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Effects of food quality, particularly nitrogen concentrations, of *Eucalyptus blakelyi* foliage on the growth of *Paropsis atomaria* larvae (Coleoptera: Chrysomelidae)

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Abstract. Five groups of *E. blakelyi* seedlings were differentially fertilized to obtain a range of N concentrations from 0.8–3.0% dry wt in the foliage. Groups of *P. atomaria* larvae were reared from eclosion to the prepupal stage on these seedlings. The effects on larval growth and development caused by foliar concentrations of N, moisture content, and tannins and leaf toughness were measured. Pupal dry weight and development time of *P. atomaria* did not differ between those reared on foliage with N levels of 1.7–3.0% but there was a significant decrease in pupal weight and increase in development time for individuals fed foliage with N below this level. Larvae fed foliage with an average of 0.8% N died before reaching instar III. Total dry matter consumption increased with a decrease in N concentration. Larval nitrogen utilization efficiency increased as foliar N level decreased until N reached a level somewhere between 1.7%–1.2% below which it decreased. There appeared to be an N concentration threshold above which *P. atomaria* larvae received adequate N by regulating consumption and nitrogen utilization efficiency but below which they could no longer accumulate enough N by compensation to maintain an optimum growth rate and development time. Effects of food quality variables on relative growth and consumption rates are presented and discussed.

During the past several years there has been a tremendous proliferation of published information regarding insect-plant interactions (eg. Visser and Minks 1982; Hedin 1983; Denno and McClure 1983). A large portion of the work has dealt with the effects of food quality of plants on the nutrition of insect herbivore larvae. Scriber and Slansky (1981) have reviewed the literature concerned with the nutritional ecology of immature insects. Many papers have focused on various plant chemicals which affect insect growth rates, such as secondary plant compounds like tannins and essential oils (eg. Feeny 1968; Fox and Macauley 1977; Morrow and Fox 1980; Bernays 1981), moisture content of plant material (eg. Scriber 1979; Tabashnik 1982), nitrogen concentrations of foliage (eg. Fox and Macauley 1977; Slansky and Feeny 1977; Scriber 1978; Tabashnik 1982), and leaf toughness (Feeny 1970).

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Nitrogen (N) plays a central role in all metabolic processes and is a critical element in the growth of all organisms. Because of its importance a considerable amount of work has been done on the effects of N on insect growth and development (see McNeill and Southwood 1979; Mattson 1980 for reviews). Nitrogen concentrations in tree foliage tend to be lower than those in herbaceous plants (Scriber and Slansky 1981) which has led to the hypothesis that N could be a limiting factor for insect defoliators feeding on trees. White (1978) suggested that the single most important factor in limiting the abundance of most animals is the shortage of nitrogenous food for the very young. In a series of papers White (1969, 1974, 1976) developed the theory that water stress increased N availability in plants and resulted in outbreaks of certain insect defoliators. Several studies have been done testing White's hypotheses with mixed results (McClure 1980; Myers 1981; Myers and Post 1981; Miles et al. 1982).

Fox and Macauley (1977) reported that the growth rate of *Paropsis atomaria* Oliver (Coleoptera: Chrysomelidae) larvae was directly related to N concentrations in *Eucalyptus* foliage and not affected at all by a wide range in concentrations of phenols. They concluded that N could be a limiting factor for *P. atomaria* since N concentrations in naturally–occurring eucalypt foliage were low. In a direct test of White's water stress hypothesis Miles et al. (1982) found, however, that growth of *P. atomaria* larvae was not related to N concentrations in *Eucalyptus camaldulensis* Dehnh. foliage. Water stress significantly increased N concentrations in foliage in their experiments but there was no difference in larval growth or development on control (watered) vs stressed (unwatered) plants. Miles et al. (1982) suggested that one reason their results differed from those of Fox and Macauley (1977) may have been because the range of N in their test plants was 1.8–4.2% (dry wt.) and above the level where N was limiting whereas the range in Fox and Macauley's leaf material was only 0.5–1.8% N.

