BIOMASS AND NITROGEN BUDGETS DURING LARVAL DEVELOPMENT OF *LYMANTRIA DISPAR* AND *CHORISTONEURA FUMIFERANA*: ALLOMETRIC RELATIONSHIPS

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Spruce budworm larvae grew faster than gypsy moth larvae both in a temporal and relative sense. The budworm larvae had a higher relative growth rate (RGR), biomass conversion efficiency (ECI), and nitrogen utilization efficiency (NUE) than the gypsy moth larvae. As both species matured, relative growth rates, rates of consumption, and conversion efficiencies declined.

The differences between species and the decline in rates with maturation are, at least partially, allometric (related to body size). The relationship can be expressed by the equation $y = aX^b$, where y is the rate of the process and X is the size of the animal. The importance of accounting for allometry when evaluating quantitative nutritional measurements is illustrated with budworm and gypsy moth.

INTRODUCTION

This paper will examine growth of the spruce budworm *Choristoneura fumiferana* (Clemens), and the gypsy moth, *Lymantria dispar* L., each on a representative host plant. The emphasis of the study was to obtain a better understanding of the basic nutritional physiology of caterpillars, particularly in regard to changes associated with size and/or age, rather than to examine effects of food quality on caterpillar growth.

Size attained, e.g., pupal weight, is a parameter frequently used to assess the effect of host nutritional quality on insect performance. While size measurements illuminate the extent to which an insect grows on a particular food source, they do not provide information as to why a food is superior or inferior. For example, poor growth can be the result of lowered consumption due to the absence of a phagostimulant or the result of lowered food utilization due to the presence of a toxic chemical.

The quantitative nutritional approach of Waldbauer (1968) provides a method to answer such questions. This involves measuring food consumption, excretion, and assimilation and calculating utilization and efficiency rates. The effect of insect size, e.g., absolute weight, on these nutritional indices has often been overlooked by entomological researchers.

Definitions

Terminology used in this paper is patterned after that of Waldbauer (1968):

$$G = I - E - R,$$

where G = growth (biomass gained), I = food ingested (consumed), E = excretion (feces) which includes both undigested food and metabolic waste, and R = respiratory loss from metabolism.

These values, which are expressed as dry weight, can be converted to relative rates by dividing the absolute value by the elapsed time period (Δt) and the mean weight (W) of the animal during the time period. Unfortunately, authors define mean weight according to their personal whims. Some use a simple average of the initial and final weight whereas others calculate an exponential mean based on initial and final weight. There are several methods used to do the latter. When daily or several measurements are made between the time interval, mean weight is often approximated as the sum of the individual measurements divided by the number of measurements.

Waldbauer (1964) made daily measurements and calculated mean weight by summing daily weights, after adjustment of the initial and final weights, then dividing by total number of days. This method approximates a solution by integrals. I have noted that several authors who measured only the initial and the final weight cite Waldbauer for method of calculating relative rates. What was done in these cases is unclear since Waldbauer's method is applicable only for a series of several measurements that can approximate a continuous record. Waldbauer's (1964) growth rate (GR) does not necessarily describe a true growth rate. Kogan and Cope (1974) show how this rate differs from the mean relative growth rate ($\overline{RGR}$) (Radford 1967) employed by general physiologists.

Herein, mean weight is defined as:

$$\overline{We} = W_f - W_o/\ln(W_f/W_o)$$

where W_f = body dry weight at the end of the period, and W_o = body dry weight at the start of the period. Relative rates for biomass, then, are

$$\text{Relative Consumption Rate (RCR)} = I/\overline{W}_e/\Delta t$$

$$\text{Relative Growth Rate (RGR)} = G/\overline{We}/\Delta t = \ln W_f - \ln W_o/\Delta t$$

Budgets and relative rates for nitrogen can be calculated in much the same manner as for dry matter biomass. It is assumed that nitrogen is not eliminated by the insect in gaseous form; hence, the nitrogen budget can be expressed as:

$$G(N) = I(N) - E(N),$$

where nitrogen gain G(N) in the insect body is the difference of nitrogen ingested I(N) and nitrogen excreted E(N). Relative rates for nitrogen are:

$$\text{Nitrogen Accumulation Rate (NAR)} = G(N)/\overline{W}_e/\Delta t$$

$$\text{Nitrogen Consumption Rate (NCR)} = I(N)/\overline{W}_e/\Delta t$$

$$\text{Nitrogen Excretion Rate (NER)} = E(N)/\overline{W}_e/\Delta t$$

The usefulness of relative rates is that they facilitate comparison between diets, instars, and species. Food utilization indices, expressed as percentages or ratios, are also useful in making comparisons. Utilization indices used herein are:

