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Development of *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) in Response to Constant Temperatures

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Desenvolvimento de *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) em Diferentes Temperaturas Constantes

RESUMO - O efeito da temperatura sobre o desenvolvimento da broca do broto do mogno, *Hypsipyla grandella* (Zeller), foi determinado em laboratório, em Turrialba, Costa Rica. Para tanto, duzentos ovos com menos de 24h foram colocados individualmente em frascos de vidro e expostos às temperaturas de 10; 12,5; 15; 20; 25; 30 e 35ºC. O estudo foi realizado em câmaras climáticas, com umidade de 80-90% e fotoperíodo de 8L:16D. Após a eclosão, as larvas foram alimentadas com folhas tenras de cedro (*Cedrela odorata*) e inspecionados a cada 24h para determinar a duração das fases larval e de pupa, e a emergência dos adultos em cada temperatura. As relações entre essas variáveis e a temperatura foram analisadas através de ANOVA, regressão e correlação. A temperatura teve grande influência no desenvolvimento das fases imaturas e na emergência dos adultos de *H. grandella*. A duração do ciclo biológico (ovo-adulto) variou de 30 dias (30ºC) a 104 dias (15ºC). A mortalidade do estágio larval foi alta nessas temperaturas, alcançando taxas de 90% (15°C) e 45% (30ºC). A mortalidade de larvas de primeiro instar foi também relativamente alta (51-75%) nas temperaturas dentro do intervalo de 15ºC a 30ºC, com exceção daquelas que se desenvolveram a 25ºC (14%). O peso das pupas foi menor em temperaturas extremas (15ºC e 30ºC). A estimativa da temperatura base de desenvolvimento para todos os estágios imaturos (8,5ºC) permitiu calcular a constante térmica (1320 graus dias), a qual possibilitará a previsão de picos populacionais no campo.

PALAVRAS-CHAVE: Meliaceae, taxa de desenvolvimento, limiar térmico, constante térmica, Costa Rica

ABSTRACT - Developmental response of the mahogany shootborer, *Hypsipyla grandella* (Zeller), to temperature was determined in laboratory trials in Turrialba, Costa Rica. Two hundred fresh eggs (less than 24h old) were placed individually inside glass flasks, and exposed to seven constant temperatures (10, 12.5, 15, 20, 25, 30 and 35°C), in separate experiments. These were carried out in environmental chambers, at 80-90% relative humidity and 8L:16D photoperiod. After hatch, larvae were fed tender foliage of Spanish cedar (*Cedrela odorata*) and were inspected every 24h to determine larval and pupal duration, and adult emergence, at each temperature. Relationships between these variables and temperature were analyzed by means of ANOVA, regression and correlation procedures. Temperature greatly influenced development of *H. grandella* immature stages and adult emergence; development time varied between 30 days (30ºC) and 104 days (15°C). Larval mortality was high at those temperatures, reaching values of 90% (15°C) and 45% (30ºC). Also, mortality of the first larval instar was relatively high (51-75%) at all temperatures in the range 15-30°C, except at 25ºC (14%). Pupal weight was lower at extreme temperatures (15ºC and 30ºC). Estimation of a common lower thermal threshold for all immature stages (8.5ºC) allowed calculation of a general thermal constant (1320 degree-days), which could be used to predict population peaks in the field.

KEY WORDS: Meliaceae, development rate, thermal threshold, thermal constant, Costa Rica

Two congeneric shootborer species, *Hypsipyla grandella* (Zeller) and *H. robusta* (Moore), are key pests of several Meliaceae species of high economic importance as timber trees (Mayhew & Newton 1998). The former is distributed throughout the neotropics, whereas *H. robusta* is present in the Old World tropics (Schabel *et al.* 1999). Both

of them bore into terminal shoots of young host plants, breaking the apical dominance, which causes forking of the stem and excessive production of lateral branches. In the case of *H. grandella*, this feeding habit has frustrated attempts to establish commercial plantations of mahoganies (*Swietenia* spp.) and cedars (*Cedrela* spp.) in Latin America and the Caribbean (Grijpma & Ramalho 1973).

