

NOTES ON LARVAL GROWTH AND EFFICIENCIES IN *ANTHERAEA*: *A. POLYPHEMUS* AND *A. PERNYI* (LEPIDOPTERA: SATURNIIDAE)

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ABSTRACT.— Larval growth rates and efficiencies were measured using standard gravimetric techniques for penultimate and final instar North American *Antheraea polyphemus* and Asian *A. pernyi* silkmoths to evaluate ecological hypotheses about the physiological adaptations of these two species. Contrary to expectations, the oak-feeding specialist, *A. pernyi* did not grow more efficiently nor more rapidly than the polyphagous *A. polyphemus* when fed 5 different *Quercus* species and *Prunus serotina*. In fact, the *A. polyphemus* generally grew more rapidly in spite of the lower nutritional quality (leaf water and nitrogen content) of their food, than was the case for *A. pernyi*. Several potential explanations are discussed, including body size effects.

KEY WORDS: Alaska, Asia, behavior, British Columbia, Canada, China, Fagaceae, genetics, herbivory, hostplants, Hymenoptera, larvae, Mexico, Missouri, Nearctic, Noctuidae, North America, nutrition, *Papilio*, Papilionidae, parasitoids, Pennsylvania, Rosaceae, *Spodoptera*, Trichogrammatidae, USA.

Antheraea polyphemus (Cramer), the polyphemus silkmoth, is probably the most widely distributed species of the North American Saturniidae. It occurs across temperate North America from the Gaspé Peninsula and British Columbia southward into Mexico (Ferguson, 1972). In addition to its wide geographical range, it also may contend for the title of the most polyphagous of the North American silkmoths, with a reported food plant range of at least 50 hosts from more than 30 genera (Ferguson, 1972).

Antheraea pernyi (Guérin-Méneville), the Chinese oak (or tussah) silkmoth, is an Asian relative of the North American *A. polyphemus*. This species (*A. pernyi*) has been bred and reared on oak (*Quercus* spp.) (Fagaceae) in China for centuries, and recently has been used as the source of the well-known Shantung (tussah) silk. This silk has been traced back to the Han dynasty in China (206 B.C.-220 A.D.; Peigler, 1993).

While the North American *A. polyphemus* is extremely polyphagous, it includes at least 6-10 oak species as natural hosts. In fact, it was suggested that *A. polyphemus* may still be behaviorally linked to these ancestral *Quercus* host plants for successful mating (Riddiford, 1967; Riddiford and Williams, 1967). While often assumed that monophagy is the derived, and polyphagy the ancestral condition (Brues, 1920, 1924; Dethier, 1954; Fraenkel, 1959; Ehrlich and Raven, 1964; Feeny, 1995), it appears that the generalist feeding behavior associated with the geographic spread of *A. polyphemus* across North America and may have been derived from ancestral Asian oak-feeding specialists (Michener, 1952; Ferguson, 1972).

There has been a long-standing assumption that the efficiency (E.C.D.) and/or rate of growth for a generalized feeder, would be less on any given host plant compared to a specialist (Dethier,

1954; Waldbauer, 1968; MacArthur, 1972; Scriber and Feeny, 1979). This hypothesis must be examined at both the physiological (or metabolic) level and the genetic (or evolutionary) level before the significance of negative genetic tradeoffs or physiological "costs" can be used to meaningfully address such an ecological presumption (Scriber and Ayres, 1988). While a few studies have attempted to specifically determine these assumptions, the data remain sparse and with mixed results for both individual physiological (Schoonhoven and Meerman, 1978; Scriber, 1978, 1981, 1986; Neal, 1987; Scriber and Dowell, 1991), and genetic (heritable) costs (Jaenike, 1990; Via, 1990; Thompson, 1994). Recently, studies of nicotine metabolism and detoxification cost (measured both by respirometry and E.C.D.'s) in two species of Lepidoptera have shown that nicotine-adapted specialists have little or no costs directly related to detoxication (Appel and Martin, 1992) whereas the generalist *Spodoptera eridania* (Cramer) (Noctuidae) polysubstrate monooxygenase detoxication of this allelochemical does impose significant metabolic costs on the larvae (Cresswell *et al.*, 1992).

This study was conducted to determine if the physiological efficiencies of digesting and converting food to larval body tissue and/or the rate of larval growth on a series of host plants would be greater for the more specialized silk moth, *Antheraea pernyi*, than its polyphagous congener, *A. polyphemus*. Presumably, the generalist *A. polyphemus* would exhibit greater metabolic loads and lower efficiencies than the specialists. Five different oak (*Quercus*) species were included, since these are presumed to represent the ancestral host plant favorites. Black cherry, *Prunus serotina* (Rosaceae), was included as a rosaceous outgroup yet a natural North American host plant.

