4 Trophic Shift in $\delta^{15}N$ and $\delta^{13}C$ through Galling Arthropod Communities: Estimates from *Quercus turbinella* and *Salix exigua*

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Summary. Galling arthropod communities have long been a model system for community ecologists, yet much remains to be explored concerning trophic interactions between hosts, herbivores, and natural enemies. While the utilization of stable isotope ratios can help to elucidate complex trophic interactions in such communities, estimates of trophic shift between community members are required before stable isotope analyses can be appropriately employed. In this chapter, we document the degree of trophic shift in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes within galls and hosts of a cynipid gall wasp (Cynipidae) in *Quercus turbinella* (Fagaceae), and a gall midge (Cecidomyiidae) and sawfly (Tenthredinidae) on *Salix exigua* (Salicaceae). We found trophic shift in nitrogen isotopes to be reduced relative to estimates from other systems, while carbon isotopes were considerably enriched. In combination with our current results, we review estimates of trophic shift in gall communities and compare patterns of trophic shift across studies. We discuss physiological mechanisms that determine the distribution of stable isotopes throughout gall communities and their potential effect on estimates of trophic shift ($\delta^{13}C$ and $\delta^{15}N$).

Key words. Stable isotope, Gall midge, Gall wasp, Trophic shift

4.1 Introduction

Arthropod galls often harbor diverse, complex communities of parasitoids, hyperparasitoids, inquilines, and predators. These closed communities have long served as empirical models for community ecology, yet much remains to be explored surrounding the role of direct and indirect trophic interactions in structuring communities (Plantard et al. 1996; Price et al.

1980; Raman et al. 2005; Roininen et al. 1996; Stone et al. 1995; Washburn and Cornell 1981). The complex trophic interactions within galls may be elucidated through the use of stable-isotope techniques. Stable isotopes have proven useful in determining the structure of complex communities and the trophic position of species in other biological systems (Post 2002), as well as revealing important population-level aspects of organism nutrition (O'Brien et al. 2002). This has been particularly true for trophic systems that are not amenable to more traditional dietary or behavioral analysis (Blüthgen et al. 2003; Callaham et al. 2000). The use of stable isotopes in the examination of trophic interactions in other insect communities has been fruitful (i.e. Callaham et al. 2000; Markow et al. 2000; McNabb et al. 2001).

The successful application of stable isotopes to trophic interactions requires a valid a priori expectation of *trophic shift* (McCutchan et al. 2003; Post 2002; Vander Zanden and Rasmussen 2001) — patterns of consumer–diet fractionation (Δ; e.g., $\Delta = \delta^{13}C_{\text{consumer}} - \delta^{13}C_{\text{diet}}$) in carbon ($\Delta\delta^{13}C$) and nitrogen ($\Delta\delta^{15}N$) isotopes (DeNiro and Epstein 1978, 1981) between trophic levels. Nitrogen generally becomes steadily more enriched (greater relative amount of the heavier isotope, e.g., $^{15}N/^{14}N$) at higher trophic levels. The overall level of enrichment is determined by exogenous and endogenous variation in nitrogen assimilation and excretion (Steele and Daniel 1978). Carbon becomes only slightly enriched across trophic levels, and less reliably so than nitrogen; carbon isotope enrichment is primarily balanced by the ratio of respiration to growth (McCutchan et al. 2003).

Despite these generalities, the degree of trophic shift in nitrogen and carbon through food webs is known to be variable between systems due to the underlying physiological variation between organisms (McCutchan et al. 2003; Post 2002; Vanderclift and Ponsard 2003). Further, the trophic positioning of communities with high levels of omnivory, cannibalism, or parasitism is especially susceptible to error in assumptions concerning $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$. It is important to obtain quality estimates of the isotopic baseline of the community (Vander Zanden and Rasmussen 2001), as determined by the primary consumers, and obtain estimates of trophic shift for secondary consumers. Additionally, progress depends on the documentation of patterns in the field and the integration with mechanistic physiological studies across a wide range of organisms (Gannes et al. 1997; Martínez del Rio and Wolf 2004), including endophagous insects and their parasitoids.

