

Resource uptake and host tissue chemistry:

Implications for competition and disease

By

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A Project

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Oregon State University

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In partial fulfillment of
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Abstract Approved By: _____
Elizabeth Borer

Maintenance of optimal nutrient supplies is fundamental to the functioning of vertebrate, invertebrate, bacterial and plant physiology. Organisms on this planet compete with each other primarily to fulfill nutritional needs in order to maximize their health, wellbeing, and reproductive success. Here we examine nutrient concentrations in several different grass species within the context of the causes and effects of infection by barley yellow dwarf viruses, a common and economically important pathogen of grasses worldwide. Here we examine whether there is evidence that nutrient concentration motivates the vector to seek and feed on particular grasses. We selected grass species for which we knew aphid fecundity from a previous experiment. We analyzed tissue from these plants to determine their carbon to nitrogen ratios. We found that perennial grasses contained more tissue carbon than annuals, regardless of fertilization, and fertilized annual grasses increased more in tissue nitrogen than did the perennial grass species. These results are concordant with previous findings: aphids preferred and produced more offspring on the lower carbon annual grasses, suggesting that aphid vector preference and performance may be controlled by nutrition.

Keywords: plant nutrition, carbon, nitrogen, BYDV infection, aphid vector, aphid nutrition, tissue analysis, plant infection

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Commencement

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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.

Canan Schumann, author

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Resource uptake and host tissue chemistry: Implications for competition and disease

Introduction

Resource uptake is an integral part of the physiology of all plants and animals, and this key life sustaining process also has implications for competition among species as well as the spread of vector borne pathogens. Nutrition is generally thought of in the context of human health as maintenance of a good diet to prevent both nutrient and nutritional deficiencies, as well as staving off disease and infection. It has been shown that human nutrition is a key player in regulating, treating, and possibly curing human ailments. For example, many studies strongly suggest that a diet supplemented with vitamin C, vitamin E and beta carotene will reduce the risk of cancer in both smokers and nonsmokers by reducing oxidative damage to DNA (Duthie et al. 1997). Imbalance in nutrition causes diseases such as scurvy (Vitamin C deficiency) rickets (Vitamin D deficiency), as well as cretinism and goiters (Iodine deficiency). The field of ecology suggests that nutrition has much more far-reaching implications than just uptake and allocation of environmental resources; nutrition ultimately determine a species' overall abundance in an ecological community by altering its competitive ability and can affect a species' relationships with its pathogens or consumers (Sturner & Elser 2002).

The ability of plant species to extract nutrients from its environment can be a very good predictor of its growth rate, reproduction, competitive success, invasion ability, and

extinction rate (Tilman 1982, Seabloom et. al. 2003). Plant species that are more efficient at internalizing nutrients and putting that nutrition into shoot, root, or seed production gives plant species a competitive advantage in a low nutrient environment over plants that do not utilize their resources as efficiently (Baligar, Fageria, and He 2001). The ability for a plant to more efficiently incorporate nutrients from its surrounding environment also gives species differing competitive and reproductive abilities (Gilroy and Jones 2000). Thus, nutrient availability in the environment can play a major role in controlling the composition of entire communities (Tilman 1982).

Nutrient uptake rates can also alter the stoichiometry of the an organism's tissues; this variability in nutrient makeup is becoming increasingly recognized as an important factor in infectious disease: hosts and their pathogens compete within the cells of hosts for the growth-limiting nutrients they share (Smith et al. 2005). Because the development of infectious disease on or within the host involves the processes of invasion and resource consumption, competition for growth-limiting resources potentially may occur between pathogens and cellular or sub-cellular components of the host ecosystem (Smith. 2007; Snoeijers et al. 2000). Host nutrition also can alter population dynamics of vectors, such as whiteflies, leafhoppers, and aphids (Muller and Godfray 1997, Denno et al 2003, Hilije et al. 2001). Thus, we expect that fertilization may leave plants more susceptible to infection by vector borne pathogens, because the vectors' nutrient requirements are more effectively met by high nutrient host tissue (Hilije et al. 2001).

Here we will use the results of the tissue chemistry analysis to examine the tissue carbon and nitrogen of different grass species, and use these results to provide a context in which we can more thoroughly understand previous work examining the fecundity of aphids. We also will discuss the implications of nutrition on plant nutrient allocation, bioavailability, and vector nutritional dependency on its hosts.