$$\text{Ingested matter efficiency (ECI)} = \frac{G}{I} = \frac{RGR}{RCR}$$

$$\text{Nitrogen efficiency (NUE)} = \frac{G(N)}{G(N)+E(N)} = \frac{NAR}{NCR}$$

Rearing and Data Collection

Gypsy moth larvae were reared individually from neonate to pupation on excised foliage of red oak, *Quercus rubra.* Foliage was changed at 48-hr intervals and kept turgid by placing the leaf stem or twig in a vial of water. Larvae were placed on the foliage about one week after budbreak and maintained at temperatures that approximated outdoor weekly mean temperatures. Eight to twelve of the larvae were sacrificed at the beginning of each instar just after hatch or the molt before any feeding occurred. The dry weight of the insect body including the newly molted larval skin, and the feces produced during the instar were measured. Standard micro-Kjeldahl procedure was used to find the nitrogen content of larvae and feces and the percent nitrogen of freeze-dried subsamples of the foliage provided the larvae at each feeding. Nitrogen ingestion was calculated as the sum of G(N) and E(N). Dry matter ingestion was calculated as I(N)÷N/mg foliage.

Spruce budworm larvae were reared on artificial diet until mid third instar at which time they were placed individually on a single terminal bud of balsam fir, *Abies balsamea* that had just shed the scale cap. They were maintained outdoors in a weather station box at ambient temperature. Humidity in the 28 ml plastic rearing container was at or near 100% RH. Larvae were divided into two groups: those that were sacrificed periodically to obtain dry weight and nitrogen content as percent of wet weight, and the experimental group reared to pupation. For the latter group, foliage was changed, frass separated from foliage and larval wet weight measured at 48-hr intervals. Larval dry weight biomass was estimated from the wet weight times the dry/wet weight ratios of larvae of corresponding size. This value was reduced 20% to account for gut contents except for larvae ready to enter the prepupa stage. Dry weight or N consumption of foliage was estimated by (1) counting number of needles damaged (completely or partially consumed) and measuring length of uneaten portions and (2) determining mean length ($\overline{x}$ L), dry weight, and nitrogen content of undamaged needles from the same twig which was used to calculate needles eaten as:

$$\frac{((\#\text{ damaged needles})\times(\overline{x}L))-(\text{total uneaten length})}{\text{mean length}}$$

Thus:

I = needles eaten x mean wt/needle
I(N) = needles eaten x mean N/needle

Results and Discussion

Table 1 compares spruce budworm and gypsy moth weight, development time, fecundity and conversion efficiencies. For the sake of convenience and brevity, only the data for females are presented throughout the paper. The budworm increased body weight about 2000-fold and the gypsy moth nearly 3000-fold; but the gypsy moth took 50% longer to complete development. In effect, the gypsy moth achieved a greater absolute percentage increase in size, but did so at a slower rate of growth (RGR). The gypsy moth also fed less efficiently than the budworm both in terms of dry matter and nitrogen. This may have contributed to the lower RGR of the gypsy mo however; as will be pointed out the difference in rate could also be explained by size differences.

The RGR, ECI, and NUE values, as presented in Table 1, represent averages for the entire larval period (*L. dispar*) or for the third instar until pupation (*C. fumiferana*). It is common practice to make measurements across instar or the entire larval stage and to express the results as a constant value independent of absolute body weight. This is an arbitrary simplification that fosters the idea that rate of growth and food conversion efficiency remain unchanged as the larva grows. In reality, such rates and indices are not constant as the animal grows but change, usually in a systematic manner with time or the weight of the insect. It would seem, therefore, that a parameter which depicts change in rate (=slope) would be as useful as mean relative rate.

Table 1. Bionomic data for female larvae

Insect Host	*C. fumiferana* Fir	*L. dispar* Red Oak
Initial dry weight (ug)	18	140
Pupal dry weight (mg)	30	400
Development time (days)	30	48
Relative growth rate (µg/mg/ °day)	15.6	11.1
Biomass conversion efficiency (%)	9.1	6.6
Nitrogen utilization efficiency (%)	40	30

