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BRIEF REVIEW

A Top Ten list for economically important plant viruses

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Abstract The concept of "Top Ten" lists of plant pathogens is in vogue in recent years, and plant viruses are no exception. However, the only list available has more to do with historical and scientific worth than it has to do with economic impact on humans and their animals. This review will discuss the most important plant viruses that cause serious harm to food plants that sustain the bulk of humankind.

Introduction

In 2011 the journal Molecular Plant Pathology published a "Top Ten" ranking for plant viruses [1]—at least, those of

> *"…perceived importance, scientifically or economically, from the views of the contributors to the journal".*

Specifically, the article authors

> *"…survey[ed] all plant virologists with an association with Molecular Plant Pathology and ask[ed] them to nominate which plant viruses they would place in a 'Top 10' based on scientific/economic importance".*

They got more than 250 votes from the international community, and came up with the following list:

1. Tobacco mosaic tobamovirus (TMV)
2. Tomato spotted wilt tospovirus (TSWV)
3. Tomato yellow leaf curl begomovirus (TYLCV)
4. Cucumber mosaic cucumovirus (CMV)
5. Potato virus Y (potyvirus, PVY)
6. Cauliflower mosaic caulimovirus (CaMV)
7. African cassava mosaic begomovirus (ACMV)
8. Plum pox potyvirus (PPV)
9. Brome mosaic bromovirus (BMV)
10. Potato virus X (potexvirus, PVX)

There were also honourable mentions for viruses just missing out on the Top 10, including citrus tristeza closterovirus (CTV), barley yellow dwarf luteovirus (BYDV), potato leafroll polerovirus (PLRV) and tomato bushy stunt tombusvirus (TBSV).

There is considerable interest in this paper, and it has been cited more than 60 times at the time of writing. However, while the list most certainly recognises the important contribution of plant virus studies in the development of molecular biology, it does not reflect the economic impact of the viruses mentioned—and nor does it accurately reflect the most economically important viral crop pathogens. In fact, there is only one virus in the "Top Ten"—African cassava mosaic begomovirus (ACMV)—that infects and causes severe losses in just one of the four major food crops grown on this planet. All the rest, excepting viruses infecting potato, are pathogens of fruits, vegetables or horticulturally important plants.

There is an obvious bias in the list to first, "scientific" favourites from the history of plant virology (e.g., TMV, BMV); and second, to viruses from the northern hemisphere and in particular, developed countries.

The bias for scientific importance is most evident with BMV: this has an interesting history in molecular plant virology, in that it was the first virus found with a divided genome [2], a characteristic later also found for other

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related bromoviruses [3], and there have been extensive molecular virological studies, especially of its replication, over nearly thirty years [4–9], as well as structural studies continuing to the present day [9–13]. However, as far as its disease potential is concerned, there appears to very little at all: the Free State streak disease in South Africa that it was implicated in during the 1980s [14] turned out to have more to do with the toxicity of the so-called Russian wheat aphid *Diuraphis noxia* and the presence of BYDV, and BMV was discounted eventually as being a serious problem in its own right—an experience that has been repeated worldwide, where it is only ever a very minor problem for cereal production [15].

The authors of the Top 10 article say this of their effort:

> *"This review article presents a short review on each virus of the Top 10 list and its importance, with the intent of initiating discussion and debate amongst the plant virology community, as well as laying down a benchmark…"*

Accordingly, I would like to respond to the invitation to discussion and debate, and I would like to fundamentally shift their benchmark—by building a list of plant viruses that cause major economic damage, and in some cases can actually lead to people dying.

An economic Top Ten for plant viruses

In 1999 I co-authored a paper entitled "Plant virus disease problems in the developing world" [16]. We took the view that the most important plant viruses in the world were those affecting the major food crops in the developing world specifically, seeing as these would affect the greatest number of people and would probably be the least well controlled. We used Food and Agriculture Organisation (FAO) data to determine that the most important crops in the developing world as far as local populations are concerned were bulk foods such as (in order of economic importance) rice, maize, cassava, bananas, and sweet potatoes; supplementary vegetables such as beans and pumpkins; and fruits such as mangoes and coconuts.

I note this list contains no tobacco, that neither tomatoes nor potatoes are particularly important, that there is no wheat, and that there are no tree-grown temperate fruits. Thus, seven of the "Top Ten" viruses are effectively unimportant as far as economic impact on the majority of humanity is concerned. The ACMD (African cassava mosaic disease) begomovirus complex would still be there because it has such an impact on cassava; CMV too would still be allowed, seeing as it infects almost anything, including maize and most vegetables; the TYLCD (tomato yellow leaf curl disease) begomovirus complex would also possibly have a place.

