Virus infection moderates plant response to water stress

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Introduction

Plant viruses are abundant in many ecosystems, though potentially positive effects resulting from viral infection are seldom explored. It is typically assumed that viral infection negatively impacts plant performance, however; there is mounting evidence to suggest that viral infection can induce plant resistance to environmental stress under certain conditions (Malmstrom et al. 2011).

Utilizing *Triticum aestivum* (Poales: Poaceae) and the insect-transmitted *Barley yellow dwarf–Padi-avenae virus* (BYDV-PAV; Luteoviridae) as a model system, we tested the hypothesis that the impacts of phytovirus infection on plant performance are mediated by water availability, using a series of water limitation and withholding experiments.

We performed three experiments to address this hypothesis:

- A test of low and high water availability delivered over the lifetime of plants;
- A test of low water delivery for a short period followed by recovery;
- A test of water withholding for several weeks followed by recovery

Our experiments demonstrate a clear element of context-dependency in plant-virus in interactions, and our results suggest that viral infection can potentially benefit plants by inducing resistance to stressful environmental conditions.

1

Treatments to manipulate plant water stress

- Prior to experiments testing interactions between water stress and viral infection, we established watering treatments to ensure that plant water availability could be reliably manipulated.
- Experimental watering regimes were applied on a gravimetric basis (g water/g soil), and consisted of four treatments: 0.1 g H_20/g soil, 0.2 g H_20/g soil, 0.3 g H_20/g soil, and 0.4 g H_20/g soil (10%, 20%, 30%, and 40%).
- Plant tissues were destructively sampled for measurements of leaf water potential (ψ_{leaf}; MPa). Predawn leaf water potential for the apical (flag) leaf on the main tiller of each plant was measured using a Scholander pressure chamber.

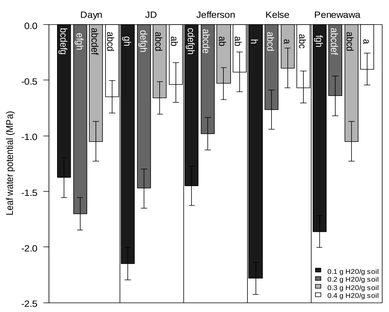

Figure 1. Predawn leaf water potential measurements (ψ_{leaf}) for five genotypes of *Triticum aestivum* maintained on four gravimetrically applied (g water/g soil) watering regimes for 15 d. Bars represent one standard error.

2

Interactions between water availability and virus infection

- Our first experiment was designed to test how interactions between water availability and viral infection would impact plant performance and fitness when watering treatments were applied over the life of plants.
- Experimental watering treatments were initiated at 15 d following inoculation, with half the plants receiving a 'high' water treatment (0.8 g H_20r/g soil), and half the plants receiving a 'low' water treatment (0.2 g H_20/ g soil, for a total of n = 6 possible treatment combinations (three infections statuses x two watering regimes) with ten replications per treatment.
- We analyzed the effects of plant infection status and watering regime and their interaction on above-ground plant biomass , seed production, mean seed mass, relative germination rate (%), total number of germinated seeds.

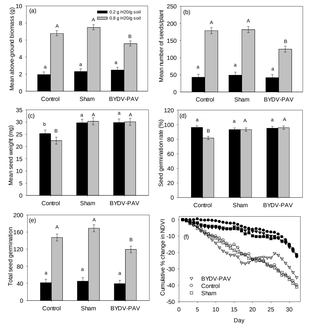

Figure 2. (a) Above-ground biomass, (b) seed production, (c) mean seed weight, (d) seed germination rate, (e) total number of germinating seeds for virus- and sham-inoculated *Triticum aestivum*, and undamaged control plants, and (f) cumulative changes in NDVI over time. In (a)-(e) gray bars represent plants receiving the 'high' water treatment (0.8 g water/g soil), and black bar bars represent plants receiving the 'low' water treatment (0.2 g water/ g soil). Error bars show ± SE. Lower-case letter denote Tukey's HSD test within the low-water group, and upper-case letters denote Tukey's HSD test within the high-water group. In panel (f), the high water treatment is denoted by closed symbols, and the low water treatment is denoted by open symbols.

3

Low water and recovery

- At 15 d following inoculation, predawn ψ_{leaf} was measured for each plant.
- We then initiated a drought watering regime that consisted of watering all plants at the lowest (0.1 g H_20/ g soil) level for 7 d.
- At the end of the 7 d period, we again measured ψ_{leaf} for each plant. After the second measurement of ψ_{leaf}, we watered *ad libitum* until plants reached maturity and yield.

