

INVITED REVIEW

VIRUSES OF GLOBE ARTICHOKE: AN OVERVIEW

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SUMMARY

An account is given of the current knowledge of viruses that infect globe artichoke (*Cynara scolymus* L.) and cardoon (*Cynara cardunculus* L.) and the diseases they cause. Most of the 23 viruses found in these crops were recorded from Europe and the Mediterranean Basin, where they constitute serious threats to the artichoke industry. They are: 10 viruses with isometric particles *ca* 30 nm in diameter that belong to six genera [*Nepovirus* (*Artichoke Italian latent virus*, *Artichoke yellow ringspot virus*, *Artichoke Aegean ringspot virus*, and *Tomato black ring virus*), *Cheravirus* (*Artichoke vein banding virus*), *Fabavirus* (*Broad bean wilt virus*), *Ilarvirus* (*Tobacco streak virus*), *Cucumovirus* (*Cucumber mosaic virus*), *Tombusvirus* (*Artichoke mottled crinkle virus*), and *Anulavirus*, a newly proposed genus in the family *Bromoviridae* (*Pelargonium zonate spot virus*)]; two viruses with rod-shaped rigid particles that belong to the genera *Tobamovirus* (*Tobacco mosaic virus*) and *Tobravirus* (*Tobacco rattle virus*); nine viruses with filamentous particles that belong to four genera [*Potyvirus* (*Artichoke latent virus*, *Bean yellow mosaic virus*, and *Turnip mosaic virus*), *Carlavirus* (*Artichoke latent virus M*, *Artichoke latent virus S*, an unnamed virus distantly related serologically to *Poplar mosaic virus*), *Potexvirus* (*Artichoke curly dwarf virus*, *Artichoke degeneration virus*, and *Potato virus X*), and *Crinivirus* (*Tomato infectious chlorosis virus*)]; two viruses with enveloped particles that belong to the family *Rhabdoviridae* (*Cynara virus*) or the genus *Tospovirus* (*Tomato spotted wilt virus*), respectively. The main properties of these viruses are illustrated and the techniques used for their detection and identification are reviewed. Micropropagation techniques for obtaining virus-free artichoke plants are also outlined.

Key words: globe artichoke, cardoon, virus, virus diseases, diagnosis, sanitation.

This review is largely based on a presentation given in 2000 at the 4th International Congress on Globe Artichoke, Bari, Italy.

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INTRODUCTION

Italy, Spain, and France are world leaders in the growth of globe artichoke (*Cynara scolymus* L.) and their industries account for about 80% of the world production. It is no wonder that most studies on viruses of this crop have been done in these countries.

Investigations of some consequence began in the late 1950s with a peak in the 1960s and 1970s. At the 1st International Congress on Globe Artichoke (Bari, Italy, 1967), Ciccarone (1967) reported only two filamentous particle viruses, namely *Artichoke curly dwarf* (ACDV) (genus *Potexvirus*) (Leach and Oswald, 1950; Morton, 1961) and *Artichoke latent virus S* (ArLVS) (genus *Carlavirus*) (Costa *et al.*, 1959), both recorded from California, and the isometric particle virus *Artichoke mottled crinkle virus* (AMCV) (genus *Tombusvirus*) recorded from Italy (Martelli, 1965; Quacquarelli and Martelli, 1966). At that time, the viral aetiologies of a bright yellow mosaic reported from Sicily (Gigante 1951), a generalized yellowing condition from California (Smith, 1940), and a chlorotic mottling accompanied by a degenerative condition from Tunisia (Laudank, 1958), were not supported by experimental evidence.

Six years later, at the 2nd International Congress on Globe artichoke (Bari, 1976), Martelli and Rana (1976) listed nine additional viruses from *C. scolymus*, *Cynara syriaca* L., and cardoon (*Cynara cardunculus* L.), namely two nepoviruses, *Artichoke Italian latent virus* (AILV) and *Artichoke yellow ringspot virus* (AYRSV), two potyviruses, *Artichoke degeneration virus* (ADV) and *Artichoke latent virus* (ArLV), plus *Cucumber mosaic virus* (CMV, genus *Cucumovirus*), *Tobacco streak virus* (TSV, genus *Ilarvirus*), *Cynara virus* (CraV, unassigned species in the family *Rhabdoviridae*), *Tobacco mosaic virus* (TMV, genus *Tobamovirus*) and *Tobacco rattle virus* (TRV, genus *Tobravirus*).

At the 3rd International Congress on Globe artichoke (Bari, 1981), the number of viruses had grown to 16 (Martelli *et al.*, 1981) and by 2000 had reached 23 (Table 1).

In this paper, the essential information on these viruses (morphology, taxonomy, symptomatology, cytopathology, epidemiology, diagnosis and sanitation) is briefly

Table 1. Viruses infecting *Cynara* species in nature: taxonomic allocation, epidemiology and geographical distribution.

Viruses	Particle size (nm) genus family	Epidemiology	Vector	Natural <i>Cynara</i> host	Geographical distribution
A. With isometric particles					
<i>Artichoke Italian latent virus</i> (AILV)	30 <i>Nepovirus</i> (Subgroup B) <i>Comoviridae</i>	soil-borne	<i>Longidorus apulus</i>	<i>C. scolymus</i>	Italy, Bulgaria, Russia
<i>Artichoke mottled crinkle virus</i> (AMCV)	30 <i>Tombusvirus</i> <i>Tombusviridae</i>	soil-borne	vectorless transmission	<i>C. scolymus</i>	Italy, Morocco, Malta, Greece, Tunisia
Artichoke vein banding virus (AVBV)	30 <i>Cheravirus</i>	soil-borne	unknown	<i>C. scolymus</i>	Italy, Turkey (?), France (?)
<i>Artichoke yellow ringspot virus</i> (AYRSV)	30 <i>Nepovirus</i> (Subgroup C) <i>Comoviridae</i>	soil-borne	unknown	<i>C. scolymus</i> <i>C. cardunculus</i>	Italy, Greece
<i>Broad bean wilt virus</i> (BBWV)	30 <i>Fabavirus</i> <i>Comoviridae</i>	insect-transmitted	several aphid species	<i>C. scolymus</i>	Italy, France
<i>Cucumber mosaic virus</i> (CMV)	30 <i>Cucumovirus</i> <i>Bromoviridae</i>	insect-transmitted	several aphid species	<i>C. scolymus</i> <i>C. cardunculus</i>	Italy, Greece, France Tunisia
<i>Pelargonium zonate spot virus</i> (PZSV)	26-35 <i>Anulavirus</i> <i>Bromoviridae</i>	insect-transmitted	several thrips species	<i>C. scolymus</i>	Italy
<i>Artichoke Aegean ringspot virus</i> (AARSV)	30 <i>Nepovirus</i> (Subgroup A) <i>Comoviridae</i>	soil-borne	unknown	<i>C. scolymus</i>	Turkey, Greece
<i>Tobacco streak virus</i> (TSV)	26-35 <i>Ilarvirus</i> (Subgroup 1) <i>Bromoviridae</i>	insect-transmitted	several thrips species	<i>C. scolymus</i>	Brazil
<i>Tomato black ring virus</i> (TBRV)	30 <i>Nepovirus</i> (Subgroup B) <i>Comoviridae</i>	soil-borne	<i>Longidorus attenuatus</i>	<i>C. scolymus</i>	France
B. With rod-shaped particles					
<i>Tobacco mosaic virus</i> (TMV)	300 <i>Tobamovirus</i>	transmission by contact	unknown	<i>C. cardunculus</i>	Italy