We selected *P. atomaria* as a test animal to further examine White's hypotheses as well as to look at the effects of other food quality variables on the population dynamics of eucalypt defoliators. The first step was to clear up the apparent discrepancy between the results of Fox and Macauley (1977) and Miles et al. (1982) by establishing the quantitative relationship between a broad range of N concentrations in eucalypt foliage and the growth and development of *P. atomaria* larvae. We also examined the effects

of moisture content of foliage, leaf toughness, and concentrations of tannins on larval growth and development.

Materials and methods

Insect and plant material

Paropsis atomaria is widely distributed in southeastern Australia and feeds on a wide range of eucalypts. *Eucalyptus blakelyi* Maiden is one of its preferred hosts in the Australian Capital Territory where this experiment was carried out. Larvae feed gregariously on terminal leaves of new shoots and develop from eggs to pupae in about 3 weeks under optimum conditions (Carne 1966). There are 4 larval instars. Larvae used in the study were obtained from eggs laid by females from a colony of beetles that had been maintained on *E. blakelyi* in the laboratory. Approximately 180 *E. blakelyi* seedlings were grown from seed in a nutrient-free vermiculite-perlite-sand mixture and watered daily with a standard Hoaglands solution[1] until 30 cm tall. To obtain groups of seedlings with a range of foliar N concentrations they were then divided into 5 treatments and watered daily with a modified Hoaglands solution[2] diluted with demineralized water as follows: treatment 1 received full strength; 2, 1 in 5; 3, 1 in 10; 4, 1 in 25; and 5 received only demineralized water. The larval feeding experiment was begun when the seedlings were 40–50 cm tall (after about 1 month).

Larval measurements

Five seedlings were selected from each fertilization treatment and a newly-hatched *P. atomaria* egg batch was tied to the tip of each seedling (ie. 5 replicates in each of 5 treatments). The larvae fed on their egg shells for 2 days before travelling *en masse* to the nearest newly-expanding leaf. Four days after hatching the larvae in each replicate were counted, weighed and approximately 20 individuals placed on a leaf of known area in the third or fourth position down from the tip of the seedling. A small sample of known area was removed from the leaf for analyses of food quality variables (see below). Larvae were kept in groups to allow expression of their natural gregarious feeding behavior. They were confined to the leaf in a ventilated petri dish clamped over it and suspended by a wire stand. The remaining larvae were frozen in liquid nitrogen, freeze-dried, and stored in a freezer for later determination of N concentration and wet weight – dry weight ratios. All leaf area measurements were made with a portable area meter (LI-COR model LI-3000, LI-COR Ltd., Lincoln, Nebraska).

On days 8, 10, 12, and 14 the larvae in each replicate were weighed and moved to new leaves of known area. The area of the remainder of the old leaf was determined to calculate the leaf material consumed by the larvae. Faeces were collected, air-dried, weighed and analyzed for N concentrations. Two or 3 larvae were removed from each replicate at every leaf change and frozen in liquid N for later analyses. By day 14, 8–10 larvae remained in each replicate and from this point to the end of the experiment only about 5 larvae were removed from each treatment for destructive sampling. After day 16 the larval groups were weighed, the faeces removed, and the remaining larvae moved to new leaves daily. When 7 or 8 of the terminal leaves of a seedling had been used a new seedling was selected from their respective pool of treatment seedlings. Each replicate was measured until all the larvae had reached prepupal stage and stopped feeding. After pupation they were weighed.

The experiment was carried out in a temperature controlled glasshouse with 16 h day at 24° C and 8 h night at 18° C nights.

Leaf measurements for food quality variables

The sample was measured for toughness, after removal from the leaf on which the larvae were placed, using a penetrometer with a 3 mm diameter brass plunger similar to the one described by Lowman and Box (1983). It was then weighed and immediately frozen in liquid nitrogen. Samples were later freeze-dried and stored in a freezer until analyzed. Each leaf sample was measured for moisture content, dry weight per unit area, and concentration of total N. The leaf opposite the one on which the larvae were placed was removed and analyzed for tannins. Total N concentrations were determined using a modified Kjeldahl technique (Ohmart et al. 1983). Tannin concentrations were measured using a haemoglobin precipitation technique described by Schultz et al. (1981).