METHODS

Cocoons of *A. polyphemus* were collected in Northhampton Co., Virginia. Emerging adults were mated and confined to paperbags or plastic boxes with oak leaves for oviposition. We obtained eggs in a similar way for *A. pernyi* which were obtained from captive cultures at Klingerstown, Pennsylvania, and St. Louis, Missouri. Eclosing larvae were allocated in 6-10 groups into rearing containers each containing one of the foodplants under examination. To minimize any effects to larval conditioning (Jermy *et al.*, 1968) and host switching effects (Scriber, 1979, 1981, 1982; Stoyenoff *et al.*, 1994) each group of larvae was reared to the molt preceding the penultimate instar on the plant species upon which the feeding experiment was to be conducted. We do not know the host plant of the parents nor the potential maternal or paternal effects on offspring (Mousseau and Dingle, 1991).

Each caterpillar used in the feeding experiments was weighed immediately after molting into the penultimate (and ultimate) instar and transferred into its own clear plastic petri dish (15 cm diameter x 2.5 cm height), and provided a foodplant leaf of known fresh weight. Eight larvae per plant species were used as replicates in the penultimate instar, with 4-5 larvae used in the final instar. Leaf petioles were inserted into water-filled, rubber-capped plastic vials to maintain leaf turgor (see Scriber 1977). All dishes were then held in a large walk-in controlled environment chamber, maintained at a 16:8 photo-scoto-phase with corresponding day/night temperatures of 23°C/19°C and a relative humidity of 75 ± 10%. Unfortunately, the silkmoth species were not available for precisely concurrent studies; however, identical procedures and analyses were conducted with these slightly staggered bioassays during the same summer.

At intervals of 24-48 hours, each caterpillar was reweighed and the feces and unconsumed leaf material were collected for freeze-drying. Each caterpillar was replaced in the dish with a new weighed leaf. A subset of 3-6 larvae were weighed live, frozen and freeze-dried to determine dry weight ratios. A subset of 6-10 leaves for each experiment were similarly weighed at each replacement and dried for dry weight determination. Larval growth was measured as weight gained during the entire instar and standard gravimetric methods (Waldbauer, 1968; Scriber and Slansky, 1981) were used to calculate the relative growth rates (R.G.R.), efficiency of conversion of ingested (E.C.I.) and digested food (E.C.D.), and approximate digestibility (A.D.). Larvae were weighed and set up immediately after molting to avoid the incorrect attribution of gut content to larval weight gain (Bernays and Simpson, 1990; Barbehenn and Keddie, 1992).

In addition to dry weight ratios, the freeze-dried larvae, feces, and leaves were stored in desiccators and later analyzed for caloric values and total nitrogen. Caloric contents were determined in triplicate in a Phillipson (1964) microbomb calorimeter. Total nitrogen was measured from triplicate samples by the micro-kjeldahl technique of McKenzie and Wallace (1954). This determination allowed calculation of the relative nitrogen accumulation rate (RNAR; mg nitrogen gained per mg of larval weight per day) and the nitrogen utilization efficiency (NUE; ratio of nitrogen gained to nitrogen ingested). These values for efficiency of conversion of ingested nitrogen into larval biomass

slightly underestimate true efficiencies because a small fraction of nitrogen is excreted in the form of uric acid, allantoin, allantoic acid, or perhaps other compounds (Bhattacharya and Waldbauer, 1972).

The concern about uncritical use of nutritional ratios for interpretation of behavioral, physiological, and ecological implications has resurfaced recently, emphasizing new points and several brought up as unresolved since earlier reviews (Waldbauer, 1968; Scriber and Slansky, 1981). The largest source of error in the gravimetric methodology for insects is generally in estimating the food consumption: this can be due to difficulties measuring small amounts eaten by early instars, fresh weight variation among leaves and during the experiment, magnification of measurement errors, too much or too little food presented, and changes in foliage mass/composition during the experiment (Axelsson and Agren, 1979; Grabstein and Scriber, 1982; Schmidt and Reese, 1986; Bowers *et al.*, 1991; Stamp, 1991). Other complications remain even with the necessary use of dry mass budgets, since energy content varies with lipid, protein, carbohydrates of insect and host plant (Gordon, 1968; Slansky and Scriber, 1985; van Loon, 1991, 1993). Volatile lipids and highly variable, or unrealistic caloric budgets can result from oven-drying rather than freeze-drying the samples to be weighed. Comparisons of gravimetric and respirometric estimates of metabolic efficiencies are useful and desirable (van Loon 1993), however are not always possible, as was the case here.