Patterns in the trophic shift of stable isotopes have only recently been reported for gall-formers or their associated parasitoids (Langellotto et al. 2005; Tooker and Hanks 2004; Yarnes et al. 2005). The establishment of an isotopic baseline of primary consumers (gall-formers) and quality esti-

mates of trophic shift in gall-forming communities are critical. Global estimates of trophic shift based on metadata compiled across different taxa may be invalid for gall communities due to physiological differences between organisms (Martínez del Rio and Wolf 2004). In this chapter, we establish the baseline isotopic composition of an oak gall cynipid, *Andricus reticulatus* (Hymenoptera: Cynipidae), in the oak *Quercus turbinella* Greene, and for two separate taxa in *Salix exigua* Nuttall, *Rhabdophaga strobiloides* (Diptera: Cecidomyiidae) and *Euura exiguae* (Hymenoptera: Tenthredinidae). We also document patterns of trophic shift in carbon and nitrogen ($\Delta\delta^{13}C$, $\Delta\delta^{15}N$) for a torymid parasitoid in *R. strobiloides*. We compare the degree of $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ in these communities relative to global estimates constructed from a wide variety of ecosystems, and estimates from other gall-forming arthropods. We also discuss physiological characteristics of galling arthropods important to the analysis of trophic shift in gall communities.

4.2 Trophic Shift in Gall-forming Arthropods in *Quercus turbinella* and *Salix exigua*

4.2.1 Collection of Galls

On October 15th 2004, *A. reticulatus* galls were collected from *Q. turbinella* near Aguirre Springs Campground in the Organ Mountains, Dona Ana County, New Mexico U.S.A. Here *Q. turbinella* forms dunes of shrubs, 1–2 m. Six trees were haphazardly chosen from a small stand of *Q. turbinella* and examined for cynipid galls. All galled leaves were collected from each tree (range: 1–32 galls·species^{-1}·tree^{-2}). Galls were transported to the laboratory, placed in Petri dishes, and monitored for galler and parasitoid emergence.

On July 13th 2005, *E. exiguae* and *R. strobiloides* were collected from *S. exigua* clones along the Rio Grande south of the Picacho Street Bridge in northwestern Las Cruces, Dona Ana County, New Mexico U.S.A. *S. exigua* forms expansive clones 2–3 m in height and care was taken to sample from distinct clones. Ten clones bearing galls were examined for *E. exiguae* and *R. strobiloides* galls. Galls were placed on ice during transport and samples processed immediately. In *R. strobiloides*, an unknown torymid parasitoid (Torymidae) was found to emerge from mature bud galls on *S. exigua*.

4.2.2 Analysis of Trophic Shift in Gall Communities

Samples were prepared and analyzed through continuous-flow isotope-ratio mass spectrometry according to Yarnes et al. (2005). Results of the batches processed for this experiment yielded a level of precision of equal to ±0.2‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. Significance in the pair-wise trophic shift between plant tissues, gall tissues, and insects within trees was analyzed using Student's Paired *t*-Test. All analyses were carried out using SYSTAT Version 10.2 (© 2002, SSI, Richmond, CA U.S.A.). All reported estimates of trophic shift are accompanied by their respective standard error of the difference (± SE).

4.2.3 Results

The $\delta^{13}C$ composition of adult *A. reticulatus* was significantly enriched relative to gall tissue in *Q. turbinella* ($\delta^{13}C_{consumer-diet}$ = 4.3 ± 0.4‰) and leaves bearing galls ($\delta^{13}C_{consumer-diet}$ = 5.1 ± 0.7‰), while galls were slightly enriched (≈1‰; not significant) relative to galled leaves in *Q. turbinella* (Table 1). Galled leaf tissue was marginally depleted in $\delta^{13}C$ relative to gall tissue (Table 1). The $\delta^{15}N_{consumer-diet}$ between *A. reticulatus* and their galls on *Q. turbinella* was significantly enriched (2.3 ± 0.5‰); a similar level of enrichment was observed for $\delta^{15}N_{consumer-diet}$ between *A. reticulatus* and *Q. turbinella* leaves (Table 1). Galls and galled leaves were similar in their $\delta^{15}N$ composition (Table 1).