Data analysis

The following indices were calculated on a dry weight larva^{-1} day^{-1} basis (after Waldbauer 1968; Tabashnik 1982):

RGR: Relative Growth Rate = $\dfrac{\text{wt gain day}^{-1})}{\text{Mean larval wt}}$[3]

RCR: Relative Consumption Rate = $\dfrac{\text{Food ingested day}^{-1}}{\text{Mean larval wt}}$

ECI: Efficiency of Conversion of Ingested Food = $\dfrac{\text{wt gained}}{\text{wt food ingested}}$

AD: Approximate Digestibility = $\dfrac{\text{wt food ingested} - \text{wt of faeces}}{\text{wt of food ingested}} \times 100$

NUE: Nitrogen Utilization Efficiency = $\dfrac{\text{wt N gained}}{\text{wt N ingested}}$

Relationships between RGR and RCR with the food quality variables measured were tested using analysis of

1 Hoaglands solution contains 15 mM N. Proportions (by weight) of elements in Hoaglands solution; N: 100, K: 112, Ca: 78, S: 31, Mg: 23, P: 16, Fe: 2.4, Cl: 0.055, Mn: 0.054, B: 0.050, Zn: 0.010, Cu: 0.006, Mo: 0.004, Co: 0.002

2 1.167 g per l $Ca(NO_3)_2 \cdot 4H_2O$ added to increase N concentration to 25 mM

3 Mean larval wt $= (W_i - W_f)/2$
W_i = initial wt for measurement period (1 day)
W_f = final larval wt for measurement period

Table 1. Nitrogen concentrations, moisture content, and toughnesses of *E. blakelyi* leaves fed to *P. atomaria* larvae in each treatment and significant pairwise contrasts at $a=0.05$[a]. Standard deviations in parentheses

Treatment	1	2	3	4	5
	% N dry wt				
Instar I & II (Day 0–14)	3.01 (0.43)	2.36 (0.35)	1.69 (0.33)	1.17 (0.16)	0.84 (0.17)
No. samples	25	25	25	30	36
All pairwise contrasts significant					
Instar III & IV (Days 16–pupa)	2.74 (0.28)	2.16 (0.30)	1.79 (0.36)	1.27 (0.32)	–[b]
No. samples	35	30	50	42	
All pairwise contrasts significant					
	% Moisture				
Instar I & II (Days 0–14)	59.9 (4.0)	62.6 (3.0)	61.2 (3.0)	61.9 (4.0)	61.2 (6.0)
No pairwise contrasts significant					
Instar III & IV (Days 16–pupa)	59.7 (3.0)	60.9 (5.0)	61.5 (4.0)	60.6 (4.0)	–
No pairwise contrasts significant					
	Leaf Toughness (gms/mm^2 to puncture leaf)				
Instar I & II (Days 0–14)	40.9 (12.7)	35.3 (9.6)	39.3 (11.4)	43.2 (13.9)	61.5 (15.5)
Significant pairwise contrasts: 1 vs 5, 2 vs 5, 3 vs 5, 4 vs 5					
Instar III & IV (Days 16–pupa)	41.1 (11.5)	41.8 (12.6)	47.0 (12.8)	65.4 (25.1)	
Significant pairwise contrasts: 1 vs 4, 2 vs 4, 3 vs 4					

[a] Tukey's method of multiple pairwise contrasts (Marascuilo 1971)
[b] All larvae in treatment 5 died before Instar III

variance, linear regression, and stepwise multiple regression. Analyses were done using the ELF computer package written by the Winchendon Group for an APPLE II microcomputer. Differences between means were tested using Tukey's method of multiple pairwise contrasts (Marascuilo 1971).

Results

Effects of nitrogen on growth, development, and consumption

The data set was divided into two parts, one containing measurements for instars I and II and the other for instars III and IV based on the evidence that the performance of young larvae may differ from that of older larvae on a given diet (Scriber and Slansky 1981; Montgomery 1982).

The method of differential fertilization used for the *E. blakelyi* seedlings gave a good separation of N concentrations between treatments (Table 1). Moisture concentrations did not differ between treatments (Table 1). Leaf toughness increased with decreasing N concentrations in the leaves of treatment 5 during the first half of the experiment and in treatment 4 in the second half (Table 1).

