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Overview of key virus problems in Europe

Expert group list

EG1
Overview of key virus problems in Europe
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1. Introduction

Text books of Plant Pathology and Plant Virology, and articles in scientific journals abound in expressions on the high economic impact of viral diseases in crops, or on how a particular viral disease is one of the most important diseases of a specific crop: No one questions these assertions, and it is widely accepted that viruses are responsible for important losses in crop productivity. However, these views mostly derive from anecdotic observations or rest on the wisdom of growers and agriculturalists. Indeed, quantitative analyses of losses due to viral diseases are not abundant, even less so than for other plant pathogens. In addition, available data are often of limited value by a number of reasons: i) data were obtained for a short period of time, or for a single cultivar or for a reduced geographic area, ii) data derive from experimental plots, and are difficult to extrapolate to commercial crops, iii) usually only the largest of a range of values is provided (Waterworth and Hadidi, 1998). Although losses due to viral diseases in Europe are better documented than for most regions of the world, during the preparation of this review it has become apparent that reports are often 30 or more years old, and it is unclear in which instances control strategies have improved, resulting in a decrease of losses, and in which the efficiency of control has not varied. This is particularly the case for viruses that have been present in Europe, and have been considered of importance, for long periods of time, i.e., mostly viruses infecting field crops. Thus, it must be pointed out that when the data presented here derive from old reports it is due to a lack of more recent analyses.

World-wide analyses of crop losses due to biological agents (pathogens, pests and weeds) indicate that, within pathogens, losses due to viral diseases in crops range second only to those caused by mycelial plant pathogens (i.e., fungi and oomycetes), and provide estimates that range between 3 and 8% for eight major crops (Oerke and Dehne, 2004). This is most certainly an underestimate and these figures probably do not apply to Europe, for several reasons: i) only for two of the eight analysed crops (potato and sugar beet) does a viral disease reach the status of key pest, and crops for which key pests include one or more viral diseases (e.g., vegetable and fruit crops) were not considered in the analysis. While vegetables and fruit crops made a small fraction of the world crop production, and use a smaller fraction of agricultural land, its economic and social importance in Europe is paramount; ii) the efficiency of crop protection practices for viral diseases (13%) is about one third smaller than for other plant diseases or pests (32-39%) and much smaller than for weeds (68%) (Oerke and Dehne, 2004). These world-wide data reflect the limited range of strategies available to control viral diseases, and their relatively low efficiency. As a consequence, the relative importance of virus-caused losses in crop production increases with increased technification of agricultural practices and with intensity of cropping systems, a trait of advanced agricultures, which is maximal in EU countries (Oerke et al. 1994; Oerke and Dehne 2004). In agreement with these considerations, losses due to viruses in Europe on field crops are about 10-15%, and figures are much higher for vegetables and fruits.

In this report we will analyse separately virus problems in field crops and in horticultural crops, including ornamentals, as the relative importance of viral diseases, and the possibility of implementing efficient control strategies, largely depends on how intensive (i.e., how much capital and labour is invested per hectare) is the crop system. Throughout this report we will use the terminology of crop losses (e.g., direct loss, actual loss, potential loss, etc) as defined by FAO (Chiarappa, 1971), which are those most currently used in Plant Pathology (Zadoks and Schein, 1979). We will only treat in detail diseases caused by viruses that are major pathogens of a major crop, other viruses are listed in the Annex Table, where the full name of viruses is also presented.

2. Field crops (including potatoes)

Viral diseases are relevant for the production of all major field crops in Europe, and even are limiting factors for some of them, conditioning their distribution, agricultural practices and/or the varieties that can be grown in a region. Well known examples are rhizomania disease of sugar beet, which limits the choice of cultivars to those incorporating resistance genes to the causal agent, BNYVV(a) (Rush 2003, OEPP 1988), or aphid-transmitted viral diseases of potato, which condition the choice of areas for the production of seed potato (Valkonen 2007). These limitations of agricultural practices result in indirect losses due to viral diseases which are difficult to quantify but should be added to actual direct losses.

All the relevant viral diseases of field crops fall into two major categories according to transmission, being either aphid transmitted or soil borne. The relevant soil borne viruses are transmitted through the zoospores and resting spores of Plasmodiophoromycetes in the genera *Polymyxa* and *Spongospora*, which are widespread in agricultural soils. Nematode-transmitted viruses may also cause serious problems locally, an example being TRV, which affects the quality of potato crops in Scotland (Dale et al. 2004).

2.1.- Control strategies

Of the various strategies available for the control of plant viruses (Hadidi et al. 1998), reducing virus spread through the control of vector populations is only feasible in field crops for aphid transmitted viruses. As a consequence, the spread of soil borne viruses can only be limited through sanitary measures aimed at exclusion of the pathogen from new soils or regions. However, given that often only relatively small amounts of soil are required to start an infection, this approach can only really help to slow (albeit significantly) any progress, rather than providing a complete protection in the long-term. Thus, the spread of BNYVV was delayed for some time after it was first reported from Italy (Canova 1959), but 30 years later it was present in all sugar beet-growing areas of Europe (OEPP 1988). Thus, plasmodiophorid-transmitted viruses present a particular problem to agriculture, and as the viruses can survive in the resting spores of the vector for long periods of time (Lubicz 2007), once the soil becomes infested it is likely to remain in that condition for decades, the actual elimination of soil-borne viruses being virtually impossible.

Control strategies for aphid-borne viruses, based on limiting virus spread by controlling aphid populations with insecticide treatments have a history of more than 50 years. Because of the low economic productivity of field crops, the number of insecticide treatments that can be applied is limited, and extensive efforts have been done to analyse the epidemiology of the diseases and to implement forecasting systems that optimise the efficiency of insecticide treatments and reduce the number of applications. Perhaps the highest success of this strategy is the control of yellows diseases of sugar beet, caused by BYV and, mainly, BMYV. Forecasting models optimising aphicide treatments were developed since the 1950s, and significantly decreased the impact of this disease in northern Europe from about 60% to about 5-9% of sugar beet production (Duffus, 1977). Still, in years of atypical weather resulting in particularly high aphid populations, losses could amount to more than 50%, and yellows of sugar beet has remained a potentially serious problem of sugar beet production (Dewar & Smith, 1999) although presently it is efficiently controlled by seed dressing with insecticides.