Viruses	Particle size (nm) genus family	Epidemiology	Vector	Natural <i>Cynara</i> host	Geographical distribution
<i>Tobacco rattle virus</i> (TRV) C. With filamentous particles	55-200 <i>Tobravirus</i>	soil-borne	<i>Thrichodorus christiei</i>	<i>C. scolymus</i>	Brazil
Artichoke curly dwarf virus (ACDV)	582 <i>Potexvirus Flexiviridae</i>	unknown	unknown	<i>C. scolymus</i>	USA (California)
<i>Potato virus X</i> (PVX)	580 <i>Potexvirus Flexiviridae</i>	transmission by contact	unknown	<i>C. scolymus</i>	Tunisia
Artichoke latent virus M (ArLVM)	697 <i>Carlavirus Flexiviridae</i>	insect-transmitted	unknown	<i>C. scolymus</i>	Italy
Artichoke latent virus S (ArLVS)	673 <i>Carlavirus Flexiviridae</i>	insect-transmitted	aphids	<i>C. scolymus</i> <i>C. cardunculus</i>	USA, Italy, Morocco Spain (?), Brazil (?)
Unnamed putative carlavirus	664 Non classified	insect-transmitted	unknown	<i>C. scolymus</i>	Italy
<i>Artichoke latent virus</i> (ArLV)	725 <i>Potyvirus Potyviridae</i>	insect-transmitted	<i>Myzus persicae</i> , <i>Brachycaudus cardui</i> , <i>Aphis fabae</i>	<i>C. scolymus</i> <i>C. cardunculus</i> <i>C. syriaca</i>	Mediterranean basin, Brazil
<i>Bean yellow mosaic virus</i> (BYMV)	750 <i>Potyvirus Potyviridae</i>	insect-transmitted	several aphid species	<i>C. scolymus</i>	Italy, Greece
<i>Turnip mosaic virus</i> (TuMV)	750 <i>Potyvirus Potyviridae</i>	insect-transmitted	several aphid species	<i>C. scolymus</i>	Italy
Artichoke degeneration virus (ADV) Putative potyvirus	585 (?) Non classified	insect-transmitted (?)	unknown	<i>C. scolymus</i>	Italy
<i>Tomato infectious chlorosis virus</i> (TICV)	850-900 <i>Crinivirus Closteroviridae</i>	insect-transmitted	<i>Trialeurodes vaporariorum</i>	<i>C. scolymus</i>	USA (California)
D. With enveloped particles					
<i>Cynara virus</i> (CraV) Putative cytorhabdovirus	260x75 un assigned <i>Rhabdoviridae</i>	insect-transmitted	unknown	<i>C. scolymus</i> <i>C. syriaca</i>	Italy, Spain
<i>Tomato spotted wilt virus</i> (TSWV)	70-90 <i>Tospovirus Bunyaviridae</i>	insect-transmitted	several thrips species	<i>C. scolymus</i>	Argentina, Australia, Italy, Spain

reviewed, thus updating previous reports (Martelli and Rana, 1976; Martelli *et al.*, 1981; Rana and Martelli, 1983).

VIRUSES WITH ISOMETRIC PARTICLES

Four of the ten isometric particle viruses that infect artichoke belong to the genus *Nepovirus*, family *Comoviridae* (Murrant *et al.*, 1996). All possess the major properties of the genus, i.e. isometric particles with angular contours and diameters of *ca* 30 nm that form three components when centrifuged in density gradients or to equilibrium, and a bipartite, positive sense, single-stranded RNA genome. Two of these viruses, *Artichoke Italian latent virus* (AILV) and *Tomato black ring virus* (TBRV) have recognized nematode vectors.

Artichoke Aegean ringspot virus (AARSV) was originally found in symptomless plants from Turkey (Smyrna) (Kyriakopoulou and Bem, 1982), then in Greece (Marathon and Nauplion), in cvs Black and Argitiki that had yellow blotches and mild mottling, and was identified as a serotype of *Raspberry ringspot virus* (RpRSV) (Rana *et al.*, 1985). The Greek and Turkish isolates were serologically very closely related (SDI = 1) and were distantly related to RpRV-S and RpRV-E (SDI = 5) (Rana *et al.*, 1985). However, when analyzed by molecular methods, these isolates proved to share 73% sequence homology with one another, but had only 7% homology with RpRSV-E (Robinson and Clark, 1987), indicating that they belonged to a different species. The virus was therefore given its present name (Murrant *et al.*, 1996). AARSV has a moderately wide experimental host range, infecting 22 species out of 40 in 7 dicotyledonous families (Rana *et al.*, 1985). Its vector is unknown (Roca *et al.*, 1986).