Study System

Plant nutrition

Nutrition is essential for growth, immune function, and overall well-being of all facets of life, from the fungus *Saccharomyces cerevisiae* (brewing yeast) to the charismatic megafauna *Balaenoptera musculus* (Blue Whale). Plants are no exception and use many macro and micro resources. Research has determined that plants require 17 nutrients, also called ‘essential elements’ (Marschner, 1995). Each nutrient assists with different plant functions that vary from allowing the plant to grow to controlling its rate of reproduction. Each plant nutrient is needed in different amounts by the plant, and varies in how mobile the nutrient is within the plant (Jones and Jacobson 2001). From an ecological perspective, these nutrients can mediate a plant’s success or failure by altering rates of resource uptake, herbivory, vector attack, and pathogen infection.

Plant immune system

Nutrition affects every area of biological development including growth, reproduction, and immunity. A plant’s immune system is a vital defense mechanism

against infection and disease and is heavily influenced by the resources that can be obtained from its environment. A plant's immune system is different from the human immune system because a plant's immunity stems from an innate immune response versus an adaptive immune response (i.e. it lacks mobile immune responses such as lymphocytes, macrophages, or a vascular system to actively move an immune response; Jonathan et. al 2006). Instead plants rely on an innate immune response to localized infections; whether topical or systemic plants use signals from these invaders to elicit a response usually in the form of a chemical (alkaloid) or a chemical secretion (wax) (Jonathan et. al. 2006). As in humans, plants are susceptible to a compromised immune state when nutrients and resources are limited. These compromised immune states can lead to longer than normal recovery times which can result in irreversible systemic damage, or if the infection persists, death.

Plant susceptibility to herbivory

Nutrient concentration within a plant can alter mortality and reproductive rates. For example, nitrogen is an essential element and often a limiting resource in the natural environment. Although it makes up a relatively large portion of the atmosphere, its bioavailability in a plant's environment can sometimes be limiting during periods of high growth and reproduction (Mattson 1980). If evolution has selected for a plant species to uptake and retain nitrogen, then also it can become a target for herbivores that are similarly nitrogen limited (Mattson 1980). The relationship between nutrient

concentration and herbivory becomes more complex when the herbivore is also a vector, as the increased attack rates may also lead to increased infection rates. Thus, nutrient status can be a determinant of transmission for vector-borne pathogens.

Aphid Nutrition

Aphid nutrition, just like plant nutrition, is an integral aspect of the life cycle and proliferation of the species. Nutrition plays a dynamic role in aphid physiology with special importance given to nitrogen and its crucial importance in amino and nucleic acid synthesis. The nitrogen content in the phloem of the host species seems to indicate the levels and the extent of infestation and infection on particular plant species. The interesting aspect is that these varying nitrogen levels within the host phloem are mostly in the form of amino acids whose amounts and relative abundance are dictated by plant life history (Sandstrom 2004). The availability of nitrogen in plant phloem is, in turn, under the control of seasonal influence that directly controls the available amounts of nitrogen in phloem due to the plants reallocation of internal resources because of seasonal demands (Sandstrom 2004) (Fig. 1). These fluctuations in the bioavailability of nitrogen control fecundity of aphids on any particular plant species. For example, on a barley grass with nitrogen in the soil, non-essential amino acids were scarce and plant-specific essential amino acids were abundant in the phloem. They hypothesized that a reduction in non-essential amino acids may limit the bioavailability of excess amounts of nitrogen needed to synthesize essential amino acids in the aphid (Ponder, K. 2000).

