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# Temperature affects performance of *Lymantria dispar* larvae feeding on leaves of *Quercus robur*

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**Abstract:** Future climatic warming may modify insect development, sex ratio, quantitative changes in populations that could affect the frequency of outbreaks. Here we analyzed the influence of temperature on larval growth and development in the gypsy moth (*Lymantria dispar* L.). The larvae were reared at three constant temperatures: 15, 20 or 25°C, and fed with leaves of the English oak (*Quercus robur* L.). Larval mortality, duration of development (DD), relative growth rate (RGR), total mass of food eaten (TFE), and pupal mass (PM) were estimated. Larval mortality was lowest at 20°C, higher at 25°C, and highest at 15°C. DD significantly decreased with increasing temperature and depended on sex. The influence of temperature on the shortening of DD was stronger in males than in females. RGR significantly depended on temperature and was the highest at 25°C, and lowest at 15°C. At 15°C, RGR did not change markedly with time. In contrast, RGR at 20°C was characterized by a continuous decreasing trend. At 25°C, RGR was very high for 2 weeks but quickly declined afterwards. Temperature did not affect the TFE. PM was significantly correlated with temperature and sex. PM of females was higher at 20°C than at 15 and 25°C, in contrast to that of males, which was similar at 20 and 25°C, and higher than at 15°C. For larval growth and development, the most favourable was the medium temperature (20°C). The least favourable temperature for females was 25°C, for males 15°C. The results suggest that global warming may modify the future sex ratio of gypsy moths that may affect insect development and outbreaks.

**Additional key words:** herbivore insect, sex ratio, pedunculate oak

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## Introduction

Global average surface temperature is projected to increase by 1.4 to 5.8°C by the year 2100 (Houghton et al. 2001). This temperature rise is expected to affect the growth, development and distribution of animals, including insect herbivores (Klimetzek and Yue 1997; Fleming et al. 1998; Tenow et al. 1999; Harrington et al. 2001; Bale et al. 2002; Walther 2004). The temperature increase may also indirectly disturb the functioning of the plant-insect herbivore system, due to: (1) physiological changes in plant defence mechanisms (Buse et al. 1998; Dury et al. 1998; Graglia et al. 2001; Dixon 2003), (2) changes in abundance of natural enemies, such as predatory insects and parasites, and competition with other insect herbivores (Bezemer et al. 1998; Coley and Barone 1996), and (3) direct influence on insect development and mortality (Coley and Barone 1996; Williams et al. 2003). Because of the short life cycles, great mobility, high reproductive potential, and physiological sensitivity to temperature, it is likely that even small clima-

tic changes will strongly affect the distribution and abundance of insects (Fleming 1996, 2000; Régnière and Sharov 1999; Ayres and Lombardero 2000). The current diversity of insects and their impact on plants generally increases with decreasing latitude (Wilf and Labandeira 1999). Those authors also report that at constant latitude, the diversity and abundance of insect herbivores increases with increasing temperature.

Previous research on effects of elevated temperature on insect growth and development has usually concerned tropical plants, mostly herbs. The results generally show that under conditions of high temperature and/or drought the nutritive value of leaves declines and the concentration of carbon-based repellents increases, which leads to more intensive insect grazing (Coley and Barone 1996). On the other hand, it is well-known that under higher temperatures energetic needs are lower, and a diet lower in calories will allow achievement of a given growth rate and level of performance. Furthermore, Lindroth et al. (1997) found that elevated temperature stimulated increase in consumption and efficiency of conversion of ingested food.