Aphicide treatments have serious limitations that condition their efficiency in virus disease control. Aphids have developed resistance to many toxic compounds over the years, and currently the best results are obtained with the use of seed dressings with neonicotinoid or compounds such as imidacloprid (Dewar & Smith, 1999) and its successors, which provide systemic protection to young plants for several weeks post emergence, often the highest risk period. Their efficiency has been demonstrated on both cereals and sugar beet. Also, insecticide sprays are limited to the more productive crops (e.g, seed potato, sugar beet, maize) in the most productive areas, what means that its use is practically none in extensive areas of dry farming in Southern Europe in crops such as small-grain cereals. Last, and perhaps most important, aphicide treatments are most efficient for the control of persistently-transmitted viruses, which include important viruses of field crops such as those causing beet yellows, cereal yellow dwarf disease (BYDV and CYDV) or potato leaf roll (PLRV). Aphicide treatments are largely inefficient for controlling non-persistently transmitted viruses (Raccah, 1986; Perring *et al.* 1999) such as TuMV in oil-seed rape or PVY in potato, and it has even been reported that aphicides promote an increased dispersal of these viruses (Fernández-Calvino *et al.* 2007), probably due to an increase in the mobility of stressed aphids. Thus, in spite that seed certification and breeding for resistance in potato has been applied to control both PLRV and PVY, PLRV, traditionally the most important virus in potato, is currently a marginal problem, while PVY continues to be a major problem for potato production all over Europe, with losses of 10-15%, only second to those caused by *Phytophthora infestans* (Valkonen, 2007).

Given that few of the important viruses of field crops are seed-borne, the use of certification schemes to ensure virus-free planting material is rare in this area. Notable exceptions are potatoes and pulse crops (pea and beans), where virus control is a vital part of any national seed certification scheme. In most cases this involves a combination of field inspections and post-harvest laboratory virus testing (mostly compulsory). Given the fact that these schemes set grade-dependant tolerances for permitted virus levels, seed crops often experience very intensive aphid control programs to ensure virus control.

As is the case for viral diseases in all crops, the use of resistance is the preferred strategy for the control of viruses of field crops. Resistance is extensively used both against aphid borne (e.g., in potato against PVY and PLRV, in pea against PSbMV, in barley against BYDV, etc) and soil-borne (e.g., in barley against BaYMV, in sugar beet against BNYVV, etc) viruses. Although resistance breaking (RB) strains have been described for most viruses, many deployed resistance factors have remained effective for long periods of time, an important exception being resistance to PVY in potato (García-Arenal and McDonald, 2003).

2.2.- Major virus problems

Two viruses are key pathogens of field crops in Europe: PVY in potato and BNYVV in sugar beet.

In potato, PVY is the second cause of loss after late blight, as recently reviewed by Valkonen (2007). Losses are most important when growing plants from infected seed, and data from different varieties indicate that they can vary between 30 and 80%. Because of the devastating effects of secondary infection, regulations exist in all countries about potato seed certification that set the allowed thresholds according to risks that vary for the different local conditions. This measure considerably increases the costs in the potato production chain, which are unavoidable. Still the fraction of the crops sown with certified seeds varies, a common value being two thirds of the crop. This conditions incidence in the field, which is related to the actual losses only above a certain threshold due to compensation from non-infected plants. Thus, below 10-20% of infection no losses may occur, and losses are 10-15% with a 30% incidence, what seems to be a common figure for European countries. Extreme resistance, effective towards all PVY strains, has been introduced in some cultivars, but strain-specific hypersensitive resistance has been most used. Resistance is overcome by the recently spread strain PVY^{NTN}, which causes tuber necrosis, with serious losses. PLRV used to be the major virus in potato, but at present is satisfactorily controlled through seed certification, breeding for resistance, and insecticide treatment of vectors (Valkonen, 2007).

BNYVV affects 66% of the sugar beet area of Europe (Hermann, 2005) and where present, only resistant varieties that incorporate the resistance gene *Rz1* or both *Rz1* and *Rz2*, can be grown, as potential losses of 60% of sugar production would occur if susceptible varieties were grown (Hermann, 2005). As a consequence, in regions where soil infestation is extensive (e.g., Belgium, France, Finland, Germany, The Netherlands, Northern Spain, Romania), resistant varieties make a large percentage (above 80%) of the crop (Hermann 2005). Although resistant varieties have given an excellent control for more than 20 years, resistance has been recently reported to be broken in several parts of the world, including areas in Europe (Harju et al, 2002; Varrelmann, 2007), which raises important concerns about the impact of rhizomania in the near future. Yellows disease comes second after rhizomania in sugarbeet, affecting about 25% of the surface in Europe (Hermann, 2005). Seed dressing with nicotinoid or imidacloprid insecticides since the mid 1990s has lead to its very efficient control, but the modification of EU regulation 91/914 does not consider the approval of these compounds in sugar beet, what may cause a return to the situation before their widespread use (see 2.1).

