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Temperature and food quality influences feeding behavior, assimilation efficiency and growth rate of arctic woolly-bear caterpillars

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Summary. The energy budget for feeding activity and growth of larval *Gynaephora groenlandica* was investigated on the tundra and in the laboratory. Larvae fed only in June when the buds and young leaves of *Salix arctica*, its principal host plant, contained the highest concentrations of macro-nutrients and total nonstructural carbohydrates (TNC). The mid-summer hiatus in larval feeding was coincident with an abrupt decline in the TNC content of leaves and a buildup of plant secondary metabolites in the leaves of *S. arctica*. Following cessation of feeding the larvae remained concealed from the sun within crevices and vegetation mats. Growth rates of larvae incubated at 15 and 30° C were similar (4.7–5.0 mg/larva/day), but the assimilation efficiency at 15° C was four times greater (40%) than at 30° C. Growth rates were lowest at 5° C (0.22 mg/larva/day) as was the assimilation efficiency (6.6%) because of the extended residence time of food in the gut. The high rate of ingestion and excretion at 30° C was caused by elevated maintenance metabolism. Changes in metabolic state influenced oxygen consumption, which was highest for feeding larvae (0.29 ml/g/h) and significantly lower for each, digesting, moving, starved larvae, and lowest for inactive larvae (0.06 ml/g/h). An influence of temperature and leaf quality on digestion rate and maintenance metabolism is the most likely cause of the feeding behavior pattern in *G. groenlandica*. The larvae may undergo "voluntary hypothermia" in order to avoid an energy deficit resulting from high maintenance metabolism during mid-season when the energy content and food quality declines. The restriction of growth and development to a very short period prior to mid-summer may have contributed to the extended 14-year life cycle of this species.

Key words: Insect-plant interaction – Arctic – Assimilation efficiency – *Gynaephora groenlandica* – *Salix arctica*

Evolution of insect life cycles has been ascribed to variation in consumption and utilization of food (Slansky and Scriber 1985). In spite of the difficulties associated with the construction of nutritional energy budgets (Wightman 1981; McEvoy 1985), numerous insect species have been examined (see reviews, Scriber and Slansky 1981; Slansky and Scriber 1985). The focus of previous investigations, however, has been on insects inhabiting regions less physically-limiting than the arctic environment (Danks 1986). In this study we investigate the nutritional energy budget of a high arctic insect with an unusual life cycle.

The "arctic woolly-bear caterpillar", *Gynaephora groenlandica* (Wöcke) (Lepidoptera: Lymantriidae), is endemic to the Canadian High Arctic Archipelago (above 70° N Lat.) where it survives low annual and seasonal energy budgets (Downes 1964; Danks 1981; Svoboda and Freedman 1989). Despite the extremely short growing seasons (45–70 days), the larvae cease foraging after 3–4 weeks and prior to mid-summer (Kukal et al. 1988a). This abbreviated summer feeding behavior contributes to the long life cycle of the moth, estimated to be at least 14 years on Ellesmere Island (Kukal and Kevan 1987). Only the larvae overwinter; other developmental stages (pupation, emergence, mating, egg laying, eclosion and molting to the second instars) are confined to 3–4 weeks in a single summer season (Kukal and Kevan 1987).

Seasonal solar radiation limits the development of organisms in the High Arctic (Bliss 1977; Danks 1981; Svoboda and Freedman 1989). During their short period of summer activity in June, larvae of *G. groenlandica* raise their body temperature to ca. 30° C, 20° C above average ambient temperatures, by basking more than 60% of the time (Kukal et al. 1988a). Basking likely increases the developmental rate (May 1979) but also interferes with maintenance activities such as feeding.

The preferred, although not entirely exclusive food for arctic woolly-bear caterpillars is the arctic willow, *Salix arctica* Pall. (Salicaceae) (Kukal and Kevan 1987). *Salix arctica* is a deciduous species, which each season synthesizes new leaves. These new tissues are rich in nutrients and carbohydrates and favored by herbivores over other arctic plant species which are predominantly evergreens and wintergreens (Chapin et al. 1980; Chapin et al. 1986; Dawson 1987). Together with the purple saxifrage, *Saxifraga oppositifolia* L. (Saxifragaceae), the arctic willow has the earliest new growth available at the onset of the growing season (Bliss 1977; Svoboda and Freedman 1988). The young buds

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and shoots contain very high levels of macro-nutrients and TNC which decline and are translocated to other plant parts by mid-season (Dawson 1987). Depletion of nutrients and carbohydrates from *S. arctica* is accompanied by a mid-summer buildup of secondary metabolites (Dawson 1987). Could this change in food quality influence the feeding behavior and metabolic state of *G. groenlandica* larvae?