Artichoke Italian latent virus (AILV) was recovered from symptomless artichokes in Apulia (southern Italy) (Majorana and Rana, 1970a), later, again in Apulia, from chichory showing chlorotic mottling of the leaves often accompanied by bright yellow spots (Vovlas *et al.*, 1971), from grapevine with fanleaf-like symptoms in Bulgaria (Jankulova *et al.*, 1977), from pelargonium with severe leaf deformation (Martelli *et al.*, 1977), and from artichoke in northeast Peloponnesus (Greece), where it caused a disease called artichoke patchy chlorotic stunting (APCS) (Rana and Kyriakopoulou, 1982; Kyriakopoulou, 1995; Brown *et al.*, 1997). AILV type strain (Apulian) is transmitted by *Longidorus apulus* (Roca *et al.*, 1975; Vovlas and Roca, 1975; Rana and Roca, 1976) and the Greek strain is transmitted by *L. fasciatus* (Roca *et al.*, 1982). The natural host range is wide, like the experimental host range, which includes 63 species in 12 dicotyledonous families (Quacquarelli *et al.*, 1976; Savino *et al.*, 1977; Camele *et al.*, 1991). Virus survival in horticultural areas of southern Italy is

facilitated by infection of susceptible weeds in which AILV is seed-transmitted, and of artichoke and chicory that are often cropped in succession in the same plots. The physico-chemical properties and cytopathology of AILV are summarized by Martelli *et al.* (1977).

Artichoke yellow ringspot virus (AYRSV) was first reported from Greece in plants showing bright yellow blotches, ringspots and line patterns in the leaves, occasionally followed by extensive necrosis (Kyriakopoulou and Bem, 1973). This virus was later isolated in Sicily (southern Italy) from cardoon (*C. cardunculus*) cv Bianco avorio with striking yellow ringspots and line patterns in the leaves (Rana *et al.*, 1978). Isolates of Italian and Greek origin differ in host range but not serologically. In nature, AYRSV infects 35 plant species in 14 families, six of which are agricultural crops (artichoke, cardoon, tobacco, broad bean, French bean, and cucumber) and 30 are wild plants (Kyriakopoulou *et al.*, 1985; Avgelis and Vovlas, 1989; Avgelis *et al.*, 1992). The experimental host range is also wide, including 56 species in 11 dicotyledonous families (Rana *et al.*, 1980). AYRSV has no known vector but was shown to be seed-transmitted in tobacco and to infect *Nicotiana cleavelandii* via pollen. The virus was purified and characterized biologically, physicochemically and cytopathologically by Rana *et al.* (1980, 1983) and identified as a member of subgroup C of the genus *Nepovirus* (Wellink *et al.*, 2000). AYRSV is not related serologically to 28 isometric plant viruses including 14 nepoviruses.

Tomato black ring virus (TBRV) in nature infects several plant species, including globe artichoke (Murrant *et al.*, 1996). It was first isolated in France in an experimental plot of cv Camus de Bretagne that showed mild mottling (Migliori *et al.*, 1984b). In commercial French artichoke fields, it was transmitted by *Longidorus attenuatus* at a rate of 5-10%. Experimental infection of artichoke seedlings of the hybrid "Bianco tarantino x Nostrano di Ascoli Piceno" induced systemic chlorotic ringspot of the leaves (Rana *et al.*, 1987a). The globe artichoke strain of the virus (TBRV-A), is more closely related to TBRV-W from beet (Harrison 1957) (SDI = 1) than to TBRV-BU from potato (Harrison, 1958) or TBRV-Ce from celery (Hollings, 1965) (SDI = 2 - 3), and is very distantly related to AILV-S and AILV-G (SDI = 11 and 12, respectively) (Dodd and Robinson, 1984; Rana *et al.*, 1987). Infected cells show inclusion bodies typical of those induced by nepoviruses, consisting of accumulations of membranous vesicles, endoplasmic reticulum strands and ribosomes. Virus particles are in groups in the cytoplasm or in rows within tubular structures that are sometimes connected to plasmodesmata (Rana *et al.*, 1987a).

Other viruses with non-enveloped isometric particles reported from artichoke are: Artichoke vein banding virus (AVBV), *Artichoke mottled crinkle virus* (AMCV), *Cucumber mosaic virus* (CMV), Broad bean wilt virus

(BBWV), *Pelargonium zonate spot virus* (PZSV), and *Tobacco streak virus* (TSV).

Artichoke vein banding virus (AVBV), described by Gallitelli *et al.* (1978, 1984), was found originally in Apulia in the Turkish artichoke cvs Bayrampasa and Sakiz, in which it caused mild chlorotic discoloration along the leaf veins, and in the Italian cv Mazzaferrata. Due to its bipartite ssRNA genome it was originally classified as a tentative species in the genus *Nepovirus* (Harrison and Murrant, 1977). More recently it was transferred to the newly established genus *Cheravirus* (Le Gall *et al.*, 2004) with which it shares a major characterizing feature, namely the presence of three coat protein subunits with Mr 22,000, 24,500, and 27,000. AVBV does not seem to be widespread, has no known vector and a moderately wide experimental host range comprising 20 species in 7 dicotyledonous families (Gallitelli *et al.*, 1978).

Artichoke mottled crinkle virus (AMCV) was the first fully characterized artichoke virus (Quacquarelli and Martelli, 1966; Martelli *et al.*, 1981). It seems to be endemic in the Mediterranean since it was recovered from symptomatic plants in southern Italy (Martelli, 1965), Morocco (Fischer and Lockhart, 1974a), Malta (Martelli *et al.*, 1976), and Tunisia (Rana and Cherif, 1981) and was also isolated from symptomless plants in several horticultural areas of southern Italy and Greece (Rana and Kyriakopoulou, 1982). Symptoms induced are severe deformation, mottling, and crinkling of the leaves. Growth and yield of symptomatic plants are severely affected. AMCV is a species of the genus *Tombusvirus*, and is very closely related serologically to *Petunia asteroid mosaic virus* (PAMV) (SDI = 1). The two viruses, however, occupy different ecological niches (natural hosts and environment), which justifies their retention as different species. Italian, Moroccan, Tunisian and Maltese isolates are serologically uniform, whereas a serological variant was identified in Greece (Rana and Kyriakopoulou, 1982). AMCV persists in the soil from where, like other tombusviruses, it can be acquired by healthy plants without the intervention of vectors. The cytopathology of AMCV infection is very complex. Among other features, infected cells were shown for the first time to contain cytopathic structures (Martelli and Russo, 1973) later denoted "multivesicular bodies", the hallmark of tombusvirus infections (Martelli and Russo, 1984). The satellite RNA associated with AMCV was studied as a possible means of biological control (Gallitelli, 1989).

