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Annual Review of Phytopathology Ecology of Yellow Dwarf Viruses in Crops and Grasslands: Interactions in the Context of Climate Change

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Abstract

Our understanding of the ecological interactions between plant viruses, their insect vectors, and their host plants has increased rapidly over the past decade. The suite of viruses known collectively as the yellow dwarf viruses infect an extensive range of cultivated and noncultivated grasses worldwide and is one of the best-studied plant virus systems. The yellow dwarf viruses are ubiquitous in cereal crops, where they can significantly limit yields, and there is growing recognition that they are also ubiquitous in grassland ecosystems, where they can influence community dynamics. Here, we discuss recent research that has explored (a) the extent and impact of yellow dwarf viruses in a diversity of plant communities, (b) the role of vector behavior in virus transmission, and (c) the prospects for impacts of climate change—including rising temperatures, drought, and elevated CO₂—on the epidemiology of yellow dwarf viruses.

INTRODUCTION

The barley and cereal yellow dwarf viruses (YDVs) that infect grain crops are among the most widespread plant pathogens globally, causing substantial yield losses that can reach 80% in crops (100), reducing grain quality (16), reducing the performance of noncultivated grasses (13, 78), and potentially impacting grassland community structure (e.g., 13). The luteoviruses that constitute the YDVs are distributed broadly in grain crops throughout temperate regions in both the Northern and Southern Hemispheres. They have also been detected in grasslands across the globe, including in North America (e.g., 51, 74, 105, 117), Europe (46, 80), Australia (99), New Zealand (26), the Middle East (6), and East Africa (11). Although not all grasslands have been surveyed for viruses, evidence to date suggests that YDVs are ubiquitous.

The YDVs are phloem-limited, single-stranded RNA viruses in the Solemoviridae and Tombusviridae families (129) that are obligately transmitted in a persistent circulative manner by several species of grass-feeding aphids to a wide range of cultivated and wild grasses (52, 88). YDVs in the Tombusviridae include five species of barley yellow dwarf virus (BYDV) in the genus *Luteovirus* (BYDV-PAV, BYDV-PAS, BYDV-MAV, BYDV-kerll, BYDV-kerll). YDVs in the Solemoviridae include (*a*) three species in the genus *Polerovirus*, including two species of cereal yellow dwarf virus (CYDV-RPS, CYDV-RPV) and one of maize yellow dwarf virus (MYDV-RMV) (66), and (*b*) two species in the genus *Sobemovirus* (BYDV-GPV, BYDV-SGV). Finally, the genus *Sobemovirus* includes BYDV-GPV and BYDV-SGV. The viruses in these groups tend to have broad, overlapping host ranges in the Poaceae grasses, with somewhat more specificity in vector relations (88, 104). The experimental host range of the YDVs includes well over 100 species of grasses, although virus prevalence varies significantly among different virus and host species (23, 42).

Globally, the most important vectors of YDVs include the major grain aphids: the English grain aphid, *Sitobion avenae* (F.); the bird cherry-oat aphid, *Rhopalosiphum padi* (L.); the corn leaf aphid, *Rhopalosiphum maidis* (Fitch); the rose-grain aphid, *Metopolophium dirbodum* (Walker); and the greenbug, *Schizaphis graminum* (Rondani). However, aphid species differ in transmission specificity and efficiency. Some aphids can transmit only a single YDV species, whereas others can transmit two or more. For a given virus species, some species of aphids can be extremely efficient at acquiring and transmitting the virus, whereas others are relatively inefficient (41, 105). BYDV-PAV is efficiently transmitted by *R. padi* and *S. avenae. R. padi* also transmits CYDV-RPV, and *S. avenae* also transmits BYDV-MAV. *R. maidis* transmits MYDV-RMV, and *S. graminum* transmits BYDV-SGV most efficiently (23). The efficiency of acquisition and transmission interacts with host preferences and plant-to-plant movement rates, which also vary between aphid species, to produce variable rates of disease spread (105).

DISTRIBUTION OF YELLOW DWARF VIRUSES IN CROPS AND WILD GRASSES

YDVs occur globally because of their broad host ranges and their transmission, at least experimentally, by 25 different species of aphid (23). During the twentieth century, significant outbreaks of YDVs occurred in Finland, New Zealand, the Czech Republic, and Ethiopia as well as the United States (12, 62, 67, 68, 97, 127). Many studies map the geographic distribution of different YDVs and occurrence of aphid vectors (e.g., 98, 99) (see **Supplemental Material Table 1** for global occurrences of YDVs). Because transmission efficiency varies significantly, the presence or absence of an aphid species can determine the species composition and relative abundance of YDVs in an area. Although the local prevalence of YDVs can be linked to the population dynamics of particular aphid species, the most common YDV species is not always the most harmful to crop

Supplemental Material >

yields. For example, in wheat and barley in the Czech Republic, BYDV-PAS is more common, but BYDV-PAV causes more symptoms and may cause greater yield losses (20, 53).

Agricultural grain crops are just one of many ecologically relevant grass-dominated systems that host YDVs and their vectors (23). YDVs are also important in unmanaged grasslands, where they have the potential to disrupt endangered or sensitive ecosystems and may also be exacerbated by global climate change. These viruses typically persist in the roots of perennial host plants but cannot be transmitted through seeds. Although perennial grasses are often better competitors than annual grasses (120), an uninfected annual may have a competitive advantage over a perennial carrying YDVs from year to year. Weeds and crops infected with YDVs can result in spillover of the pathogen via shared grain aphid vectors to native perennial grasses, which may then be outcompeted over time. In California grasslands, wild oats (*Avena fatua*), an introduced annual weed, are a highly competent host of YDVs that can increase the prevalence of YDVs and reduce the fitness of native perennial grasses (77, 78). The discovery of YDVs in native and introduced grasses in endangered grasslands in the northwestern United States and in a fragile sub-Antarctic ecosystem has raised concerns about YDVs disrupting ecosystem function in these systems (49, 130).