The general aim of this study was to investigate the energy budget for feeding activity of *G. groenlandica* larvae and relate it to growth rate and assimilation efficiency as a function of temperature and food quality. Specifically, we investigated: 1) The seasonal phenology and tissue compartmentalization of macro-nutrients, TNC, caloric content and secondary metabolites of *Salix arctica*, 2) Seasonal changes in feeding behavior and metabolic state of *G. groenlandica* larvae, 3) The effect of temperature, feeding activity and digestion on the larval metabolic rate, 4) Influence of temperature on the growth rate and assimilation efficiency of the larvae. Ultimately, we wish to provide a scheme for food utilization in a High Arctic insect limited by low temperatures and variations in host-plant food quality.

Materials and methods

Study site

Investigations were conducted during 1982–1987 at two sites classified as High Arctic "oases" (Bliss 1977; Svoboda and Freedman 1989): Truelove lowland, Devon Island (75° 33′ N; 84° 40′ W) and Alexandra Fiord lowland, Ellesmere Island (78° 53′ N; 75° 55′ W). These lowlands are considered "arctic oases" and are typified by unusual physiographic properties which gave rise to a relatively rich flora and fauna (Courtin and Labine 1977). Insect feeding behavior was examined mostly at Alexandra Fiord. Climate and microclimate were monitored at both sites using Campbell CR-5 and CR-21 data acquisition stations (Campbell Scientific, Logan, Utah) following the methods of Dawson (1987) and Henry (1987).

Larval feeding behavior on the trundra

The phenology of larval feeding behavior and general above-ground activity has been observed throughout the arctic summer (May–September) for 6 years at the Alexandra Fiord lowland and for 2 years at Truelove lowland. Host plant preference was determined by observation of larvae feeding on the trundra over a period of 3 days at the onset and 3 days at the end of their feeding season in June 1987. The species and plant part eaten were recorded for 200 larvae observed at each of the two time periods. Preference for certain parts of *Salix* was estimated as the feeding periods allocated to leaves, buds, or catkins for 30 larvae, other than the 200 scored for host preference. Feeding larvae ($N=10$) were brought back into the laboratory, their guts were dissected into saline, placed on microscope slides and examined for microbial symbionts at $\times 600$ and $\times 1000$ magnifications.

Seasonal trends in food quality and availability

Six entire plants of *Salix arctica* were carefully excavated each week over the growing season (early June–late August). Each plant was washed of all soil, blotted dry and sorted into leaves, reproductive structures, above- and below-ground shoots, fine roots and taproots. These tissues were weighed fresh and subsequently dried at 80° C in a force-draft oven to a constant weight. Dried samples were diced, thoroughly mixed, ground to 1 mm (20 mesh screen) in a Wiley Mill and analyzed for macronutrients (N,P,K) and caloric content. Tissues were digested using a modified micro-Kjeldahl procedure with a sulphuric acid-hydrogen peroxide digestion (Allen et al. 1974). Samples were analyzed by ICP spectrophotometry for K and for N and P with a Technicon Auto Analyser II. The mean nutrient concentrations are expressed as the percent of total dry weight in each compartment. To provide check on the analytical accuracy, a standard orchard leaf (U.S. Department of Commerce) was analyzed concurrently with the harvest samples. Caloric content was obtained with the use of an adiabatic bomb calorimeter (Parr Inst., model 1241, Moline, Illinois, USA). Values are expressed on an ash-free basis. Total non-structural carbohydrates (TNC) analyses followed a modified version of the methods outlined by Allen et al. (1974). Six individuals of *S. arctica* harvested four times during the 1984 growing season were used for the carbohydrate analyses. Plants were harvested and prepared as above, fixed immediately in boiling 80% EtOH (plus ca. 1 g of sodium bicarbonate) and sealed in glass jar for transport back to the laboratory. The partially extracted tissues were filtered and dried at 80° C to a constant weight. Samples were then ground in a Wiley Mill and extracted a second time (6 h in 80% EtOH) using a Soxhlet apparatus. The initial filtrate and the first Soxhlet extract were combined for the determination of reducing sugars. The remaining residue was dried for 24 h at 80° C and weighed as the alcohol insoluble dry weight. The dried residue was digested for starch at 37° C for 24 h in the dark by combining a subsample of the dried plant tissue with 0.2 g of *Aspergillus*-type alpha-amylase in distilled water. The digested residue was filtered, and extracted again for additional 6 h in 80% EtOH in a Soxhlet apparatus. The filtrate and the extract were combined for the determination of total starch concentration. The analyses of reducing sugar and digested starch extracts were accomplished using the procedures outlined by Allen et al. (1974) using an anthrone reagent and a colorimetric analysis. Tissue samples from the 1983 and 1984 samples were also prepared and analyzed for tannins and phenols as in Dawson (1987).