Cucumber mosaic virus (CMV) was recorded by Lisa (1971) in northern Italy from mottled cardoon plants and was successfully transmitted to cardoon seedlings by *Myzus persicae*. Globe artichoke seedlings mechanically inoculated using the cardoon virus isolate remained symptomless. CMV strains belonging to subgroup II were also isolated in France (Migliori *et al.*, 1984a) and in southern Italy (Paradies *et al.*, 2000) in mixed infec-

tion with either the potyvirus *Artichoke latent virus* (ArLV) or *Tomato spotted wilt virus* (TSWV) in plants showing severe stunting, leaf malformation, and necrosis. A further well-substantiated record of infection by CMV is from Tunisia (Chabbou and Cherif, 1990), but a report from Slovenia is dubious (Baricevic *et al.*, 1995).

Broad bean wilt virus (BBWV) was first isolated in southern Italy, along with ArLV and, occasionally, *Cynara virus* (CraV) and *Bean yellow mosaic virus* (BYMV), from plants of cv Castellammare showing yellow mottle, mosaic or line patterns (Russo and Rana, 1978). The virus was further studied by Rana *et al.* (1987b) who, in mechanically inoculated artichoke seedlings of cv Locale di Mola, reproduced a yellow mottle very similar to that observed in the past in Italy in different artichoke cultivars (Gigante, 1951; Martelli and Rana, 1976; G.P. Martelli, G.L. Rana and A. Ragozzino, unpublished data). This virus also occurs in Greece (Kyriakopoulou, 1995). Inoculation of *Gomphrena globosa* or *Chenopodium quinoa* can be used to separate BBWV from ArLV as they are infected only locally by ArLV but systemically by BBWV. Because of aphid transmissibility in a non-persistent manner, BBWV spreads very rapidly in the field and can reach a high incidence, as in France where in crops of cv Camus de Bretagne infection rates of 40 to 70% have been recorded (Migliori *et al.*, 1987). In experimental tests, the most efficient vector was *Capitophorus horni* Börner. Migliori *et al.* (1987) showed that BBWV infection reduces the yield remarkably in terms of weight of the first flower head and the number of marketable heads per plant. A comparative biological, physico-chemical, serological and cytopathological characterization of a French (BBWV-FA) and an Italian (BBWV-IA) strain of the virus was done by Migliori *et al.* (1988). In serological tests, BBWV-FA appeared to be more closely related to BBWV-IA than to BBWV serotypes I and II (Uyemoto and Provvidenti, 1974).

Pelargonium zonate spot virus (PZSV), a virus originally described by Gallitelli (1983), has been recently characterized in molecular detail (Finetti-Sialer and Gallitelli, 2003) and proposed to be the type species of a new genus, *Anulavirus*, in the family *Bromoviridae* (Gallitelli *et al.*, 2005). PZSV has quasi-spherical particles 25-35 nm in diameter, a positive sense ssRNA genome consisting of three functional species with sizes of 3,383 nt (RNA-1), 2,435 nt (RNA-2), and 2,569 nt (RNA-3), and a complex cytopathology, differing somewhat from that of other members of the family (Castellano and Martelli, 1981). The virus was isolated in Apulia from artichokes cv Romanesco with stunting and chlorotic mottling of the leaves (Rana and Martelli, 1983). It had been recovered previously from tomato and pelargonium in the same area (Martelli and Cirulli, 1969; Quacquarelli and Gallitelli, 1979). An isolate from *Chrysanthemum coronarium* induced yellowish

ringspot and line patterns when artificially inoculated to globe artichoke seedlings of cv Locale di Mola (Rana *et al.*, 1990). The virus is apparently limited to the south of Italy, Spain, and France, where it is more commonly found in tomato (Vovlas *et al.*, 1986; Luis-Arteaga and Cambra, 2000; Gebre-Selassie *et al.*, 2002). PZSV is endemic in Apulia, where it infects *Diplotaxis eruroides* latently and from which it is carried in pollen by thrips, to spread to crops, especially tomato (Vovlas *et al.*, 1989). The virus is pollen-borne and transmitted through seed in *Nicotiana glutinosa*.

Tobacco streak virus (TSV), a member of the genus *Illarvirus* with particles 26 to 35 nm in diameter, was reported only once from globe artichoke in Brazil, where it was isolated from stunted plants with malformed leaves (Costa and Tasaka, 1971). This isolate did not differ from other TSV strains from potato, tobacco and tomato occurring in the same agricultural area and did not seem to have clear-cut detrimental effects on the artichoke crop.

VIRUSES WITH FILAMENTOUS PARTICLES

Of the viruses with filamentous particles that infect globe artichoke, three are definitive members of the genus *Potyvirus* (Berger *et al.*, 2000), three are putative members of the genus *Carlavirus*, and two are members of the genus *Potexvirus*. The last two genera belong to the recently established family *Flexiviridae* (Adams *et al.*, 2004).

Potyriviruses. *Artichoke latent virus* (ArLV) was first recovered from symptomless globe artichoke plants by Marrou and Mehani (1964) in Tunisia, then by Fischer and Lockhart (1974b) and Foddai *et al.* (1977) in Morocco and Sardinia (Italy), respectively. ArLV is a typical potyvirus with particles *ca* 730 nm long, that can be transmitted experimentally in non-persistent manner to artichoke seedlings by *Myzus persicae*, *Brachycaudus cardui*, and *Aphis fabae* (Rana *et al.*, 1982). Transmission efficiency is very high, as shown by the quick re-infection rate (over 75% in two years) registered in a field trial carried out with virus-free plants in Sardinia (Foddai *et al.*, 1985). The host ranges of ArLV isolates from eight different countries were studied by Rana *et al.* (1982), who also characterized an Italian isolate of the virus, proving that it is serologically unrelated to the following potyriviruses: *Bean common mosaic virus* (BCMV), *Bean yellow mosaic virus* (BYMV), *Clover yellow vein virus* (CYVV), *Beet mosaic virus* (BMV), *Lettuce mosaic virus* (LMV), *Zucchini yellow fleck virus* (ZYFV), *Papaya ringspot virus* (PRSV), *Watermelon mosaic virus* (WMV), *Turnip mosaic virus* (TuMV), *Potato virus Y* (PVY), *Soybean mosaic virus* (SMV), and *Dasheen mosaic virus* (DsMV). Originally, ArLV was thought not to have any