Beyond some methodological sources of variation, one of the recent concerns involving nutritional ecology is the uncritical use of ratios and the statistical problems these may create. A series of excellent reviews (Raubenheimer, 1995; Raubenheimer and Simpson, 1992, 1994; Simpson and Raubenheimer, 1995) has been modelled directly on previous examples (Atchley, 1978; Packard and Boardman, 1987, 1988) which were derived from earlier statistical evaluations (e.g., Cochran, 1957). Common terms in the "X" and "Y" variables (as in ratios) may lead to spurious self-correlations, among other problems (see discussion in Raubenheimer, 1995).

These studies were analyzed by plotting the efficiencies (AD, ECD, ECI) and rates (RCR, RGR) against the mean larval weight during each instar (the initial and final weight data were not retained and were unavailable for using in the desirable analysis of covariance; Packard and Boardman, 1987, Raubenheimer and Simpson, 1992).

RESULTS AND DISCUSSION

The efficiency of converting digested food into larval biomass (E.C.D.) was not significantly greater for penultimate instar *A. pernyi* (oak specialist) compared to the generalist *A. polyphemus* on any host plant species (Table 1a). In the final instar, only the white oak treatment resulted in a significantly higher efficiency (E.C.D.) for *A. pernyi* than *A. polyphemus*. The same basic pattern is observed for E.C.I. (Table 1b). The mean relative growth rates (R.G.R.) of penultimate instar *A. polyphemus* generalists were also significantly greater than those of the specialized *A. pernyi* on chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), white oak (*Q. alba*), and black cherry (*Prunus serotina*), with no significant difference on swamp white oak (*Q.*

TABLE 1a. Efficiencies of conversion of digested (E.C.D.) and 1b. ingested (E.C.I.) food to larval growth for penultimate and final instars of *Antheraea* moth species (data are presented as a mean \pm SE).

| Species (and instar) | Chestnut Oak | Red Oak | Swamp White Oak | White Oak | Pin Oak | Black Cherry |
|-----------------------------|-----------------|------------|--------------------|--------------|------------|-----------------|
| E.C.D. (penultimate instar) | | | | | | |
| <i>pernyi</i> | 74.4 (4.4) | 42.2 (2.8) | 41.2 (3.8) | 40.9 (1.5) | 29.3 (3.2) | 17.2 (3.0) |
| <i>polyphemus</i> | 62.5 (2.9) | 81.6 (8.6) | 63.5 (4.8) | 83.4 (6.1) | 33.0 (2.9) | 14.3 (8.9) |
| (F - ratio) | (N.S.) | (*) | (*) | (*) | (N.S.) | (N.S.) |
| E.C.D. (final instar) | | | | | | |
| <i>pernyi</i> | 23.8 (1.2) | 11.7 (1.6) | 14.7 (1.4) | 23.4 (0.4) | 17.1 (4.7) | - |
| <i>polyphemus</i> | 54.7 (11.8) | 10.3 (5.9) | 34.7 (8.6) | 17.1 (1.7) | 29.7 (5.0) | - |
| (F - ratio) | (*) | (N.S.) | (N.S.) | (*) | (N.S.) | - |

TABLE 1b.

| Species (and instar) | Chestnut Oak | Red Oak | Swamp White Oak | White Oak | Pin Oak | Black Cherry |
|-----------------------------|-----------------|------------|--------------------|--------------|------------|-----------------|
| E.C.I. (penultimate instar) | | | | | | |
| <i>pernyi</i> | 20.3 (0.6) | 12.4 (0.5) | 15.4 (0.5) | 16.2 (0.6) | 8.7 (0.4) | 8.1 (0.8) |
| <i>polyphemus</i> | 14.1 (0.7) | 22.2 (1.4) | 18.7 (1.0) | 18.5 (0.6) | 7.9 (0.5) | 7.4 (2.6) |
| (F ratio) | (*) | (*) | (*) | (*) | (N.S.) | (N.S.) |
| E.C.I. (final instar) | | | | | | |
| <i>pernyi</i> | 8.6 (0.5) | 3.6 (0.5) | 4.9 (0.5) | 10.8 (0.4) | 4.7 (1.0) | - |
| <i>polyphemus</i> | 11.5 (0.5) | 8.9 (3.5) | 10.7 (2.0) | 6.0 (0.7) | 6.9 (1.0) | - |
| (F ratio) | (*) | (N.S.) | (*) | (*) | (N.S.) | - |

* Significant differences between the means are indicated (*) at the $p = 0.05$ level (Snedecor and Cochran, 1967). N.S. = non-significance.

