Fecundity of the aphid *Rhopalosiphum padi* on selected Oregon grasses

by

Vincent T. Adams

A PROJECT

submitted to

Oregon State University

University Honors College

in partial fulfillment of
the requirement for the
degree of

Honors Baccalaureate of Science in Environmental Science (Honors Scholar)

Presented May 31, 2007
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AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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Elizabeth Borer

Barley yellow dwarf virus (BYDV) is a globally distributed pathogen of grasses that is transmitted by aphids. Little research has been done examining the response of aphids to different host grasses in naturally mixed communities. We measured the short-term fecundity of the aphid *Rhopalosiphum padi*, a widely distributed vector of BYDV, on a broad array of Oregon *Poaceae* in field and laboratory experiments to quantify the effect of host grass life history, provenance, phylogeny, and nutrient status on the number of nymphs produced. In both field and laboratory trials aphids had significantly higher rates of fecundity on annuals over perennials regardless of host grass provenance, phylogeny, or age class (in the case of perennials). Nitrogen addition resulted in higher aphid short-term fecundity. Thus, host life history and nitrogen status have an influence on the number of vector insects within a community. This suggests that the presence of infected annual host grasses in a community may cause an increase in overall viral prevalence.

Key words: Rhopalosiphum padi, Barley Yellow Dwarf virus, BYDV, aphids, short-term fecundity, virus vector, grasslands

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APPROVED:

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I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

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INTRODUCTION

Vectored and generalist pathogens have a profound influence over biotic systems worldwide, and have long been known to alter the relationships between invaders and native species. Much of the current invasion theory has focused around the gain or loss of natural enemies (enemy-release theory) and the introduction of novel pathogens altering the progression of invasion (novel-weapons theory) (Borer, 2007). Most of the community ecology research on host-parasite systems has explored a limited range of pathogen-host interactions; largely a single pathogen infecting a community or a community of pathogens infecting a single host. Less research has been devoted to interactions between multiple pathogens in multihost communities (Collinge, 2006). Here we examine the relationship between the vector of a suite of generalist viral pathogens and a community of host species.

Seabloom et al. (2003) demonstrated that annual grass invaders in California systems are inferior competitors for resources compared to native perennials. Despite this, annual grasses have successfully invaded >9 million hectares of grassland in that state. This seemingly paradoxical result has been attributed to anthropogenic disruption and grazing (Baker, 1978). However, new research in this system on the effects of BYDV on exotic annuals and native perennials has revealed that because perennials are reproductively more limited than annuals they suffer more from the viral pathogen (Borer et al., 2007). Conversely, annuals benefit from the partial mortality due to the virus by the reduction of

intraspecific competition, conferring them a competitive advantage over perennials (Malmstrom et al., 2005, Borer et al., 2007). Malmstrom et al. (2005) suggested the invasion of annual grasses into California may have changed aphid population dynamics sufficiently to have altered the prevalence of the Barley Yellow Dwarf virus (BYDV), generating positive feedbacks that maintain and enhance this annual grass invasion. According to Malmstrom et al. (2005), the aphid *Rhopalosiphum padi*, a wide spread aphid vector of BYDV, has greater fecundity on annuals than perennials thus explaining the increase in viral prevalence in perennials as a function of annual presence. However, this research was limited to two invasive annuals, *Avena fatua* and *Bromus hordaeceus*, and three native perennials, *Elymus glaucus*, *Elymus multisetus*, and *Nasella pulchra*.

Here we used a broader array of Oregon *Poaceae* in field and laboratory experiments to determine if the positive relationship between the fecundity of *R. padi* on annual hosts can be generalized. We further compared aphid fecundity across phylogenetic pairing of host grasses to discriminate aphid performance as a function of host genetic similarity. We included invasive perennials in the suite of host plants to further examine the effect of host provenance on aphid fecundity and all hosts in the laboratory experiment were placed in a factorial array of nitrogen and phosphorus fertilizer additions to reveal any differences in aphid fecundity due to changes in host nutrient status.