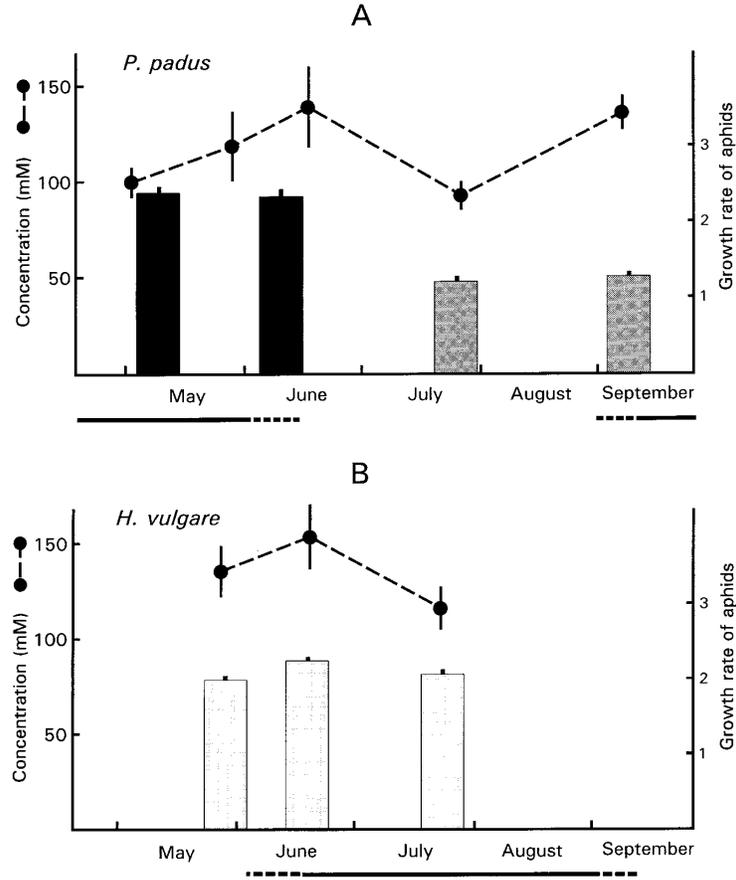


Fig. 1 Seasonal fluctuation in total amino acid concentration in phloem from *Prunus padus* (A) and *Hordeum vulgare* (B) collected from stylets of *Rhopalosiphum padi* (line and filled circles, left scale). Mean relative growth rates (mg:mg \cdot 100 day $^{\circ}$ C) of *R. padi* on *P. padus* (A) and *H. vulgare* (B) at different growth stages (bars, right scale). On *P. padus* (A) black bars are growth rates of second spring generation aphids, and stippled bars are rates of sexual females. Standard error of means shown as vertical bars. Lines under months indicate normal presence of *R. padi* on the two plants in Uppsala, Sweden. For phloem samples n_6–15, for aphid growth rate n_10 (reproduced from Sandstorm 2004)

Aphid Symbiosis and Nutrition

The symbiotic relationship shared with the aphid and its microflora provides the aphid with some of the essential amino acids it would otherwise not be able to obtain from plant phloem. The aphid shares a special intracellular relationship with the bacteria of the genus *Buchnera*, this bacterium is thought to be unculturable outside its natural environment, the mycetocytes, inside the aphid. In the absence of the bacterium, the aphid performs poorly and has a low fecundity rate (Douglas A. 1998). The bacterium is believed to be a crucial source of nutrients for the aphid, just as *E.coli* plays an important role in the natural flora of the human gastrointestinal system, providing us with constant vitamin B supplementation. (Mittler 1971) showed an important relationship between the bacteria and aphid by synthesizing the aphid's diet and supplementing it with an antibiotic, the aphids were then able to produce progeny. This is critical because the bacterium is transferred from the parent to the progeny through the ovum via mycetocytes. The aphid's progeny were then fed a diet that omitted all 10 essential amino acids. The larva of aphids fed antibiotic showed decreased growth versus the larva of aphids not fed the antibiotic and had no trouble synthesizing all the essential amino acids except histadine, isoleucine, and methonine (Mittler, T. 1971). Thus, the intricate and essential symbiotic relationship that is required to supply the essential amino acids to the aphid in absence of the amino acids it cannot obtain from plant phloem.

Methods

The plant tissue analyzed in the current study was collected at the end of an experiment conducted in 2006 by Elizabeth Borer, Vincent Adams, Gareth Engler, and Autumn Adams, to examine aphid fecundity on selected Oregon grasses that had been subjected to a factorial combination of nitrogen and phosphorus fertilization (Adams 2007). At the end of the 2006 experiment, the aboveground growth was removed from each pot at the level of the growing medium, dried for 24 hours, and weighed. For the current study, I homogenized these samples via mechanical grinding and stored them in glass vials. Samples with >0.5g dry tissue (n=119) were analyzed for %C and %N (Central Analytical Lab, Oregon State University) using a Leco CNS-2000 Macro Analyzer.

Results

Carbon Analysis

The carbon tissue chemistry analysis shows that perennials have a higher percent tissue carbon than annual grasses in the same phylogenetic group ($p < 0.001$) (Fig1.). The percent tissue carbon of the different grass species is not affected by fertilization. There is a small phylogenetic signal, such that bromes have more tissue carbon than the avena (oat) group ($p = 0.048$).

Table 1. Statistical significance of the tissue carbon analysis. Numbers in bold highlight statistically significant factors.