However, cassava is not just affected by ACMV, nor are tomatoes devastated just by TYLCV: rather, there are groups of distantly related generic begomoviruses such as ACMV, EACMV, SACMV and ICMV, among others [17, 18], that infect cassava; likewise, TYLCV, TYLCThV and a host of other distinct begomoviruses infect tomatoes worldwide to cause TYLCD [19]. Singling out just one example each of a complex of viruses that cause major disease problems is therefore arbitrary, and two virus disease complexes would have to be in my Top Ten.

I also find the omission of maize streak virus (MSV) from any Top Ten list to be seriously questionable: MSV has, after all, been an object of serious historical as well as molecular virological significance over more than 100 years [20]. However, maize streak disease (MSD) is also the most significant viral disease of Africa's most important food crop, with losses of up to US$480M per year based on average annual yield losses of only 6 %–10 % [21]. As losses can be up to 100 %, this is almost certainly an underestimate—therefore, MSV must be a serious contender too.

So what would I consider to be my Top Ten? I would not go as far as ranking them in importance; however, from the basis of considering only viruses with sufficient economic impact to kill people if crops are affected, it would be these—ordered by crop importance.

Rice: the rice tungro disease agents RTBV, a dsDNA badnavirus, and rice tungro spherical virus (RTSV), an ssRNA waikavirus, in Asia [22, 23]; rice yellow mottle (RYMV) ssRNA sobemovirus in Africa [24]; and rice hoja blanca virus (RHBV, ssRNA(-) tenuivirus) in South America [25].

Wheat: Barley yellow dwarf luteoviruses (BYDV)—again, actually a complex of ssRNA viruses which in fact belong in different species—is almost certainly the worst viral pathogen of wheat worldwide [26].

Maize: The ssDNA geminiviral pathogen maize streak mastrevirus (MSV) is unarguably the worst viral pathogen of maize in the whole of Africa, where maize is the most common staple food [20].

Maize rayado fino virus (MRFV, an ssRNA marafivirus) is possibly the most important virus in North and especially South America [27]. The ssRNA potyviruses maize dwarf mosaic virus and sugarcane mosaic virus are probably the most widespread viruses of maize, having essentially a worldwide distribution, and often being associated with severe disease [16].

Sweet potato: Sweet potato feathery mottle potyvirus (SPFMV) is probably the worst pathogen affecting this increasingly used crop worldwide, but pathology is

exacerbated by co-infection with sweet potato sunken vein closterovirus (SPSVV) [28, 29].

Cassava: The Africa-limited ACMD complex of ACMV, EACMV, SACMV and others together constitute a major threat to food security in the continent, especially given an increased use of cassava continent-wide [18]. As an object example of why I choose to go with the viruses mentioned, it is worth revisiting what Pietersen and I wrote in 1999 [16]:

> *"It is quite remarkable to pass within a few kilometers from areas with mild ACMD to areas where there are almost no cassava plants left growing. The inevitable lag in replacement of the crop by sweet potato, for example, results in severe hardship for farming families accustomed to using it as a staple in their diet. The wave of ACMD across Uganda may be a good example of the devastating effect of a plant virus on the human population."*

Fifteen years on, I see no reason to revise the statement.

Bananas: the worst virus affecting bananas worldwide has to be banana bunchy top nanovirus (BBTV) [30, 31]. This ssDNA pathogen has been identified in numerous developing countries in Oceania, Africa, and Asia and has caused devastating epidemics. Also-rans include the dsDNA banana streak badnavirus (BSV) [32]—also found integrated into the genome of many members of the genus *Musa*—and the ssRNA cucumber mosaic cucumovirus (CMV) [33].

Vegetables: As noted previously [14], possibly the most important groups of viruses affecting vegetables worldwide are geminiviruses, potyviruses and tenuiviruses—with tomato spotted wilt virus(es) the prominent of the latter. The ubiquitous tomato is probably worst affected by TYLCD [19], then tenuiviruses [34]; bean production in Central America is badly affected by bean golden mosaic and other begomoviruses [35].

So, my Plant Virus Top Ten is, in alphabetical order:

- African cassava mosaic disease (ACMD) begomovirus complex
- Banana bunchy top nanovirus (BBTV)
- Banana streak badnavirus (BSV)
- Barley yellow dwarf disease luteovirus complex
- Cucumber mosaic cucumovirus
- Maize streak mastrevirus (MSV)
- Maize dwarf mosaic/Sugarcane mosaic potyviruses
- Rice tungro disease complex
- Rice yellow mottle sobemovirus (RYMV)
- Sweet potato feathery mottle potyvirus (SPFMV)

Also-rans:

- The legion of tomato begomoviruses worldwide, but especially in Asia
- Tomato spotted wilt tospovirus, because it is ubiquitous
- Various South American (mainly Brazilian) vegetable begomoviruses
- Various potyviruses, mainly in vegetables, in Asia

I consider these to be the most important plant viruses in terms of causing severe hardship and affecting large numbers of people. I would rank the ACMD complex, MSV and the rice tungro complex as the top three in global importance; however, any finer ranking would have to be subject to an exhaustive economic evaluation that is beyond the scope of the review.

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