Only a small proportion of the studies concerned with effects of elevated temperature on insect growth and development have taken into account the most harmful polyphagous insects feeding on leaves of the economically important forest tree species of Europe. Therefore, we here focus on the gypsy moth (*Lymantria dispar* L.), which is a major insect pest feeding chiefly on leaves of oaks, beeches, hornbeams, maples, poplars, and birches (Sharov et al. 1999; Lazarević et al. 2002). It is found in forests, parks and orchards all over Europe, but also in Africa, North America and Asia, except for submontane and montane zones. In our experiment, larvae of this insect were fed with their preferred food, i.e. leaves of English oak (*Quercus robur*), which plays an important role in silviculture nearly all over Europe (Meusel et al. 1965). To identify the effects of temperature on larval growth and development, larvae were raised at three different constant temperatures: 15, 20 and 25°C. These temperatures are commonly observed within the ranges of distribution of both the studied insect pest (*L. dispar*) and its host plant (*Q. robur*) (Walter 1976).

The objectives of this study were: (1) to determine how temperature directly affects larval mortality, growth and development in *L. dispar*, and (2) to identify the influence of insect sex on these traits.

# Material and methods

## Plant material

The larvae were fed with leaves of pedunculate oak (*Quercus robur* L.), collected from three ca. 30-year-old trees of local provenance, growing at the Experimental Forest 'Zwierzyniec' in Kórnik, Poland (52°14'36"N and 17°05'00"E). For all temperature treatments, the leaves were collected on the same day from the sunlit part of the tree crown, at about 1/3 of its height (measured from the apex). Large size of the trees and alternating leaf collection among trees during the experiment minimized stimulation of plant defence mechanisms.

## Insect

Eggs of the gypsy moth (*Lymantria dispar* L.) from northeastern Poland were obtained from Lidia Sukovata (Forest Research Institute, Warsaw, Poland) and they were prepared according to the methods described by Giertych et al. (2005).

The larvae were fed with oak leaves in 15 cm diameter Petri dishes. The dishes were kept in a phytotron at 15±1°C (low temperature), 20±1°C (medium temperature) or 25±1°C (elevated temperature). The caterpillars were fed with leaves for 2.5 months (between 17$^{th}$ June and 1$^{st}$ September). One larva at the developmental stage L2–3 was placed with an oak leaf (its petiole was stuck in a hole drilled in the lid of an Eppendorf tube filled with water, so that the water could not leak out) in each dish, and there were 16 replicates for each temperature treatment (total 48 dishes). The leaves for all temperature treatments were changed every two days. Each leaf was weighed when placed in the dish and the uneaten residue was oven-dried and weighed after 2 days.

The larvae were checked daily for mortality and stage of development. Duration of development (DD) was defined as time from the beginning of the experiment to pupation. Once a week, each larva was weighed. Relative growth rate (RGR) was calculated from the formula:

$$RGR = (M_t - M_0)/(T_{t\text{-}0} \times M_0),$$

where $M_0$ and $M_t$ = initial and final larval mass (in mg), and $T_{t\text{-}0}$ = number of days between the initial and final measurement. The RGR value was calculated for a 4-week period. Additionally, ontogenetic changes in RGR were assessed for 1-week intervals, with $M_0$ and $M_t$ = larval mass at the beginning and end of each week, respectively. RGR was calculated in relation to the initial mass (Hwang and Lindroth 1997; Lazarević et al. 2002).

We determined the pupal mass (PM) and the total mass of food eaten (TFE).

The mass of food eaten (as dry leaf mass) was calculated by subtracting the dry mass of leaf remnants from the dry mass of the leaf before placing it in the Eppendorf tube. In parallel, the fresh mass of leaves were compared with their oven-dried mass (65°C), to calculate the fresh/dry mass ratio.

## Statistical analyses

Analysis of covariance (ANCOVA) was conducted with JMP software (version 4.0.4, SAS Institute Inc. USA). ANCOVA was used to assess the influence of temperature treatment, sex and their interaction on the DD, TFE, and PM. The initial mass was used as a covariate as suggested by Lazarević et al. (2002) and Raubenheimer and Simpson (1992). For statistic analysis of RGR (after 4 weeks of the experiment) ANOVA was used.

# Results

The thermal conditions of rearing markedly affected the mortality of gypsy moth larvae (Fig. 1). Mortality was the lowest at 20°C (6.3%), and twice as high (12.5%) at the highest of the applied temperatures (25°C). Their mortality increased dramatically (62.5%) when larvae were reared at 15°C.