In other field crops virus diseases are also important. Thus, in small grain cereals BYDV and CYDV cause losses that vary from up to 30% in barley in the UK (Plumb et al. 1986), to 10-15% in wheat in UK and France (Plumb, 1983; Bayon and Ayrault, 1987) to negligible in Spain (Jordá et al. 1989). BYDV was also the cause of rice “giallume” in Italy and “enrojat” in Eastern Spain, which caused losses of 5% in the 1970-80s (Prescini, 1987, Jordá et al. 1987). This rice disease has disappeared with the change of cropping system from transplantation to direct sowing, which introduced a temporal shift of the crop cycle relative to the aphid vector’s, a good but infrequent example of efficient control linked to a change in cultural practices. In the Ebro Valley (Spain), MDMV-caused losses of maize seed production were of

13 to 40% according to the variety (Achón et al. 1995). Soil-borne viruses may also be key pathogens of small-grain cereals in some regions. In barley, losses due to soil-borne mosaic (BaYMV and BaMMV) are reported to amount to 30-50% in susceptible varieties in the UK and Germany (Oerke et al., 1994; Lapierre and Signoret 2004). Similar losses are reported for soil-borne mosaic of wheat (SBCMV) (Vallega et al. 1999; Clover et al. 2001). In oilseed rape, TuYV (previously BWYV) is the most important virus disease, emerging as a serious threat to the crop in the UK and in Germany. Infection does not cause obvious symptoms, but affects all components of yield: seed weight, oil content of seeds, and oil quality, with increased glucosynolate content (Stevens et al, 2008). Seed yield losses of 10-26% have been estimated in the UK, and of 12-34% in Germany (Jay et al. 1995; Graichen and Schliephake, 1999). Control by aphid treatment is inefficient and resistant varieties are not available. In the UK it is estimated that if half of the losses (10-15%) could be prevented, the value of the yield would be increased £ 100-150 hA (Stevens et al., 2008).

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2. Horticultural crops (including grapevines)

The impact of virus diseases is highest on the productivity of horticultural crops, i.e., fruit, vegetable and ornamental crops. There are different reasons for this: Horticultural crops differ from field crops in crop intensity, with higher inputs and productivity per hectare, and allow for a deeper modification of the environment, including higher costs devoted to crop protection. As a result, the impact of virus diseases relative to those caused by other pathogens is, on the average, higher. Also, intensive breeding of horticultural crops for higher production and quality has lead to high vulnerability to pathogens, the link between high productivity and vulnerability in crops being a well known though incompletely understood phenomenon (Oerke et al. 1994). Last, horticultural crops are characterised by smaller plots, fast rotations and a high turnover of varieties and cultural practices, in part lead by changes in the consumer's demands. This is particularly the case for vegetable crops, but for both fruits and vegetables the result is a highly artificial, complex and variable ecosystem that favours the emergence, or re-emergence, of new pathogens, and it is well documented that viruses make the larger fraction of emerging pathogens of animals and plants (Woolhouse et al., 2005). The repeated emergence of new virus diseases is best exemplified in vegetable crops under protection (greenhouses, tunnels etc). So, in the last 30 years tomato production in the Mediterranean coasts of the Iberian Peninsula has been threatened by a series of epidemics of new viruses or strains: CMV strains supporting necrogenic satellite RNAs were first reported in 1986, TSWV in 1989, TYLCV in 1992, TBSV in 1994, ToCV in 1997, PepMV in 2000, TICV in 2001 and ToTV in 2001 (Accotto et al, 2003; Aramburu et al. 1994; Cuadrado et al. 1995; Font et al., 2003; Jordá et al. 1992; Jordá et al. 2001; Jordá et al. 2003, Luis-Areteaga et al. 1996, Moriones et al. 1993; Navas-Castillo et al. 2000 Verbeek et al, 2007). All these viruses caused severe losses, reducing the yield above 50% and up to 80% in the affected areas, and occasionally leading to the abandon of traditional areas of tomato production. Some of these viruses occurred in transient epidemics (e.g., those caused by CMV and TBSV lasted 6 and 3 years, respectively), other have caused long-lasting problems. Also, all these viruses occurred at about the same time in other horticultural areas of the Mediterranean basin. Although this represents an extreme situation, the fact is that, except for pome fruits, viruses are key pathogens of horticultural crops, and that viral diseases condition the production of stone fruits, citrus, grapevines, vegetables and ornamentals.

At odds with field crops, relevant diseases of horticultural crops are caused by viruses that spread through many different mechanisms: insect vectored by aphids, whiteflies, mealybugs and thrips, soil borne by nematodes or through the zoospores of Chytridiomycetes, transmitted by contact or transmitted with the seed or with the vegetative propagation material.

3.1 Control

Control strategies for insect-borne viruses, based in limiting virus spread by controlling vectors with insecticide treatments, do not have the economic limitations signalled for field crops, and growers can apply a high number of treatments. Thus, in vegetable crops, sprays aimed at the control of whiteflies or thrips have been done in the past with weekly or even more frequent periodicities (Riudavets et al, 1992). However, control was never satisfactory. Various reasons explain this failure, in addition to those associated with the mechanisms of transmission described in *2.1*. On the one hand, the Economic Threshold of Damage (ETD) for these crops is usually very low, and low incidence of disease, or small decreases in the quality or the aesthetics of the product, result in important actual losses, so that the control of vector populations should be almost total to achieve virus control. Also, in fruit tree crops that stay in the field for long periods of time vector treatment is not efficient because disease incidence is the result of cumulative spread over the years. Moreover, EU regulations on admitted pesticide residues on horticultural products, mostly directed to the fresh market, pose an important constraint to this approach of virus control. In recent years, integrated pest control strategies directed to virus vectors (mostly to thrips and whiteflies), based on the use of predators and parasitoids, plus sanitation practices, including the use of physical barriers, have been developed and are being applied with success to increasingly larger areas (e.g. Contreras et al., 1994).

Measures to decrease the transmission of soil borne viruses are economically feasible in the small plots of intensive vegetable crops, particularly in protected crops. Thus, solarisation or fungicide treatments may efficiently decrease the populations of chytrid fungi in the soil, but even in soil-less crops, in which fungicides are applied with irrigation water, virus disease control may be inefficient due to small EDT, as was the case for MNSV in melon in SE Spain (Cuadrado, 1994).