STUDY SYSTEM

Hosts

The native plant composition of Willamette Valley prairies prior to 1800 was dominated by perennial forbs and grasses including *Bromus carinatus*, *Elymus glaucus*, and *Festuca roemeri* (*idahoensis*) (Wilson et al., 1998), all known to be susceptible to BYDV (*F. roemeri* is symptomless) (D'Arcy, 1995a). Willamette Valley grasslands (Oregon, USA) were invaded significantly by non-native grasses as early as 60 years after settlement (Habeck, 1961). Today most Willamette Valley prairies are a mix of native and exotic species, although some aggressive invaders can form monoculture patches (Wilson et al., 1998). Common exotic grass hosts include *Arrhenatherum elatius*, *Brachypodium sylvaticum*, *Bromus diandrus*, *Bromus hordaeceus*, *Dactylis glomerata*, *Holcus lanatus*, *Festuca arundinacea*, *Poa pratensis*, and *Taeniatherum caput-medusae* (Wilson et al., 1998).

Pathogen

The BYDV suite of pathogens are a group of RNA viruses that infect the phloem carrying structures of cereals and other grasses, and annex a portion of the plants' metabolism for viral reproduction, resulting in chlorosis and stunting in above- and below-ground plant tissues (D'Arcy, 1995a). Because agricultural grains are among the target hosts, BYDV is an economically significant pathogen on a global scale (Lister & Ranieri, 1995). BYDV is

widespread and prevalent in California grasslands, infecting a broad range of native and introduced grasses (Lister & Ranieri). A comprehensive evaluation of BYDV prevalence in the Willamette Valley was not available at the time of writing (Mundt, per com, 2007).

Vector

BYDV is transmitted between host grasses by viral strain-specific aphid vectors. An aphid feeding on an infected grass inserts its stylet-shaped mouthparts through the outer tissues of the plant into the phloem bearing sieve-tube elements where the virus resides (Gray, 2003). Viral uptake can occur in as short as 1-5 minutes after phloem access

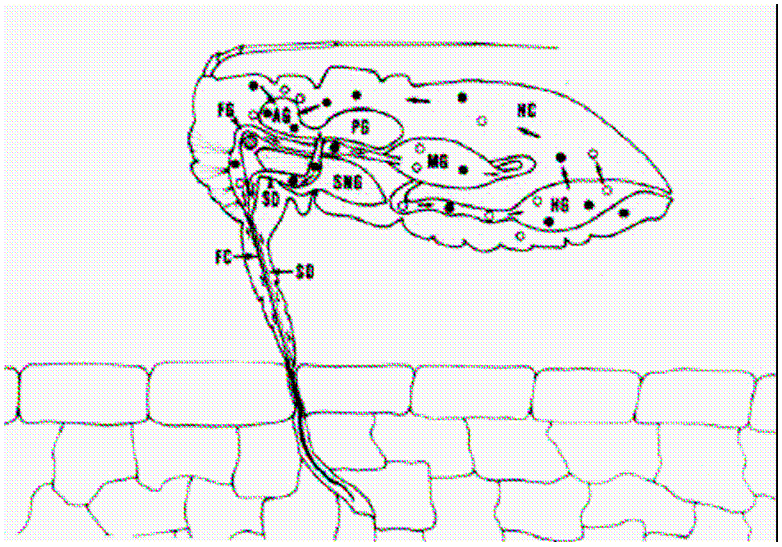

Figure 1 The circulative route of luteoviruses through an aphid. Ingested virus moves up the food canal (FC), through the foregut (FG) and accumulates in the midgut (MG) or hindgut (HG). Virus is then acquired into the hemocoel (HC). Virus may also accumulate in the hemocoel and remain viable for weeks. Transmissible viruse (black hexagons) is transported into the accessory salivary gland (AG), but does not associate with the principle salivary gland (PG). Transmissible virus is then injected into the plant through the salivary duct (SD) when the aphid feeds on a plant. (reproduced from Gray, 2003)

(Leonard, 1978), after which the virus is selectively transported across the tissues of the aphid's hind gut into the hemocoel (Gray, 2003). The dormant virus travels in the hemolymph until it is expressed in the salivary glands of the aphid. When an aphid carrying the virus feeds on an uninfected plant, the virus is injected into the potential host with the salivary fluids (Gray, 2003).

