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Review

Advances and prospects in biogenic substances against plant virus: A review

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ABSTRACT

Plant virus diseases, known as 'plant cancer', are the second largest plant diseases after plant fungal diseases, which have caused great damage to agricultural industry. Since now, the most direct and effective method for controlling viruses is chemotherapeutics, except for screening of anti-disease species. As the occurrence and harm of plant diseases intensify, production and consumption of pesticides have increased year by year, and greatly contributed to the fertility of agriculture, but also brought a series of problems, such as the increase of drug resistance of plant pathogens and the excessive pesticide residues. In recent years, biopesticide, as characterized by environmentally safe due to low residual, safe to non-target organism due to better specificity and not as susceptible to produce drug resistance due to diverse work ways, has gained more attention than ever before and exhibited great development potential. Now much progress has been made about researches on new biogenic anti-plant-virus substances. The types of active components include proteins, polysaccharides and small molecules (alkaloids, flavonoids, phenols, essential oils) from plants, proteins and polysaccharides from microorganisms, polysaccharides from algae and oligochitosan from animals. This study summarized the research advance of biogenic anti-plant-virus substances in recent years and put forward their further development in the future.

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Abbreviations: BMV, brome mosaic virus; ChiVMV, chilli veinal mottle virus; CMV, cucumber mosaic virus; HIV, human immunodeficiency virus; HSV, herpes simplex virus; PAL, phenylalanine ammonia lyase; PRs, pathogenesis-related proteins; PVX, potato virus X; PRSV, papaya ringspot virus; PVY, potato virus Y; RIPs, ribosome-inactivating proteins; RBSDV, rice black-streaked dwarf virus; RSV, rice stipe virus; SA, salicylic acid; SRV, sunn-hemp rosette virus; TBSV, tomato bushy stunt virus; TMV, tobacco mosaic virus; TNV, tobacco necrosis virus; ToMV, tomato mosaic virus; TuMV, turnip mosaic virus; WMV, watermelon mosaic virus.

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1. Introduction

Plant virus diseases, known as 'plant cancer', are the second largest plant diseases after plant fungal diseases, and have caused great damage to agricultural industry. The International Committee on Taxonomy of Viruses published a variety of 950 kinds of plant viruses throughout the world in the Ninth Report [1]. Plant viruses have been a major problem in many crops, vegetables and ornamental plants, which seriously affect product quality and yields of different crops (Fig. 1). Every year throughout the world, plant viruses causes economic losses as much as $60 billion, and the loss of food crop alone has reached to $20 billion [2]. Once virus invades the host, its replication may be integrated with the metabolism of the host plants. It often happens that drugs aiming to inhibit replication of virus may also do harm to the host, thus making it difficult to control plant virus diseases.

Since now, the most direct and effective method for controlling viruses is chemotherapeutics, except for screening of anti-disease species. As the occurrence and harm of plant diseases and insect pests intensify, production and consumption of agricultural agents have increased year by year, and greatly contributed to the fertility of agriculture. The 1930s successively witnessed the new creation of high reactive DDT, organochlorine and organophosphorus and so on. From then on, control of agricultural pathogens and pests was usually based on synthetic organic pesticides. Pesticides have the advantages of increasing yield, saving labor, reducing risk of fertilizer use [3], but have also brought a series of problems, such as the increase of drug resistance of plant pathogens and environmental pollution, the excessive pesticide residues, the explosion of poisoned human and animals and also the declining quality of agricultural products [4,5]. But in 1960s, high toxicity and residue of synthetic organic pesticides caused more and more serious consequences and even threatened human health [4,5]. Carson [6] exaggeratively described the damage of chemical pesticides to human in her book *Silent spring*. Since then, there formed growing calls to improve pesticides and preserve the ecological environment. In the 21st century, with relative lower toxicity and less residue, chemical pesticides are still predominantly used, and have become one of the most important inputs in crop, with the application amount up to 3 billion kg annually [7]. Meanwhile, the problems caused by chemical pesticides are still severe [8]. Pimentel [7] estimated the annual indirect costs caused by pesticides in the U.S. of about $1.1 billion due to adverse impact on public health, $1.5 billion due to pesticide resistance, $1.4 billion due to crop loss, $2.2 billion due to bird loss, and $2 billion due to ground water contamination.

In recent years, the rapid development of science and technology, especially the development of biotechnology, biology and chemistry of natural product, have greatly pushed forward the development of biogenic pesticides. Biopesticide, as characterized by environmentally safe due to low residual, safe to non-target organism due to better specificity and not as susceptible to produce drug resistance due to diverse and synergetic work ways, has gained more attention than ever before and exhibited great development potential. The production of biopesticide is currently growing at 16% per year, almost three times as that of conventional agrochemicals which is growing at a rate of 5.5% per year [9]. Now much progress has been made about researches on new biogenic anti-plant-virus substances. The types of active components include proteins, polysaccharides and small molecules (alkaloids, flavonoids, phenols, essential oils) from plants, proteins and polysaccharides from microorganisms, polysaccharides from algae and oligochitosan from animals [10–15]. These compounds are highly active, highly specific, with less environmental pollution and less residual. This study summarized the research advance of biogenic anti-plant-virus substances in recent years and put forward their further development in the future.