Sanitation and the use of genetic resistance are the only strategies that can be applied for contact-transmitted viruses, and are the most efficient ones for all viruses of horticultural crops. Thus, seed certification regulations are applied to different viruses of vegetable crops, such as LMV in lettuce and tobamoviruses in pepper, which, together with control of virus spread in seedbeds and nurseries, including insecticide treatments, can significantly decrease disease incidence in the field. Certification programmes are most important for fruit and ornamental crops, with zero tolerance for certain viruses in certified propagation material to be sold to growers. Most countries within Europe run centralised national certification schemes for both soft and tree fruit, utilising a combination of nursery inspection and laboratory testing. The citrus certification scheme in Spain, in which nurseries can only multiply virus-free material provided by official institutions which also survey virus-free status of daughter plants, is an excellent example of how effective these campaigns can be (Navarro, 1986). Roguing of diseased plants, including large scale eradication programmes, such as those carried to prevent the spread of sharka disease of stone-fruit trees (see next section) are also part of sanitation strategies for virus control

Resistance has been effectively deployed in vegetable crops, and examples abound of species for which susceptible varieties cannot be grown anymore, due to the very high potential losses. Examples of this are tomato and ToMV and TSWV, pepper and PMMoV (in greenhouses) or PVY (in the open), melon and MNSV in greenhouses. For most deployed resistance factors resistance-breaking strains have been reported to occur in the field, and in some virus-crop systems have resulted in a short life of the resistant varieties. Even when this has not been the case, and resistance-breaking strains have not become prevalent in the field, most deployed resistances in vegetable crops are under the threat of being overcome sooner or later (García-Arenal and McDonald, 2003).

3.2 Major virus problems

Many viruses are key pathogens of fruits and vegetable crops in Europe. We will treat here *in extenso* only the most relevant ones.

3.2.1 Fruit crops

Sharka, caused by the aphid- transmitted PPV, is the most devastating disease of stone-fruit trees, and the direct and indirect losses that it causes in the production of apricots, plums and peaches is particularly well documented (reviewed in Cambra et al., 2006). Sharka was first described in Bulgaria in 1932, and by 1994 it had spread to all countries of Europe and the Mediterranean basin. PPV has different strains that differ in virulence towards the various *Prunus* species and in aphid transmissibility, PPV-D and PPV-M being the main strains in Europe. Infection causes a decrease in fruit production, an increase of early fruit drop and, most important, a decrease of fruit quality that makes it unmarketable even for the industry. To these direct losses, the cost of producing PPV-free plants, of surveys and of eradication programmes should be added. PPV has lead to a reduction of 40% in apricot production in Europe, with an estimated loss of 3600 M€ for the last 30 years. In addition, sharka has lead to the indirect cost of substituting the more sensitive early varieties for the more tolerant late ones. In the European plum, losses were even higher, of 50%, amounting to an estimate of 5400 M€ in the last 30 years. In peach, losses are estimated at about 5% of the production, amounting to about 576 M€ in the last 20 years. The recent spread of the PPV-M strain, most pathogenic to peach, to the Mediterranean basin threatens to increase these figures. The only feasible control strategies are eradication and use of virus-free propagation material. Costs of mandatory or voluntary eradication programmes are only available for Spain, where 2.3 million trees were eradicated since 1989 at a cost of 63 M€, including compensations to growers. Costs of surveys in Europe, including nursery surveys for the production of PPV-free plants, amount to 39 M€, involving the analysis of more than 13 million samples, and investment in research on PPV was of 73 M€. Transgenic plums resistant to PPV have been produced and assayed in the field (Fuchs et al., 2007; Malinowski et al., 2006) under the auspices of several EU-funded projects (including project QLK3-CT-2002-02140 Transvir “Environmental impact assessment of transgenic grapevines and plums on the diversity and dynamics of virus populations”) The FP7-KBBE-2007-1 project SharCo (Sharka Containment, started March 2008) aims at helping the EU face the accession of Member States known as endemic of sharka disease by providing the EU with tools such as marker-assisted selection, PPV resistant plant materials, guidelines, warning systems, decision-support system.

The most devastating disease of citrus, tristeza, is again a viral disease, caused by the aphid-transmitted CTV. Spain is the region of the world that has most suffered from the disease, with more than 40 million trees killed between the first reported outbreak, in 1956 until 2000, what represent more than 35% of sweet orange and mandarin trees (Cambra et al., 2000; Piquer et al., 2005). About half of these losses occurred between 1957 and 1989, and the other half between 1990 and 2000, because of a faster field dispersion of the disease after the efficient vector *Aphis gossypii* became the prevalent species in aphid populations (Cambra et al. 2000). CTV isolates in Spain only cause decline in sweet orange and mandarins when grafted on sour orange, and are efficiently controlled by grafting on tolerant rootstocks. Hence, since 1975 a certification programme, the Citrus Variety Improvement Programme, was started (Navarro et al. 1986) and it is compulsory to plant virus-free trees grafted on tolerant rootstocks. More than 100 million pathogen-free trees, grafted mostly on citrange rootstocks have been planted, meaning the replacement of more than 75% of sweet orange, mandarin and grapefruit plantations. Still, CTV potential losses are high, because of the risk of introduction of severe strains that cause tree decline on their own roots, and because of the risk associated to a citriculture based on only one type of rootstock, as citranges, tolerant to CTV, are sensitive to other diseases, such as citrus exocortis (Cambra et al., 2000) which at present do not occur in Spain.