R. padi or Birdcherry-oat aphid is a broadly distributed insect that feeds on a variety of grasses and is a frequently reported vector of BYDV (Halbert and Voegtlin, 1995). In the spring, this species moves from its overwintering host, *Prunus* cherry trees, to grasses and grain fields where it reproduces asexually bearing live nymphs throughout the growing season.

METHODS

Field Experiment

Short-term aphid fecundity was examined by Borer et al. (2006) in an outdoor experiment that compared the performance of *R. padi* on a single invasive annual host species and a single native perennial host species in California grasslands. The experiment performed in Oregon closely followed the design of the California experiment to determine if host life history, phylogenetic grouping, or provenance has an influence on the fecundity on

Table 1 Field experiment host species

species	common name	life span	provenance	group
Bromus hordeaceus	soft brome, soft chess	A	X	brome
Bromus carinatus	California brome	P	N	brome
Avena fatua	wild oat	A	X	oat
Arrhenatherum elatius	tall oat	P	X	oat
Taeniatherum caput-medusae	medusa-head rye	A	X	rye
Elymus glaucus	blue wild-rye	P	N	rye
Cynosurus echinatus	bristly dogs-tail grass	A	X	fescue
Festuca arundinaceae	tall fescue	P	X	fescue

(A) annual; (P) perennial; (X) exotic; (N) native aphids.

We performed the field fecundity experiment in June of 2006 at Basket Butte National Wildlife Reserve, an area characterized by upland prairie interspersed with young upland oak groves. The reserve is surrounded largely by grass seed agriculture. The climate is mild with a long growing season. The region receives 40 – 60 inches of precipitation

annually and the temperature ranges from approximately 27°C in the summer to a winter mean of 7°C.

We selected eight host grass species for use in the experiment (see Table 1). Of these, two were native perennials and the rest were either annual or perennial exotics. Each species was grouped with one other species based on phylogenetic similarity, thus yielding four groups: bromes, oats, ryes, and fescues. Sleeves of 118 µm polyester mesh (Sefar America Inc. Kansas City, MO) were constructed, each 8 cm long by 2 cm wide, and were affixed to individual grass blades with pressure sensitive laboratory tape (VWR brand) forming a pouch. A single mature apterous *R. padi* was placed into each pouch and sealed. A sleeve containing an aphid was applied to single host grass individuals, and blades were chosen based on health. Individual host grasses were selected randomly but were in groups for ease of sleeve recovery. Aphids used were cultured from individuals collected locally from corn plants found near Corvallis, OR. For the field fecundity experiment they were raised on *Avena sativa* in Percival Intellus environment chambers at 22°C, 75% humidity, and a 24 hr light cycle. The aphids were left in the pouches four days. The pouches were clipped from the plants and returned to the laboratory where each was opened under a dissection microscope (Zeiss, Stemi 2000), the status of the aphids was assessed, adult and young aphids counted, and enclosed leaf area measurements taken. A total of 160 pouches were deployed (20 pouches per host species), in two groups of 80 pouches; the deployments were separated by five days. Data from both deployments were combined, and were analyzed with poisson regression analysis.

Laboratory Experiment

Short-term aphid fecundity was examined by Malmstrom et al. (2005) in a greenhouse experiment that compared the performance of *R. padi* on two invasive annual host species and three native perennial host species in California grasslands. Borer et al. (2006) examined the effect of nitrogen addition on aphid fecundity in field plots. To determine the effect of varying soil nutrient status on short-term aphid fecundity the design of the field experiment repeated in the laboratory with a factorial addition of fertilizer.