Temperature significantly influenced the duration of development (DD = number of days from the beginning of the experiment to pupation - Table 1). As the temperature increased, DD decreased (averaged for both sexes) to about a half. The interaction between sex and temperature was significant, due to a stronger decrease in DD in males (28 days) with increasing temperatures as compared to females (38 days). The shortening of larval development at higher temperatures was also associated with higher values of relative growth rate (RGR - Table 1). The interaction between sex and temperature was not significant. During the first 4 weeks, the RGR of larvae reared at 25°C was about 15-fold higher for females and about 32-fold higher for males than at 15°C. Patterns of changes in RGR over time were different for each temperature treatment (Fig. 2). At 15°C, RGR values were relatively stable but low. Higher but decreasing values of RGR over time were recorded for larvae raised at 20°C. Yet another pattern of changes in RGR was observed at 25°C: values increased during the first weeks and decreased afterwards (Fig. 2). Apart from the lowest temperature, where considerable fluctuations in RGR were observed in both sexes, the changes in RGR observed at higher temperatures (20 and 25°C) were similar in larvae of both sexes.

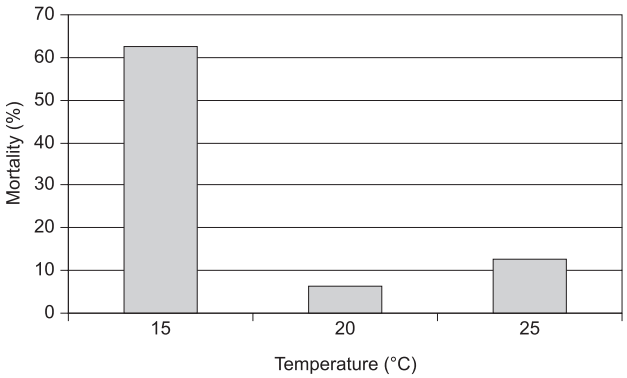


Fig. 1. Influence of temperature (15, 20 and 25°C) on larval mortality in *Lymantria dispar*

The mass of food eaten by females was significantly higher than of food eaten by males: 2.6-fold at 15°C, 3.1-fold at 20°C, and 2.7-fold at 25°C. However, the total mass of food eaten by larvae was not significantly affected by temperature and no interaction was observed between temperature and sex. Despite the considerable differences in the mass of food eaten by females and males, the efficiency of conversion of ingested food (described as the relationship between the dry mass of food eaten to pupal mass Fig. 3) was similar in both sexes, and did not depend on temperature. The sex x temperature interaction was marginally significant (*P=0.083*). The efficiency of conversion of ingested food for female larvae at 20°C was higher than at 25°C, while for male larvae these values were similar at both temperatures (Fig. 3).

Pupal mass was significantly correlated with temperature and sex, which interacted with each other (Table 1). Among female larvae, those reared at 20°C were characterized by the highest pupal mass. Pupal mass in males was similar at both higher temperatures (20 and 25°C), but much lower at 15°C.

Table 1. The mean (*SE) and summary of ANCOVA results for duration of development (DD; days), total food eaten (TFE; g dry mass), and pupa mass (PM; g), and ANOVA for relative growth rate after 4 weeks (RGR; mg $mg^{-1}$ $d^{-1}$), by temperature (°C) and sex. Initial larva mass was used as covariate to adjust initial mass differences between insect