Even though a great deal of research aimed at managing *H. grandella* has been conducted (Newton *et al.* 1993, Mayhew & Newton 1998), the response of the insect to abiotic factors has been poorly documented. For instance, available information on the *H. grandella* life cycle in response to varying temperature is inadequate, as published figures are either general estimates from field or laboratory data, or data have been gathered at only a single temperature under controlled conditions (Ramírez-Sánchez 1964, Roovers 1971, Becker 1976).

From biological and ecological standpoints, this lack of reliable information prevents rigorous comparisons of development among *H. grandella* stages and between *H. grandella* and other insect species. Furthermore, it precludes using degree-day approaches (Wigglesworth 1972, Pruess 1983) to predict field population peaks of this pest, in order to improve timing for application of management tactics. Therefore, the objective of this research was to determine the response of *H. grandella* to a range of constant temperatures and estimate both its lower thermal threshold and thermal constant as a basis for predicting population peaks in the field.

Materials and Methods

Study Site. Research was conducted at the Tropical Agricultural Research and Higher Education Center (CATIE), in Turrialba, in the Caribbean watershed of Costa Rica. CATIE is located at 9º52'N, 83º38'O and 590 masl, within the premontane wet forest life zone (Tosi 1969).

Laboratory trials were carried out in environmental chambers (Percival I-35L), in which relative humidity (80-90%) and photoperiod (8L:16D) were kept constant for all experiments. Response to temperature was assessed by exposing *H. grandella* eggs to six constant temperatures (10, 15, 20, 25, 30 and 35°C) in individual experiments; an additional temperature evaluation (12.5°C) was included later on for those cases in which there was no response at 10ºC, but it would be expected to obtain some response above 10° C and below 15ºC.

Procedures. *H. grandella* eggs were taken from colonies maintained at CATIE, where larvae were initially reared on tender foliage of Spanish cedar (*Cedrela odorata* L.) and later transferred to an artificial diet (Vargas *et al.* 2001).

For determining development time, a cohort of 200 fresh eggs (less than 24h old) was placed individually inside 30 ml glass flasks containing a disk of *C. odorata* tender foliage (2.3 cm in diameter). Flasks were turned upside down and each egg was placed above the disk. A piece of paper towel was fastened with the lid and was moistened periodically. Eggs were inspected every 24h, in order to determine hatching rates and development time at each constant temperature.

Once eggs hatched, each first-instar larva was kept in the respective flask, where it was fed with tender foliage, until reaching instar III. Afterwards, each larva was transferred to a flask containing about 5 ml of artificial diet (Vargas *et al.* 2001), where it was allowed to complete development. Larvae were inspected every 24h, in order to determine instar duration by observing morphological changes (size and larval signs, such as their old head capsule and exuviae), at each constant temperature.

Each pupa was weighed using an analytical scale and sexed (Hidalgo-Salvatierra 1973) to determine sex ratio. The pupa was subsequently transferred to a dry, 30ml plastic flask, where it was inspected daily until adult emergence. Dates for adult emergence were recorded, and experiments were carried out to study adult longevity and oviposition patterns. However, these experiments failed, because pairs of *H. grandella* did not mate when they were in small cages placed inside the environmental chambers, except at 25°C. In order to determine mating success, females were dissected to count the number of spermatophores in their bursa copulatrix, as each one of them represent a successful mating (Lara 1974).

Analysis. The relationship between development time (by instar and sex) and temperature was analyzed by means of ANOVA procedures, and means were compared by Tukey's HSD test (SAS Institute 1985), at a significance level of $\alpha = 0.05$. Also, regression and correlation analyses were performed to examine the relationships between temperature and the rates of development of immature stages and adult emergence.