detrimental effect on infected plants. However, a number of trials conducted in France and Italy have demonstrated that it has a distinct depressive effect on the crop. Recent studies have shown that accessions of *C. cardunculus* and *C. syriaca* are susceptible to ArLV, whereas an interspecific hybrid between these two species has a high level of resistance (Manzanares *et al.*, 1995). It is worth mentioning that ArLV does not seem to occur in Albania, Yugoslavia, Slovenia, Lebanon, Portugal and Greece (Rana *et al.*, 1982; Baricevic *et al.*, 1995). In Apulia, ArLV has been found in *Petunia hybrida* in mixed infection with CMV (Di Franco and Gallitelli, 1985).

Bean yellow mosaic virus (BYMV). This virus was initially recorded from globe artichoke by Russo and Rana (1978) in Apulia (southern Italy) and later in Greece (Rana and Kyriakopoulou, 1980). Apulian artichokes were also infected by BBWV and ArLV and showed vein yellowing, yellow flecking and line patterns on the leaves. These symptoms closely resembled those characterizing the aetiologically undetermined "mosaic" described by Gigante (1951), and the yellow mottle from Campania and Apulia with which BBWV was associated (Rana *et al.*, 1987b). In artificial inoculation tests, a BYMV isolate from cv Castellammare, maintained in broad bean, was unable to infect globe artichoke seedlings of cvs Mazzaferrata and Vert globe systemically but caused only erratic local lesions (Russo and Rana, 1978). The same BYMV isolate was purified from broad bean and the cytopathology of infected *Vicia faba*, was typical of that induced by potyriviruses (Russo and Rana, 1978).

Turnip mosaic virus (TuMV) was isolated in southern Italy (Sardinia and Apulia) from symptomless artichoke plants of cvs Spinoso sardo (Foddai *et al.*, 1993) and Brindisino (D. Gallitelli, M. Padula and M. Finetti-Sialer, unpublished information), which were also infected by ArLV. The artichoke isolate of TuMV has particles *ca* 730 nm long that could be decorated by an antiserum to a German isolate of the virus. The incidence of TuMV infections and their economic importance, if any, have not been determined.

Carlaviruses. *Artichoke latent virus M* (ArLVM) was found in Apulia in mixed infection with one or two of the following viruses: AILV, AMCV, ArLV (Di Franco *et al.*, 1989). Virus particles in leaf dip preparations from naturally infected globe artichoke leaves measured 697 nm in length and contained a single species of RNA with an estimated size of *ca* 7.5 kb and a coat protein with an Mr of 31,000. ArLVM was not associated with any particular symptom in the field and was not mechanically transmitted to a number of hosts (*C. quinoa*, *C. amaranticolor*, *Cucumis sativus*, *Cucurbita pepo*, *C. scolymus*, *G. globosa*, *N. benthamiana*, *N. clevelandii*, *N. megalosiphon*, *N. tabacum* cvs White Burley and Xanthi, and *Phaseolus vulgaris* cv La Victoire). In immuno-elec-

tron microscopy tests, ArLVM was weakly decorated by antisera to *Carnation latent virus* (CarLV) and *Poplar mosaic virus* (PopMV), both members of the genus *Carlavirus*. The cytopathology of globe artichoke cells infected by ArLVM did not differ from that induced by other carlaviruses in their hosts. The cells contained complex cytoplasmic inclusions composed of deranged organelles, lipid droplets and accumulations of membranes (Di Franco *et al.*, 1989). ArLVM is a tentative species in the genus *Carlavirus* (Adams *et al.*, 2004).

Artichoke latent virus S (ArLVS) was probably identified for the first time in symptomless Californian artichoke plants (Costa *et al.*, 1959), although no information was given on virus particle length and cytopathology. Two viruses causing the same symptoms as those induced by ArLVS in three herbaceous hosts (*C. amaranticolor*, *N. clevelandii*, and *Zinnia elegans*) were later found in symptomless globe artichoke plants in Apulia (Majonara and Rana, 1970b) and Morocco (Fischer and Lockhart, 1974b). The particle lengths of these viruses were 678 and 674 nm, respectively. There is no evidence that a virus found in Brazil in symptomless artichoke plants (Costa and Camargo, 1969; Kitajima *et al.*, 1970) was the same as ArLVS as infected plants contained the cylindrical inclusions (pinwheels and laminated aggregates) typical of potyviral infections. However, degenerated artichoke plants from Spain (Peña-Iglesias and Ayuso-Gonzales, 1972), were possibly infected by ArLVS (or another carlavirus) and a potyvirus because infected cells had cytopathological modifications suggestive of the simultaneous presence of a carlavirus and a potyvirus. No antiserum to ArLVS is available. ArLVS is a tentative species in the genus *Carlavirus* (Adams *et al.*, 2004).

Unnamed putative carlavirus. A virus with filamentous particles was isolated in Apulia from symptomless globe artichoke plants of cvs Terom and Romanesco obtained by *in vitro* meristem tip culture. Its biological, physico-chemical, and cytopathological properties resembled those of members of the genus *Carlavirus* (Rana *et al.*, 1989). This virus differed from ArLVM because of its sap-transmissibility to herbaceous hosts, genome size (7.7 kb versus 7.5 kb), coat protein subunit size (29,000 versus 31,000 Da), and particle length (664 nm versus 697 nm). Like ArLVM, it was serologically related to PopMV. However, the relationship was distant enough (SDI = 4-5), to support its identification as an artichoke isolate of PopMV, as suggested by Rana *et al.* (1989). Since the characterization of the virus has not been completed, its taxonomic allocation has remained undetermined. Thus this virus does not appear among recognized carlavirus species (Adams *et al.*, 2004).

Potexviruses. *Potato virus X* (PVX) was isolated in Tunisia by Chabbouh (1989) from artichoke plants showing mosaic, leaf deformation and a strong reduc-

tion in size of the leaf blade. The virus was mechanically transmitted to a number of herbaceous hosts and identified serologically. Cytopathological alterations were those expected in cells infected by PVX.

