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DIRECT AND INDIRECT EFFECTS OF PRIOR GRAZING OF GOLDENROD UPON THE PERFORMANCE OF A LEAF BEETLE¹

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Abstract. A plant's grazing history can influence the nutritional quality of its leaves and directly affect herbivore performance. In addition, leaf nutritional quality can indirectly affect herbivore performance by influencing food consumption. We examined the direct and indirect influences of prior grazing of *Solidago missouriensis* upon leaf nutritional quality and the growth and fecundity of *Trirhabda canadensis* (Coleoptera: Chrysomelidae). We fed leaves from both previously grazed (during 1988 and 1989) and ungrazed goldenrod plots derived from a single *S. missouriensis* clone to larvae and adults of *T. canadensis* in laboratory performance trials. We computed standard insect performance indices and used structural equation modeling and path analysis to interpret the results of these trials. Prior grazing of goldenrod had a direct negative impact upon the growth of *T. canadensis* larvae in spring of 1990; a concomitant reduction in foliage consumption accentuated this effect. Larvae fed leaves from grazed plots accumulated biomass and N more slowly, used them less efficiently, and reached a lower final mass than did larvae fed leaves from plots without prior folivory. Goldenrods produced a new flush of leaves following larval grazing in the spring of 1990. Therefore, adults feeding in plots defoliated by larvae ate younger leaves than those feeding in undefoliated plots. Leaves from defoliated plots had direct positive impacts upon the growth and egg production of adult *T. canadensis*. Adults converted these young leaves into biomass with greater efficiency and preferred them to older leaves from ungrazed plots in choice tests. However, negative indirect effects of prior grazing upon initial adult mass and total foliage consumption negated any positive influence that these more nutritious leaves had upon growth, and made the overall impact of prior grazing upon egg production negative. These results indicate that impacts of food availability and quality must be considered jointly to understand how prior grazing influences herbivore performance.

Key words: goldenrod; insect growth and reproduction; insect herbivory; nutritional quality; path analysis; prior grazing; *Solidago missouriensis*; structural equation modeling; *Trirhabda canadensis*.

INTRODUCTION

The availability and nutritional quality of vegetation influence the population dynamics of herbivores, especially those that feed in the same area or upon the same plant for several successive generations (Werner 1979, McNaughton 1984, Myers and Williams 1984, Tuomi et al. 1984, Williams and Myers 1984, Bryant et al. 1985, Day and Detling 1990). Folivores can alter the availability of vegetation by reducing standing crop and by influencing survivorship, growth, resource allocation, and reproduction of plants (Waloff and Richards 1977, Morrow and La Marche 1978, Rausher and Feeny 1980, Marquis 1984, Cain et al. 1991, Dyer et al. 1991). Concomitantly, grazers can alter basic foliage nutritional characteristics such as water, nitrogen, or fiber content (Cargill and Jefferies 1984, McNaughton

1984, 1985, Archer and Detling 1986). In addition, folivores may influence production of allelochemicals that deter feeding or reduce assimilation efficiency, growth rate, or fecundity (Bryant 1981, Lincoln et al. 1982, Baldwin 1988, Brown 1988, Haukioja 1990).

Chrysomelid beetles of the genus *Trirhabda* are important folivores of goldenrods (*Solidago* spp.) (Messina and Root 1980, Messina 1981, McBrien et al. 1983, Root and Cappuccino 1992). Both larvae and adults of *Trirhabda* eat goldenrod, and often feed upon the same clone for several successive years (Balduf 1929, Messina 1981). These beetles typically exhibit localized outbreaks on goldenrod clones. Extensive defoliation during outbreaks greatly reduces the availability of leaves and increases the availability of light, water, and soil nitrogen to plants (Brown 1994). Availability of these resources influences both leaf nutritional quality and insect growth rates (Fox and Maccauley 1977, McNeill and Southwood 1978, Mattson 1980, Scriber and Slansky 1981, Bryant 1987, Waring and Cobb 1992). The *Trirhabda*–*Solidago* system of-

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TABLE 1. Leaf consumption in the field by larvae and adults of *Trirhabda canadensis* in experimental *Solidago missouriensis* plots between July 1988 and August 1990 (mean ± 1 SE; n = 12).

Folivory treatment	Leaf area consumed (%)				
	1988		1989		1990
	By adults	By larvae	By adults	By larvae	By adults
Zero	1.58 ± 0.37	0	10.5 ± 11.60	7.32 ± 2.80	9.45 ± 0.45
Low	6.53 ± 1.11	0	35.77 ± 4.11	87.96 ± 5.77	16.29 ± 1.47
High	14.52 ± 2.58	0	47.83 ± 5.79	97.97 ± 2.03	16.68 ± 2.13

fers an opportunity to address the following questions: (1) Does prior folivory affect the nutritional characteristics of goldenrod leaves? (2) How does feeding upon leaves from previously grazed goldenrod affect components of *Trirhabda's* performance such as consumption, conversion efficiency, growth, or fecundity? (3) Do female *Trirhabda* adults distinguish between leaves from plants with different defoliation histories?