Two viral diseases are key in grapevine production: fan-leaf degeneration, caused by the nematode-transmitted GFLV and leaf roll, caused by a complex of viruses of which the mealybug-transmitted GLRaV3 seems to be the most important one. Fan leaf degeneration is the oldest disease of grapevine, recorded in Europe for more than 200 years, and antedating the introduction of American rootstock hybrids. Losses due to fan-leaf degeneration vary according to the tolerance of the cultivar to the virus. Tolerant cultivars are little affected in their production, while losses in the most susceptible ones can amount to 80% of the yield (Martelli 1990). For example, reported reductions in yield were of 78-98% in cvs. Chasselas, Merlot and Pinot Noir in France (Bovey 1970), of 44-94% in cv. Traminer in Germany (Rüdel 1985), 55-65% in cv. Savagnin and 30% in cv. Nebbiolo in Italy (Legin et al. 1993; Mannini et al. 1994). Fruit quality is also affected, with a reduction of tritable acidity of –1.33 (Mannini et al. 1994). Vigour of the vine is reduced by 30-50% (Legin et al. 1993; Mannini et al., 1994), leading to progressive decline and reduced productive life of the vineyard. In France, 65% of the acreage is affected by GFLV, and 30% is severely affected (Demangeat et al. 2005), and yearly losses can be estimated at 1000-1500 M€, M. Fuchs, personal communication). Losses due to leaf roll have been reviewed recently (Charles et al. 2006). Leaf roll infected vines have a reduction of photosynthetic activity of 50-65% (Cabaleiro et al. 1999), leading to yield declines of 14%, resulting into cumulative decays in production of up to 70% in 7 years in some varieties (Credi and Babini, 1997). In addition, grape quality is severely affected, with a reduction in sugar content of –1.5ºBrix, and an increase in tritable acidity of 1.2; also, anthocyanin content is lower, with an impact on wine quality difficult to quantify (Charles et al., 2006). Control of both viruses is based on certification regulations, still to be implemented in some European countries, which for GLRaV3 should include the symptomless American grapevine rootstocks and hybrids. The nematode vectors of GFLV are widespread, and their control is not feasible in field conditions. Spread of GLRaV3 by mealybug vectors is only important in some regions of Europe, e.g., NW Spain (Cabaleiro & Segura, 1997), and can be decreased by treatments with organophosphate insecticides. Transgenic grapevine rootstocks resistant to GFLV have been produced and are currently being assayed in the field by INRA (Fuchs et al., 2007) with support from EU FP5 (project QLK3-CT-2002-02140 Transvir “Environmental impact assessment of transgenic grapevines and plums on the diversity and dynamics of virus populations”).

Viruses are also key pathogens of soft fruits. Thus, RBSV causes important losses in red raspberry and in blackberry, pending on the species and variety. So, in red raspberry, but not in blackberry, cane growth and fruit number are affected. In both species it causes a reduction of yield (of 40-50%), berry weight (of 25-40%) and druplet number per fruit (35-40%), considerably reducing the value of the crop both for the freshmarket and for processing (Strik and Martin, 2003). Resistance and planting of virus-free canes are efficient control measures.

3.2.2. Vegetable crops

In vegetables, viruses are also often key pathogens, and may be the major cause of loss (e.g., Cuadrado, 1994). In field-grown vegetable crops, losses are mostly due to aphid transmitted viruses. Thus, actual losses in lettuce yield caused by BWYV and LMV have been reported of 30% and 15%, respectively (Walkey and Payne, 1990). Losses in tomato due to CMV can be of 20-50% (Tien and Wu 1991), but are much higher when CMV isolates supporting necrogenic satellite RNAs occur in epidemics, as the tomato plant undergoes a systemic necrosis, so that the whole crop, or that from the second bunch on, is completely lost. Epidemics of CMV-caused tomato necrosis in Spain and Italy resulted in 80% of plants undergoing necrosis in 70% of the fields in large regions (Jordá et al. 1992; Gallitelli 2000), with the subsequent abandon of the crop in many traditional areas. CMV losses in pepper can also be high (up to 80%) (Avilla et al., 1997), but in this crop PVY is the most prevalent virus in field conditions, with losses up to 70% (Avilla et al., 1997) In melon, CMV and WMV are the two most prevalent viruses in field-grown crops (Luis-Areteaga et al., 1998), and in central Spain cause losses of 60% and 30% of yield, respectively, in the case of early infection (before the set of the first fruit). Losses are about half this value when infection occurs after this stage. Losses are due to the lower size and weight of fruits, but quality is unaffected (Alonso-Prados et al. 1997). ZYMV also causes severe losses (60-90%) in field-grown cucurbits (Al-Shawan et al., 1995; Blua & Perring 1989). The large host range of all these viruses, ZYMV excepted, and limitations in the possibility of management of aphid populations, makes control very difficult. Resistance is used in lettuce against LMV, and the wide-spread use of *mo1* resistance, together with seed certification provides a satisfactory control of LMV, at risk due to the potential spread of resistance-breaking, seed-transmitted strains (German-Retana et al 2008). Resistance to PVY is also widely used in pepper, but RB strains have been reported for all deployed resistance factors (Moury et al 2004).

Thrips- and whitefly-transmitted viruses become more important than aphid-transmitted ones where populations of these insects are established, i.e., in field-grown crops in the coastal areas of the Mediterranean basin and, particularly, in green-house-grown crops, where thrips and whiteflies survive around the year, with high populations and overlapping generations. The thrips-transmitted TSWV causes important losses since the late 1980s in several vegetable crops, including lettuce, artichoke, pepper and tomato. In tomato, TSWV losses in yield in the 1990s varied from 50 to 80% depending on the time of infection but, both for early and late infections, 85% of the fruits had discolorations that made them unsuitable for the fresh market (Moriones et al. 1998). Insecticide treatment of the vector, *Frankliniella occidentalis*, results in high costs, residue problems and is largely inefficient. *Sw-5* resistance to TSWV in tomato is widely used and gives a good protection. Resistant-breaking strains have been reported since 2001, but apparently they do not spread in the population and the resistance remains stable so far, but RB strains pose a potential risk (Aramburu and Marti 2003). Resistance to TSWV has also been widely deployed in pepper, but RB strains, first reported in 2002 (Roggero et al. 2002) are becoming widely prevalent. In some areas of pepper cultivation, integrated management of TSWV and the thrips vector has lead to a very satisfactory control (Contreras et al 1994)