Development time (T) data were transformed by dividing 1/T, to obtain the rate of development at each temperature. The regression lines between development rate and temperature were extended to obtain the lower thermal threshold (LTT), which corresponds to the intersection with the abscissa (Davidson 1944, Wigglesworth 1972). The LTT was then used to calculate the thermal constant, which represents the physiological time required to complete development at each temperature. This was achieved by means of the algorithm $K = y\ (t\text{-}a)$, where: K (thermal constant), y (development time), t (temperature) and a (LTT) (Wigglesworth 1972). Afterwards, a general thermal constant was calculated, by averaging thermal constants obtained at 15, 20, 25 and 30°C (Wigglesworth 1972).

Results and Discussion

Development Time. Temperature greatly influenced the development time of immature stages (egg, larva and pupa) of *H. grandella*, as it occurs with many insect species (Davidson 1944, Bursell 1964, Wigglesworth 1972, Dent 1991). Except for the larval stage at 25°C and 30°C, development time for immature stages decreased as temperature increased ($P < 0.05$) (Table 1). Total development time, which ranged from 104 (15ºC) to 30 days (30ºC), also decreased with increasing temperatures ($P < 0.05$), except between 25°C and 30°C. There were no differences in development times between sexes for any stage ($P > 0.05$), except for the pupal stage at 20°C, in which females spent 18.1 ± 1.5 days and males 20.1 ± 2.1 days.

Development time curves for eggs, larvae and pupa were best fitted by the potential model (Fig. 1). Because larvae and pupae were unable to develop beyond 30°C, the linear tendency for calculating development rate was obtained only up to that temperature.

Table 1. Development time (days) of the immature stages of *H. grandella*, at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D.

°C	Egg		Larva		Pupa		Total	
	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.
10	0	ND		ND		ND		ND
12,5	8	23.0 ± 2.66 a		ND		ND		ND
15	99	12.7 ± 1.20 b	10	65.9 ± 8.70 a	3	29.0 ± 1.00 a	3	104.0 ± 2.00 a
20	143	7.6 ± 0.68 c	54	39.2 ± 8.66 b	32	19.2 ± 2.11 b	30	61.5 ± 4.15 b
25	113	4.3 ± 0.64 d	91	18.7 ± 2.47 c	58	13.4 ± 1.20 c	58	36.1 ± 2.58 c
30	126	3.8 ± 0.49 e	57	17.2 ± 2.23 c	22	9.9 ± 1.85 d	20	29.7 ± 2.46 c
35	83	3.1 ± 0.33 f		ND		ND		ND

ND = No data, because development did not occur at these temperatures; X = Mean; S.D. = Standard deviation
Means followed by the same letter in each column were not significantly different (P < 0.05), according to Tukey´s HSD test.

