2000). RNA 3 is also thought to be involved in foliar symptom expression (McGeachy and Barker, 2000). Serological (ELISA) and molecular (RT-PCR) methods to detect PMTV in potato leaves and tubers are already widely used. Both methods rely on the presence of the coat protein, encoded by RNA 3 (McGeachy and Barker, 2000) as this is a highly conserved region of the PMTV genome. There is evidence that RNAs 1 and 2 can accumulate and spread systemically in infected plants in the absence of RNA 3 and that these plants do not display symptoms (McGeachy and Barker, 2000).

PMTV has been found in South America, Canada, Europe, China and Japan (Arif *et al.*, 1994; Jeffries, 1998); it is a consistent and major constraint in potato production within Scandinavian countries (Sandgren, 1996; Nielsen and Mølgaard, 1997; Nielsen *et al.*, 2003) and has been found recently for the first time in the USA (Lambert *et al.*, 2003; Xu *et al.*, 2004). Within Scotland, SASA has collected data on the incidence of PMTV infection and spraing symptoms in tuber samples from Scottish seed and ware crops collected for statutory ring rot and brown rot testing in 1999 and 2001. In 1999, spraing was found in 13% of 277 seed crops and 23% of 53 ware crops. PMTV alone was present in 7.2% out of the 277 seed crops, TRV alone in 2.9% and both viruses in 2.2% of affected crops. Results for 2001, from a much larger sample

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(977 crops) showed that, although incidence of spraing was lower with only 4.2% of crops having some tubers affected by spraing, the proportion of PMTV to TRV causing spraing was roughly 2:1 (2.5% PMTV to 1.3% TRV), similar proportions to that of 1999. These results indicate that, in Scotland, PMTV was twice as likely to be the cause of spraing as TRV. At present, losses attributable to PMTV occur primarily through the rejection of ware potatoes by processors and packers. In future, however, it is likely that the disease will impact increasingly on exporters of seed potatoes as a number of seed-importing countries (Bangladesh, Brazil, China, Indonesia, Iran, Jordan, Kuwait, Saudi Arabia, Thailand and Uruguay) designate PMTV to be a quarantine organism and impose a nil tolerance for the virus in imported seed potatoes.

Jones and Harrison (1969) demonstrated that the powdery scab pathogen, the plasmodiophorid; *Spongospora subterranea*, was a vector in the transmission of PMTV. Infection from infective spore balls could produce symptoms on plants and in tubers. Arif *et al.* (1995) demonstrated conclusively that PMTV could be acquired from the roots of infected plants by *S. subterranea* and then subsequently transmitted to healthy bait plants. It is now widely accepted that *S. subterranea* is the only vector for PMTV.

Powdery scab has become increasingly important in recent years (Qu, *et al.*, 2006). This may, in part, be due to the popularity of cultivars that are particularly susceptible, the increased use of irrigation that leads to optimal conditions for disease development, inadequate crop rotations or the absence of an effective seed tuber inspection scheme (Qu, *et al.*, 2006, Wale, 2000, De Haan and van den Bovenkamp, 2005, Harrison *et al.*, 1997). Changes in marketing practices have affected the importance of this disease. Powdery scab usually only causes cosmetic damage to tubers, making them appear unsightly so they are difficult to market (Wale, 2000), especially as potatoes are now mostly presented to customers washed. A clean, blemish free appearance is, therefore, a critical marketing attribute. Seed lots are often rejected or re-classified during inspection if a high incidence of powdery scab is observed on tubers (De Haan and van den Bovenkamp, 2005); this in turn may have a detrimental effect on export opportunities and may also be a financial burden on the grower.

On mature tubers, powdery scab develops as hollow lesions filled with brown powder consisting of cystosori (sporeballs) (Germundsson *et al*., 2002). Under wet conditions, cystosori germinate and release primary zoospores which can infect potato roots, stolons, young shoots and tubers (Hims and Preece, 1975). After penetration of the host cells, the zoospore becomes a multinucleate plasmodium divided into segments to form zoosporangia. Each of these contains 4 to 8 secondary zoospores that can again infect roots (Hims and Preece, 1975). The zoospores can acquire virus particles of PMTV when *S. subterranea* develops in virus-infected host cells but the mechanism of acquisition is still uncertain (Germundsson *et al*., 2002). Infection occurs soon after the vector has penetrated the host cell. PMTV is located inside the zoospores emerging form vegetative sporangia and it also resides in resting spores which may survive in soil for more than 15 years (Jones and Harrison, 1969, 1972, Campbell, 1996). Soils may, therefore, be infected by PMTV for a long period of time (Germundsson *et al*., 2002) and can still be detected in soils 12 years after potatoes were grown (Jones and Harrison, 1972).

The powdery scab pathogen is ubiquitous: however; the extent to which populations of *S. subterranea* are infested with PMTV has yet to be determined. Infection with *S. subterranea* is favoured by cool conditions (14-20°C) and high humidity (Teakle, 1988), which are also the optimal conditions for PMTV infections. In Scotland, the disease is more closely associated with higher annual rainfall than with soil characteristics (Cooper and Harrison, 1973). The probability of infection increases with increasing annual rainfall.

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Current control measures for powdery scab, and as a consequence, PMTV, are limited. There are no fungicides or fumigants specifically licensed for the control of powdery scab on tubers although Fluazinam has been given a specific off label approval for application to soil pre-planting to control powdery scab. No varieties are known to be immune to PMTV; however PMTV infection in certain varieties can result in few or no spraing symptoms. There are still no known sources of resistance to PMTV for incorporation into modern potato cultivars.

Despite the fact that transmission of PMTV from seed to daughter tubers is restricted and may lead to elimination of the virus from a seed potato stock over a few years, control of PMTV may be difficult and is hampered by our incomplete understanding of its epidemiology. There is little information on the extent of symptomless infection in the growing plant and tubers, the rate of transmission of PMTV from seed to daughter tubers, the relative importance of soil and seed inoculum and the extent to which populations of *S. subterranea* are infected with PMTV. Such information is essential in order to assess the risk of PMTV to the overall yield and quality of the potato crop, the effectiveness of potential control measures, e.g. roguing, and the provision of advice to assist growers with decisions on affected crops.

2.2 Material and methods

2.2.1 Seed transmission experiments

The aim of these experiments was to determine the amount of transmission of PMTV which occurs from an infected seed tuber to the growing plant and then to daughter tubers for a range of cultivars. The experiments were conducted over 2 years at one site, SASA's Gogarbank Farm. Powdery scab and PMTV have rarely been seen on tubers produced on this farm.

2.2.1.1 2004 experiment

Transmission of PMTV from seed to daughter tubers was examined for four cultivars (cvs Cara, Maris Piper, Nicola and Slaney) in experiments at SASA's Gogarbank Farm. Soil from the area designated for the experiment was sampled prior to planting and tested for the presence of PMTV (see Section 2.2.7). Tubers of cv. Nicola from crops in different fields (Field 1 and Field 2) on the same farm were included in this study as both had a relatively high incidence of PMTV infection (15.8% and 19.2 %, respectively). Tubers from the 5 crops were tested by ELISA for PMTV to obtain 120 infected tubers and 120 PMTV-free tubers. The experiments were laid out in a randomised block design with 3 or 4 replications (cv. Slaney only). Each plot consisted of 2 (cv. Slaney only) or 4 drills, each containing 10 tubers spaced 0.38m apart. Each plot was guarded lengthwise and across drills by planting blue coloured tubers of cvs Edzell Blue or Arran Victory. Tubers were planted on 18 May, 2004. Plants were assessed for visual symptoms characteristic of PMTV infection during June and July, and affected plants identified by a cane. Leaflets from all affected and a sample of non-affected plants were collected in July and tested for PMTV by ELISA (leaflets tested from all affected plants and at least 4 healthy plants per drill). Haulm was killed on 2 September, 2004 by applying diquat dibromide (Reglone) at the manufacturer's recommended rate. Produce of plants affected by viruses, other than PMTV, and blackleg was discarded just before harvesting. In each plot, daughter tubers from affected plants were harvested by fork on 28 September 2004 and the remainder of plants was harvested by single row digger and hand lifting. For each plot, all tubers from affected plants were tested by ELISA for PMTV and a random sample of 150 tubers from the unaffected plants was also tested. Yield of tubers from unaffected and affected plants was also measured.

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2.2.1.2 2005 experiment

Transmission of PMTV from seed to daughter tubers was again examined in a randomised experiment at Gogarbank using four cultivars (cvs Cara, Nicola, Rooster and Winston). Tubers from two crops of cv. Cara (Cara 1 and Cara 2) with a high incidence of PMTV infection (52% and 35%, respectively) were included in this study. As in 2004, 120 infected tubers and 120 PMTV-free tubers were identified for each crop by testing by ELISA for PMTV. The experiments were laid out in a randomised block design with 3 replications. Each plot consisted of 4 drills, each of 10 tubers spaced at 0.38m apart. Each plot was guarded lengthwise and across drills, as in 2004. Tubers were planted on 10 May, 2005. Plants were examined visually during June and July and those with symptoms characteristic of PMTV infection were marked by canes. Leaflets from all affected and a sample of non-affected plants were collected in July and tested for PMTV by ELISA, as in 2004. Haulm was killed on 18 August, 2005 by applying Reglone at half of the manufacturer's recommended rate followed by a second application 1 week later. Produce of plants affected by viruses, other than PMTV, and blackleg were discarded just before harvesting. In each plot, daughter tubers from affected plants were harvested by fork on 4 October, 2005 and the remainder of plants was harvested by single row digger and hand lifting. For each plot, all tubers from affected plants were tested by ELISA for PMTV and a random sample of 150 tubers from the unaffected plants was also tested. Yield of tubers of unaffected and affected plants was also measured.

2.2.2 Transmission of PMTV on seed crops of cv. Cara in relation to site and generation of production

The aim of this study was to examine the health of crops grown from seed potatoes from a common origin at a wide range of sites in eastern Scotland and to determine their health in two succeeding generations. Cv. Cara was chosen for this purpose because seed potatoes for most of the marketing of basic classes of this cultivar are grown over 2 years on a range of Scottish farms after receipt of the initial seed potatoes from a producer in the north of Scotland. The health of seed and daughter tubers from these crops was studied over two multiplication seasons: 2004-2005 and 2005-2006. In presenting the results, each grower has been assigned a unique number. However, farm numbers only indicate different farms in any year.

2.2.2.1 cv. Cara 2004 study

Seed potatoes of 2 Super Elite crops (0.5% tubers infected by PMTV and 5.5% tubers affected by powdery scab) grown on a farm in the North of Scotland were distributed to 31 farms for the commercial production of Super Elite 2 or 3 class seed potatoes. Crops were grown according to farm practice. Soil samples were collected from the drills of all 31 crops when the plants were already established and tested for the presence of PMTV (see Section 2.2.7). Just after harvest, a random sample of 200 daughter tubers from each stock was collected into new bags by seed potato inspectors and despatched to SASA. After all samples were received, they were stored for 2 weeks at 16°C, followed by 1 week at 6°C which are the conditions reported by Harrison and Jones (1971) to be conducive to spraing development. After rose and heel end cores were taken for ELISA testing, the severity of powdery scab in a range of categories and the incidence of spraing after cutting tubers was recorded.

2.2.2.2 cv. Cara 2005 study

The effect of site on the development of powdery scab and PMTV was assessed in 84 potato crops of cv. Cara being grown commercially to produce Super Elite 3 and Elite 1 class seed potatoes. The Elite 1 class crops were derived from some of the 31 crops of Super Elite 2 & 3 class seed potatoes studied in 2004. The other crops were derived from class SE seed potatoes

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from the producer in the north of Scotland (0.7% of tubers in each crop infected by PMTV). Crops were grown according to farm practice. Just after harvest, a random sample of 150 daughter tubers from each crop was collected by seed potato inspectors and dispatched to SASA. Tubers were stored and assessed for PMTV, spraing and powdery scab as in 2004.

2.2.2.3 cv. Cara 2006 study

The effect of site on the development of powdery scab and PMTV was assessed in 28 potato crops of cv. Cara being grown commercially to produce Elite 1 class seed potatoes and which had been planted with seed potatoes from some of the crops of Super Elite class seed potatoes studied in 2005. Soils from crops of cv. Cara were sampled in all 28 fields prior to planting crops and after harvesting. Pre-planting soils samples were collected in April and May, 2006 and post harvest soil samples were collected in March, 2007. All soils were tested for PMTV as described in Section 2.2.7. Crops were grown according to farm practice. Just after harvest, a random sample of 150 daughter tubers from each crop was collected by seed potato inspectors and dispatched to SASA. Tubers were stored and assessed for PMTV, spraing and powdery scab as in previous years.

2.2.3 Survey of the incidence of PMTV in Scottish seed crops

A random selection of crops of 4 commonly grown cultivars (cvs Hermes, Nicola, Maris Piper and Saturna) known to be susceptible to PMTV were selected from sixteen counties representing all the major seed producing areas of Scotland. All crops were Super Elite class seed potatoes. For the purpose of selecting crops and for analysis, the various counties were allotted to one of 4 main regions: The Borders, Central, North-Eastern & Northern (see Table 14) and approximately 10 crops of each cultivar were sampled for each region. In all, 128 crops were selected with no more than one crop on a farm where possible. One hundred and fifty tubers from each crop were tested for PMTV by ELISA, and cut tubers examined for spraing.

2.2.4 Tuber testing

Tubers were individually numbered and a tissue core (approximately 0.5g) was taken with a cork borer from the rose and heel end (stolon attachment point). The two cores were placed in a Bioreba homogenisation bag (Bioreba AG, CH) and 5ml tuber extraction buffer was added to the sample prior to homogenisation.

