



Expectations for habitat-adapted symbiosis in a winter annual grass



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ABSTRACT

The habitat-adapted symbiosis hypothesis predicts that the most positive effects of symbiosis are expected in the most stressful sites for a plant host. Stress varies with site characteristics but also during the life cycle of a plant, with winter annuals experiencing the most stress after fall emergence. For *Bromus tectorum*, fecundity can vary tremendously from a few to thousands of seeds per plant. We used endophytic *Sordaria fimicola* to test the hypothesis in three sites in western Montana. We hypothesized that the effects of *S. fimicola* inoculation would be most positive in the most stressful site after fall application. As predicted, the most positive effects on growth and fecundity were observed in the most stressful site after fall application of *S. fimicola*. However, the effects of treatments varied within and between sites considerably, and are best understood as an example of context-dependency in plant-microbe interactions rather than habitat-adapted symbiosis.

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1. Introduction

Endophytic fungi have been isolated from above- and below-ground tissues of all plants examined thus far (Arnold et al., 2000). Endophytes are phylogenetically diverse, but apart from well-studied examples, their ecological functions are largely hypothetical. One hypothesis regarding endophyte function is that of 'habitat-adapted symbiosis' (Rodriguez et al., 2009). According to this hypothesis, some non-clavicipitaceous, systemic endophytes help or enable plants to grow in unproductive, high-stress habitats. Habitat-adapted symbiosis is hypothesized to be critical or even obligate for plants in these habitats (Rodriguez et al., 2008). An outstanding example is that of the complex symbiosis in geothermally heated soil that involves a plant, a fungus, and a virus (Marquez et al., 2007). Another is the increased fitness of *Oryza sativa* in saline environments that has been attributed to infection by endophytic *Fusarium culmorum* (Rodriguez et al., 2004; Rodriguez and Redman, 2008; Redman et al., 2011).

Similarly, drought is an abiotic stress that can be alleviated by

endophytes (Rodriguez et al., 2008). Disease represents a more complex biotic stress for plants, because the severity of a given disease can be modified by a large number of endophytes in either direction, and a single plant can simultaneously experience multiple diseases (Busby et al., 2015). However, for abiotic stresses such as heat and drought, a generalized form of the habitat-adapted symbiosis hypothesis of Rodriguez et al., (2009) can be stated as follows: the positive effects of endophyte-plant symbiosis are expected to be greatest in the most stressful environmental conditions a plant can tolerate.

Stress for plants varies not only along abiotic, environmental gradients, but also phenologically during the life cycle of a plant. Winter annual grasses, such as *Bromus japonicus* and *Bromus tectorum*, experience greatest stress during the winter after fall germination (Baskin and Baskin, 1981; Mack and Pyke, 1984). This is likely to mean that the timing of endophyte infection matters, although most of the literature relating to this area is focused on order of assembly of members of the symbiont community rather than on life cycle of hosts. For example, the order of assembly of microbial communities can produce endophyte-pathogen interactions that vary from inhibitory to facilitative (Adame-Álvarez et al., 2014), or it can affect microbiome structure (Pan and May 2009; Cannon and Simmons, 2002).

In our test of the habitat-adapted symbiosis hypothesis, we

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simply predicted first that fall applications of a symbiont would affect *B. tectorum* more positively than spring applications within a given site. Secondly, we predicted that as site productivity increased for *B. tectorum* symbiont effects would become less positive. In other words, we predicted that the most positive overall effect would follow fall application in the least productive site. We employed a strain of *Sordaria fimicola* (CID 323) that was previously shown to increase growth and fecundity of *B. tectorum* (Newcombe et al., 2016), an invasive annual grass in western North America. Three sites with different biotic and abiotic stress characteristics, predicted to vary in *B. tectorum* productivity, were chosen at a location in the Bitterroot Valley, MT, and sites were divided into plots which were treated as uninoculated controls and others in which *B. tectorum* plants were inoculated in either fall or spring with *S. fimicola* spore suspension.

2. Materials and methods

2.1. Isolation and culturing of *S. fimicola* (CID 323)

The Moscow strain of *S. fimicola*, designated as CID 323, was isolated from *B. tectorum* plants collected on Moscow Mountain (near W Twin Rd, 46°48'45.7"N 116°55'11.0"W) at approximately 1,280 m elevation at a site with minimal slope, an aspect of ~300, on the roadside in a mixed conifer stand where *B. tectorum* was estimated at < 5% cover. Endophytic *S. fimicola* was isolated from surface-sterilized plant tissue incubated on potato dextrose agar (PDA) using methods previously described (Baynes et al., 2012a; Newcombe et al., 2016). Cultures were maintained by subculturing onto PDA from reference cultures stored at 4 °C. Each plate of *S. fimicola* was examined microscopically (for appropriately formed and colored asci and ascospores) when producing perithecia to ensure that cultures were viable. Cultures with malformed or discolored perithecia, asci, or ascospores were discarded.