Two native perennials were added to the list of eight host species used in the field experiment (see Table. 2) for a total of ten host species retaining the four phylogenetic groups. Seed for the original eight species was obtained from the Basket Butte

Table 2 Lab experiment host species

species	common name	life hx.	provenance	group
Bromus hordeaceus	soft brome, soft chess	A	X	brome
Bromus carinatus	California brome	P	N	brome
Avena fatua	wild oat	A	X	oat
Koeleria cristata	prairie junegrass	P	N	oat
Arrhenatherum elatius	tall oat	P	X	oat
Taeniatherum caput-medusae	medusa-head rye	A	X	rye
Elymus glaucus	blue wild-rye	P	N	rye
Cynosurus echinatus	bristly dogs-tail grass	A	X	fescue
Festuca roemeri	Romer's fescue	P	N	fescue
Festuca arundinaceae	tall fescue	P	X	fescue

(A) annual; (P) perennial; (X) exotic; (N) native

site in mid summer of 2006. The seed for the two additional species was purchased from a local commercial seed grower that specializes in native plants.

The seeds were started with various techniques that resulted in the highest germination rates. *E. glaucus*, *F. arundinaceae*, *A. elatius*, *B. carinatus*, and *K. cristata* were germinated in commonly available zipper-style plastic bags with a single 23.6cm x 26cm

square brown paper towel (Envision brand, Georgia Pacific Inc.) folded in quarters and moistened to provide substrate. *B. hordeaceus* and, *C. echinatus*, were germinated in 9 cm x 9 cm x 1.5 cm covered square plastic Petri dishes with the same paper towel folded to fit as moist substrate. Inducing *T. caput-medusae* to germinate required a 6-day cold stratification in a refrigerator (approximately 2°C), and *F. roemeri* required 18 days of cold stratification, after which these seeds were started in dishes as above. *A. fatua* proved to be challenging to start in the lab, but sufficient germination rates were achieved by after-ripening the seeds for two weeks at 26°C, then using three daily applications of 100ppm concentration gibberellic acid solution during the germination process in square Petri dishes.

Two hundred 656 cm^3 (7cm dia x 45cm depth) black polyethylene planter cones were filled with planting medium (Sunshine Grower's Mix A, Sungro Inc., Vancouver, Canada) to 2 cm from the top. Nitrogen and phosphorus fertilization was applied in a factorial arrangement (N, P, N +P, and none). There were five replicates of each treatment for each species (5 reps × 4 treatments × 10 species) for a total of 200 cones. Where indicated, 0.993g ± 0.005g of $Ca(NO_3)_2$ and 0.342g ± 0.005g of $Ca(H_2PO_4)_2$ were added to the top of the soil in the cones, then mixed in to depth of 5cm to simulate typical fertilizer application levels. The cones were then topped with untreated growing medium. The individual pre-germinated starts were planted in the cones and placed in racks of 20 cones each. The racks were arranged approximately 0.5m from west facing windows in the laboratory and fixtures holding four fluorescent tubes (General Electric plant & aquarium, 40w/1400 lumens) were mounted above the plants on a 16 hour light cycle to reinforce the fall sunlight. The plants were watered every 3 days and were grown under ambient temperature and humidity until all individuals had leaves large enough to mount mesh

sleeves on (approximately 6 weeks). The procedure used for applying the aphids to the plants in the laboratory experiment was identical to that used in the field experiment. All 200 aphids were applied on the same day and likewise removed after four days and counted at the same time. After the aphids were counted, the top of each plant was removed at the level of the growing medium, dried for no less than 24 hours, and weighed. A linear model was created from the top biomass data, and a poisson regression was again used on the indoor aphid count data as in the field experiment.