2.2.5 Leaf testing

Samples for testing consisted of four leaflets. For an affected plant, one leaflet was collected from each of four compound leaves on a stem or, for four unaffected plants, one leaflet was taken from a compound leaf on each plant. Leaflet samples were placed into the back of the Bioreba homogenisation bag (Bioreba AG, CH) and were tested immediately after sampling. However, if this was not possible, they were stored at 4°C and tested within 24 h of sampling. Five ml of leaf extraction buffer was added to the sample prior to homogenisation, and a further 5 ml leaf extraction buffer was added to the sample after homogenisation.

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2.2.6 ELISA testing procedure

All ELISA testing was carried out using polystyrene microtitre plates (Nunc, DK) that had been precoated with a PMTV specific monoclonal antibody (http://www.sasa.gov.uk/about_sasa/antibodies/index.cfm). Two hundred microlitres of the homogenised samples were added to each well and analysed in duplicate. Samples from negative (tuber) and negative (leaf) control material were also added to each plate.

Plates were incubated at 7°C for 18 h, washed, and a PMTV alkaline phosphatase conjugate (SASA) was added to each well. The plates were incubated for a further 2 h at 37°C. P-nitrophenyl phosphate substrate (Sigma) was then added at 1mg ml^{-1}. After 1 h, the reactions were assessed using a microplate reader (Dynatech Laboratories) at 405nm. Samples were judged to be positive when the mean OD values were greater than twice that of the negative controls.

2.2.7 Detection of PMTV in soil

2.2.7.1 cv. Cara survey soil samples
Soil samples were collected from fields of all 31 crops of cv. Cara (**2.2.2.1 cv. Cara 2004 study**). Soil was sampled in August, 2004 (see Section 2.2.7.2). In 2006, soil was sampled from all 28 fields (**2.2.2.3 – cv. Cara 2006 study)** in April and May, prior to planting the crops of cv. Cara. Fields were sampled again after harvest in March, 2007. The need to validate the existing test method meant that there were insufficient resources available to collect and test soils in 2005.

2.2.7.2 Sampling field soil
For each field, in 2004 and 2006, soil was sampled from an area which did not exceed four hectares. Fields over 4 hectares were split into units of 4 hectares or less for sampling purposes. The area to be sampled was walked in an extended 'W' pattern and sub samples (cores) were taken using a 5 cm x 1 cm borer at various points covering the entire unit of the 'W' shaped walk. The number of cores taken per unit varied between sites with wet, sticky, clay soils requiring fewer cores per unit than dry, sandy, clay soil which does not core as well. In total, approximately 600 ml soil was collected from each sample unit or each sub-divided (< 4 ha) sample unit. Soils were laid on paper towel on 30 x 40cm plastic trays and, when necessary, broken up to remove large lumps. Soils were then air-dried at room temperature then stored at 5°C until testing.

2.2.7.3 Soil bait test
Sample soils were air-dried as described in Section 2.2.7.2. Approximately 20 g of soil was placed in each well of a tray containing 84 wells (well - 25mm wide at top. Amprica, Italy). There were 3 replicate wells for each soil sample. A single 2-week-old seedling of *Lycopersicon esculentum* (cv. Moneymaker) or *Nicotiana benthamiana (N. benthamiana)* was planted into each well. Plants were grown under natural light conditions in a glasshouse at temperatures between 17-21ºC with daily watering of plants. After 14 days, plants were removed from the wells and soil carefully washed from the roots. Approximately 100 mg of root tissue from each bait plant was excised using a scalpel and placed into an individual labelled Bioreba homogenization bag (Bioreba AG, Switzerland). Total RNA extractions were carried out using the Kingfisher™ system (Thermo Labsystems, Finland) and MagExtractor®-

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RNA- reagents (Toyobo, Japan), according to the manufacturer's instructions. Extracted RNA template was stored at -20°C prior to testing by real-time RT-PCR.

2.2.7.4 PCR assay

In order to optimise the test for detecting PMTV, preliminary experiments examining primers, probes and type of bait plant (see 2.2.7.3) were conducted because McGeachy and Barker (2000) indicated that infection by PMTV occurred in the absence of RNA 3 molecule which was the current target for existing tests. It, therefore, seemed prudent to examine this possibility.

Real-time PCR was performed on 1µl of RNA template in 25µl reactions. PCR mastermix contained; JumpStart^{TM} Taq ReadyMix^{TM} for Quantitative PCR (Sigma, USA) 12.5µl, 3 mM $MgCl_2$ 4µl, PMTV Forward primer @ 7.5 pmol/µl 1µl, PMTV Reverse primer @ 7.5 pmol/µl 1µl, PMTV Probe @ 5.0 pmol/µl 0.5µl, M-MLV Reverse Transcriptase (Promega, USA) 0.05µl, H_2O 4.95µl. Six primer/probe combinations were assessed for their effectiveness in detecting PMTV. Primer sequences are shown in Table 1a and probes in Table 1b. Amplification and detection was performed on a Applied Biosystems 7900HT PCR System (Applied Biosystems, USA) cycling conditions were as follows, an initial hold step at 48ºC for 30 min, preliminary denaturation at 94ºC for 2 min followed by 40 cycles of 95ºC for 15 seconds and 60ºC for 1 min.

TABLE 1A. PRIMER SEQUENCES FOR REAL-TIME PCR DETECTION OF PMTV. THE NUMBER OF EACH PRIMER PAIR DENOTES THE RNA MOLECULE OF PMTV THAT IT TARGETS. PRIMER PAIR 3B HAS BEEN PREVIOUSLY DESCRIBED (MUMFORD *ET AL*., 2000)

Primer Name	Forward Sequence	Reverse Sequence
1A	5'-AGGACAGCTATGCCCGAGAA-3'	5'-GGTGCAGCCATATTTCGCTT-3'
1B	5'-TGGGTCGTGCATGGACCTA-3'	5'-GACCGAAGTCTTGTAAGCACTAACAT-3'
2A	5'-CCGACATAAGTTTG(CT)GCTTG-3'	5'-TCGATG(CT)CAATTCTCCGTTAA-3'
2B	5'-AGAATTG(AG)CATCGAAACAGCA-3'	5'-GTCGCGCTCCAATTTCGTT-3'
3A	5'-GGTTACGCTGGGCTGGTG-3'	5'-CGATAGCGGTGACG-3'
3B	5'-GTGATCAGATCCGCGTCCTCCTT-3'	5'-CCACTGCAAAAGAACCGATTTC-3'

TABLE 1B. PROBE SEQUENCES FOR REAL-TIME PCR DETECTION OF PMTV. THE NUMBER OF EACH PRIMER PAIR DENOTES THE RNA MOLECULE OF PMTV THAT IT TARGETS. PROBE 3B HAS BEEN PREVIOUSLY DESCRIBED (MUMFORD ET AL., 2000)

Primer Name	Probe
1A	5' -AGCGGTTTGGCAGAAGGTTTGG-3'
1B	5' -TCAAAACATGCCGTGGACATTACGTCA -3'
2A	5'-AATCCGTTGTAATCCAGAACTGTTCATGCAG-3'
2B	5'-CCACAAACAGACAGGTATGGTCCGGAA-3'
3A	5'AGCAATTAACCGCTCAGGCTYTTTTGGTTTG-3'
3B	5' -ACCAGAACTACGGTGCCGCGTCG-3'

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2.2.7.5 Sensitivity of soil assay
In order to assess the sensitivity of the developed test, six of the 2004 soil samples from Cara crops were diluted using sterilised horticultural sand (w/w) to the following concentrations: 50, 20 and 10% and tested using the bait plants. A soil from a field near Auchterarder, Perthshire, Scotland known to infested by PMTV acted as positive control. A sample from a batch of John Innes No 2 compost acted as negative control and a sample of the positive control soil which had been sterilised was also tested.

2.2.8 Temperature in relation to infection from soil inoculum

This experiment was designed to examine, in a glasshouse, the effect of temperature on infection of plants of five potato cultivars by PMTV when the virus was present in the growing medium. The range of temperatures could only be provided using different sections within SASA's glasshouse complex which meant that the experiment design had to be an incomplete randomised block. Five cultivars and two growing media were used.

2.2.8.1 Cultivars and seed tubers
Tubers from five PMTV susceptible cultivars (cvs Nicola, Cara, Slaney, Rooster and Saturna) were selected from produce of plants grown at SASA's Gogarbank Farm in 2006 and tested for PMTV by ELISA, as described in section 2.2.4 & 2.2.6. Only PMTV-free tubers were used in the experiment. Prior to planting in pots, the tubers were covered with paper towel and stored at room temperature for 3 weeks to chit.

2.2.8.2 Test soils
Soil known to be infested by PMTV from previous testing was collected from a field near Auchterarder, Perthshire, Scotland. The field soil was mixed with John Innes No 2 compost (1:1, v/v) in a cement mixer to give a homogeneous lot. Pots were filled with either the mixture of field soil and compost or compost alone.

2.2.8.3 Experimental layout
Tubers were planted on 7th February, 2007 in 1.5 litre pots placed in 3 different glasshouse units set at a constant temperature of 12°C, 19°C or 26°C and a 16 h daylight regime. In each unit, pots were placed on the middle bench in a randomised block layout with 5 replications for each combination of cultivar and soil. Each tuber was planted to a depth of 7 cm and soils watered generously on a daily basis to encourage zoospores to spread. Soil moisture sensors (SM200) (Delta-T Devices Ltd, Cambs, UK) were placed in the soil and soil moisture was monitored daily using a GP1 Data logger (Delta-T Devices Ltd, UK) as a basis for the watering regime.

Leaves from all plants were sampled on 23rd March 2007 as described in section 2.2.5 and tested for a range of potato viruses (Potato Viruses Y, X, A, S, M, V, Potato Leaf Roll Virus, Tomato Black Ring Virus, Potato Mop Top Virus and Tobacco Rattle Virus). Daughter tubers from each pot were harvested into new paper bags on 22 May, 2007 and stored in a refrigerated cabinet for 2 weeks prior to being subject to a storage regime to enhance spraing development (2.2.2.1). All daughter tubers were tested for PMTV by ELISA, visually assessed for powdery scab lesions, and cut and examined for spraing assessment.

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2.2.9 Statistical analysis

Many of the data sets contained treatments which produced nil or very low values e.g. PMTV-free seed and treatments which produced very high values e.g. PMTV-infected seed. The extreme nature of the values rendered conventional analysis of variance inappropriate and redundant. However in some cases, logistic regression modelling for binomial data was conducted using Genstat® version 8.1 to determine differences. Analysis of variance (ANOVA) and correlation analysis were also conducted as appropriate.

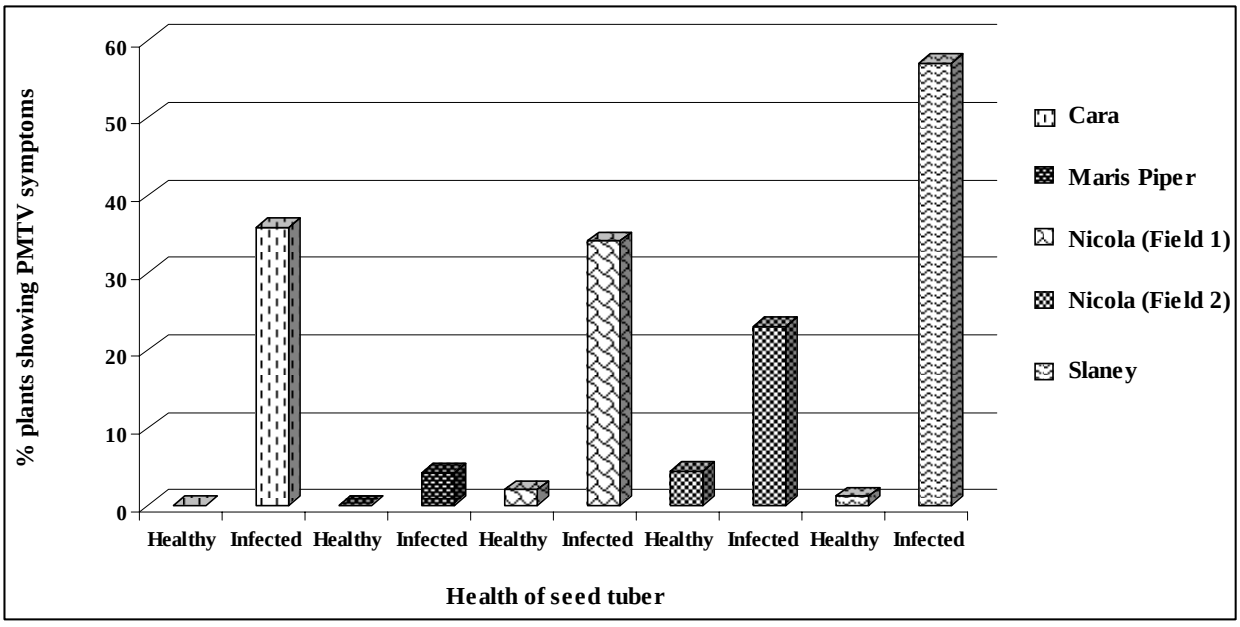
2.3 Results

2.3.1 Seed transmission experiments

2.3.1.1 2004 experiment

PMTV was not detected in the samples of soil collected from the site before planting. In this experiment, infected seed tubers of cv. Cara were also divided into those that were symptomlessly infected (tested positive for PMTV by ELISA; no spraing) and those that had spraing symptoms (also positive for PMTV by ELISA). The incidence of PMTV in plants and daughter tubers was similar for symptomlessly infected and spraing affected seed tubers, therefore only the mean results for these treatments (infected, spraing/infected, no spraing) are presented. The incidence of plants with symptoms of PMTV infection grown from PMTV-infected and PMTV-free seed of cvs Cara, Maris Piper, Nicola and Slaney is presented in Figure 1. Symptoms of PMTV infection were rare on plants derived from healthy seed tubers. When plants were grown from infected tubers, the incidence of affected plants was greatest for cv. Slaney (57.1%) while plants of cv. Maris Piper were rarely affected (4.2%). Analysis by logistic regression of the binomial data confirmed that symptom expression on the growing plant was cultivar dependent ($P < 0.05$).