Dry weight of pupae and development time to prepupal stage were the same for treatments 1 to 3 but were significantly different from those of treatment 4 (Table 2). Larvae fed leaves with an average N concentration of 1.69% and higher (ie. treatments 1–3) reached a uniformly higher pupal weight and developed at a much faster rate than those fed leaves with N concentrations below this level. All larvae in treatment 5 died before reaching instar III. Although N concentrations in this treatment may have been limiting it seemed apparent from observations that leaf toughness played a major role in larval mortality. In most cases larvae eventually died after encountering a leaf which was too tough for them to initiate feeding.

Table 2. Average pupal dry weight (mg) and length of development time (days) from egg to prepupa for *P. atomaria* larvae in treatments 1 to 4 and pairwise contrasts significantly different at $a=0.05$. Larvae in treatment 5 died before reaching instar III. Standard deviations in parentheses.

Treatment	1	2	3	4
Pupal dry wt (mg)	25.2 (6.1)	25.5 (4.7)	25.6 (5.2)	17.9 (4.1)
No. samples	43	42	46	29
Significant pairwise contrasts: 1 vs 4, 2 vs 4, 3 vs 4				
Development time (days)	26.4 (2.4)	23.5 (1.3)	25.8 (1.7)	41.1 (6.3)
No. samples	43	42	46	29
Significant pairwise contrasts: 1 vs 4, 2 vs 4, 3 vs 4				

Table 3. Average dry matter and nitrogen consumed by *P. atomaria* larvae and nitrogen utilization efficiencies (NUE) for all four instars.

Treatment	1	2	3	4
Dry matter consumed (mg)	208.5 (26.0)	225.8 (26.6)	258.4 (36.6)	306.6 (54.5)
No. samples	5	5	5	6
N consumed (mg)	5.75 (0.49)	4.92 (0.55)	4.53 (0.95)	3.99 (1.16)
No. samples	5	5	5	6
NUE (%)	49.2	55.1	59.3	45.5

Table 4. Approximate digestibility (AD) and efficiency of conversion of ingested food (ECI) for all four instars of *P. atomaria* larvae and significant pairwise contrasts at $a=0.05$. Standard deviations in parentheses.

Treatment	1	2	3	4
AD (%)	33.2 (10.0)	33.8 (2.9)	23.8 (2.1)	24.1 (4.4)
No. samples	5	5	5	6
Significant pairwise contrasts: 1 vs 3, 1 vs 4, 2 vs 3, 2 vs 4				
ECI (%)	15.7 (1.1)	14.1 (1.7)	12.3 (1.3)	7.1 (0.5)
No. samples	5	5	5	6
Significant pairwise contrasts: 1 vs 3, 1 vs 4, 2 vs 4, 3 vs 4				

Total consumption of dry matter per larva increased with a decrease in N concentration (Table 3). Since larvae in treatments 1–3 reached the same final weight in the same length of time and yet fed on leaves with decreasing levels of N it appeared that they compensated for a decrease in foliar N by increasing their total consumption. Larvae in treatments 1–3 would have consumed about the same amount of N if they had compensated completely for decreased foliar N concentrations. However, N consumption decreased as N levels declined (Table 3). Larvae in treatments 1–3 compensated for decreased N concentrations in leaves, in part by increasing nitrogen utilization efficiency (NUE) and in part by consuming more leaf material (Table 3).

Digestion efficiencies of the larvae decreased as N concentrations in leaves decreased (Table 4). There was a gradual decline in efficiency of conversion of ingested food (ECI) with a decline in N concentrations whereas the approximate digestibilities (AD) of treatments 1 and 2 were similar with a sharp decline between treatments 2 and 3.

Effects of food quality variableson relative growth and consumption rates

Tannin concentrations increased with decreasing foliar N concentrations (Table 5). Pupal weight and length of development time were not affected by tannin concentrations even though the leaves in treatments 2 and 3 had significantly more tannin than those of treatment 1 (Table 1). Tannin concentrations were not correlated with relative growth rate

Table 5. Tannin concentrations in the *E. blakelyi* foliage fed to *P. atomaria* larvae in each treatment and significant pairwise contrasts at $a=0.05$. Standard deviations in parentheses.