The $\delta^{13}C$ composition of larval gall-forming arthropods on *S. exigua* was depleted relative to inner gall tissues (*R. strobiloides*: $\delta^{13}C_{consumer-diet}$ = –0.2 ± 0.2‰; *E. exiguae*: $\delta^{13}C_{consumer-diet}$ = –0.5 ± 0.2‰), but enriched over

Table 1. $\Delta^{15}N$ ± SE, $\Delta^{13}C$ ± SE for adult cynipid gall wasps on *Quercus turbinella*

Species	Isotope	$\Delta_{herbivore-gall}$	$\Delta_{herbivore-leaf}$	$\Delta_{gall-leaf}$	$\Delta_{parasitoid-herbivore}$
Neuroterus sp. (Yarnes et al. 2005)	^{15}N	0.7 ± 0.2	0.5 ±0.3	–0.2 ± 0.2	2.1 ± 0.2
	^{13}C	4.4 ± 0.5	6.0 ± 0.5	1.6 ± 0.2	–0.3 ± 1.1
Andricus reticulatus	^{15}N	2.3 ± 0.5 t_3 = 5.099 P = 0.02	2.2 ± 0.4 t_3 = 6.116 P = 0.009	–0.1 ± 0.3 t_3 = -0.444 P = 0.687	n/a
	^{13}C	4.3 ± 0.4 t_3 = 11.052 P = 0.002	5.1 ± 0.7 t_3= 7.677 P = 0.005	0.9 ± 0.5 t_3 = 1.908 P = 0.15	n/a

Table 2. $\Delta^{15}N \pm SE$, $\Delta^{13}C \pm SE$ for larval gall-forming arthropods on *Salix exigua*

Species	Isotope	$\Delta_{herbivore-inner}$	$\Delta_{herbivore-outer}$	$\Delta_{inner-outer}$	$\Delta_{herbivore-mean\ gall}$	$\Delta_{parasitoid-herbivore}$
Rhabdophaga strobiloides	^{15}N	1.1 ± 0.2 $t_9 = 5.94$ $P < 0.001$	1.0 ± 0.5 $t_{10} = 2.20$ $P = 0.05$	0.0 ± 0.7 $t_8 = 0.065$ $P = 0.95$	1.1 ± 0.2 $t_8 = 4.821$ $P = 0.001$	2.2 ± 0.5 $t_1 = -4.657$ $P = 0.135$
	^{13}C	-0.2 ± 0.2 $t_9 = -1.073$ $P = 0.311$	0.8 ± 0.2 $t_{11} = 4.397$ $P = 0.001$	0.9 ± 0.2 $t_8 = 6.059$ $P < 0.001$	0.2 ± 0.2 $t_8 = 0.247$ $P = 0.287$	1.2 ± 0.3 $t_1 = 4.460$ $P = 0.14$
Euura exiguae	^{15}N	1.3 ± 0.3 $t_4 = 4.104$ $P = 0.02$	1.7 ± 0.2 $t_4 = 8.102$ $p = 0.001$	0.4 ± 0.2 $t_4 = 1.789$ $P = 0.15$	1.5 ± 0.2 $t_4 = 6.278$ $P = 0.003$	n/a
	^{13}C	-0.5 ± 0.2 $t_4 = -2.478$ $p = 0.07$	-0.9 ± 0.3 $t_4 = -3.737$ $P = 0.02$	-0.4 ± 0.2 $t_4 = -2.227$ $P = 0.09$	0.7 ± 0.2 $t_4 = 3.410$ $P = 0.03$	n/a

outer gall tissue (*R. strobiloides*: $\delta^{13}C_{consumer-diet} = 0.8 \pm 0.2‰$; *E. exiguae*: $\delta^{13}C_{consumer-diet} = -0.9 \pm 0.3‰$). The $\delta^{13}C_{consumer-diet}$ between larvae and mean gall tissue (inner + outer) were not different in *R. strobiloides* ($\delta^{13}C_{consumer-diet} = 0.3 \pm 0.2‰$), but was significantly depleted in *E. exiguae* ($\delta^{13}C_{consumer-diet} = -0.7 \pm 0.2‰$). The $\delta^{13}C$ composition of inner gall tissue was not significantly different from that of outer gall tissue in *E. exiguae*, but was significantly enriched within galls of *R. strobiloides* (Table 2). The $\delta^{13}C_{consumer-diet}$ between the torymid parasitoid and *R. strobiloides* appeared to be enriched ($1.2 \pm 0.2‰$; Table 2), however the small sample size (n = 2) precluded a robust statistical test. The $\delta^{15}N_{consumer-diet}$ between both larval *R. strobiloides* and *E. exiguae* and their inner and outer gall tissues in *S. exigua* were ≈1‰; the same relationship was true when estimating $\delta^{15}N_{consumer-diet}$ from mean gall $\delta^{15}N$ (Table 2). Torymid parasitoids appeared enriched in $\delta^{15}N$ relative to *R. strobiloides* ($\delta^{15}N_{consumer-diet} = 2.2 \pm 0.3‰$). The inner and outer gall tissues were similar in their $\delta^{15}N$ composition (Table 2).

