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On the canopy structure manipulation to buffer climate change effects on insect herbivore development

Marc Saudreau · Sylvain Pincebourde ·
Mathieu Dassot · Boris Adam · Hugh D. Loxdale ·
David G. Biron

Abstract Insect pest development is often linearly related to air temperature, without taking into account the multiple interactions between the particular host plant and pest, the microclimatic conditions actually experienced by the insect, and the non-linear response of insect development rate to temperature. In this study, using an integrative biophysical model, we have investigated effects of both climatic and tree structure changes on the development of a phytophagous leaf mining moth (*Phyllonorycter blancardella*), taking into account the heterogeneous microclimatic conditions provided by its host plant, the domestic apple (*Malus domestica*), the larval body temperature rather than the ambient air temperature, and a non-linear development rate model. Hourly body temperature dynamics of larvae homogeneously dispersed in tree canopies were simulated from hourly meteorological conditions (medium IPCC climate change scenario) within the canopy of apple trees. To analyse the effect of tree architecture on leaf miner development, both pruned and unpruned trees, and one, two and three scaffold branched trees were used. Body temperature dynamics was used to compute larval development time and mortality following the non-linear developmental model for this insect. The results showed that tree pruning influences significantly larval development time and mortality. Nevertheless, the effects of manipulating tree structure on larval development and survival were relatively weak compared with the impact of chosen climate variations. This survey also showed that the variability in insect development time within a year and insect mortality change markedly with climatic variations, and highlights the importance of using non-linear rate curves and insect body temperatures instead of air temperature in forecasting models of climate-related insect pest outbreaks.

M. Saudreau (✉) · M. Dassot · B. Adam · D. G. Biron
INRA, UMR0547 PIAF, 63100 Clermont-Ferrand, France
e-mail: marc.saudreau@clermont.inra.fr;
saudreau@clermont.inra.fr
URL: http://www2.clermont.inra.fr/piaf/index_eng.php

M. Saudreau · M. Dassot · B. Adam · D. G. Biron
Clermont Université, Université Blaise Pascal,
UMR547 PIAF, 63039 Clermont-Ferrand, France

S. Pincebourde
Institut de Recherche sur la Biologie de l'Insecte
(IRBI, CNRS UMR 6035), Faculté des Sciences et Techniques,
Université François Rabelais, 37200 Tours, France

H. D. Loxdale
Institute of Ecology, Friedrich-Schiller-University,
Dornburger Strasse 159, 07743 Jena, Germany

D. G. Biron
CNRS, UMR 6023, LMGE, 24 Avenue des Landais,
63177 Aubière, France

Introduction

In agro-ecosystems, tree canopy structures are manipulated to optimise radiation interception by leaves which enhance their physiological activity and results in higher yield (Jackson 1980; Robinson and Lakso 1991). More recently,

many authors have highlighted the fact that plant architecture management could provide (1) an innovative lever for low pesticide pest management systems (Simon et al. 2006), and (2) provide an appealing way to control pest development under the expected changing climate (Coakley et al. 1999; IPCC 2007; Pangga et al. 2011).

Relationships between the canopy structure and the tree physiology have been widely investigated and modelled (Sinoquet et al. 2001; Bauerle et al. 2004; Willaume et al. 2004), but much more less attention has been paid to effects on pest development, especially on trees. Plant canopies are highly structured environments set by the size, shape, orientation and density of plant organs—for example, leaves, branches, flowers and fruits. Such complex structures can act at least at two levels. First, insect herbivores, predators and hymenopterous parasitoids are not evenly distributed within plant canopies and their movements depend on the level of connectedness between plant organs (Casas and Djemai 2002; Skirvin 2004). Second, architecture directly sets the heterogeneity of microclimatic conditions which in turn influences the performance of insects (Pincebourde et al. 2007). Manipulating plant canopy architecture is likely to influence these aspects of insect ecology. Indeed, the hypothesis that there should be canopy configurations minimising insect herbivore population development or maximising insect mortality has been evoked (Simon et al. 2006, 2007). This hypothesis has however never been tested properly, and it is not known whether climate change reduces or magnifies this property of canopy architecture.