TABLE 2. Relative growth rates ($\text{mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$) of two *Antheraea* moth species on six host plant species.

| Species (and instar) | Host Plant Species | | | | | |
|-------------------------|--------------------|------------|--------------------|--------------|------------|-----------------|
| | Chestnut Oak | Red Oak | Swamp White Oak | White Oak | Pin Oak | Black Cherry |
| R.G.R. (penultimate) | | | | | | |
| <i>pernyi</i> | .16 (.00) | .18 (.01) | .18 (.01) | .16 (.01) | .16 (.01) | .04 (.01) |
| <i>polyphemus</i> | .19 (.01) | .23 (.02) | .18 (.01) | .22 (.01) | .14 (.01) | .07 (.01) |
| (F ratio) | (*) | (*) | (N.S.) | (*) | (N.S.) | (*) |
| R.G.R. (final instar) | | | | | | |
| <i>pernyi</i> | .05 (.01) | .03 (.01) | .05 (.00) | .05 (.00) | .03 (.00) | - |
| <i>polyphemus</i> | .10 (.01) | .06 (.01) | .10 (.00) | .07 (.01) | .07 (.01) | - |
| (F ratio) | (*) | (*) | (*) | (N.S.) | (*) | - |

* Significant differences between the means are indicated (*), $p = 0.05$ level.

bicolor) or pin oak (*Q. palustris*; Table 2). The final instar *A. polyphemus* larvae also grow faster than *A. pernyi* larvae on all 5 oak species, although this does not reach significance for white oak (Table 2).

These results indicate that the extremely polyphagous North American silkworm, *A. polyphemus*, is both more efficient and more rapid in larval growth than the *A. pernyi* oak specialist. This is precisely the opposite result that ecological theory might predict based simply on the assumption that the more specialized *A. pernyi* larvae would be more efficient at conversion on a given host than would larvae of their generalized congeners, *A. polyphemus*. To determine if the larval performance of *A. polyphemus* was the result of host nutritional differences, analyses of the leaves were conducted independently for each species and each instar on every host plant. In no case (penultimate or final

instars) was an explanatory correlation of relative growth rate observed with total leaf nitrogen (% of dry mass), caloric density (cal/mg), or leaf water content (% of fresh weight). In fact, the faster growth rates of *A. polyphemus* larvae, compared to *A. pernyi*, were in spite of generally lower leaf water contents (Fig. 1-2), which is also contrary to general observations for immature insects (Scriber and Slansky, 1981) and tree-feeding Lepidoptera in particular (Mattson and Scriber, 1987). In addition, for most host plant pairs the leaves were slightly lower in total nitrogen for the generalist *A. polyphemus* than for *A. pernyi* (Fig. 1-2). Caloric density of plant leaves ranged from 4.8 to 5.2 cal/mg and were not correlated with any index of larval growth or efficiency.

The poorer performance of *A. pernyi* on 5 *Quercus* species, compared to *A. polyphemus*, was unexpected based on the assumption that a polyphagous "super-generalist" would be less efficient than the oak specialized species. This exceptional performance of *A. polyphemus* larvae was not due to better nutritional leaf quality, which was the case for *A. pernyi* larvae. In fact, the *A. pernyi* hosts were of higher nutritional quality. Perhaps the explanation of poorer larval conversion efficiency and growth performance of *A. pernyi* is simply that these particular host plant species are not their ancestral *Quercus* species. An apparent lack of specific physiological adaptations for efficient metabolic processing of North American trees may be due to insufficient time since the recent importation of *A. pernyi* into the USA (brought in during the last couple of decades by lepidopterists, research physiologists, and biological control specialists for mass-rearing of *Trichogramma* (Hymenoptera: Trichogrammatidae) egg parasitoids for use against forest pest species; Peigler, 1993).

While the efficiency of assimilating and converting tree leaf biomass to insect herbivore biomass and the subsequent rate of larval growth is determined primarily by the nutritional quality of the food (Scriber, 1984; Mattson and Scriber, 1987; Slansky, 1992, 1993), we did not observe this to be the case with these oak-feeding silk moths. In fact, a weak but negative correlation of penultimate instar growth rate (RGR) and leaf water content was observed (Fig. 1a). *Quercus* leaf nitrogen concentrations are also less for the fast-growing generalists on every oak species in both instars (Fig. 1b-2b).

Metabolic costs of detoxification will depend on the specific mechanisms involved and the affiliated evolutionary adaptations of each herbivore in question. For example, one allelochemical, nicotine, is metabolically costly for the polysubstrate oxygenase detoxification system of a generalist caterpillar (Cresswell *et al.*, 1992) but specialist caterpillar species with rapid excretion abilities and target site insensitivity has insignificant metabolic costs for detoxification (Appel and Martin, 1992). Perhaps these differences in mechanisms of detoxification with differential associated metabolic costs explain the mixed results in past attempts to quantify differences for specialist insects and generalist insects since Krieger *et al.* (1971) and Whittaker and Feeny (1971) suggested that selection for detoxification energy efficiency would be expected in specialists compared to generalists (which were presumed to have a greater number of detoxification systems to maintain and operate as a "metabolic load"; Slansky, 1993). While the North American generalist *A. polyphemus* is