RESULTS

Table 3 Baskett Butte field experiment regression

	estimate	standard error	z-value	Pr
intercept	1.342	0.071	18.932	< 2e-16
exotic perennial	-1.259	0.212	-5.932	3.00e-9
native perennial	-0.578	0.149	-3.870	1.09e-4

Field experiment

The first deployment of 80 aphids in the field experiment performed at Baskett Butte received rain during the first part of the 4-day experiment duration resulting in some of the tape closures failing; however some of these aphids remained in their enclosures. In the second deployment the *T. caput-medusae* at Baskett Butte had senesced and were not tested; for this host species n = 10.

In the field experiment, *R. padi* had lower short-term fecundity on perennial hosts than on annual hosts regardless of phylogenetic grouping (regression analysis, $p<0.001$) (see Fig. 2). Based on Akaike information criterion (AIC), phylogenetic group was dropped from the final model shown in Table 1; the final model includes only "type," a term that combines host provenance and life history. Figure 3 more clearly shows the higher fecundity performance observed in the annual host grass species surveyed in the aphid application experiment performed in the field.

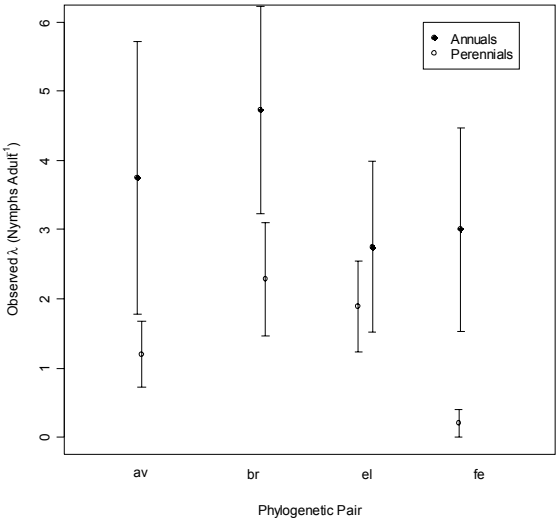

Figure 2 In field assays, aphid short-term fecundity differs significantly among annual (n=4), native perennial (n=2), and exotic perennial (n=2) grass hosts ($p<0.001$ for both comparisons). Error bars are 2 SE.

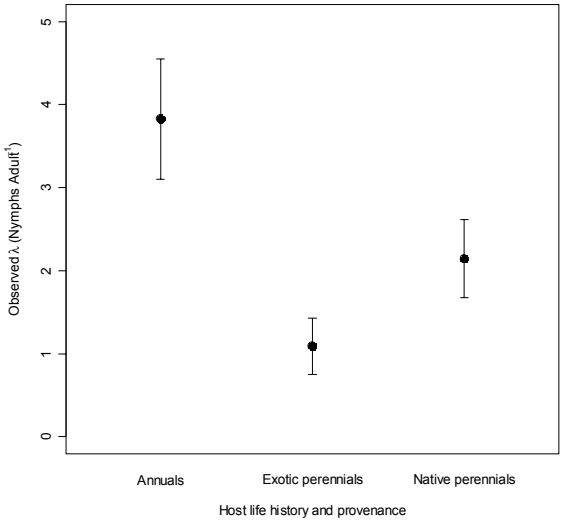

Figure 3 In field assays, observed number of aphid nymphs per adult on annual vs. perennial host by phylogenetic grouping. Aphids show lower fecundity on perennials vs. annual, regardless of phylogenetic grouping.

Table 4 Lab experiment linear regression for host grass biomass

	estimate	st. error	t-value	P-value
intercept	0.120	0.064	1.876	0.063
nitrogen (N)	**0.228**	**0.082**	**2.771**	**6.23e-3**
phosphorus (P)	0.075	0.082	0.915	0.362
exotic perennial	0.124	0.106	1.165	0.246
native perennial	0.023	0.082	0.283	0.778
brome group	**0.423**	**0.056**	**7.510**	**3.67e-12**
rye group	-0.011	0.056	-0.204	0.839
fescue group	0.046	0.489	0.934	0.352
N by P	0.060	0.117	0.513	0.609
N by exotic perennial	**0.357**	**0.144**	**2.479**	**0.014**
N by native perennial	0.012	0.121	0.101	0.919
P by exotic perennial	0.018	0.144	0.122	0.903
P by native perennial	-0.124	0.117	-1.053	0.294
N by P by exotic perennial	-0.026	0.200	-0.131	0.896
N by P by native perennial	0.025	0.169	0.149	0.882