Nitrogen content of larvae at the onset and end of their feeding season

According to the previously determined phenology of larval feeding, fifteen larvae (instar IV, V) were collected immediately at the onset of snowmelt (12 June, 1987) and also at the time when most larvae ceased feeding (26 June). Another group of 16 larvae was kept at near 0° C in the dark for the duration of their feeding period. All 3 groups of larvae were killed by ethyl acetate, dried and later analyzed in the laboratory for nitrogen content in the same manner as described above.

Temperature influence on growth rate and assimilation efficiency

Larvae collected at Alexandra Fiord throughout their feeding period in June 1987 were maintained in the laboratory

at 5° C, 15° C, and 30° C under constant light for one month (July). *Salix arctica* was collected at Alexandra Fiord between 15–29 June and kept near 0° C in the dark. Thirty larvae (instar IV, V) at each of the three incubation temperatures were kept in separate containers in groups of ten and fed ample arctic willow. Each week the larvae and their dried frass were weighed, old food removed, dried and weighed and ~50 g of fresh food replenished. The low temperature larvae required only bi-weekly feeding. Ten larvae incubated at 5° C were fed ample willow and their gut content was removed and weighed every week in order to estimate the residence time of food in the gut and its mean weight. Because leaves were removed (preventing translocation) and kept in the dark (preventing photosynthesis and other light reactions) at low temperature (suppressing respiration) (cf. Dawson 1987), we estimate that carbohydrate content did not change more than 10–13% over the experimental period. Dry weight of larvae was estimated from a standard proportion of fresh to dry weight. Dissections indicate food retention within the larval guts at 5° C incubation temperature. The mean weight of food retained in guts was 2.11 ± 0.08 mg/larva/day ($N=5$). The assimilation efficiency of larvae incubated at 5° C was computed using this value by subtracting it from the food ingested. Amount ingested was determined from a standard relationship between fresh and dry weight of willow which precluded an error introduced by desiccation of food over the feeding period. Rates of growth and efficiencies of food consumption at different temperatures were computed as in Slansky and Scriber (1985). The nitrogen levels in frass excreted by larvae incubated in the laboratory at 15 vs. 30° C were compared with those of frass collected from larvae in nature. Two hundred larvae were held in a wooden box exposed to daily temperature and light changes. They were fed ample willow (i.e. more than was ever estimated to be ingested) throughout June and then their frass was collected, desiccated and analyzed for nitrogen content as described above.

The effect of feeding and digestion on larval metabolism

Metabolic rates of late instars were measured with an oxygen analyser (S-3A Applied Electrochemistry) accurate to 0.001% oxygen concentration. The analyser was interfaced to a computer, using a customized program (H. Esch, U. of Notre Dame, unpubl.) to enable monitoring of oxygen uptake and body temperature at 15 s intervals over 1–48 h. Individual larvae ($N=10$) were placed in a 10 ml flask with or without *Salix* leaves and their oxygen uptake was detected by a Model N-37M sensor in a flow-through system where the intake and outlet air was filtered through water and carbon dioxide absorbant. The flow rate of air was maintained at 12.5 ml O_2/h by a pump, and the oxygen inside the flask was continuously compared to the ambient O_2 concentration.

Comparisons were made between oxygen uptake at 25° C by feeding larvae, digesting larvae and inactive larvae in hibernacula. The length of digestion period was estimated from a continuous computer record of post-feeding larvae, as was the resting (i.e. standard) metabolic rate of larvae with an empty gut. A temperature profile of oxygen consumption at 5, 10, 15, 20, 25, 30° C was obtained for larvae acclimated to 5 and 15° C for a period of 2 months.

Results

Feeding behavior on the tundra

Ninety-seven percent of actively feeding larvae ($N=200$) fed primarily on new leaf-buds of *Salix arctica* at the onset of their feeding season. However, at the end of June, just prior to cessation of feeding, only 9% of feeding larvae fed on new leaf growth while the remaining 81% had stopped feeding altogether. At the onset of summer, <3% of feeding larvae fed on the flowers of *Saxifraga oppositifolia* L. (Saxifragaceae) and on senescent leaves of *Dryas integrifolia* M. Vahl. (Roseaceae). As the frequency of feeding decreased there was no switch to a different food source or to a different plant part. The length of larval feeding period was only ca. 30% of the degree days available for growth as indicated the microclimatic measurements (cf. Dawson 1987; Henry 1987). Feeding was usually followed by basking (while digesting) for approximately 5 h; dissections of larval guts showed food present in basking larvae. Previously starved or shaded larvae began feeding when exposed to the midday sun and fed for 20% of the time thereafter. Most of their time (60%), however, was allocated to basking (see Kukal et al. 1988a). Bacterial symbionts were not detected in the gut ectoperitrophic spaces of feeding larvae ($N=10$).