The prevalence, host response to infection, vector abundance and host preference, and overall epidemiology of YDVs are better characterized in agricultural systems because of the economic consequences for grain crops. However, there is increased potential for YDVs to spill over into noncrop grasses and spill back into agricultural grasses, along with their vectors, as a result of climate-induced range shifts, introduction and spread of invasive weedy grass hosts, and the overall expansion of agricultural landscapes relative to noncrop grasslands (5). It is likely that YDVs and their vectors regularly move across the agroecological interface between cropping systems, weeds, and native noncrop grass hosts despite the relative paucity of studies (**Figure 1**)



Figure 1

Current understanding of the dynamics of the yellow dwarf viruses within and across crop and noncrop grasslands. Substantial research has been conducted in grain crops and cool-season pasture grasslands in North America and globally (*black arrow*). Virus dynamics in noncrop native perennial grasslands are less well understood except in some western and coastal grasslands in North America (*gray arrow*). Virus and vector movement (spillover) between the two systems at local and landscape scales are significantly understudied (*yellow dashed arrows*). Photos by J.S. Peters. Adapted with permission from Reference 5.

Rhopalosiphum maidis aphids tended by ants

Alate aphids on Andropogon gerardi



Figure 2

A *Rhopalosiphum maidis* colony tended by ants (*left*). Unidentified alate aphids (*right*) on native perennial bunchgrass *Andropogon gerardi* in New York. Photos by J.S. Peters.

(5, 38, 101, 108). There is limited understanding of the geographic range and host effects of YDVs in most native grass communities globally, and impacts on host fitness have not been characterized for most noncrop grass species in ecologically relevant contexts. Host preference and transmission efficiency of aphid vectors are also understudied in noncrop hosts, although a suite of vector aphids do colonize most, if not all, of these grasses (**Figure 2**).

Yellow Dwarf Viruses in Prairie Grass Communities in North America

The ecology of YDVs has been studied in detail in several grassland communities in North America. Land-use change in the Great Plains of the midwestern United States has driven the conversion of most prairie grassland to agricultural land use, with the predominant crops being corn and wheat (45), both seasonal hosts of YDVs and their vectors (23). However, native prairie is still present in smaller patches and is being restored in some areas (9, 43). Native prairie grasses have been surveyed for YDVs in the remnant tallgrass prairie at the Konza Prairie Biological Station in Kansas (37). The most common native grasses of this plant community include Sorghastrum nutans (Indiangrass), Schizachyrium scoparium (little bluestem), Panicum virgatum (switchgrass), and Andropogon gerardi (big bluestem). When surveyed, all but S. nutans were found to be infected with at least one species of the five YDVs that were tested for (PAV, MAV, RMV, RPV, SGV). Interestingly, in this region PAV is known to be the most common of the YDVs in wheat but was not found in any of the tested native prairie grass species. In contrast, little bluestem was primarily infected with SGV (60%), switchgrass primarily with MAV (31%), and big bluestem with MAV (31%) (37). Although it is possible that these native perennial prairie grasses may be a reservoir of YDVs that could infect grain crops, more research is needed to investigate the mismatch between viral species in these systems.

Several studies have evaluated the potential fitness impacts of YDVs on grasses in the Great Plains. For example, *Panicum virgatum*, the native prairie grass that is of interest to the biofuel industry, exhibited stunting and reduced root biomass and depth when coinfected with PAV and RPV (75). This native grass showed drought sensitivity that could impact plant productivity in both its native habitat and its performance as a biofuel crop, particularly in the context of climate change. When infected with PAV, two common switchgrass ecotypes (lowland and upland) remained asymptomatic but had reduced fitness (30%) in a multiyear study (4). The lowland ecotype appeared more resistant to infection and recovered over time, whereas the upland ecotype responded to infection with a phenological delay and reduction in seed set. The differences between ecotypes are significant because both the wild type and cultivars of this species are strong candidates to be biofuel crops and therefore for plant breeding. Susceptibility and host response to PAV infection in the form of biomass accumulation were measured across wild type and cultivars of switchgrass in greenhouse and field trials, in both experimentally planted and naturally occurring switchgrass communities (117). Compared to the wild type, the cultivars were more susceptible to PAV, had greater reductions in biomass, and were preferred by grain aphids. More work on vector preference and transmission between perennial grasslands and annual cropping systems could elucidate the potential impact of this process.

Yellow Dwarf Viruses in Western Grasslands of North America

Environmental and land-use factors also influence the prevalence and viral diversity of YDVs in at-risk noncrop landscapes like the remnant Palouse Prairie in the US Pacific Northwest and cooccurring Conservation Reserve Program (CRP) grasslands (51). Here, thirty annual and perennial grass species were surveyed, including native species like Idaho fescue (*Festuca idaboensis*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). YDVs were found across all prairie and CRP sites surveyed and PAV and SGV were detected. Grass host identity, as well as season, were the most important determinants of pathogen prevalence, and annual grasses were less likely to be infected than perennial grasses (51). Another important factor driving pathogen prevalence was proximity to agriculture. The presence of grain crops within 1 km of prairie or CRP grasslands was correlated with increased pathogen prevalence in both native and introduced perennial and annual grasses.