FIG. 1. PERCENTAGE OF GROWING PLANTS SHOWING PMTV SYMPTOMS IN THE FIELD IN 2004 IN RELATION TO THE PMTV HEALTH OF THE SEED TUBER AND CULTIVAR.



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The effect of cultivar and PMTV health of the seed tuber on the incidence of PMTV in the growing plant, as measured by ELISA, is shown in Table 2. Virtually all plants from PMTV-free mother tubers were free of PMTV although an occasional symptomatic plant was recorded in plants derived from PMTV-free seed tubers of cvs Nicola (Field 2) and Slaney. With PMTV-infected seed, the incidence of PMTV infection in asymptomatic plants was less than that for symptomatic plants in 4 out of 5 comparisons. In general, the detection of PMTV was correlated only weakly with symptoms. For example, 60% of plants of cv. Slaney from infected seed showed symptoms of PMTV infection but PMTV was detected in only 25% of these plants when tested by ELISA.

TABLE 2. THE INCIDENCE OF PMTV INFECTION AND SYMPTOMS ON THE GROWING POTATO PLANT IN 2004 AT GOGARBANK IN RELATION TO PMTV HEALTH OF SEED TUBER AND CULTIVAR.

		% plants infected with PMTV		
Cultivar	**PMTV health of seed tuber**	**Asymptomatic plants**	**Symptomatic plants**	**Mean % plants infected by PMTV**
Cara	Healthy	0 (36)*	-†	0
	Infected	19 (74)	29 (85)	25
Maris Piper	Healthy	0 (40)	-†	0
	Infected	33 (45)	25 (4)	33
Nicola (Field 1)	Healthy	0 (51)	0 (5)	0
	Infected	16 (51)	41 (22)	23
Nicola (Field 2)	Healthy	2 (44)	0 (5)	2
	Infected	8 (52)	18 (34)	12
Slaney	Healthy	1 (79)	0 (1)	1
	Infected	16 (32)	25 (48)	21

* Total number of plants tested is shown in parentheses.
† Symptomatic plants not observed

PMTV infection in daughter tubers from PMTV-free seed was generally very low or absent (Table 3). The incidence of infection by PMTV in daughter tubers derived from infected seed ranged from 31% for cv. Nicola (Field 2) to 49% for cv. Cara. With cv. Maris Piper, the incidence of infected daughter tubers (33%) was considerably greater than the incidence of symptomatic plants (4%) (Figure 1). With daughter tubers from PMTV-infected seed tubers, the incidence of PMTV in tubers was broadly similar for symptomatic and asymptomatic plants (Table 4). Asymptomatic plants produced a lower proportion of infected tubers in only 2 out of 5 comparisons.

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TABLE 3. THE INCIDENCE OF PMTV IN DAUGHTER TUBERS IN 2004 AT GOGARBANK IN RELATION TO PMTV HEALTH OF SEED TUBERS AND CULTIVAR

	% daughter tubers infected with PMTV	
Cultivar	**PMTV-free seed**	**PMTV-infected seed**
Cara	2.7 (150)*	49.4 (1363)
Maris Piper	0 (150)	32.9 (797)
Nicola (Field 1)	0 (398)	33.4 (682)
Nicola (Field 2)	0.8 (269)	31.5 (537)
Slaney	0.6 (505)	42.2 (637)

* Total number of tubers tested is shown in parentheses

TABLE 4. PERCENTAGE OF PMTV-INFECTED DAUGHTER TUBERS PRODUCED FROM PMTV-INFECTED SEED IN RELATION TO SYMPTOMS ON THE GROWING PLANT IN 2004

	% daughter tubers infected with PMTV	
Cultivar	**Symptomatic plants**	**Asymptomatic plants**
Cara	39.0 (387)*	43.8 (881)
Maris Piper	23.7 (187)	32.8 (610)
Nicola (Field 1)	51.5 (224)	25.5 (458)
Nicola (Field 2)	14.0 (88)	13.6 (450)
Slaney	22.2 (222)	36.2 (415)

* Total number of tubers tested appears in parentheses

The effect of PMTV infection of seed tubers on tuber yield is presented in Figure 2. In the majority of comparisons, plants from PMTV-infected tubers produced tuber yields which were slightly smaller than, but not significantly different from, those from PMTV-free seed tubers.

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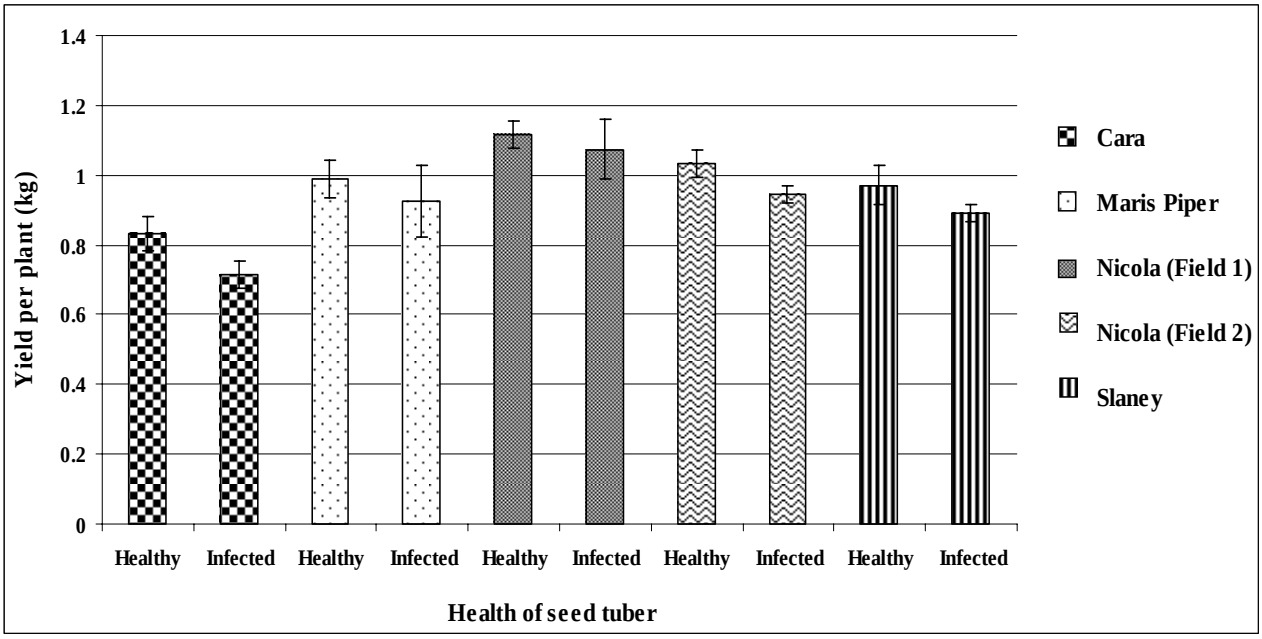
FIGURE 2. HEALTH OF SEED AT A COMMON SITE (GOGARBANK STUDY – 2004). TUBER YIELD OF PLANTS OF 4 CULTIVARS IN RELATION TO PMTV HEALTH OF SEED TUBER



2.3.1.2 2005 experiment

The incidence of symptomatic plants derived from PMTV-infected and PMTV-free tubers of cvs Cara, Nicola, Rooster and Winston is presented in Figure 3. As in the 2004 experiment, symptoms of PMTV infection were rare on plants derived from PMTV-free seed tubers. On plants from infected seed, symptoms were most common on plants of cv. Nicola and were not observed on plants of cvs Rooster and Winston. However, the incidence of symptomatic plants of cv. Cara was lower in 2005 than in 2004. As in 2004, the logistic regression analysis confirmed that symptom expression on the growing plant differed amongst the cultivars ($P < 0.05$).

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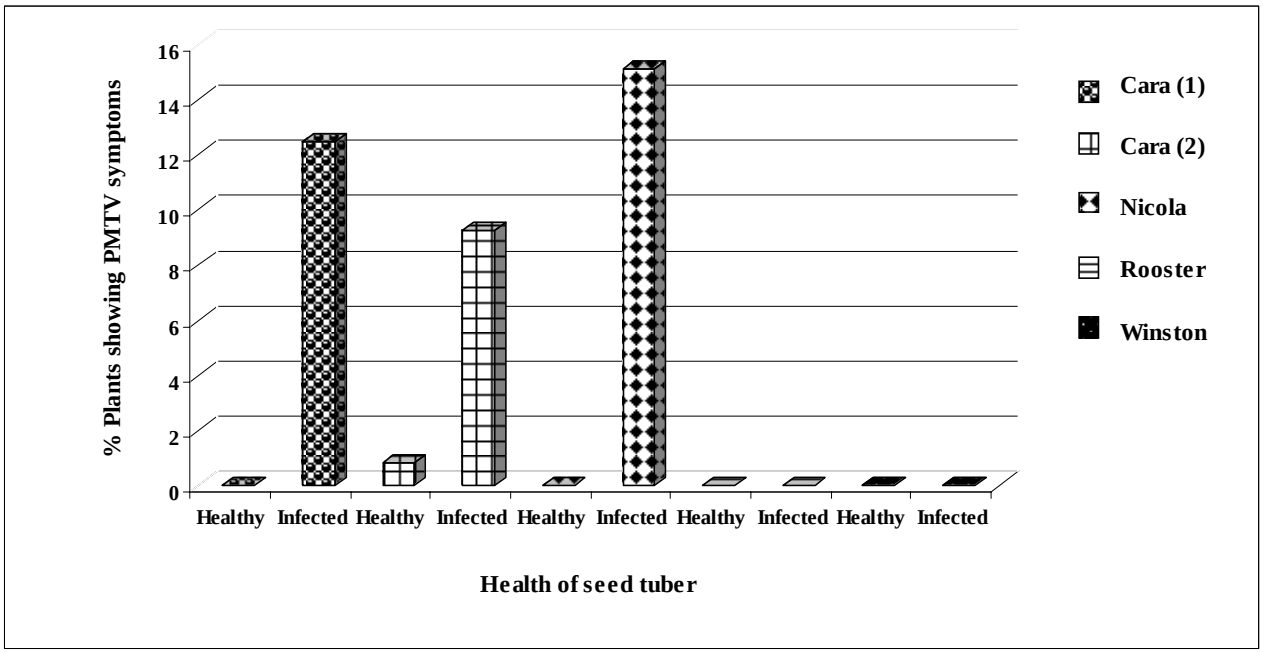
FIGURE 3. HEALTH OF SEED AT A COMMON SITE (GOGARBANK STUDY – 2005). PERCENTAGE OF PLANTS SHOWING PMTV SYMPTOMS IN THE FIELD IN 2005 IN RELATION TO THE PMTV HEALTH OF THE SEED TUBER AND CULTIVAR



The effect of cultivar and PMTV health of seed tuber on the incidence of PMTV in the growing crop is shown in Table 5. Virtually all plants derived from PMTV-free tubers tested negative for PMTV although PMTV was detected in the two 'healthy' symptomatic plants of cv. Nicola but not in the symptomatic plant of cv. Cara 2. No symptoms developed on plants of cvs Rooster and Winston derived from PMTV-infected seed but the incidence of PMTV in plants of these cultivars was 27% and 40% respectively. The incidence of PMTV infection in plants from infected seed tubers did not appear to be affected by the extent to which symptoms developed on the growing plant. For example, the mean incidence of PMTV in plants of cv. Winston whose plants developed no symptoms was 40% compared with 30% of those of cv. Nicola of which 56% of plants developed symptoms. As in 2004, the detection of PMTV in affected plants of cvs Cara and Nicola was relatively low, ranging from 40 to 64%. The incidence of PMTV infection in asymptomatic plants was less than that in symptomatic plants in all 3 comparisons.