2. Biogenic anti-plant-virus substances from plants

2.1. Abundant plant resources provided for antiviral substances

In 1914, Allard firstly found that juice from pokeberry could suppress viral activity, from then on, focus was gradually shifted to looking for antiviral substances from plant resources [16], which are rich, cost effective and easy to develop. In the world, there are about more than 250,000 known plant species (but actually, maybe up to 500,000), of which, about 10% plant species have been studied for their chemical components [17]. Over the past 50 years, plants have provided key structures and compounds that possess potential applications for industrial development and used as cosmetics, nutritional supplements, fine chemicals, agrochemicals and therapeutic agents for a variety of diseases [18]. Grange et al. [19] reported that there are about 2400 plant species which possess inhibition activities against detrimental bio-organisms. In 1989, out from more than 500 Chinese medicinal herbs, Zhu and Qiu [20] screened 30 species that are antiviral effective against cucumber mosaic virus (CMV), among which, the best control effects were obtained from *Forsythia suspensa* Vahl, *Rheum officinalle* Bail and *Isatis tinctoria* L extracts. Over the next 20 years, more and more scientists carried out research on screening of plant materials with anti-plant-virus effects, and many kinds of plants from different families were gradually discovered to have the ability of inhibiting viruses, the discovered families including Amaranthaceae, Nyctaginaceae, Asteraceae, Chenopodiaceae, Asclepiadaceae, Polygonaceae, Simaroubaceae, Acanthaceae, Liliaceae, Cruciferae, Leguminosae sp., Boraginaceae, Oleaceae, Taxaceae, Ranunculaceae, Juglandaceae, Saxifragaceae, Theaceae, Schisandraceae, Cupressaceae, Labiatae and Caryophyllaceae and so on [21–23]. Details about antiviral substances from plant resources are shown in Table 1.

2.2. Antiviral components from plants

Plants contain plenty of polysaccharide, protein, alkaloids, anthocyanins, carotenoids, flavonoids, phenolic acids and many other phytochemicals [24,25]. Some kinds of secondary metabolites with specific bioactivities in plants are formed after a long period of competition for survival and resistance to stresses. Swain [26] reported that there are more than 400,000 kinds of secondary metabolites in plants, most of which possess antiviral, anti-inflammation, antibacterial, antifungal and anti-cancer activities [27]. And they are widely used in medicine for health care and curing diseases [28,29]. Among all of the antiviral substances, protein accounts for the largest number, followed by alkaloids, flavonoids, phenols, essential oils and polysaccharides (see Table 1).

2.2.1. Proteins

Plants usually produce defense-related proteins upon infection with pathogens such as viruses, fungi, oomycetes, and bacteria [30]. Several types of these proteins have been classified into 17 families of pathogenesis-related proteins (PRs) [31]. Others formed more specifically in

