Recent advances in the nutritional ecology of Thysanoptera, or the lack thereof

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Introduction.

In the past several years, some of the most innovative research on Thysanoptera has centered on intra and interspecific chemical ecology of thrips. These studies have documented exceedingly complex responses by Thysanoptera to chemical cues elicited by conspecifics or other arthropods. Responses include aspects such as seeking webbing as refuge when volatiles associated with thrips predation are detected (Venzon et al., 2000), and the presence and detection of certain food sources (pollen) altering thrips behavior and predator/prey interactions (van Rijn et al., 2002). On a more technical level, both quantitative and qualitative analyses of the chemical components of thrips alarm pheromones (MacDonald et al., 2002) and defensive secretions (Suzuki et al., 2000) have been comprehensively described.

In contrast, there has been conspicuously little progress made in the chemical basis of thrips/host plant interactions since Kirk's review in 1995. For many insect taxa, this type of research is the cornerstone of chemical ecology, as it is has direct bearing on insect fitness and host resistance. A diversity of recent studies have documented the variability in thrips performance and host selection based on plant genotype (e.g. Berg and Le Blanc, 1997; Jager et al., 1996; Kogel et al., 1997a), plant parts (e.g. Kogel et al., 1997 b, c), plant age (e.g. Kogel et al., 1997c) or the influence of cultural conditions on thrips preference and performance (e.g. Vos and Frinking, 1997; Harris et al., 1999). Advances have also been made in the identification of volatile attractants (e.g. Teulon et al., 1999; Jurgens et al., 2000; Murai et al., 2000). Very few studies, however, have advanced to the critical level of identifying ingested plant compounds that account for variable performance and host selection. An understanding of the chemical/nutritional basis driving thrips/host plant interactions is essential to understanding host plant resistance.

The lack of empirical data in the nutritional ecology of thrips has resulted in an even greater paucity in ecological theory concerning thrips nutrition. Notable exceptions exist, such as the effects/responses of thrips to plant inducible responses (Agrawal et al., 2000; Agrawal and Colfer, 2000) and the phylogenetic considerations of Kirk (1995). Yet many of the central nutritional questions addressed in studies on other insects have received little attention. What are the comparative roles of primary nutrients versus secondary compounds in determining thrips distribution (Rosenthal and Janzen, 1979)? Do thrips follow 'co-evolutionary theory' in that species with limited host range are more greatly influenced by secondary compounds produced by hosts than are generalist species (Rhoades, 1979)? What is the role of dietary nitrogen in determining thrips success (Slansky and Scriber, 1985)? What are the primary feeding and ovipositional cues, and which are most likely to determine thrips distribution?

We do not presume to know all of the reasons for the lack of research concerning the nutritional ecology of Thysanoptera. As relatively new participants in this line of thrips research, we will present several of our studies in the context of the difficulties encountered, and also examine how other key research has dealt with these problems. Clear identification of difficulties in this line of research may lead to protocols that can assist in bringing these research efforts up to speed with the rapid advances being made in other branches of Thysanopteran chemical ecology.

Logistical Limitations

The dimensions of thrips do not lend themselves easily to quantification of mass for determination of growth rates, nor can enough insect tissue be collected to provide sufficient sample for analyses of nutrient retention and accumulation. Consequently, many of the typical measurements taken by nutritional ecologists are compromised whether measurements are for traditional indices (Waldbauer, 1968) or more recently proposed indices (Raubenheimer and Simpson, 1993). In a similar fashion, the extremely short developmental period of many thrips preclude repeated measurements on individual insects (e.g. daily consumption rates), particularly when many species of Thysanoptera feed only during limited intervals in development. Size and developmental limitations in themselves should not prohibit advances in nutritional ecology. As noted above, Thysanopterists have made advances in other fields of research despite these same limitations. And while individuals may be difficult to analyze and measure, population attributes of many species of thrips (high fecundity, short generation time, high polyphagy) make them suitable candidates for study on a population level.