| Temperature | Number of individuals | | DD | | RGR | | TFE | | PM | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| 15 | 2 | 4 | 65.5 ±1.5* | 67.0 ±1.2 | 0.56 ±0.08 | 0.18 ±0.03 | 4.56 ±0.22 | 1.77 ±0.14 | 1.81 ±0.14 | 0.58 ±0.04 |
| 20 | 6 | 8 | 49.0 ±2.3 | 38.5 ±0.7 | 3.75 ±1,08 | 2,48 ±0.46 | 4.70 ±0.37 | 1.53 ±0.04 | 2.09 ±0.12 | 0.63 ±0.02 |
| 25 | 7 | 8 | 37.1 ±1.4 | 28.8 ±1.1 | 8.41 ±1.17 | 5.67 ±0.23 | 4.30 ±0.28 | 1.58 ±0.06 | 1.49 ±0.05 | 0.66 ±0.01 |
| ANCOVA | d.f. | Error | F | *P* | F | *P* | F | *P* | F | *P* |
| Temperature | 2 | 28 | 146.1 | *0.000* | 23.22 | *0.000* | 1.19 | *0.318* | 8.04 | *0.002* |
| Sex | 1 | 28 | 18.80 | *0.000* | 3.42 | *0.076* | 212.7 | *0.000* | 414.0 | *0.000* |
| T x S | 2 | 28 | 5.70 | *0.008* | 0.76 | *0.479* | 1.25 | *0.302* | 13.8 | *0.000* |
| Initial larva mass (covariate) | 1 | 28 | 0.34 | *0.562* | - | - | 1.22 | *0.277* | 0.44 | *0.512* |

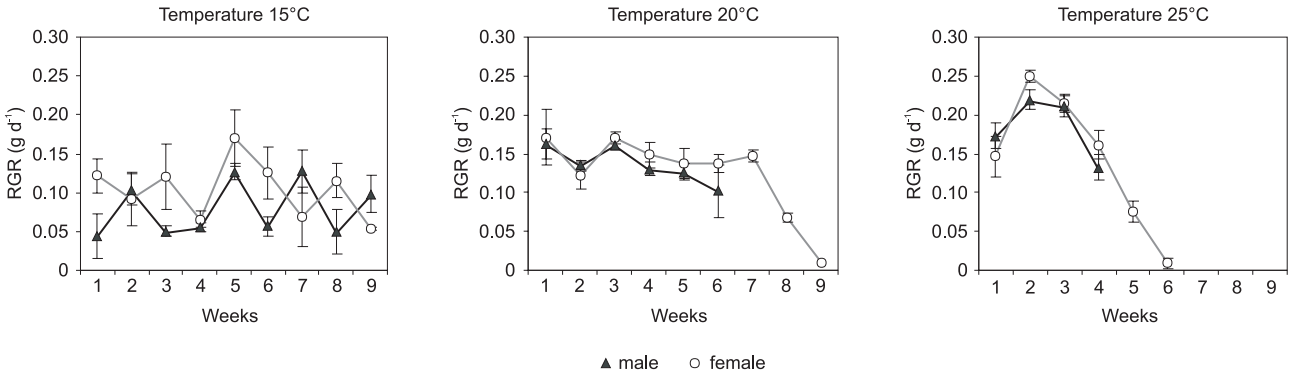


Fig. 2. Influence of temperature (15, 20 and 25°C) on temporal change of relative growth rate (RGR) in male and female larvae of *Lymantria dispar*; given are means ±SE