A few decades ago, ecologists began to simulate the development rate of insect species using phenological models dependent upon local climatic factors. These models simulate insect development according to air temperature. Therefore, they inherently assume that the insect microhabitat and body temperatures both equate with local ambient air temperature, but this assumption is not generally true. The body temperature of ectotherms such as insects results from multiple interactions between microclimatic conditions, the inherent properties of the animal (colouration, transpiration, size, shape, etc.), and the behaviour of the organism, e.g. behavioural thermoregulation (Gates 1980; Kingsolver 1983; Helmuth 1998; Pincebourde and Casas 2006a). Moreover, the microclimatic conditions are quite heterogeneous in both space and time, especially for small organisms like insects (Pincebourde et al. 2007; Scherrer and Korner 2009). For example, the architecture of plant canopies interacts with environmental factors such as radiation level to create a mosaic of various microclimates which shifts spatially according to sun elevation (Sinoquet et al. 2001). In combination with the heat budget of a leaf, the microclimatic mosaic can influence the development and the

distribution of insects within a plant canopy (Pincebourde et al. 2007). Simulating what the amplitude of insect body temperature change may be following climate warming is however challenging because of the non-linearity in the link between climate, the microclimate within plant canopies, the heat budget of a leaf, and an insect. The biophysical modelling approach alleviates this difficulty by integrating plant canopy architecture and microclimate functioning into a single mechanistic framework (Pincebourde et al. 2007).

The aim of the present study was to analyse and quantify how much plant architecture manipulation by altering the within-tree canopy microclimate may buffer variations in climatic conditions and then lower climate change impacts on a phytophagous insect.

In this study, we focused on a phytophagous insect, the fifth larval instar of the endophytous spotted tentiform leafminer moth, *Phyllonorycter blancardella* (F.) (Lepidoptera: Gracillariidae), and considered several tree canopy structures of its host plant, domestic apple, *Malus domestica* L. (Rosales: Rosaceae), and climatic conditions following a 21st climate change scenario proposed by the IPCC (2007). Interactions were modelled by the biophysical model of Pincebourde et al. (2007), which simulates the spatial distribution and the temporal dynamics of leaf and mine temperatures within the tree crown. A developmental rate model was integrated into this biophysical framework.

Materials and methods

Integrative biophysical model

As mentioned above, a biophysical model (Pincebourde et al. 2007) was used to predict the body temperature of a leafminer larva at a given position within a tree crown from local climatic conditions. This model was built by coupling (1) a model for radiation and leaf energy budget distribution within a tree canopy (Sinoquet et al. 2001); (2) a biophysical model for mine energy budget (Pincebourde and Casas 2006a); and (3) an empirical model of larval body temperature (Pincebourde and Casas 2006b). We then connected this cascade of models to a non-linear biophysical model of insect development rate. This integrative biophysical model (Fig. 1) (1) simulates the hourly dynamics of the spatial distribution of leaf microclimate into an apple tree taking into account the tree architecture, the orchard structure and local climatic conditions; (2) accurately predicts temperature within *P. blancardella* mines at different positions within an apple tree crown from the leaf microclimate; and (3) simulates the development time and the survival rate of the fifth (L5) larval