Seasonal trends in resource availability and insect feeding

Nutrient, TNC and caloric content of *S. arctica* leaves declined steadily over the course of the summer (Figures 1, 2). A particularly sharp decrease at the end of June was evident in the TNC content of leaves (Fig. 1). Secondary plant metabolites (tannins and phenols), on the other hand, increase in concentration over the summer season (Fig. 3), however, this increase occurs primarily after larvae cease feeding. Nutrient concentrations of leaves compared to nutrients in larval frass suggest removal of nitrogen and potassium by the larvae (Table 1). Carbohydrate concentrations and caloric content of different parts of *S. arctica* indicate the high starch concentration in leaf buds and high caloric content of catkins (Table 2). Despite their high caloric value, catkins were rarely consumed by larvae.

Influence of temperature and seasonal phenology on the nitrogen content of larvae and their frass

Mean nitrogen content of larvae was not significantly different (ANOVA: $P=0.247$, d.f. 2,6) between larvae from the onset of the feeding season, larvae from the end of the season and larvae that "missed" the feeding season altogether (Table 3). However, the mean concentration of nitrogen excreted by larvae incubated at 15° was significantly lower ($P<0.05$, d.f. 8) than the levels excreted by larvae at 30°. Neither of the laboratory incubations differed significantly in the N content of larval frass (for 15° $P=0.52$; for 30° $P=0.10$) from the levels of nitrogen excreted by the larvae on the tundra (Table 3).

Temperature influence on growth rate and assimilation efficiency

Growth rates were similar at 15 and 30° C, approximately 20-fold the rate at 5° C (Table 4). At the lowest temperature

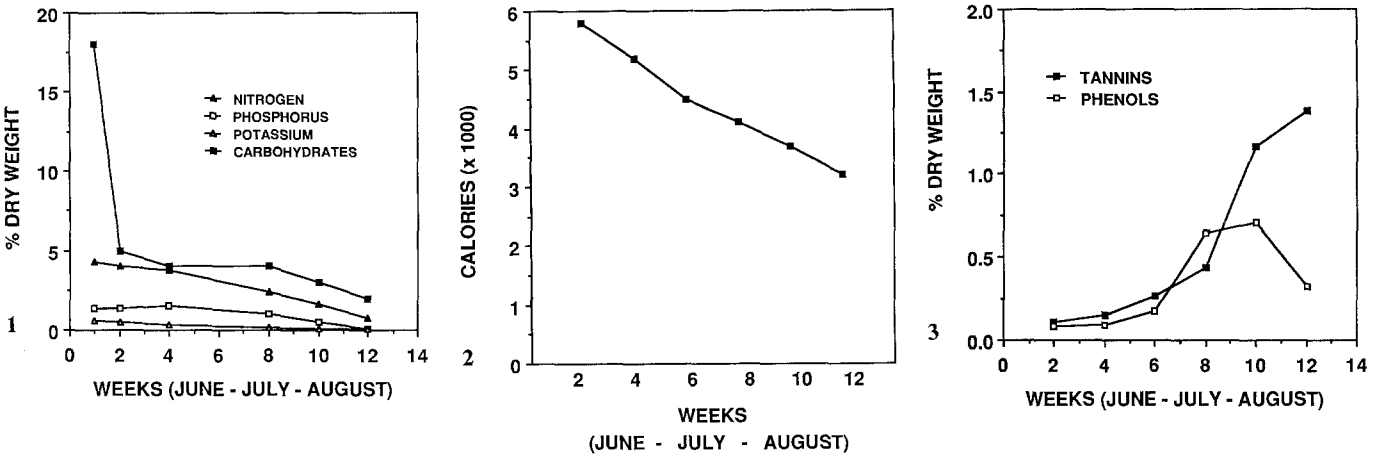

Fig. 1. Seasonal variation in nutrient and carbohydrate (TNC) content of *Salix arctica* leaves in the High Arctic. ($N=17$; mean values $\pm$ S.E. ≤ 1 for TNC; S.E. ≤ 0.1 for macro-nutrients) The larvae of *G. groenlandica* feed only during June of each summer season; they stop feeding at the beginning of July

Fig. 2. Seasonal variation in the caloric content of *Salix arctica* leaves in the High Arctic. ($N=5$; mean values in cal/g/dry wt. $\pm$ S.E. $\leq 3\times10^3$) The feeding activity of *G. groenlandica* is suspended at the beginning of July each summer. The larvae are active on the tundra surface only during June

Fig. 3. Seasonal variation in the plant secondary metabolites (tannins and phenols) of *Salix arctica* leaves in the High Arctic. ($N=5$; mean values $\pm$ S.E. ≤ 0.1)

the amount of *Salix* ingested and egested was very low compared to the amounts of food processed at higher temperatures (Table 4). The amount ingested at 30° C was about four times the amount ingested at 15° C and the amount excreted was approximately three times greater at the higher temperature. The ingestion rate at 5° C was 4.5-fold lower than in larvae held at 15° C, and the rate of egestion temperature was decreased 15-fold at the lower temperature. The corresponding assimilation efficiencies were 9.5% at 30° C, 40% at 15° C and 6.6% at 5° C. Dissection of guts indicate that food was retained in the guts of larvae incubated at 5° C. The mean weight of food retained was 2.11 ± 0.08 mg/larva/day ($N=5$). This value was used to adjust the calculation of assimilation efficiency of larvae incubated at 5° C.

