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Food induced variation of thermal constants of development and growth of *Autographa gamma* (Lepidoptera: Noctuidae) larvae

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Abstract. The development stages of a species may have an identical lower development threshold (LDT) and proportionally different durations. This phenomenon called "rate isomorphy" (RI) has been demonstrated for a number of insect species. In contrast, the growing day degrees accumulated over the period of larval development (sum of effective temperatures SET) should be plastic and vary with environment conditions. The prediction from RI is that, with changing conditions, the uniform LDT should be accompanied by differences in development time which remain proportional at different temperatures. This was tested by investigating the effect of diet on thermal requirements for development of larvae of the polyphagous species *Autographa gamma* (L.) (Lepidoptera: Noctuidae). The larvae were kept at 15.0, 20.3 and 26.7°C and fed on leaves of 13 dicotyledoneous herb and tree species. The proportion of total development time spent on a particular diet was plotted against temperature. The existence of RI was inferred from a zero change in development time proportion with changing temperature. This rigorous test supported RI for 3 of 9 diets where development was completed in all temperatures. The LDT observed on 11 diets where the larvae completed development in at least 2 temperatures varied between 9.3 and 11.0°C while SET varied between 167 and 353 day degrees (dd). Assuming RI, LDT and SET for those 9 diets were recalculated. The recalculated LDT was 10.0°C and SET varied between 177–257 dd. The SET increased with decreasing water content and decreasing nitrogen content of food. Worsening food quality decreased food consumption, metabolic and food conversion efficiency, and the relative growth rate of the larvae. Increasing metabolic costs of development were thus positively correlated with SET. The standardized rate of growth (mg.dd^{-1}) was typical for particular diets. Pupal mass decreased with increasing temperature and, within each temperature, with development length.

INTRODUCTION

In insects the development rate (a reciprocal of development duration) increases with temperature. The increase is linear over a range of ecologically relevant temperatures, although at temperatures approaching the lower point where development ceases and at temperatures approaching the upper limits of thermal tolerance, the relationship may become non-linear. The linear relationship enables the calculation of thermal constants, such as the lower development threshold (LDT), which is a temperature at which the development rate is zero, and the sum of effective temperatures (SET), which is equal to the amount of growing day degrees (dd) needed to complete a development stage.

A huge quantity of data (reviewed by Honěk & Kocourek 1990, Honěk 1996, Kiritani 1997) became available over the past eighty years, during which time the temperature effects on insect development have been intensively studied. The data revealed not only a large variation of thermal constants between species, but also among populations within species. However, these differences are not only caused by biological variation, but also due to bias in the experimental data. This bias appears even in carefully performed experiments and becomes enormously important when comparing the data of different authors. A recently developed method (Jarošík et al., in press) enabled a test to be made of the relevance of differences in LDT. The method consists of testing the hypothesis of "rate isomorphy". "Rate isomorphy" means that, with changing temperature, the development stages of a population of a species take constant proportions of total development time. Then the LDT is identical for all development stages. A comparison of published data for 342 species from 11 insect orders revealed "rate isomorphy" in 57% of populations. In the rest of the data violation of the "rate isomorphy" principle was very small. Thus LDT is probably uniform in developmental stages within populations and species, and probably also in taxonomically related groups of species (Dixon et al., 1997). In contrast to LDT, SET is plastic and reflects the variation in environment conditions other than temperature, including food quality of the growing stage (larva), humidity, photoperiod etc. (Squire & Trudgill, in litt.).

With testing for "rate isomorphy" we may prove the identity of LDT of developmental stages but not to establish its correct value. A method of calculating the true LDT value may consist in looking at variation of development times of larvae of a highly polyphagous species fed with several diets. A common development threshold may be calculated using a modified application of the "rate isomorphy" principle (described in the Material and Methods). Thermal constants for development were therefore established in larvae of *Autographa gamma* (L.), an extremely polyphagous noctuid species occurring throughout the Europe which periodically becomes a pest of several agriculture crops. The species has 1–3 generations per year, according to weather conditions. Its development was first described by Ostreykowna (1924) who first supposed overwintering in central Europe. Cayrol (1962, 1965) and Novák (1971, 1972, 1988) revealed that the central European populations consist of two constituents, a part overwintering in the 4th larval instar and a part immigrating each spring from the southern Europe. The rate of larval development is influenced by temperature and humidity (Kozhantshikov, 1939; Hill & Gatehouse, 1992), population density (Cayrol, 1957; Long, 1953, 1955, 1959) and food (Novák, 1960, 1974, Cayrol, 1962;). The widely polyphagous larvae may eat the leaves of more than 200 host plant species (Schwitulla, 1963). The preferred food plants change with the course of the season as a consequence of host plant senescence (Novák, 1960, 1974; Steudel, 1963). In addition to the wide range of natural host plants, under laboratory conditions the larvae eat many plant species not accepted in the open. The food induced plasticity of development rate provides an opportunity for studying the variation of thermal constants. By looking at parallels in variation of growth rate and food assimilation under different temperatures, we may determine the causes of variation in SET.

In our experiments we tested the hypothesis of "rate isomorphy" in *A. gamma* larvae provided with leaves of several host plant species. Development time, pupal mass, and food assimilation were studied at 3 experimental temperatures. The data enabled (1) the determination of the thermal constants of larval development, (2) testing for "rate isomorphy", (3) the establishment of variation in body growth under different trophic conditions and (4) calculations of the relationship between food assimilation and larval development.

MATERIAL AND METHODS

Rearing of larvae. Adult *A. gamma* moths were collected at Prague Ruzyně (50°06′N, 14°15′E), in August, 1988. The moths flying in an alfalfa stand were captured by use of entomology net when feeding on flowers. Groups of three female and three male moths were placed into cardboard cylinders of 15 cm diameter and 15 cm height covered by a glass lid and provided with a diluted commercial mixed fruit syrup. This source of water and carbohydrates was offered in a petri dish (7 cm diam.) covered with a thin stiff nylon fabric (1.5 mm mesh size) which prevented the moths from drowning. Eggs were laid overnight, on the side-walls of the cylinder. Each day the moths were moved to a new cylinder, the pieces of cardboard with groups of eggs were cut out and until hatching placed into 3.5 × 12 cm glass tubes covered with dense nylon fabric. The freshly hatched larvae were removed at 24 h intervals and used for experiments. Adults and eggs were placed until hatching at room temperature (25 ± 1°C) and natural photoperiod.