TABLE 5. THE INCIDENCE OF PMTV INFECTION AND SYMPTOMS ON THE GROWING POTATO PLANT IN 2005 AT GOGARBANK IN RELATION TO PMTV HEALTH OF SEED TUBER AND CULTIVAR

% plants infected with PMTV				
Cultivar	**PMTV health of seed tuber**		**Asymptomatic plants**	**Symptomatic plants**
Cara (1)	Healthy	0(48)	-†	0
	Infected	29(48)	40(15)*	32
Cara (2)	Healthy	0(48)	0(1)	0
	Infected	29(48)	64(11)	36
Nicola	Healthy	0(48)	50(2)	2
	Infected	27(48)	56(18)	30
Rooster	Healthy	0(48)	-†	0
	Infected	40(48)	-†	27
Winston	Healthy		-†	0
	Infected		-†	40

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† Symptomatic plants not observed
* Total number of plants tested is shown in parentheses

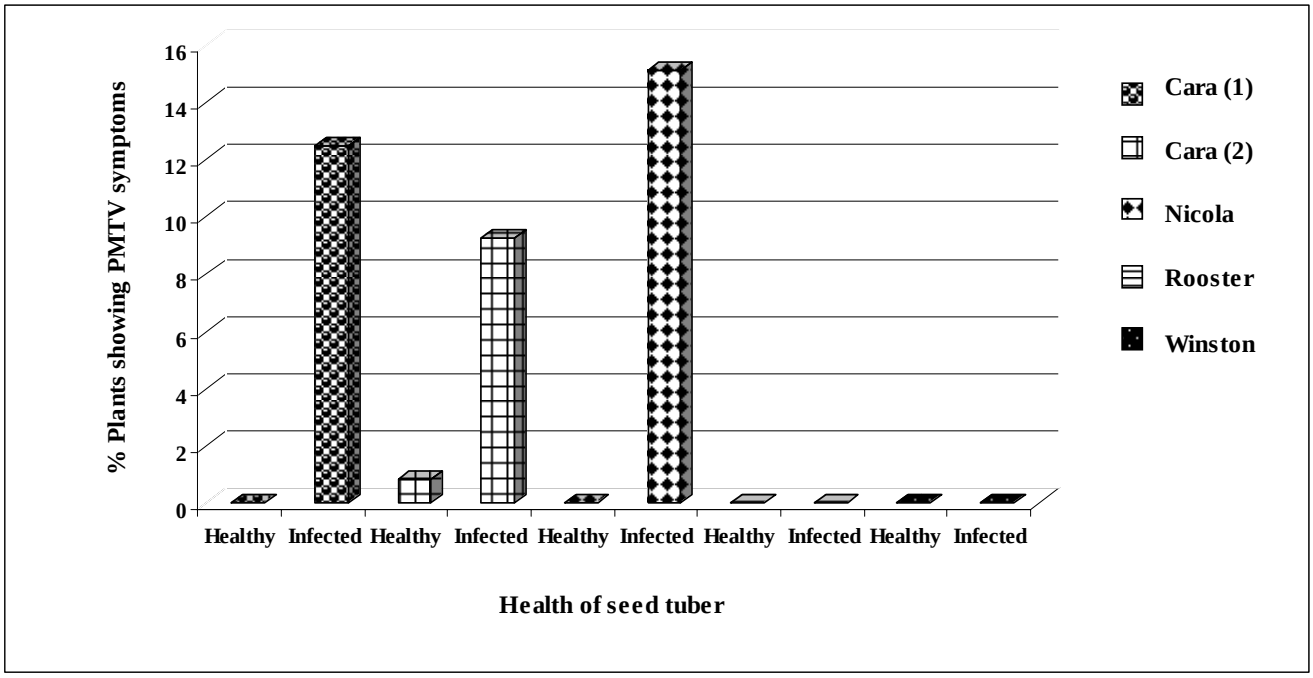
Although PMTV infection was detected in daughter tubers produced from PMTV-free seed of all cultivars, the amount of infection was very low (Table 6). The incidence of PMTV infection in daughter tubers derived from PMTV-infected seed ranged from 23.3% for cv. Rooster to 40.9% for crop 2 of cv. Cara. As in 2004, the incidence of tuber infection was greater than the incidence of symptomatic plants (Table 6, Figure 3). Asymptomatic plants derived from PMTV-infected seed tubers produced a lower proportion of infected tubers than symptomatic plants in 2 out of 3 comparisons (Table 7).

TABLE 6. THE INCIDENCE OF PMTV IN DAUGHTER TUBERS IN 2005 AT GOGARBANK IN RELATION TO PMTV HEALTH OF SEED TUBERS AND CULTIVAR

	% daughter tubers infected with PMTV	
Cultivar	**PMTV-free seed**	**PMTV-infected seed**
Cara (1)	1.1 (450)*	34.1 (671)
Cara (2)	0.2 (457)	40.9 (633)
Nicola	0.9 (450)	32.0 (662)
Rooster	0.2 (450)	23.3 (450)
Winston	0.2 (450)	38.0 (450)

* Total number of tubers tested is shown in parentheses

FIGURE 3. HEALTH OF SEED AT A COMMON SITE (GOGARBANK STUDY – 2005). PERCENTAGE OF PLANTS SHOWING PMTV SYMPTOMS IN THE FIELD IN 2005 IN RELATION TO THE PMTV HEALTH OF THE SEED TUBER AND CULTIVAR



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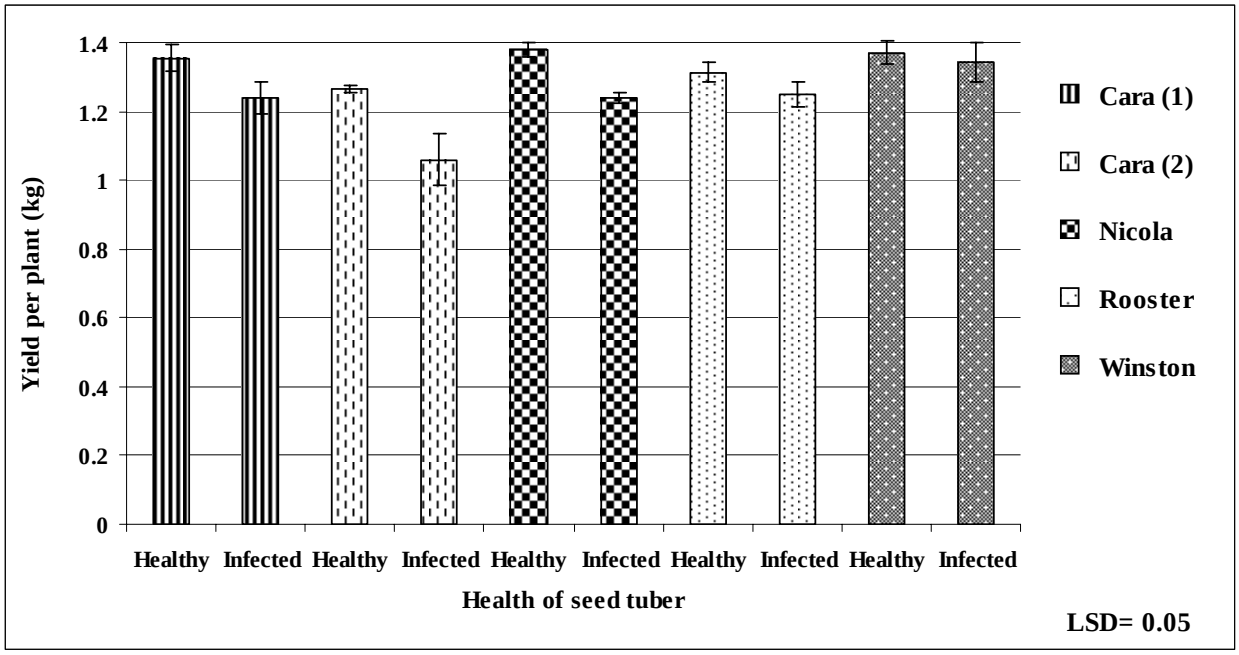
The effect of PMTV health of seed tuber on tuber yield is presented in Figure 4. With all cultivars, plants from infected seed tubers produced a smaller yield than those from PMTV-free seed tubers. The mean yield of 1.34 kg of daughter tubers per plant from PMTV-free seed was significantly ($P<0.05$) different from the yield of 1.23 kg per plant from PMTV-infected seed (Data not shown).

TABLE 7. PERCENTAGE OF PMTV-INFECTED DAUGHTER TUBERS PRODUCED FROM PMTV-INFECTED SEED IN RELATION TO SYMPTOMS ON THE GROWING PLANT IN 2005

	% daughter tubers infected with PMTV	
Cultivar	**Symptomatic plants**	**Asymptomatic plants**
Cara (stock 1)	41.33 (221)*	33.78 (450)
Cara (stock 2)	40.01 (183)	40.22 (450)
Nicola	40.05 (212)	30.64 (450)
Rooster	NA	23.33 (450)
Winston	NA	38.00 (450)

* Total number of tubers tested appears in parentheses

FIGURE 4. HEALTH OF SEED AT A COMMON SITE (GOGARBANK STUDY – 2005). TUBER YIELD OF PLANTS OF 4 CULTIVARS IN RELATION TO PMTV HEALTH OF SEED TUBER



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2.3.2 Transmission of PMTV on cv. Cara in relation to site and generation of production

2.3.2.1 cv. Cara 2004 study

The incidence of PMTV and powdery scab in seed tubers from the initial producer was 0.5% and 5.8% respectively. Only 1 out of 31 daughter crops had no powdery scab on daughter tubers (Table 8). The highest incidence of powdery scab on daughter tubers was 85.6% in a Perth-grown crop (no. 26). Overall, 45% of crops had fewer than 20% tubers affected by scab (Table 9). The distribution of crops relative to the incidence of powdery scab within a crop was fairly even over the range >10 to 90% of affected tubers By contrast, only 9.7% of crops had more than 5% of tubers affected by PMTV (Table 9) while 67.7% of crops had less than 1% tuber infection (Table 8). Two stocks (nos 25 and 26) had a relatively high incidence of PMTV (52 and 34.9%) with a correspondingly high incidence of spraing (52 and 31.2%, respectively) (Table 8). However, the occurrence of a high incidence of powdery scab was not generally associated with a high incidence of PMTV. For example, in Perth-grown crops, nos 29 and 31, which had 72.4 and 76.1% of their tubers affected by powdery scab, the incidence of PMTV infection was only 0.2 and 0%, respectively.

TABLE 8. OCCURRENCE OF PMTV, SPRAING AND POWDERY SCAB ON DAUGHTER TUBERS FROM 31 CROPS OF CV. CARA PRODUCED IN 2004 FROM COMMON ORIGIN SEED IN RELATION TO SITE OF PRODUCTION

Site no.	County	% PMTV	% spraing	% powdery scab
1	Aberdeen	0	1	40.3
2	Angus	11.9	11.4	47.9
3	Angus	2.5	0.5	9.5
4	Angus	2.4	3.3	37.6
5	Angus	1.9	0	11.4
6	Angus	1.5	0.5	76
7	Angus	1.4	2.9	38.8
8	Angus	1.4	0.5	52.8
9	Angus	1.0	0.5	13.6
10	Angus	0.5	0.5	60.5
11	Angus	0.5	0.5	23
12	Angus	0.5	0.5	5.5
13	Angus	0.5	0.5	7.6
14	Angus	0.5	0	0
15	Angus	0.5	0.5	55.0
16	Angus	0	0	27
17	Angus	0	0	54.8
18	Angus	0	0	13.7
19	Angus	0	0	6
20	Angus	0	0	15.2
21	Banff	0.5	0	5
22	Fife	1.0	0.5	7.1
23	Fife	0	7.6	63.3
24	Moray	0.5	0.5	1.0
25	Perth	52	52	67.5
26	Perth	34.9	31.2	85.6
27	Perth	1.4	1.4	59.1
28	Perth	0.5	0.5	1.0
29	Perth	0.2	7.6	72.4
30	Perth	0	0	3.5
31	Perth	0	0	76.1

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TABLE 9. DISTRIBUTION OF 31 CROPS OF CV. CARA IN 2004 IN RELATION TO INCIDENCE OF POWDERY SCAB AND PMTV WITHIN CROPS.

% tubers affected by powdery scab	No. of crops	% tubers infected by PMTV	No. of crops
0-10	10	0-5	28
10-20	4	5-10	0
20-30	2	10-15	1
30-40	2	15-20	0
40-50	2	20-25	0
50-60	4	25-30	1
60-70	3	30-35	0
70-80	3	35-40	0
80-90	1	> 40	1

2.3.2.2 cv. Cara 2005 study

Three seed potato crops were grown in 2004 by the initial producer (no. 1) to provide seed potatoes for the multiplication of 27 crops of basic seed potatoes by commercial producers in 2005 (Table 10). The incidence of PMTV in each of the initial seed crops was 0.7%, even although they had been produced on different farms. Powdery scab was not found on the tuber sample from 5 out of 27 daughter crops from this seed and 11 crops were free of PMTV. Four of these 27 crops had more than 4% of tubers infected by PMTV, with the greatest incidence being 35% and each was produced by a different grower (6, 10, 25 and 31) in Angus and Perthshire. Of the crops produced by these growers in 2004, three were free of PMTV and one contained 0.2% infected tubers. Furthermore, one of these growers (6) planted 2 fields in 2005 with the initial seed potatoes; one produced a crop with 13% PMTV and the other produced a crop with no PMTV.

Of the 58 daughter crops produced by the basic producers (growers 2 to 28), largely from their own 2004 seed potatoes, only five had no powdery scab on daughter tubers (Table 10). Overall, 27% of crops had fewer than 4% tubers affected by powdery scab (Table 11). The distribution of crops relative to the incidence of powdery scab was fairly evenly between 0 and 30% of tubers affected by powdery scab, thereafter the frequency of crops in each category declined as the incidence of powdery scab increased. The highest incidence of powdery scab was 84.7% in a crop grown in Angus by grower 14 from seed potatoes with 8% of tubers affected by powdery scab. The incidence of powdery scab on a sister crop grown on the same farm in 2005 was 0% and, on 2 sister crops on another farm, the incidence was 56 and 65%. In general, there did not appear to be a good relationship between the incidence of powdery scab on seed tuber and that on daughter tubers. For example, grower 13 planted a 2005 crop with seed potatoes which had 60% of tubers affected by powdery scab and this produced a crop in which only 3% of tubers were affected by powdery scab. The reverse occurred with grower 14. Further evidence of the absence of a relationship can be seen with grower 12. The incidence of powdery scab on seed tubers was 53% but the amount of powdery scab on 10 sister crops ranged from 0 to 56%. This was confirmed by correlation analysis of the incidence of powdery scab on seed tubers and mean incidence of powdery scab for all crops grown from those seed potatoes by a producer which revealed a correlation coefficient of 0.23 (26df).