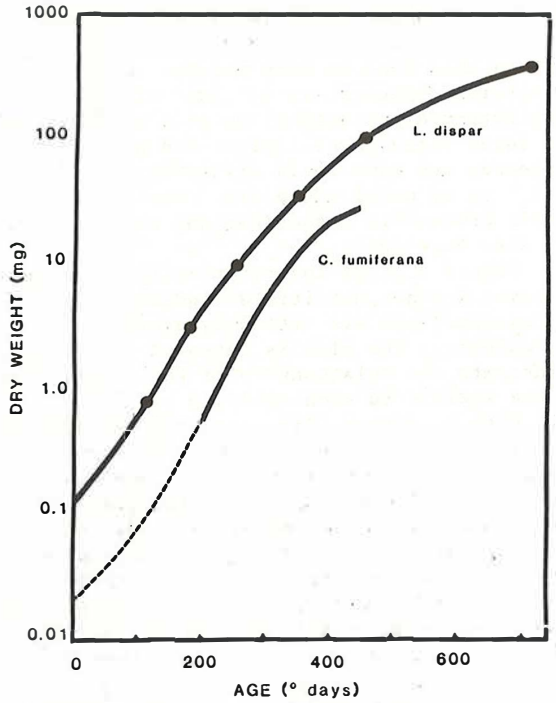

Figure 1. L. dispar and C. fumiferana growth against time. Measurements for L. dispar were made at each instar molt; for C. fumiferana every 2 days beginning at 200 degree days, the dashed line is an extrapolation.

It is also common practice to plot against time the log weight of the developing organism (Fig. 1). An easy and frequently used method to mathematically describe such growth is to regress the logarithm of the weight on time. This type of regression is appropriate if growth was exponential; i.e., weight increases at a constantly increasing rate until death or metamorphosis interrupts the process. If the growth of the two caterpillars was exponential, the data sets plotted on a log linear scale, as in Figure 1, would produce a straight line. The growth curves though are clearly sigmoid; i.e., the weight increases exponentially but with a rate of increase that changes with time. Curves used to describe this type of growth are, among others, the power, Gompertz, logistic, and Bertalanffy (Kaufman 1981).

The Bertalanffy equation has been used to describe the growth of plants, fish, mammals, and humans. It can can be written as:

$$dW/dt = {}_nW^a - {}_kW \qquad (1)$$

where W = weight, t = time and a, k, and n are parameters.

A closed form solution of this equation is:

$$W = \left[\frac{n}{k} - \left(\frac{n}{k} - W_o^{(1-a)t}\right) e^{-k(1-a)t}\right]^{1/1-a}$$

where W_o = weight at time, t=0. Needless to say, fitting this and other nonlinear models to data requires knowledge of calculus and matrix algebra and a computer programmed to do a nonlinear least-squares analysis. Such process is beyond many while to others proposing plausible equations and seeking "the" formula that most closely approximates the experimental data is great mental sport. The goal however should not be to achieve high statistical fit via complex equations but to describe and use data in a manner that facilitates evaluation of effects of substrate and environment on the growth process.

Graphical plots are a convenient, straightforward method that allows one to describe changes in growth rate as a function of size.

Figure 2 shows that body size and RGR of L. dispar and C. fumiferana are allometric functions. With both species, the log of RGR more or less decreased in direct proportion to the log of the weight. Although the overall RGR of the budworm was higher than that of the gypsy moth, it was more sensitive to size and decreased at a faster rate as the larvae grew.

The initial value for L. dispar represents the first larval stadium and may underestimate RGR. L. dispar neonates normally spend the first 24-48 hours wandering and not feeding; a period of dispersal. To account for this, the time interval for the stadium was shortened 17 degree-days which may have been insufficient. On the other hand, the first instar RGR may actually be lower since the larva must replenish the moisture and energy expended during the nonfeeding interval before a net increase can occur.

The greater fluctuation of the C. fumiferana data about the regression line reflects the higher variability in measurements for this species. Standard errors of budworm larval weight and consumption ranged from 10-20% of the mean whereas gypsy moth standard errors were always less than 10% of mean values.

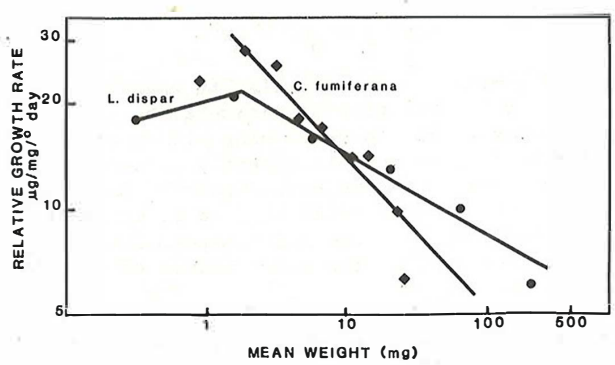

Figure 2. Relative growth rate (RGR) of L. dispar and C. fumiferana against mean weight ($\overline{W}_e$).