Food. Experimental larvae were supplied with fresh leaves picked from the plants growing in the open. Thirteen plant species (Dostál, 1989) covering the range of preferred and non-preferred hosts were selected: *Amaranthus retroflexus* L. (Amaranthaceae), *Pastinaca sativa* L. (Apiaceae), *Achillea millefolium* L., *Cirsium arvense* (L.) Scop., *Matricaria maritima* L., *Taraxacum officinale* Weber in Wiggers (Asteraceae), *Sambucus nigra* L. (Caprifoliaceae), *Medicago sativa* L., *Robinia pseudoacacia* L. (Fabaceae), *Geranium pratense* L. (Geraniaceae), *Plantago major* L. (Plantaginaceae), *Salix babylonica* L. (Salicaceae), *Urtica dioica* L. (Urticaceae). Experiments were made in August (development duration) and September 1988 (food assimilation). Water and total nitrogen content of leaves were measured in early September. For each host plant species c. 200 g of fresh leaves were weighed and dried to a constant mass at 90°C. The dry mass and nitrogen content of each sample was then determined and the water content of the fresh leaves calculated. The determination of N content was made commercially, by a laboratory using a standard (Kjeldahl) method.

Development time and pupal mass. Cohorts of 0–24 h old larvae hatched at room conditions were transferred to constant temperatures of 15.0, 20.3 and 26.7°C and 18L : 6D photoperiod where the larvae were kept in 3.5 × 12 cm glass tubes covered with dense nylon fabric. First and second instar larvae were reared in groups of 20, and at the end of the 2nd instar the larvae were placed in individual tubes and then kept alone until pupation. The larvae were provided with leaves of the 13 host plant species mentioned above. Fresh leaves were supplied and faeces removed every 2 or 3 (weekends) days. Pupation was observed daily, at 07:00 and 19:00. The pupae were sexed and their live body mass was established within 24 h from pupation, with an accuracy of 0.1 mg. Ten randomly selected pupae were killed, dried to constant mass and their dry matter content was determined.

Food utilization. The cohorts of 0–24 h old larvae hatched at room conditions were isolated. The larvae were then kept in 500 ml glass cylindric vials covered with dense nylon fabric. Until the 4th instar the larvae were reared in groups of 15–20 per vial, kept at room conditions (25 ± 1°C, natural photoperiod) and in 2 or 3 d (weekends) intervals supplied with fresh *T. officinale* leaves. The larvae of early 4th instar were removed from food and starved for 24 h to empty the gut contents. The larvae were then divided into groups of 5 randomly selected individuals and the groups of larvae were weighed. Each group was then placed into a 500 ml vial and supplied with a weighed quantity of fresh leaves. The leaves were collected within 4 h of establishing the experiment and maintained in plastic sacks to prevent desiccation during handling. Dry matter content of these leaves was determined in 5 samples randomly selected from the leaf supply of each plant species. The vials with larvae and food were then put in constant temperatures of 15.0, 20.3 and 26.7°C and 18L : 6D photoperiod. The larvae were allowed to feed on the leaves for 2 d (at 26.7°C), 3 d (20.3°C) or 5 d (15.0°C). At the end of this feeding period the larvae were removed from food, starved for 24 h and weighed. Dry matter content of the larval body was determined by weighing the fresh and dry mass of 10 randomly selected larvae. For each group, the remaining non-consumed leaves (food) and faeces produced during feeding and post-feeding starvation period were collected, dried to constant weight and weighed.

Data elaboration. In each temperature T, larval development length D was measured as number of days elapsed from the egg hatching (isolation of the 1st instar larvae cohort) until larval-pupal ecdysis. Development rate R was calculated as D^{-1}. The regression $R=a+b\times T$ (where a and b are constants) was calculated. From here lower development threshold (°C) was calculated as $LDT= -b\times a^{-1}$ and sum of effective temperatures (day degrees dd) as $SET=b^{-1}$. Standard deviations of LDT were calculated according to Janáček et. al (in litt.). Multiple regression of SET on water and N content was calculated using Statistica® (StatSoft, 1994). High SET for poor diets that had been calculated from only 2 temperatures were included because they increased the significance of the regression. The mass of neonate larvae was below the limits of weighing precision and thus negligible compared to pupal mass PM. The growth rate GR

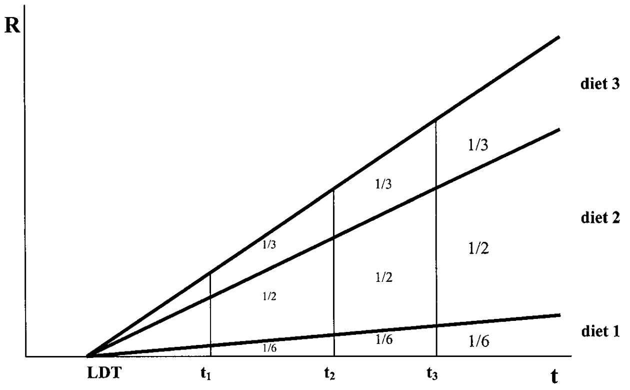

Fig. 1. An illustration of the effect of temperature (t) and three different diets on rate of development (R) of larvae within the linear range of the relationship between R and t. The larvae are isomorphic, and at each temperature (t_1, t_2, t_3), 1/6 of the total time spent on the three diets is spent on diet 1, 1/2 on diet 2, and 1/3 on diet 3. Larvae on all three diets have a common lower developmental threshold (LDT).

average body mass increment per day) was therefore calculated as $GR=PM\times D^{-1}$. Standardized growth rate SGR (average body mass increment per day degree) was calculated as $SGR=PM\times SET^{-1}$. SGR compensated for differences in growth rate caused by temperature and revealed the variation caused by food. In food utilization experiments, dry mass of ingested food (F), dry mass of excrement (E) and dry body mass increments (I) were calculated. These values were used to calculate the indices of food assimilation, efficiency of food conversion $ECI=I\times F^{-1}$ and metabolic efficiency $ECD=I\times(F-E)^{-1}$. Relative growth rate was calculated as $RGR=\exp((\ln Wf-\ln Wi)\times d^{-1})\times Wi^{-1}$ where Wi is initial mass and Wf final mass of an individual larva in the feeding experiment, and d is duration of the experiment (days) (Barbehenn et al., 1999). Means are accompanied by ± SE throughout the paper.