Tomato leaf curl disease, caused by a variety of related begomovirus species (here collectively designed as TYLCV) transmitted by the whitefly *Bemisia tabaci*, causes important losses in tomato production in the Mediterranean areas since the early 1990s. Losses in susceptible cultivars have been estimated to be of 90%, due to a lower production of the severely stunted plants and, as for TSWV, to severe discoloration of the fruits even in newly infected plants (Lapidot et al. 1997). Partially-resistant cultivars give a reasonable protection, which is dependent on inoculum potential (Moriones & Navas-Castillo, 1999). Still, recombinant strains with an enlarged host and vector range can multiply more efficiently in the resistant tomato genotypes and, although currently this has not been associated to an increased virulence, pose an important potential threat (Monci et al., 2002). The losses caused by other, more recently emerged, whitefly transmitted viruses in tomato, such as TICV and ToCV, have not been estimated. Whitefly-transmitted viruses also affect severely other vegetable crops. This is the case of CYSDV in cucurbits, which causes yield reductions of 40-50% (Eid et al., 2006).

Vegetable crops grown in greenhouses are also severely affected by soil borne and by contact-transmitted viruses. Soil-borne MNSV, transmitted by *Olpidium bornovanus*, was a limiting factor of melon production in SE Spain in the 1980s, causing total loss of the crop in infested greenhouses due to the collapse and necrosis of the vines after fruit set. Since the 1990s, only resistant cultivars, based in the *nsr* gene, can be grown, due to the widespread infestation of soil and substrates. This resistance factor gives a very satisfactory protection, but RB strains have been reported that, once again, pose a potential threat to melon production (Díaz et al., 2002). Contact-transmitted viruses are also key pathogens of greenhouse-grown vegetables. This is the case of different species of tobamoviruses infecting pepper, mainly ToMV, TMGMV and PMMoV. Infection causes discoloration and altered texture of the fruits of infected plants, which are not marketable. Virus incidence in greenhouses may be very high, up to 80%, what often lead to the abandon of the crop even before the first fruit was harvested (García-Arenal and Fraile, unpublished). Different tobamovirus species and strains are successfully controlled by different alleles at the *L* locus, all of which have been overcome, except allele *L4*, which has given a stable protection for more than 25 years (García-Arenal & McDonald, 2003). Recently, strains overcoming *L4* resistance have been reported in Japan and in Israel (Genda et al, 2007, Antignus et al 2008), with a high risk of fast spread and serious potential losses to pepper production. A similar case is that of ToMV in tomato, successfully controlled with $Tm2^2$ resistance for more than 30 years (García-Arenal & McDonald, 2003). Still, potential losses due to ToMV can be estimated to be about 80%, as in older susceptible varieties (Pelham et al., 1970), because all commercial tomato cultivars must incorporate this resistance factor and, wherever susceptible cultivars are grown, infection by ToMV occurs. Currently, the most important contact-transmitted virus in Europe is PepMV, which causes severe epidemics in tomato crops all over Europe since it was first reported in 1999 (Lesemann et al., 2000, van der Vlugt, 2002). In the milder syndrome, PepMV infection only causes a loss of quality by fruit discoloration, which can affect from 30 to 50% of the crop, according to the incidence and the environmental conditions (Guerrero et al 2001), but PepMV may also be involved in much more severe syndromes, such as collapse and death of tomato plants in SE Spain, with losses of more than 80% (Soler-Aleixandre et al. 2005). No resistance is yet available for PepMV and its control is based on sanitary measures or, for the collapse syndrome, on grafting on tolerant rootstocks.

3.2.3 Ornamental crops

Viruses are a major cause of loss in the production of ornamentals, both for the flower and for the plant market. Because aesthetics is the main value of ornamentals, and virus-caused diseases most often result in stunting, distortions and/or discolorations, infected plants are not acceptable, and losses can be equated with incidence. As a result, only virus-free plants are grown for most species, and the production of these plants makes an important fraction of the ornamental crop industry. As the ETD is very small, estimates of actual losses are scarce.

Moreover, viruses that do not cause obvious symptoms, or are latent, may be the source of actual losses due to poor vigour, poor rooting, or enhanced disease symptoms when in co-infection with other viruses. An example of this, and one of the few instances of loss estimates, is the impact of viruses in the production of carnation flowers or plants, where CarMV is difficult to eliminate from some varieties and is often very mild or asymptomatic (Devergne et al., 1982), although in red varieties infection results in a paler colour of the flowers at low temperatures (Devergne, 1988). Flower yield is reduced by 15% by CarMV, which in addition reduces plant vigour and rooting ability (Brige et al., 1970).

4. Conclusions and prospects

As it has been shown in this report, viral diseases cause important actual losses in yield and quality in both field and horticultural crops in Europe, in spite that Europe is the world's region in which the efficiency of crop protection is highest (Oerke and Dehne, 2004). Moreover, potential losses could be much higher, and it is capital to avoid them: relatively few of the key virus problems of European crops are successfully controlled through sanitation (e.g., viruses of strawberry or ornamentals), cultural practices (e.g., grafting on tolerant rootstock for CTV) or the use of resistant varieties (e.g., BNYVV in sugar beet, MNSV in melon or TSWV in tomato). All these strategies are at stake because there is the risk of new strains spreading and becoming prevalent in the virus population against which current control strategies would be no longer efficient. Those strains could be introduced from other regions of the world or may arise in the European virus population through the many mechanisms of virus genetic variation (García-Arenal et al. 2001). Examples are RB strains on currently deployed resistance factors, or severe strains of CTV causing decline of trees grafted on tolerant rootstocks. Thus, surveys and regulations must be implemented, which are additional sources of economic loss, both direct (e.g., as estimated for sharka disease of stone-fruit crops) or indirect, by imposing limitations to the trade of propagation material and crop products (e.g., in the case of citrus for CTV) or to the cultivars or varieties that can be grown in a certain region (e.g., in the case of sugar beet and BNYVV or in the case of apricots and sharka). If actual data on the amount of direct losses are few, data on indirect losses are virtually non-existent. Hence, a first conclusion of this report is that research efforts directed at evaluating the losses (direct or indirect, economical or others including social) caused by viruses to the European agriculture and environment, and to the society at large, should be promoted.