The relationship between metabolic rate and absolute body size is one of the classical topics of comparative physiology. That the normal or basal metabolic rate of plants and homeothermic and poikilothermic animals is inversely related to body size; i.e., smaller organisms have higher metabolic rates, is something learned by introductory biology students (Keeton 1972). This relationship can be approximated by allometric formula (Huxley 1932):

$$M = {}_bW^{\alpha} \qquad (2)$$

where M = metabolic rate per unit of time, W = body weight, and α and b are constants. For weight-specific metabolic rates, the equation becomes:

$$\frac{M}{W} = {}_b W^{\alpha-1} \qquad (3)$$

On a log-log graphical plot, an empirical data set that follows this function would afford a straight line regression, the slope of which indicates α. If α= 2/3, then the surface rule is being followed; i.e., the change in rate decreases in proportion to the change of surface area. If the slope is 45°,α= 1, then change in rate is directly proportional to the change in weight. Bertalanffy (1957) has proposed that metabolic rates of most animals are proportional either to surface area, to weight, or, more rarely, lie between these two types. Brody (1945) however, indicated that basal metabolic rate varies at the 3/4 power of weight. Most laboratory measurements are close to this value (Fenchel 1974).

It is not unreasonable to assume that rules similar to those regarding the size dependency of metabolic rates would extend to growth rates. After all, is not growth in its simplest terms but the product of anabolism minus catabolism? Adolph (1949) showed that, at least in first approximation, the rate of all physiological processes can be expressed as allometric formulae. Thus, change in body weight can be expressed as a function of the difference between building up and breaking down; i.e.:

$$dW/dt = {}_nW^a - {}_kW^b$$

This is similar to the Bertalanffy equation except for the addition of parameter b. Bertalanffy (1957) in developing his equation argued that catabolism is directly proportional to weight and since the basic equation is rather insensitive to minor deviations in b, it can be regarded as equal to one. The exponent a then more or less depicts the relationship of growth rate to body weight.

Less predictable is the effect of body size on food consumption rates and food conversion efficiencies. Food consumption would be expected to be proportional to body weight if the insect simply feeds to repletion once or twice daily. In this case, digestive efficiency would likely decrease with increasing body size, since gut surface area decreases at about 2/3 power of gut volume. Conversely, if digestive rate rather than gut volume delimits the rate of food consumption, one would expect digestive efficiency to be rather independent of body size and consumption to be more proportional to surface area than to body volume. Food conversion, however, is not just digestion but also intermediary metabolism plus several complex and intertwined physiological and metabolic processes and thus it is difficult to predict what type of model would fit. The final net result however is measurable and can be tested for size dependency.

Figure 3 plots logarithmically RGR as well as several other nutritional indices. The regression lines are fitted by eye and approximate. The plot is intended only to illustrate the relationship of the general trend of the indices to each other.

With L. dispar (Fig. 3a), RCR followed the same pattern as RGR except that RCR decreased at a slower rate as size increased. Consequently, ECI (Fig. 3c) decreased. The nitrogen budget (Fig. 3b) followed a similar pattern. NAR decreased at a steeper rate than NCR; hence, NUE (Fig. 3c) also decreased as size increased. Note that the NER changed much less with weight than either NAR or NCR. Both NUE and ECI had about the same slope; an indication that they were not affected differentially.

The C. fumiferana data are more complex. They are also less precise; hence, interpretation must be taken lightly. In this case, RCR decreased but then began to increase as pupation neared while RGR changed at a constant rate (Fig. 3d). NCR exhibited a similar pattern even though NAR decreased continuously as size increased (Fig. 3e). NER was apparently little affected by larval size. Since RCR and NAR decreased at a decelerating rate and rate of decrease of RGR and NER remained constant, ECI and NUE decreased at an accelerating rate (Fig. 3f).

My starting hypothesis was that since RGR is affected by weight, RCR and ECI would also be influenced by weight since RGR = RCR x ECI. Indeed, a general pattern was observed where growth, accumulation, and efficiency decreased as body size increased. However, each index had a different slope which indicates independent influence and/or compensation mechanisms.

Rate/efficiency interactions involve the complex area of feedback and homeostasis and is an area largely unexplored by insect physiologists. Slansky and Feeny (1977) proposed that rate of growth or accumulation is held stable, maximal, by compensatory changes in consumption and efficiency. Their data supported the hypothesis of Odum and Pinkerton (1955) that power and efficiency cannot be maximized simultaneously and that power (i.e., assimilation rate) would be selected for.