Testing for "rate isomorphy". Rate isomorphy implies no change in the proportion of time spent on a particular diet with change in temperature (Fig. 1). Therefore, within the range of the linear relationship between development rate *R* and temperature *t,* the consequence of rate isomorphy is common *LDT* for larvae on all diets, in spite of different development rates on each diet. The prediction of rate isomorphy, namely uniform LDT accompanied by proportional variation of SET, was tested by designating the $arcsin \sqrt{proportion}$ of the time spent on particular diet as the response variable, and temperature and diet as factors. The data were analysed by two-way ANOVA with temperature and diet as fixed effects. The existence of rate isomorphy was inferred from a zero change in the development time proportion at changing temperature, and the existence of variation in SET from differences in the development time proportions on individual diets. A zero change in the development time proportion at different temperature accompanied by differences in the proportions on individual diets indicated rate isomorphy. Different development time proportions on individual diets accompanied by variation in the proportions at different temperatures violated the assumptions of rate isomorphy.

RESULTS

Thermal constants of development. The duration of larval development decreased and development rate increased with increasing temperature (Tables 1 and 2). Mortality was generally high, and was not correlated with temperature or kind of food. This might be caused by diseases introduced to laboratory cultures by food contaminated in the open. Thermal constants were calculated for development on 11 host plant species of which 9 permitted complete larval development at 3 temperatures while with 2 host plant species development was completed at 2 temperatures. Experimental LDT for all species were similar (9.3–11.0°C, average 9.9 ± 0.2°C) (Table 2). As development rate was largely affected by food, larvae fed with leaves of some host plant species extended their development time by up to 3 times compared that found with optimum food. Consequently, the variation in SET was large and the slow growing larvae

TABLE 1. Number of pupated individuals (N), per cent mortality (M), larval development time (D) and fresh pupal mass (W) of larvae kept at 3 constant temperatures and fed with leaves of 13 host plant species.

Host plant	Temperature (°C)											
	15.0				20.3				26.7			
	N	M	D	W	N	M	D	W	N	M	D	W
A. millefolium	6	67	36.3±1.2	336±33	6	67	18.3±0.2	307±6	13	28	11.8±0.2	254±6
A. retroflexus	4	78	56.9±0.5	86a	7	61	24.4±0.7	227±4	15	17	14.5±0.3	187±7
C. arvense	8	56	34.2±0.4	352±14	5	72	19.4±0.2	318±8	9	50	10.7±0.2	272±9
G. pratense	5	72	47.2±1.9	258±28	9	50	20.2±0.3	324±4	7	61	14.5±0.5	249±7
M. maritima	0	100	--	--	9	50	23.8±0.4	182±8	6	67	14.8±0.9	191±17
M. sativa	1	94	42.0	202	3	83	20.3±0.6	226±15	11	39	11.8±0.2	183±10
P. sativa	4	78	41.9±2.6	305±43	3	83	16.9±0.1	354±10	6	67	11.7±0.2	289±10
P. major	9	50	39.5±0.3	350±15	5	72	19.6±0.2	339±7	10	44	12.5±0.3	287±7
R. pseudoacacia	0	100	--	--	0	100	--	--	3	83	27.5±0.9	117±13
S. babylonica	1	94	64.9	--	0	100	--	--	11	39	20.6±0.6	195±11
S. nigra	0	100	--	--	0	100	--	--	10	44	14.1±0.3	227±9
T. officinale	11	39	36.4±1.0	375±9	24	4	17.4±0.1	335±4	8	56	10.3±0.2	284±8
U. dioica	13	28	35.6±0.4	362±6	20	20	18.7±0.2	329±4	15	17	11.2±0.1	265±5

a – other pupae malformed

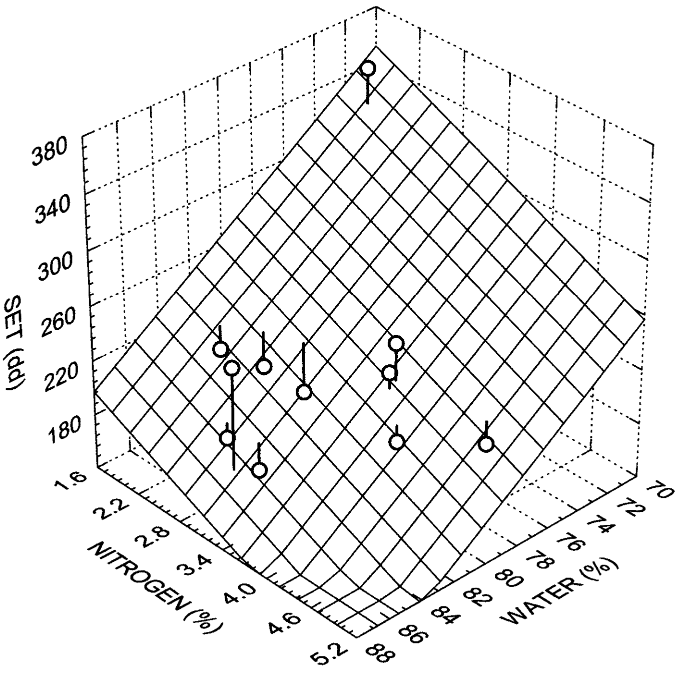

Fig. 2. The influence of food quality, the water content ($t_{(8)} = -3.034$, $p = 0.016$) and N content ($t_{(8)} = -1.957$, $p = 0.086$) of host plant leaves on SET of the larval development ($R^2 = 0.614$, $F_{(2,8)} = 6.367$, $p = 0.022$). Data for each host plant is represented by one point.

fed with *S. babylonica* leaves had 2.3 times greater SET (353 dd) than larvae fed with *T. officinale* (167 dd) (Table 2).