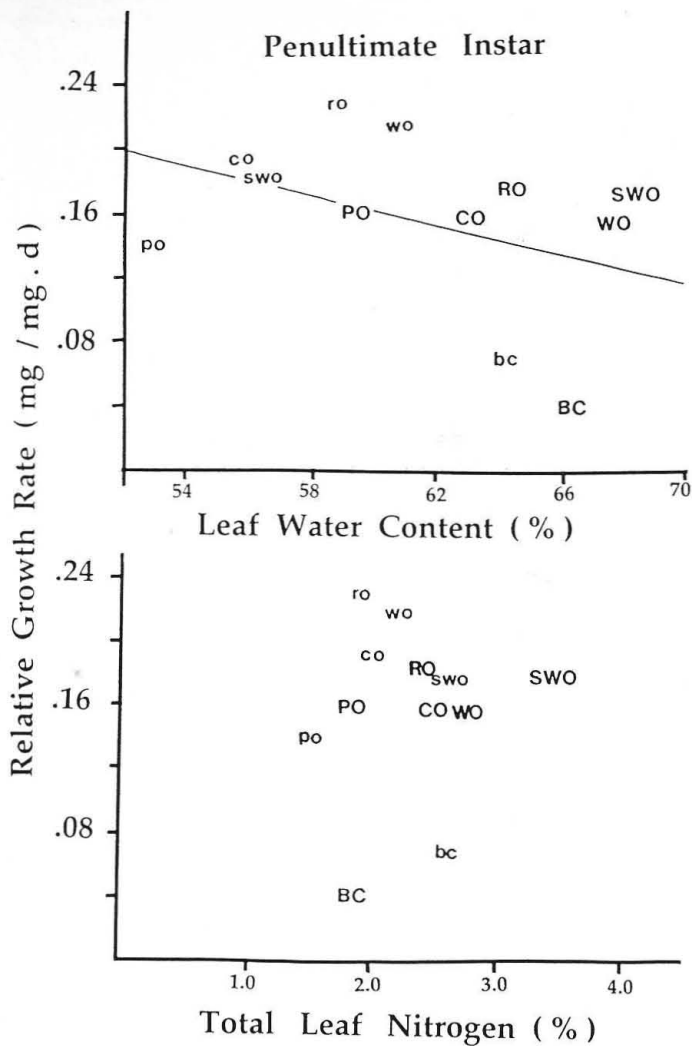


Fig. 1. The relative growth rates of penultimate instar larvae ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) of *Antheraea pernyi* (large letters) and *A. polyphemus* (small letters) on Chestnut oak (co), Red oak (ro), Swamp white oak (swo), White oak (wo), Pin oak (po), and Black cherry (bc) as a function of leaf water content (percent fresh weight; top, $r = 0.40$) and total nitrogen (percent dry weight; bottom, $r = 0.21$).

believed to be derived from the Asian oak specialists (e.g., a proto-*pernyi*; Ferguson, 1972), we see no evidence that there has been any loss of efficiency or growth rate in this polyphagous derivative and if anything, they do better on nutritionally poorer host tissues. No simple explanation is available for such atypical results (Slansky and Scriber, 1985).

BODY SIZE EFFECTS

Body size can have major significance in the feeding ecology of Lepidoptera (Scriber and Slansky, 1981; Mattson and Scriber, 1987; Reavy, 1993). The initial size can be of primary importance for establishment on the host plant and in successful completion of a given generation in certain thermally constrained situations, as described for *Papilio* in Alaska (Ayres and Scriber, 1994). It is clear that bigger larvae eat more and analysis of general trends in nutritional indices indicate that with more food eaten, more weight is gained, but lower relative consumption rates and relative growth rates exist for larger larvae (later instars; Slansky and Scriber, 1985; Reavy, 1993). Use of ratios in calculating the RGR (weight gained/mean weight \cdot d) may not adequately correct