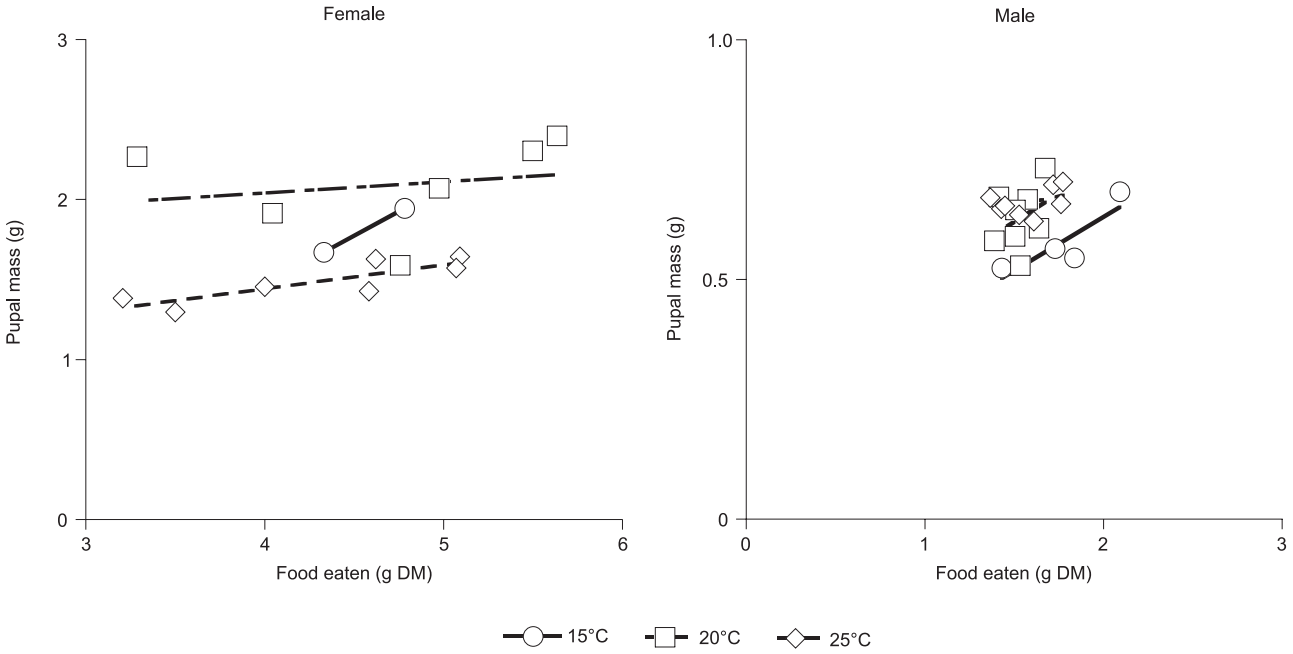


Fig. 3. Relationship between the dry mass (DM) of food eaten to pupal mass for each temperature treatment, for female and male *Lymantria dispar*

## Discussion

Among the traits studied that characterize insect reactions to various temperatures of rearing, the most important is obviously the mortality rate. Results of this study showed that within the experimental temperature range (15–25°C), the medium treatment (20°C) was the most favourable for the growth of gypsy moth larvae. Raising temperature by 5°C increased larval mortality 2-fold, while its lowering by 5°C caused a 10-fold increase in mortality. Contrasting results were reported by Lindroth et al. (1997), who fed larvae of the same species with an artificial food. In their study, an increase in temperature by 6°C within a comparable temperature range (19–25°C during the day) did not exert any significant influence on larval mortality. Also Williams et al. (2003) did not detect any effect of a 3.5°C increase in temperature (in relation to ambient temperature) on the survival of gypsy moth larvae. The comparison of our results with those reported by Lindroth et al. (1997) suggests that an interaction between food type and temperature may affect the outcome of experiments. The study by Williams et al. (2003) was conducted with the use of growing seedlings. In that case, the increase in temperature could affect the larvae also indirectly, because of metabolic changes in plants, such as initiation of defence mechanisms in leaves. Moreover, Ayers and MacLean (1987) recorded the most negative influence on the growth and development of caterpillars of *Epirrita autumnata* at the highest temperature, due to leaf aging. We collected leaves for the larvae from the same trees, which were growing in equal thermal conditions. Thus our results reflect only the direct effect of temperature on insects.