Rate isomorphy. Proportion of the total development time spent on a particular diet significantly interacted with temperature and type of diet (ANOVA: F = 9.236; df = 16, 225; $p < 0.001$). At particular temperatures, the proportion significantly varied with diet (Table 3). This confirms that the SET is very plastic and changes with food quality. The proportion did not significantly vary with temperature for larvae reared on *Medicago sativa, Pastinaca sativa* and *Taraxacum officinale* (Table 4). It means that on these diets, the variation of SET is proportional with changing temperature. The larvae fed by these diets have a common LDT and their development is thus isomorphic. The development time proportion varied with temperature on other diets. Larval development thus violated rate isomorphy. However, the variation in larval development time on particular diets at different temperatures (Table 4) was much less than the variation on different diets at any given temperature (Table 3). The violation of rate isomorphy thus appeared to be generally negligible and the differences in LDT for larvae reared on different diets were small compared to differences in SET

TABLE 2. Food quality as indicated by per cent water (WC) and total N content (NC) in leaves, regression constants a, b (development rate = a × temperature + b), thermal constants SET (dd) and LDT (°C) calculated from experimental data, and SET recalculated under assumption of "rate isomorphy" principle (SET_{rec}).

Host plant	WC	NC	a ($\times 10^3$)	b ($\times 10^2$)	LDT	SET	SET_{rec}
A. millefolium	81.4	2.50	4.886	–4.535	9.3±0.2	205	188
A. retroflexus	79.2	3.75	4.397	–4.833	11.0±0	227	257
C. arvense	84.9	2.77	5.509	–5.587	10.1±0.8	182	182
G. pratense	78.8	3.75	4.060	–3.729	9.2±1.2	246	227
M. maritima	85.9	3.54	4.000	–3.915	9.8	250	
M. sativa	77.3	4.64	5.216	–5.516	10.6±0.3	192	205
P. sativa	80.5	2.86	5.201	–5.149	9.9±0.9	192	192
P. major	82.5	2.14	4.688	–4.471	9.5±0.1	213	202
R. pseudoacacia	68.8	3.17					
S. babylonica	71.9	2.16	2.833	–2.709	9.6	353	
S. nigra	82.1	3.57					
T. officinale	84.5	3.12	5.995	–6.308	10.5±0.2	167	177
U. dioica	80.0	4.02	5.250	–5.154	9.8±0.3	190	185
Average					9.9±0.2	219.7±14.7	201.7±7.3

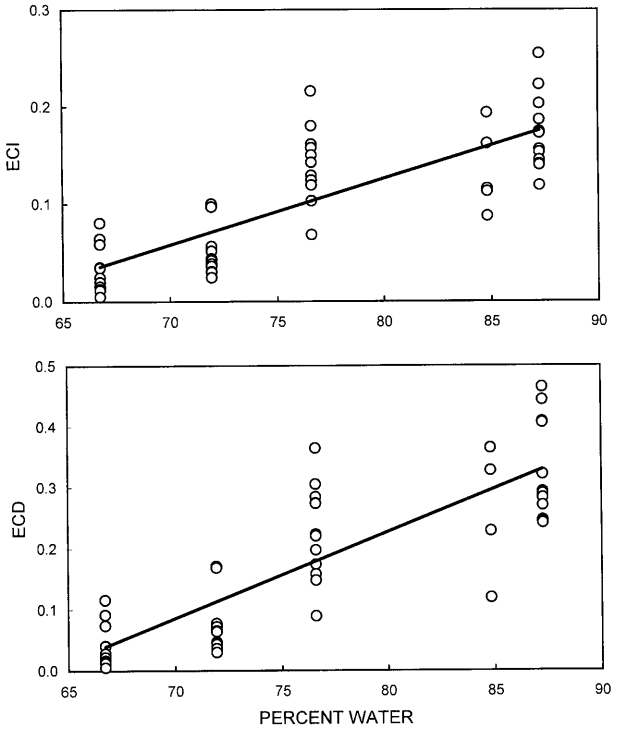

Fig. 3. Proportion of water content (W) in the food in relation to efficiency of food conversion ($ECI = 0.0068W - 0.4514$, $R^2 = 0.645$, $p < 0.001$) and metabolic efficiency ($ECD = -0.0141W - 0.9047$, $R^2 = 0.694$, $p < 0.001$). Each point represents an experiment replicate, a group of 5 larvae.

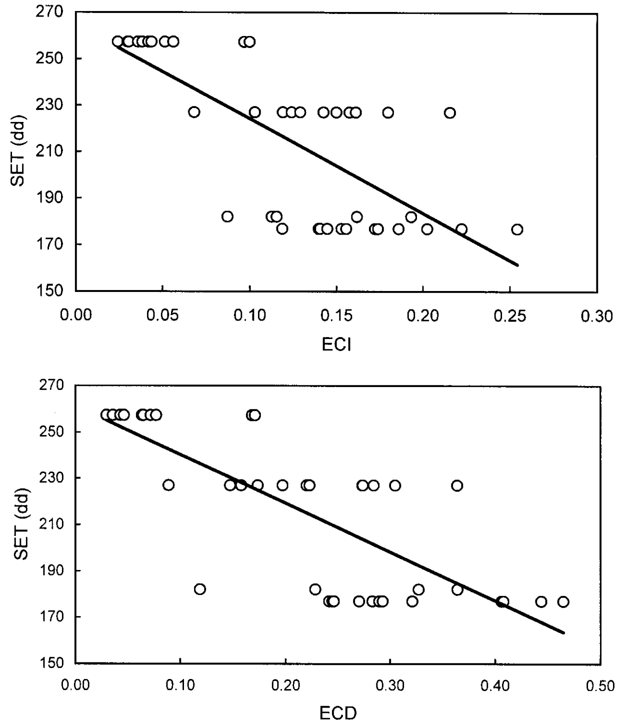

Fig. 4. Sum of effective temperatures SET for development of larvae on 4 host plants (from above: *A. retroflexus*, *G. pratense*, *C. arvense* and *T. officinale*) in relation to the efficiency of food conversion ECI ($SET = -406.3ECI + 264.8$, $R^2 = 0.515$, $p < 0.001$) and metabolic efficiency ECD ($SET = -210.4ECD + 261.4$, $R^2 = 0.584$, $p < 0.001$). Meaning of points as in Fig. 3.