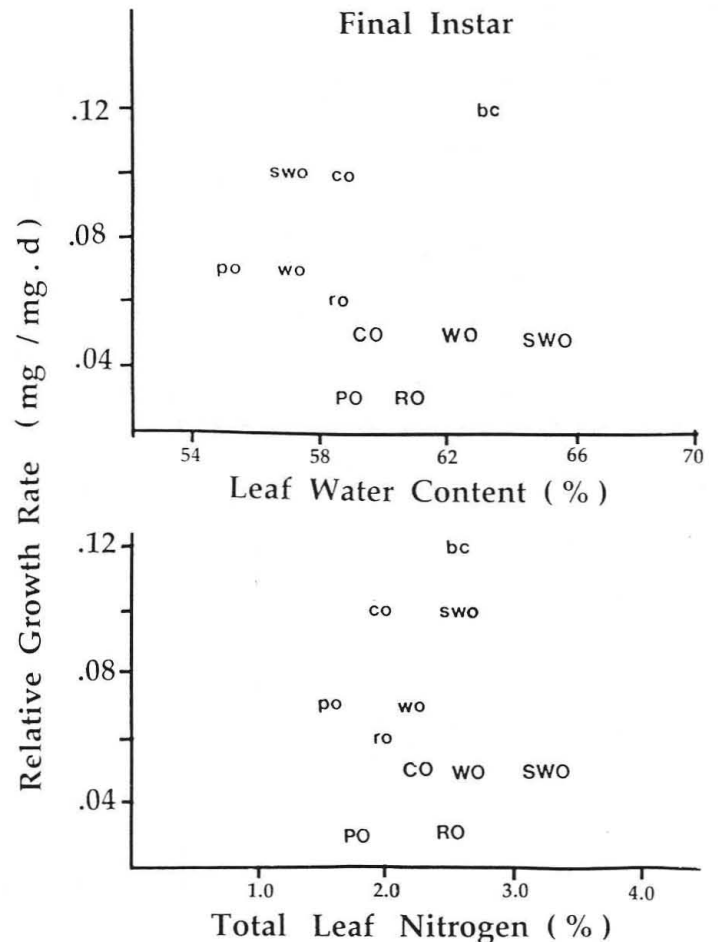


Fig. 2. The relative growth rates of final instar *Antheraea pernyi* and *A. polyphemus* on various hosts as a function of leaf water ($r = 0.12$) and leaf nitrogen content ($r = 0.06$) (same coding as in Fig. 1).

for size in attempting to assess the tissue growth rates (Waldbauer 1968). This and related statistical problems described recently (Raubenheimer and Simpson, 1992, 1994; Raubenheimer, 1995) led to an evaluation of raw data for all of the *A. pernyi* and *A. polyphemus* comparisons with regard to their size differences.

The *A. polyphemus* larvae were generally smaller than *A. pernyi* in both the penultimate and final instars. This was most pronounced for larvae on chestnut oak and pin oak (Tables 3-4). While mean size (B) is not included in the calculation of the 3 efficiencies (AD, ECD, or ECI), it certainly could have an effect, due to a smaller gut surface area relative to body weight for example. However, the increased volume of gut epithelial cells in larger larvae (rather than surface area of the lumen) may have equalizing effects on the assimilation efficiency (Reavy, 1993).

When plotted against the average size during the penultimate and final instars of both species, there is no significant interaction of mean weight with the approximate digestibility (AD) and only a slight hint of an effect in the final instar for the conversion efficiency of digested food (ECD), but the overall conversion efficiency of ingested food ($\text{ECI} = \text{AD} \times \text{ECD}$) shows no size effect for either instar (Fig. 3).

In contrast, the relative consumption rates (RCR) and the relative growth rates (RGR) of *A. polyphemus* and *A. pernyi* do show an effect of average size in the final instar (but not the

TABLE 3. Penultimate instar weight gain and mean weight during the instar for different host species. Data are presented as a mean (\pm SE).

| | Biomass increase (mg dry) | | | | Average weight (mg dry) | |
|-----------------|---------------------------|-------------------|-----|---------------|-------------------------|---------------|
| | (n) | <i>polyphemus</i> | (n) | <i>pernyi</i> | <i>polyphemus</i> | <i>pernyi</i> |
| Chestnut Oak | (6) | 125 \pm 11 | (8) | 452 \pm 14 | 107 \pm 6 | 439 \pm 14 |
| Red Oak | (5) | 360 \pm 12 | (8) | 363 \pm 18 | 292 \pm 4 | 313 \pm 9 |
| Swamp White Oak | (6) | 263 \pm 15 | (5) | 301 \pm 14 | 235 \pm 11 | 256 \pm 8 |
| White Oak | (5) | 239 \pm 14 | (8) | 389 \pm 24 | 202 \pm 18 | 329 \pm 17 |
| Pin Oak | (6) | 180 \pm 17 | (8) | 311 \pm 23 | 189 \pm 12 | 293 \pm 20 |
| Black Cherry | (2) | 120 \pm 29 | (4) | 167 \pm 15 | 136 \pm 24 | 215 \pm 9 |

TABLE 4. Final instar weight gain and mean weights during the instar for different host species. Data are presented as a mean (\pm SE).