Artichoke curly dwarf virus (ACDV) is currently classified as a tentative species in the genus *Potexvirus* (Adams *et al.*, 2004). It was recovered by Leach and Oswald (1950) and Morton (1961) in California (USA) from stunted artichoke plants with distorted leaves, variously extended vein necrosis, delayed flower head development, and low quality crop. Mechanically inoculated artichoke and cardoon seedlings reproduced the field syndrome (Leach and Oswald, 1950). ACDV is poorly characterized; its particles are filamentous, 582 x 15 nm in size. Its epidemiology is unknown. In California, this virus was reported to occur consistently in mixed infections with another virus with longer filamentous particles (Morton, 1961) that may be the same as the putative carlavirus ArLVS.

Artichoke degeneration virus (ADV) is a virus with filamentous particles that infects globe artichokes in Spain. It was identified by Peña-Iglesias and Ayuso-Gonzales (1972) in dwarfed plants of cv Tudela with mottling, curling and crinkling of the leaves. Virus particles from partially purified preparations had an estimated length of 585 nm. The cytopathology of infected cells resembled that induced by potexviruses. Attempted transmissions by aphids were unsuccessful. According to Peña-Iglesias and Ayuso-Gonzales (1972), ADV and the putative potexvirus ACDV are not the same. This, however, was not ascertained experimentally. In any case, the information available on ADV is too limited to allow its classification. Thus, ADV was not included among tentative potexvirus species (Adams *et al.*, 2004).

Criniviruses. In California, natural infections by *Tomato infectious chlorosis virus* (TICV) were detected in artichoke and weeds (*Nicotiana glauca*, *Picris echioides*) that were host to high populations of *Trialeurodes vaporariorum* (www.eppo.org/QUARANTINE/Alert_List/viruses/tmicxx.htm). Known in the USA since 1993, TICV elicits interveinal yellowing and necrosis of the leaves of tomato plants. Symptoms in artichoke are undetermined. In Italy, TICV was recorded from tomato plants in Liguria, Sardinia, Latium, and Campania. The virus is transmitted by *T. vaporariorum* but not by *Bemisia tabaci*, and is included in the EPPO alert list as it is regarded as an emerging pathogen with a high potential to have an economic impact.

FILAMENTOUS VIRUSES AND GLOBE ARTICHOKE DEGENERATION DISEASE

Under the name of degeneration of globe artichoke, disorders characterized by foliar mottling, leaf deforma-

tion and crinkling, stunting and decreased yield have been reported from several countries of the Mediterranean region. Common to all these diseases are the progressiveness of the degenerating condition, which becomes increasingly severe as the crop ages, and the consistent presence of filamentous viruses of one kind or another in diseased plants (Marrou and Mehani, 1964; Pochard *et al.*, 1964; Mehani 1969; Peña-Iglesias and Ayuso-Gonzales, 1972, Welvaert and Zitouni, 1974, Welvaert and Van Vaenenberg, 1981). That artichoke degeneration is only of virus origin was questioned by Welvaert and Zitouni (1974) and Welvaert and Van Vaenenberg (1981), who suggested the possible involvement of bacteria and perhaps other undetermined biotic factors. Since no real advances have been made in establishing its nature, artichoke degeneration remains an ill-defined disease. Nevertheless, viruses seem to figure largely in its aetiology due to the consistent presence of infections by multiple agents of diverse taxonomic position. In this connection, the identification of individual filamentous "latent" viruses reported in the literature as single different potyviruses, carlaviruses or potexviruses is not always substantiated by unequivocal experimental evidence and may be incorrect.

VIRUSES WITH RIGID ROD-SHAPED PARTICLES

The presence of *Tobacco mosaic virus* (TMV, genus *Tobamovirus*) in symptomless and apparently unaffected *C. cardunculus* was recorded by Lisa (1971) in Piedmont (Italy). The cardoon isolate of TMV is serologically identical to its so-called tomato strain, now classified as *Tomato mosaic virus* (ToMV) (Brunt, 1986). Thus this artichoke virus should be reclassified as ToMV.

Tobacco rattle virus (TRV), the type species of the genus *Tobravirus*, was isolated by Chagas *et al.* (1969) and Chagas and Silberschmidt (1972) in Brazil (Sao Paulo State) from globe artichoke plants with a disease characterized by bright yellow discoloration of the leaves. The virus could not be transmitted back to artichoke seedlings by mechanical inoculation but was transmissible by *Trichodorus christiei* (Salomao, 1976). Virus particles were 25 nm thick and had two main lengths, 200 and 55 nm. Another TRV isolate was found in France in mixed infections with ArLV and BBWV in globe artichoke plants of cv Camus de Bretagne by Migliori and Marzin (1985). The French TRV was recognized by antisera to the following TRV isolates: PRN, CAM and *Solanum nigrum* L. (Migliori and Marzin, 1985). The French TRV isolate was transmitted by *Trichodorus primitivus*. A natural source of inoculum for it is *S. nigrum*, a weed which was identified in an artichoke field in Sicily as a host of an Italian isolate of TRV, transmitted by *Paratrichodorus tunisiensis* (Roca and Rana, 1981).

VIRUSES WITH ENVELOPED PARTICLES

Globe artichoke-infecting viruses with enveloped particles are members of the genus *Tospovirus*, family *Bunyaviridae*, or of the family *Rhabdoviridae*.

Tomato spotted wilt virus (TSWV) was first recorded from Argentina (Gracia and Feldman, 1978), where it was observed in artichoke plants with yellowing and withering of the leaves. The virus is also present in Australia (Martelli *et al.*, 1981) and was isolated in southern Italy from artichokes cv Catanese and from seed-propagated cultivars. Infected plants showed severe stunting, generalized chlorosis and bronzing of the apical leaves, distortion of the head stalk, and necrosis of more or less extended portions of the inner and outer scales (Vovlas and Lafortezza, 1994; Camele and Rana, 1999). TSWV is transmitted in a persistent manner by several thrips species, among which *Frankliniella occidentalis* is the most efficient. The physico-chemical properties of the virus were described by Ie (1970), and the cytopathology of its infection in globe artichoke was investigated by Gracia and Feldman (1978) and Vovlas and Lafortezza (1994). In Apulia, infection by TSWV is very detrimental because of the severity of the disease and the fact that infected artichoke plants form inoculum reservoirs for transmission by thrips to other susceptible crops.