An examination of the regression coefficient of the indices (Table 2) for L. dispar not only supports the thesis that power or accumulation rate is stabilized at a high rate but also offers an explanation why efficiency decreases as size increases. The reason for suggesting that L. dispar RGR and NAR are maximal is that the constant of proportionality, a-1, was very close to the 3/4 power rule for metabolic rate. In other words, the caterpillar's accumulation of biomass and nitrogen changed at the theoretical, expected rate despite changes in food supply. (Effect of food will be discussed later.)

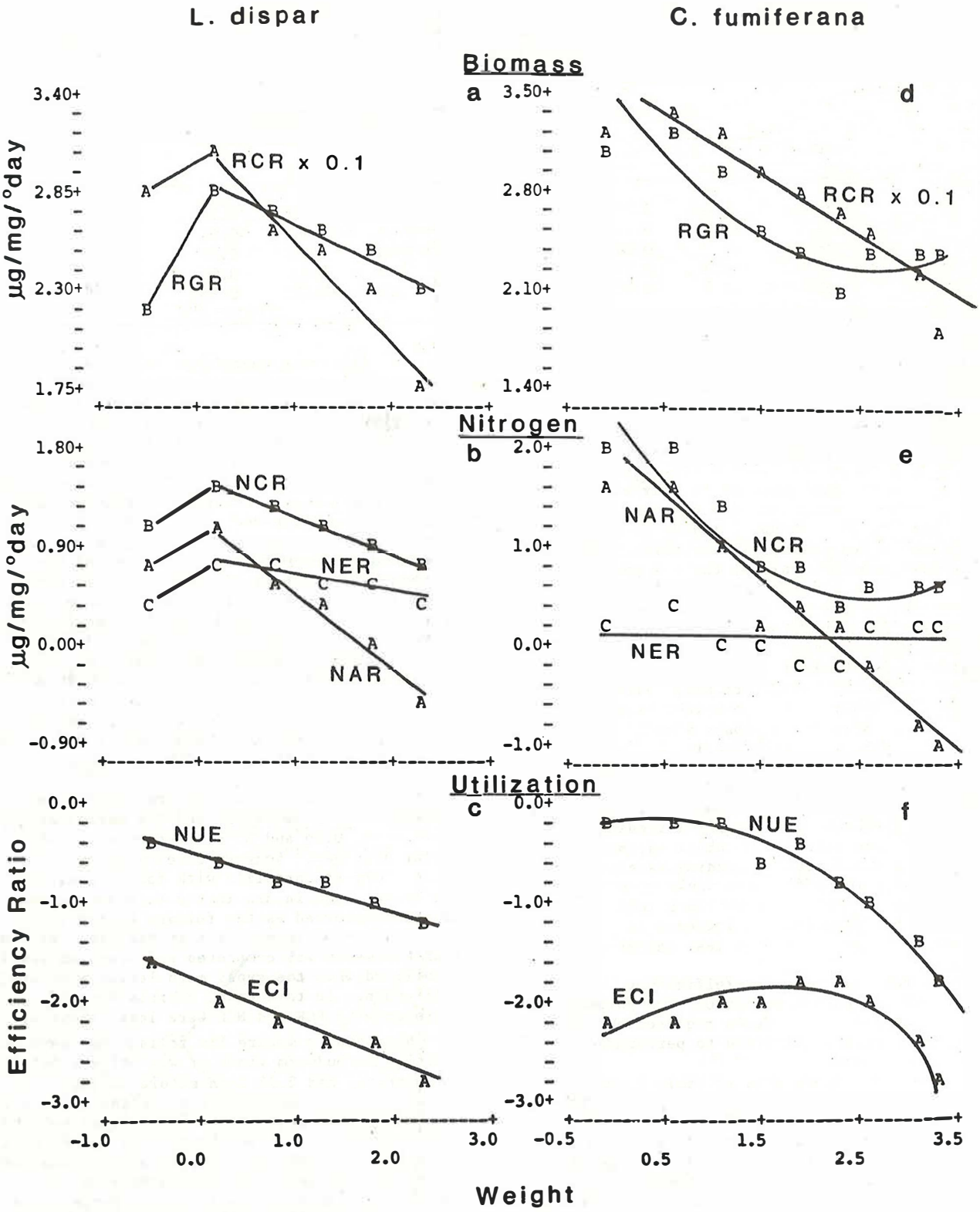

Figure 3. Weight dependency of nutritional indices. Values have been converted to natural logarithms. (See Definitions section for abbreviations.)

Table 2. Regression equations and coefficients of determination of nutritional indices on log $\overline{We}$. The equations have the form: log (index) = a log $\overline{We}$ + log b. (Index units = µg/mg/°day, weight = mg).