Nutritional characteristics of leaves are often evaluated using familiar consumption and growth indices developed by Waldbauer (1968; see Table 2). These indices are algebraic combinations of a few variables (initial mass, final mass, food consumption, duration of the experiment, and excretion) measured in con-

trolled performance trials. While these measures succinctly document differences between treatment groups, the causes of these differences may not be evident. For example, biomass conversion efficiency is a commonly used index of leaf quality that is computed by dividing insect biomass gained by leaf biomass consumed. Conversion efficiency may differ between groups because of differences in starting biomass, consumption, final biomass, or an interaction among these three determinants. Since insects collected from natural systems usually vary in all of these components, difficulties in interpretation can arise. In addition, since many indices are computed from a few measured variables, autocorrelation between indices presents a sta-

TABLE 2. Formulae and interpretation for insect performance indices.

Performance index	Formula	Interpretation
Relative consumption rate	$\frac{(\text{total leaf mass consumed})/(\text{no. days in trial})}{\exp\left(\frac{\ln(\text{initial dry mass}) + \ln(\text{final dry mass})}{2}\right)}$	Mean daily leaf consumption per unit body mass over the course of an entire performance trial
Relative N consumption rate	$\frac{(\text{total leaf N consumed})/(\text{no. days in trial})}{\exp\left(\frac{\ln(\text{initial dry mass}) + \ln(\text{final dry mass})}{2}\right)}$	Mean daily N consumption per unit body mass over the course of an entire performance trial
Biomass conversion efficiency	$\frac{\text{increase in insect mass}}{\text{leaf mass consumed}} \times 100$	Efficiency with which an insect converts ingested leaf biomass into insect biomass; egg production was included for adults
Nitrogen use efficiency	$\frac{\text{increase in insect N}}{\text{mass of N consumed}} \times 100$	Analogous to biomass conversion efficiency, but focuses strictly on nitrogen; egg production was included for adults
Relative growth rate	$\frac{\ln(\text{final mass}) - \ln(\text{initial mass})}{\text{no. of days in trial}} \times 100$	Mean compound growth rate required to produce the final mass of insect material from the initial insect mass during a performance trial; egg production was included in the final mass for adults
Relative N accumulation rate	$\left(\frac{\ln(\text{final N mass}) - \ln(\text{initial N mass})}{\text{no. of days in trial}}\right) \times \left(\frac{\text{mean mg N}}{\text{g biomass}}\right)$	Similar to relative growth rate but focuses strictly on nitrogen; for adults the N content of eggs was incorporated into the final N mass and mean N content
Reproductive allocation	$\frac{\text{mass of eggs (or mass of N in eggs)}}{\text{total biomass (or N) gained}} \times 100$	Percentage of insect biomass or N production which is allocated to egg production, an index of reproductive effort

tistical problem and an experimental limitation. We use structural equation modeling (Loehlin 1987) and path analysis (Wright 1934, Li 1976) to augment the interpretation of performance indices. These techniques examine causal relationships among the measured variables in a performance trial. A virtue of the structural-equation approach is that it disentangles foliage quality's direct effects on insect performance from its indirect effects upon consumption or other factors.

METHODS

Experimental system

We worked at the Cedar Creek Natural History Area located in east-central Minnesota, USA, about 60 km north of Minneapolis/St. Paul. Descriptions of Cedar Creek and the study site are available elsewhere (Grigal et al. 1974, Inouye et al. 1987, Brown 1994).

Solidago missouriensis (Nutt.) (Missouri goldenrod) is a short, rhizomatous, perennial herb (20–40 cm tall) typically found in dry, infertile sites (Werner 1976). It grows in discrete clones throughout Cedar Creek, generally in fields of mid-successional age (20–30 yr) through undisturbed oak savanna. *S. missouriensis* is one of several goldenrods consumed by both the larvae and adults of *Trirhabda canadensis* (Kirby) (Coleoptera: Chrysomelidae). Eggs oviposited beneath a goldenrod clone during the preceding summer hatch from early- to mid-May. Larvae feed for about ≈ 1 mo and subsequently pupate in the soil under their host. Adults emerge in late June to early July and simultaneously feed and mate on goldenrods through July and into August (see Balduf [1929] for greater detail). Populations of *T. canadensis* erupt asynchronously on clones of *S. missouriensis* and other goldenrods at Cedar Creek. During these eruptions *T. canadensis* can consume all leaf tissue in their host clone (D. G. Brown, *personal observation*). Larvae of *T. canadensis* generally will not leave a goldenrod clone unless the availability of leaves is limited. Adults are also relatively sedentary (Messina 1982; D. G. Brown, *personal observation*), but will emigrate if there is a local shortage of food or mates (Morrow et al. 1989).

Imposition of folivory treatments

To study how prior grazing affected leaf nutritional quality while controlling for genetic factors, we collected *S. missouriensis* ramets from a single clone that was free of *T. canadensis* in June 1987. We transplanted these ramets into 36 circular plots 1 m in diameter (0.785 m²) arrayed in three 3 × 4 blocks with the center of each plot 7 m from that of its neighbors. Aluminum flashing 20 cm deep, approximately the maximum rooting depth of *S. missouriensis* (D. G. Brown, *personal observation*), surrounded each plot. We assigned plots randomly within each block to one of three *T. canadensis* folivory treatments: zero (zero adults per ramet),

low (one adult per ramet), or high (five adults per ramet). The density of *T. canadensis* can reach five adults per ramet or higher on native goldenrod clones during outbreaks (D. G. Brown, *personal observation*). We initiated folivory treatments in July 1988 and concluded them in August 1990. In early July of each year, we collected beetles from colonies maintained by P. A. Morrow and G. M. Puttick and released them into the low and high folivory plots. We did not enclose the plots, but maintained adult densities by regular censuses and appropriate removal, transfer, or restocking. Few *T. canadensis* larvae eclosed in the experimental plots in 1989 and their grazing was negligible. In contrast, a large number of larvae eclosed in low and high folivory plots in 1990 and inflicted extensive damage. We sprayed first instar larvae in zero folivory plots with insecticidal soap (Safer, Ringer Coompany, Eden Prairie, Minnesota, USA) in early May 1990 and subsequently removed survivors by hand. Table 1 summarizes the grazing history in the field of plots assigned to each folivory treatment.