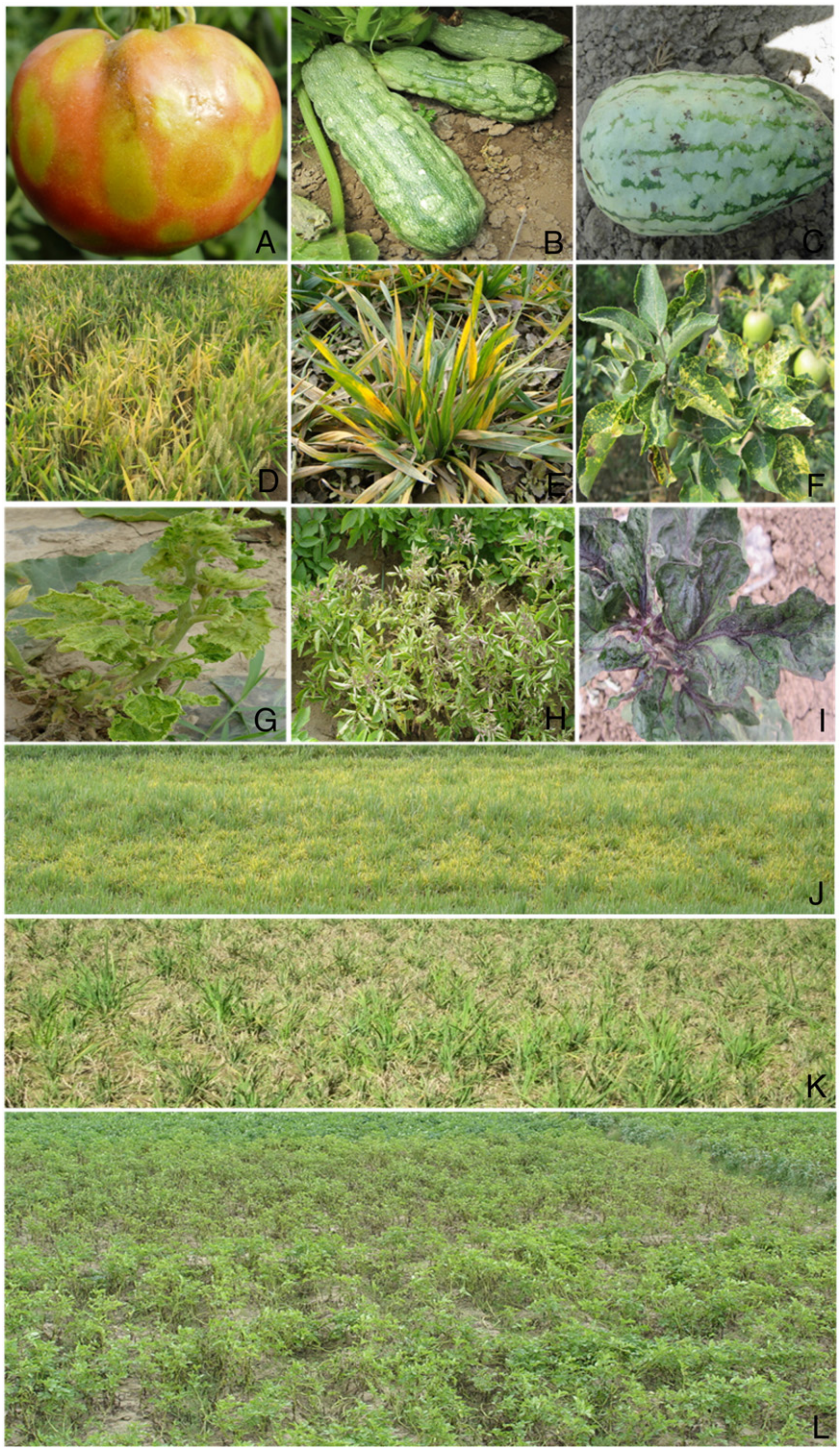


Fig. 1. The harm of virus diseases on different crops. A: Symptom of tomato spotted wilt virus (TSWV) on tomato fruit; B: symptom of zucchini yellow mosaic virus (ZYMV) on zucchini fruit; C: symptom of watermelon mosaic virus (WMV) on watermelon fruit. D: Symptom of barley yellow dwarf virus (BYDV) on wheat; E: wheat yellow mosaic virus (WYMV) on wheat; F: symptom of apple mosaic virus (ApMV) on apple plants; G: ZYMV on zucchini; H: symptom of potato leaf roll virus (PLRV) on potato; I: symptom of CMV on eggplant; J: WYMV in the wheat field; K: symptom of rice black streaked dwarf virus (RBSDV) in the rice field; L: symptom of PLRV in the potato field.

some certain plant species have also been reported, including cell wall hydroxyproline-rich glycoproteins, amylases, polygalacturonase-inhibiting proteins, glycine-rich proteins, lipase-like gene products, lipoxygenases, lectins, cysteine-rich peptides and ribosome-inactivating proteins (RIPs) [30]. Rosario et al. [31] reported the antiviral protein Beetin 27, which is a ribosome-inactivating protein (RIP) from sugar beet (*Beta vulgaris* L.) leaves and induced by virus and signaling compounds such as hydrogen peroxide and salicylic acid (SA), displayed biological activities in vitro that could result in a broad action against several types of pathogens. Its role as a defense protein has been attributed to its RNA polynucleotide: adenosine glycosidase activity. Nandlal et al. [32] Cloned and expressed another antiviral/ribosome-inactivating protein from *Bougainvillea xbuttiana* and found it exhibited a high level of resistance against tobacco mosaic virus (TMV). Frank et al. [33] also found several elderberry ribosome-inactivating proteins with better anti-TMV activity. Aparana et al. [34] purified CAP-34, a systemic

Table 1
Details about anti-plant-virus components extracted from all kinds of plants throughout the world.

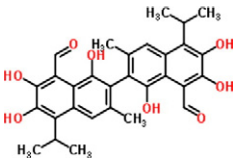
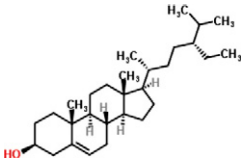
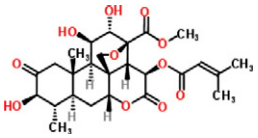
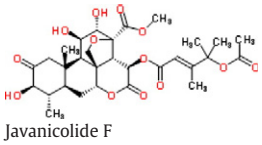
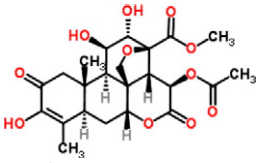
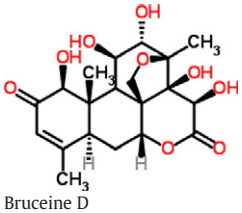
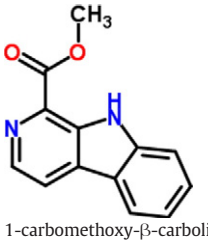
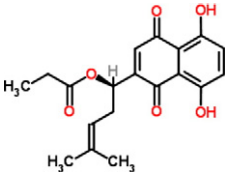
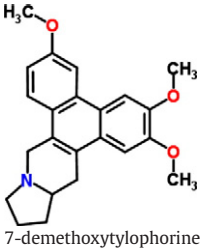
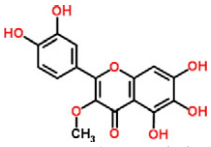
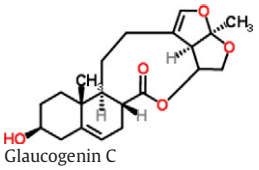
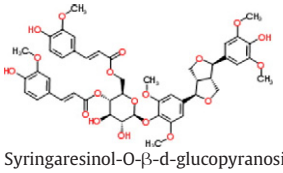
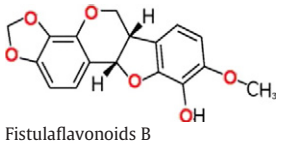
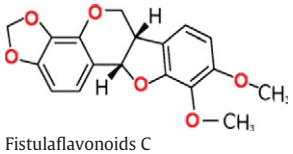
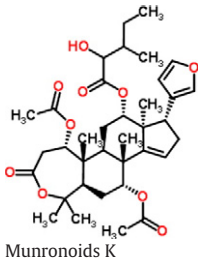
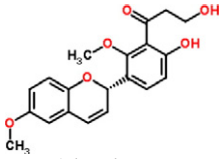
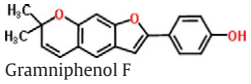
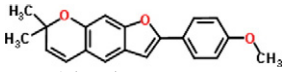
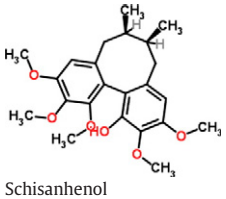
Family	Species	Active ingredients	Virus	Reference
Phytolaccaceae	*Phytolacca americana* L.	Protein	BMV, CMV	[10,117]
Malvaceae	*Gossypium spp.*	 Gossypol	TMV, RBSDV, RSV	[12]
		 β-sitosterol		
Chenopodiaceae	*Beta vulgaris*	Protein	TMV	[31]
	Spinacia oleracea L.	Leaf juice	TMV	[118]
	Chenopodium amaranticolor	Leaf extract	TNV	[119]
	Chenopodium album L	Protein	TMV	[120]
	Chenopodium serotinum L.	Whole plant extract	TMV	[121]
Liliaceae	*Hosta plantaginea* Aschers	 7-deoxytrans-dihydronarciclasine	TMV	[45,121]
Amaranthaceae	*Celosia cristata* L.	Glycoprotein	TMV, SRV, CRSV	[36]
Simaroubaceae	*Ailanthus altissima*	Leaf extract	RSV	[122]
	Brucea javanica (L.) Merr.	 Javanicolide E	TMV, CMV, PVY	[46,47]
		 Javanicolide F		
		 Bruceine B		
		 Bruceine D		
	Picrasma quassioides		TMV	[48]