$R^2 = 0.56$

Laboratory Experiment

Host grasses in the laboratory were raised in a factorial array of nutrients (nitrogen, phosphorus, both, and neither). The plants were grown in blocks of 40 individuals that were further subdivided in half to account for proximity to a nearby window and edge of artificial lighting. Growth blocks were not significant and were removed from all final models.

A linear model was created to explain host grass biomass as shown in Table 4, which showed that plant above-ground biomass was increased by N-addition ($p = 0.006$), and the Bromus group had higher overall mass than any of the other three groups ($p < 0.001$).

Table 5 Lab experiment regression for aphid fecundity

	estimate	st. error	t-value	P-value
intercept	1.739	0.116	15.059	<2e-16
nitrogen (N)	**0.270**	**0.137**	**1.969**	**0.049**
phosphorus (P)	0.232	0.141	1.650	0.099
exotic perennial	**-1.102**	**0.279**	**-3.948**	**7.89e-5**
native perennial	**-0.612**	**0.182**	**-3.367**	**7.60e-4**
brome group	**-0.228**	**0.105**	**-2.163**	**0.031**
rye group	**-0.410**	**0.111**	**-3.681**	**2.32e-4**
fescue group	-0.016	0.091	-0.170	0.865
N by P	**-0.423**	**0.196**	**-2.158**	**0.031**
N by exotic perennial	-0.257	0.372	-0.691	0.489
N by native perennial	0.097	0.239	0.405	0.686
P by exotic perennial	0.056	0.356	0.156	0.876
P by native perennial	0.356	0.231	1.538	0.124
N by P by exotic perennial	**0.975**	**0.470**	**2.077**	**0.038**
N by P by native perennial	-0.634	0.333	-1.906	0.057

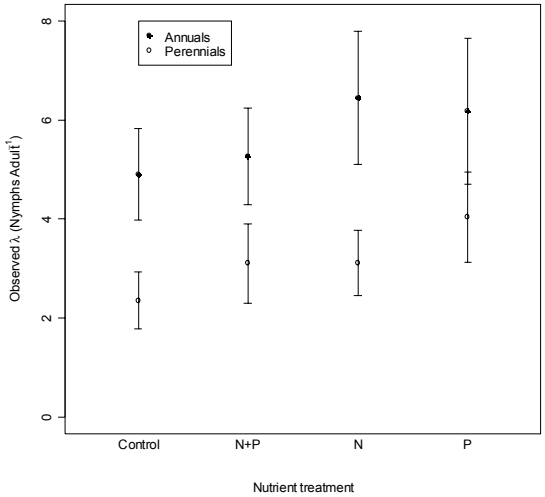

Figure 4 In laboratory assays, aphid short-term fecundity was consistently higher on annual hosts than on either exotic or native perennial hosts ($p<0.001$). Short-term fecundity was also significantly increased by N ($p=0.048$), but not P ($p=0.098$). There was an N*P interaction such that nutrient in combination led to lower juvenile production than did individual nutrients ($p=0.031$). Error bars are 2 SE.

In general, fertilization caused similar increases in mass among plant types (native perennials, exotic perennials, and annuals); however, the mass of exotic perennials increased disproportionately with nitrogen addition (N by exotic perennial interaction term, p = 0.014).