It may be more accurately stated that the study of the nutritional ecology of thrips has not benefited from interdisciplinary research. Many of the advances in the nutritional ecology of other insects have resulted from the interdisciplinary approach suggested by the very name given to this line of research – plant-insect ecology. A review of either the presentations at the Seventh International Congress of Thysanoptera or a general literature review of recent research on Thysanoptera shows a paucity of collaboration by researchers specializing in the 'plant' component of these trophic interactions.

Taxonomic discrimination is evidenced even within disciplines of entomology. Nutritional ecology has advanced greatly by the merging of insect ecology with insect physiology; establishment of the physiological basis for phenomena noted at the whole organism (or population) level have been one of the major advances in recent entomology. Not so for Thysanoptera. For example, despite the growth of thrips research world-wide, the *Journal of Insect Physiology* published only four studies on Thysanoptera in the five year period from 1997 to 2001. All four of these dealt with cold-hardening or cold-tolerance; none dealt with nutrition which is a staple of this journal. Although it is clear why insect physiologists would not consider thrips as ideal subjects, this lack of interest may be a limitation to thrips research for years to come. Progress has been made by Thysanopterists in specific areas, such as the feeding mechanisms of thrips (for review see Kirk, 1997).

Some progress can (and is) being made in nutritional ecology. A key factor may be realizing and identifying limitations of working with thrips, and selecting dependent variables (thrips response) based on thrips 'limitations' rather than conforming to indices typically used by nutritional ecologists. Even relatively crude criteria such as measurements of thrips damage or total population sizes can offer useful information in relation to host plant nutrients. In one of the most comprehensive studies to date, Mollema and Cole (1996) contrasted the nitrogen chemistry of a wide variety of accessions of four host species to damage by thrips in greenhouse tests. While some questions have been raised regarding analytical techniques, the wide chemical database acquired allowed them to formulate one of the few nutritional hypotheses for Thysanoptera to date. Specifically, they postulated that aromatic amino acids (AAA) were consistently correlated with thrips performance, and that concentrations of these amino acids were related to plant susceptibility to thrips herbivory.

Our subsequent two-year study on seasonal and fertilization effects of *F. occidentalis* feeding on *L. esculentum* under field conditions suggested that the 'AAA hypothesis' may have some validity, although there were several key differences in our results (Brodbeck et al., 2001). Populations of *F. occidentalis* responded strongly to fertilization treatments during seasonal peaks in 1996 and 1997. We did not find correlations between total aromatic acids and thrips populations, yet we did find strong correlations between concentrations of the primary aromatic amino acid (phenylalanine) in flower tissue and *F. occidentalis* populations during the seasonal peak in both years (Figure 1). Fairly similar correlations were found with leucine, another 'essential' amino acid (amino acids that insects typically cannot synthesize; Taylor and Medici, 1966). Correlations with specific essential amino acids suggested a role

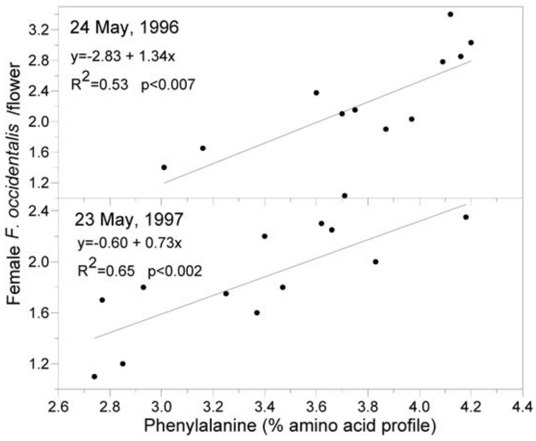

Figure 1. Abundance of female *F. occidentalis* on *L. esculentum* during the seasonal peaks in 1996 and 1997 in relation to concentrations of phenylalanine found in flower tissue (modified from Brodbeck et al., 2001).

for these compounds in explaining fertilization effects, but were not well correlated throughout the season indicating that other factors such as flower number and total flower nitrogen may predominate in explaining seasonal trends.