4.3 Discussion

Several distinct patterns in the trophic shift within gall communities emerge when comparing the results from these species coupled with that of published data. Most striking may be the $\Delta\delta^{13}C$ between cynipids and their galls. In many systems $\Delta\delta^{13}C$ is much less variable (0–1‰; Table 3) across trophic levels than is $\Delta\delta^{15}N$. However, in rare instances $\Delta\delta^{13}C$ may

Table 3. Published estimates of $\Delta^{15}N \pm SE$, $\Delta^{13}C \pm SE$ for larval gall-forming arthropods and their parasitoids in other host plants. Meta-data estimates of $\Delta^{15}N$ and $\Delta^{13}C$ are given by McCutchan et al. (2003)

Species	Isotope	$\Delta_{herb-host}$	$\Delta_{P.\ californica-herb}$	$\Delta_{Tetrastichus-herb}$	$\Delta_{T.\ baccaridis-herb}$	$\Delta_{T.\ koebelei-herb}$
Rhopalomyia californica (Langaletto et al. 2005[a])	^{15}N	3.3 ± 0.4	1.8 ± 0.3	0.4 ± 0.8	2.1 ± 0.4	2.3 ± 0.3
	^{13}C	1.1 ± 0.3	0.4 ± 0.2	1.6 ± 0.3	1.0 ± 0.3	1.2 ± 0.2
Species	Isotope	$\Delta_{A.\ rufus-S.\ terebinthinaceum}$		$\Delta_{A.\ rufus-S.\ laciniatum}$		
Antistrophus rufus (Tooker and Hanks 2004[b])	^{15}N	≈2.5		≈0.5		
	^{13}C	not reported		not reported		
Source of estimate	Isotope	$\Delta_{consumer-diet}$				
McCutchan et al. 2003	^{15}N	2.3 ± 0.2				
	^{13}C	0.5 ± 0.1				

[a]Trophic shift estimates are reported for *R. californica* ("herb") on its host, *Baccharis pilularis* and four parasitoids.
[b]Reported trophic shifts are rough estimates as they were reported through figures. They report estimates of $\Delta^{15}N$ for *A. rufus* in two host plants.

range to near 7‰ (Buckeye butterfly, *Junonea coenia*; McCutchan et al. 2003). The leaf-galling cynipids on *Q. turbinella* (*A. reticulatus* and *Neuroterus* sp.) exhibit relatively large $\Delta\delta^{13}C$ (4.27–6.02‰ over gall tissue, Table 1). While, $\Delta\delta^{13}C$ is determined by the balance of assimilation and respiration, it is unlikely that cynipids would require the abnormally high respiration rate for growth leading to such an elevated $\Delta\delta^{13}C$. Gleixner et al. (1998) found primary plant carbon storage compounds (sucrose, starch) in sink tissues to be enriched in $\delta^{13}C$ composition over their counterparts in source tissues owing to post-transport metabolic conversions of primary compounds. Galls are known to be metabolically intense and similar source-sink dynamics and patterns of post-transport metabolic activities within galls (Harper et al. 2004; Larson and Whitham 1991) would contribute to variation in $\delta^{13}C$ between different gall tissues. Notably, we do not see the same pattern in bud-galling Cecidomyiidae (Langellotto et al. 2005; Yarnes et al. 2005; Tables 2, 3). Nor do we see high estimates of $\Delta\delta^{13}C$ in stem-gallers representing other taxa (Tables 1, 3). At this time, an estimate of $\Delta\delta^{13}C$ near zero for all non-cynipid gall-formers may be appropriate. All the endoparasitoids of gall-forming arthropods examined so far (Tables 1, 2) exhibit only a marginal degree of $\Delta\delta^{13}C$ (–1‰ to 1‰) from their hosts, as expected from meta-data estimates (Table 3).