| | Biomass increase (mg dry) | | | | Average weight (mg dry) | |
|-----------------|---------------------------|-------------------|-----|---------------|-------------------------|---------------|
| | (n) | <i>polyphemus</i> | (n) | <i>pernyi</i> | <i>polyphemus</i> | <i>pernyi</i> |
| Chestnut Oak | (4) | 505 \pm 92 | (4) | 849 \pm 28 | 460 \pm 60 | 1066 \pm 36 |
| Red Oak | (3) | 557 \pm 173 | (4) | 388 \pm 36 | 770 \pm 87 | 683 \pm 32 |
| Swamp White Oak | (4) | 557 \pm 14 | (4) | 524 \pm 45 | 666 \pm 71 | 823 \pm 40 |
| White Oak | (4) | 342 \pm 108 | (4) | 739 \pm 46 | 476 \pm 65 | 963 \pm 60 |
| Pin Oak | (4) | 560 \pm 105 | (4) | 478 \pm 35 | 695 \pm 96 | 836 \pm 61 |
| *Black Cherry | (1) | 441 | (-) | - | 376 | - |

* Poor survival in the final instar (only one larva completed development).

penultimate instar; see Fig. 4-5). Unfortunately, the initial weights and final weights of larvae for each instar were not retained (after the weight gained and the average weights were calculated), and therefore, it is not possible to do the desired analysis of covariance (Packard and Boardman, 1987; Raubenheimer and Simpson, 1992; Horton and Redak, 1993). Even if these values were available, they might not be useful since the instar weights for each host plant treatment were influenced by previous feeding on that host and not randomly assigned across host treatments.

What is clear is that ratio transformation of consumption rates and growth rates by mean size do not entirely remove the effects of size for the final instars. It appears that a general size-related

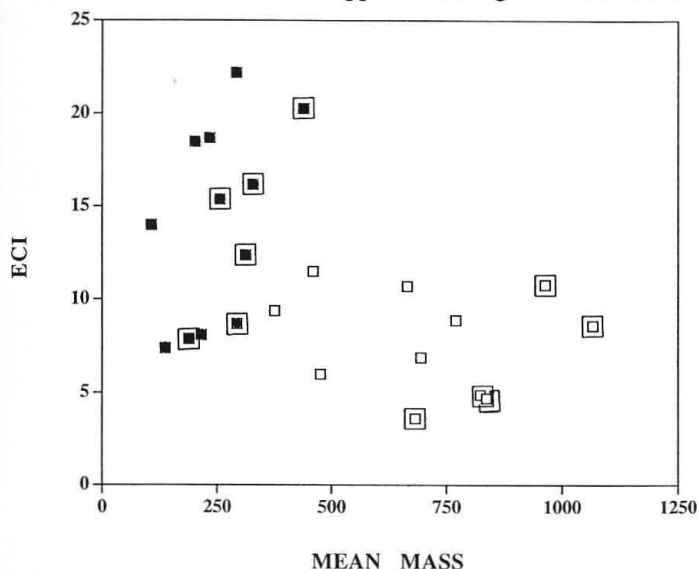


Fig. 3. The overall efficiency of conversion of ingested mass into larval biomass gain (E.C.I. = A.D. \times E.C.D.) as a function of average size of larvae in penultimate and final instars. Solid symbols represent penultimate instars, open symbols are final instars. Large squares are *A. pernyi*; the small are *A. polyphemus*.

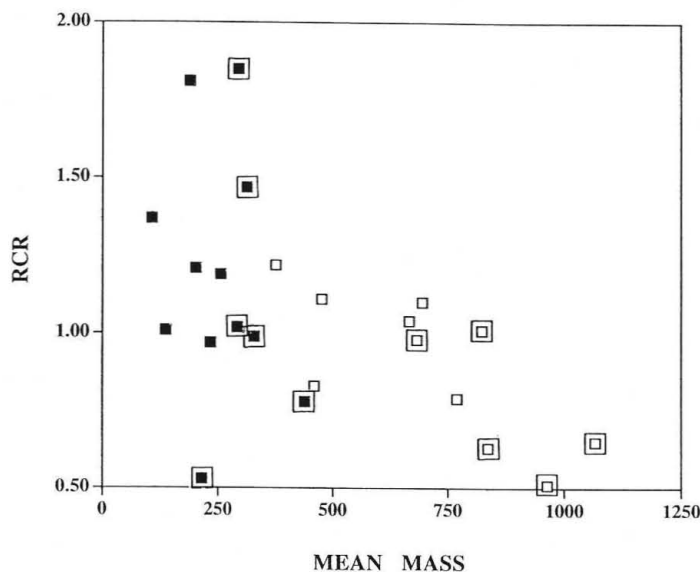


Fig. 4. The relative consumption rate (R.C.R. = mg ingested/mg \cdot d; dry weight basis) as a function of average weight of larvae of *A. polyphemus* and *A. pernyi* during the penultimate and final instars on 5 oak species and black cherry. Symbols are described in Fig. 3 caption.