Performance of T. canadensis and leaf nutritional quality

General procedure.—We conducted performance trials to ascertain how the grazing history of their host influenced the growth and reproduction of a generation of *T. canadensis*. Insects lived in 250 ml plastic containers during performance trials. We melted a hole in each container's side to admit an Aquapik, which maintained leaf hydration. We dried all containers at 40°C for 48 h and weighed them before use. We performed the trials in the laboratory at ambient temperature (21°–24°C), humidity, and light conditions.

We used only fully expanded, non-senescent leaves that had <1% of their area removed by folivores in performance trials. We haphazardly collected suitable leaves for each folivory treatment on a rotational basis from all experimental plots assigned to that treatment; each insect therefore consumed leaves representative of those available in the field. We collected leaves between 0900 and 1000 and immediately placed them in a dish of water to maintain hydration. We measured the area of each leaf with a leaf area meter (LI-COR). We then haphazardly selected a subset of the leaves for the performance trial. We inserted leaves into Aquapiks with their blades parallel to the bottom of the container and placed insects upon the leaves. We dried the remainder of the leaves for each folivory treatment at 105°C for 24 h to estimate the water content and specific leaf mass (mass per unit area) of the leaves used in the performance trial. We then ground these leaves and determined their N content with a Carlo Erba combustive C-N-S autoanalyzer (Tilman and Wedin 1991).

We starved *T. canadensis* larvae and adults for 24 h before a trial. We replaced their leaves every other day during a trial and measured the remaining area of each outgoing leaf. We determined leaf area consumption

by the difference between remaining leaf area and that measured before feeding; the product of leaf area consumed and specific leaf mass yielded the mass of foliage consumed. When we changed leaves, we scraped excreta off outgoing leaves with an X-acto knife and placed it back into the container. During the adult performance trial, we also collected egg clutches if present. We replaced dishes if mold began to appear on excreta. At the end of a trial, we removed leaves and starved the insects for 24 h. We then removed the Aquapiks and dried the containers and their contents at 40°C for 48 h and weighed them to determine the mass of excreta produced. We included molted larval cuticles with excreta for the calculation of larval performance indices. We dried insects at 105°C for 24 h to determine final dry mass, and determined the N content of insects, eggs, and excreta as described above. We calculated the performance indices shown in Table 2 using data obtained from the performance trials (cf. Waldbauer 1968, Slansky and Feeny 1977, Slansky and Scriber 1985).

Larval performance.—We collected second instar *T. canadensis* larvae of similar size on 25 May 1990 from a second clone of *S. missouriensis* and haphazardly assigned them to eat leaves from one of the three folivory treatments. We could not accurately determine the initial live mass of individual larvae. Therefore, we determined the live mass of the group of larvae assigned to eat leaves from a given folivory treatment and assumed that each larva in that group had the same initial live mass. We then dried a fourth group of larvae at 105°C for 24 h to convert live masses into dry mass estimates. We had 24 replicates for each folivory treatment. We placed two larvae in each container because we anticipated significant larval mortality from manipulation during setup. If both survived the trial, then we used their mean response for statistical analyses. In cases where one larva died or escaped within the first day of the trial, we used the results for the remaining larva. We omitted cases where one larva died late in the trial since these gave inaccurate results for the remaining larva. We concluded the trial on 4 June when no suitable leaves remained in low or high folivory plots. Nearly all experimental larvae were then in their third instar.

Adult performance.—We collected teneral female *T. canadensis* from experimental plots on 3 July 1990 and separately stored those collected from each folivory treatment. Dispersal in other *Trirhabda* species occurs in a brief post-teneral period (Messina 1982); *T. canadensis* will usually not disperse at this time unless no goldenrod foliage is available (Morrow et al. 1989; D. G. Brown, *personal observation*). Therefore, we assumed that adults emerged in the plots from which we collected them. We randomly selected 12 females from each folivory treatment and determined the initial live mass of each. We dried the remainder of the females from each folivory treatment for 24 h at 105°C to es-

timate the initial dry mass and N content of the beetles in the trial. During the trial, we fed females leaves like those they would have consumed had they remained in their emergence plots (i.e., females from zero folivory plots ate leaves from zero folivory plots, females from low folivory plots ate leaves from low folivory plots, and those from high folivory plots ate leaves from high folivory plots). We retained beetles in the trial until they perished or until 1 mo elapsed after they produced their first clutch.

Paired-choice tests

We conducted paired-choice tests to determine whether or not adult female *T. canadensis* could distinguish between leaves from plots defoliated by larvae and those from plots not defoliated. We collected adult female *T. canadensis* from colonies and starved them for 24 h. Females lived in 9 cm diameter plastic Petri dishes during the test. We placed a piece of damp filter paper in the dish to reduce water loss from leaves. We collected leaves and determined biomass consumption as described above. We placed leaves from two of the folivory treatments at opposite sides of each dish. In half of the 24 replicates of each paired comparison, we placed leaves from the lower folivory treatment on the right. In the other half, we placed them on the left. We placed a female between the two leaves and allowed her to feed for 24 h. We performed this test in the laboratory at ambient temperature, humidity, and light conditions.