We consider these studies preliminary in aiding our understanding of thrips nutrition, but both studies have made contributions by comparing chemical analysis of food sources with relatively simple measurements of thrips response. While the general applicability of the AAA-hypothesis merits further investigation, this hypothesis has already provided a framework for subsequent studies. Many other studies have suggested a role for dietary nitrogen in thrips performance and distribution, and the AAA hypothesis has correctly placed dietary nitrogen form at the center of this discussion.

Thrips Diversity

Thrips species exhibit an incredible diversity of feeding behavior at the trophic (predacious to herbivorous to omnivorous), tissue (animal tissue, foliage, pollen, and specific flower parts) and polyphagy (monophagous to highly polyphagous) levels. Wide diversity of feeding habits occur even within a particular thrips species, and may also be evident at the insect/host plant level; a given thrips species may respond differently to chemical changes in one host plant than to similar changes in another host. Diversity of feeding behavior inhibits general theory about thrips nutritional ecology.

This diversity can be seen in much of our early research with thrips. We have shown that *F. occidentalis* populations consistently respond to increasing soil nitrogen, yet we have also documented that other thrips species commonly found feeding on *L. esculentum* do not respond to varying soil nitrogen (Stavisky et al., 2002). In a more recent series of experiments, we examined laboratory colonies to more closely examine relationships between dietary components and thrips performance. We selected *Frankliniella fusca* for a series of choice and no-choice experiments as it is closely related to *F. occidentalis*, yet feeds primarily on foliage (hence, the exact tissue ingested can be analyzed). In each phase of the experiment, 30 adult *F. fusca* were released in each of five plastic cages that provided a range of host plants for thrips. Adult and immature thrips were counted after two to three weeks and abundances were related to plant size, foliar nitrogen concentration, and foliar amino acid profiles. Selection experiments included alternative host species utilized by *F. fusca* (*L. esculentum, Arachis hypogaea* and *Gossypium hirsutum*), and variations within the preferred host *A. hypogaea* including genotype, plant age, soil nitrogen and *Rhizobium* inoculation.

F. fusca exhibited the strongest variations in regard to plant type (host species and genotypes), although distribution patterns sometimes varied with stage of development (Figure 2). Manipulations within plant genotypes (plant age, fertilization and inoculation) did not result in significantly different distribution of thrips. Different plant species grown under the same conditions provided significantly different amounts of foliar nitrogen (Figure 2), and plant age significantly impacted foliar nitrogen as well (Figure 3). In none of the choice tests, however, was foliar nitrogen positively related to *F. fusca* host selection. *L. esculentum* provided significantly higher foliar nitrogen, yet was the least preferred host for immature thrips. Young *A. hypogaea* provided 25-60% higher foliar nitrogen than plants of the same genotype that were three

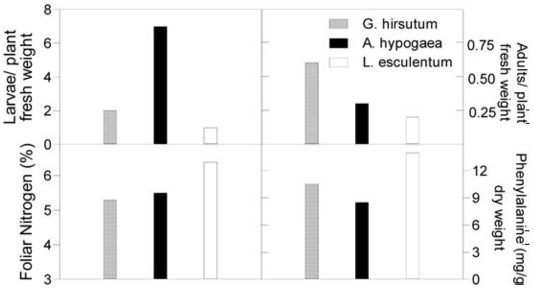

Figure 2. Abundances of adult and larval *F. fusca* in selection tests (two to three weeks) with a choice of *L. esculentum*, G. *hirsutum* and *A. hypogaea*. Each selection test was replicated 5 times. Abundances are expressed per plant wet weight to standardize for difference in plant size. Total nitrogen and phenylalanine concentrations of foliar tissue from plants used in the tests are presented as well.