Treatment	1	2	3	4	5
Tannin conc. (% dry wt)	19.8 (2.0)	22.9 (2.8)	25.7 (2.4)	27.1 (3.2)	27.6 (3.8)
No. samples	38	37	37	29	10
Significant pairwise contrasts: 1 vs 2, 1 vs 3, 1 vs 4, 1 vs 5 2 vs 3, 2 vs 4, 2 vs 5					

(RGR) within any of the five treatments analyzed separately or with the data pooled. The dramatic decline in pupal weight and increase in development time experienced by the larvae in treatment 4 were therefore not related to tannin concentrations.

Simple correlation coefficients between RGR and leaf toughness, moisture content, N concentration, and N consumption appear in Table 6. Leaf toughness was very important in explaining day – to – day fluctuations in RGR's of young larvae in all treatments except treatment 5, whereas for older larvae it was only important in treatment 4. Consumption of N by older larvae explained more variation in RGR than any other food quality variable in all treatments. Larvae in treatments 1–3 were undoubtedly large enough by instar III to consume almost any foliage, regardless of its toughness, and RGR depended solely on the rate of N consumption. Instar III larvae in treatment 4, however, were smaller and may have been physically less able to feed efficiently on some of the tougher leaves. Total leaf consumption by treatment 4 larvae was not affected by leaf toughness, since they consumed more foliage than those in all the other treatments.

Food quality variables explained larger amounts of variance of RGR in multiple regression equations as N levels decreased, indicating that leaf properties other than N concentration also became important as foliar N levels declined (Table 6). More food quality variables were significantly correlated with RGR in treatment 4 than in the other treatments in both young and old larvae (Table 6).

Moisture content was important in explaining variation in RGR in treatment 4 for all instars and in treatments 1 and 3 for the young larvae. Small fluctuations in moisture contents in these treatments had an important influence on RGR since the range of moisture contents was small and did not differ between treatments (Table 1).

There were no correlations between RGR and any food quality variables in treatment 5. The young larvae were so stressed, owing to the extremely low N level and high leaf toughness in their diet, that feeding was totally disrupted and no relationships were evident. The situation encountered by these larvae was probably unrealistic since young larvae feed on newly-expanding foliage in the field and would never encounter young leaves with these extremely low N concentrations and high toughnesses.

The relative consumption rates (RCR) of young larvae were negatively related to N concentration in treatments 1–3 (Table 7). Relative consumption rates of older larvae were not related to any of the food quality variables measured in the study except with leaf toughness in treatment 4. However, total consumption per larva for all 4 instars was negatively related to N concentration (Table 3).

Table 6. Simple correlation coefficients (r) between daily relative growth rates (RGR) and the food quality variables leaf toughness (gms/mm^2), moisture concentration (%), N concentration (% dry wt), and N consumed (dry wt mg day^{-1}), measured on the leaves fed to *P. atomaria* larvae in each treatment and total adjusted multiple R^2 from stepwise multiple regression with RGR as the dependent variable.

Treatment	1	2	3	4	5
Instar I & II					
Toughness	−0.601[a]	−0.415[a]	−0.723[a]	−0.789[a]	*
Moisture content	0.495[a]	*	0.444[a]	0.679	*
N content-tration	*	*	*	0.505	*
N consumed	*	0.537[a]	0.816[a]	0.503	0.479[a]
Adj. R^2	0.45	0.49	0.79	0.62	0.23
Instar III & IV					
Toughness	*	*	*	−0.652[a]	–[b]
Moisture content	*	*	*	0.525	–
N concen-tration	*	*	*	*	–
N consumed	0.410[a]	0.765[a]	0.753[a]	0.742[a]	–
Adj. R^2	0.17	0.59	0.58	0.60	–

* Not significantly correlated with RGR at $a=0.05$
[a] Variables which contribute significantly to total adjusted R^2 in stepwise multiple regression
[b] Larvae died before reaching instar III

Table 7. Simple correlation coefficients (r) between daily relative consumption rates (RCR) and the food quality variables leaf toughness (gms/mm^2), moisture concentration (%), and N concentration (% dry wt) measured on leaves fed to *P. atomaria* larvae in each treatment.