(Table 2). The data for 9 diets where development rate was established in 3 experimental temperatures were recalculated assuming rate isomorphy. The recalculated LDT was 10.0°C (identical with the average LDT calculated as the arithmetical mean of the experimental data for these foods). The recalculated SET_{rec} differed by up to 30 dd from SET calculated from experimental data (Table 2).

Effect of food quality. The SET increased with decreasing water content and decreasing nitrogen content of food (Fig. 2). Multiple regression analysis indicated a significant contribution of variation in food dry matter content ($t_{(8)} = 3.152$, $p = 0.014$) while the effect of nitrogen content was below the limit of statistical significance ($t_{(8)} = -2.011$, $p = 0.079$). The increase of SET was paralleled by decreasing efficiency of food assimilation which also was largely determined by food quality. ECD and ECI (Fig. 3) decreased with decreasing water content in food. SET established on 4 host plants were consequently significantly correlated with ECI and ECD (Fig. 4). Food ingestion and RGR were also negatively influenced by decreasing water content of the food and RGR significantly increased with ECD and ECI (Fig. 5). By contrast, the effect of temperature on larval metabolism was not significant when data were pooled across foods. Food consumption, growth rate, as well as metabolic efficiency ECD and efficiency of food conversion ECI (Fig. 6) did not significantly change with temperature.

TABLE 3. ANOVA of the proportion (angular transformation) of the total development time spent on different diets at 15, 20.3 and 26.7°C.

Temperature (°C)	Source of variation	Df	SS	MS	F	P
15	Among diets	8	0.0365	0.00456	37.02	< 0.001
	Within diets	51	0.00629	0.000123		
20.3	Among diets	8	0.0237	0.00296	63.49	< 0.001
	Within diets	73	0.00341	0.0000467		
26.7	Among diets	8	0.0382	0.00477	309.70	< 0.001
	Within diets	85	0.0105	0.000123		

Body growth. Pupal mass increased with temperature and, within each temperature, decreased with the length of development time (Fig. 7). Pupal mass was thus determined by growth rate GR which significantly increased with temperature (Fig. 8). Recalculation of data to SGR which removed the effect of temperature revealed that pupal mass increased with SGR and the increase was typical for particular food types (Fig. 8). The increasing SET was inversely proportional to decreasing SGR (Fig. 9).

DISCUSSION

Constraints on LDT. The prediction of uniform LDT derived from the assumption of rate isomorphy (RI) was confirmed only on 3 from 9 diets where development was completed in all temperatures. It is not surprising because we had available only 3 experimental temperatures. Even

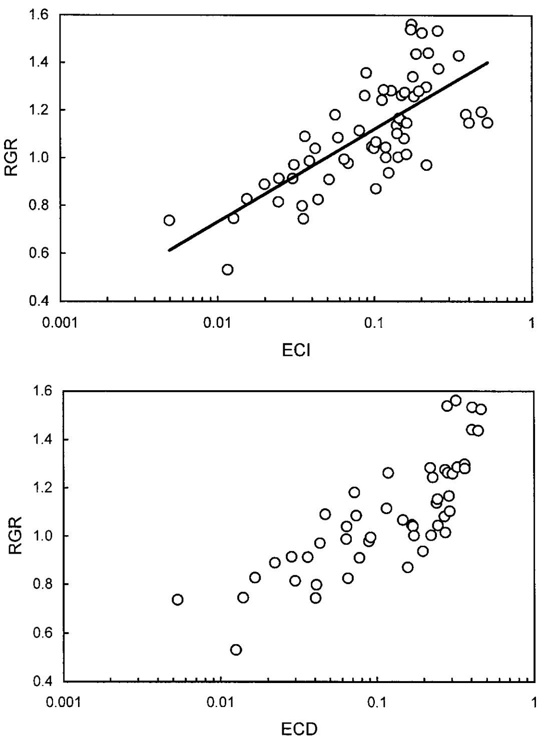

Fig. 5. Relative growth rate RGR (mg.mg^{-1}.d^{-1}) in relation to efficiency of food conversion ECI (RGR = 0.169lnECI + 1.509, $R^2 = 0.539$, $p < 0.001$) and metabolic efficiency. The significance of the RGR vs. ECD relationship was not tested because of autocorrelation. Meaning of points as in Fig. 3.

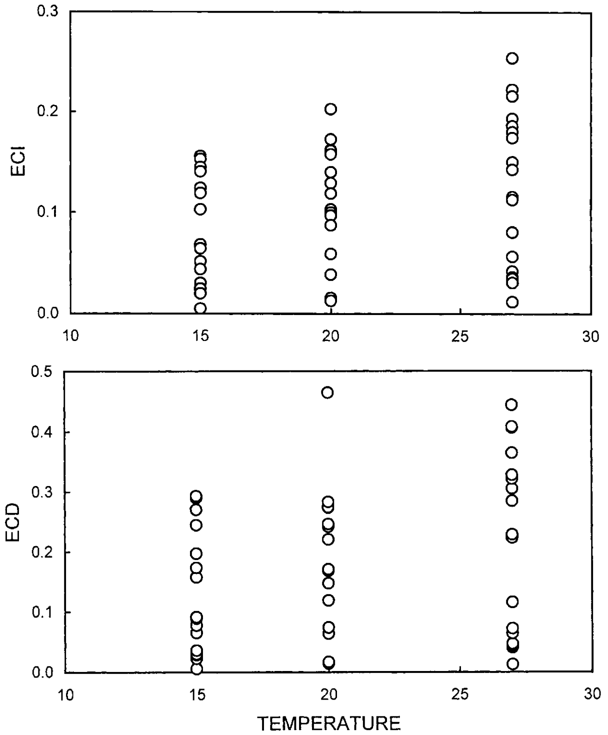

Fig. 6. Efficiency of food conversion ECI ($R^2 = 0.060$, $p > 0.05$) and metabolic efficiency ECD ($R^2 = 0.034$, $p > 0.05$) in relation to temperature (°C). Meaning of points as in Fig. 3.

if LDTs are calculated from data collected over a range of ecologically relevant temperatures, and the regression of development rate on temperature is linear, the accuracy of the estimates is affected by errors in the estimates of the development rate (Campbell et al., 1974). The low precision of LDTs is obvious from their large standard errors (Table 2).