	L. dispar			*C. fumiferana*		
Index	b	a-1	r^2	b	a-1	r^2
RCR	182.6	0.90	0.94	236.1	0.69	0.71
RGR	25.2	0.75	0.97	31.4	0.62	0.81
NCR	4.7	0.85	0.99	6.6	0.53	0.76
NAR	2.8	0.73	0.96	6.2	0.18	0.93
NER	2.1	0.93	0.97	0.5	-0.71	0.38

Consumption and excretion also seem to be following ideal case models. These indices are fairly close to one and hence more directly proportional to volume (= weight) compared to accumulation where direct proportionality is closer with surface area ($A = V^{2/3}$). Since gut volume is roughly proportional to body volume (= weight), then a proportionality constant for RCR of near zero (0.9 - 1 = -0.1) indicates the insect eats to repletion. Assimilation of the food however proceeds only at the 3/4 power of the rate of intake; hence, assimilation efficiency decreases as intake increases. This scenario implies little feedback control over feeding rate, the insect simply eats until it is full if food is available and palatable.

The data suggest an intriguing, alternative scenario. Catabolism is also weight proportional (cf. *L. dispar* NER) and responds more to weight change than anabolism (Bertalanffy 1957). This fact also can explain size related decrease in efficiency. Further, if catabolism and/or elimination of metabolic waste were rate limiting, it, through feedback, could control feeding rate. An excess of nonutilizable metabolites that must be eliminated would depress feeding rates. Better assimilation efficiency would result in faster growth not only from the increased conversion, but also from an increase in consumption the production of less wastes would afford.

These remarks about rate/efficiency interactions are pure speculation. Its purpose is more to illustrate the caution required and the difficulty in relating indices to performance or to cause and effect.

The spruce budworm data in Table 2 were ignored in the preceding discussion because the data apparently illustrate effect of substate more than ontogeny. The budworm proportionality constants were lower than expected and suggest that phenological changes in the fir foliage placed increasing stress on the budworm as it matured. On the other hand, the gypsy moth data seem to reflect mainly a scaling effect. One would need to suppose that young oak foliage was relatively less suitable than older foliage or that the lower early season temperatures were more favorable in order to account for a phenological effect on the gypsy moth constants.

To illustrate phenologic relationships between foliar chemistry and the indices, I have plotted some of my unpublished foliar analyses on logarithmic axes with the corresponding mean larval weight substituted for sample date on the axis of the abscissas (Fig. 4). Significant correlations of chemical levels with nutritional indices are almost a foregone conclusion simply because the indices decline with size (time) and most of the chemicals either increase or decrease in concentration with time. Because of the overbearing effect of allometry, few of these correlations can be rationalized. For example, condensed tannin in oak leaves increased as the leaves matured whereas in fir tannin decreased after budbreak. In the first case, the correlation coefficient with RGR is -0.96 and in the second, 0.99. Total phenol in oak is obviously poorly correlated with RGR, but it cannot be ruled out that total phenol was without influence if the change in RGR is mainly ontological.

The situation with nitrogen seems more informative. Budworm RGR and NCR were strongly correlated, 0.96 and 0.99, respectively, with foliar nitrogen. Budworm development was rapid and closely synchronized with foliar expansion. The larvae were in 3rd instar at budbreak and pupation occurred as the foliage became fully expanded and nitrogen level stabilized. With oak, leaf expansion was completed and nitrogen level stabilized when the gypsy moth larvae were about half grown. In this case, correlations of nitrogen with RGR and NCR were less, about 0.7.

Nitrogen in mature fir foliage may have been limiting to budworm since it was below 1.5%. Oak, by contrast, had 2.3% N in mature foliage. It would seem to be advantageous for the budworm to complete development before the foliage matures. Both its habit of attacking foliage before buds break and its small size may be adaptations that aid this. Decline in growth rates with increasing size occurs also among species, i.e., small animal species tend to have higher RGR (Schmidt-Nielsen 1975). McNab (1978) stated that herbivores of equal size feeding on woody foliage have significantly lower metabolic rates than those feeding on richer plant tissues. The budworm gypsy moth comparisons do not support this. (See Mattson 1980 for more on body size.)