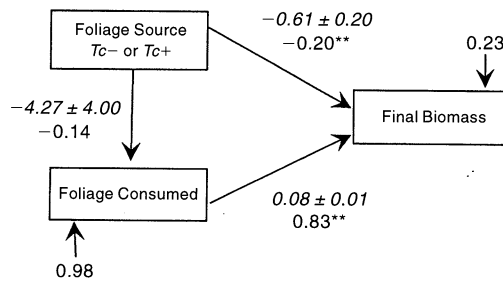
Statistical analysis

Low and high folivory plots had similar grazing histories, and preliminary analyses revealed that these treatments generated similar responses for factors considered in this study. Therefore, we pooled the low and high folivory treatments into a single *T. canadensis* folivory treatment ($Tc+$) to simplify data presentation. We contrasted this composite treatment with the zero folivory treatment ($Tc-$).

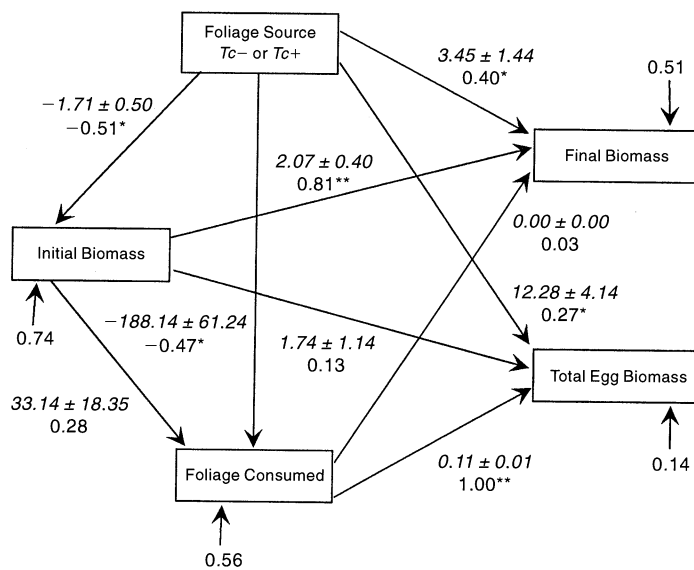
We analyzed data on leaf characteristics with a mixed-model ANOVA. The F ratio reported is that for the effect of *T. canadensis* grazing (fixed) using the sampling date (random) \times grazing interaction as the error term. We first analyzed data for larval growth, adult growth, and adult reproduction using MANOVA to determine whether or not there was a significant overall effect of prior folivory upon the suite of response variables. We then examined the significance of individual response variables using linear regression. The t statistic reported is that for the dummy variable $Tc+ - Tc-$ in the regression model after inclusion of block effects and other background variables. We analyzed the paired-choice test with a paired t -test.

We performed additional analyses to reveal how changes in foliage quality caused by prior grazing influenced *Trirhabda* performance through a network of direct and indirect causes. For instance, reduced foliage

a) Larval Performance



b) Adult Performance



* $P < 0.05$
 ** $P < 0.01$

FIG. 1. (a). Structural equation model for the final mass of *T. canadensis* larvae as a function of foliage source (T_{c+} or T_{c-}) and amount of foliage consumed. Arrows indicate causal influence of one variable upon another. Structural equation coefficients ± 1 SE (upper, large italic type) show how incrementing a predictor variable (e.g., switching from T_{c-} to T_{c+} foliage or increasing foliage consumption by 1 mg) would alter the target variable (foliage consumption or final mass) (in mg) with all other factors held constant. Path coefficients (lower, small type) indicate how changing a predictor variable (foliage source or foliage consumption) by one standard deviation would directly alter the target variable in SD units with all other factors held constant. Values associated with vertical arrows show the correlation of a target variable with unexamined background factors and experimental error. (b). Structural equation model for final mass and egg biomass production of adult female *T. canadensis* as a function of foliage source, initial mass, and amount of foliage consumed.

nutrient content may lower final larval biomass directly. Indirect influences on growth may occur if *Trirhabda* compensates for low foliage nutrient quality by increasing foliage consumption. Compensatory consumption might then mitigate the adverse effect of low-quality foliage (Scriber and Slansky 1981). To reveal such direct and indirect effects, we used structural equation modeling (Loehlin 1987). This statistical technique is a generalized form of multiple linear regression related to path analysis.

To analyze an experiment with structural equation

modeling, one starts with an ad hoc model that depicts the experimental situation. Fig. 1a depicts the model we used for the larval experiment. We expected the final mass of a *Trirhabda* larva to depend upon both foliage source and the amount of foliage ingested. However, foliage consumption could also depend upon foliage source. Thus, both foliage source and foliage consumption could affect final mass directly, while foliage source could affect final mass indirectly by altering foliage consumption. We analyzed this model by calculating structural equation coefficients for the ef-

TABLE 3. Water content, specific leaf mass, and N content of *Solidago missouriensis* leaves for the two folivory treatments during the larval and adult feeding periods of *Trirhabda canadensis* in 1990 (mean \pm 1 SE). NS = not significant.