The largest departure from expected proportions assuming the existence of rate isomorphy is at the lowest

TABLE 4. ANOVA of the proportion (angular transformation) of the total development time spent at different temperatures on individual diets.

Diet	Source of variation	Df	SS	MS	F	P
Achillea millefolium	Among temperatures	2	0.00119	0.000596	6.746	0.005
	Within temperatures	22	0.00194	0.0000883		
Amaranthus retroflexus	Among temperatures	2	0.00282	0.00141	8.189	0.002
	Within temperatures	23	0.00396	0.000172		
Cirsium arvense	Among temperatures	2	0.00290	0.00145	22.15	< 0.001
	Within temperatures	19	0.00124	0.0000654		
Geranium pratense	Among temperatures	2	0.00299	0.00150	8.279	0.003
	Within temperatures	18	0.00325	0.000181		
Medicago sativa	Among temperatures	2	0.000344	0.000172	2.639	0.11
	Within temperatures	12	0.000782	0.0000651		
Plantago major	Among temperatures	2	0.000714	0.000357	3.841	0.04
	Within temperatures	21	0.00195	0.0000929		
Pastinaca sativa	Among temperatures	2	0.00126	0.00063	3.68	0.06
	Within temperatures	10	0.00171	0.000171		
Taraxacum officinale	Among temperatures	2	0.000473	0.000236	3.075	0.06
	Within temperatures	39	0.00300	0.0000770		
Urtica dioica	Among temperatures	2	0.00249	0.00124	23.95	< 0.001
	Within temperatures	45	0.00234	0.0000520		

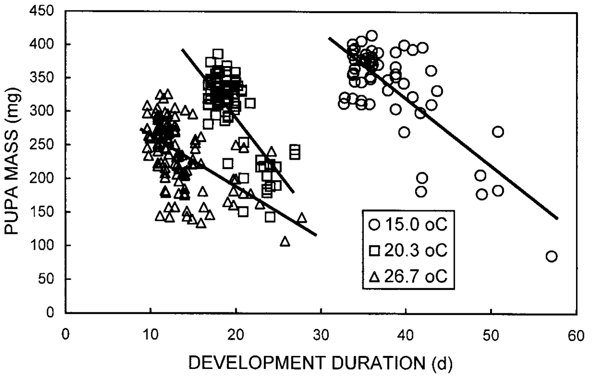

Fig. 7. The relationship between pupal mass and development duration at different temperatures. 15°C: pupal mass = 0.71 – 0.0098 development duration; 20.3°C: pupal mass = 0.63 – 0.017 development duration; 26.7°C: pupal mass = 0.34 – 0.0077 development duration. F = 100.4; df = 5, 262; $p << 0.001$; $R^2 = 65.7\%$. Each point represents 1 individual.

or the highest temperatures (Jarošík et al., in prep.). There are three reasons why these temperatures may violate rate isomorphy. At low temperature there may be differential mortality. The individuals with the fastest development complete their development early while the rest succumb to adverse conditions, the more so if their development is prolonged. The second reason is an imprecise measuring of developmental time at high temperatures. As developmental time decreases with temperature, the number of observations per stage also decreases if monitoring is made at constant intervals at low and high temperatures. The third reason is crucial from a statistical point of view. An important determinant of the slopes of the linear regressions, from which the LDTs are inferred, are the highest and the lowest values (see Crawley 1993, p. 78–82). Therefore, a relatively small bias in the developmental rates measured at the highest or the lowest temperatures will cause a large shift in the LDT.

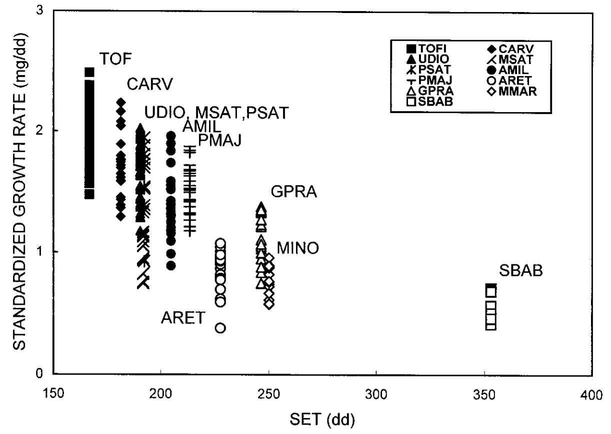

Fig. 9. Standardized growth rate (mg/dd) in relation to SET for different host plants (data pooled over temperatures). Regression for average value for each host plant: growth rate = 2.9 – 0.0073 SET. F = 16.80; df = 1, 9; $p < 0.003$; $R^2 = 65.1\%$. Acronyms as in Fig. 8, meaning of points as in Fig. 7.