In coastal grasslands in California and Oregon, local relative abundance of perennial grasses was also correlated with increased pathogen prevalence, and this effect was stronger than the impact of regional climate (15, 77). Although prevalence differed somewhat among host species, infection rates did not vary with host traits like life history or phylogeny. The similarity of infection rates among species at the end of the experiment suggested that local factors like the background prevalence of YDVs in the local context outweighed host species traits or vector preferences that could otherwise influence susceptibility (15). Virus prevalence in this system appeared to be decoupled from vector preference, as has sometimes been found in other contexts (14, 78). Abiotic factors, including nutrients such as phosphorus, and biotic factors like the presence of herbivorous vertebrates, including small mammals, mule deer (*Odocoileus bemionus*), and European wild boar (*Sus scrofa*), were also found to increase virus prevalence in annual and perennial grasses in western US grasslands (107).

Coinfection by multiple related or unrelated pathogens is common in plant communities (14, 106, 118). However, the diversity of YDVs within a single host and its effects on transmission and host response remains understudied in most noncrop hosts (but see 119). Infection with multiple YDVs was extremely common and nonrandom in a native perennial grass (*Elymus*)

glaucus) in California grasslands (121). The YDVs found co-occurring most frequently were those that shared a vector. In this study, more than 50% of the samples were coinfected and, of those, 28% had three or more co-occurring viruses. An additional outcome of coinfection by multiple YDVs is transcapsidation in which the RNA of one virus species is encapsidated by the protein capsid of a different species, which can allow transmission by normally incompetent vectors (21, 112). Coinfection with YDVs may also affect plants differently depending on host identity. In a greenhouse experiment, a native California perennial grass (*Nassella pulcbra*) and an introduced annual (*Bromus hordeaceus*) were challenged with infection by YDVs (91). The native perennial was the least susceptible to single infections and no coinfection of PAV/MAV occurred. In contrast, the introduced annual showed reduced above- and belowground biomass in single infections of PAV, and coinfection greatly reduced biomass overall (91). Further comparisons of the responses to single infections and coinfections of annual versus perennial grasses, as well as introduced versus native grasses, are needed, particularly under field conditions.

Introduced annual grasses and resulting biodiversity loss may play an important role in the dynamics of YDVs in some noncrop grasslands. Malmstrom et al. (78) showed that the introduced annual grass Avena fatua amplified aphid vector populations in California grasslands, driving increased virus prevalence in nearby perennial species. These infected perennials had reduced growth and fecundity, suggesting that YDVs may play a role in apparent competition between the native perennials and introduced annuals (79). Reduced host diversity and introduced species prevalence were also shown to increase infection with YDVs in both native and non-native grass hosts in grasslands from British Columbia to California (69). A total of 27 grass species were identified and surveyed for YDVs with the most common species being the introduced annuals Bromus diandrus and B. hordeaceus, indicating significant biodiversity loss of the native bunchgrasses that dominated these communities previously. Four YDV species were detected (PAV, RPV, MAV, SGV), with infection levels ranging from 0% to 85% depending on the host. Prevalence of YDVs in the sentinel host B. hordeaceus was correlated with reduced overall host species richness across sites. Annual hosts surveyed in this study were again determined to be better hosts when susceptibility to experimental inoculation was measured (121). The introduction and subsequent ubiquity of competent hosts like B. hordeaceus, along with the concurrent decline of native, less susceptible species, resulted in disease amplification in these grasslands. Other common introduced grasses such as Achnatherum, Danthonia, Poa, and Sporobolus were also susceptible when experimentally inoculated with YDVs (49). These introduced invasives are frequently found across degraded perennial grasslands in North America and highlight the need to understand how global change and ecosystem management may interact with YDVs and introduced hosts in grassland conservation.

Vector Behavior and the Epidemiology of Yellow Dwarf Viruses

The transmission of YDVs depends on the behavior and population dynamics of their aphid vectors. It is well established that YDVs can influence aphids indirectly by altering the physiology of host plants, thereby modifying aphid–plant interactions that are critical to the transmission of YDVs: landing, settling, reproduction, and dispersal (16). More recent studies indicate that YDVs can also influence aphid behavior directly when aphids are carrying the viruses. Many studies have examined aphid movement in relation to plant infection status using choice bioassays with wingless apterous aphids and winged alate aphids at various spatial scales.

Alates use visual cues to distinguish between plants and bare soil and land on surfaces reflecting preferred wavelengths and intensities of light (30, 60). Attraction to specific colors and the strength of attraction varies by species, but many aphids are attracted to the color yellow (for review, see 30). High numbers of alates in fields infected with YDVs appear to be linked to the aphids' preference

for symptomatic leaves (e.g., 2). Alates are thought to use both visual and olfactory cues in flight above host plants (96), but relatively few studies have examined the influence of olfactory cues on alates in flight (16). In lab bioassays conducted in darkness to eliminate visual cues, *R. padi* alates chose uninfected PAV-resistant wheat significantly more than infected resistant wheat but showed no preference between infected and uninfected susceptible wheat (85). Aphids that are consistently attracted to visual or olfactory cues of infection may acquire YDVs from symptomatic infected plants more quickly than species with no preference, but the transmission of YDVs within a plant population also depends on settling, reproduction, and dispersal.

Once aphids land, they distinguish between host and nonhost plants by probing. Persistently transmitted viruses like the YDVs take hours for an aphid to acquire, and probing behavior has generally been found to remain similar regardless of plant infection status. No significant differences in the probing behavior of *R. padi* are apparent between RPV-infected oats and uninfected oats, but *S. graminum* began feeding more quickly and fed longer on RPV-infected oats than on uninfected oats (90). *S. avenae* showed no significant difference in probing behavior between uninfected oats and oats infected with either RPV or PAV (34). However, the recent finding that *R. padi* is able to transmit PAV into barley during brief intracellular punctures adds importance to investigations of probing behavior and plant infection status (55).