Treatment	1	2	3	4	5
Instars I & II					
Toughness	−0.403	*	*	−0.599	*
Moisture content	*	*	*	0.673	*
N concentration	−0.413	−0.437	−0.500	*	*
Instars III & IV					
Toughness	*	*	*	−0.472	–[a]
Moisture content	*	*	*	*	–
N concentration	*	*	*	*	–

* Not significantly correlated with RCR at $a=0.05$
[a] Larvae died before reaching instar III

Discussion

It appeared that there was a foliar N concentration threshold between 1.2% and 1.7% above which *P. atomaria* larval growth and development were optimum and independent of foliar N concentration since they were able to regulate N intake and utilization by altering consumption and NUE. Below this threshold growth and development were directly correlated with N levels, since larvae were unable to obtain an adequate amount of N resulting in longer larval development time and lighter pupae. Poor larval performance could have been due to the physical constraints of digesting large amounts of poor quality food rapidly passed through the gut as well as from biochemical problems of N availability.

The results of the analyses of the data presented here demonstrate why Fox and Macauley (1977), working with N concentrations between 0.5% and 1.8%, obtained positive correlations between RGR's of fourth instar *P. atomaria* larvae and foliar N concentrations, while Miles et al. (1982), working with N concentrations above 1.8%, found no relation between foliar N levels on growth and development of *P. atomaria* larvae. They were working on opposite sides of the N threshold for this species.

Total larval consumption was negatively related to N concentration in the leaves (Table 3) and, above the limiting N threshold, growth rates were independent of N concentration (Table 6). Digestion efficiencies were negatively related to N concentration (Table 4). This indicated that larvae handled food in a way similar to other herbivores when N concentrations ranged above this threshold (eg. Baker 1975; House 1965; Taylor and Bardner 1968; Slansky and Feeny 1977). Fox and Macauley (1977), on the other hand, reported that the feeding rate of *P. atomaria* larvae was independent of leaf N and growth rate was positively related to leaf N. They concluded that *P. atomaria* differed from other insects in these relationships. Their exposure of larvae to a low range of N concentrations and lack of opportunity to measure total consumption by all larval stages and final pupal weight, did not allow them to see the complete spectrum of the relationships between leaf N, consumption, and growth.

The present study differs from many other recent insect feeding studies which have looked at the relationships between food quality variables and insect growth and development by the fact that all larval stages were subjected to the experimental treatments. Most studies examined only one or two instars (eg. Feeny 1970; Slansky and Feeny 1977; Fox and Macauley 1977; Scriber 1978; Morrow and Fox 1980) and some have examined larval growth for only 24 h (Tabashnik 1982). It is important to measure growth and development in absolute as well as relative terms in order to obtain a complete understanding of the effects of food quality on insect populations. Insect population dynamics are affected by absolutes such as adult weight, with which fecundity is correlated, and total larval development time, which influences larval mortality by length of exposure to biotic and abiotic mortality factors, rather than by relative rates of growth, consumption, etc. during one or two instars. For example, knowing that lower foliar N reduces RCR does not give any indication of how long the larvae will take to develop or what weight they will finally attain.

In this study the relative measures RGR and RCR masked relationships that were clearly demonstrated by absolute measures. For example, Table 7 shows no relation between RCR of old larvae, which do most of the feeding, and leaf N concentrations in any treatment. Table 3, however, clearly shows a negative relationship between total consumption and leaf N. Another example is that Table 6 shows no relation between leaf N concentrations and RGR of older larvae, which accumulate most of the biomass, in any treatment, yet leaf N had a dramatic effect on pupal weight and development time (Table 2).

There are several problems inherent in the determina-

tion of RGR owing to measurement limitations. For example, larval weight is affected by faeces in the digestive tract or changes caused by moulting. Relative measures decrease in value as larvae get larger, regardless of the diet, owing to the allometric relationship between body size and the rate of the process, eg. growth, consumption, etc. (Montgomery 1982; Montgomery pers. comm.).