	<u>Estimate</u>	<u>Probability</u>
(Intercept)	38.414855	<0.001
Nitrogen (N)	0.048388	0.9622
Phosphorus (P)	0.624173	0.5509
Exotic perennial	2.730069	0.0427
Native perennial	2.299506	0.0387
Group Brome	1.384609	0.0481
Group Elymus	-0.529485	0.5192
Group Fescue	0.011793	0.9847
N to P	-0.757499	0.6013
N x Exo. peren.	-0.246331	0.8875
N x Nat. peren.	-0.004122	0.9979
P x Exo. peren.	-1.353968	0.4469
P x Nat. peren.	0.455879	0.7714
N x P x Exo. peren.	0.571416	0.8077
N x P x P x Nat. peren.	-0.453678	0.8366

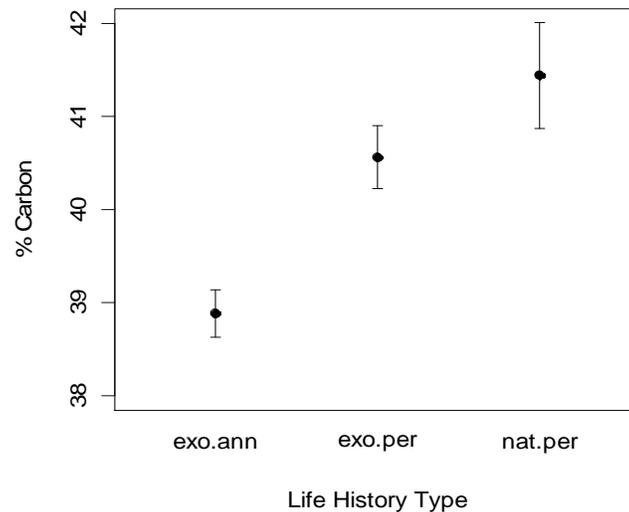


Figure 2. Annual and perennial life history groups differ strongly in tissue %C, whereas native and exotic perennials have similar tissue %C. Y-axis shows percent tissue carbon, X-axis is the life history of the grass species that were measured.

Nitrogen Analysis

The nitrogen tissue chemical analysis results give some interesting insight to the nutritional needs of the grass species that were investigated. All grasses increased in percent tissue nitrogen with fertilization ($p < 0.001$) (Fig. 2). Grasses with an annual life history can take up more nitrogen into their tissues when fertilized than can closely related perennial grasses (Fig. 3). The basal percentage of nitrogen in the tissues of all the plant species before fertilization, regardless of life history, was approximately the same.

Table 2. Statistical significance of the nitrogen tissue analyses. Numbers in bold highlight statistically significant factors.

	<u>Estimate</u>	<u>Probability</u>
(Intercept)	1.44257	<0.001
Nitrogen	2.85693	<0.001
Phosphorus	-0.24957	0.2709
Exotic perennial	-0.54372	0.0718
Native perennial	0.27955	0.2599
Group Brome	-0.38738	0.0143
Group Elymus	-0.27769	0.1342
Group Fescue	-0.03307	0.8107
N to P	-0.02425	0.9406
N X Exo. peren.	-0.78585	0.0467
N X Nat. peren.	-1.41380	<0.001
P X Exo. peren.	0.23742	0.5526
P X Nat. peren.	-0.18470	0.6006
N X P X Exo. peren.	0.16172	0.7592
N X P X Nat. peren.	0.52435	0.2812

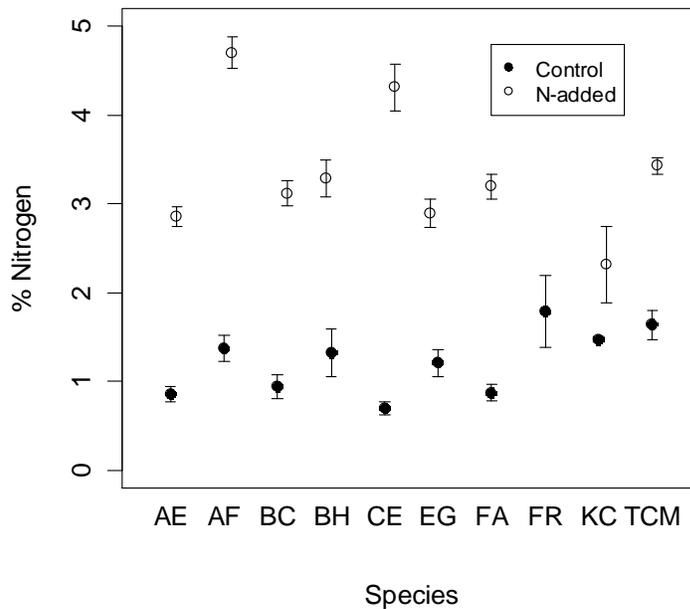


Figure 3. The addition of nitrogen through fertilization increased percent nitrogen in the tissues of all plant species observed regardless of life history or phylogeny. Y axis shows the percent nitrogen in the tissues of the above ground plant biomass, X axis shows the species that were analyzed.