Table 1 (*continued*)

Family	Species	Active ingredients	Virus	Reference
		 1-carbomethoxy-β-carboline		
Nyctaginaceae	*Mirabilis jalapa* L.	Protein, root extract	TMV, CGMMV, PVY, TuMV, CMV	[123]
	Bougainvillea xbuttiana	Protein	TMV	[32]
Taxaceae	*Taxus cuspidata*	Bark extract	CMV	[124]
Boraginaceae	*Lithospermum erythrorhizon*	 Propionylshikonin	TMV	[125]
Polygonaceae	*Rheum palmatum* L.	Whole plant extract	ToMV	[126]
Asclepiadaceae	*Cynanchum komarovii* Al	 7-demethoxytylophorine	TMV	[49]
	Centaurea rupestris L.	 Quercetagetin 3-methyl ether	TBSV	[52]
	Bidens pilosa	Flavonoid glycoside	TMV	[127]
	Arctium lappa L.	Fructooligosaccharide	TMV	[78]
	Eupatorium adenophorum	Leaf extract	TMV	[115]
	Artemisia argyi H. Lév. & Vaniot	Essential oil	TMV	[62]
	Lactuca tatarica (Linn.) C.A. Mey	Whole plant extract	TMV	[21]
	Syneilesis aconitifolia (Bge.) Maxim.	Whole plant extract	TMV	[21]
Rosaceae	*Chaenomeles sinensis* (Thouin) Koehne	Fruit extract	TMV	[21]
	Rubus flosculosus Focke	Whole plant extract	TMV	[21]
Leguminosae	*Thermopsis lanceolata* R. Br.	Leaf extract	TMV	[21]
Juglandaceae	*Juglans regia*	Leaf extract	TMV	[128]
Acanthaceae	*Strobilanthes cusia*	 Glaucogenin C	TMV	[14]
Anacardiaceae	*Rhus javanica* L. var. roxburghiana (DC.) Rehd. & Willson	 Syringaresinol-O-β-d-glucopyranoside	TMV	[129]
	Cotinus coggygria Scop.	Leaf extract	TMV	[21]
Saxifragaceae	*Rodgersia podophylla* A. Gray	Whole plant extract	TMV	[21]
Ranunculaceae	*Semiaguilegia adoxoides* (DC.) Makino	Earthnut extract	TMV	[131]
	Pulsatilla chinensis (Bunge) Regel	Leaf, root, stem extract	TMV	[21]
Brassicaceae	*Thlaspi arvense* L.	Whole plant extract	TMV	[21]
Portulacaceae	*Portulaca oleracea* L.	Whole plant extract	TMV	[132,133]
Oleaceae	*Forsythia suspensa* (Thunb.) Vahl	Whole plant extract	CMV	[20]
Papilionaceae	*Cassia fistula*		TMV	[53]

(*continued on next page*)

Table 1 (*continued*)

Family	Species	Active ingredients	Virus	Reference
		 Fistulaflavonoids B		
		 Fistulaflavonoids C		
	Satureja montana L.	Essential oil and phenolic compounds	TMV, CMV	[63]
Caprifoliaceae	*Sambucus williamsii*	Protein	TMV	[33]
Verbenaceae	*Clerodendrum aculeatum*	Protein	PRSV	[34]
Cucurbitaceae	*Momordica charantia* Linn.	Protein	ChiVMV, CMV, TMV, TuMV	[134]
Papilionaceae	*Cyamopsis tetragonoloba* (L.) Taub.	Protein	TMV, SRV, PRSV	[35]
Meliaceae	*Munronia unifoliolata*	 Munronoids K	TMV	[135]
Orchidaceae	*Arundina graminifolia*	 Gramniphenol C	TMV	[56]
		 Gramniphenol F		
		 Gramniphenol G		
	Zingiber officinale	Essential oil	TMV	[62]
Rutaceae	Lemon	Essential oil	TMV	[62]
	Tangerine peel	Essential oil	TMV	[62]
Theaceae	*Camellia sinensis*	Essential oil	TMV	[62]
Crassulaceae	*Rhodiola eurycarpa* (Frod.) S. H. Fu	Whole plant extract	TMV	[21]
	Cymbopogon citratus	Essential oil	TMV	[62]
Poaceae	*Cymbopogon citratus* (DC.) Stapf	Essential oil	TMV	[62]
	Achnatherum splendens (Trin.) Nevski	Whole plant extract	TMV	[21]
Schisandraceae	*Schisandra rubriflora*	 Schisanhenol	TMV	[22]
Cupressaceae	*Thuja orientalis*	leaf, shoot and fruit extract	WMV	[23]