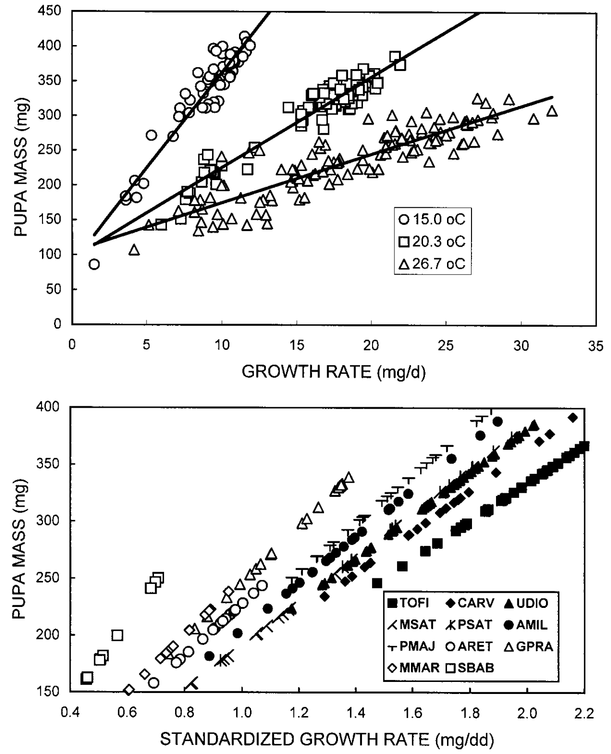

Fig. 8. Above: The relationship between pupal mass and growth rate (GR) at different temperatures. 15°C: pupal mass = 99.2 + 25.9 GR; 20.3°C: pupal mass = 99.2 + 12.8 GR; 26.7°C: pupal mass = 99.2 + 7.3 GR. F = 889.3; df = 3, 264; $p << 0.001$; $R^2 = 91.0\%$. Below: The relationship between pupal mass and standardized growth rate SGR (pooled over temperatures) at different host plants. F = 22.1; df = 21, 234; $p << 0.001$; $R^2 = 66.5\%$. Increase in pupal mass is host-plant specific (F = 2.982; df = 11, 245; $p < 0.001$). TOFI – T. *officinale*, MSAT – *M. sativa*, PMAJ – *P. major*, MMAR – *M. maritima*, CARV – *C. arvense*, PSAT – *P. sativa*, ARET – *A. retroflexus*, SBAB – *S. babylonica*, UDIO – *U. dioica*, AMIL – *A. millefolium*, GPRA – *G. pratense*. Meaning of points as in Fig. 7.

The common LDT for *A. gamma* larvae calculated using data for 11 host plant species was 9.9 ± 0.2°C, by 2.3°C higher than the LDT calculated for a UK population of this species (Hill & Gatehouse, 1992) which was 7.7°C (male) and 7.6°C (female) (Table 5). The difference, tested using SD calculated for the UK data (Janáček et al., in litt.), was not significant ($t_{2,4} = 1.434$, $p > 0.05$). In fact it is smaller than variation observed between populations of other species studied by more than one author, e.g. *Heliothis armigera* (Hübner) (LDT between 8.6–12.9°C), *Heliothis virescens* (F.) (7.6–11.8°C), or *Trichoplusia ni* (Hübner) (9.0–14.7°C) (Table 5). The difference was apparently caused by variation of methods used in the two studies. Data on variation of LDT between populations were available for 12 noctuid species (Table 5). If we exclude the outlier data for populations of *A. ipsilon* (Hufnagel), *Pseudaletia unipuncta* (Haworth) and *Spodoptera frugiperda* (Smith) because of the large extent of variation in the differences between local populations, which were in the order of 1.7–5.7°C (mean = 3.9 ± 0.4°C). In general differences between the studies of different authors were greater than the differences "within" the studies.

Dixon et al. (1997) extended the idea of rate isomorphy (existence of a LDT constraint) to higher taxonomic

TABLE 5. Thermal constants for larval development in noctuid moths of temperate regions. Number of populations investigated in a study (Pn), number of experimental temperatures where development length was determined (N), range of experimental temperatures (Range), lower development threshold (LDT) and sum of effective temperatures (SET).

	Pn	Temperature (°C)		LDT (°C)	SET (dd)	Reference
		N	Range (°C)			
Agrotis fucosa Butler	1	3	20–28	13.4	273.1	Hasegawa & Chiba, 1969
Agrotis ipsilon (Hufnagel)	1	3	13–27	7.2	502.7	Archer et al., 1980
	2	2	20–25	8.5–10.8	601.4–720.5	Fahmy et al., 1973
	1	6	18–28	8.8	322.5	Hasegawa & Chiba, 1969
	1	4	18.3–26.7	11.0	322.5	Luckmann et al., 1976
	1	2	21–25	16.8	143.8	Poitout & Bues, 1974
Agrotis segetum (Denis et Schiffermüller)	7	2	20–25	10.5–12.4	397.7–738.5	Weismann & Podmanická, 1971
Anticarsia gemmatalis (Hübner)	1	2	21.1–26.7	16.4	154	Leppla et al., 1977
Autographa biloba (Stephens)	2	2	20–25	10.6–11.6	211.8–231.2	Beach & Todd, 1988
Autographa californica (Speyer)	1	5	14–30	11.5	189.6	Miller et al., 1984
Autographa gamma (L.)	2	5	13–25	7.6–7.7	281.3–281.8	Hill & Gatehouse, 1992
Dargida procincta (Grote)	1	2	15–27	7.0	410.3	Kamm, 1991
Eudocima salaminia (Cramer)	1	4	15–27	11.9	280.2	Sands et al., 1991
Heliothis armigera (Hübner)	1	2	21–25	8.6	254.2	Poitout & Bues, 1974
	1	3	20–30	12.9	185.7	Quareshi et al., 1999
	1	3	20–30	10.2	298.4	Sharma & Chaudhury, 1988
	1	5	13.1–27.1	11.8	235.7	Twine, 1978
	1	3	15–25	9.0	267.1	Wu et al., 1980
Heliothis subflexa (Guenée)	1	6	15–27.5	12.2	222.5	Butler et al., 1979
Heliothis virescens (F.)	1	6	15–27.5	11.4	230.7	Butler & Hamilton, 1976
	3	6	1 5–27.5	11.1–11.8	199.9–229	Butler et al., 1979
	1	3	20–30	7.6	405.7	Nadgauda & Pitre, 1983
Heliothis zea (Boddie)	3	3	15.6–25	8.0–11.8	225.2–419.6	Butler, 1976
	8	2	20–25	7.0–12.7	187.5–498.2	Wiseman & Isenhour, 1989
Hydraecia immanis (Guenée)	1	4	18–27	4.7	779.7	Giebink et al., 1985
Hydraecia micacea (Esper)	1	4	18–27	6.6	558.2	Giebink et al., 1985
Leucania loreyi Dupont	1	3	15–25	8.9	432.6	Hirai, 1975
Leucania separata Walker	1	3	15–25	7.3	409.9	Hirai, 1975
	1	3	15–25	9.0	293.1	Sinchaisri & Sogawa, 1969
Mamestra brassicae (L.)	1	2	21–25	11.4	212.2	Poitout & Bues, 1974
Mamestra configurata Walker	1	5	8–24	4.7	434.4	Bailey, 1976
	1	2	21–25	9.5	275.6	Poitout & Bues, 1974
Mythimna convecta (Walker)	3	3	15–25	5.8–6.2	461.4–502.9	Smith, 1984
Orthosia hibisci (Guenée)	1	8	7.5–25	4.1	258.5	Judd et al., 1994
Papaipema nebris (Guenée)	1	5	12.8–23.9	3.1	1480.8	Levine, 1983
Peridroma saucia (Hübner)	1	4	10–25	3.7	471.9	Shields, 1983
	1	5	10–26.7	6.6	384.3	Simonet et al., 1981
Phlogophora meticulosa (L.)	2	4	11–21	3.6–4.2	572.1–678.4	Bues & Poitout, 1980
Plathypena scabra (F.)	2	4	15.6–26.7	6.2	376.2–401.5	Hammond et al., 1979
Pseudaletia unipuncta (Haworth)	1	4	13–28	7.7	368.3	Guppy, 1969
	1	2	21–25	0	460.5	Poitout & Bues, 1974
	1	2	18–23	11.0	292.1	Taylor & Shields, 1990
Simyra henrici (Grote)	3	3	18.3–23.9	9.6–10.3	454.5–548.6	Decker & Maddox, 1971
Spodoptera exigua (Hübner)	3	3	18–26	11.4–13.1	128.0–185.9	Ali & Gaylor, 1992
	1	4	15–25	10.2	231.6	Butler, 1966
	1	2	21–25	16.1	97.8	Poitout & Bues, 1974