Species Codes

Table 3 Lab experiment host species

species	common name	life hx.	Provenance	group
<i>Bromus hordeaceus</i> (BH)	soft brome, soft chess	A	X	brome
<i>Bromus carinatus</i> (BC)	California brome	P	N	brome
<i>Avena fatua</i> (AF)	wild oat	A	X	oat
<i>Koeleria cristata</i> (KC)	prairie junegrass	P	N	oat
<i>Arrhenatherum elatius</i> (AE)	tall oat	P	X	oat
<i>Taeniatherum caput-medusae</i> (TCM)	medusa-head rye	A	X	rye
<i>Elymus glaucus</i> (EG)	blue wild-rye	P	N	rye
<i>Cynosurus echinatus</i> (CE)	bristly dogs-tail grass	A	X	fescue
<i>Festuca roemerii</i> (FR)	Romer's fescue	P	N	fescue
<i>Festuca arundinaceae</i> (FA)	tall fescue	P	X	fescue

(A) annual; (P) perennial; (X) exotic; (N) native
(reproduced from Adams 2007)

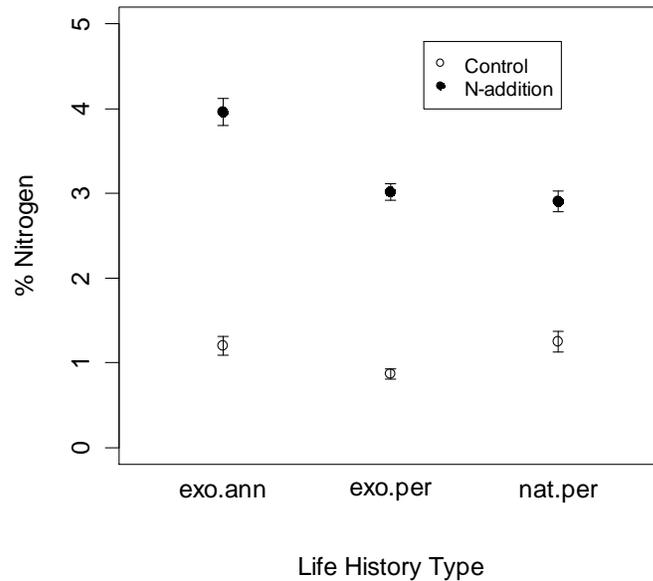


Figure 4. Nitrogen fertilization increases tissue nitrogen in both annual and perennials, but the increase in annuals is far more substantial than in the increase in perennials. Y axis shows the percent tissue nitrogen, X axis shows the life history of the grass species that were measured.

Discussion

Nutritional requirements are the basis of the behavioral and foraging needs of both plant and aphid species, and these nutritional requirements may play an important role in the spread of the infectious agent, BYDV through their effects on aphid performance. We found that annual plants had lower percent tissue carbon and their tissue nitrogen increased more strongly than did perennial plants when fertilized (Fig 3). These differences in tissue chemistry could play an important role in a plant's ability to avoid viral infection. Aphids had higher fecundity on annual vs. perennial grasses

(Adams 2007). The work presented here suggests that differences in tissue chemistry may drive the differences in aphid fecundity.