Table 1. Pre-digestion levels of nutrients in the leaves of *Salix arctica* during June compared to post-digestion nutrient levels in the frass of *G. groenlandica* larvae. (Values = mean % dry wt. $\pm$ 1 S.E.) (leaves $N=17$; frass $N=9$)

Nutrient	Leaves	Frass
Nitrogen	4.35 ± 0.13	1.48 ± 0.22
Phosphorus	0.50 ± 0.001	1.66 ± 0.06
Potassium	1.40 ± 0.04	1.01 ± 0.04

Table 2. Soluble carbohydrate allocation and the caloric content of different parts of *Salix arctica* compared to their concentrations in frass after digestion by *G. groenlandica* larvae during their feeding season in June. (*Salix* $N=9$; frass $N=5$)

Carbohydrates	Buds	Leaves	Catkins	Frass
	(Values = mean % dry wt. $\pm$ 1 S.E.)			
Sugars	4.37 ± 0.89	7.75 ± 2.1	8.55 ± 0.49	2.47 ± 1.3
Starches	29.4 ± 2.8	17.1 ± 6.6	8.95 ± 1.4	1.40 ± 0.49

Date:	Calories (Values = mean cal./g dry wt. $\pm$ 1 S.E.)		
	Leaves	Catkins	Frass
15 June	5437 ± 251	5707 ± 177	
20 June	5098 ± 208	5919 ± 109	2598 ± 97
25 June	4749 ± 371	6081 ± 338	

The effect of feeding and digestion on larval metabolism

Starved larvae and inactive larvae in hibernacula maintained standard metabolic rates (Table 5). This rate increased during movement and further increase was evident when feeding ensued. Following feeding, approximately 5 h of elevated metabolic rate indicated a digestion period. The oxygen consumption rate by digesting larvae was greater than by actively moving larvae. Metabolic rate of larvae increased as a function of increasing temperature with no significant difference ($P<0.01$) between their Q_{10}/O_2 (Fig. 4).

Table 3. Nitrogen content of larvae in nature (at the onset of feeding season; end of season; after missing their feeding season), of their frass in nature, and nitrogen in frass from larvae incubated at 15 vs. 30° C

	Nitrogen (mean % dry wt. $\pm$ S.E.)
Larvae ($N=3$/group)	
1) Onset of season	25 ±1
2) End of season	24 ±1
3) Missed season	27 ±1
Frass ($N=5$/group)	
1) Tundra	3.2 ± 0.3
2) Laboratory 30°	3.4 ± 0.1[a]
3) Laboratory 15°	2.7 ± 0.05[b]

[a, b] Values significantly different by ANOVA ($P<0.05$, d.f. 8)

Table 4. Temperature influence on growth rate and assimilation efficiency of *G. groenlandica* larvae feeding on *Salix arctica*. Each incubation temperature contained 3 groups of 10 larvae. Assimilation efficiency = % mass gain per mass ingested; Metabolic rate = (food ingested − excreted) − mass gain (Values = mean ± 1 S.E.) (mean dry wt. of larva = 300 ± 5 mg)

Incubation temp. °C	Larval growth rate	Food ingested	Frass excreted	Metabolic rate	Assimilation efficiency %
		mg dry wt./larva/day [mg dry wt./mg larva/day]			
5	0.22 ±0.41[a] [0.001±0.0005]	3.67 ±0.67 [0.012±0.002]	0.33 ±0.13 [0.001±0.0004]	1.0 [0.003]	6.6
15	4.67 ±2.00 [0.016±0.007]	16.67 ±4.00 [0.056±0.018]	5.00 ±2.67 [0.017±0.009]	7.0 [0.023]	40
30	5.00 ±2.00 [0.017±0.007]	68.33 ±5.00 [0.227±0.006]	16.00 ±2.33 [0.053±0.008]	47 [0.157]	9.6

[a] Corrected for the extended residence time of food in the gut (mean dry wt. of food in the gut = 2.11 ± 0.08 mg/larva/day)

Table 5. Oxygen consumption at 25° C by larvae in different metabolic states; feeding, digesting, starved, in hibernacula and following cold acclimation. ($N = 10$; Values = mean* ± S.E.)