TABLE 5 (continued).

Spodoptera frugiperda (Smith)	3		17–33	12.4–12.9	192.3–270.7	Ali et al.,1990
	4	2	20–25	5.5–8.8	262.7–331.2	Combs & Valerio, 1980
	5	2	25–30	15.3–18.6	180.6–240.8	Isenhour et al., 1985
Spodoptera littoralis (Boisduval)	1	2	20–22.5	12.7	227.9	Baker & Miller, 1974
	3	2	25–30	8.6–9.7	280.0–305.8	Nasr et al., 1973
	1	2	21–25	16.5	119.2	Poitout & Bues, 1974
	1	3	15–25	11.7	236.8	Sidibé & Lauge, 1977
Spodoptera litura (F.)	1	2	26–30	7.2	307.2	Bilapate & Thombre, 1979
	3	5	16–28	10.8–12.9	248.3–260.6	Miyashita,1971
	1	3	15–25	11.5	252.1	Rao et al., 1989
Trichoplusia ni (Hübner)	2	5	19–26	12.0–14.7	119.3–165.3	Butler et al., 1975
	1	4	15–26.7	9	252.3	Jackson et al., 1969
	1	3	16.6–27.7	12.9	164.6	Toba et al., 1973
Trichoplusia orichalcea (F.)	4	2	15–28	8.0–11.3	194.1–269.0	Cabello, 1988
Uraba lugens (Walker)	3	3	15–25	11.5–13.2	453–460	Allen & Keller, 1991
Average 106				10.2±3.3	329.6±177.1	

groups of similar biology. Noctuid moths may be considered in this respect because they have a similar larval biology. To compare the available data we compiled a review of 48 studies on larvae of noctuid species of the temperate zone (Table 5). The included species are all folivorous facultatively polyvoltine phytophagans. In fact, the average LDT for 108 populations of 34 species, 10.2 ± 0.3°C, is surprisingly close to the average LDT of *A. gamma* established in this study. Thus, despite the enormous variation of the literature data the assumption of rate isomorphy for the family of Noctuidae could not be rejected.

Plasticity of SET. The time (or heat) requirements for completing development of a stage as reflected by variation of the SET are plastic. At the species level this variation parallels taxonomic differences between species, but also trophic specialization of the taxa and the differences in body size (Honěk, 1999). Within populations of some species there exist adaptive differences between the sexes in development time (Nylin et al., 1993). However, in many other species the importance of sex linked differences is small (Honěk, 1997). Probably the most important differences in SET are caused by variation of food quality (Slansky & Scriber, 1985; Slansky, 1993). In this study the differences in food quality caused a 2.6 fold variation in the SET. The leaves of 13 host plant species differed in their water and nitrogen content, which both together explained 62.2% of the variance in SET. This indicates a small effect of secondary factors, leaf surface quality and allelochemicals, on food acceptability for *A. gamma* larvae. This is apparently consistent with the broad polyphagy of this species which should overcome the defence barriers of a wide range of plant species.

The water content of food is an important factor in food utilization by caterpillars (Slansky, 1993). Its importance has been demonstrated with natural foods (Scriber, 1977, 1979a), synthetic diets (Schmidt & Reese, 1988) and with stored products of different humidity (Nawrot, 1979; Hagstrum & Milliken, 1988). The effects of water content on food digestibility and larval growth was also demonstrated in other insect orders (e.g. Merkel, 1977). The importance of water content of food (47.2% of variance in SET explained) for larval performance of *A. gamma* thus parallels other polyphagous insect species. The nitrogen content of food explained only 19.3% of total variance in SET of *A. gamma*. Although N content is an important factor of food quality for Lepidoptera larvae (Scriber 1979b; Lindroth et al., 1991; Bauce et al., 1994; Soontiens & Bink, 1997), its relative importance is apparently smaller than in sucking insects where nitrogen content of phloem or xylem sap may become a limiting factor of larval growth and adult reproductive performance (e.g. Honěk et al., 1998; Ponder et al., 2000).

Growth. As with other insects, temperature and development time influenced final size (pupal mass) of the larva. The effect of temperature on body size is unimodal, with a monotonic decrease of body size below and above the "optimum" temperature (e.g. David et al., 1994). The temperature where insects grow to largest body size is always below the optimum for development time and reproduction efficiency. In *A. gamma* this temperature is less than or equal to 15.0°C, since the average pupal mass decreased over the range of experimental temperatures (15.0–26.7°C). Within each temperature pupal size decreased with increasing development time. There was no trade-off between body size and development time which might be expected under optimum trophic conditions (Begon et al., 1990). Extended larval development accompanied by lower final mass was apparently associated with the inability to compensate for reduced food quality (Slansky, 1993). In fact, the indices of efficiency of food assimilation decreased in parallel with decreasing growth rate and pupal mass. The variation of pupal size thus may appear as a non-adaptive result elicited by an environmental constraint. However, if we consider a wide spectrum of situations that the organism may face in the open, decreasing body size might still be adaptive (Wiklund et al., 1991; Nylin & Gotthard, 1998). Pupating at small size may be advantageous in areas with constrained thermal unit availabilty (Ayres & Scriber, 1994; Scriber, 1996). The study of fitness consequences of body size variation in *A. gamma* remains to be studied.

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