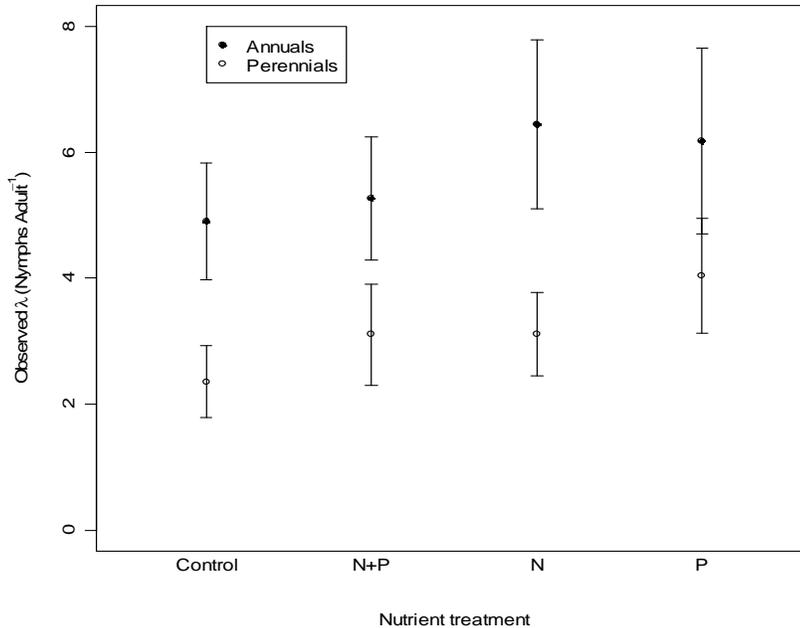


Fig 5. In laboratory assays, aphid short term fecundity was consistently higher on annual host than on either exotic or native perennial host ($p < 0.001$). Short term fecundity was also significantly increased by N ($p = 0.048$), but not P ($p = 0.098$). There was an N*P interaction such that nutrient in combination led to lower juvenile production than did individual nutrients ($p = 0.031$). Error bars are 2 SE. (reproduced from Adams 2007)

The higher tissue nitrogen in annual species may account for the higher vector attack rates relative to perennial grasses, but as shown by Borer et. al the preference of aphids seems to decline with an increase in percent tissue carbon. Annuals also have a lower percent tissue carbon than perennials at the early stages of life, so if the aphid is deterred by the carbon-rich perennials, then more annuals should become infected during a season.

If carbon is inaccessible to an aphid i.e. being used to construct cell walls, versus a bioavailable form i.e. carbohydrates, then it is possible that an increase in carbon that is used in cell wall construction would not meet aphid nutritional requirements. Higher carbon in perennial grasses also may be caused by a thicker shoot. Physiology and foraging theory suggest that animals will tend to favor a lower quality food that is easy to obtain versus high quality food that requires high energy cost.

Although annuals and perennials have similar tissue nitrogen content, the more carbon-poor annuals may provide a more convenient nutritional source for aphids. Analysis of the relationship between tissue chemistry and phloem chemistry may clarify this relationship. The data show that unfertilized perennials and annuals have similar tissue nitrogen, but upon fertilization, the annuals' ability to uptake nitrogen is significantly greater than the perennials'. . It is possible that the soil nutrient availability in the natural environment is quite different than in our laboratory investigation; the role of nutrient pools on tissue chemistry and aphid fecundity warrants further investigation. Finally, a better understanding of which element drives the nutritional requirement of aphids, carbon (in the form of carbohydrates), nitrogen (in the form of amino acids), or the stoichiometric balance of these two elements will help sort out these results.

Annuals start each season uninfected as the pathogen is not transmitted via seed. Thus the annuals may increase vector abundance and pathogen transmission, while suffering less from infection relative to their perennial competitors. This may be true if aphids seek high nitrogen diet with a low relative percent tissue carbon, but this is speculation under the assumption that the wild grassland mimics the fertilized parameters that were produced in the lab. Even though infection appears to be dictated, at least in

part, by plant carbon content, the viral infections resulting from this interaction are likely to have caused a change in grassland dominance from native perennial to exotic annuals (Borer et. al. 2007).

Seasonal fluctuations in grass species composition are also an indication of how the aphids preferentially seek a nutrient. As Sandstrom (2004) has shown, in the summer months the concentration of nitrogen in the form of amino acids in the phloem of *P. padus* increases and has a slight decrease in the fall. With this increase in available amino acid concentration in the phloem, the growth rate of the aphid increases, as well. In the West Coast grassland system, annual infection rate may dramatically increase during the summer months because of annuals' ability to uptake more nitrogen than perennials as well as the lower percent tissue carbon compared to perennials. Thus, not only does the variation in tissue chemistry among annuals and perennials play an important role for pathogen transmission, but the season in which the aphids are most active may also be important because of seasonal variation in tissue chemistry.

These results suggest that tissue chemistry may provide predictions about BYDV infection. The research has laid down basic fundamental ideas to what the different grass species chemical make up looks like in regards to nitrogen and carbon, but much needs to be done with respect to what these different essential elements are stored as and what bioavailable form they are assessable in if any. Determining the relationship between soil chemistry, tissue chemistry, and phloem chemistry is a critical future step which will further clarify the role of plants and insect nutrition in determining pathogen dynamics in natural communities.

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