antiviral resistance inducing protein from *Clerodendrum aculeatum* and found its inhibiting effect on papaya ringspot virus (PRSV) infection in *Carica papaya*. Vivek et al. [35] isolated a systemic antiviral resistance inducing protein named CT-VIA-62, which can induce systemic resistance against sunn-hemp rosette virus (SRV) in *Cyamopsis tetragonoloba*. They found that all CT-VIA-62 peptides share homologies with the proteins from *Medicago truncatula* that possess a mannose-binding lectin domain. Balasubrahmanyam et al. [36] isolated CCP-25 and CCP-27 proteins from the leaves of *Celosia cristata*, which showed anti-TMV activities, with suppression rates of 92.4% and 91.8% at the concentration of 30 μg mL^{-1}, respectively. Pokeweed antiviral protein, a heatedly researched antiviral protein at the end of last century, is composed of eight alpha helices and a beta sheet consisting of six strands. It is the main antiviral-active constituent from *Phytolacca americana* L., which exhibits a broad spectrum antiviral activity against TMV, poliovirus, herpes simplex virus (HSV), influenza virus, cytomegalovirus and human immunodeficiency virus (HIV) and so on. It can effectively inhibit replication of viruses at concentrations which do not suppress protein

synthesis of the host cells [37–43]. Other plants in which the anti-plant-virus effective compounds are proteins include *Chenopodium amaranticolor*, and *Mirabilis jalapa* L. (see Table 1).

2.2.2. Alkaloids

Alkaloids are a large group of naturally chemical compounds with diverse structures, many of which have pharmacological effects on human or animals. Alkaloids are usually bioactive constituents contained in many medicinal plants, especially many Chinese herbal medicines. At present, there are more than 18,000 alkaloids that have been discovered [44]. Wang et al. [45] separated 5 new alkaloids from *Hosta plantaginea* Aschers, among which a known alkaloid 7-deoxy-trans-dihydronarciclasine showed strong anti-TMV activity, with IC_{50} value at 1.80 μM. Bruceine-D, a kind of alkaloid extracted from *Brucea javanica* (L.) Merr, exhibited better inhibition effect against potato virus Y (PVY), TMV and CMV [46]. When the concentration of Bruceine-D was 100 μg mL^{-1}, at 15 min after incubation, the inhibition rates for PVY and CMV in *Chenopodium amaranticolor* were 94.2% and 91.7%, respectively, [46]. Yan et al. [47] separated two new quassinoids (javanicolide E and javanicolide F) and fifteen known C-20 quassinoids, all of which showed potent anti-TMV activity. Eight compounds including brusatol, bruceine B, bruceoside B, yadanzioside I, yadanzioside L, bruceine D, yadanziolide A and aglycone of yadanziolide D, showed strong antiviral activities, with IC_{50} values in the range of 3.42–5.66 μM. Chen et al. [48] isolated 10 known β-carboline alkaloids and one quassinoid in MeOH extract from the wood of *Picrasma quassioides* Benn. All of them showed moderate anti-TMV activities and exhibited synergistic effects when combined with nigakilactone B. When these ten β-carboline alkaloids were used alone at the concentration of 50 μg mL^{-1}, the anti-TMV rates varied from 25% to 47.4%. When added 25 μg mL^{-1} of quassinoid, the anti-TMV rates were increased and varied from 36.4% to 68.4% [48]. An et al. [49] isolated two alkaloids with anti-TMV activities from *Cynanchum komarovii* Al Ilginski, i.e., 7-demethoxytylophorine and 7-demethoxytylophorine N-oxide, with inhibition rate of 65% for the former at a concentration of 1.0 μg mL^{-1} and 60% for the latter at 500 μg mL^{-1}.

2.2.3. Flavonoids

Flavonoids have been isolated from diverse plants [50]. They share a common carbon skeleton of two benzene rings, which are joined by a 3-carbon bridge (C6-C3-C6). There are about 10,000 kinds of flavonoids that are currently known [51]. Due to the development of more sensitive analysis methods, the amounts of flavonoids reported continues to increase [50]. Gordana et al. [52] discovered that flavonoid quercetagetin 3′-methyl ether isolated from *Centaurea rupestris* L. showed prominent inhibition effect against tomato bushy stunt virus (TBSV), with the inhibition rate of 99% at the concentration of 1 mg mL^{-1}. Zhao et al. [53] isolated 2 new and 5 known flavonoids, with fistulaflavonoids B and C showing high anti-TMV rates of 28.5% and 31.3% at the concentration of 20 μM, respectively.

2.2.4. Phenols

Phenolic compounds are present in many plants, especially in berries. These kinds of compounds include anthocyanins, procyanidins, ellagitannins and hydroxycinnamates [54]. There are also higher levels of phenols in tea and cotton seed. Phenols have been reported to have many kinds of bioactivities such as free radical scavenging/antioxidant actions, anti-inflammatory effects, anti-carcinogenic properties and anti-microbial activities [55]. In the respect of their antiviral activities, Hu et al. [56] isolated five new phenolic compounds from *Arundina gramnifolia*, among which compounds 1 (Gramniphenol C), 4 (Gramniphenol F) and 5 (Gramniphenol G) showed anti-TMV rates of 48.2%, 35.8% and 32.1% at the concentration of 20 μM, respectively. Zhao et al. [12] isolated gossypol from cottonseed oil sludge, which exhibited good anti-TMV activity. The curative effect of gossypol against TMV was 54.4% at the concentration of 500 μg mL^{-1}. Since now, because of the distinctive antiviral effect and the inexpensive raw material, Cottonseed Oil Sludge extract has been successfully industrialized in China with the brand name of 'ZaiXiChun', which contains gossypol as one of the bioactive components. Wang et al. [22] isolated schisanhenol from *Schisandra rubriflora* and designed a series of derivatives (1–16, 15a-16a, and 15b-16b) by chemical modification. The anti-TMV activity test indicated that Dibromoschisanhenol at 0.25 mM exhibited the strongest protective activity (83.5%), and 14-(3, 5-dibenzyloxy)-benzoyloxyschisanhenol showed a significant curative effect (78.0% at 0.15 mM), which was much stronger than that of the commercial virucide Ningnanmycin at the same concentration (34.3%).

