



Drought stress alters a host-vector-pathogen interaction

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Viral pathogens are ubiquitous and can impose limitations on agricultural productivity. Despite their prevalence, host-virus interactions are seldom considered as potentially beneficial, and until recently studies of plant viruses focused primarily on the damaging physiological effects of infection on host plants. However, recent evidence suggests that virus infection is not always harmful to plants, and many viruses found in plant tissues exhibit few, if any, symptoms in their hosts, leading researchers to question whether plant viruses have ecological significance that extends beyond their role as pathogens.

IMPACT

Plant viruses do not always harm their hosts, and in some situations may even benefit them. Our recent research suggests that Barley yellow dwarf virus–*Padi-avenae* virus (BYDV) infection does not harm host wheat plants when water is limited, and that under severe drought stress, infection may help plants to survive.

We tested whether environmental stress alters host-virus interactions in an agroecosystem comprising an herbivore virus vector (*Rhopalosiphum padi* L.), wheat, and an insect-borne viral pathogen (Barley yellow dwarf virus–*Padi-avenae* virus, BYDV-PAV). Our approach evaluates interactions

between water stress and virus infection in this system. Prior to experiments testing interactions between water stress and host plant infection, we confirmed that plant water stress could be reliably manipulated by top-watering plants at different quantities. We performed experiments to answer the following two questions: (1) Do water quantity and pathogen infection interact to affect host plant growth and seed set when watering treatments are applied over the life of hosts? and (2) Does host infection have consequences for host vital rates when plants are challenged by drought and subsequently allowed to recover? For this question we tested two different types of water stress: short-term water scarcity and longer-term water withholding.

Results. There were significant interactions between host infection status and water quantity when watering treatments were applied over the lifetime of plants. Under low water there was no significant difference in the total number of germinating seeds resulting from plant infection status, indicating a pattern consistent with higher seed set by noninfected plants at high water inputs but no effect of pathogen infection on seed set at low water inputs (Figure 1).

When water inputs were low, infected plants retained more water (Figure 2). Before we imposed water scarcity, host infection status had no effect on leaf water potential, but following a seven-day period of water scarcity, BYDV-PAV-infected plants



Figure 2. *Triticum aestivum* cultivar 'JD' following a challenge with seven days of water scarcity. Infected plants were visibly more turgid and robust at the end of the experimental period. Photo by Seth Davis.

had significantly higher leaf water potentials than either sham-inoculated or undamaged plants. After we resumed watering, host infection status had no effect on seed set, seed mass, germination frequency, or total number of germinated seeds. However, aboveground biomass was greater for virus-infected plants at the end of the experiment than for either sham-inoculated or undamaged plants. After long-term water stress (withholding) followed by recovery, infected plants surpassed uninfected control plants in biomass growth, seed set, absolute and relative seed germination frequency, and seed mass. Also, the onset and progression of water stress symptoms were delayed for infected host plants in comparison to uninfected control plants (Figure 3).

Discussion. Our results suggest that applying moderate stress through water limitation and withholding shifted host-pathogen interaction from negative to neutral over the lifetime of hosts, but that host wheat plants actually benefited from the infection when abiotic stress became severe. These effects translated directly to host vital rates and productivity, with infected hosts producing more viable seed under severe abiotic stress. Altogether, our results are consistent with a hypothesis of context dependency in this pathosystem and suggest that environmental factors may mediate disease dynamics in agroecosystems, potentially favor-

ing coexistence of hosts, vectors, and pathogens in stressful environments.

Several physiological hypotheses could underlie the patterns we describe here, particularly hydraulic failure, carbon starvation, and biochemical induction. We are focusing our efforts on determining whether systemic induction of broadly bioactive phytohormones in response to infection may be responsible for the effects we observed. In particular, the abscisic acid stress hormone pathway has been implicated in conferring tolerance to water stress following viral infection. There is significant genetic variation in wheat for the induction of this pathway following virus infection, which may have important biotechnology applications and could allow geneticists to select for wheat resistance to drought stress using pathways that are elicited by viruses. We conclude that the ecology of agricultural viruses is not intuitive and cannot be understood without considering both costs and benefits to host organisms: in the wheat-BYDV-aphid system, we propose that control efforts for viruses may not be necessary in drought years. Future research in this area will evaluate how these complex symbiotic interactions may be exploited to promote agroecological resilience under climate change, with efforts focused on identifying genetic patterns underlying the effects we report here.