A second conclusion is that all efforts must be made to prevent the emergence or re-emergence of new viral diseases, either through the introduction of new viral species or by the introduction or appearance of new strains that would compromise the success of current control strategies. Emergence and re-emergence of pathogens, including viruses, may be favoured by a series of factors external to agricultural production itself, which may be particularly difficult to manage. These include globalisation of the trade in agricultural goods and particularly of seeds and plants, which on the one hand increases the connectivity of potential pathogens and hosts, and on the other imposes a relaxation of quarantines and other regulatory measures in European agriculture. In addition, there is increasing evidence that climatic change is leading to variation in the geographic range of many biological species, including hosts and vectors of plant viruses, what may result in geographic- and host-range expansion of viral diseases. Examples are the expansion of begomoviruses world-wide, including in Europe, as reported here. A last factor is the concern of European society for an environmentally safe agriculture, which has lead to a more strict control of the use of pesticides. Although the benefits of these regulations for the society at large cannot be questioned, they may have a negative impact on the efficiency of crop protection in the short term. Hence, a second conclusion is that efforts must be put to increase our understanding of virus epidemiology and ecology, two scientific disciplines that have been out of favour in the recent past, so that emergence and re-emergence of viral diseases can be anticipated, if it cannot be avoided.

Lastly, the most efficient, specific and environmental friendly strategy for controlling viral diseases of crops is the breeding of genetic resistance into crop cultivars. As shown in this report, most instances of successful control of plant viruses rest on this strategy. However, resistance can be eroded, and the phenomena that lead to the overcoming of resistance or to its durability are poorly understood. These phenomena relate to the mechanisms of virus evolution, on the one hand, and to the intrinsic mechanisms of resistance, e.g., to the molecular biology of virus-plant interactions. These have been subjects of active research in the recent past, but we are still far from understanding why some resistance factors are durable while others are overcome in a short time. Thus, a third conclusion of this report is that increased efforts should be made in order to understand the nature of the resistance mechanisms of plants to viruses, and the sustainability of resistance in agroecosystems, which is the core of this European network.

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ANNEX 1. Names of virus species in the main text

BYDV- *Barley yellow dwarf virus*
BaMMV- *Barley mild mosaic virus*
BaYMV- *Barley yellow mosaic virus*
BNYVV- *Beet necrotic yellow vein virus*
BWYV- *Beet western yellows virus*
CMV- *Cucumber mosaic virus*
CTV – *Citrus tristeza virus*
CYDV- *Cereal yellow dwarf virus*
CYSDV- *Cucurbit yellow stunting disorder virus*
CarMV – *Carnation mottle virus*
GFLV – *Grapevine fanleaf virus*
GLRaV3 – *Grapevine leafroll-associated virus 3*
LMV – *Lettuce mosaic virus*
MNSV – *Melon necrotic spot virus*
MDMV- *Maize dwarf mosaic virus*
PLRV – *Potato leaf roll virus*
PMMoV – *Pepper mild mottle virus*
PPV – *Plum pox virus*
PLRV- *Potato leaf roll virus*
PSbMV – *Pea seedl borne mosaic virus*
PVY- *Potato virus Y*
PepMV- *Pepino mosaic virus*
SBCMV- *Soil-borne cereal mosaic virus*
TBSV- *Tomato bushy stunt virus*
TICV- *Tomato infectious chlorosis virus*

TMGMV – *Tobacco mild green mosaic virus*
TRV – *Tobacco rattle virus*
TSWV- *Tomato spotte wilt virus*
TYLCV – *Tomato yellow leaf curl virus*
ToCV – *Tomato chlorosis virus*
ToMV – *Tomato mosaic virus*
ToTV- *Tomato torrado virus*
TuMV – *Turnip mosaic virus*
TuYV- *Turnip yewllows virus*
WMV – *Watermelon mosaic virus*
ZYMV – *Zucchini yellow mosaic virus*

ANNEX 2. Summary of significant virus problems in Europe

The major virus problems at a European level are listed below in relation to the sector of agriculture/horticulture. The viruses are those that were indicated by a significant number of the experts responding to the questionnaire as being of economic significance.

Virus name	Transmission	Crop	Estimated losses (ref.)
Barley yellow dwarf virus (BYDV) and *Cereal yellow dwarf virus* (CYDV)	Aphid	Cereals (wheat, barley, and oats)	Early infection causes biggest losses, up to 80% (Perry et al. 2000). Up to 30% in barley in UK (Plumb et al 1986),10-15% in wheat in UK and France (Plumb 1983; Bayon & Ayrault, 1987)
Barley yellow dwarf virus (BYDV)	Aphid	Rice	5% in Italy and Spain (Prescini, 1987; Jorda et al, 1989)
Barley yellow mosaic virus (BaYMV) or *Barley mild mosaic virus* (BarMMV)	*Polymyxa graminis*	Barley	Susceptible cultivars may suffer 30-50% yield loss (Lapiere & Signoret 2004)