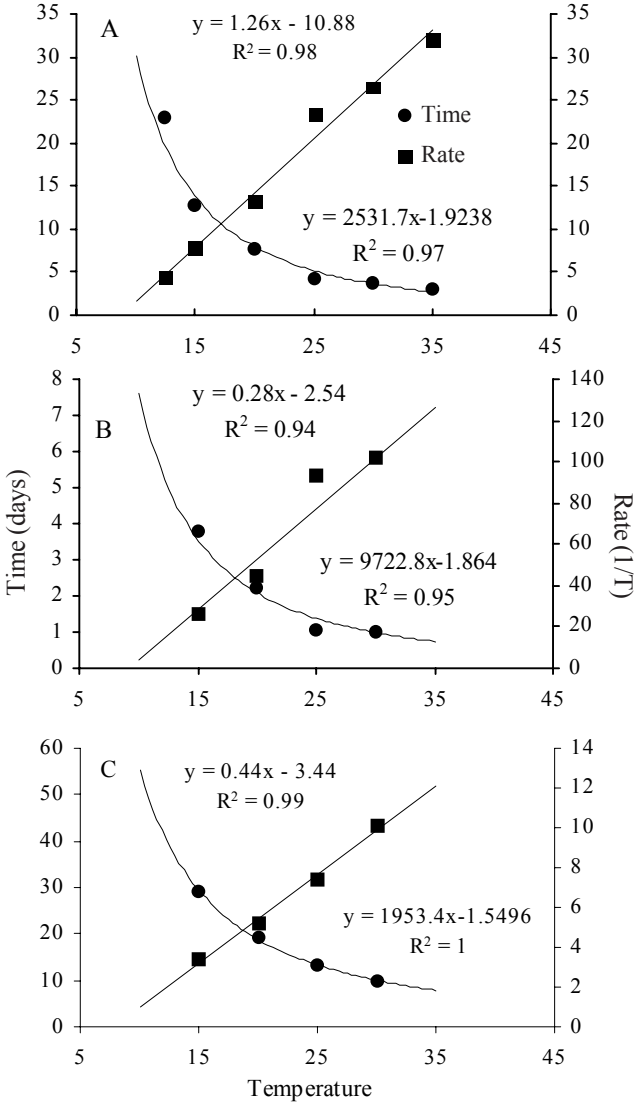

Figure 1. Time (days) and development rate for eggs (A), larvae (B) and pupae (C) of *H. grandella*, at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D. The continuous lines depict the responses predicted from the regression model.

Development rate was highest for eggs (1.26), followed by pupae (0.44) and larvae (0.28) (Table 2). These values allowed calculation of the lower thermal threshold for each stage: 8.7°C (egg), 9.1°C (larva) and 7.8°C (pupa) (Table 2). These theoretical thresholds did not exactly coincide with real values, as at 10°C no one of the stages showed any signs of development. Egg hatching was arrested at 10°C, and although at 12.5°C egg hatching occurred, development did not proceed further (Table 1). Thermal constants were estimated for each temperature (Table 3), and a general constant of 1320 degree-days was calculated.

Larvae did not develop at temperatures below 15ºC or above 30ºC (Table 1). They normally passed through six instars, but at the two lowest temperatures (15°C and 20°C) there were additional instars (Table 4). Supernumerary instars have been reported for *H. grandella* (Ramírez-Sánchez 1964, Roovers 1971, Hidalgo-Salvatierra & Berríos 1973), but their occurrence had not been related to temperature. At 20°C there were two additional instars, which lasted for 10.5 and 26 days, respectively, whereas the rest of the instars varied between 4

Table 2. Regression equations, coefficients of determination (R^2) and variation (C.V.) , and lower thermal thresholds for development rates of each one of the immature stages of *H. grandella*, at constant temperatures between 12.5ºC and 35°C.

Stage	Equation	R²	C.V.	Threshold (°C)
Egg	Y = 1.26X - 10.88	0,98	9,30	8,66
Larva	Y = 0.28X - 2.54	0,94	14,54	9,09
Pupa	Y = 0.44X - 3.44	0,99	4,81	7,74

Table 3. Thermal constants for *H. grandella* at each of four temperatures, expressed in both Celsius (°C) and Fahrenheit (°F) degrees, assuming a development threshold of 8.5°C.

°C	°F	Development time (days)	Thermal constant (K)	
			°C	°F
15	59	141,33	918,65	1685,56
20	68	61,53	707,60	1305,67
25	77	36,13	596,15	1105,06
30	86	29,75	639,63	1183,33

Table 4. Development time (days) of larval instars of *H. grandella* at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D.

°C	Instar I		Instar II		Instar III		Instar IV		Instar V		Instar VI		Instar VII		Instar VIII	
	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.	N	X ± S.D.
15	24	8.7 ± 1.79a	22	9.1 ± 2.91a	22	8.4 ± 2.32a	19	10.1 ± 3.70a	19	9.6 ± 3.73a	17	18.1 ± 11.89a	7	22.0 ± 6.73a		ND
20	59	5.4 ± 0.99b	57	3.8 ± 0.73b	57	3.9 ± 0.97b	57	5.5 ± 1.50b	56	6.2 ± 2.04b	54	13.3 ± 4.97a	4	10.5 ± 7.19b	1	26.0 ± 0.00
25	97	2.7 ± 0.94c	93	2.1 ± 1.01c	91	2.3 ± 1.00c	91	3.1 ± 0.81c	91	3.4 ± 1.20c	91	5.1 ± 2.65b		ND		ND
30	61	2.2 ± 0.61cd	58	1.8 ± 0.68cd	58	1.8 ± 0.82c	57	3.0 ± 0.80c	57	2.6 ± 0.73cd	57	5.9 ± 1.73b		ND		ND
35	35	1.6 ± 0.49d	26	1.1 ± 0.33d	19	1.7 ± 0.65c	14	2.3 ± 0.47c	9	1.9 ± 0.93d	2	3.0 ± 1.41b		ND		ND