	Leaf characteristic	Folivory treatment		F	df	P
		+ <i>T. canadensis</i>	- <i>T. canadensis</i>			
Larval feeding period	Water content (%)	75.23 \pm 0.08	76.65 \pm 0.20	1104.58	1, 1	0.05
	Specific leaf mass (g/m ²)	74.07 \pm 1.22	69.15 \pm 1.68	41.55	1, 3	0.01
	N content (%)	3.28 \pm 0.17	3.25 \pm 0.16	0.10	1, 3	NS
Adult feeding period	Water content (%)	73.70 \pm 0.42	68.33 \pm 0.45	322.15	1, 17	0.0001
	Specific leaf mass (g/m ²)	73.95 \pm 1.98	100.20 \pm 1.98	186.10	1, 17	0.0001
	N content (%)	2.48 \pm 0.12	1.78 \pm 0.10	33.15	1, 6	0.01

fects of foliage source and foliage consumption on final larval mass. These are partial regression coefficients that predict the expected change in final mass when larvae eat leaves from previously grazed plants vs. ungrazed plants (statistically holding foliage consumption constant), and the change in final mass caused by a 1-mg change in foliage consumption (statistically holding foliage source constant). We then determined a third structural equation coefficient that predicts the change in foliage consumption when larvae eat leaves from previously grazed vs. ungrazed plants. This coefficient thus shows the direct effect of foliage source on foliage consumption. The indirect effect of foliage source upon final biomass mediated by changes in foliage consumption is estimated by the product of the coefficient for effect of foliage source on foliage consumption and that for the effect of foliage consumption on final mass (shown numerically in Table 5). The observed difference in mean final mass of larvae fed leaves from grazed plants and those fed leaves from ungrazed plants should be equal to the sum of the direct and indirect effects of foliage source calculated from the structural equation model (see Table 5). We used the same procedure to analyze a more complex model of the adult performance experiment that examined direct and indirect influences of foliage source on final adult female mass and the mass of eggs produced.

We also used conventional path analysis to analyze these models. The procedure is the same as for structural equation modeling, except that the partial regression coefficients calculated are called path coefficients

and are expressed in standard deviation units. (Wright 1934, Li 1976). We calculated partial coefficients of determination (analogous to R^2 of linear regression) from the path coefficients for the direct and indirect effects of foliage source on the target variables (Li 1976; see Weis et al. 1989 for a detailed computation of partial coefficients of determination from path coefficients.). We determined the goodness-of-fit for the path models when possible. This is assessed by comparing the correlation matrix observed among the variables in the experiment to that predicted by the estimated regression coefficients. (See Mitchell 1992 for an excellent account of this method.) The test statistic is distributed as a chi-square, and a nonsignificant value indicates that the predicted correlation matrix does not differ from the observed, i.e., the path model provides a good fit to the data. We calculated structural equation coefficients, path coefficients, and the goodness-of-fit statistic using the maximum likelihood option of the CALIS procedure of SAS (SAS Institute 1988).

RESULTS

Leaf characteristics

During the larval feeding period, leaves from *Tc-* plots had higher leaf water content and lower specific leaf mass than did those from *Tc+* plots (Table 3). Leaf N content did not differ between the folivory treatments. During the adult feeding period, in contrast, leaves from *Tc+* plots had higher leaf water and N content and lower specific leaf mass than did those from *Tc-* plots.

TABLE 4. Consumption and growth indices for *Trirhabda canadensis* larvae fed *Solidago missouriensis* leaves from the two folivory treatments in laboratory performance trials in 1990 (mean \pm 1 SE). NS = not significant.

Performance index	Folivory treatment		t	P
	+ <i>T. canadensis</i> (n = 41)	- <i>T. canadensis</i> (n = 20)		
Relative consumption rate (g·g ⁻¹ ·d ⁻¹)	4.29 \pm 0.14	4.11 \pm 0.18	0.96	NS
Relative N consumption rate (mg·g ⁻¹ ·d ⁻¹)	130.5 \pm 5.6	121.7 \pm 5.4	1.74	NS
Biomass consumed (mg)	41.9 \pm 2.22	46.2 \pm 3.38	-1.15	NS
N consumed (mg)	1.3 \pm 0.1	1.4 \pm 0.1	-0.83	NS
Biomass conversion efficiency (%)	6.85 \pm 0.31	8.38 \pm 0.37	-3.58	0.001
N use efficiency (%)	21.94 \pm 1.11	25.07 \pm 1.05	-2.62	0.05
Relative growth rate (%/d)	24.61 \pm 0.82	28.68 \pm 1.10	-3.08	0.01
Relative N accumulation rate (mg·g ⁻¹ ·d ⁻¹)	23.6 \pm 0.77	26.8 \pm 1.11	-2.51	0.05
Final mass (mg)	3.2 \pm 0.2	4.2 \pm 0.3	-2.70	0.01

TABLE 5. Impact of grazed vs. ungrazed goldenrod upon performance (larval, adult, and egg biomass) of *Trirhabda canadensis*, partitioned by direct and indirect effects of foliage source ($Tc+$ or $Tc-$). Effects were calculated using structural equation coefficients (Fig. 1); indirect effects were calculated using individual coefficients along appropriate causal paths (indicated in parentheses).