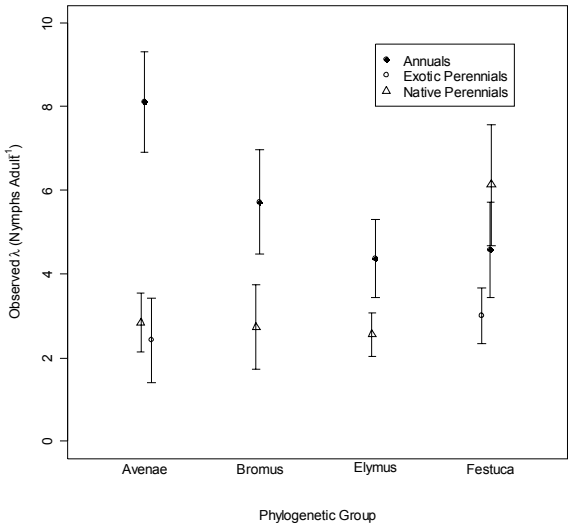

Figure 5 Overall, in laboratory assays aphid fecundity was lower on both native and exotic perennials than on phylogenetically matched annual grass hosts ($p<0.001$). Aphids had higher fecundity on host species in the Avena and Festuca groups than on species in the Bromus ($p=0.031$) and Elymus ($p<0.001$) groups. Error bars are 2 SE.

Poisson regression of the laboratory aphid fecundity count data showed an increase in fecundity across all species with addition of nitrogen (p = 0.049). Aphid fecundity was significantly lower on exotic perennials (p < 0.001) and native perennials (p < 0.001) when compared to annual grasses in the experiment. Addition of both nitrogen and phosphorus was associated with a slight decrease in fecundity across all species (p = 0.031), save for the exotic perennials group, which demonstrated a notable increase in aphid fecundity with addition of both fertilizers (P = 0.038). Moderate reductions in fecundity were found in both the brome group (P = 0.031) and rye group (P < 0.001) as well.

DISCUSSION

The field experiment showed strongly that overall perennial grasses are inferior hosts for aphids when compared to annuals. However, within perennials, it appeared that natives were a better resource for aphids than exotic perennials (see Figure 2). It is important to note that the grasses in the laboratory experiment were the same age, whereas in the field experiment the perennial grasses were aged multiple years. Since the results of both experiments were similar, this suggests that annual grasses serve as superior hosts to perennials regardless of perennial host age. Nitrogen addition in the laboratory experiment predictably resulted in increased plant mass, but also had an indirect effect of increasing aphid fecundity. This indicates that nitrogen addition changes host plant quality for aphids. In California field experiments, viral prevalence in annual and perennial grasses correlated with increased aphid fecundity due to nitrogen addition (Borer et al., 2006). Agriculture liberally uses nitrogenous fertilizers to increase yields, but within the pathogen-vector-host framework of BYDV this practice may be exacerbating the infection of crops and grasses in surrounding uncultivated lands by artificially elevating the population of the pathogen vector.

Results from both experiments indicate that *R. padi* experiences substantially higher fecundity on annual grasses, at least in the short term, which supports the results found by Malmstrom et al. (2005) and Borer et al. (2006); that increased annual grass presence in grassland communities will result in higher prevalence of BYDV in perennial grasses due to a higher rate of transmission of the pathogen. The higher pathogen load on California perennials in turn cause a shift in the competitive interactions between annuals and

perennials (Borer et al., 2007). This could explain the dramatic transition from perennial grasses to annuals seen in California grasslands. Annual exotic grasses do not dominate grassland communities in Oregon (Wilson et al., 1998), which suggests that other factors are preventing a strong competitive reversal as seen in California. Climate may play a significant role in perennial grasses retaining competitive advantage. Since the prevalence of BYDV in the Willamette Valley is poorly described, it may be that the pathogen is not as broadly distributed in Oregon as it is in California.

Based on the clear indication that the BYDV-vector mechanism in Oregon is similar to that observed in California, we suggest that viral prevalence trials between annual and perennial grasses including the role of aphid fecundity be performed in the Willamette Valley. Since Willamette Valley grasslands are being invaded more by exotic perennials (e.g. *Arrhenatherum*, *Agrostis*)(Stanley, per. com. 2007) competitive dominance and resource use surveys integrating both provenance and life history should be undertaken to more clearly reveal the interaction forces at work, both locally and in all grassland communities.

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