ND = No data, since development did not occur at these temperatures; X = Mean; S.D. = Standard deviation
Means followed by the same letter in each column were not significantly different (P < 0.05), according to Tukey´s HSD test.

and 13 days; also, the additional instar at 15°C lasted for 22 days, whereas the rest of the instars ranged from 8 to 18 days.

Mean development time for each larval instar tended to decrease as temperature increased. Differences in development time at adjacent temperatures were significant (P < 0.05), with the exception of some instars at either 25, 30 or 35ºC. Also, there were no differences in development times (data not shown) between sexes for any stage (P > 0.05), except for a few isolated cases.

Pupal Weight and Sex Ratio. Pupal weight was lower (P < 0.05) at the two extreme temperatures (15ºC and 30ºC) and did not differ between them. It was higher (P < 0.05) at intermediate temperatures (20ºC and 25ºC) than at the two extremes (Table 5). There were no differences between pupal weights of females and males at the two extreme temperatures (P > 0.05), but at the intermediate ones females were heavier (P < 0.05) than males (Table 6). This may be explained by the higher levels of food storage normally present in the fat body tissue of the female (Chapman 1998).

There was a sex ratio bias to females at the two extreme temperatures, whereas at the intermediate temperatures the proportion of both sexes was nearly equal (Table 5). The large female bias obtained at 15°C may be due to low sample size.

Mortality Patterns. Temperature clearly influenced mortality during development (Fig. 2). Eggs survivorship was lowest at the two extreme temperatures (4% at 12.5°C and 42% at 35°C); at the latter, larvae that hatched were unable to reach the pupal stage. At the highest temperature, survivorship was nil through the larval stages. This can be explained because high temperatures constrain insect development either by protein denaturing or because of accumulation of toxic wastes resulting from metabolic imbalances (Chapman 1998).

In addition to eggs, larval instar I showed moderate to low survivorship levels, ranging from 24% to 48%, except at 25°C, at which it was 86%. Once instar II was reached, survivorship remained stable until the pupal stage, except at 35ºC, but in the transition between pupa and adult emergence it decreased from 42 to 30% at 25, 30 and 15°C; at 20°C, it reached 59%. Pupal mortality was generally high. Thus, the most vulnerable *H. grandella* stages to temperature extremes were the egg, larval instar I, and the pupa.

Adult Emergence Patterns. Data for adult emergence at 15ºC were omitted, due to the small sample size (n = 3). Emergence ocurred only at intermediate temperatures, between 20°C and 30ºC. Cumulative emergence at these temperatures was best described by logarithmic curves with decreasing increments over time (Fig. 3), possibly because of the acceleration of metabolic processes during the pupal stage.

Emergence rates increased with temperature, so that 100% emergence was attained earliest at 30°C (10 days), followed by 25°C (12 days) and 20°C (25 days); 50% emergence was

Table 5. Weight and sex ratio for *H. grandella* pupae at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D.

°C	Weight (g)		Sex ratio		F: M
	N	X ± S.D.	F	M	
15	10	0.070 ± 0.026 a	8	2	4.00 *
20	54	0.134 ± 0.033 b	24	30	0.80 ns
25	91	0.124 ± 0.035 b	44	47	0.94 ns
30	57	0.081 ± 0.033 a	36	21	1.71 *

X = Mean; S.D. = Standard deviation
Means followed by the same letter were not significantly different (P < 0.05), according to Tukey´s HSD test.
Sex ratio values were significant (*) or non-significant (ns) (P < 0.05), according to Tukey's HSD test.

