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Effects of crop viruses on wild plants

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Global land conversion and intensification of agriculture mean that remnant native plant populations are increasingly exposed to crop viruses. What are the consequences for wild plants? In natural unmanaged systems, the key consideration is how crop virus infection influences plant fitness. Field studies of virus effects on wild plant fitness are scant. Approaches include (i) observational studies, (ii) studies of experimental plants with natural infection, and (iii) studies of experimental plants with experimental infection, with most studies focused on viruses in the *Luteoviridae* and *Potyviridae* families. Fitness effects documented are largely neutral to negative. Crop virus influence on wild plants merits attention in ecological conservation and restoration.

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Introduction

Humanity's appetite for food, fuel, and fiber is growing. To feed it, approximately one-half of the Earth's terrestrial surface has been converted to agricultural crops and rangeland [1], and this fraction will likely increase. When agriculture first developed some 10,000 years ago, cultivated fields were a small fraction of the landscape, with crops surrounded by a matrix of wild vegetation. Farmers, and later plant pathologists, worked hard to defend crops from what must have seemed to be an overwhelmingly large natural reservoir of viruses and other pests. Now in many regions the landscape balance has been reversed, with natural vegetation present in ever-shrinking remnants within an expansive sea of crops and managed fields. Wildlands are regularly exposed to viruliferous vectors effluxing from agroecosystems, and there is increasing evidence about the potential for deleterious effects [2,3•]. Thus, a new question must be asked: What influence(s) are domesticated landscapes having on plant virus ecology and evolution? Specifically, what effects do crop viruses have on the fitness of wild plants? This is an urgent question whose timeliness is compounded by the need to protect wild plant populations from the rising threats of climate change. Unfortunately, due to a number of constraints including disciplinary history [4] and biosafety logistics [3•], there is a surprising lack of empirical data. We thus explore relevant published studies from the beginning of modern plant virology (1960s) to the present and call for a new era of investigation.

Are crop viruses pathogenic in wild plants?

Most of the viruses that are central to our knowledge of plant virology are crop-associated, and were first recognized because of their presence in, and often damage to, agricultural plants [5]. We thus define 'crop viruses' as those known to cause notable yield or economic loss in crops, including forage, in contrast to 'wild' viruses that are associated primarily with non-crop vegetation. Many crop viruses are generalists that also can infect 'wild' or unmanaged plant populations, which we define as non-cultivated plant populations in which changes in population size or genetic composition are not under direct human control [6•]. It is clear from retrospective analyses that agricultural expansion and intensification have capacity to drive changes in viral taxa, such as the proliferation of potyviruses that occurred in parallel with the first development of cropping systems [7]. Does association with crops make plant viruses more or less pathogenic? The classical hypothesis has been that agricultural association would tend to favor pathogenicity [8]. Given that crop plants represent a subset of plant life styles (mostly annual, fast growing) and environments (highly managed in modern agriculture), selective pressures might favor viruses that could propagate quickly and be readily transmitted to new hosts, characteristics associated with pathogenicity (in fact, the situation is likely more complex [8]).