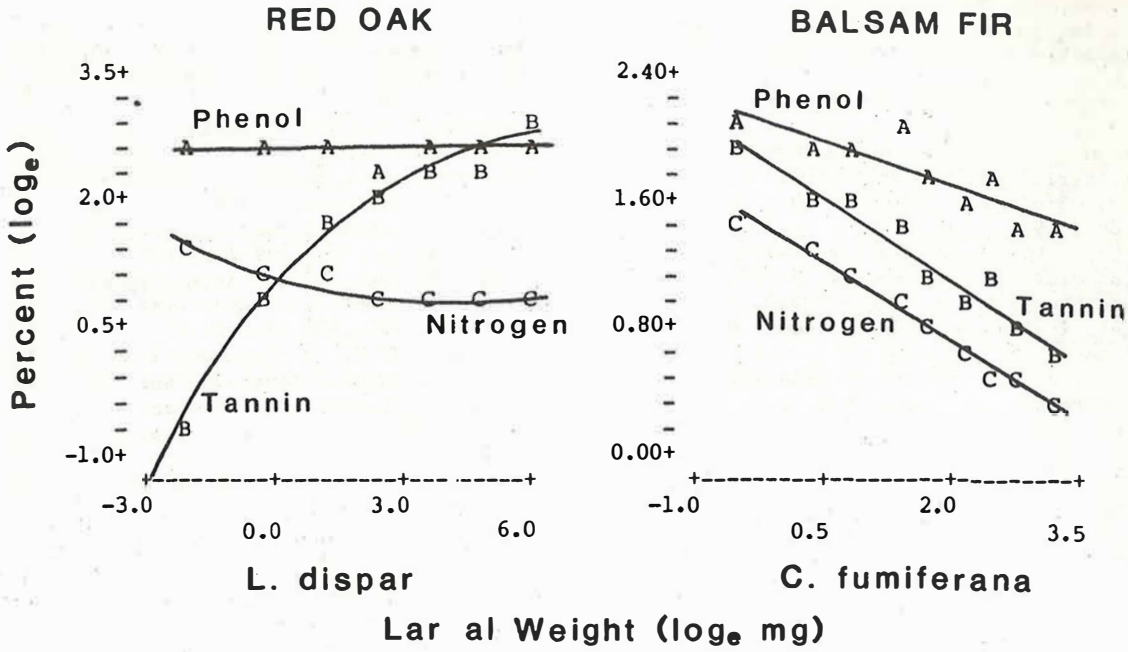

Figure 4. Seasonal change in concentration of foliar chemicals in relation to larval weight at time of sampling. Values have been converted to natural logarithms.

Gypsy moth is a rather large caterpillar with a rather long development time for a spring-feeding arborivore. Speed may have been sacrificed to efficiency (Fig. 5). Budworm by contrast had higher NUE on spruce where growth was less. The plants that supported poor budworm growth also had lower foliar nitrogen levels (Montgomery, unpublished). This observation complements the data for developing larvae (Figs. 3 and 4) where, as nitrogen became in apparent critical supply, NUE decreased more than expected while NAR was maintained. Both host and development data for budworm support the thesis of Odum and Pinkerton (1955) that efficiency is of lesser importance than rate. It should be clarified that although changes in RGR due to size applies to different sized individuals, species, etc., there is no evidence (see Banse 1979) that the weight (= age) dependent efficiency that occurs in a growing individual applies to individuals of different size. Thus, the size/efficiency relationship of budworm in Figure 5 may or may not be allometric.

Although firm statements about the weight dependency of nutritional indices cannot be made, that such effects may exist is sufficient reason to consider the role of allometry when interpreting quantitative nutritional data.

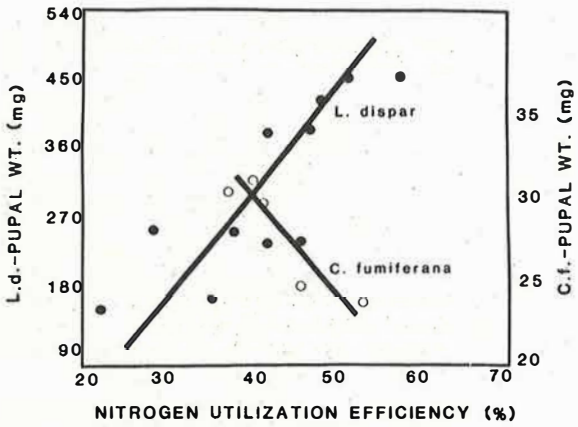

Figure 5. Mean nitrogen utilization efficiency against mean female pupal weight for L. dispar (L.d.) on eleven different host species and for C. fumiferana on white spruce hosts differing in age and vigor (Montgomery, unpublished).

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Literature Cited

Adolph, E. F. Quantitative relations in the physiological constitutions of animals. Science 109: 579-585; 1949.

Banse, K. On weight dependence of net growth efficiency and specific respiration rates among field populations of invertebrates. Oecologia (Berl.) 38: 111-126; 1979.

Bertalanffy, L. von. Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32: 217-231; 1957.

Brody, S. Bioenergetics and Growth. Missouri Agric. Res. Bull. 89: 1-123; 1945.