2.2.5. Essential oils

Essential oils are complex mixtures with low molecular weight, which are usually stored in oil ducts, resin ducts, glands or trichomes (glandular hairs) of the plants [57]. Since they are commonly used as flavouring agents in food products, drinks, perfumeries, pharmaceuticals and cosmetics [58,59], consumption of essential oils is increasing all over the world [60]. Known for their antiseptic, fragrant and medicinal properties, essential oils also play an important role in the protection mechanisms of the plants as antivirals, antibacterials, antifungals and insecticides, and so on [61]. Min et al. [62] tested the effect of 29 kinds of plant essential oils on inhibition of TMV and found that oils from ginger, lemon, tea tree, tangerine peel, artemisia and lemongrass had the inhibition rate of more than 50% against TMV at the concentration of 100 μg mL^{-1}. Valerija et al. [63] discovered that carvacrol and thymol were the major compounds of the essential oil extracted from *Satureja Montana* L. ssp. Variegate (Host) P. W. Ball (Lamiaceae) and both of them were biologically active in reducing TMV and CMV infection. When the concentrations were 4.2 mm L^{-1} for carvacrol and 1 mm L^{-1} for thymol, the inhibiting rates were 34.3% and 26.1% respectively against TMV, and 28.3% and 33.2% respectively against CMV.

2.2.6. Polysaccharides

Polysaccharides are carbohydrate molecules that widely exist in plants. These molecules have an extensive range of biological activities and have been widely investigated in recent decades due to their limited side effects, relative low toxicity and broad spectrum of biological activity [64–66]. It has been reported that plant polysaccharides have the capacity of anti-aging, anti-oxidation, anti-rheumatism, immune-strengthening, hypoglycemic, anti-cancer and lipid-lowering activities and so on [67–71]. There are also many reports on some kinds of plant polysaccharides with the bioactivities against viruses from human and animal, such as *Lycium barbarum* polysaccharide [72], sulfated *Chuanminshen violaceum* polysaccharide [73], sulfated *Caesalpinia ferrea* polysaccharide [74], *Achyranthes bidentata* polysaccharide [65], *Eupatorium adenophorum* polysaccharide [75], *Portulaca oleracea* L. polysaccharide [76] and sulfated astragalus polysaccharide [77]. As for anti-plant-virus activities, burdock fructooligosaccharide, isolated from the root tissue of *Arctium lappa*, has been found active in controlling plant virus, which could induce resistance of the plants against TMV and increase the levels of transcription of PR genes (acidic PRs) and defense-related enzymes [(PAL, EC 4.3.1.5), and 5-epi-aristolochene synthase (EAS, EC 2.5.1.35)] genes [78]. In their experiment, burdock fructooligosaccharide reduced the level of TMV-CP transcripts (7.0-fold lower compared with the control) 24 h after inoculation, induced accumulation of hydrogen peroxide (2.2-fold higher) at the 6 h time point and increased the concentration of SA and SA 2-O-b-D-glucoside.

3. Biogenic anti-plant-virus substances from microorganisms

Microorganisms are the most widely distributed organisms and is spread throughout water, soil, air, and the surface and in vivo of all kinds of organisms. Characterized by rapid propagation and diverse biological activities, microorganisms play an important role in material transformation and circulation in the nature [79,80]. Fungi, bacteria

and actinomycetes are the main microorganisms that contain anti-plant-virus substances, and each of them is described as follows.

3.1. Fungi

The main antiviral active components in fungi are polysaccharide, polysaccharide peptide and protein. There are a large number of fungi that can produce polysaccharide and polysaccharide peptide. Fungal polysaccharides and polysaccharide peptide have a wide range of biological activities and have been paid more attention in recent years [64–66]. In the past few years, fungal polysaccharides and polysaccharide peptide with antiviral activities have been extracted from *Coriolus versicolor*, *Coprinus comatus*, *Lentinus edodes* (Berk.) sing, *Pleurotus ostreatus* and *Flammulina velutiper* (Fr.) Sing (Table 2). Coriolus versicolor polysaccharide peptide is the newly discovered fungal polysaccharide peptide exhibiting good anti-TMV effects. The rates of its curative effects upon TMV infection were 85.4% at the concentration of 500 μg mL^{-1} and 64.8% at 100 μg mL^{-1}, respectively (see Fig. 2) [11]. Wang et al. [64] reported that lentinan showed anti-TMV activities with curative rate of 58.7% at the concentration of 10 μg mL^{-1}. It was found that *Coriolus versicolor* polysaccharide peptide and lentinan may promote expression of disease resistance-related enzymes in host plants such as PAL and peroxidase and also that of the PR proteins, thus increasing the plant's resistance and tolerance to diseases [11,64, 81]. Lentinan now has been successfully registered as an anti-plant-virus agent in China and has become industrialization.

For fungi-derived proteins, Kulye et al. [82] selected from plenty of pathogenic fungi with low pathogenicity, and found that *Alternaria tenuissima* can effectively promote plant immunization. They isolated a heat-stable protein with high activity, which may induce resistance of the plant, and simulate the growth metabolism and the immune system of the plant. There are also other fungi that contain antiviral-active proteins, including *Lentinus edodes* (Berk.) sing, *Agrocybe aegerita*, *Flammulina velutipes*, *Pleurotus citrinopileatus* and *Pleurotus eryngii* (Table 2). In addition, crude methanolic extracts of *Neosartorya fischeri* and *Penicillium oxalicum*, also exhibited inhibitory activity toward TMV [83].