Performance index	Difference between treatment means ($Tc+$ minus $Tc-$)	Direct effect of foliage source	Difference attributed to:			
			Indirect effects via:			Unexplained difference
			Foliage consumption	Initial adult biomass		
Final larval biomass	-1.00 mg	-0.61 mg	-0.34 mg (-4.27×0.08)	NA*	-0.05 mg	
Final adult biomass	-0.20 mg	3.45 mg	0.00 mg ($(-1.71 \times 33.14 \times 0.00)$ $+ (-188.14 \times 0.00)$)	-3.54 mg (-1.71×2.07)	-0.11 mg	
Total egg biomass	-19.06 mg	12.28 mg	-26.93 mg ($(-1.71 \times 33.14 \times 0.11)$ $+ (-188.14 \times 0.11)$)	-2.98 mg (-1.71×1.74)	-1.43 mg	

* NA: not applicable.

Performance of *T. canadensis*

Larvae.—Prior grazing of *S. missouriensis* by *T. canadensis* significantly affected the suite of larval performance characteristics (MANOVA: Wilks' Lambda = 0.482; $F = 5.74$; $df = 9,48$; $P < 0.001$; Table 4). Although larvae fed leaves from both $Tc+$ and $Tc-$ plots had the same initial mass (0.3 mg), those fed foliage from $Tc+$ plots were 1 mg lighter at the trial's end. Neither the consumption rate nor the overall consumption of biomass and N by *T. canadensis* larvae differed between the $Tc+$ and $Tc-$ treatments. Therefore, reduced conversion efficiencies and accumulation rates of both biomass and N for larvae fed leaves from $Tc+$ plots indicate that these leaves were of lower nutritional quality than those from $Tc-$ plots.

The structural equation model for larval growth (Fig. 1a) indicated that nearly two-thirds of the reduction in final mass of larvae fed leaves from $Tc+$ plots was directly attributable to the lower nutritional quality of these leaves relative to those from $Tc-$ plots (Table 5). Reduced consumption of leaves from $Tc+$ plots explained about one-third of the difference in final mass. The coefficient for this indirect effect of prior grazing was not statistically significant, however. Path coefficients revealed that leaf consumption should generally be a stronger determinant of final mass (69% of variance explained) than foliage source (6% of variance

explained) (Table 6). This seemingly contradictory result was due to the relatively large path coefficient for the influence of foliage consumption upon final mass, coupled with the lack of significant variation in consumption between the treatment groups. No goodness-of-fit test was possible for the larval structural equation model.

Adults

1. **Growth.**—Prior folivory significantly affected the suite of adult growth characteristics (MANOVA: Wilks' Lambda = 0.092; $F = 18.81$; $df = 11,21$; $P < 0.001$; Table 7). Females collected from $Tc+$ plots were lighter than those collected from $Tc-$ plots. However, females fed leaves from both sources reached nearly identical final mass. Both relative consumption rate and total biomass consumption of females fed leaves from $Tc-$ plots were higher than those of females fed leaves from $Tc+$ plots. In contrast, prior grazing did not affect either relative N consumption rate or total N consumption. Females fed leaves from $Tc+$ plots had significantly higher biomass conversion efficiency but lower N use efficiency than did those fed leaves from $Tc-$ plots. The folivory treatment did not affect female lifespan, relative growth rate, or relative N accumulation rate.

The structural equation model for final adult mass (Fig. 1b) indicated that the similar final masses of fe-

TABLE 6. Proportions of variance in *Trirhabda canadensis* performance explained by foliage source ($Tc+$ or $Tc-$), foliage consumption, and initial adult biomass. Values are calculated along causal paths in the models in Fig. 1.

Performance index	Foliage source			Foliage consumption			Initial adult biomass			Total variance explained
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total	
Final larval mass	0.040	0.023	0.063	0.689	NA*	0.689	NA	NA	NA	0.752
Final adult mass	0.160	-0.172	-0.012	0.001	NA	0.001	0.656	0.007	0.663	0.652
Total egg mass	0.073	-0.183	-0.110	1.000	NA	1.000	0.017	0.036	0.053	0.943

* NA = not applicable.

TABLE 7. Consumption and growth indices for adult female *Trirhabda canadensis* fed *Solidago missouriensis* leaves from the two folivory treatments in laboratory performance trials in 1990 (mean ± 1 SE). NS = not significant.

Performance index	Folivory treatment		t	P
	+ <i>T. canadensis</i> (n = 23)	- <i>T. canadensis</i> (n = 12)		
Initial mass (mg)	8.33 ± 0.23	10.05 ± 0.52	-3.47	0.01
Lifespan (d)	34.8 ± 2.3	37.1 ± 1.6	-0.68	NS
Relative consumption rate (g·g ⁻¹ ·d ⁻¹)	0.85 ± 0.04	1.25 ± 0.07	-5.09	0.0001
Relative N consumption rate (mg·g ⁻¹ ·d ⁻¹)	22.0 ± 1.0	22.0 ± 1.7	-0.03	NS
Biomass consumed (mg)	345.6 ± 31.8	590.3 ± 44.2	-4.48	0.001
N consumed (mg)	9.1 ± 0.8	10.7 ± 1.1	-1.24	NS
Biomass conversion efficiency (%)	11.46 ± 0.53	9.64 ± 0.57	2.36	0.05
N use efficiency (%)	36.15 ± 1.66	44.47 ± 1.83	-3.08	0.01
Relative growth rate (%/d)	5.31 ± 0.38	5.27 ± 0.30	0.08	NS
Relative N accumulation rate (mg·g ⁻¹ ·d ⁻¹)	4.71 ± 0.35	4.69 ± 0.28	0.05	NS
Final mass (mg)	17.4 ± 0.9	17.6 ± 1.0	-0.16	NS