Beet mild yellowing virus (BMYV), *Beet yellowing virus* (BYV), *Beet chlorosis virus* (BCV)	Aphid	Sugarbeet	Affects 25% of surface in Europe (Hermann 2005)
Beet necrotic yellow vein virus (BNYVV)	*Polymyxa betae*	Sugarbeet	Yield losses between 53-75% (Henry, 1996) Potential losses in susceptible cultivars 60% (Hermann 2005)
Beet western yellows virus (BWYV)	Aphid	Lettuce	30% in yield (Walkey & Payne, 1990)
Carnation mottle virus (CarMV)	No vector	Carnation	15% flower yield (Brige et al, 1970)
Citrus tristeza virus (CTV)	Aphid	Citrus	The most significant disease on citrus. Causes death of trees on susceptible root stocks 35% of sweet orange and mandarin trees killed in Spain (Cambra et al 2000)
Cereal yellow dwarf virus (CYDV)	Aphid	Cereals	See *Barley yellow dwarf virus*
Cucumber mosaic virus (CMV)	Aphid	Tomato, pepper, cucumber	Up to 80% due to quality loss in peppers (Avilla et al, 1997) 50%-80% in tomato infected with CMV+satRNA necrogenic (Jorda et al,1992)
Cucumber mosaic virus (CMV)	Aphid	Beding and pot plants, cut flowers	Can cause entire loss due to quality problems above a threshold of affected product
Cucumber yellow stunt disorder virus (CYSDV)	Whitefly	Cucurbits	40-50% (Eid et al, 2006)
Grapevine fan leaf virus (GFLV)	Nematode	Grapevine	Yield decline of 14% (Credi & Babini 1997)
Grapevine leaf roll associated virus complex (GLRaV)	Mealybugs	Grapevine	Reduced quality and sugar accumulation. Yield reduction between 5-8% (Goheen, 1970; Duffus, 2977)
Impatiens necrotic spot virus (INSV)	Thrips	Beding and pot plants, cut flowers	Can cause entire loss due to quality problems above a threshold of affected product
Lettuce mosaic virus (LMV)	Aphid	Lettuce, some ornamentals	15% in lettuce yield (Walkey & Payne, 1990)
Maize dwarf mosaic virus (MDMV)	Aphid	Maize	13-40% in maize seed production in Spain (Achon et al 95)
Melon necrotic spot virus (MNSV)	*Olpidium bornovanus* and seeds	Melon, cucumber	100% in SE Spain in 1980 (Cuadrado et al, 1993)

Pepino mosaic virus (PepMV)	Contact	Tomato	50-80% losses (Jorda et al, 2001)
Pepper mild mottle virus (PMMoV)	Contact	Pepper	80% loses in greenhouses
Plum pox virus (PPV)	Aphid	Stone fruit	More damaging in mixed infections, but the growth of trees can be reduced by 9.2-69.1% (Nemeth 1992). 50% losses in European plumb (Cambra et al, 2006)
Potato virus Y (PVY)	Aphid	Potato	Losses dependent on cultivar. Largest losses from infected seed. Data from multiple varieties range from 50-85% for 2° infection Hunnius & Arenz, 1959)
Potato virus Y (PVY)	Aphid	Tomato, pepper	Up to 70% loss in peppers (Avilla et al1997)
Potato leafroll virus (PLRV)	Aphid	Potato	Up to 90% can include quality problems due to internal necrosis (Jeffries, 1998) Losses in potato production 10-15% (Valkonen 2007)
Potato mop-top virus (PMTV)	Fungus	Potato	Causes quality problems mostly in northern regions (Nielsen & Molgaaard, 1997)
Prunus necrotic ringspot virus (PNRSV)	Pollen and planting material	Stone fruit	Yield of infected trees reduced by 8-47% (Pusey 1991)
Raspberry bushy dwarf virus (RBDV)		Raspberries	Most damaging in combination with other viruses, causes quality problems and reduces productive life of fields. 40-50% reduction in yiel (Strik and Martin. 2003)
Soil borne cereal mosaic virus (SBCMV)	*Polymyxa graminis*	Wheat/Rye	Loss to cereal furovirus have been estimated at 48% and between 30-50% in two recent studies (Clover et al, 2001; Vallega et al, 1999)
Strawberry crinkle virus (SCV) often in complex with *Strawberry mild yellow edge virus* (SMYEV) and *Strawberry mottle virus* (SMoV)	Aphid	Strawberry	Fruit losses in commercial strawbwrries can range from 30% in single infections to 80% in mixed infections (Thompson et al, 2003)
Tobacco mild green mosaic virus (TMGMV)	Contact	Pepper	
Tobacco rattle virus (TRV)	Nematode	Potato	Causes quality problems mostly in northern regions (Dale et al, 2004)
Tomato bushy stunt virus (TBSV)	No vectors, seed	Tomato	50-80% losses (Cuadrado, 1995)
Tomato chlorosis virus (ToCV)	Whitefly	Tomato	50-80% losses in tomato

Tomato infectious chlorosis virus (TICV)	*Trialeurodes vaporariorum*	Tomato	50% losses
Tomato mosaic virus (ToMV)	Contact	Tomato	80% potential losses (Pelham et al., 1970)
Tomato spotted wilt virus (TSWV)	Thrips	Tomato, pepper	Up to 85% losses in tomato (Moriones et al., 1998)
Tomato spotted wilt virus (TSWV)	Thrips	Beding and pot plants, cut flowers	Can cause entire loss due to quality problems above a threshold of affected product
Tomato torrado virus (ToTV)		Tomato	50-80% losses (Jorda et al,2003; verbeek et al 2007).
Tomato yellow leaf curl virus (TYLCV)	Whitefly	Tomato	100% losses in Israel (Lapidot et al 1997) 50-80% losses in Spain (Moriones & Navas-Castillo,1999)
Turnip mosaic virus (TuMV)	Aphid	Brassica	Up to 10% annually due to leaf necrosis in white cabbage (Hunter et al, 2002)
Turnip yellows virus (TuYV) previously *Beet western yellows virus* (BWYV)	Aphid	Oilseed rape	Seed yield losses 10-26% in UK (Stevens et al 2008), 12-34 in Germany (Jay et al, 1995: Graichen 1999)
Watermelon mosaic virus (WMV)	Aphid	Melon	30% of yield in Central Spain (Luis-Arteaga et al, 1998)
Zucchini yellow mosaic virus (ZYMV)	Aphid	Cucurbits	Losses ranging from 64-85 % in cucumbers (Al-Shawan et al,1995)and up to 94% in melon (Blua & Perring, 1989).