Metabolic state	Oxygen consumption (ml/g/h)
Standard metabolism	0.06 ± 0.02[a]
Starved larvae	0.06 ± 0.02[a]
Moving larvae	0.11 ± 0.03[b]
Feeding larvae	0.29 ± 0.03[c]
Digesting larvae**	0.17 ± 0.02[d]
Larvae in hibernacula	0.07 ± 0.02[a]
Low temperature acclimation***	0.07 ± 0.02[a]

* Means followed by a different letter are significantly different by *t*-test ($P < 0.05$)
** The digestion period estimated from the length of time of elevated metabolism
*** Larvae held at 5° C and dark for 2 months

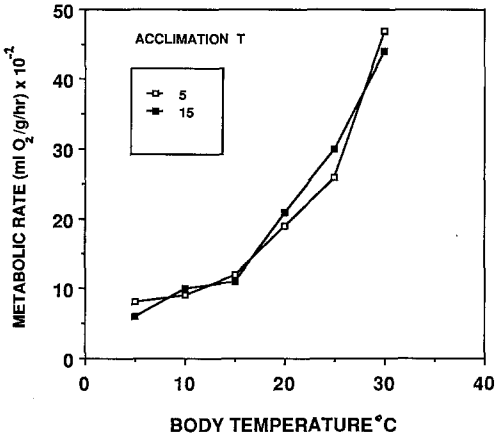

Fig. 4. Influence of body temperature on the oxygen consumption by *G. groenlandica* larvae following acclimation at 5° and 15° C for 2 months ($N = 10$; mean values ± S.E. ≤ 0.02)

Table 6. Food utilization by *Gynaephora groenlandica* (A) compared to 29 species of Lepidoptera (B) (data from Slansky and Scriber 1985)

	RGR (mg dry wt./day/mg)	RCR (mg dry wt./day/mg)	AD %	ECD %	ECI %
A: *Gynaephora* at 5, 15, 30° C					
5[a]	0.001	0.012	33.3	9.1	3.0
15	0.016	0.056	69.6	41.0	28.5
30	0.017	0.227	76.7	9.8	7.5
B: Other Lepidoptera (Values = $\bar{x}$/range; $N = 444$–629)					
0.38/0.03–1.50		2.03/0.27–6.90	53/16–97	40/2–87	20/1–78

RGR = relative growth rate
RCR = relative consumption rate
AD (approx. digestibility) = (food ingested-frass)/food ingested
ECD (efficiency of conversion) = biomass gained/(food ingested-frass)
ECI (efficiency of conversion of ingested food) = AD × ECD

[a] Values adjusted for food remaining undigested in the gut

Discussion

Gynaephora groenlandica exists "on the edge" in the High Arctic owing to severe developmental constraints including, 1) low temperature threshold for metabolism and feeding activity (Kukal et al. 1988a; Kukal et al. 1989), 2) preparation for overwintering by carbohydrate storage (Kukal et al. 1988b), and 3) parasitoid pressure causing above 60% mortality (Kukal and Kevan 1987). These three factors interact to prolong the developmental time of *G. groenlandica*, extended to last ~14 years at Alexandra Fiord lowland, Ellesmere Island (Kukal and Kevan 1987). The extended developmental time of *G. groenlandica* reduces its reproductive potential (cf. Price et al. 1980). Reproductive potential and overall fitness of *G. groenlandica* may be enhanced by changes in its feeding strategy involving, 1) maximized energy intake from food by spatial and temporal selectivity, and (2) minimized energy expenditure in activities (i.e. feeding, mobility, molting) while food quality is relatively poor. This study demonstrates that retardation of larval development is at least in part due to the declining quality and energy content in the host plant, *Salix arctica*.

The growth rate of *Gynaephora* is extremely low compared to other species of Lepidoptera (Table 6) and the late instars (III–VI) molt only once every 3–4 years (Kukal and Kevan 1987). Low growth rate may stem from the diel pattern of larval feeding activity. Unlike other Lepidoptera which spend most of their time feeding, *Gynaephora* larvae bask more than 60% of the time in order to elevate their body temperature by ~25° C (Kevan et al. 1982;

Kukal et al. 1988a). Basking larvae can therefore regulate their metabolic and digestion rates, however, at maximal body temperatures (> 30° C) the maximal energy gain from digestion appears to be counterbalanced by simultaneous increase in maintenance metabolism. When larvae begin to feed or move, their body temperature drops (Kukal et al. 1988a) and their maintenance metabolism simultaneously decreases. As a consequence, the time spent feeding compared to basking is an essential determinant of larval energy balance. During sunny conditions the larvae tend to feed during the highest temperatures at mid-day and bask at "night" when they cannot attain the higher temperatures required for activity (> 5–10° C) because of reduced incoming radiation. Since digestion requires approximately 5 hours, it is probably necessary for the larvae to maintain elevated body temperature by basking in order to enhance the activity of digestive enzymes. The lack of bacterial symbionts underscores the importance of raised body temperature to aid digestion in *G. groenlandica*. The lack of symbionts may influence the length of ingestive vs. digestive phase. Compared to the cinnabar moth with a feeding period of 40 min (McEvoy 1984), the relatively short feeding periods in *Gynaephora* larvae are interspaced with long periods of digestion while basking.