males fed leaves from the two folivory treatments resulted from two counteracting influences (Table 5). *Tc+* foliage was of higher nutritional quality, as evinced by the nearly 20% higher biomass conversion efficiency enjoyed by females that ate *Tc+* foliage relative to those that ate *Tc-* foliage. If all else were equal, this higher quality foliage would have directly produced heavier females. Instead, reduced initial mass, an indirect effect of feeding on *Tc+* foliage as a larva, canceled out the positive effect of nutritional quality. The model also indicated that the heavier females collected from *Tc-* plots should have attained a higher final mass, but these females ate leaves of lower nutritional quality than did females from *Tc+* plots. The net effect of these two opposing influences was similar final mass for the two treatments. Path coefficients revealed that initial mass explained most of the variance in final adult mass (Table 6). Surprisingly, foliage consumption and foliage source explained almost none of the variation in final mass, the latter because indirect effects nullified direct effects.

2. *Reproductive output.*—Prior folivory significantly affected the suite of reproductive characteristics (MANOVA: Wilks' Lambda = 0.557; *F* = 2.39; *df* = 8,24; *P* < 0.05; Table 8). Females fed leaves from *Tc+* plots took longer to lay their first clutch and had a longer inter-clutch interval than did those fed leaves

from *Tc-* plots. As a result, these females produced fewer clutches than did those fed leaves from the *Tc-* plots. Since prior grazing of foliage did not affect clutch size, females fed leaves from *Tc+* plots produced fewer eggs than those fed leaves from *Tc-* plots. Females fed leaves from *Tc-* plots produced a greater biomass of eggs and allocated a greater percentage of both assimilated biomass and N to egg production than did those fed leaves from *Tc+* plots. However, eggs produced by females fed leaves from *Tc+* plots were heavier than those of females fed leaves from *Tc-* plots.

The structural equation model for egg mass (Fig. 1b) indicated that if all else were equal, adults that ate high-quality foliage from *Tc+* plots would have produced a greater mass of eggs than did those that ate *Tc-* leaves (Table 5). However, two negative indirect effects of feeding upon *Tc+* foliage (greatly reduced foliage consumption and, to a lesser extent, smaller initial size) dwarfed the direct positive effect of *Tc+* foliage upon egg production. Path coefficients revealed a nearly one-to-one correspondence between foliage consumption and egg biomass production (Table 6). The structural equation model for adult performance shown in Fig. 1b adequately describes the causal influences determining final biomass and egg biomass production (goodness-of-fit $\chi^2 = 0.90$, *df* = 1, *P* > 0.30).

TABLE 8. Reproductive performance indices for adult female *Trirhabda canadensis* fed *Solidago missouriensis* leaves from the two folivory treatments in laboratory performance trials in 1990 (mean ± 1 SE).

Reproductive index	Folivory treatment		t	P
	+ <i>T. canadensis</i> (n = 23)	- <i>T. canadensis</i> (n = 12)		
Time to first clutch (d)	11.8 ± 1.1	7.9 ± 0.8	2.36	0.05
Clutches produced	6.9 ± 0.7	10.6 ± 0.5	-3.35	0.01
Time between clutches (d)	4.6 ± 0.4	3.0 ± 0.1	2.69	0.05
Total eggs produced	195.5 ± 26.8	353.6 ± 40.9	-3.28	0.01
Total mass of eggs (mg)	30.88 ± 4.34	49.94 ± 5.69	-2.58	0.05
Reproductive allocation [biomass] (%)	71.99 ± 3.66	85.96 ± 1.10	-2.63	0.05
Reproductive allocation [N] (%)	71.66 ± 3.79	84.91 ± 1.13	-2.41	0.05
Mean egg mass (mg)	0.156 ± 0.004	0.142 ± 0.003	2.30	0.05

Paired-choice test

Adult female *T. canadensis* did not distinguish between leaves from low and high folivory plots (paired $t = 0.11$, $df = 21$, $P > 0.9$). However, they preferred leaves from *Tc+* plots to those from *Tc-* plots (5.38 ± 0.78 mg consumed [mean ± 1 SE] vs. 3.76 ± 0.54 mg; paired $t = 2.77$, $df = 47$, $P < 0.05$).

DISCUSSION

Prior grazing and larval performance

Prior grazing of *S. missouriensis* by *T. canadensis* reduced leaf nutritional quality for *T. canadensis* larvae. The direct negative impact of eating *Tc+* foliage revealed by the structural equation model for larval growth reflects the 22% reduction in biomass conversion efficiency and 14% reduction in N use efficiency for larvae fed *Tc+* leaves relative to those fed *Tc-* leaves. Since prior folivory did not affect biomass and N consumption by *T. canadensis* larvae, we conclude that this reduction in food processing efficiency led to the reduced relative growth rate, relative N accumulation rate, and final larval mass (Slansky and Scriber 1985). Variation in foliage consumption by larvae may have been minimal because larvae consumed food at nearly their maximal capacity (Slansky and Scriber 1985). This lack of variation in consumption probably facilitated detection of the effect of leaf quality upon larval growth. The structural equation model indicated that leaf consumption may generally be a better predictor of larval performance in *T. canadensis* than leaf nutritional quality.