The trophic shift in nitrogen isotopes ($\Delta\delta^{15}N$) has been proposed as an index for diet protein quality for consumers (Martínez del Rio and Wolf 2004) as it represents the balance between nitrogen assimilation and excretion. As the quality and assimilation efficiency of diet protein increases, trophic shift decreases. The $\Delta\delta^{15}N$ between *A. reticulatus* and their galls in *Q. turbinella* was nearly equal to meta-data estimates (≈2.5‰; McCutchan et al. 2003) and similar to estimates of trophic shift in other gall-forming arthropods (Langellotto et al. 2005; Tooker and Hanks 2004; Table 3). However, the $\Delta\delta^{15}N$ in *A. reticulatus* on *Q. turbinella* is drastically different from that reported in another species of cynipid, *Neuroterus* sp., on *Q. turbinella* (Yarnes et al. 2005; Table 1). This result indicates that separate species of cynipids can exhibit different $\Delta\delta^{15}N$ on the same host plant. Further, Tooker and Hanks (2004) found that the $\Delta\delta^{15}N$ for *Antistrophus rufus* significantly differed across host plants (Table 3). These results may indicate differences in the physiological mechanisms of gall nitrogen supply across different galling arthropods, as well as differences in nutritional quality of different hosts. Clearly, ecological patterns of $\Delta\delta^{15}N$ in gall-formers are still in need of considerable study before researchers can rely upon published estimates. Literature surveys of predator-based studies point to a generalized 3‰ shift in $\delta^{15}N$ across trophic levels for secondary consumers (Post 2002). The lower observed trophic shift for a torymid parasitoid of *R. strobiloides* of ≈ 2‰ is consistent with the high nitrogen assimilation efficiency often observed in parasitoids (Greenblatt et al. 1982) and other parasitoids (Tables 1–3). While it appears reasonable to assume an estimate of ≈ 2‰ for $\Delta\ \delta^{15}N$ in parasitoids of gall-forming arthropods (Langellotto et al. 2005; Yarnes et al. 2005), additional estimates for gall-formers are necessary due to interspecific differences between gall-formers and on both the same and different host plants.

4.4 Analytical Considerations and Future Directions

The continued application of stable isotope analyses in gall-forming arthropod communities requires a number of analytical considerations. While significant differences in the trophic shift of isotopes exist within galls of most species, the magnitude of the trophic shift is typically reduced from that of meta-data estimates. This puts an increased demand upon analytical precision, particularly when measurements are performed in continuous-flow isotope ratio mass spectrometry (CF-IRMS). This may be further exacerbated by the sample size requirement of $^{15}N/^{14}N$ measurements in CF-IRMS (60 μg elemental N) when considering the body

mass of many inhabitants of gall communities. While considerably more time consuming, the use of traditional dual-inlet techniques would provide better precision and reduced sample consumption requirements (typically a ten-fold reduction in sample gas requirements). It is our suggestion that dual-inlet techniques be strongly considered when available.

Recent technological developments in IRMS technologies now allow for the high-precision measurement of the isotope-ratios of individual compounds through the coupling of a gas chromatograph to an IRMS (GC-C-IRMS). In particular, this technique has been successfully applied to the measurement of isotope ratios in both amino acids and lipids (Teece and Fogel 2004). The application of GC-C-IRMS has the potential to elucidate long-standing physiological and biochemical aspects of cecidogenesis, as well as the nutrition of gall-forming arthropods. This may be particularly true for the role of lipids in the inner nutritive cells of cynipid galls (Bronner 1992, Harper et al. 2004) or the regulation of host amino acid production and supply by gall-formers (Hartley and Lawton 1992; Koyama et al. 2003).

The utility of stable isotopes goes far beyond any potential applications to the biology of gall-forming arthropods and their associates. Stable isotopes offer a risk-free alternative to the radioactive isotopes historically used in studies of cecidogenesis. Stable isotopes are safe both at the natural abundance level and in studies requiring the use of stable isotopic tracers. The broad capabilities and increasing availability of IRMS technologies leaves little room for the future consideration of radioactive tracers in ecological and biochemical studies of galls.

4.5 Conclusions

Significant differences in the trophic shift in carbon and nitrogen isotopes between gall community consumers and their hosts indicate that stable isotopes have the potential to provide considerable insight into the trophic interactions within gall communities. Additional information is still needed to set an isotopic baseline for $\Delta\ \delta^{15}N$ within gall communities. $\Delta\ \delta^{13}C$ appears to be fairly reliable across systems — with the exception of cynipid gall wasps. In particular, the examination of different gall tissues and compound-specific isotope studies may profoundly illuminate the physiological ecology of gall-forming insect larvae. The ultimate utility of stable isotopes to the study of food web ecology within galls will depend on the further documentation of patterns in trophic shift and the demonstration of

applicability to more complex communities that include inquilines, predators, and hyperparasitoids.

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