Besides temperature, the larvae are limited by the quality of their major food source, the buds and young leaves of *Salix arctica*. Larval feeding behavior and assimilation efficiency are therefore expected to vary with seasonal changes in nutrient, carbohydrate and caloric content of *Salix* tissues (MacLean and Jensen 1985; Chapin et al. 1986; Ayres and MacLean 1987a). This variation in food quality is reflected in the restriction of larval feeding behavior to the month of June when both the nutrient and carbohydrate content of host plant is maximal. At this time the buds and new leaves contain the greatest concentrations of nutrients and carbohydrates which, subsequently in July are translocated to other tissues including the reproductive parts (Dawson 1987). The catkins, however, are rarely consumed by the larvae. The observed larval response (i.e. cessation of feeding) to changing quality of their host plant is neither compensatory or inductory (cf. Slansky and Scriber 1985); larvae do not increase their rate of feeding in response to decreased food quality and do not show a genetically programmed summer aestivation. Larval metabolic rate is not suppressed and, if provided with fresh willow, the larvae continue feeding beyond June. This feeding pattern leads to physiological modification of assimilation efficiency and growth rate. These physiological changes are a direct consequence of larval "voluntary hypothermia" (Kukal et al. 1988a) induced by their hiding in vegetation or cracks near the permafrost, presumably in order to conserve energy. This energy stored as glycogen is the source for cryoprotectant synthesis crucial for overwintering in frozen state (Kukal et al. 1988b).

The molting process in at least two other arctic species can be inhibited by near zero temperatures and comprises 43–50% developmental time of an instar (Ayres and MacLean 1987b). Molting requires an expenditure of as much as 27% of the nitrogen or caloric content of a gypsy moth larva (Montgomery 1982). The decline in July levels of plant nutrients, nitrogen in particular, may affect the larval molting. The energy expenditure in molting may be a key factor in determining the developmental rate of *Gynaephora*. Moreover, the decreased amount of energy available from the host plant in the form of carbohydrates could result in a decreased larval growth during July (Kukal et al. 1988a).

The link between decreasing food quality and cessation of larval feeding may be further enhanced by a slight increase in secondary metabolites in the older leaves of *Salix*. Although not directly correlated, the buildup of tannins and phenols may also act as a feeding deterrent to the larvae of *G. groenlandica* (Feeney 1970; Rosenthal and Janzen 1979; Haukioja et al. 1985). Recently, Price et al. (1987a, b) have demonstrated that the sawfly, *Euura mucronata* shows shifts in its feeding behavior correlated with shoot length and age of its principal host plant, *Salix cinerea*. The authors concluded that the survivorship of larvae was correlated with shoot age, length and vigor. Furthermore, the plant secondary metabolites were lower and resources higher in shoots preferred by these insects.

Our laboratory experiments indicate that larvae assimilate food most efficiently at 15° C as opposed to 5° or 30° C. Assimilation efficiency decreases with increasing temperature (30° C) despite the similar larval growth rate. This decrease is caused by increased maintenance metabolism through increased activity, ingestion and egestion rates. In contrast to other Lepidoptera inhabiting warmer regions, the assimilation efficiency of *G. groenlandica* decreases rather than increases with a temperature rise to 30° C (Slansky and Scriber 1985). Despite the relatively low rates of food consumption and growth, the efficiency of conversion of ingested food in *G. groenlandica* larvae exceeds the mean value for other species of Lepidoptera (Table 6).

In his review of insect-plant relationships in the arctic, Danks (1986) addresses the relative importance of physical vs. biological constraints on the interdependence between herbivores and their plant hosts. He suggests that the decreasing ratio of herbivores to host plant species indicates an increasing influence of physical constraints over herbivores at high latitudes. The prevailing physical constraints may result in decreased specialization of arctic plant feeders i.e., more frequent polyphagy or oligophagy and lack of synchrony with plant phenology and resource allocation (Danks 1986). The insect-plant interaction between *G. groenlandica* larvae and *Salix arctica* reveals the importance of both, physical and biotic factors in influencing the insect's life cycle and development. Temperature plays a crucial role in optimizing growth rate offset by maintenance metabolism. Host plant phenology and resource allocation influences the feeding pattern of *G. groenlandica* larvae. Concurrent increase in temperature and decrease in food quality probably confines the larval feeding activity to June, thereby extending the moth's life cycle to 14 years at the Alexandra Fiord lowland.