Another problem in examining these relationships using only relative measures of growth regressed with food quality variables is best illustrated by the relationship between N consumed and RGR (Table 6). There was a significant positive correlation between N consumption and growth rate for all instars in every treatment but one. This seems to imply that the more N a larva consumes the faster it will grow. The natural conclusion is that an increase in N level in the diet would increase growth. Table 2 and 3, however, readily illustrate that as N level increases consumption of foliage declines, the amount of N consumed increases slightly and NUE decreases. The outcome is that, although the food quality appears to improve in treatments 1–3 as N increases, there is no effect on growth and development. The correlation between N and growth only occurs in treatment 4.

This experiment demonstrates that below a certain threshold not only is leaf N important to larval growth and development but at these low N levels leaf toughness and moisture content are highly correlated with RGR. This indicates that at low N levels fluctuations in these leaf properties could also have an impact on growth and development. In some low N leaves N concentrations, leaf toughness and moisture contents were intercorrelated, low N leaves tend to be tougher and lower in moisture. Both these factors inhibit larval growth. When N is limiting it may be important to consider the total effects of all these food quality variables rather than consider each one individually.

White (1978) hypothesized that it was the very young larvae for which N accumulation was critical. However, table 6 indicates that in treatments 1 and 3 leaf toughness was more important than N consumption in explaining variation in RGR of young larvae and almost as important as N in treatments 2 and 4. At the same time, leaf toughness was, in these experiments, caused by the low nitrogen status of the plant. In that sense, although as stated earlier, leaf toughness probably was the immediate cause of larval mortality in treatment 5, low N could be counted as an ultimate cause. If survival of the first instar larva is crucial to the population dynamics of *P. atomaria* this experiment indicates nevertheless that N level may be only one of several factors – some possibly interrelated – that influence survival.

White (1969, 1974, 1976) suggested that water stress could bring about increases in leaf N resulting in population outbreaks. Our experiment showed that *P. atomaria* larval growth was limited by leaf N if it occurred below a certain threshold. Concentrations of foliar N below this threshold would extend development time exposing the larval stages to mortality factors for a longer period. Low N produces lighter females which lay fewer eggs (Carne 1966). The end result would be lower fecundity and higher larval mortality. Survival of first instar larvae may also be affected but this study was not designed to test this hypothesis. Based on the above conclusions the important question to ask is: What levels of leaf N do *P. atomaria* larvae encounter in the field? Unfortunately no one has thoroughly examined this question and there are extremely few studies of N levels in eucalypt canopies (Fox and Macauley 1977; Lamb 1976; Ashton 1975; Cromer 1971; Schonau 1981) and almost no information for *E. blakelyi* (but see Journet and Cochran 1978). Most published data suggest that leaf N of eucalypts varies from 1 to 2%. If this is true *P. atomaria* larvae must feed on foliage with N levels that fluctuate above and below the threshold where N is limiting. If foliar N occurs at levels where it is limiting during most years but in some years occasionally rises above the threshold, owing to water stress, etc., then larval growth and development would be optimum and population performance dramatically affected. Detailed studies of N dynamics in *E. blakelyi* canopies are being initiated to answer these questions.

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References

Ashton DH (1975) Studies of litter in *Eucalyptus regnans* forests. Aust J Bot 23:413–433

Baker JG (1975) Protein utilization by larvae of the black carpet beetle, *Attogenus megatoma*. J Insect Physiol 21:613–621

Bernays EA (1981) Plant tannins and insect herbivores: an appraisal. Ecol Ent 6:353–360

Carne PB (1966) Ecological characteristics of the eucalypt-defoliating chrysomelid *Paropsis atomaria* 01. Aust J Zool 14:647–672

Cromer RN (1971) Fertilizer trials in young plantation eucalypts. Aust For Res 5:1–10

Denno RF, McClure MS (1983) Variable plants and herbivores in natural and managed systems. Academic Press NY, p 712

Feeny PP (1968) Effects of oak leaf tannins on larval growth of the winter oak moth *Operophtera brumata*. J Insect Physiol 14:805–817

Feeny PP (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecol 51:565–581

Fox LR, Macauley BJ (1977) Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia (Berlin) 29:145–162

Hedin PA (ed) (1983) Plant resistance to insects. Amer Chem Soc, Wash DC Symp Ser 208, p 375