As the temperature increased from 15 to 25°C, the time from the beginning of the experiment to pupation (DD) was shortened by 33 days and the RGR of larvae increased. In relation to those traits, our results are consistent with those reported by Lindroth et al. (1997), Åsman (2001) as well as Williams et al. (2003), who studied the same insect species. Lindroth et al. (1997) found that a rise in temperature results in a shortening of the larval period by 14–16 days, for a slightly a narrower range of diurnal temperatures (19–25°C). Also Williams et al. (2003) showed that an increase in rearing temperature by 3.5°C shortens larval development by about 8 days. However, the data on interaction between sex and temperature and their influence on DD are inconsistent. Williams et al. (2003) found, as in our study, that with increasing temperature, larval development is accelerated more strongly in males than in females. However, the difference between sexes was small (0.5 day) in comparison with that recorded in our study (9.8 days). Contrasting results are reported by Lindroth et al. (1997). In their study, the shortening of DD caused by increasing temperature was greater (by 1.6 days) in females than in males. The influence of higher temperature on shortening of larval development is currently indisputable and has been confirmed also in other species of insect herbivores (Leather and MacKenzie 1994; Åsman 2001; Stillwell and Fox 2005). However, further research is needed to determine its interactions with other factors (e.g., food quality) that may differentiate the duration of larval duration depending on sex. As temperature increased, the relative growth rate (RGR) of larvae also increased (Table 1). Increasing RGR at higher temperatures enables the larvae to reach similar body masses as larvae at lower temperatures at reduced development times. Therefore, a reduction in development time (which is assumed to be favourable) needs to be accompanied by increased RGR to ensure that larvae reach optimal body sizes. A similar trend was observed in gypsy moth larvae also by Lindroth et al. (1997). Their study revealed an interaction between sex and temperature, as a rise in temperature did not affect RGR in males, but increased it in females. Our results did not show any interaction between temperature and sex, both for RGR calculated for the first 4 weeks of larval growth (Table 1) and for changes in RGR over a longer time, analysed separately for each temperature (Fig. 2). The analysis of changes in RGR with time, conducted for each temperature separately, indicated that in larvae reared at 20°C it was relatively high and gradually decreased until pupation (Fig. 2B). In larvae reared at 15°C, RGR was lower and fluctuated considerably (Fig. 2A), while at 25°C, it rapidly declined after the 2$^{nd}$ week of growth (Fig. 2C). A decrease in RGR with time, associated with an increase in temperature, was also observed in other insect species (Ayres and MacLean 1987). The time-course of RGR observed in this study at different temperatures helps to explain why, regardless of the shortening of larval development at higher temperatures, no negative effect on pupal mass was observed (Table 1). Our results indicate that an increase in temperature is favourable for this insect species. Due to the acceleration of larval development they are exposed for a shorter time to negative effects of stress factors, both abiotic (drought, mechanical injury) and biotic (parasites, insect predators). Simultaneously, the shorter duration of larval development exerts no negative influence on their growth.

Rearing temperature in our experiment did not affect the total mass of food eaten in larvae of either sex. The highest values of pupal mass for a given mass of food eaten were observed at the medium temperature (20°C) in individuals of both sexes, although the difference between 20°C and 25°C was small for males (Fig. 3). These relationships were reflected in values of pupal mass (PM). PM in females was the highest at 20°C, while in males it increased with temperature. PM in females is positively correlated with reproductive success (Leather and MacKenzie 1994; Hough and Pimentel 1978).

Our results indicate that the temperature of 15°C, which is lower than the optimum (20°C), is unfavourable for the growth and development of gypsy moth larvae of both sexes, while a higher temperature (25°C) is unfavourable for female larvae but favourable for male larvae. Our results contrast with those reported for the same insect species by Lindroth et al. (1997) and Williams et al. (2003). The former researchers observed only a marginally significant influence of elevated temperature on pupal mass, while the latter reported a lack of such an influence. In the study carried out by Lindroth et al. (1997), a temperature increase also caused a significant increase in the efficiency of conversion of ingested food. Thus, the aforementioned disparity in experimental results can be explained by the application of different types of food. Williams et al. (2000), who studied the influence of temperature on the growth and development of gypsy moth larvae, used leaves of two maple species: the red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*). In their study, an increase in temperature by 3.5°C in relation to ambient temperature did not affect conversion of ingested food in larvae fed with red maple leaves, but significantly increased its values in larvae fed with sugar maple leaves. The host plant species may play an important role here because both research teams cited above reported that the increase in temperature did not cause any changes in the concentrations of components favourable or unfavourable for larval growth and development such as nitrogen, nonstructural carbohydrates (soluble sugars and starch), tannins, and interactions between