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References

Allen SE, Grimshaw HM, Parkinson JA, Quanrmby C (1974) Chemical analysis of ecological materials. John Wiley and sons, New York

Ayres MP, MacLean SF (1987a) Development of birch leaves and the growth energetics of *Epirrita autumnata* (Geometridae). Ecology 68:558–568

Ayres MP, MacLean SF (1987b) Molt as a component of insect development: *Galerucella sagittariae* (Chrysomelidae) and *Epirrita autumnata* (Geometridae). Oikos 48:273–279

Bliss LC (ed) (1977) Truelove lowland, Devon Island, Canada. A High Arctic ecosystem. The University of Alberta Press, Edmonton, p 714

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Chapin FS, Johnson DA, McKendrick JD (1980) Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. J Ecol 68:189–209

Chapin FS III, McKendrick JD, Johnson DA (1986) Seasonal changes in carbon fractions in Alaskan tundra plants of differing growth form: Implications for herbivory. J Ecol 74:707–731

Courtin GM, Labine CL (1977) Microclimatological studies of the Truelove lowland. In: Bliss LC (ed) Truelove lowland, Devon Island, Canada. A High Arctic ecosystem. The University of Alberta Press, Edmonton, pp 73–106

Danks HV (1981) Arctic arthropods. A review of systematics and ecology with particular reference to the North American Fauna. Entomol Soc of Canada, Ottawa, p 608

Danks HV (1986) Insect plant interactions in arctic regions. Revue d'Entomologie du Quebec 31:52–75

Dawson TE (1987) Comparative ecophysiological adaptations in arctic and alpine populations of a dioecious shrub, *Salix arctica* Pall. PhD thesis, University of Washington, Seattle, USA, p 208

Downes JA (1964) Arctic insects and their environment. Can Ent 96:279–307

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

Haukioja E, Hiemela P, Siren S (1985) Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation in the mountain birch *Betula pubescens* spp *tortuosa*. Oecologia 65:214–222

Henry GHR (1987) Ecology of sedge meadow communities of a polar desert oasis: Alexandra Fiord, Ellesmere Island, Canada. PhD thesis, U. of Toronto, Toronto, Canada, p 272

Kevan PG, Jensen TS, Shorthouse JD (1982) Body temperatures and behavioral thermoregulation of high arctic woolly-bear caterpillars and pupae (*Gynaephora rossii*, Lymantriidae: Lepidoptera) and the importance of sunshine. Arctic and Alpine Research 14:125–136

Kukal O, Kevan PG (1987) The influence of parasitism on the life history of a high arctic insect, *Gynaephora groenlandica* (Wöcke) (Lepidoptera: Lymantriidae). Can J Zool 65:156–163

Kukal O, Heinrich B, Duman JG (1988a) Behavioural thermoregulation in the freeze-tolerant arctic caterpillar, *Gynaephora groenlandica*. J Exp Biol 138:181–193

Kukal O, Serianni AS, Duman JG (1988b) Glycerol metabolism in a freeze-tolerant arctic insect: an *in vivo* ^{13}C NMR study. J Comp Physiol B 158:175–183

Kukal O, Duman JD, Serianni AS (1989) Cold-induced mitochondrial degradation and cryoprotectant synthesis in freeze-tolerant arctic caterpillars. J Comp Physiol B 158 (in press)

May LM (1979) Insect thermoregulation. Ann Rev Entomol 24:313–349

MacLean SF, Jensen TS (1986) Food plant selection by insect herbivores in Alaskan arctic tundra: the role of plant life form. Oikos 44:211–221

McEvoy PB (1984) Increase in respiratory rate during feeding in larvae of the cinnabar moth *Tyria jacobaeae*. Physiol Entomol 9:191–195

McEvoy PB (1985) Balancing insect energy budgets. Oecologia 66:154–156

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

Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weiss AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Ann Rev Ecol Syst 11:41–65

Price PW, Roininen H, Tahvanainen J (1987a) Plant age and attack by the bud galler, *Euura mucronata*. Oecologia 73:334–337

Price PW, Roininen H, Tahvanainen J (1987b) Why does the bud-galling sawfly, *Euura mucronata* attack long shoots? Oecologia 74:1–6

Rosenthal GA, Janzen DH (eds) (1979) Herbivores: Their interaction with secondary plant metabolites. Acad Press, New York

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

Slansky F Jr, Scriber JM (1985) Food consumption and utilization. In: Kerkut GA, Gilbert LI (eds) Comprehensive Insect Physiology, Volume 4 Chapter 3. Pergamon Press, Oxford, pp 87–163

Southwood TRE (1978) Ecological Methods. Wiley, New York

Svoboda J, Freedman B (1989) Ecology of a high arctic oasis, Alexandra Fiord lowland, Ellesmere Island, N.W.T., Canada. University of Toronto Press, Toronto

Wightman JA (1981) Why insect energy budgets do not balance. Oecologia 50:166–169

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