Cynara virus (CraV) was first observed in degenerated globe artichokes in Spain (Peña-Iglesias *et al.*, 1972) and then in *C. scolymus* and *C. syriaca* in Apulia (Russo *et al.*, 1975). CraV particles are bacilliform, enveloped, measure 170-260 nm (modal length = 243 nm) x 60-65 nm, and are localized within dilations of the endoplasmic reticulum, from which they appear to acquire the envelope (Peña-Iglesias *et al.*, 1972; Russo *et al.*, 1975; Rana *et al.*, 1988). Thus, in principle, CraV could be classified in the genus *Cytorhabdovirus*, but the limited knowledge of its properties has suggested its inclusion among the unassigned species in the family (Walker *et al.*, 2000). CarV has always been found in mixed infections, with an unidentified potyvirus (ArLV?) in Spain (Peña-Iglesias *et al.*, 1972) and, in Apulia, with filamentous particle (ArLV or BYMV) and isometric particle viruses (AILV or BBWV) (Russo *et al.*, 1975). The virus has an experimental host range virtually restricted to plants in the Solanaceae (Rana *et al.*, 1988); a good host for maintaining virus cultures and from which to purify the virus is *Nicotiana langsdorffii*. An antiserum to CraV with a titre of 1:16-1:64 (Rana *et al.*, 1988) did not decorate Ivy vein clearing virus, another cytoplasmic rhabdovirus (Castellano and Rana, 1981) classified as unassigned species to the family *Rhabdoviridae* (Walker *et al.*, 2000).

EFFECT OF VIRUS INFECTION ON THE CROP

Although there is no doubt that virus infections have a detrimental effect on the growth and yield of artichoke plantings, as exemplified by the degenerating condition reported from many countries, detailed information on the damage caused by single viruses is limited. ACDV was reported to induce a 25% reduction in the yield of marketable heads in Californian artichoke crops (Morton, 1961).

Comparative trials carried out in France and Italy on some cultivars (Camus de Bretagne, Spinoso Sardo, and Brindisino) and hybrids (Talpiot, H137, and H044) artificially infected with one or two viruses showed that ArLV causes significant reductions of the number and size of marketable heads (and thus yield), premature opening and colour breaking of head scales, and shortening of the head stalk. In particular, yield losses varied from 38 to 53% and were accompanied by delayed harvesting (Foddai *et al.*, 1983a, 1983b; Migliori *et al.*, 1987; Rana *et al.*, 1992; Camele *et al.*, 1999). Field control trials for preventing the spread of ArLV in cv Spinoso sardo showed that treatments with deltamethrin and mineral oils reduced the infection from 32% (control) to 7% (treated plots) over a three-year period.

Migliori *et al.* (1987) showed that single infections by BBWV, CMV and TBRV in cv Camus de Bretagne caused, respectively, 11, 15 and 19% decrease of the first head weight and a reduction by 19, 29 and 42% of the number of heads per plant.

DIAGNOSIS

Mixed infections are common in globe artichoke, thus making symptom-based diagnosis almost impossible. Most of the plants, even when they are infected by a single virus, do not show distinct symptoms, either because infections are latent or because symptom expression is influenced by factors such as varietal reactions, environmental conditions, agronomic practices and plant age.

The use of herbaceous indicators may only occasionally be of help since many of the viruses found in globe artichoke share a common host range and often induce similar symptoms in the same host. Although the use of an extended host range can sometimes allow a rough identification of the virus in question, biotests are time- and labour-consuming and demand space and controlled environment facilities in order to be done properly. Thus, the use of herbaceous indicators is usually restricted to those viruses for which no serological or molecular detection tools are available.

Serology has been used in several circumstances either as gel diffusion tests or ELISA (Migliori *et al.*, 1989; Foddai *et al.*, 1992). ELISA has become very popular because of its distinct advantage over immunodiffu-

sion, but it is not free of drawbacks. Artichoke sap oxidizes rapidly, which often causes borderline results, especially when antigen concentration is very low, so that background readings prevent differentiation between infected and healthy samples.

Because virus distribution in the host may vary with the season, the success of any detection technique is strongly dependent upon the choice of an appropriate time for sampling. In our experience collecting samples between the beginning of September and mid-November from young leaves of at least one-year-old artichoke plants, gives the best and most reproducible results (Repetto *et al.*, 1997).

Electron microscopy (EM) has been used extensively, as viruses that infect artichoke may occur in a sufficiently high concentration (e.g. AMCV, TMV) in the host tissues to be seen in leaf-dip mounts and identified by immune electron microscopy (IEM) (Milne and Luisoni, 1977). Immunosorbent electron microscopy (ISEM) (Derrick, 1973) has also been successfully applied to samples containing low amounts of virus. EM-based diagnosis has been further modified by using various decoration techniques and, in particular, gold-conjugated antibodies. Finally, as cytopathological alterations may be specific at the genus or the species level, observation of thin-sectioned tissues can prove useful for preliminary identification (Martelli and Russo, 1977, 1984).

Accurate diagnosis combined with rapid and early virus detection can be accomplished by using nucleic acid-based assays. Cloning of virus nucleic acid and the development of non-radioactive detection methods have increased the use of hybridization techniques. For artichoke, dot blotting represents a suitable assay for routine tests and sanitary certification schemes. In a dot blot protocol developed in our laboratory (Gallitelli and Saldarelli, 1996; Repetto *et al.*, 1997), artichoke tissues are crushed in an alkaline solution that prevents oxidation, spotted onto a positively-charged Nylon membrane, and hybridized with digoxigenin-labeled riboprobes. Since mixed infections are very common in artichoke, specific probes contained in the same hybridization solution must be used for each individual virus (Saldarelli *et al.*, 1996).

Diagnostic tools for artichoke viruses that can identify multiple infections reliably in a single test are highly desirable. The polymerase chain reaction (PCR) has this potential. Grieco and Gallitelli (1999) have described a method for the independent amplification of genome sequences of ArLV, AILV and AMCV (i.e. three viruses belonging to different genera) in a six primer-driven reverse transcriptase-PCR (RT-PCR) using samples in artichoke plant sap. This allowed the simultaneous and specific identification of each virus with a single test. In this RT-PCR protocol, antisense primers for the synthesis of first strand cDNA using a viral RNA template, represented the most crucial factor for obtaining specific

amplification. To ensure high specificity, even at the strain level, these primers were selected within regions of the genome that differed greatly among members of the same taxon.