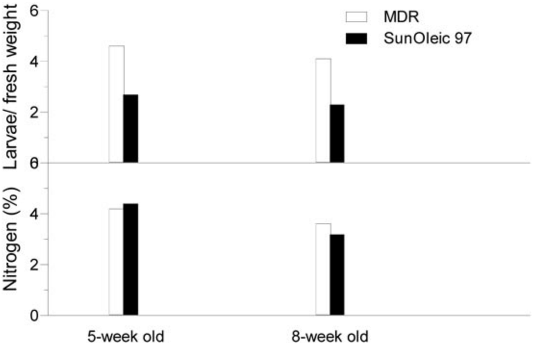

Figure 3. Abundance of *F. fusca* in selection tests on two genotypes of *A. hypogaea* of different age classes (five and eight weeks; 5 replications per test). Abundances are expressed per plant wet weight to standardize for difference in plant size. Total nitrogen concentration of foliar tissue from plants used in the tests are also presented.

weeks older, but were not more highly selected by thrips. Similarly, our preliminary analyses of aromatic acids indicate that these are not predominant factors in host selection by *F. fusca*. For example, the preferred host *A. hypogaea* had the lowest concentrations of phenylalanine. We are currently examining other aspects of amino acid profiles to decipher more subtle effects on *F. fusca*, but our initial results suggest that other plant factors such as secondary compounds or plant architecture may be more central to host selection by *F. fusca* than is form or concentration of dietary nitrogen. Our preliminary conclusions are that the effects of dietary nitrogen on *F. fusca* are radically different than effects previously recorded on *F. occidentalis*.

A portion of thrips feeding diversity results from the fact that some thrips species may use different hosts for very different aspects of performance. In Florida, *F. occidentalis* is a pest species on both *L. esculentum* and *Capsicum* spp. Field experiments suggest fairly high abundances of thrips on both species, yet the latter is a good reproductive host for *F. occidentalis* while *L. esculentum* is not. As such, we should not expect that nutritional requirements for *F. occidentalis* feeding on both hosts to be similar. In a parallel fashion, our feeding experiments with *F. fusca* and the experiments of Mollema and Cole (1996) measured thrips throughout development, whereas our field tests recorded only selection by adult *F. occidentalis* on the non-reproductive host *L. esculentum.*

Thus, while we suggest that fairly broad measurements of thrips response are suitable as dependent variables we offer the caveat that the role of the host plant needs to be accounted for in each study. Understanding of host plant usage will allow identification of the effects of specific nutrients on individual processes (selection, survivorship, fecundity, etc.) and also allow us to delineate what is contradictory or anomalous data and what is not. Nutritional ecologists may avoid the pitfalls long in evidence in other population studies of thrips, where observations of populations on nonreproductive hosts (Andrewartha and Birch, 1954) may have been inappropriately extrapolated to thrips on other hosts as noted by Funderburk et al. (2000).

Tissue Diversity

Of all the limitations of research on Thysanoptera, we consider tissue diversity most problematic for nutritional ecologists. For most phytophagous insects, the food source can be identified, isolated and analyzed. Foliage, or even layers of foliage, can be excised; pure xylem fluid or phloem fluid can be collected. Many thrips species have the capacity to feed on a variety of plant tissues, and it is often difficult to establish exactly what food source is being consumed (for detailed discussion, see Kirk, 1995). Even when the tissue can be identified, it may be difficult to establish the nutritional portion of tissue being ingested. The typical thrips feeding method of puncturing cells and 'sucking' cell contents (Kirk, 1985) makes for difficult analysis as the emptying of cell contents may or may not be complete depending on a variety of factors (Kirk, 1985; van de Wettering, 1999).

Flower thrips may be particularly problematic, as a variety of flower tissues may be consumed. While nutrient levels of foliar tissue may vary somewhat with host species, some commonality is guaranteed by the preponderance of Rubisco enzymes in all foliar tissue (for summary see FAO Report, 1970). In contrast, the nutrient levels of flower components may vary much more drastically. Pollen provides a good example as it is a common thrips food source, and a commonly studied food source. Pollen is widely cited as being a good food source due to comparatively high nitrogen content. In actuality, comparative studies suggest that mean nitrogen values are comparable to foliar tissue (Slansky and Scriber, 1985). Moreover, pollen nitrogen concentrations vary radically with species and are often below those typically reported for foliar tissue.