Bioassays in small experimental arenas (9-15 cm) have demonstrated that nonviruliferous aphids settle preferentially on plant tissue infected with YDVs. In a dual-choice bioassay, nonwinged apterous R. padi preferred both the leaves and the volatile organic compounds near the leaf surface (headspace) of PAV-infected wheat over those of uninfected wheat (56). PAV-infected wheat gives off a significantly higher concentration of volatiles compared to uninfected plants (56, 61). Using a single-choice bioassay, Medina-Ortega et al. (85) showed that preferential settling on PAV-infected plants is due to attraction, not arrestation. Nonviruliferous R. padi apterae walked toward the headspace volatiles emitted by infected wheat significantly more than toward uninfected wheat and chose paper carrying volatile blends that mimic the headspace of infected plants significantly more than paper with volatiles mimicking the headspace of uninfected plants. Apterous *R. padi* placed over the headspace of infected plants did not differ significantly in their movement from aphids placed over the headspace of uninfected plants. Interestingly, transmission efficiency of an aphid clone appears to influence attraction to infected plants. R. padi clones with high transmission efficiency showed a preference for PAV-infected barley, whereas clones with medium and low transmission efficiency did not differ significantly in their attraction to infected barley versus uninfected barley (61). Studies conducted in greenhouses at slightly larger spatial scales that allowed aphids to encounter both visual and olfactory cues of entire plants found that nonviruliferous aphids settled preferentially on uninfected plants or had no clear preference (63, 106). Overall, the results of small-scale arenas and greenhouse studies suggest that the preferences of aphids of a single species can differ according to morph, season (1), aphid transmission efficiency, virulence of the virus strains, and the severity of symptoms being displayed as well as the particular experimental setup (33).

Once an aphid has acquired one of the YDVs and becomes viruliferous, its host preferences may change, resulting in a process called conditional preference. Ingwell et al. (50) allowed apterous *R. padi* to acquire PAV from artificial phloem and demonstrated that direct interaction between PAV and aphids' bodies resulted in nonviruliferous aphids preferring to settle on infected plants. Apterous *R. padi* that became viruliferous from feeding on either infected plant tissue or artificial infected phloem both settled significantly more on uninfected plants than on PAV-infected plants. In contrast, some studies have shown no significant difference in attraction by viruliferous *R. padi* apterae toward the volatiles of uninfected versus PAV-infected wheat leaves (31, 85) or oat leaves (125). Although evidence is insufficient to declare that viruliferous aphids show a clear reversal

of nonviruliferous aphids' preference for infected plants, at a minimum, aphid acquisition of PAV appears to lessen the difference in responses between infected and uninfected plants. This change in behavior could help viruliferous aphids spread YDVs to uninfected plants. Early in the season when relatively few plants in a field are infected, the increased attractiveness of plants infected with YDVs should increase virus spread because plants have a finite window of susceptibility (131, 133). However, when many plants are infected, attraction to infected plants is likely to limit spread, whereas attraction to uninfected plants would increase spread (83).

Aphids feeding on plants infected with YDVs often experience improved fecundity, shorter development times, and/or increased survival (31, 56, 90). Although YDVs have been found to increase amino acid concentrations and carbohydrate content in plant phloem (3, 34), the causal link between the changes in phloem composition induced by YDVs and aphid fecundity has not been demonstrated. Aphid changes in fecundity may depend on host plant identity. *S. avenae* raised on wheat infected with YDVs have higher fecundity than those raised on uninfected wheat (34, 87, 110). *R. padi* experiences increased fecundity on PAV-infected wheat but not oats (7). Higher fecundity and subsequent overcrowding can increase dispersal from the overcrowded plant (39, 40). Moreover, *R. padi* and *S. avenae* living on YDV-infected (PAV, RPV, and MAV) oats and barley produce more alates than on uninfected plants (39, 40, 90). Although Fiebig et al. (35) found that *S. avenae* was less fecund on infected plants, which also had lower amino acid and carbohydrate content than uninfected plants. These results indicate that YDVs indirectly alter aphid reproduction and morphology via changes in host plant nutritional content, thereby facilitating the dispersal of viruliferous alates and leading to increased transmission.

Persistently transmitted viruses are predicted to modify host plant physiology so that nonviruliferous aphids preferentially land and settle on infected plants and stay long enough to acquire the virus (82). Studies conducted in small (15 cm) arenas with apterae provide evidence for this pattern, but greenhouse and field experiments would elucidate aphid behavioral patterns and movement ecology at larger spatial scales. At a smaller scale, the general aphid preference for younger leaves could affect the acquisition of YDVs because new leaves can contain lower titers of YDVs in some infected host plants (33). Experiments have often brought aphids into contact with detached leaves or volatiles, and studies of how aphids respond to infected plants across a plant's life span are limited. Different aphid species also have preferred locations for feeding, so using the entire host plant to investigate aphid behavior may further knowledge of location-specific aphid behavior (16). Once an aphid has acquired one of the YDVs, selection is predicted to favor viruses that encourage viruliferous aphids to preferentially land, settle, and feed on uninfected plants. Clarifying the preferences of both viruliferous apterae and alatae is essential to understanding the transmission of YDVs. Contradictory results may be due to variation in the virulence of different strains of YDVs and in the symptoms that plants display (33). We further emphasize that because of this variation, it is important to understand the mechanisms by which viruses affect aphid behavior, both directly and indirectly via host plants. Although our understanding of aphid response to changing host plant physiology is well-developed, there is much less information about direct virus effects on aphid behavior.