2.2. Choice of field sites

Field plots were established at three different sites (Table 1) on MPG Ranch land in the Bitterroot Valley, MT. The site judged to be the least stressful, or most productive, for *B. tectorum* was at the bottom of a wide draw with a 2% slope. The draw collects water from surrounding upland areas in the spring, and soils at this site are loamy in texture and contain little to no gravel to a depth of 20 cm. The site chosen as moderately stressful was more westerly (SSW) and mid-slope on the side of a wide draw, with more afternoon sun and gravelly sandy loam. The most stressful site was the steepest, with soils and aspect similar to the moderate site, but with more exposure to wind and sun than the other sites. It had the highest percentage of gravel and bare ground. To these site observations was added an assessment of soil resistance to root

penetration at each site with a soil hammer penetrometer. In the center of nine sub-plots at each site, we counted the number of hammer strikes needed to drive a 1.12 cm steel bar to a depth of 20 cm (Donaldson, 1986), in the expectation that soil resistance to root penetration would be inversely correlated with growth and fecundity of *B. tectorum*. In order to reach 20 cm, the least stressful site required an average of 12 strikes of the hammer; the moderately stressful site required an average of 19 strikes of the hammer; and the most stressful site required an average of 31 strikes of the hammer.

2.3. Inoculation of *B. tectorum* with *S. fimicola* in the field

Inoculum was produced by incubating cultures on PDA at ambient laboratory conditions (20 °C with a 10:14 light:dark photoperiod) for 28 d. Petri dishes with mature perithecia were scraped into sterile deionized water (SDW) and shaken to form a suspension of spores and mycelium. In total, 14 plates of mature *S. fimicola* were suspended in 5 L SDW. Final concentration of spores and mycelial fragments were estimated using a hemocytometer at ~1.05 million fungal units per mL of SDW.

Each site was divided into 9 sub-plots of 3 × 5 m, with 1 m strips separating sub-plots, and treatments assigned to sub-plots so that each row and column contained each treatment level (control, spring application, and fall application). In early December 2012, after germination and emergence of *B. tectorum* was confirmed at the field sites, and there was sufficient precipitation (primarily light snow) to ensure constant leaf moisture, *S. fimicola* inoculum was applied to the three fall application sub-plots at each of the three sites at a rate of approximately 0.5 L per sub-plot with a backpack sprayer.

In March of 2013, after snowmelt and during a period of continuous light rain, *S. fimicola* inoculum was applied to a further three sub-plots of each site at a rate of approximately 0.5 L per sub-plot with a backpack sprayer (with inoculum prepared in the same manner and quantities as described above). The final three sub-plots of each of the three sites were treated as uninoculated controls (treated with SDW rather than *S. fimicola*). Infection was confirmed by isolating *S. fimicola* from leaf samples from treatment plots using standard surface sterilization and plating on potato dextrose agar (c.f., Baynes et al., 2012a; Newcombe et al., 2016).

2.4. Observations and sampling

Beginning in early summer, weekly observations of plots were made to monitor progress towards seed ripening and plant senescence in *B. tectorum*. When plants had dried sufficiently that little additional growth was expected, but before seed shatter, 5 cm × 10 cm cotton bags were tied around at least 100 inflorescences per sub-plot to collect the seeds. We left the plants to

Table 1
Site descriptions.

| Site | Aspect (°) | Elevation (m) | Slope (%) | Plant Species (>5%) | Cover Estimates | Habitat-type | Average Penetrometer Strikes |
|----------------------|------------|---------------|-----------|---|--|--------------------------------|------------------------------|
| Least Stressful | 170 | 1113 | 2 | <i>Bromus tectorum</i> (50%) <i>Sisymbrium altissimum</i> (5%) | bare ground (5%) litter (40%) | annual grass monoculture | 12 |
| Moderately Stressful | 205 | 1200 | 11 | <i>Poa bulbosa</i> (18%) <i>Hesperostipa comata</i> (17%) <i>Poa secunda</i> (7%) <i>Euphorbia esula</i> (6%) <i>Bromus tectorum</i> (5%) <i>Centaurea stoebe</i> (5%) | bare ground (2%) litter (39%) moss/lichen (53%) gravel (3%) | shrubland | 19 |
| Most Stressful | 204 | 1177 | 15 | <i>Bromus tectorum</i> (41%) <i>Hesperostipa comata</i> (32%) <i>Pseudoroegneria spicata</i> (6%) <i>Thinopyrum intermedium</i> (6%) | bare ground (9%) litter (60%) moss/lichen (4%) gravel (12%) | non-irrigated grass plantation | 31 |

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