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TABLE 10. OCCURRENCE OF PMTV, SPRAING AND POWDERY SCAB IN DAUGHTER TUBERS OF 84 CROPS OF CV. CARA GROWN IN 2005 IN RELATION TO THE INCIDENCE OF SEED INFECTION IN 2004, REGION, AND GROWER

2004				2005			
County/Grower/Farm*	**% PMTV**	**% spraing**	**% powdery scab**	**County/Grower/Farm***	**% PMTV**	**% spraing**	**% powdery scab**
Cromarty/1/1	0.7	0	NA	Angus/6/2	0	20	16.7
				Aberdeen/29/1	0	12	0
				Aberdeen/29/2	0.7	0	18.7
				Angus/13/1	2.7	1.3	12.7
				Angus/17/1	0	0	0
				Angus/18/2	0.7	2	0.7
				Angus/30/1	1.3	1.3	6
				Angus/12/2	30	25.3	36.7
				Angus/11/2	0.67	0.7	2
				Angus/7/2	0	0.7	6
				Angus/2/2	3.3	1.3	37.3
				Angus/14/2	2	1.3	12
				Fife/23/2	0	0	0
				Fife/16/1	4	3.3	32.7
				Perth/10/1	34.7	25.3	28
				Perth/31/1	2	1.3	8
Cromarty/1/2	0.7	0.7	NA	Angus/22/1	0	0	3.3
				Angus/6/2	13.3	10.7	28
				Moray/4/1	0	0	0
				Perth/9/2	0	0.7	77.3
				Perth/31/1	9.3	10	22.7
Cromarty/1/3	0.7	0	NA	Aberdeen/21/1	0	0	7.3
				Angus/27/2	0	0	0
				Angus/25/2	12.7	11.3	19.3
				Banff/28/1	0.7	0	3.3
				Perth/3/2	0.7	0	0.7
				Perth/19/2	0	0	6.7
Angus/2/1	1	0.5	13.6	Angus/2/2	1.3	2	27.3
				Angus/2/3	8	6.7	41.3
				Angus/2/3	3.3	1.3	22
Perth/3/1	0.5	0.5	0.1	Perth/3/3	0	0	9.3
				Perth/3/4	0	0	15.3
				Perth/3/1	0	0	9.3
				Perth/3/1	0	0	2
Moray/4/1	0.5	0.5	0.1	Moray/4/2	10	10	24.7
				Moray/4/1	0	0	4
				Moray/4/	0	0	2.7
Angus/5/1	2.4	3.3	37.6	Angus/5/2	24	7.3	22.7
				Angus/5/3	2	1.3	20
Perth/6/1	0.2	7.6	72.4	Perth/6/1	4	11.3	48
				Perth/6/2	3.3	12	17.3
Angus/7/1	11.9	11.4	47.9	Angus/7/1	3.3	4.7	19.3
Angus/8/1	0	0	15.2	Angus/7/3	5.3	6.7	47.3
				Angus/7/3	0.7	1.3	19.3

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TABLE 10 (CONTD). OCCURRENCE OF PMTV, SPRAING AND POWDERY SCAB IN DAUGHTER TUBERS OF 84 CROPS OF CV. CARA GROWN IN 2005 IN RELATION TO THE INCIDENCE OF SEED INFECTION IN 2004, REGION AND GROWER

2004				2005			
County/Grower/Farm*	**% PMTV**	**% Spraing**	**% Powdery scab**	**County/Grower/Farm***	**% PMTV**	**% Spraing**	**% Powdery scab**
Perth/9/1	34.9	31.2	85.6	Perth/9/2	2.0	0.0	38.7
				Perth/9/3	1.3	0.0	12.0
				Perth/9/4	0.0	0.0	0.0
Perth/10/1	0.0	0.0	76.1	Perth/10/1	39.3	32.0	65.3
Angus/11/1	0.5	0.5	5.5	Angus/11/2	0.7	0.0	20.7
				Angus/11/3	2.0	1.3	8.7
Angus/12/1	1.4	0.5	52.8	Angus/12/3	1.3	1.3	6.0
				Angus/12/3	3.3	0.7	50.7
				Angus/12/3	47.3	24.7	56.0
				Angus/12/4	2.7	2.7	13.3
				Angus/12/4	2.0	4.0	12.7
				Angus/12/4	7.3	6.0	22.7
				Angus/12/4	0.7	4.3	2.8
				Angus/12/2	28.0	25.3	55.3
				Angus/12/5	0.0	0.7	0.0
				Angus/12/5	0.0	0.0	6.0
Angus/13/1	0.5	0.5	60.5	Angus/13/1	4.0	7.3	3.3
Angus/14/1	0.5	0.5	7.6	Angus/14/1	0.7	0.0	56.0
				Angus/14/1	31.3	19.3	64.7
				Angus/14/2	2.0	24.7	0.0
				Angus/14/2	0.0	0.0	84.7
Perth/15/1	1.4	1.4	59.1	Perth/15/1	2.7	0.7	17.3
Fife/16/1	1.0	0.5	7.1	Fife/16/1	1.3	0.0	6.7
Angus/17/1	0.0	0.0	27.0	Angus/17/3	2.0	1.3	28.0
				Angus/17/2	26.0	10.0	45.3
Angus/18/1	1.9	0.0	11.4	Angus/18/2	14.7	8.0	27.3
Angus/30/2	2.5	0.5	9.5	Angus/30/1	0.0	0.0	24.0
				Angus/30/1	0.0	7.3	0.0
Perth/19/1	0.0	0.0	3.5	Perth/19/2	0.0	0.0	3.3
Angus/20/1	0.5	0.5	55.0	Perth/20/2	0.0	0.0	24.7
				Angus/20/3	0.7	0.7	0.0
Aberdeen/21/1	0.5	0.0	5.0	Aberdeen/21/1	0.7	0.7	20.0
Angus/22/1	0.0	0.0	6.0	Angus/22/1	0.0	0.7	9.3
				Angus/22/2	0.7	0.7	10.0
Fife/23/1	0.0	7.6	63.3	Fife/23/3	0.0	0.0	2.7
				Fife/23/4	0.0	2.7	5.3
Angus/24/1	0.5	0.5	23.0	Perth/9/5	2.0	0.0	20.7
Angus/25/1	0.0	0.0	54.8	Angus/25/3	2.7	1.3	26.0
Angus/26/1	1.5	0.5	76.0	Roxburgh/32/1	2.0	1.3	35.3
Angus/27/1	0.5	0.0	0.0	Angus/27/2	0.0	0.0	5.3
Banff/28/1	0.5	0.0	5.0	Banff/28/1	0.0	1.3	40.0

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TABLE 11. DISTRIBUTION OF 84 CROPS OF CV. CARA IN RELATION TO THE INCIDENCE OF PMTV, SPRAING AND POWDERY SCAB IN DAUGHTER TUBERS IN 2005

% tubers infected with PMTV	No. of crops	% tubers affected by spraing	No. of crops	% tubers affected by powdery scab	No. of crops
0	30	0	30	0	10
0-4	39	0-4	30	0-4	13
4-10	5	4-10	12	4-10	14
10-20	3	10-20	7	10-20	15
20-30	4	20-30	5	20-30	15
30-40	3	30-40	1	30-40	6
40-50	1	40-50	0	40-50	4
50-60	0	50-60	0	50-60	4
60-70	0	60-70	0	60-70	2
70-80	0	70-80	0	70-80	1
80-90	0	80-90	0	80-90	1
90-100	0	90-100	0	90-100	0

Only 19% of crops had more than 4% of tubers affected by PMTV while 35% were free of PMTV (Table 11). Two crops (growers 10 and 12) had a relatively high incidence of PMTV (39% and 47%) with a correspondingly high incidence of spraing (32% and 25%, respectively) (Table 10). The incidence of PMTV in the seed potatoes planted to produce these crops was 0 and 1.4% respectively. Overall, the mean incidence of PMTV in daughter tubers from each producer was not correlated (r=-0.097, 26 df) with the amount of PMTV in the seed potatoes used for planting. This can illustrated further by examining the results for individual growers. For example, the incidence of PMTV in daughter tubers of three 2005 crops (grower 9) was 2, 1.3 and 0% although the planted seed potatoes contained 35% PMTV. Similarly, of 10 daughter crops produced in 2005 by grower 12 from seed potatoes containing 1.4% of tubers infected by PMTV, seven had less than 4% of tubers infected by PMTV, one had 7.3% infection and two had more than 25% infected tubers.

2.3.2.3 cv. Cara 2006 study

All crops grown by each producer in 2006 were planted with seed potatoes produced by that grower in 2005 (Table 12). The highest incidence of powdery scab was 71.3% in a Perth-grown crop (grower 19). Of the 28 daughter stocks studied in 2006, only three had no powdery scab on daughter tubers and 46% of crops had fewer than 4% of tubers affected by powdery scab (Table 13). The distribution of crops in relation to incidence of powdery scab between >4 and 71.3% was fairly even. As in 2005, there did not appear to be a good relationship between the amount of powdery scab on seed tubers and that on daughter tubers (Table 12). For example, with grower 19, two crops were produced in 2006 from 2005 seed potatoes with 7% powdery scab. One daughter crop had 5% of tubers affected while the other had 71% affected.

Only 25% of crops had more than 4% of tubers affected by PMTV while 35.7% were free of PMTV (Table 13). Two crops (growers 19 and 7) had a relatively high incidence of PMTV (45.3% and 30.4%) with a correspondingly high incidence of spraing (35.3% and 24.5%, respectively). The incidence of PMTV in seed tubers used to grow both crops was 0%. As in 2005, the incidence of PMTV in the seed tubers did not correlate (r= -0.18, 11 df) with the mean amount of PMTV in daughter tubers. For example, the same seed planted on two

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different farms by grower 19 produced daughter crops with 71 and 5% of tubers infected by PMTV. Similarly, one seed crop (grower 5) in 2005 had a PMTV infection of 13.3% of tubers but only 4.6% and 0.7% of tubers were affected by PMTV in two daughter crops in 2006.

TABLE 12. OCCURRENCE OF PMTV, SPRAING AND POWDERY SCAB IN DAUGHTER TUBERS OF 28 CROPS OF CV. CARA GROWN IN 2006 IN RELATION TO THE INCIDENCE OF SEED INFECTION IN 2005, REGION AND GROWER

2005				2006			
County/Grower/Farm*	**% PMTV**	**% Spraing**	**% Powdery scab**	**County/Grower/Farm***	**% PMTV**	**% Spraing**	**% Powdery scab**
Perth/3/2	0.7	0.0	0.7	Perth/3/1	0.3	0.3	0.7
				Perth/3/2	0.0	0.0	5.7
Angus/6/2	13.3	10.7	28.0	Angus/6/2	4.7	3.3	8.7
				Angus/6/3	0.7	1.3	0.0
Angus/7/2	0.0	0.7	6.0	Angus/7/2	30.4	24.5	53.9
Perth/9/2	0.0	0.7	77.3	Perth/9/6	1.3	2.0	6.7
				Perth/9/5	1.3	2.0	6.7
				Perth/9/1	2.7	0.7	1.3
Angus/11/2	0.7	0.7	2.0	Angus/11/4	0.0	0.0	22.7
Angus/13/1	2.7	1.3	12.7	Angus/13/1	0.0	0.0	3.3
Angus/14/2	2.0	1.3	12.0	Angus/14/3	4.5	4.5	16.5
				Angus/14/4	2.7	2.0	2.0
Angus/17/1	0.0	0.0	0.0	Angus/17/1	0.0	0.0	0.0
				Angus/17/4	0.0	0.0	0.0
Perth/19/2	0.0	0.0	6.7	Perth/19/3	45.3	35.3	71.3
				Perth/19/4	5.3	2.0	4.7
Aberdeen/21/1	0.0	0.0	7.3	Aberdeen/21/1	0.0	0.0	0.7
Angus/22/1	0.0	0.0	3.3	Angus/22/2	0.0	0.0	1.3
				Angus/22/1	0.0	0.0	10.0
				Angus/22/3	0.7	0.0	0.7
Fife/23/2	0.0	0.0	0.0	Fife/23/5	0.0	2.7	7.7
				Fife/23/1	0.7	0.0	0.7
Angus/25/2	12.7	11.3	19.3	Angus/25/2	1.3	0.7	10.7

* County/grower identity is constant. Farm identity may change each year.

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TABLE 13. DISTRIBUTION OF 28 CROPS OF CV. CARA IN RELATION TO THE INCIDENCE OF PMTV, SPRAING AND POWDERY SCAB IN DAUGHTER TUBERS IN 2006

% Tubers infected with PMTV	No. of crops	% Tubers affected by Spraing	No. of crops	% Tubers affected by Powder scab	No. of crops
0	10	0	12	0	3
0-4	11	0-4	12	0-4	10
4-10	5	4-10	2	4-10	7
10-20	0	10-20	0	10-20	2
20-30	0	20-30	1	20-30	3
30-40	1	30-40	1	30-40	0
40-50	1	40-50	0	40-50	0
50-60	0	50-60	0	50-60	1
60-70	0	60-70	0	60-70	1
70-80	0	70-80	0	70-80	1
80-90	0	80-90	0	80-90	0
90-100	0	90-100	0	90-100	0

2.3.2 Survey of incidence of PMTV in seed crops of PMTV susceptible cultivars

The incidence of PMTV and spraing in 128 crops of cvs Hermes, Maris Piper, Nicola and Saturna is presented in Tables 14 and 15 respectively. Only 48 crops (38%) were infected by PMTV and spraing was seen in only 24 crops (19%). PMTV in tubers was detected around 80% more frequently in crops of cv. Nicola than in those of the other three cultivars. Overall, PMTV was more frequent in crops from Central Scotland (Angus, Perthshire and Fife) than those from Northern and North-Eastern regions of Scotland (Table 14). Crops in Border areas were least infected by PMTV although the number of sampled crops was less than for the other regions. The distribution of spraing symptoms was broadly similar to that for PMTV with symptoms being most frequent in crops from Central Scotland and Northern Scotland (Table 15).