These complex interactions between viruses, vectors, and hosts have important implications for our ability to elucidate the epidemiology of YDVs. For decades, some of the processes described above have been incorporated into models of the spread of YDVs at the field scale. For example, using a spatially explicit model, McElhany et al. (83) examined the influence of vector preference for plants infected or uninfected with YDVs on spatial spread of the virus at different levels of pathogen prevalence. This model predicted that vector preference for infected plants would result in greater rates of spread when virus prevalence is low. When virus prevalence is

high, however, vector preference for infected plants should result in lower rates of spread. In contrast, under conditions of high virus prevalence, preference for uninfected plants would lead to greater rates of spread. Preference strength and vector movement rates can influence the prevalence level at which the switch would occur, along with the realistic spatial autocorrelation that leads to clumped infections, driven by local plant-to-plant movement by apterous aphids (105). Spatial autocorrelation resulted in a lower switch point, such that vector preference for uninfected plants would lead to greater rates of spread at a lower overall virus prevalence.

Models have continued to be used to explore the outcome of aphid preferences for infected or uninfected plants. For example, Sisterson (126) partitioned preference into orientation preference (response to visual and olfactory cues) and feeding preference (response to gustatory cues). Results of this model supported the findings of McElhaney et al. (83) for the effects of orientation preference but indicated that the effects of feeding preference did not depend on overall infection rates because feeding preference allows virus transmission during discrimination between infected and uninfected plants. Based on the behavioral studies of aphid conditional preference described above (e.g., 50), Roosien et al. (113) developed a model to explore the impact of vectors' host preferences that depend on whether a vector carries the virus. In contrast to previous models, this model predicted that changes in host preference following acquisition of the virus should increase virus spread throughout the epidemic, regardless of virus prevalence, as long as nonviruliferous vectors prefer infected plants and viruliferous vectors prefer uninfected plants. Several subsequent models have assessed the relative importance for virus spread of vector life history (population growth rate and carrying capacity) and movement rates that are conditional on whether the host plant is infected and whether the vector is viruliferous (123, 124). Overall, both vector life history and vector movement rates strongly influenced virus spread, with or without conditional preference. However, conditional preference tended to amplify contact between hosts and vectors with different infection statuses, which also contributed to greater virus spread. Shoemaker et al. (125) extended this approach to a multispecies host community and predicted less virus spread in diverse communities based on the host preferences of viruliferous vectors.

EPIDEMIOLOGY OF YELLOW DWARF VIRUSES UNDER CLIMATE CHANGE

Previous reviews have comprehensively examined the direct and indirect effects of climate change on a wide array of plant hosts, vectors, and viral pathogens (58, 59). Here, we address the implications of rising temperatures, increasing frequency of drought, and elevated atmospheric CO₂ on the epidemiology of YDVs by considering the effects of the changing environment on aphid vectors of YDVs, virus dynamics in hosts, and the performance of infected host plants (**Figure 3**).

Effects of Increased Temperature

Higher global temperatures are expected to increase the prevalence and spread of many plant viruses as a result of four processes: (*a*) changing geographic ranges of viruses and their insect vectors; (*b*) temperature effects on the population dynamics and activity of insect vectors; (*c*) temperature effects on virus replication, within-host movement, and transmission; and (*d*) temperature effects on host resistance mechanisms. Higher temperatures are predicted to result in more rapid population growth of aphid species that transmit YDVs because of faster development, shorter generation times, increased proportion of winged morphs, and increased flight activity (59). Although optimal temperatures for population growth of major grass-feeding aphids are typically around 20°C, some lineages have been shown to be capable of very rapid adaptation to temperatures up to 36°C (25). Higher temperatures during the growing season would lead to



Climate change effects on the yellow dwarf virus (YDV) pathosystem. Barley yellow dwarf virus-PAV virions magnified 200,000×. Virions figure adapted with permission from Reference 29. Abbreviation: N, nitrogen.

faster development and higher reproductive rates, resulting in greater intrinsic growth rates, while warmer winter temperatures would lead to increased overwintering, earlier reproduction, and earlier flight activity (86). Due to this accelerated life cycle, an increase in average global surface temperatures of 2°C has been predicted to result in 4–5 additional generations of aphids per year in temperate regions (142). Rates of vector development and reproduction differ significantly among host plants; thus, temperature-driven changes in host plant distributions and community structure will also modify population growth rates.

Vector dispersal and movement among host plants are also likely to be enhanced under climate change. For vector insects to undergo long-distance flights, temperatures must rise above a minimum threshold (59). With climate change, that threshold is likely to be exceeded more often and earlier in the season, leading to greater opportunities for virus transmission to new areas. Vector movement patterns may also respond to large-scale changes in vegetation that are driven by climate change, such as modifications in cropping patterns and changes in unmanaged plant communities (36). Local interplant movement by walking vectors is also more common at higher temperatures, leading to greater rates of virus transmission among host plants (128). In general, heat stress causes greater aphid movement as a behavioral response to avoid physiological damage, along with higher rates of dropping from plants (73, 74). These responses lead to longer development times and slower population growth but higher rates of movement to new hosts, potentially resulting in increased virus transmission. Porras et al. (103) showed recently that acquisition of PAV by *R. padi* significantly increased expression of thermal tolerance genes and enhanced the thermal tolerance of this aphid by a remarkable 8°C. It is not clear whether this increased tolerance could outweigh the negative effects of higher temperatures on aphid population growth. More research is needed to assess the potential effects of increased aphid thermal tolerance on virus spread.

Many studies have demonstrated increased virus replication rates, within-host virus concentrations, and within-host virus movement with higher temperatures, for a variety of plant virus species, including the YDVs (e.g., 93). Because higher virus concentration in hosts is linked to more efficient virus transmission for several YDVs (41), increased virus concentrations due to higher temperatures would be expected to lead to greater rates of successful virus transmission. There are, however, upper limits to the positive association between temperature and virus concentration, and virus accumulation begins to slow at higher temperatures, likely due to increased gene silencing. The optimal temperature for virus replication varies among different viruses, and expression of disease symptoms also attenuates at high temperatures. The latent period—the period between virus inoculation and sufficient virus replication to allow transmission by vectors decreases with increasing temperature (137), also leading to more rapid virus spread at higher temperatures.