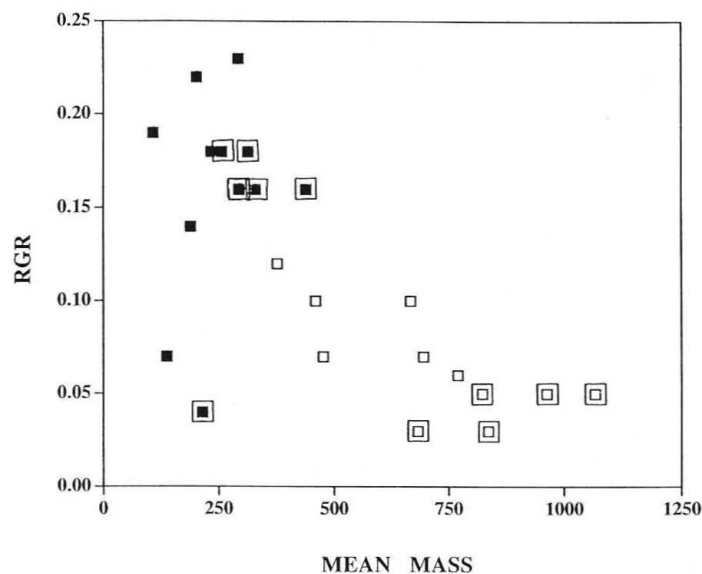


Fig. 5. The relative growth rate (R.G.R. = mg gained/mg \cdot d; dry weight basis) as a function of average weight of the larvae during each instar (see caption Fig. 3).

difference between *A. pernyi* and *A. polyphemus* relative growth rate and relative consumption rate (not efficiency) exists in the final instar stage. This could indicate that for every host species except red oak (where *A. pernyi* is smaller than *A. polyphemus*), the smaller *A. polyphemus* appear to consume food faster (RCR, Fig. 4) and grow faster (RGR, Fig. 5) simply because of their size, and not because of their adaptations for processing North American species of tree leaves. This conclusion might also be reached in pairwise comparisons of penultimate instars for chestnut oak, white oak, and black cherry (but not swamp white oak or pin oak; Fig. 5). However on red oak the mean size is the same but the growth rate of *A. polyphemus* is significantly higher than *A. pernyi* (see Tables 2-3).

Why *A. polyphemus* is smaller than *A. pernyi* may be ecologically more significant than the possibility that they are able to consume and process North American hosts for faster growth than are their Asian congeners. For example, if the seasonal degree day (thermal) accumulations for these *A. polyphemus* source populations are restrictive, smaller size may allow completion of the generation. It has previously been suggested that small size of adults is selected for in such thermally constrained areas (Ayres and Scriber, 1994; Scriber, 1994, 1996). It is also important to understand the entire environment on the larval performance of any species. Natural photoperiods or thermoperiods may cue a caterpillar's behavior and affect its physiological performance on different species with different allelochemicals (Scriber and Slansky, 1981; Slansky, 1992; Matsuki and MacLean, 1994; Stamp, 1994a, 1994b). Other variables of potential ecological significance that were not measured in this study include: 1) the egg size of the two silkmoths, 2) the duration of the molt (which in some temperatures is longer than the instar duration; Ayres and MacLean, 1987; Ayres and Scriber, 1994).

Since so little is known about the ecology of *A. pernyi* in Asia, it is with great caution that comparisons of nutritional physiology must be considered. For example, if Asian *Quercus* host species are allelochemically very different as a group than the five North American species used in these comparative bioassays, one might hypothesize that the biochemical detoxication mechanism of the Asian oak-feeding *A. pernyi* is inefficient on the American host species; however, such speculation is not justified. We know little about the phytochemistry of Asian oaks in regard to insect toxins, deterrents and nutrients, or their interactions (but see Gavrilchik, 1991). Also, the five American oak species used in these studies can have significant differences in gallotannins, total phenolics, foliar astringency, and proanthocyanidins (Hunter, 1994). It would seem logical that such differences among these North American *Quercus* species would elicit differential interspecific larval growth efficiencies or growth rates if differential adaptations (or "exaptations"; Lauder *et al.*, 1993) existed for these silkmoths. Perhaps the only way to evaluate the differential *Quercus* chemistry hypothesis would be to test both *Antheraea* species concurrently on Asian oaks to see if the larval growth performances are reversed.

Although the few larvae that died during these studies did not look to be diseased, it is certainly feasible that other sub-lethal pathogen influences were, for unknown reasons, more prevalent in *A. pernyi* than *A. polyphemus*. Such differences in microbial susceptibility deserve additional study, since microbe/plant/herbivore interactions are very poorly understood yet may be responsible in part for significant differences in population responses and maternal effects (Mousseau and Dingle, 1991; Rossiter, 1994; Scriber and Haas, 1996).

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