Analysis by logistic regression confirmed that the incidence of crop infection by PMTV differed amongst regions ($P< 0.005$), with a greater proportion of crops from the Central Scotland being infected by PMTV than those from the other regions. However, statistically, the differences amongst cultivars in crops infected by PMTV and those developing spraing was much weaker (P value 0.058 and 0.075 respectively) than for regions. Logistic regression analysis showed that the evidence ($P = 0.075$) for differences in the development of spraing symptoms amongst cultivars was weak. Comparing the means, the incidence of crops with spraing affected tubers was greater for cv. Nicola than for cvs Maris Piper and Hermes (Table 15).

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TABLE 14. INCIDENCE OF CROPS CONTAINING TUBERS INFECTED BY PMTV IN RELATION TO REGION OF PRODUCTION AND CULTIVAR

Region	Cultivar				Mean % crops infected by PMTV
	Hermes	Maris Piper	Nicola	Saturna	
North-Eastern (Aberdeenshire, Banff & Kincardine)	0/6	3/8	6/9	1/7	33.3
Central (Angus, Perth & Fife)	7/10	5/10	7/10	5/11	58.5
Northern (Caithness, Inverness, Moray, Nairn, Ross & Sutherland)	3/11	2/13	3/7	2/5	27.7
The Borders (Berwick, East Lothian, Dumfries & Roxburgh)	1/8	3/9	0/1	0/3	19.0
Mean % crops infected by PMTV	31.4	32.5	59.3	30.8	38%

TABLE 15. INCIDENCE OF SEED POTATO CROPS CONTAINING TUBERS AFFECTED BY SPRAING IN RELATION TO REGION OF PRODUCTION AND CULTIVAR

Region	Cultivar				Mean % crops affected by spraing
	Hermes	Maris Piper	Nicola	Saturna	
North-Eastern (Aberdeenshire, Banff & Kincardine)	0/6	0/8	1/9	1/7	6.7
Central (Angus, Perth & Fife)	3/10	1/10	4/10	4/11	29.3
Northern (Caithness, Inverness, Moray, Nairn, Ross & Sutherland)	1/11	4/13	3/7	0/5	29.3
The Borders (Berwick, East Lothian, Dumfries & Roxburgh)	0/8	0/9	1/1	1/3	9.5
Mean % crops affected by spraing	11.4	12.5	33.3	23.1	18.8%

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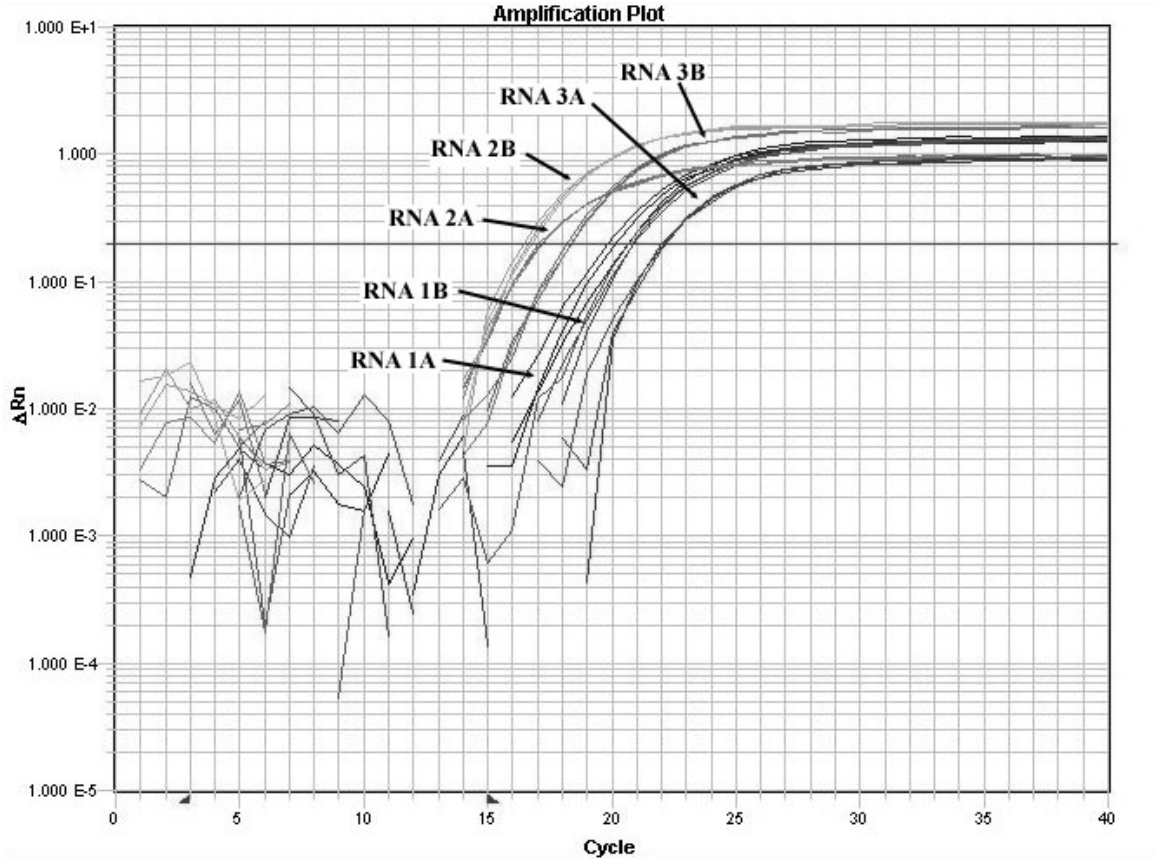
2.3.3 Detection of PMTV in soil

An example of the amplification plots produced using the six primer/probe combinations is shown in Figure 5. Primer/probe combination RNA 2B consistently gave the lowest C_T value of all six primer/probe combinations tested. In real time PCR analysis, a lower C_T value means more DNA detected; thus the RNA 2B combination was the most sensitive in these tests. This was confirmed by the results of tests conducted on soil samples from a selection of 2004 Cara crops (Table 16). These tests compared RNA 3B, the primer/probe combination, originally described by Mumford *et al* (2000), and RNA 2B probe. Both primer/probe combinations detected PMTV in all 10 test soils with similar results for number of positive replicates. However, the RNA 2B probe gave consistently lower C_T values than the RNA 3B probe for soil bait assays using identical total RNA extracts.

FIGURE 5. AMPLIFICATION PLOT OF SIX PRIMER/PROBE COMBINATIONS USING PMTV INFECTED TUBERS OF CV. CARA AS POSITIVE CONTROL MATERIAL



Assays for PMTV in soil were also performed using two indicator plants, *L. esculentum* and *N. benthamiania*, on the same samples as tested above, with the inclusion of one additional soil. Results are shown in Table 17. As in the previous experiment, RNA 2B and RNA 3B were equally effective in detecting PMTV in the bait plant, however RNA 2B produced consistently lower C_T values than RNA 3B. Comparing the performance of indicators plants in Table 17, it is evident that assays using *L. esculentum* produced more positive replicates than those using *N. benthamiana*. In addition, the *L. esculentum* plant proved easier to work with than *N. benthamiana* because it was more robust and amenable to transplanting.

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TABLE 16. ASSAY OF FIELD SOILS USED FOR GROWING SEED CROPS OF CV. CARA IN 2004 FOR PMTV USING TOMATO AS THE INDICATOR PLANT AND RNA 2B AND RNA 3B PRIMER/PROBE COMBINATION, THE LATTER AS DESCRIBED BY MUMFORD ET AL. (2000)

		RNA 3B		RNA 2B	
Crop no	**% PMTV**	**No. of replicates +ve**	**Mean* Ct value**	**No. of replicates +ve**	**Mean Ct value**
1	52.0	3/3	21.2	3/3	16.3
2	34.9	3/3	18.4	3/3	16.0
3	11.9	3/3	23.8	3/3	17.0
4	2.5	1/3	23.7	2/3	23.9
5	1.4	1/3	30.6	1/3	26.1
6	1.4	3/3	23.7	3/3	19.1
7	0.5	1/3	27.8	1/3	24.7
8	0.5	1/3	28.1	2/3	25.3
9	0.5	1/3	32.9	1/3	28.4
10	0.5	3/3	19.0	3/3	16.9
11	0.0	2/3	24.6	2/3	19.3
+ve control soil	NA	3/3	22.9	3/3	16.4
Compost	NA	2/3	20.5	3/3	26.4

TABLE 17. ASSAY OF FIELD SOILS USED FOR GROWING SEED CROPS OF CV. CARA IN 2004 FOR PMTV USING TOMATO AND N. BENTHAMIANA AS INDICATOR PLANTS AND 2 SETS OF PRIMER/PROBE COMBINATIONS; A RNA 3B PRIMER/PROBE COMBINATION (MUMFORD ET AL., 2000) AND A RNA 2B PRIMER/PROBE COMBINATION DEVELOPED BY SASA.

		No. of replicates PMTV +ve				Mean Ct value			
		Tomato		***N. benthamiana***		**Tomato**		***N. benthamiana***	
Crop	% PMTV in tubers	RNA 2B	RNA3B	RNA 2B	RNA3B	RNA 2B	RNA3B	RNA 2B	RNA3B
1	52.0	3/3	3/3	3/3	3/3	16.3	21.2	18.1	18.9
2	34.9	3/3	3/3	2/3	2/3	16.0	18.4	19.0	20.4
3	11.9	3/3	3/3	2/3	2/3	17.0	23.8	16.8	17.2
4	2.5	2/3	1/3	0/3	0/3	23.9	23.7	0.0	0.0
5	1.4	1/3	1/3	0/3	0/3	26.1	30.6	0.0	0.0
6	1.4	3/3	3/3	2/3	2/3	19.1	23.7	19.1	19.9
7	0.5	1/3	1/3	0/3	0/3	24.7	27.8	0.0	0.0
8	0.5	2/3	1/3	0/3	0/3	25.2	28.1	0.0	0.0
9	0.5	1/3	1/3	0/3	0/3	28.4	32.9	0.0	0.0
10	0.5	3/3	3/3	1/3	1/3	16.9	19.0	18.9	20.3
11	0.0	0/3	0/3	1/3	0/3	0.0	0.0	19.5	0.0
12	0.0	2/3	2/3	0/3	0/3	19.3	24.6	0.0	0.0
+ve control soil	NA	3/3	3/3	1/3	1/3	16.4	22.9	16.8	17.3
-ve control soil (Compost)	NA	3/3	2/3	0/3	0/3	26.4	30.8	0.0	0.0

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The soil bait assay was further tested in a subsequent experiment in which the soil, collected from fields in which infected tubers had been produced, was diluted using sterile sand to 50, 20 & 10 % w/w. PMTV was not detected at any dilution in 4 out of 6 soils from commercial fields, in compost or in known infested soil which had been autoclaved. Of the remaining 3 samples in which PMTV was found, the test using RNA 2B combination detected in 7 replicate samples out of 36 compared with 4 out of 36 using RNA 3B combination. Given the low number of detections of PMTV, it is not possible to be definitive on the effectiveness of the RNA 2B assay in detecting PMTV at different dilutions, except to note that the number of replicates in which PMTV was found was the same for undiluted soil and those diluted by 90%.

2.3.3.1Detection of PMTV in soils sampled before planting and after harvest of cv. Cara crops in 2006.

Using primer/probe combination RNA 3B, assays were conducted on soil samples from fields used to grow the 28 crops of cv. Cara studied in 2006. The results are shown in Table 18 together with the % PMTV infection found in seed tubers from 2005 crop and in daughter tubers from 2006 crops. PMTV was detected in 50% of fields when sampled before planting and in 60% of fields after harvest. For the eight crops produced in a soil free of PMTV and from PMTV-free seed, 3 of the crops contained daughter tubers infected by PMTV and one of the fields was infested after harvest (Table 19). For the 6 crops derived from infected seed and planted in uninfested soil, 4 crops had tubers infected by PMTV and PMTV was detected in 3 fields. Planting PMTV-free seed in infested soil resulted in 5 crops being infected, with 2 of these crops being the most infected, 30 and 45%. All fields sampled after harvest were also infested.