The efficiency of virus transmission by vectors can also increase as temperature rises. Increasing temperatures in transmission experiments from 5° C to 25° C resulted in significantly greater transmission of YDVs by *R. padi* (reviewed in 36). There is also evidence that warmer temperatures can increase transmission rates by vector species that are typically inefficient vectors (72). Thus, rising temperatures could lead to a broader range of vectors capable of transmitting YDVs and to greater virus spread.

Increasing average global temperatures may either impair or enhance host plant resistance mechanisms. Higher temperatures are known to affect two types of antiviral resistance: (*a*) RNAibased viral defense such as gene silencing and (*b*) resistance based in protein–protein recognition (reviewed in 18, 59). Gene silencing becomes much more effective at higher temperatures in some model hosts, such as *Arabidopsis thaliana* and *Nicotiana benthamiana* (18, 132), and studies have indicated that this is true for other plants as well (e.g., 19). In contrast, protein-induced dominant resistances can be negatively affected by increasing temperatures. In this type of resistance, a viral determinant is recognized by the host, leading to the activation of salicylic acid and systemic acquired resistance. Depending on the host, this type of resistance can be disrupted by temperatures above a certain threshold. Therefore, some protein-elicited resistances could be impaired by temperature increases, and broad-spectrum gene silencing resistance could be enhanced (18).

The responses of viruses, vectors, and hosts to increasing temperatures are clearly complex, and the outcome of increased temperatures is a result of many distinct biological processes. Most predictions about the impacts of increased temperature are derived from lab or growth chamber experiments carried out under highly controlled conditions. These studies are informative and have the advantage of precision, but they clearly lack realism. Recently, some researchers have attempted to address the effect of warming in field experiments, which have the advantage of integrating multiple virus, vector, and host processes under more realistic environmental conditions. For example, in a 3-year field experiment that used infrared heaters to elevate growing season temperatures by 3°C, Rúa et al. (114) found increased aphid colonization and a higher prevalence of YDVs in tall fescue-dominated grasslands with elevated temperatures. This suggests that any enhancement of gene silencing resulting from higher temperatures was outweighed by increased growth rates of aphid populations. On the basis of this study, we would expect rising temperatures to favor increased viral disease in temperate grasslands and potentially in grain crops.

Effects of Drought

Other predicted impacts of climate change include changes in precipitation regimes and increased frequency, intensity, and duration of extreme weather events, which may have significant impacts on the epidemiology of YDVs. Drought can negatively affect productivity in both natural and agricultural ecosystems and impair plant growth by altering plant physiology, such as water use efficiency (65, 111). Monneveux et al. (89) emphasized that 40% of the world's cereal growing areas are in arid regions, and as much as 60% of the total area experiences drought. Recent estimates suggest that from 1964 to 2007, drought reduced cereal yields by 10% globally (71). Given current and predicted occurrence of drought, understanding the interaction of drought and infection by YDVs on cereal crops and grasslands is essential.

Studies of both natural and experimental drought indicate that yield losses to YDVs are exacerbated by drought (89). Infected plants are associated with decreased shoot growth and reduced grain quality (16) as well as reduced root system growth and root-to-shoot ratios, resulting in shorter roots that provide insufficient water supply (47). Shah et al. (122) suggested that diminished root systems due to infection with YDVs may reduce plant resistance to abiotic stressors in general. In early attempts to breed crops for tolerance to YDVs, it was thought that tolerance could be achieved through selection for drought tolerance and that variability in drought tolerance may be partly related to the presence or absence of YDVs (89). More recently, a greenhouse drought experiment demonstrated that the order of stressor events (drought and infection by YDVs) is important in both predicting and understanding the incidence of YDVs (24). The authors found that when PAV infection occurred before water deprivation, plant performance was not reduced by virus infection, and infected plants recovered from severe stress more readily than uninfected plants. Smyrnioudis et al. (128) examined the effects of different levels of experimental drought stress on the dispersal of wingless R. padi and examined spread of YDVs at different temperatures. In this study, drought-stressed wheat plants were more likely to become infected than nonstressed plants. Moreover, drought-stressed wheat plants grown in the higher temperature treatment (15°C) were more frequently visited by R. padi and consequently had more infection with YDVs.

Future climate regimes are highly likely to alter the abundance of insect virus vectors (109). Insect pest abundance and resulting plant damage are expected to rise with increasing temperatures due to faster population growth and increased consumption rate (27). Although temperature can be used to predict changes in insect abundance, effects of drought are harder to predict. Past drought studies on vectors have shown variable results. For example, *R. padi* can respond positively (10), negatively (44), or neutrally (102, 115) to drought.

Wade et al. (140) combined a controlled growth chamber study with an experimental field study to better understand the impact of predicted precipitation scenarios on barley performance, aphid herbivory, and aphid predation. In the growth chamber experiment, aphid biomass increased by 15% in drought treatments where water was severely reduced, consistent with a previous study that found increased *R. padi* fecundity in conditions with low humidity (70). However, the field

experiment detected no effect of soil drought on *R. padi* abundance or biomass (140). This suggests that other environmental factors that vary under field conditions, such as temperature or humidity, may buffer the potential effects of soil drought on aphids. There is some evidence that the beginning of a dry period may be particularly important in the annual cycle of YDVs, which involves aphid migrations (89).