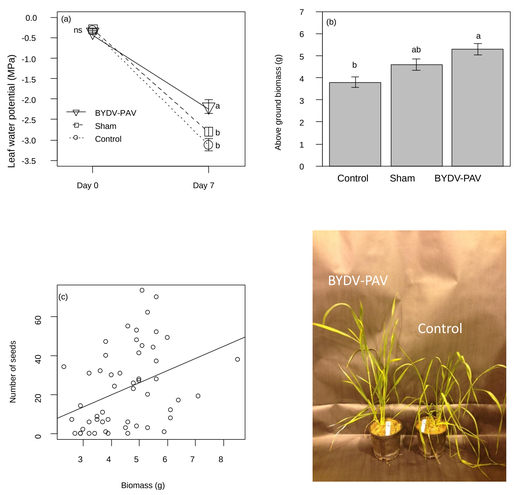

Figure 3. (a) Predawn leaf water potential measurements (ψ_{leaf}) from 30 d-old *Triticum aestivum* inoculated with *Barley yellow dwarf virus–Padi avenae virus* (BYDV– PAV; ▼), sham inoculated plants (nonviruliferous aphids; □), and undamaged control plants (○) prior to (Day 0) and following (Day 7) exposure to experimental drought. Bars represent one standard error, and lower case letters denote Tukey's HSD test. Plants inoculated with BYDV-PAV were visibly more turgid than uninfected plants by Day 7 (see picture). (b) The effect of plant infection status on above-ground biomass following exposure to episodic drought. (c) The relationship between plant biomass and seed production ($F_{1, 51}$ = 8.319; P = 0.005; Equation: number of seeds = -4.821+6.204[biomass].

4

Water withholding and recovery

- At 15 d following inoculation, water was withheld from plants, and plant decline was recorded daily for 15 d using the leaf water stress symptom index developed in O'Toole & Cruz (1980).
- After withholding water for 15 d, plants were subsequently watered *ad libitum* to initiate recovery.
- We analyzed onset and severity of drought symptoms, above-ground biomass, seed production, mean seed mass, and absolute and relative (%) rates of seed germination.

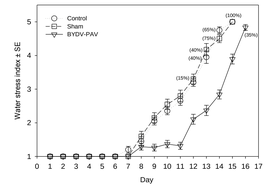

Figure 3. Time series showing the onset and progression of visual water stress symptoms in *Triticum aestivum* following water withholding. Values in parentheses denote the proportion of plants in each treatment group exhibiting severe visual stress symptoms (water stress index = 5).

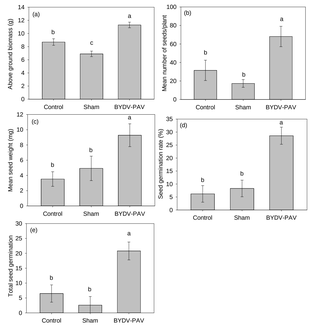

Figure 4. Differences in (a) above-ground biomass, (b) seed production, (c) mean seed mass, (d) seed germination rate, and (e) total germination due to infection status of *Triticum aestivum* following 15 d water withholding and recovery. Letters indicate Tukey's HSD test.

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Summary & Future Directions

- Our experiments suggest that the outcomes of this plant-phytovirus interaction (*T. aestivum-Barley yellow dwarf virus*) are context dependent, and can shift relative to water availability.
- Virus infection exerted a cost on plant fitness when water availability was high, but had neutral effects on fitness when water availability was low.
- Moreover, under short-term water stress conditions followed by recovery, virus infection promoted water retention in plants with no apparent fitness cost
- When water stress conditions were prolonged, viral infection actually enhanced plant fitness relative to uninfected plants

Follow up work on this project will employ chemical analyses to evaluate shifts in phytohormones that may confer tolerance to water stress, particularly abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA).

We will test how phytohormones vary with plant infection and across time, and use hormone knockout mutants (as well as hormone-sensitive and hormone-insensitive mutants) to evaluate whether the effects we describe here are moderated by specific genes. We will also test whether the stress resistance we document here is transferred to offspring via gene activation.

References

Malmstrom, C.M., Melcher, U., & Bosque-Pérez, N.A. (2011). The expanding field of plant virus ecology: historical foundations, knowledge gaps, and research directions. *Virus Res.*, 159, 84-94.

Jiménez-Martínez, E.S., & Bosque-Pérez, N.A. 2004. Variation in Barley yellow dwarf virus transmission efficiency by *Rhopalosiphum padi* after acquisition on transgenic and nontransformed wheat genotypes. *J. Econ. Entomol.*, 97, 1790-1796.

O'Toole, J.C., & Cruz, R.T. (1980). Response of leaf water potential, stomatal resistance, and leaf rolling to water stress. *Plant Physiol.*, 65, 428–432.

Roossinck, M.J. (2011). The good viruses: viral mutualistic symbioses. *Nat. Rev. Microbiol.*, 9, 99-108.

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