those substances. The factors that affect the influence of temperature on survival may be different from those affecting its influence on the growth and development of insect herbivores. It is possible that in our study the unfavourable effect of low temperature on gypsy moth larvae of both sexes is mainly due to the direct impact of low temperature on insects, as suggested by Coley and Barone (1996) as well as Williams et al. (2003). Results of some studies suggest that relatively high temperatures affect larval development indirectly through the influence of temperature on the chemical composition of host plant leaves. For example, Buse et al. (1998) and Dury et al. (1998) found that even a modest rise in temperature (by 3°C) for 2 months caused a significant increase in concentrations of phenolic compounds (of condensed tannins in particular) and a decrease in nitrogen content in leaves of *Q. robur*. Thus a higher temperature would increase the chance of metabolic defence against insect grazing on leaves. Those authors in their experiments used leaves of plants growing at various temperatures. In our experiment, as mentioned above, we fed the larvae with leaves growing in the same outdoor thermal conditions. Besides, an unfavourable, indirect influence of plant metabolic defence on larvae should be observed in both sexes, but we recorded it only in females, indicating that we observed a direct influence of temperature.

In summary, our study revealed that under controlled laboratory conditions, the growth and development of male gypsy moth larvae (characterized by DD, RGR, TFE, and PM), was unchanged or more favourable at 25°C than at 20°C. By contrast, in female larvae both an increase and a decrease in temperature by 5°C was much less favourable for growth and development (except DD and RGR) than the temperature of 20°C. In contrast to prior reports (Lindroth et al. 1997; Williams et al. 2003) our results show that elevated temperature (25°C) is unfavourable for female but favourable for male larvae, resulting in modification of the sex ratio of adult gypsy moths. Additional studies taking into account temperature, insect sex, and food quality are necessary to forecast insect development, quantitative changes in populations, and frequency of outbreaks in the future, warmer world.

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## References

Åsman K. 2001. Effect of temperature on development and activity periods of the leel moth *Acrolepiopsis assectella* Zell. (Lep., Acrolepiidae). Journal of Applied Entomology 125: 361–364.

Ayres M.P., Lombardero M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262: 263–286.

Ayres M.P., MacLean S.F.Jr. 1987. Development of birch leaves and their growth energetics of *Epirrita autumnata* (Geometridae). Ecology 68: 558–568.

Bale J.S., Masters G.J., Hodkinson I.D., Awmack C., Bezemer T.M., Brown V.K., Butterfield J., Buse A., Coulson J.C., Farrar J., Good J.E.G., Harrington R., Hartley S., Jones T.H., Lindroth R.L., Press M.C., Symrnioudis I., Watt A.D., Whittaker J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16.

Bezemer T.M., Jones T.H., Knight K.J. 1998. Long-term effects of elevated $CO_2$ and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. Oecologia 116: 128–135.

Buse A., Good J.E.G., Dury S., Perrins C.M. 1998. Effects of elevated temperature and carbon dioxide on the nutritional quality of leaves of oak (*Quercus robur* L.) as food for the winter moth (*Operophtera brumata* L.). Functional Ecology 12: 742–749.

Coley P.D., Barone A. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27: 305–335.

Dixon A.F.G. 2003. Climate change and phenological asynchromy. Ecological Entomology 28: 380–381.

Dury S.J., Good J.E.G., Perrins C.M., Buse A., Kaye T. 1998. The effect of increasing $CO_2$ and temperature on oak leaf palatability and implications for herbivorous insects. Global Change Biology 4: 55–61.

Fleming R.A. 1996. A mechanistic perspective of possible influences of climate changes on defoliating insects in North America's boreal forests. Silva Fennica 30: 281–294.

Fleming R.A. 2000. Climate change and insect disturbance regimes in Canada's boreal forests. World Resources Review 12: 520–555.

Fleming R.A., Candau J.N., Munn R.E. 1998. Influences of climatic change on some ecological processes of an insect outbreak system in Canada's boreal forests and the implications for biodiversity. Environmental Monitoring and Assessment 49: 235–249.