3.2. Bacteria

Scince now, researchers have screened some bacteria which can inhibit plant virus and isolated bioactive components from them. Zhou et al. [84] isolated bacterial strain ZH14 from Anxi Oolong, which may produce bioactive proteins with strong resistance to TMV. Shen et al. [85] applied *Pseudomonas fluorescens* CZ to control TMV and obtained better control efficiency. Ju et al. [86] identified an antiviral cyclic peptide against TMV from the cell-free supernatant of *Pseudomonas chlororaphis* O6. Thapa et al. [87] discovered that culture filtrate from *Serratia marcescens* Gsm01 showed anti-CMV activity. Details about anti-plant-virus substances from bacteria resources are shown in Table 2.

3.3. Actinomycetales

The Actinomycetales are composed of approximately 80 genera and produce a diversity of secondary metabolites with great significance in medicine. About more than 50% of the antibiotics identified are extracted from Actinomycetales [88,89]. The most successful researches on anti-plant-virus substances from actinomycetes are those on Ningnanmycin and Cytosinpeptidemycin. Ningnanmycin, isolated from *Strepcomces noursei* var. xichangensis, is a new cytosine nucleoside peptide antibiotic and has been widely applied to agricultural production. Its curative effect upon TMV infection was 58.1% at the concentration of 500 μg mL^{-1} [12]. It was reported that Ningnanmycin may induce the plants to increase resistance to TMV [90]. Cytosinpeptidemycin, isolated from *Streptomyces ahygroscopicus*, showed efficient anti-plant-virus activity [91,92], and has been successfully registered and industrialized as an anti-plant-virus agent in China. In addition, Zhang et al. [93] isolated a novel glycoprotein GP-1 from *Streptomyces sp.* ZX01, with anti-TMV rate of more than 80% at the concentration of 1 mg mL^{-1}, which exhibited potential applications.

4. Anti-plant-virus substances from algae and animals

4.1. Algae

Micro- and macroalgae were one of the first discovered sources of natural compounds that exhibit in vitro anti-HIV activity [94]. Algae include a wide variety of plants that range from diatoms characterized by microscopic and unicellular, to seaweeds extending over 30 m. Reports on the antimicrobial properties of seaweed extracts have been published since the middle of last century [95,96]. Seaweeds polysaccharide, especially polysaccharides from brown algae and sulfated polysaccharides, possess efficient anti-plant-virus activities [97–100]. Alginate, an abundant polysaccharide of brown algae, exhibited inhibition rate of 95% against potato virus X (PVX) at the concentration of

Table 2
Biogenic anti-plant-virus substances from microorganisms.

Cultures	Strains	Active ingredients	Virus	References
Fungus	*Coriolus versicolor*	Polysaccharide peptide	TMV	[12]
	Lentinus edodes	Lentinan	TMV	[64]
	Alternaria tenuissima	Protein	TMV	[82]
	Agrocybe aegerita	Protein	TMV	[135]
	Flammulina velutipes	Protein	TMV	[136,137]
	Pleurotus citrinopileatus	Protein	TMV	[136,137]
	Pleurotus eryngii	Protein	TMV	[136,137]
	Coprinus comatus	Protein, polysaccharide	TMV	[130,138]
	Pleurotus ostreatus	Polysaccharide	TMV	[139]
	Flammulina velutiper (Fr.) Sing	Polysaccharide	TMV	[139]
	Trichoderma pseudokoningii SMF2	Antimicrobial peptide	TMV	[140]
	Neosartorya fischeri	Methanolic extract	TMV	[83]
	Penicillium oxalicum	Methanolic extract	TMV	[83]
Bacteria	*Bacillus cereus* ZH14	Culture filtrate	TMV	[84]
	Pseudomonas fluorescens CZ	Protein	TMV	[85]
	Pseudomonas chlororaphis O6	Peptide	TMV	[86]
	Bacillus subtilis	Culture filtrate	TMV	[141]
	Serratia marcescens Gsm01	Culture filtrate	CMV	[87]
Actinomycetes	*Strepcomces noursei var.-xichangensis*	Ningnanmycin	TMV	[90]
	Streptomyces ahygroscopicus	Cytosinpeptidemycin	TMV	[91,92]
	Streptomyces sp. ZX01	Glycoprotein GP-1	TMV	[93]

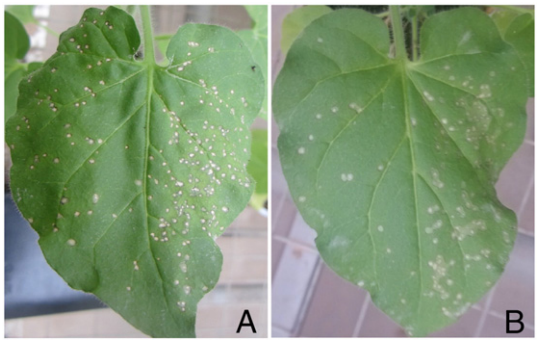


Fig. 2. Curative effects of the Polysaccharide peptide against TMV in *Nicotiana glutinosa* leaves using half-leaf methods. TMV (6×10^{-3} mg mL^{-1}) was inoculated on the whole tobacco leaves. Then the leaves were washed with water and dried. Polysaccharide peptide was smeared on the left side, and purified water was smeared on the right side for control after 6 h. The local lesion numbers were recorded 4–5 days after inoculation. A: Polysaccharide peptide at 100 μg mL^{-1}; B: polysaccharide peptide at 500 μg mL^{-1}.

10 mg mL^{-1} [100]. Nagorskaia et al. [101] found that kappa/beta-carrageenan from red marine alga *Tichocarpus crinitus* can suppress the infection of TMV in Xanthi-nc tobacco leaves. Wang et al. [102] and Liu et al. [103] isolated lectin from the marine algae *Ulva pertusa* with the anti-TMV activity. Pardee et al. [100] tested anti-PVX effects of methanol extracts from 30 species of marine algae, out of which those from 6 species exhibited inhibition rates of more than 80%, at the concentration of 10 mg mL^{-1}.