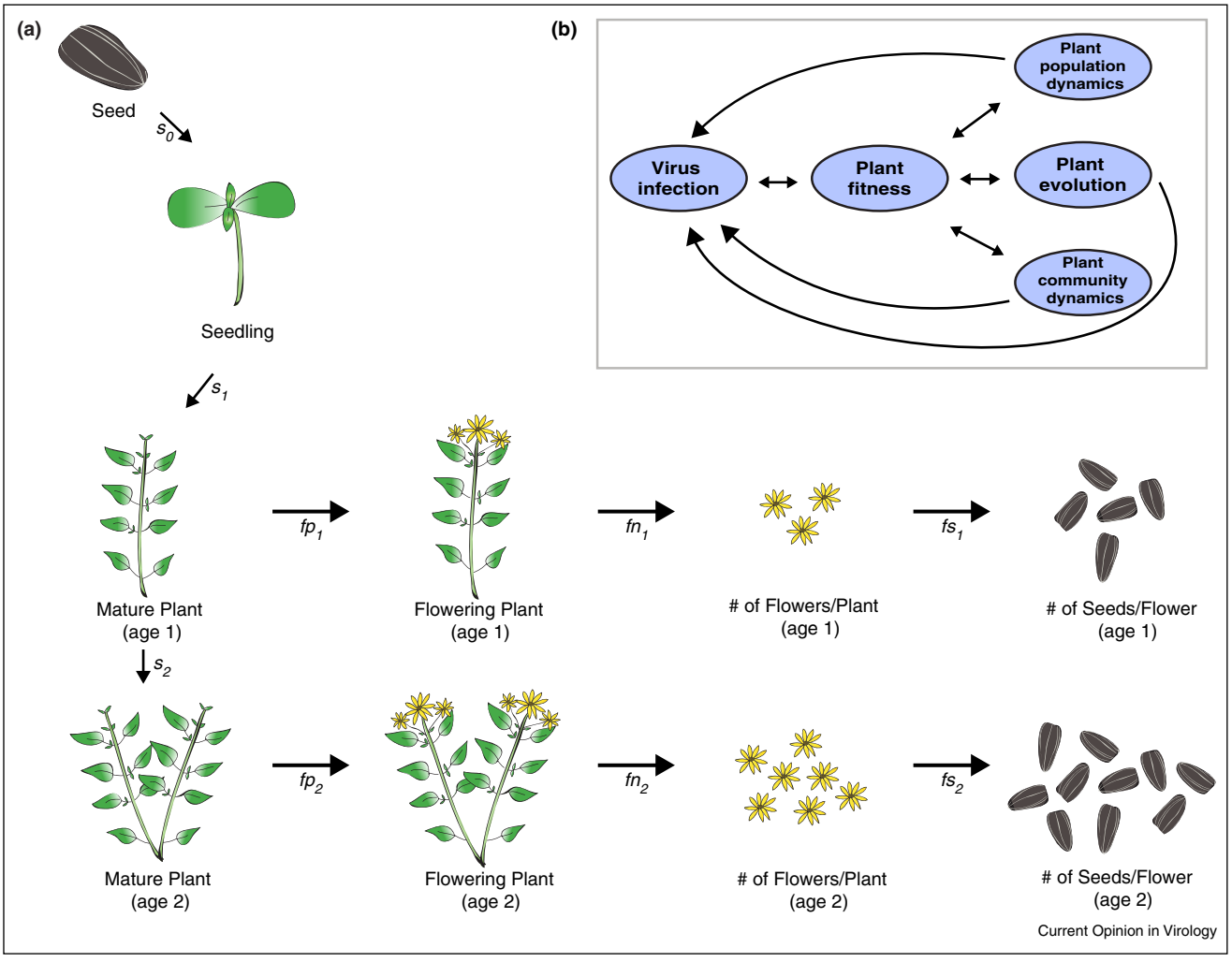
Our focus here is on whether pathogenic crop viruses have consequences for wild plants. One expectation is that effects will be negative — that is, viruses pathogenic on crops will also be pathogenic on wild plants. However, plant breeding has sometimes increased crop growth rates at the expense of crop resistance [9,10], so it is possible that viruses operating in such hosts might maintain fewer defenses (e.g., silencing suppressors) themselves. Thus, crop viruses might be pathogenic in crops, but have little effects on better defended wild hosts. Finally, it has also been suggested that crop viruses may provide some

benefits to plants, such as tolerance to dessication [11,12] or drought [13] (but see [14]).

Quantifying virus influence on plant fitness in the field

There is much less empirical data about the effects of crop viruses on wild plants than on crop and model species. Nonetheless, there are interesting indications that virus infection in wild plants, as in crop plants, can modulate plant physiology and response to environmental resources and stresses. For example, infection increases the response of native grasses to resource release with simulated grazing [15]. Evaluation of the molecular and physiology mechanisms of wild plant–crop virus interactions is thus valuable. Here we wish to highlight the critical need for investigation of virus effects at the whole plant level, namely effects on wild plant fitness in the field. 'Fitness' is an evolutionary biology term that describes how successfully an individual propagates its genes [16]. We thus use the term 'fitness' to mean the contribution of an individual, in terms of

Figure 1



(a) Fitness components. The lifetime fitness of an individual plant depends on fitness components including its probabilities of survival to different life stages (s_0, s_1, s_2), and, if it survives, on the probability that it flowers (*fp*), the number of flowers it produces (*fn*), and the number of seeds it produces per flower (*fs*) at each age (two-year life cycle shown). Virus infection, whether naturally occurring or experimentally induced, can occur at different points in the life cycle. For example, experimental inoculations can be performed on seedlings [23] or on mature plants [18]. The effect of the virus on plant fitness may depend on the timing of infection relative to plant life history events. (Note: We used a perennial sunflower as the focus of this figure; for this species, each inflorescence ('head') consists of many flowers). **(b)** Fitness as a central mediator of effects in plant ecology and evolution. Virus infection can affect plant fitness (either negatively or positively), which in turn can alter plant population dynamics (changes in plant numbers over time), plant evolution, or plant community dynamics (changes in plant species composition over time). These three processes can in turn alter patterns of virus infection. For example, virus infection could decrease plant fitness, and if there is genetic variation in susceptibility, plants may evolve to become more resistant. Greater resistance in the plant population may reduce rates of virus infection (and possibly lead to evolutionary changes in the virus). Note that to keep the figure simple, we have not included arrows between the ovals for plant population dynamics, evolution, and community dynamics, even though these processes certainly interact.