It is not clear what accounted for the differences in larval performance between the folivory treatments. Basic nutritional factors such as N content, water content, and leaf toughness, which are often excellent predictors of the growth of insect larvae (Scriber 1977, Scriber and Slansky 1981), were similar between the two treatments. Anti-herbivore chemicals might have influenced *T. canadensis* performance (Erickson and Feeny 1974, Blau et al. 1978, Lincoln et al. 1982, Slansky and Scriber 1985). *Solidago* clones at Cedar Creek with different defoliation histories do not differ in their concentrations of terpenoids that might have anti-herbivore properties (P. A. Morrow and G. M. Puttick, *personal communication*), but some other class of chemical may have been involved. The similar relative consumption rates of larvae fed leaves from the two folivory treatments indicate that any potential anti-herbivore agent did not function as a feeding deterrent (Slansky and Scriber 1985).

Prior grazing and adult performance

Goldenrod leaves flushed in *Tc+* plots following defoliation by *T. canadensis* larvae were of higher nutritional quality than those available in *Tc-* plots. These younger *Tc+* leaves were similar in their basic nutritional characteristics to those available during the

larval feeding period. We expected that these younger leaves would be more nutritious than their older counterparts (Feeny 1970, Scriber and Slansky 1981, Raupp and Denno 1983). That this was partially true is indicated by: (a) the higher conversion efficiency of adults fed *Tc+* leaves, (b) the preference for *Tc+* leaves shown by females in the paired-choice experiment, and (c) the positive direct effects of *Tc+* foliage upon growth and egg biomass production within the structural equation model. However, the value of the structural equation approach now becomes clear, for it plainly shows that strong negative indirect effects outweighed the positive influence of *Tc+* leaves upon growth and egg production. Female *T. canadensis* that ate *Tc+* foliage had a lower mass at emergence and, more significantly, consumed far less leaf material than those that fed upon *Tc-* foliage. Despite large differences in leaf nutritional quality, foliage source wielded no explanatory power for either egg biomass production or final adult mass. Variation in the amount of foliage consumed explained nearly all the variation in egg biomass produced, and variation in initial mass accounted for the bulk of the variation in final adult biomass. Note, however, that larval mass at pupation determined initial adult mass, and foliage consumption explained most of the variation in final larval mass during the larval performance trial. Therefore, foliage consumption during the larval stage strongly influenced initial adult mass. These results from the structural equation models strongly suggest that the quantity of food consumed by *T. canadensis* was a more important determinant of growth and reproductive output than was food quality.

Reduction in leaf availability due to heavy grazing is probably a more important determinant of the growth and reproductive success of *T. canadensis* in its habitat than is any grazing-induced change in leaf quality. Heavy consumption during outbreaks, especially by larvae, can eliminate all leaf material in goldenrod clones (McBrien et al. 1983; D. G. Brown, *personal observation*). This can lead to mass mortality of larvae (D. G. Brown, *unpublished data*). Adults that successfully emerge from defoliated clones may be smaller, take longer to reach reproductive maturity, and be more likely to die before reproduction. Consequently we expect such adults to have lower reproductive output than those that had sufficient larval food. In addition, if food and potential mates are relatively scarce, these adults will be more likely to emigrate in search of them (Morrow et al. 1989). This will further reduce the time available for feeding and mating and will lower reproductive output. As a result of these factors, outbreaks of *T. canadensis* on *Solidago* clones can often entirely vanish within a single year (P. A. Morrow, *personal communication*).

Paired-choice test

Not surprisingly, adult female *T. canadensis* preferred to eat leaves from *Tc+* plots that were more

nutritious and had direct positive effects upon growth and egg production. This preference seems paradoxical if one considers the indirect consequences of consuming *Tc+* leaves and the reduced growth potential for offspring of females that oviposit in a grazed clone of *S. missouriensis*. However, since situations resembling the paired-choice test seldom occur in the field, such extrapolation is unwarranted. *T. canadensis* often spends its entire life cycle in a single isolated goldenrod clone. The ability to choose between leaves of different nutritional quality in separate clones is probably not a relevant factor in the life history of this species.

CONCLUSION

Folivory by *T. canadensis* elicited two distinct responses in the quality of goldenrod foliage. Adult grazing in prior years reduced leaf nutritional quality and impaired the performance of *T. canadensis* larvae. Many experiments involving terrestrial insect herbivores (Werner 1979, Schultz and Baldwin 1982, Myers and Williams 1984, Tuomi et al. 1984, Williams and Myers 1984, Haukioja 1990, Bryant et al. 1991) and some involving vertebrates (e.g., Bryant et al. 1985) report similar results. In contrast, available *S. missouriensis* foliage following larval defoliation was younger and of higher nutritional quality than that in plots not grazed by larvae. Intense and predictable vertebrate grazing often generates this response (Ellison 1960, Cargill and Jefferies 1984, McNaughton 1984, 1985, Jaramillo and Detling 1988). However, negative indirect effects upon total foliage consumption and insect mass overshadowed any positive impact of these more nutritious leaves. Adults that ate the younger leaves did not perform as well as those that ate the older, lower quality leaves from ungrazed plots. This study demonstrates that the impacts of prior folivory on leaf quality and of leaf quality upon herbivore performance are not necessarily transitive. Structural equation modeling and path analysis are important tools allowing researchers to examine jointly the influences of food availability and quality to better comprehend the dynamics of herbivore populations.

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