Giertych M.J., Bąkowski M., Karolewski P., Żytkowiak R., Grzebyta J. 2005. Influence of mineral fertilization on feed quality of oak leaves and utilization efficiency of feed components by the gypsy moth. Entomologia Experimentalis et Applicata 117: 59–69.

Graglia E., Julkunen-Titto R., Shaver G.R., Schmidt I.K., Jonasson S., Michelsen A. 2001. Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. New Phytologist 151: 227–236.

Harrington R., Fleming R.A., Wolwod I.P. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agricultural and Forest Entomology 3: 233–240.

Hough J.A., Pimentel D. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. Environmental Entomology 7: 97–102.

Houghton J.T., Ding Y., Griggs D.J., Noguer M., van der Linden P.J., Dai X., Maskell K., Johnson C.A. 2001. Working Group I: The Scientific Basis. Intergovernmental Panel on Climate Change (IPCC). Third Assessment Report: Climate Change: 2001. Available from: http://www.ipcc.ch/

Hwang S-Y., Lindroth R.L. 1997. Clonal variation in foliar chemistry of aspen: effects on gypsy moth and forest tent caterpillars. Oecologia 111: 99–108.

Klimetzek D., Yue C.F. 1997. Climate and forest insect outbreaks. Biologia 5: 153–157.

Lazarević J., Perić-Mataruga V., Stojković B., Tucić N. 2002. Adaptation of the gypsy moth to an unsuitable host plant. Entomologia Experimentalis et Applicata 102: 75–86.

Leather S.R., MacKenzie G.A. 1994. Factors affecting the population development of the bird cherry ermine moth, *Yponomeuta evonymella* (L.). Entomologist 113: 86–113.

Lindroth R.L., Klein K.A., Hemming J.D.C., Feuker A.M. 1997. Variation in temperature and dietary nitrogen affect performance of the gypsy moth (*Lymantria dispar* L.). Physiological Entomology 22: 55–64.

Meusel H., Jäger E., Weinert E. 1965. Vergleichende Chorologie der zentraleuropäischen Flora. VEB G. Fischer. Jena, Germany.

Raubenheimer D., Simpson S.J. 1992. Analysis of covariance: an alternative to nutritional indices. Entomologia Experimentalis et Applicata 62: 221–231.

Régnière J., Sharov A. 1999. Stimulating temperature-dependent ecological processes at the sub-continental scale: male gypsy moth flight phenology as an example. International Journal of Biometeorology 42: 146–152.

Sharov A.A., Pijanowski B.C., Liebhold A.M., Gage S.H. 1999. What affects the rate of gypsy moth (Lepidoptera: Lymantriidae) spread: winter temperature or forest susceptibility? Agricultural and Forest Entomology 1: 37–45.

Stillwell R.C., Fox C.W. 2005. Complex patterns of phenotypic plasticity: interactive effects of temperature during rearing and oviposition. Ecology 86: 924–934.

Tenow O., Nilssen A.C., Holmgren B., Elverum F. 1999. An insect (*Argyresthia retinella*, Lep., Yponomeutidae) outbreak in northern birch forests, released by climatic changes? Journal of Applied Ecology 36: 111–122.

Walter H. 1976. Strefy roślinności a klimat. PWRiL, Warszawa, Poland (in Polish).

Walther G.R. 2004. Plants in a warmer world. Perspectives in Plant Ecology Evolution and Systematics 6: 169–185.

Wilf P., Labandeira C.C. 1999. Response of plant-insect associations to Paleocene-Eocene warming. Science 284: 2153–2159.

Williams R.S., Lincoln D.E., Norby R.J. 2003. Development of gypsy moth larvae feeding on red maple samplings at elevated $CO_2$ and temperature. Oecologia 137: 114–122.

Williams R.S., Norby R.J., Lincoln D.E. 2000. Effects of elevated $CO_2$ and temperature-grown red and sugar maple on gypsy moth performance. Global Change Biology 6: 685–695.