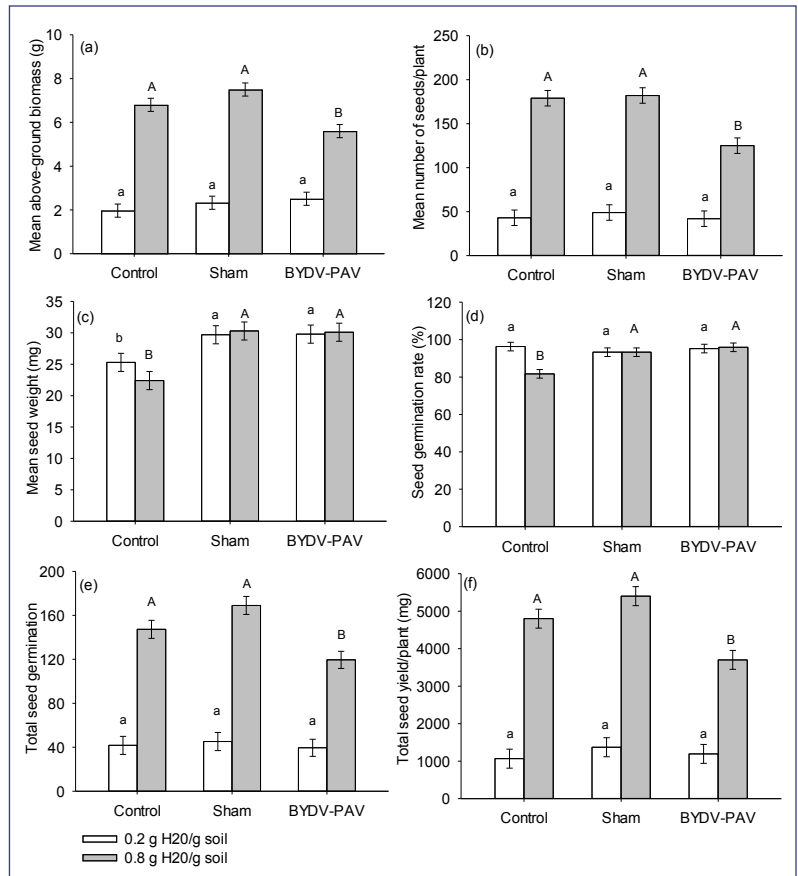


Figure 1. Interaction between water quantity and Barley yellow dwarf virus–Padi-avenae virus (BYDV-PAV) infection on (a) aboveground biomass, (b) seed set, (c) seed weight, (d) seed germination frequency, and (e) total number of germinating seeds for virus- and sham-inoculated *Triticum aestivum*, and control plants. Gray bars denote the high water treatment (0.8 g water per gram soil), and black bar bars denote the low water treatment (0.2 g water per gram soil). Error bars show \pm SE. Lowercase letters denote Tukey's honest significant difference (HSD) test within the low-water group, and uppercase letters denote Tukey's HSD test within the high-water group.

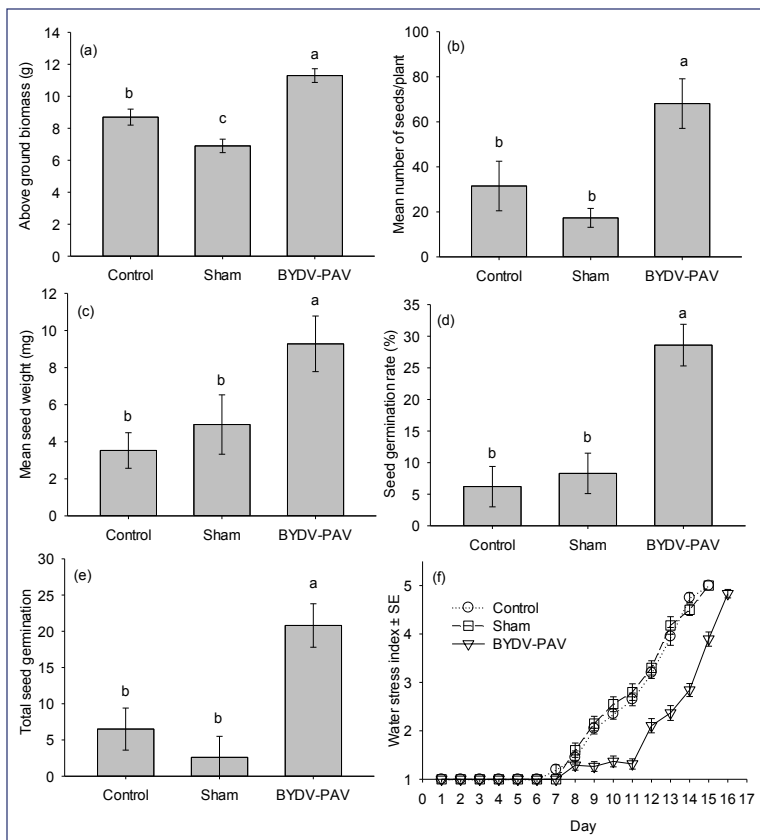


Figure 3. Plant responses following water withholding and recovery. Differences in (a) aboveground biomass, (b) seed set, (c) seed mass, (d) seed germination frequency, and (e) total germination, according to infection status of *Triticum aestivum* following 15-day water withholding and recovery. (f) Time series showing the onset and progression of visual water stress symptoms in *T. aestivum* following water withholding. In all panels, letters indicate Tukey's honest significant difference (HSD) test. BYDV-PAV = Barley yellow dwarf virus–Padi-avenae virus.