Table 6. Weight (g) of *H. grandella* pupae, according to sex at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D.

°C	Sex	N	X ± S.D.
15	Female	8	0.074 ± 0.030 a
	Male	2	0.053 ± 0.020 a
20	Female	24	0.147 ± 0.034 b
	Male	30	0.123 ± 0.029 c
25	Female	44	0.134 ± 0.030 d
	Male	47	0.116 ± 0.030 e
30	Female	36	0.086 ± 0.037 f
	Male	21	0.070 ± 0.020 f

X= Mean; S.D.= Standard deviation
Means followed by the same letter (for each sex, at the same temperature) in each column were not significantly different (P < 0.05), according to Tukey´s HSD test.

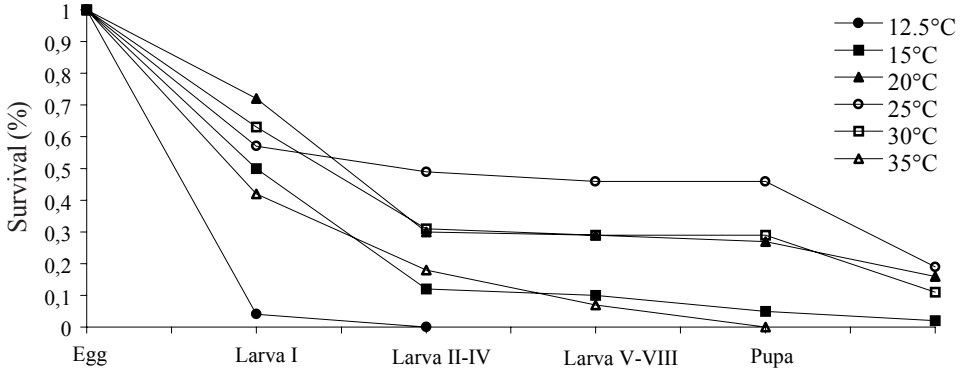

Figure 2. Survival curves for *H. grandella* stages, at several constant temperatures, RH = 80-90%, and a photoperiod of 8L:16D.

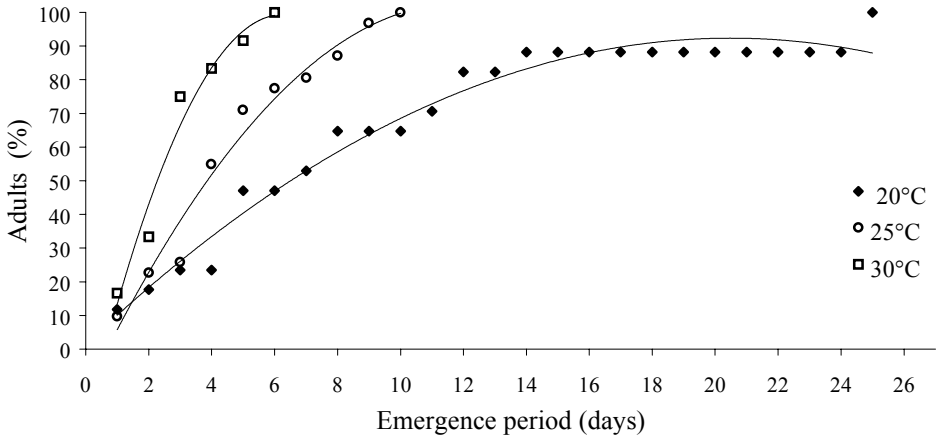

Figure 3. Cumulative emergence of *H. grandella* adults, from the first day at which emergence occurred at each constant temperature. The continuous lines depict the curves best fitting the data.

reached at four, five and seven days, respectively. Equations were: $Y = -0.26x^2 + 10.56x - 11.35$ ($R^2 = 0.98$) for 20°C, $Y = -0.66x^2 + 18.57x - 26.37$ ($R^2 = 0.96$) for 25°C, and $Y = -0.90x^2 + 21.17x - 21.51$ ($R^2 = 0.95$) for 30°C. These trends also held for each sex. Mortality followed a similar pattern, so that it was highest at the two highest temperatures (25°C and 30ºC).