4.2. Animals

There are much less anti-plant-virus compounds found from animals compared with those from plants and microorganisms. Among these compounds, oligochitosan is one of the most successfully discovered anti-plant-virus substances from animals, which is the product of enzymatic hydrolysis of chitosan polymer. Chitin and chitosan have been proved to be nontoxic, biodegradable and biocompatible, which have been shown to induce a wide spectrum of defensive reaction in plants [104–106]. Chitosan is the product of deacetylation of chitin and have shown suppressing virus infection regardless of virus type as well as plant species [107]. When at the concentration of 50 μg mL^{-1}, the inhibition rate of oligochitosan on TMV infection was 50.41% [107]. Many studies found that oligochitosan inhibits infection of pathogens through inducing the production of nitric oxide, hydrogen peroxide and protein kinase and promoting phenylalanine ammonia-lyase activity and Ca^{2+} signaling pathway [18,107–111]. Since now, oligosaccharide has been registered and industrialized as an anti-plant-virus agent in China. Moreover, Chondroitin sulfate, whey protein and its esterification products, and melittin and its analogue also have anti-plant-virus effect [99,112–114].

5. Conclusions and prospects

With the development of living level, people begin to lay stress on quality and safety of food and problems in pesticide residue. Since biogenic anti-plant-virus agent is characterized by relatively safe to human and livestock, with less pollution and less residual, it has dramatically sprung up in recent years. However, there are still some disadvantages of biogenic anti-plant-virus substances when compared with chemical pesticide. Firstly, the action effects of some biogenic drugs are lower and not so rapid. It is even more so inadequate for biogenic drugs when a sudden and destructive disease is encountered. The bioactivity declines more quickly and the guarantee period is short. Secondly, biogenic pesticide should be used with high technology and therefore there will be a process of adaptation in technical utilization for farmers. Thirdly, the amount of some biological resources are limited, thus restricting their large-scale exploitation and usage.

In order to solve these problems, not the only one crop or one kind of pest should be controlled, but the systematic control scheme concerning on all of the possible diseases, insects and weeds in one crop should be worked out. In other words, based on the idea of green and harmonious plant protection, an integrated pest management programme should be established to take temporary or even radical solutions. The usage of drugs was to maintain yield and quality of agricultural products, rather than to exceedingly kill the organisms. We should learn from the history that all plant protection activities aiming at killing as much as possible will certainly cause the rapid increase of pathogens and pests. However, some mild drugs may preliminarily solve this problem, such as protein, polysaccharide, biological medicine fertilizer and plant-based pesticide and so on. Biogenic drugs should be used scientifically, flexibly, in time, in moderation and by proper methods according to the weather, the characteristics of the protected object and the occurrence dynamics of diseases and pests.

While the prospects of biogenic anti-plant-virus substances are bright, the road has twists and turns. More efforts should be made by researchers in order for better usage of biogenic anti-plant-virus substances in agriculture. Firstly, the screening of biological antiviral resources should be unceasingly expanded, in order to obtain compounds or biological materials with higher activities. At present, the amount of anti-plant-virus substances with very high efficiency and good economic benefits is still limited, which is not able to meet the requirements of agricultural development. Moreover, the existing developed plants or microorganisms constitute only a minority of the total resources. Secondly, the structure-function relationship in bioactive components should be further investigated, and new molecular model should be found out, thus synthesizing highly active compounds and providing material basis for exploiting efficient biogenic agents. Thirdly, functional mechanism of bioactive compounds and molecular targets should be actively explored, thus providing theoretical guidance for developing new biogenic anti-plant-virus substances. Since researches on anti-plant-virus mechanisms have been mainly focused on inducing resistance of the plants and passivating viruses [11,12,64,90,115], much more need to be studied on some highly active compounds for their action mechanisms. Fourthly, researches on biosynthesis methods of anti-plant-virus compounds should be intensified, such as endophyte culture, plant cell culture and adventitious root culture, which may solve the bottleneck problems as faced by natural resources and involved in industrial production of biogenic agents. For example, biosynthesis of artemisinin has reached 25 g per litre of artemisinic acid, which greatly promoted production efficiency of artemisinin and reduced the cost [116]. Fifthly, technical research on application of biological agents to the field should be conducted, so that their regulation and control effect can be brought into full play. Since now, most studies were done in the laboratory, and there usually exists a considerable difference between the laboratory and the field. So researches in both two should be taken into consideration. Sixthly, industrialization of new drugs should be started from those components which exhibit better activities and are more easily extracted. For example, Zhao et al. [11] discovered that polysaccharide peptide showed better anti-TMV activity than the commercial agent Ningnanmycin, despite of protection, curative and inactivation effects. It can be easily extracted and efficiently purified by liquid fermentation with a low cost, making the industrialized production feasible. Moreover, Zhao et al. [12] found acetone extract from cottonseed oil sludge as a novel anti-plant-virus agent against plant viruses and isolated gossypol from it. Since now, this extract has been further optimized and successfully industrialized as an anti-plant-virus agent in China. Finally, agents in medicine should be used for reference in order to develop anti-plant-virus drugs, since medicine is more advanced than pesticides. For instance, polysaccharide peptide is good at antitumor in medicine. However, Zhao et al. [11] applied it to plant virus and discovered its preferable anti-TMV activity.

All in all, nowadays with the vigorous advocation of green agriculture, strengthening environmental protection and developing

sustainable agriculture, to exploit natural and biological anti-plant-virus substances plays an important role for food safety. In the development of pesticide science, the research and application of pesticides should return to nature, which is the inexorable trend of both social and nature sciences. It is believed that in the near future biological agents will greatly contribute to guarding health, purifying the environment, developing the economy and benefiting the society.

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