Although the procedure described by Grieco and Gallitelli (1999) had several advantages it did not completely overcome the problem of detection of mixed infections in artichoke plant sap. For example, the limit of sensitivity was lower than that reported for other virus-hosts combinations since detection limits in *ca* 70 ng leaf tissue were 400 fg of AMCV and ArLV RNAs but only 4 pg of AILV RNA. This may have been due to the simultaneous presence of primers and templates competing for the same reagents during first strand cDNA synthesis and its subsequent amplification. Another critical factor was plant sap concentration. Amplified fragments were seen only when artichoke sap was diluted 10³-fold prior to being added to the reaction. With sap diluted 10²-fold, the reaction did not proceed.

An additional possible source of problems was the relative concentration of each viral template in naturally infected plant tissue samples. In mixed infections, different amounts of each virus are likely to occur, especially if the viruses belong to different taxonomic groups. This may selectively drive the reaction in favour of one virus and mask the presence of other viruses.

Although PCR has the potential for sensitive specific and reliable detection/identification of artichoke viruses, the detection and characterization of amplicons requires downstream analysis (e.g. gel electrophoresis, Southern blotting, sequencing), which can make the technique less appealing for large-scale routine diagnosis.

Very recently, novel PCR technologies, relying on fluorescence resonance energy transfer (FRET) (Nazarenko *et al.*, 1997) between a fluorophore and a proximal quencher molecule, combined with automated fluorescent amplicon detection have been developed. With these methods, dual-labeled probes hybridize to an amplicon and changes in the quenching of the fluorophore are detected in "real time" by a fluorimeter coupled with the thermocycler. TaqMan (Holland *et al.*, 1991; Lee *et al.*, 1993), Molecular Beacons (Tyagi and Kramer, 1996) and Scorpion (Whitcombe *et al.*, 1999), are some of the formats of real-time PCR. Finetti-Sialer *et al.* (2000) have used the Scorpion-RT-PCR to detect TSWV in naturally infected artichoke plants. Amplified products of the expected size were detected either by real time measurements or by visual estimation of fluorescence emission from tubes placed over an ultraviolet light source at the end of the reaction. In serially diluted plant sap, the method allowed the detection of 7.5 pg of infected plant tissue and proved to be at least as sensitive as visual estimation of ethidium bromide-stained amplicons separated by gel electrophoresis. The use of different fluorophores for different viruses may allow multiple detection in the same test.

SANITATION

The detrimental effects of virus infections on the quantity and quality of the yield highlight the importance of establishing new artichoke fields with virus-free propagation material.

In the past, two approaches, often used in combination, were followed to free artichoke plants from viruses namely thermotherapy and *in vitro* culture of shoot tips or tissues excised from young head receptacles. Encouraging, but not conclusive, results were obtained with both techniques (Marras *et al.*, 1982; Pecaut *et al.*, 1985).

Better results were achieved with meristem tip culture (Peña-Iglesias and Ayuso-Gonzales, 1974; 1982, Harbaoui *et al.*, 1982). However, virus elimination through meristem tips can have a detrimental effect on the flowering behavior of the sanitized crop. For example, with cvs Brindisino, Violetto di Provenza and Catanese, meristem tip culture caused loss of earliness, an essential trait for the highest market value. The causes of such a change for the worse are unknown but it was speculated that the high hormone level used in tissue culture could have interfered with the physiology of the plants. Moreover, it was recently shown that meristem tip culture can eliminate ArLV (Pasquini *et al.*, 2003; Papanice *et al.*, 2004) but not AILV (Papanice *et al.*, 2004). However, AILV can be eliminated by exposing off shoots from infected plants to 38°C for 60 days, followed by excision and growing the meristem tips *in vitro* (Papanice *et al.*, 2004). Although the effect of this type of treatment on the preservation of earliness is still under evaluation, *in vivo* thermotherapy followed by meristem tip culture seems to be a suitable technique to obtain virus-free stocks of early flowering cultivars.

Propagation from seed, which has been regarded as an attractive way to obtain virus-free plants, may not represent a suitable solution, because many of the artichoke-infecting viruses are known to be seed- and pollen-transmitted in other plants in the *Compositae* and may behave similarly in artichoke. For instance, AILV and ArLV were detected in the seed coats and fully expanded cotyledons of artichoke seedlings, and AILV was also detected in the first true leaf (5-6 cm in length). Infection rates were in the range of 5-10% for both viruses (Bottalico *et al.*, 2002a,b).

CONCLUDING REMARKS

Since the last review (Martelli *et al.*, 1981), knowledge of viruses and virus diseases of globe artichoke and cardoon has undergone significant advances. Many of the viruses have been characterized at the molecular level and highly sensitive diagnostic tools have been developed. However, the role of many viruses in the aetiology of specific diseases is still undetermined, and whether or

not they can affect the yield, and to what extent, are equally unknown.

Because there is a progressive tendency to move from classical pluriennial vegetatively propagated crops to seed-propagated crops that remain in the field for no longer than a couple years, it is likely that the economic importance of virus infections will also tend to decrease in the future. In fact, the perpetuation of high infection rates in newly established plantations is primarily due to the use of off-shoots originating from sanitarly uncontrolled mother plants, which, at the most, have undergone a superficial visual selection by the farmers. The availability of certified healthy seed should decrease inoculum potential and, in the long run, have a beneficial effect on the overall level of infection.

In the meantime, some aspects of the infection pathway need to be elucidated. Transmissibility of major viruses through true seeds should be investigated, incidence and distribution of natural sources of inoculum in different environments should be identified, and the length of incubation period of single and mixed infections should be determined. This kind of information is essential if any prediction is to be made of the impact of inoculum potential on the rate of re-infection of sanitized plants.

All this leads to the conclusion that studies on artichoke virology, which are somewhat stagnating, except for the perennial interest shown by two or three laboratories, should resume momentum and also be directed towards practical applications of the extant achievements of research.

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