Drought stress has been shown to increase aphid movement and result in the increased transmission of YDVs (10). Drought leads to an increase in alate aphids, yet under more severe drought, aphid migrations can be limited by aphid desiccation (89). More recent work has also found that the effects of drought on phloem-feeding insects may depend on the strength of the drought event (48). Davis et al. (24) suggested that the interactions between wheat and YDVs shift along gradients of water stress severity and duration. In this study, chronic drought stress increased wheat tolerance to infection by YDVs while also enhancing population growth of aphid vectors. Njue et al. (95) explored the interactions between *R. padi* and ground-dwelling predators during experimental soil drought manipulations. Under drought conditions, when soil moisture was limiting, *R. padi* moved belowground, where they experienced increased predation but only in dry soil conditions. However, the net effect of soil drought on aphid abundance was neutral because an increase in aphid abundance aboveground compensated for increased predation belowground.

Drought can also influence interactions between *R. padi* and parasitoids (8, 57). Aslam et al. (8) showed that simulated summer drought did not change aphid abundance but did alter aphid population demography, resulting in more adults in drought treatments. Consequently, parasitism rates were lower in drought treatments likely due to the lower incidence of nymphs, which may be easier to parasitize. Johnson et al. (57) found that drought reduced aphid abundance by more than 50% and that the negative impact on aphid density was more severe with earthworm presence when plants were under drought stress. The reductions in aphid abundance also reduced the abundance of the aphid parasitoid, *Aphidius ervi*, which was further negatively affected by drought. Altogether, these studies continue to demonstrate that the YDVs pathosystem is complex and that the outcome of plant–vector interactions are challenging to predict under future climate change scenarios.

An increase in extended droughts may limit vector population growth, thereby reducing pathogen spread, and reduce populations of alternative hosts of vectors or viruses that can serve as reservoirs (59). However, Davis et al. (24) found that chronic drought stress in wheat increased its tolerance to infection by YDVs while also enhancing population growth of aphid vectors. Extreme rainfall events might wash vectors off plants while providing moisture that allows the survival of reservoir hosts. In the 3-year field experiment mentioned above, Rúa et al. (114) found that increased precipitation resulted in a higher prevalence of YDVs in tall fescue when it was infected with a common fungal endophyte but not when it was endophyte-free. In this experiment, temperature and precipitation had independent effects on virus prevalence, and there were no interactive effects. Overall, the epidemiology of vector-borne pathogens in response to changes in precipitation is very complex, and studies designed to predict this response have produced variable results.

Effects of Elevated CO₂

Atmospheric CO₂ concentrations are rising and are expected to continue to rise in the coming decades (17). Past studies on the effect of elevated CO₂ on plant growth have found that elevated CO₂ has a positive fertilizing effect on plants (76, 92). Elevated CO₂ can increase plant growth, agricultural yields, and water use efficiency (64, 76) via reduced stomatal conductance and transpiration (22, 32). Although many of these studies have reported positive effects of increased CO₂

on growth of uninfected plants, there are fewer studies examining the effects of elevated CO_2 on the epidemiology of YDVs. To date, studies have predicted an increase in the prevalence of YDVs under elevated CO_2 conditions (76, 134), but it is useful to consider the effects of elevated CO_2 on the complete pathosystem: the viruses, the vectors, and the virus-infected plants.

The effects of elevated CO_2 on YDVs can be assessed by measuring disease prevalence within a plant community or measuring virus titer within an individual plant. A field study over four growing seasons and across four YDVs (BYDV-PAV, BYDV-MAV, CYDV-RPV, and MYDV-RMV) and eight wheat cultivars that examined the natural incidence of YDVs under ambient and elevated levels of atmospheric CO_2 found that virus incidence was higher under elevated CO_2 than in ambient CO_2 (134). This study was the first to examine effects of elevated CO_2 on the incidence of YDVs under field conditions, with natural aphid immigration into the study plots. Greater virus incidence in plots with elevated CO_2 may indicate that aphids showed a preference for elevated CO_2 plots and plants grown under these conditions (134). Future studies should be mindful of this potential source of variation when examining the effects of elevated CO_2 on viral disease prevalence.

Experimental manipulations of CO_2 also influence virus titers in host plants. When PAVinfected plants were grown under elevated CO_2 , virus titer in wheat plants increased by 36% compared to wheat plants in ambient CO_2 treatments (135). Although these plants also had increased growth with elevated CO_2 , this did not fully explain the higher virus titer. An increase in virus titer could result in earlier, more severe symptom development and greater attractiveness to aphids, leading to greater virus spread. Furthermore, it is possible that under future elevated CO_2 , YDVs will cause more severe yield losses because high virus titer is associated with lower yields (54). Overall, these findings suggest that the YDVs are both sensitive and responsive to increases in the level of atmospheric CO_2 .

There are relatively few studies examining the effects of elevated CO_2 on plants infected with YDVs (135). Stunted growth is a characteristic symptom of the YDVs under ambient CO_2 ; however, this is not always the case in elevated CO_2 experiments. Under elevated CO_2 , oats (*Avena* sativa) infected with PAV showed an increase in both aboveground and belowground biomass when compared to healthy controls (76). This increase in the prevalence of infected biomass may increase virus reservoirs and aphid populations (76). Increased CO_2 has also been reported to increase plant physiological performance (mid-day photosynthesis and water use efficiency) in both infected and uninfected plants. Further, elevated CO_2 alters plant antioxidant defense systems (138, 139) and plant nitrogen concentrations declined by 19% and 31%, respectively, in PAV-infected plants compared with infected plants grown in ambient CO_2 . This is especially important for insect-vectored viruses because vector population dynamics and behavior depend on plant nutritional content.