Our initial research attempts with pollen were to analyze pollen used in recent life history studies (Hulshof and Vannini, 2002). The most striking data from the life history study was that dietary supplementation with *Pinus* pollen greatly enhanced fecundity rates (and hence relative growth rates) significantly more than diets with other types of pollen or diets lacking pollen. Our preliminary analysis reflects many of the facets of pollen nutrition noted in a literature review of pollen chemistry. Specifically, amino acid profiles of pollen from different host species were highly variable (as were effects on thrips fecundity). Expressed as percentage of the amino acid profile, the predominant amino acid was glutamic acid/glutamine in one species (*Pinus sylvestris*), proline in *Corylus avelana* and *Epilobium angustifolium* and leucine in *Betula pubescens* and *Typha latifolia*. *Pinus* had the highest levels of glutamic acid (17-56% higher than other species) and lysine (9-83% higher than other species) (Figure 4). Glutamine is a pivotal amino acid for many insects in the synthesis of other amino acids (Andersen et al., 1992) and may also be a phagostimulant (Brodbeck et al., 1990). Lysine is an essential amino acid for insects (Taylor and Medici, 1966). Other studies have shown amino acid composition of other plant species to vary radically, sometimes with the predominant amino acids being ones that are generally found in very low concentrations in other plant material (e.g. cysteine and histidine; Carisey and Bauce, 1997; Hollister and Mullin, 1999). Secondly, our analyses showed total amino nitrogen was highly variable ranging from ca. 1.5 to 2.8%. These values are within the range previously published for the nitrogen concentration of pollen (Slansky and Scriber, 1985), although more recent reports have ranged up to 10% (Roulston and Cane, 2000). Lastly, our analyses suggest that nitrogen concentration may be a poor indicator of thrips performance (*Pinus* had the lowest values of total nitrogen in our study). As reviewed by Kirk (1995), thrips feed on cell cytoplasm and leave cell

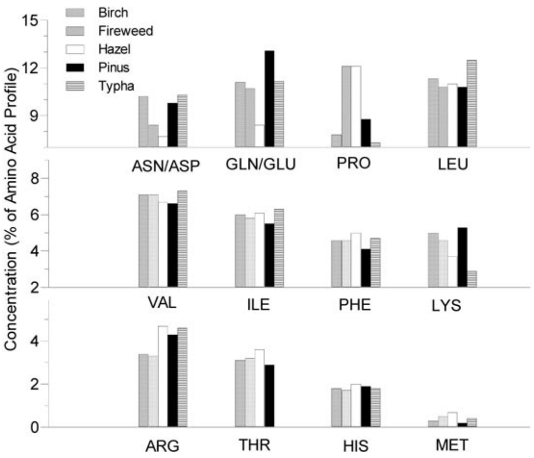

Figure 4. Concentrations of the major and essential amino acids (expressed as a percentage of the total amino acid pool) of the five pollen sources used in the life history studies of Hulshof, et. al., (2002). ASP (aspartic acid), ASN (asparagine), GLN (glutamine), GLU (glutamic acid) and PRO (proline) are major nonessential amino acids; ILE (isoleucine), LEU (leucine), PHE (phenylalanine), LYS (lysine), HIS (histidine), ARG (arginine), THR (threonine), VAL (valine) and MET (methionine) are essential amino acids (those that most insects cannot synthesize). GLU/GLN and ASP/ASN are expressed together due to deamination of amides during sample hydrolysis.

walls. In the case of pollen, walls are composed primarily of sporopollenin with a caratenoid and cellulose (both non-nitrogenous) skeleton. Pollen wall structure is intricate and can be variable for different host species (Perezmunoz et. al., 1993; Lan et al., 1995). It is likely that nitrogen (or specific nutrients) analyses of pollen expressed as a percentage of dry weight will largely reflect the contribution of this uningested material (pollen with thick exine will contain less total nitrogen).

This preliminary analysis suggests some chemical correlates to fecundity of *F. occidentalis*, yet clearly a larger database is needed prior to speculating on mechanistic relationships. Development of this nutritional database will also allow us to examine how fixed nutrient profiles are for given host species. Most importantly, this study documents the diversity of nutrient profiles found in pollen. Although documentation is not extensive, profiles of other flower components vary greatly as well and are readily altered by environment, plant phenology, etc. (e.g. Pena-Valdivia and Rodriguez-Gracia, 1999; Xie et al., 1997). Variation between profiles of different tissues suggests that thrips may encounter an array of nutrient profiles (dependent on tissue type) within a given plant.