Fenchel, T. Intrinsic rate of natural increase: The relationship with body size. Oecologia (Berl.) 14: 317-326; 1974.

Huxley, J. Problems of relative growth. Methuen, London; 1932.

Kaufmann, K. W. Fitting and using growth curves. Oecologia (Berl.) 49: 293-299; 1981.

Keeton, W. T. Biological Science. New York: Norton & Co.; 1972. 888 p.

Kogan, M.; Cope, D. Feeding and nutrition of insects associated with soybeans. 3. Food intake, utilization and growth of the soybean looper, Pseudoplusia includens. Ann. Entomol. Soc. Amer. 67: 66-72; 1974.

Mattson, W. J., Jr. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119-161; 1980.

McNab, B. F. Energetics of arboreal folivores; physiological problems and ecological consequences of food supply. p. 153-162. In Montgomery, G. G. (ed.). The ecology of arboreal folivores. Washington, D.C.; Smithsonian Inst. Press; 1978. 574 p.

Odum, H. T.; Pinkerton, R. C. Times speed regulator: The optimum efficiency for maximum power output in physical and biological systems. Amer. Sci. 43: 331-343; 1955.

Radford, P. J. Growth analysis formulae - Their use and abuse. Crop Sci. 7: 171-175; 1967.

Slansky, F. Jr.; Feeny, P. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecol. Monogr. 47: 209-228; 1977.

Schmidt-Nielsen, K. S. Animal physiology; adaptation and environment. London: Cambridge University Press; 1975. 699 p.

Waldbauer, G. P. The consumption, digestion and utilization of solanaceous and non-solanaceous plants by larvae of the tobacco hornworm, Protopace sexta (Johan.). Entomol. exp. Appl. 7: 253-269; 1964.

Waldbauer, G. P. The consumption and utilization of food by insects. Adv. Insect Physiol. 5: 229-288; 1968.

SUMMARY REMARKS

Many of the papers presented discussed foliage chemistry and/or the response of caterpillars to dietary chemicals. The concluding two papers, one by Houston on characteristics of stands resistant and susceptible to defoliation by gypsy moth, and the other by Witter et al. on management implications of budworm/host interactions, do not discuss foliage chemicals or foliage quality per se. Instead, they focus on traditional site classification systems. More than anything, this is indicative of where the "state-of-the-art" is and the gaps in knowledge that future research should fill.

Forests have traditionally been classified as to physical and phytosociological characteristics such as soil, slope, species composition, stocking density, and tree age. Because of their familiarity to the forest manager and their relative ease of measurement, they are the characters currently being incorporated into site classification schemes. Such entities are a step removed from the actual cause-effect relationship. They act on the physiology and growth habit of the host tree (the "room and board" referred to in the paper by Wallner) which in turn influences pest insect populations. The quality of the "board", at its lowest denominator, is determined by the chemicals used as food and anything that affects the ability of the insect to access or utilize them.

Research at this level may seem distant to practical payoffs. The papers presented indicate both the progress and challenges of such work. The introductory chapter by Talerico cited that a relationship between budworm growth and natural variation in foliar components had not been previously demonstrated. Papers given by Wagner and Blake, Montgomery, Mattson et al., and Schmitt et al., noted a positive correlation between budworm pupal or adult weight and concentration of foliar nitrogen. The importance of nitrogen did not extend to the gypsy moth. Lechowitz found little correlation between foliar N levels and gypsy moth host preferences and Montgomery reported a similar situation with pupal weight. The latter author did report, though, that nitrogen utilization efficiency was highly correlated with gypsy moth pupal weight. Apparently something, perhaps tannins, inhibited utilization of the foliar nitrogen. Of the several papers that presented data on tannin or phenolic foliar levels, none reported strong evidence of a negative effect on budworm or gypsy moth. Schultz and Baldwin explained however that it may not be the "mean" level of secondary chemical in the tree, but the induction or increase in concentration in response to insect attack that is important. Thus, foliage quality should not be considered as static, but dynamic and variable, not only in time, but also in space. This presents sampling problems not only to the insect, but also to the researcher. The models presented by Valentine and Fleming showed that lowering of foliage quality may not necessarily be beneficial from a pest management standpoint for populations may be prolonged at high levels instead of crashing because of starvation.

I must chide myself as well as this symposium for focusing excessively on foliage chemistry. Many other aspects of the host insect interaction such as Shepard's paper on bud phenology were also discussed. But perhaps the greatest imbalance was the focus on identifying mechanisms responsible for host suitability without documenting their action in the field under natural conditions. The second paragraph of the paper by DeHayes comments well on this.

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