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TABLE 18. ASSAYS OF SOILS USING TOMATO AS THE INDICATOR PLANT AND RNA 2B PRIMER/PROBE COMBINATION TO DETERMINE INFESTATION BY PMTV INFECTION IN SAMPLES COLLECTED BEFORE PLANTING AND AFTER HARVEST FROM FIELDS USED TO GROW SEED CROPS OF CV. CARA IN 2006

Crop no	% PMTV in 2005 crop	No. of replicates +ve for PMTV in pre-planting soil	% PMTV in 2006 crop	No. of replicates +ve for PMTV in post harvest soil
1	0.00	0/12	0.00	0/12
2	0.00	1/3	0.67	2/3
3	0.00	0/3	0.00	0/3
4	0.00	2/3	0.00	2/3
5	0.00	0/3	0.67	0/3
6	0.00	0/3	0.00	0/3
7	0.00	0/6	0.00	0/6
8	2.00	1/18	4.45	5/18
9	2.00	0/6	2.67	5/6
10	13.33	2/15	4.67	14/15
11	13.33	0/12	0.67	0/12
12	0.00	0/6	1.33	0/6
13	0.00	0/3	1.33	2/3
14	0.00	3/3	2.67	3/3
15	0.00	3/3	45.33	3/3
16	0.00	2/6	5.33	4/6
17	0.67	1/6	3.33	2/6
18	12.67	1/6	1.33	1/6
19	9.33	2/3	8.67	3/3
20	1.33	0/6	0.00	0/6
21	2.67	2/6	0.00	2/6
22	0.00	1/6	0.67	0/6
23	0.67	0/3	6.67	3/3
24	0.00	0/3	0.00	0/3
25	0.00	6/6	30.44	6/6
26	0.67	0/9	0.34	1/9
27	0.67	0/3	0.00	0/3
28	0.67	3/6	0.00	1/6

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TABLE 19. PROPORTION OF CROPS WITH INFECTED DAUGHTER TUBERS AND FIELD SOILS INFESTED BY PMTV AFTER HARVEST IN RELATION TO PMTV-HEALTH OF SEED AND INFESTATION OF SOIL PRE-PLANTING

Seed	Pre-planting soil	Daughter tubers infected	Post harvest soils infested
PMTV-free	PMTV-free	3/8	1/8
PMTV-free	Infested	6/7	6/7
Infected	PMTV-free	4/6	3/6
Infected	Infested	5/7	7/7

2.3.4 Temperature in relation to infection from soil inoculum

The weight of tubers produced by plants grown at 26°C was much less than that for plants at the two lower temperatures (Table 20). Cv Rooster produced few tubers, only very long stolons around the inside of the pot. Overall, the yield of tubers was significantly ($P<0.05$) less for plants grown in infested soil than in compost for those grown at 12°C and 19°C. Differences in yield amongst the cultivars were also apparent with cv. Nicola producing the greatest yield.

TABLE 20. EFFECT ON TUBER YIELD (KG/PLANT) OF GROWING PLANTS OF 5 CULTIVARS IN EITHER JOHN INNES NO. 2 COMPOST OR A 50:50 MIXTURE OF COMPOST AND KNOWN PMTV-INFESTED SOIL IN RELATION TO GLASSHOUSE TEMPERATURE

		Cultivar					
Temperature (°C)	Growing medium	Nicola	Cara	Slaney	Rooster	Winston	LSD (P<0.05)
12	Compost	0.9	0.7	0.6	0.6	0.5	0.1
	PMTV infested soil	0.5	0.4	0.4	0.4	0.4	
19	Compost	0.8	0.6	0.7	0.5	0.4	0.08
	PMTV infested soil	0.5	0.3	0.3	0.3	0.3	
26	Compost	0.3	0.1	0.1	0.01	0.2	0.1
	PMTV infested soil	0.2	0.02	0.01	0.0	0.1	

The incidence of PMTV infection in daughter tubers as affected by temperature and cultivar is shown in Figure 6. PMTV was not detected in any tubers produced at 26°C, but was prevalent at 12°C and 19°C in all 5 cultivars. The highest incidence of PMTV infection (87.5%) was detected in daughter tubers of cv. Nicola grown at 12°C in infested soil; however cvs Cara and Rooster had similarly high amounts of PMTV infection when grown at 19°C, with infection levels of 85.2% and 86.4%, respectively. Low amounts of infection were detected in tubers of cvs Cara and Rooster produced in compost at 12°C and those of cvs Nicola and Saturna produced at 19°C.

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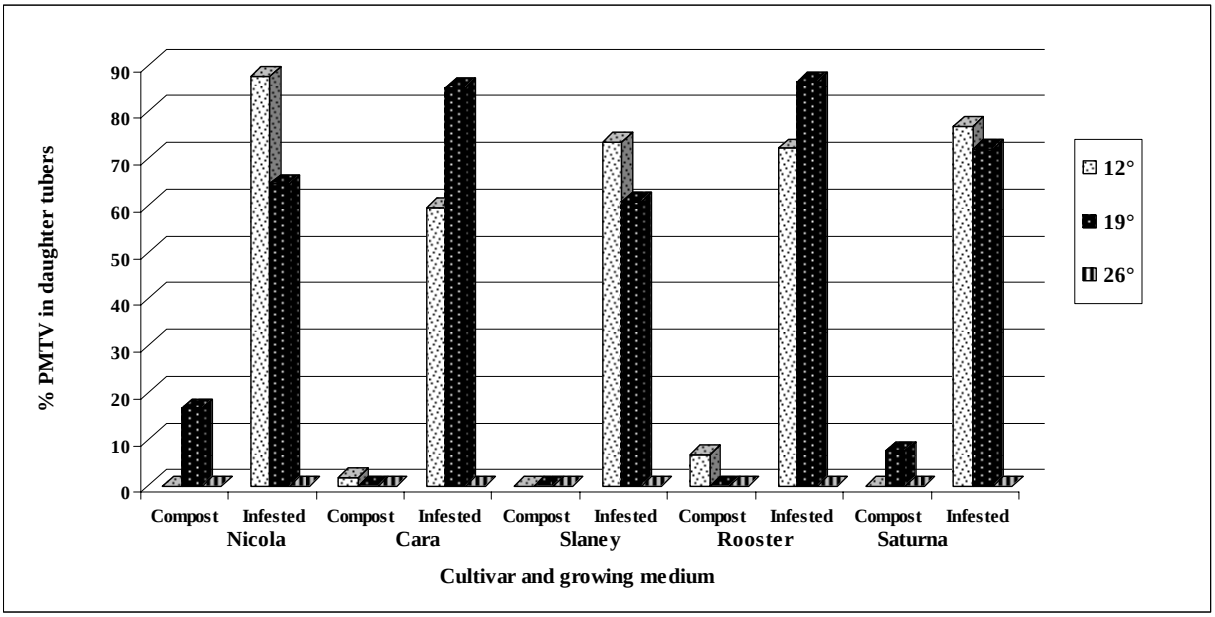
FIGURE 6. INCIDENCE OF PMTV IN DAUGHTER TUBERS DERIVED FROM HEALTHY SEED TUBERS PLANTED IN JOHN INNES NO 2 COMPOST OR A 50:50 MIXTURE OF COMPOST AND A SOIL KNOWN TO BE INFESTED WITH PMTV IN RELATION TO GLASSHOUSE TEMPERATURE



The mean incidence of spraing in daughter tubers, after post harvest conditioning, in relation to temperature is shown in Figure 7. Only tubers that were produced in a glasshouse at 12°C were found to be affected by spraing. The incidence of spraing was greatest in tubers of cvs Nicola and Cara, with 29.2% and 28.6% of tubers being affected respectively. Cv. Saturna was least affected, with only 2.6% of daughter tubers being affected.

Figure 8 shows the mean percentage of daughter tubers affected by powdery scab. Powdery scab lesions were not observed on tubers produced in the 26°C glasshouse. The incidence of powdery scab on tubers was greater at 12°C than at 19°C; this difference was greatest for cv. Saturna, with 84.6% of tubers produced at 12°C being affected by powdery scab compared with 28.0% at 19°C. Analysis by logistic regression confirmed that significantly ($P<0.001$) more tubers were affected by powdery scab when plants were grown at 12° than at 19°C.

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FIGURE 7. MEAN INCIDENCE OF DAUGHTER TUBERS WITH SPRAING PRODUCED IN GLASSHOUSES IN EITHER JOHN INNES NO 2 COMPOST OR A 50:50 MIXTURE OF COMPOST AND A SOIL KNOWN TO BE INFESTED WITH PMTV IN RELATION TO CULTIVAR AND GLASSHOUSE TEMPERATURE

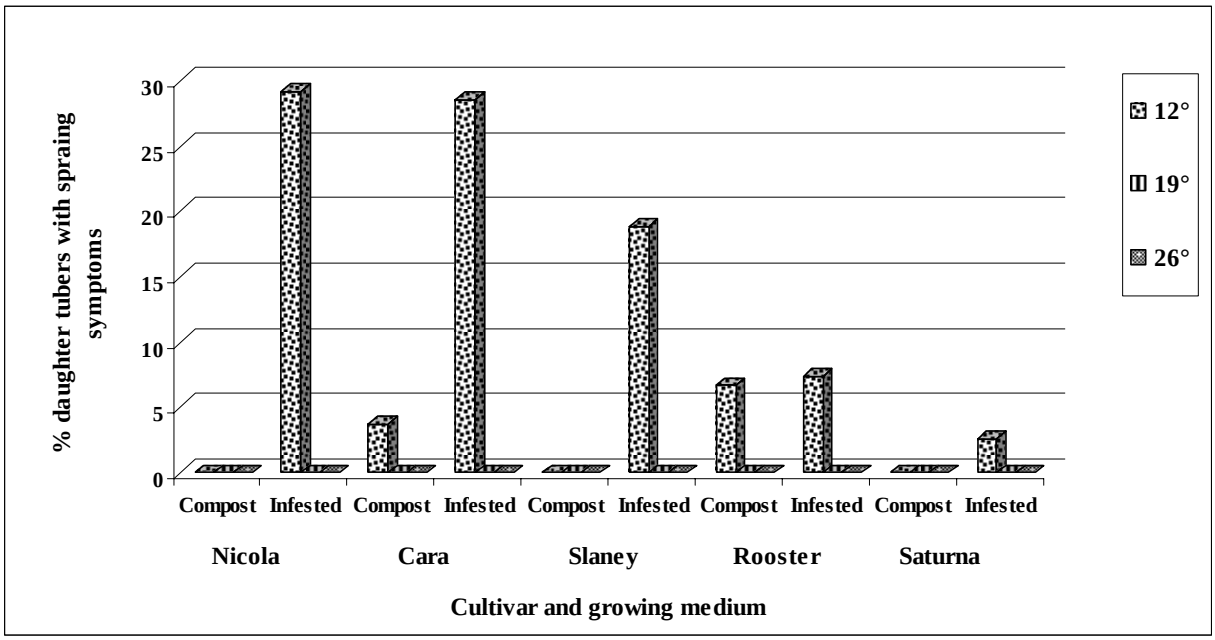
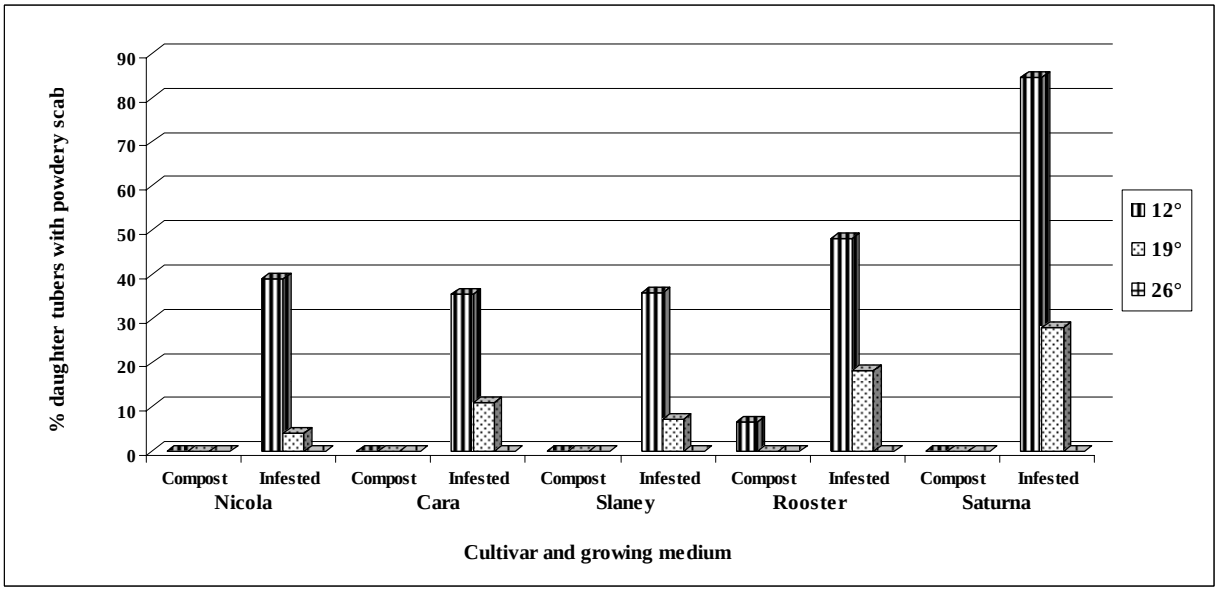


FIGURE 8. MEAN % OF DAUGHTER TUBERS WITH POWDERY SCAB LESIONS PRODUCED IN GLASSHOUSES IN EITHER JOHN INNES NO 2 COMPOST OR A 50:50 MIXTURE OF COMPOST AND A SOIL KNOWN TO BE INFESTED WITH PMTV IN RELATION TO CULTIVAR AND GLASSHOUSE TEMPERATURE



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2.4 Discussion

SASA's Gogarbank farm was chosen as the site for the seed transmission experiments because it was known that it posed a minimal risk for PMTV infection. This was confirmed by the absence or minimal amounts of PMTV found in daughter tubers derived from PMTV-free seed tubers in both years (Tables 3 and 6) and by PMTV not being detected in 2004 soil sample. The incidence of PMTV in produce of PMTV-free seed also indicates that the ELISA tuber test was effective in identifying PMTV-free tubers within a sample containing infected tubers. The development of symptoms on the growing plant differed amongst the cultivars. Symptoms developed more frequently on cvs Slaney and Cara from PMTV-infected seed than on other cultivars, although symptoms were generally relatively mild leaf and stem distortions and were largely confined to one or two stems on a plant. Infection of plants by PMTV resulted in no symptom development on cvs Winston and Rooster and only rarely on cv. Maris Piper. Testing leaves by ELISA showed that a considerable proportion of plants of these varieties were infected, despite the absence of symptoms. Similarly, asymptomatic plants produced along with symptomatic plants from PMTV-infected seed tubers were also found to be infected by PMTV although the incidence of PMTV tended to be less for asymptomatic plants. However, the incidence of PMTV in daughter tubers was similar for symptomatic and asymptomatic plants derived from infected seed. This indicates that the incidence of symptomatic plants in crops, even in cultivars known to develop symptoms attributable to PMTV infection, may be a less useful indicator of the extent of PMTV infection than spraing.