Bernays and Bright (1991) proposed that the benefits of polyphagy include obtaining a proper mix of primary nutrients and the dilution of secondary compounds from a single food source. Our previous research with highly polyphagous leafhoppers supports the benefits of nutrient mix, with the caveat that desired nutrient mix will vary with insect stage of development (Brodbeck et al., 1990, 1999). We propose that thrips may realize the same benefits within a single host plant by varying types of tissue ingested. Benefits would appear to be most pronounced for flower thrips, but as noted by Kirk (1997) the delineation between flower and foliar feeding thrips is not precise; many thrips species appear to be able to ingest a variety of plant material. In our own laboratories we have found that *F. fusca* larvae can develop adequately on foliage from several host species, but that adults benefit greatly from the addition of pollen to their diet (Sims and Funderburk, unpublished data). Thrips not only have the capacity to ingest a variety of nutrient profiles (by ingesting different tissue types), but they may also utilize varying diets to maximize different aspects of performance. For example, adult thrips frequently populate non-reproductive hosts (hosts/diets that can be used successfully for survivorship but not fecundity). This is consistent (on the population level) with the defining 'opportunism' of thrips (Mound, 1995). Thrips may subsist on a variety of diets, and undergo rapid population growth when hosts suitable to high fecundity are eventually encountered.

Summary

Size and life history traits alone should not preclude studies in nutritional ecology of thrips. Some flexibility, however, is warranted in the type of dependent variable (thrips response) that may be considered; many of the quantitative measurements typically used by nutritional ecologists will not be appropriate. Simple dependent variables (e.g. abundance, feeding damage) can give valuable information, although whenever possible, thrips usage of the host plant (reproductive, non-reproductive host) and specifics of feeding site (tissue) should be determined as accurately as possible. High variability in nutritional ecology should be expected between thrips species, although certain commonalities should result from similarities in mechanisms of thrips feeding (Kirk, 1997).

The most difficult impediment to the nutritional ecology of thrips remains the determination of specific tissues consumed (Kirk, 1995), and this should be a focal point of future research. As noted by Mound and Teulon (1995), the specific tissues ingested were known for very few thrips species; few advances have since been made in this area. The most immediate progress can be made with life history studies (e. g. Tsai et al., 1996; Hulshof and Vannini, 2002) in concert with chemical analysis of the limited and defined dietary source. Although these studies are tedious, they can most accurately link nutrients to specific aspects of thrips performance (developmental rates, fecundity, etc.). Thrips behavior/performance on whole plant material is more difficult to define. Visual examinations to determine feeding sites have been valuable (e.g. Kirk, et. al., 1985; Hansen, 2000), yet the nutrient profiles of different plant organs need to be determined, as do environmental/phenological effects on these tissues. Tissue variability may potentially provide a valuable tool for studying the nutritional ecology of thrips, and manipulations of tissue nutrient levels may be possible. Our studies on *L. esculentum* (Brodbeck et al., 2001) confirm that flower chemistry changes with plant age or environment (in this case, soil nitrogen); other studies have shown that the nutrient profiles of specific floral tissues change with phenology (Bieleski, 1995). Comparison of thrips performance on flowers at different phenological states (or flowering versus non-flowering plants) can be examined; flower chemistry can also be altered by applying specific fertilizers or other agents (Thaler, 1999; Baldwin and Hamilton, 2000). Similarly, performance on male versus female flowers can be evaluated in certain host species to examine the contribution of flower components. Other agents such as boron (Simojoki, 1991; Chen et al., 1998) or carbamate (Ozaki et al., 1999) can be used to alter the pollen load within flowers. Lastly, specific flower components may be excised in small scale studies to further delineate the dietary contribution of specific tissues. Creative manipulations of plant components (such as these) may be essential for understanding the role of nutrients in whole plants where a diversity of tissues may be ingested.

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