Females copulated only at 25°C, and they mated only once, which was revealed by the presence of a single spermatophore in the female´s bursa copulatrix. This fact coincided with findings from previous authors (Lara 1974), who reported that during copulation the male inserts a single spermatophore. Failure to mate at most temperatures in our experiments could be due to absence of air currents inside the environmental chamber. For instance, mating success of *H. robusta* can be increased by exposing caged adults to alternating or continuous air currents (Mo & Tanton 1996). The mechanism by which wind promotes mating is unclear, but may involve release or dispersal of the female´s sex pheromone. Fasoranti (1985) showed that flight strongly influences mating and oviposition in *H. grandella*. The absence of air circulation in the chambers may limit flight behavior by *H. grandella*.

The constant-temperature regimes in our study did not mimic the diurnal variation occurring in *H. grandella* habitat. For instance, in Turrialba, Costa Rica, differences as high as 13ºC can be observed between the highest and the lowest daily temperatures. Nevertheless, the information gathered at constant temperatures in environmental chambers allowed us to estimate a common lower thermal threshold for all *H. grandella* immature stages (8.5ºC), and to calculate a general thermal constant (1320 degree-days). Using these values through the degree-day method (Wigglesworth 1972, Pruess 1983, University of California 1990), Taveras *et al.* (in press) successfully predicted four population peaks, occurring at intervals close to 1881 degree-days, during a 16-month period in Turrialba.

Prediction of *H. grandella* population peaks could be used to time suppressive measures and prevent population from damaging both mahogany and cedar trees in commercial plantations. Aside from bioinsecticides, such as derivatives of neem (*Azadirachta indica*, Meliaceae) (Mancebo *et al.* 2002), such measures could include both repellent/deterrent substances (Mancebo *et al.* 2000, 2001), as well as pheromones. Research on both of these approaches is underway in Costa Rica.

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Literature Cited

Becker, V.O. 1976. Microlepidópteros asociados con *Carapa, Cedrela* y *Swietenia* en Costa Rica. p. 75-101. In J.L. Whitmore (ed.), Studies on the shootborer *Hypsipyla grandella* (Zeller). Lep. Pyralidae v. 2. IICA Misc. Publ. No. 101. San José, Costa Rica, 139p.

Bursell, E. 1964. Environmental aspects: Temperature. p. 283-321. In M. Rockstein (ed.), The physiology of Insecta. v. 1. Academic Press, New York, 640p.

Chapman, R.F. 1998. The insects. Structure and function. 4 ed. Cambridge University Press, 819p.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13: 26-38.

Dent, D. 1991. Insect pest management. CAB International, United Kingdom, 604p.

Fasoranti, J.O. 1985. Influence of flight on the mating behavior of the mahogany shootborer *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae). Turrialba 35: 300-302.

Grijpma, P. & R. Ramalho. 1973. *Toona* spp., posibles alternativas para el problema del barrenador *Hypsipyla grandella* de las Meliaceae en América Latina. p. 3-17. In P. Grijpma (ed.), Studies on the shootborer *Hypsipyla grandella* (Zeller). Lep. Pyralidae v. 1. IICA Misc. Publ. No. 101. San José, Costa Rica, 91p.

Hidalgo-Salvatierra, O. 1973. Determinación del sexo en pupas, p. 67. In P. Grijpma (ed.), Studies on the shootborer *Hypsipyla grandella* (Zeller). Lep. Pyralidae v. 1. IICA Misc. Publ. No. 101. San José, Costa Rica, 91p.