A small number of PMTV-free seed tubers, i.e., mother tubers that tested negative for PMTV prior to planting, produced plants which were infected with or without symptoms. This infection may have occurred either as result of the discontinuous distribution of virus in seed tubers, as found previously by Torrance and co-workers (1992), or the virus titre being below the level of detection by ELISA at time of testing. It is also possible that PMTV came from the soil because, although PMTV was not detected in soil samples in 2004, infestation may have been missed due to unrepresentative sampling or testing an insufficient amount of soil.

In both seed transmission experiments, it was clearly demonstrated that PMTV is only partially transmitted to daughter tubers from infected mother tubers. The most efficient transmission was found with cv. Cara in 2004 in which 49% of daughter tubers were infected. The least efficient transmission was found with cv. Rooster where only 23% of daughter tubers were infected. However, the results in the Cara study suggest that these experiments may have underestimated the rate of PMTV elimination in practice. When seven crops of cv. Cara were grown from lots of seed potatoes in which tuber infection ranged from 12 to 35%, the reductions in the incidence of PMTV in daughter crops varied from 100% to 65%. Farm also appeared to affect the rate of elimination of the virus during multiplication. For example, a 65% and a 95% reduction in PMTV in daughter tubers was recorded in two crops grown on different farms by the same producer from the same seed in which 13% of tubers were infected. Soil and environment may affect plant growth and thus virus transmission. From these results. it can be concluded that the amount of infection in a crop can be reduced with each propagation cycle which , in the absence of new infections, may lead to the elimination of the virus within one or two cycles. Certainly, one propagation cycle may be sufficient to reduce infection to an amount which will have no serious economic impact.

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The effect of PMTV infection of seed tubers on tuber yield was variable. In the majority of comparisons in 2004 (Figure 2), plants from PMTV-infected tubers produced tuber yields which were slightly smaller than, but not significantly different from, those from PMTV-free seed tubers. However, in 2005 (Figure 4), all cultivars produced a smaller yield from PMTV-infected than from PMTV-free seed tubers. In addition, a 67% reduction in the yield of plants having severe mop top symptoms caused by PMTV has been recorded in a commercial crop of cv. Hermes (SASA, unpublished data). These results contrast with the findings of Nielsen and Molgaard (1997) who reported that PMTV had no impact on yield or dry matter content in Danish-grown potatoes. It is likely that, in a crop, the relatively small reduction in yield of plants from PMTV-infected seed recorded in our study will be compensated by an increase in the yield of neighbouring healthy plants, as recorded with other diseases (Hirst *et al.*, 1973: Hide and Read, 1990). This may explain the difference between our findings and those in Denmark.

The importance of soil and seed inoculum on PMTV infection over two successive generations was examined using cv. Cara as a model in which the initial seed came from a common source. The amount of PMTV infection in initial seed was very low, <1.0%, in both years. In 2004, the incidence of PMTV infection in 31 daughter tubers was correspondingly low, except for 3 crops (Table 8). All 3 stocks had a high incidence of spraing and powdery scab. In 2005, 3 out of 27 daughter crops from common origin seed had more than 12% of tubers infected by PMTV. Similar patterns were found when basic growers re-planted their farm saved seed. These results demonstrate that high incidences of PMTV, unrelated to the health of the seed tubers, can occur and that soil is the most important source of inoculum for the infection of potato crops.

In the Cara study, the occurrence of high incidences of PMTV in tubers was not generally associated with high amounts of powdery scab. There were also many instances of prevalent powdery scab and no or minimal PMTV infection of tubers. Although powdery scab was wide spread on all stocks of cv. Cara, PMTV infection was much more limited. This indicates that, although powdery scab is widespread, the extent to which populations of *S. subterranea* carry the virus may be limited. However, attempts to test samples of spore balls extracted from soil for PMTV proved unsuccessful because of difficulties in obtaining zoospores and limited staff time.

The 2006 Cara study was further developed by performing pre-planting and post-harvest soil bioassays. When PMTV-free seed was planted in PMTV infested soil, 6 out of 7 crops produced PMTV-infected daughter tubers. However, planting infected seed tubers in PMTV-free soil resulted in 4 out of 6 crops producing PMTV-infected daughter tubers and in 3 out of 6 soils being infested by PMTV when sampled post harvest. These findings support the conclusion of the seed transmission experiments; namely, that PMTV transmission between seed and daughter tubers is less efficient than that for aphid transmitted viruses and that PMTV is primarily soil borne. However, the results also indicate that planting infected seed in PMTV-free soil can lead, in some instances, to soil becoming infested although this finding should be treated with some caution as it is based on a small number of cases. Nevertheless, it suggests that, each year, the planting of infected seed potatoes may be risking the introduction of PMTV into soils in Scotland.

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The value of an effective soil bioassay for PMTV is indicated by the findings presented in Tables 18 and 19. The assays, however, illustrate potential strengths and weaknesses of the current methodology. Of the three crops (14, 15 and 25) in which all replicate soil samples tested positive for PMTV, only two crops (15 and 25) had high amounts of tuber infection in daughter tubers. With three other crops in which at least half the replicate samples tested positive for PMTV, the incidence of tuber infection ranged between 0 and 5.3%. By contrast for the 10 crops which did not produce any infected tubers, PMTV was found in three of post harvest soil samples. Quantification of testing by real time PCR did not appear to add value to an assessment based on number of replicate samples testing positive. It is possible that these 'discrepancies' can be attributed to sampling problems, either in obtaining a representative sample of tubers or field soil. It is also possible that fields may contain PMTV 'hot-spots'. Environmental factors during the growth of plants may also play a significant role in determining the extent of infection within a growing crop. Further study is required to refine the current method and to evaluate the distribution of the virus within soils and the impact on infection within crops. Overall, the results do suggest that the use of a soil test could be of considerable value to industry in determining risk in relation to planting varieties in specific fields.

A survey of four cultivars (cvs Hermes, Maris Piper, Saturna and Nicola) known to be susceptible to PMTV infection was conducted to determine the incidence of PMTV infection in seed potato crops in Scotland. In general, the incidence of crops with more than 1% PMTV infection was relatively low. The virus was most prevalent in crops of cv. Nicola, as was spraing (Tables 14 & 15). The proportion of infected crops was broadly similar amongst the other cultivars. However, the proportion of infected crops of cv. Saturna which also developed spraing was higher (5 out of 8) than for cvs. Hermes and Maris Piper (4 out of 11 and 5 out of 13 respectively). However, in our glasshouse experiments, cv. Saturna developed significantly less spraing than the other test cultivars, although the incidence of PMTV infection did not differ amongst the cultivars. This result is in agreement with the finding of Sokmen *et al*., (1998) in which most infected tubers of cv. Saturna grown in a screenhouse in Scotland did not develop spraing. The results also suggest that varietal reaction may vary amongst countries: cv. Saturna being very susceptible in Scandanavia but apparently less so in Scotland. There was some evidence to suggest that PMTV infection was more common in Central Scotland than elsewhere, particularly The Borders which had the lowest incidence of infected crops. Similar patterns occurred with the distribution of spraing symptoms.

The glasshouse experiment confirmed that the development of powdery scab was much greater at 12°C than at 19°C (Figure 8), in keeping with the results of van de Graaf *et al*. (2005) who found powdery scab development to be most severe at 12°C. No scab was evident at 26°C and this was matched by an absence of PMTV in tubers grown at this temperature (Figure 6). Infection by PMTV was affected by temperature and cultivar; the highest incidence of PMTV in daughter tubers (87.5%) was detected with cv. Nicola grown at 12°C in an infested soil mixture. However, overall the incidence of PMTV infection in tubers was similar at 12°C and 19°C but spraing did not develop on tubers produced at 19°C. This suggests that the risk of crops grown at moderately high temperatures developing spraing caused by PMTV may be low, even if the seed tubers are infected but further work is needed to confirm this finding. This will have important implications for seed export in relation to the economic risk of the disease developing in potato production in warmer countries.

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3. CONCLUSIONS

The development of symptoms on the growing plant varied amongst cultivars; e.g., few plants of cv. Maris Piper had symptoms and none were produced on plants of cvs Rooster and Winston, even although ELISA testing of leaves had confirmed the presence of PMTV. In the cv. Cara study, however, the incidence of PMTV in the tubers was reasonably well correlated with the incidence of spraing in tubers which had been subject to storage conditions to enhance symptom development. Symptoms in the tubers may, therefore, be a better guide to infection in a crop than symptoms in the growing plant.

The seed transmission experiments confirmed that transmission of PMTV from infected seed to daughter tubers is limited, generally less than 50%, but varied with cultivar. The virus is self-eliminating with successive cycles of seed multiplication and, in cases where symptom expression is severe i.e. all stems affected and plant mopped, elimination may occur in one year or at least pose no economic risk to the crop.

The study with crops of cv. Cara over 3 years showed that, while powdery scab infection may be common in Scotland, infection of crops by PMTV was more limited. The results also demonstrate that soil inoculum of PMTV is more important than seed inoculum in producing economic outbreaks of the disease. The PMTV health of crops produced by a grower can vary from year to year and from field to field. Knowledge of the history of fields will be critical in avoiding the planting of susceptible cultivars in infested soil. Such decisions could be supported by an effective, predictive soil test for PMTV. The bioassay developed using tomato plants and real-time PCR was shown to be effective in detecting the presence of PMTV in soils from a range of fields but quantification of the results in terms of the severity of the infection which might occur given favourable conditions requires further work.

Surveying a large number of crops from 4 widely grown, PMTV-susceptible cultivars grown in Scotland showed that the majority were free of PMTV and spraing. The number of crops with spraing was generally much less than that for PMTV infection in tubers. More crops from Central Scotland were infected by PMTV and had spraing than elsewhere, suggesting that certain regions or soils may have a greater risk of producing infected and affected crops.

A preliminary glasshouse experiment with five cultivars grown at 12°C, 19°C or 26°C confirmed that the development of powdery scab was much greater at 12°C than at 19°C. There was no powdery scab at 26°C. However, the incidence of PMTV infection in tubers was similar at 12°C and 19°C but spraing was virtually absent at 19°C, even although the same post harvest treatment was applied to all tubers to enhance its development. This suggests that the risk of crops grown at moderately high temperatures developing spraing caused by PMTV may be low if the seed tubers are infected but further work is needed to confirm this finding.

- Recommend that growers test field soils for the presence of PMTV prior to planting in order to have some information on the risk of PMTV infection in daughter crops.
- Further work is required to refine the PMTV-soil bioassay in order to quantify the severity of infection which might occur given favourable conditions.
- Advise growers not to plant potatoes or a susceptible variety, particularly one which produces spraing when soils are infested with PMTV.
- Advise growers not to plant infected seed potatoes in an uninfested field, this can be achieved by testing seed potatoes of known susceptible varieties.

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- Recommend that the susceptibility of new and existing varieties is determined, whilst recognising that such testing is complicated because the vector is an obligate parasite which cannot be conveniently cultured nor can samples of powdery scab be easily tested directly for the presence of PMTV.
- Further work is required to determine whether roguing would have a positive impact on disease management. Preliminary evidence suggests that for some varieties roguing may reduce the level of infection but this is not true for all varieties as symptoms may be difficult to identify or absent.

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6. KNOWLEDGE TRANSFER ACTIVITIES

Poster Presentations:
SEERAD Growing Crop Inspectors course, entitled 'Identification of Potato varieties and their diseases course' (Gogarbank Farm, Edinburgh, 2/7/04).
BPC's Potatoes in Practice (Dundee, 5/8/04)
BPC's Seed Industry Event (Crieff Hydro, 11 - 12/11/04)
SEERAD 'Tuber Disease and Identification & Inspection Procedures Course' (SASA, Edinburgh, 16/11/04).
SEERAD Growing Crop Inspectors course, entitled 'Identification of Potato varieties and their diseases course' (Gogarbank Farm, Edinburgh, 30/6/05).
16th Triennial Conference of The European Association for Potato Research (EAPR): EAPR-2005 (17 – 22/7/05 Bilbao, Spain)
Potatoes in Practice (Dundee, 11/8/05)
British Potato 2005 (Harrogate, 30/11/05 – 1/12/05)
Crop Protection in Northern Britain 2006 (Dundee, 28/2/05 – 1/3/06)
SEERAD Growing Crop Inspectors course, entitled 'Identification of Potato varieties and their diseases course' (Gogarbank Farm, Edinburgh, 29/6/06).
Potatoes in Practice (Dundee, 10/8/06)
SEERAD Growing Crop Inspectors course, entitled 'Identification of Potato varieties and their diseases course' (Gogarbank Farm, Edinburgh, 28/6/07).
BPC's Seed Industry Event (Crieff Hydro, 2 - 3/11/06)
Potatoes in Practice (Dundee, 9/8/07)

Oral Presentations:
Association of Applied Biologist's Meeting: Advances in plant virology (Warwick, 5-7/4/06)
8th Conference of the European Foundation for Plant Pathology & BSPP Presidential Meeting 2006 (Copenhagen, 13–17/8/06)
13th European Association for Potato Research. Virology Section Meeting (Aviemore, 17-22/6/07).

Published Work:
T Davey, I Browning, SF Carnegie & GS Saddler (2006). The importance of potato mop top virus (PMTV) in Scottish seed potatoes. **Proceedings Crop Protection in Northern Britain 2006**. pp. 375-380.

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