Elevated CO_2 may affect many aspects of aphid behavior, and understanding vector responses is essential to accurately predict future viral prevalence under climate change. Here, we focus on the developmental and behavioral responses of *R. padi* to elevated CO_2 , as it is one of the best-studied vectors of YDVs, but we acknowledge that responses of other vectors might vary somewhat. Responses of *R. padi* to experimental CO_2 elevations have largely pointed toward decreased aphid fitness. A reduction in population size of *R. padi* was observed in tall fescue (*Festuca arundinacea*) under elevated CO_2 (94). Trębicki et al. (136) also found reduced fecundity and population growth rates of *R. padi* on uninfected plants under elevated CO_2 but found no change on PAV-infected plants regardless of CO_2 treatment. This finding suggests that lower aphid populations are expected on uninfected plants, whereas there may be no change or even increased aphid populations on infected plants. However, when CO_2 and temperature were simultaneously elevated, the fitness of *R. padi* was not affected regardless of the host's infection status (92). Clearly, more research is needed to clarify aphid response to elevated CO_2 .

Climate change is already affecting many climate patterns and weather extremes across the globe (81). Climate models predict increases in global surface temperatures and changes in precipitation regimes due to increasing CO_2 emissions, all of which have consequences on the YDV pathosystem (**Figure 3**). According to Saulescu et al. (116), these changes could potentially make YDVs the most dangerous disease of cereal crops.

THE MANAGEMENT OF YELLOW DWARF VIRUSES

YDVs can be difficult to manage because of their wide host range and complex vector interactions, and effective management of YDVs varies according to local conditions and geographic locations (141). In general, YDVs within agricultural landscapes have been managed by selecting tolerant or resistant cultivars, adjusting planting dates to vector phenology, or using foliar pyrethroid sprays or neonicotinoid seed treatments. These methods have provided fairly successful management of YDVs for many years now. Typically, YDVs incur relatively low yield losses in the United States, Europe, and Australia, although some northern US states are reported to experience more significant losses (84, 141). However, more recently, concerns regarding the negative environmental impacts of insecticides on nontarget pollinators have encouraged the European Union to begin moving away from the use of several insecticides against aphid vectors (84). Moreover, Dewar & Foster (28) suggest that pyrethroid resistance genes found in S. avenae populations in the UK may be related to the 2012 and 2016 BYDV outbreaks in the UK. Ongoing challenges to BYDV management in Europe include limitations on the use of insecticides, the development of pesticide resistance in aphids, the relative paucity of resistant or tolerant varieties, and climate change (84). However, a recent study has suggested that using the parasitic wasp Aphidius colemani for biocontrol of R. padi will be an effective measure of management under future environmental conditions of increased CO_2 and increased temperature (92).

Although extensive efforts have been made to manage YDVs in crops, there has been comparatively less focus on understanding the epidemiology of YDVs in natural systems at the agroecological interface (but see 5). Given that YDVs are overwintering in perennial and weedy species in noncultivated ecosystems, understanding the epidemiology in natural systems can help manage viral disease spillover into agricultural systems as well as spillback from agriculture into endangered grassland systems.

SUMMARY POINTS

- Yellow dwarf viruses (YDVs) are globally distributed and affect both agricultural and noncultivated ecosystems. Research on YDVs in agroecosystems is extensive, but research in natural systems is still limited, despite the susceptibility of noncrop hosts. Many susceptible native perennial grasses are found in imperiled or degraded grasslands that support high biodiversity, soil and water conservation, and grassland bird habitat. The impact of YDVs is an understudied threat to noncrop grasslands.
- Population dynamics, movement, and preference behavior of aphid vectors are influenced by host plant infection by YDVs and whether the vector is carrying the virus. Symptomatic changes in plant color and volatiles contribute to nonviruliferous vectors preferentially settling on infected plants; viruliferous aphids may prefer uninfected

plants. Aphids also experience higher fecundity and produce more alates on infected plants. Models indicate that changes in population dynamics on infected plants and aphid preference behavior enhance virus spread.

3. Climate change is highly likely to influence the prevalence of YDVs, although viral dynamics may differ across regions according to specific environmental conditions. Increasing temperatures are expected to result in increased vector fecundity and abundance as well as increased within-host YDV titers. Drought can increase vector movement and the transmission of YDVs. Increases in temperature and drought may amplify the prevalence of YDVs; however, elevated CO₂ has shown no effect on aphid vectors despite increasing virus titer within plant hosts. More accurate predictions of the dynamics of YDVs under climate change require more research on how vectors and plants infected with YDVs respond to current and predicted environmental change.

FUTURE ISSUES

- Current research on YDVs is heavily weighted toward studies of grain crops and weedy annual grass systems globally. However, studies indicate YDVs are ubiquitous within noncrop native perennial grasslands, including California coastal systems, tall- and shortgrass prairie, and savanna in the Pacific Northwest, the Midwest, and eastern North America. The epidemiology and ecological consequences of YDVs in these systems are unknown in most cases, as is the influence of land management and climate change on disease impacts.
- 2. The direct study of vector and movement of YDVs between grain crops and weedy annual grass systems at a landscape scale is also underrepresented in the literature.
- 3. Future studies should investigate the effects of host infection on vector behavior in lessstudied aphid species and morphs, at larger scales in the greenhouse and the field, and by using noncrop plants in behavioral assays. Determining aphid preference for infected versus uninfected plants across a plant's anatomy and throughout its life span would also help farmers and grassland managers predict the spread of YDVs.
- 4. More research is needed to predict the effects of climate change on the YDV pathosystem. Exploring the interacting effects of elevated CO₂, temperature, and climate extremes, such as drought, will enable more accurate predictions of the impacts of YDVs on both agricultural and noncultivated grass communities.

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