Hidalgo-Salvatierra, O. & F. Berríos. 1973. Growth of larvae reared on a synthetic diet, p. 77-80. In P. Grijpma (ed.), Studies on the shootborer *Hypsipyla grandella* (Zeller). Lep. Pyralidae v. 1. IICA Misc. Publ. No. 101. San José, Costa Rica, 91p.

Lara, L. 1974. Algunos aspectos en la biología, desarrollo y reproducción de *Hypsipyla grandella* (Zeller) (Lepidoptera: Pyralidae) en condiciones de laboratorio. MSc Thesis. University of Washington, Seattle, 77p.

Mancebo, F., L. Hilje, G.A. Mora & R. Salazar. 2000. Antifeedant activity of *Quassia amara* (Simaroubaceae) extracts on *Hypsipyla grandella* (Lepidoptera: Pyralidae) larvae. Crop Prot. 19: 301-305.

Mancebo, F., L. Hilje, G.A. Mora & R. Salazar. 2002. Biological activity of two neem (*Azadirachta indica* A. Juss., Meliaceae) products on *Hypsipyla grandella* (Lepidoptera: Pyralidae) larvae. Crop Prot. 21: 107-112.

Mancebo, F., L. Hilje, G.A. Mora, V.H. Castro & R. Salazar. 2001. Biological activity of *Ruta chalepensis* (Rutaceae) and *Sechium pittieri* (Cucurbitaceae) extracts on *Hypsipyla grandella* (Lepidoptera: Pyralidae) larvae. Rev. Biol. Trop. 49: 501-508.

Mayhew, J.E. & A.C. Newton. 1998. The silviculture of mahogany. CABI Publishing. Wallingford, United Kingdom, 226p.

Mo, J. & T. Tanton. 1996. Diel activity pattern and effects of wind on the mating success of cedar tip moth, *Hypsipyla robusta* Moore (Lepidoptera: Pyralidae). Austr. Forest. 59: 42-45.

Newton, A.C., P. Baker, S. Ramnarine, J.F. Mesén & R.R.B. Leakey. 1993. The mahogany shoot borer: Prospects for control. Forest Ecol. Manage. 57: 301-328.

Pruess, K.P. 1983. Day-degree methods for pest management. Environ. Entomol. 12: 613-619.

Ramírez-Sánchez, J. 1964. Investigación preliminar sobre biología, ecología y control de *Hypsipyla grandella*. Bol. Inst. For. Latino Amer. Invest. y Capacit. (Venezuela) 16: 33-37.

Roovers, M. 1971. Observaciones sobre el ciclo de vida de *Hypsipyla grandella* Zeller en Barinitas, Venezuela. Bol. Inst. For. Latino Amer. Invest. Capacit. (Venezuela) 38: 3-46.

SAS Institute. 1985. SAS user guide: Statistics, Version 5 ed. SAS Institute Inc. Cary, North Carolina. 956p.

Schabel, H., L. Hilje, K.S.S. Nair & R.V. Varma. 1999. Economic entomology in tropical forest plantations: An update. J. Trop. Forest Sci. 11: 303-315.

Taveras, R., L. Hilje, P. Hanson, R. Mesón, M. Carballo & C. Navarro. Population trends and damage patterns of *Hypsipyla grandella* (Lepidoptera: Pyralidae) in a mahogany stand, in Turrialba, Costa Rica. Agric. Forest Entomol. (in press).

Tosi, J. 1969. Mapa ecológico de la República de Costa Rica, según la clasificación de zonas de vida del mundo de L.R. Holdridge. Centro Científico Tropical. San José, Costa Rica.

University of California. 1990. DDU (Degree-Day Utility). User's guide. Version 2.0. Univ. California IPM Publ. 9.

Vargas, C., P.J. Shannon, R. Taveras, F. Soto & L. Hilje. 2001. Un nuevo método para la cría masiva de *Hypsipyla grandella* Hoja Técnica No. 39. Manejo Integr. Plagas 62: i-iv.

Wigglesworth, V.J. 1972. The principles of insect physiology, 7 ed. Chapman & Hal, London, 827p.

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