House HL (1965) Effects of low levels of nutrient content of a food and of nutrient imbalances on the feeding and the nutrition of a phytophagous larva, *Celerio euphorbiae* (Linnaeus) (Lepidoptera: Sphingidae). Can Ent 97:62–68

Journet ARP, Cochran PM (1978) Free amino acids in the leaf tissue of *Eucalyptus blakelyi*. Phytochem 17:1789–1790

Lamb D (1976) Variations in the foliar concentrations of macro and micro elements in a fast-growing tropical eucalypt. Plant and Soil 45:477–492

Lowman MD, Box JD (1983) Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. Aust J Ecol 8:17–25

Marascuilo LA (1971) Statistical methods for behavioral science research. McGraw-Hill, San Francisco, p 578

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Ann Rev Ecol Syst 11:119–161

McClure MS (1980) Foliar nitrogen: A basis for host suitability for elongate hemlock scale, *Fiorinia externa* (Homoptera: Diaspididae). Ecol 61:72–79

McNeill S, Southwood TRE (1978) The role of nitrogen in the development of insect/plant relationships. In: Harborne JB (ed) Biochemical aspects of plant and animal coevolution. Phyto Chem Soc Eur Symp Ser 15:77–98

Miles PW, Aspinall D, Correll AT (1982) The performance of two chewing insects on water-stressed food plants in relation to changes in their chemical composition. Aust J Zool 30:347–355

Montgomery ME (1982) Life-cycle nitrogen budget for the gypsy moth, *Lymantria dispar*, reared on artificial diet. J Insect Physiol 28:437–442

Morrow PA, Fox LR (1980) Effects of variation in *Eucalyptus* essential oil yield on insect growth and grazing damage. Oecologia (Berlin) 45:209–219

Myers JH (1981) Interactions between western tent caterpillars and wild rose: A test of some general plant herbivore hypotheses. J Anim Ecol 50:11–25

Myers JH, Post BJ (1981) Plant nitrogen and fluctuations of insect populations: A test with the cinnabar moth-tansy ragwort system. Oecologia (Berlin) 48:151–156

Ohmart CP, Stewart LG, Thomas JR (1983) Leaf consumption by insects in three *Eucalyptus* forest types in southeastern Australia and their role in short-term nutrient cycling. Oecologia (Berlin) 59:322–330

Schonau APG (1981) Seasonal changes in foliar nutrient content of *E. grandis*. South Afr J For 119:1–4

Schultz JC, Baldwin IT, Nothnagle PJ (1981) Hemoglobin as a binding substrate in the quantitative analysis of plant tannins. J Agr Food Chem 29:823–826

Scriber JM (1978) The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: An ecological consideration. Entomol Exp Appl 24:294–510

Scriber JM (1979) Effects of leaf-water supplementation upon post-ingestive nutritional indices of forb, shrub-, vine-, and tree-feeding Lepidoptera. Entomol Exp Appl 25:203–215

Scriber JM, Slansky F jr (1981) The nutritional ecology of immature insects. Ann Rev Entomol 26:183–211

Slansky F jr, Feeny PP (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecol Monogr 47:209–228

Tabashnik BE (1982) Responses of pest and non-pest *Colias* butterfly larvae to intraspecific variation in leaf nitrogen and water content. Oecologia (Berlin) 55:389–394

Taylor WE, Bardner R (1968) Leaf injury and food consumption by larvae of *Phaedon cochleariae* (Coleoptera: Chrysomelidae) and *Plutella maculipennis* (Lepidoptera: Plutellidae) feeding on turnip and radish. Entomol Exp Appl 11:177–184

Viser JH, Minks AK (1982) Proceedings of the 5th International Symposium on Insect-Plant Relationships. Wageningen, the Netherlands 1–4 March 1982. Wag Centre Agr Publ Doc, p 464

Waldbauer GP (1968) The consumption and utilization of food by insects. Adv Insect Physiol 5:229–289

White TCR (1969) An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecol 50:905–909

White TCR (1974) A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia (Berlin) 16:279–304

White TCR (1976) Weather, food and plaques of locusts. Oecologia (Berlin) 22:119–134

White TCR (1978) The importance of a relative shortage of food in animal ecology. Oecologia (Berlin) 33:71–86

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