Fig. 1 Description of the integrative biophysical model used to predict body temperature of a larva, and its development rate, at a given position within a tree crown from local climatic conditions
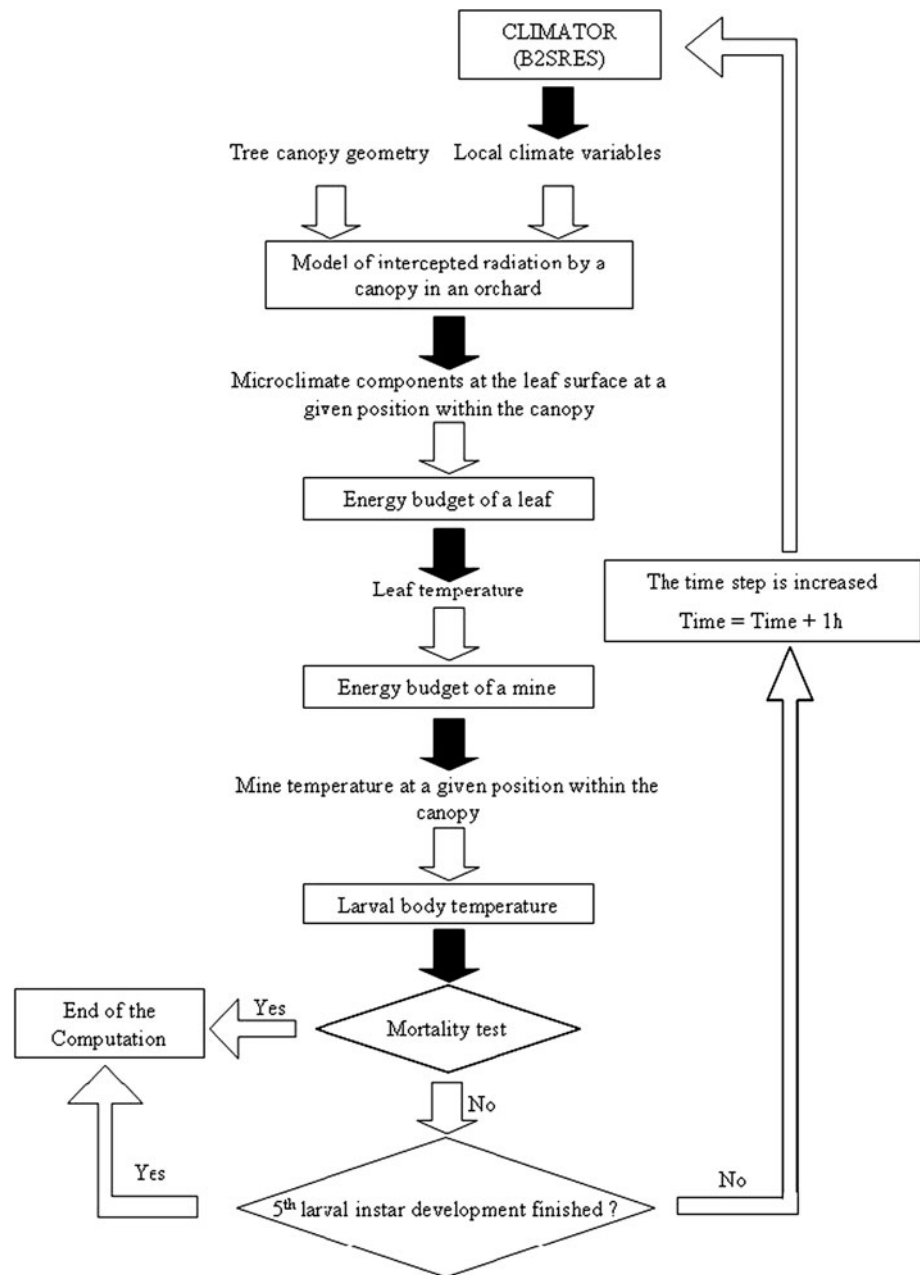
instar of *P. blancardella* as a function of its body temperature and position within the tree crown. All these models were tested and validated within a broad range of variable values (Sinoquet et al. 2001; Pincebourde and Casas 2006a; Pincebourde et al. 2007).

A key feature of our integrative model is that it considers insect body temperature rather than air temperature. For instance, the leaf miner body temperature can be above ambient air temperature by >10 °C under high irradiation level (Pincebourde and Casas 2006a). The development rate model is curvilinear and based on a poikilotherm curve (Schoolfield et al. 1981). Biophysical curve parameters (temperatures and related enthalpy activations) were

obtained by fitting experimental data of the L5 larval instar of *P. blancardella* (Baumgartner and Severini 1987) with the additional hypothetical feature of setting the developmental rate to zero when body temperature reached 42 °C in accordance with Pincebourde et al. (2007) (Fig. 2). All parameters of the integrative biophysical model are given in Tables S1 and S2.

Host plant

We tested whether the manipulation of plant architecture influences the thermal environment of the leaf miner to the point of buffering/amplifying the amplitude of climate
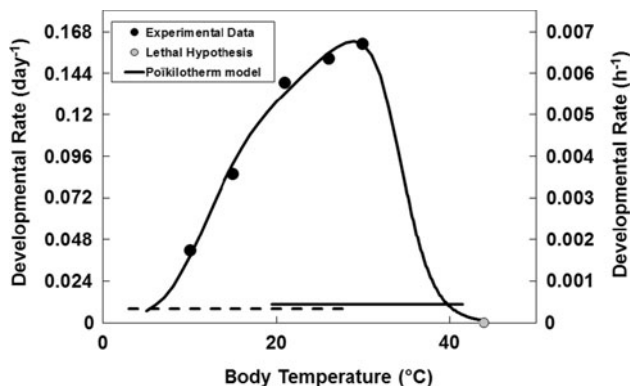
Fig. 2 Non-linear curve of development rate of *P. blancardella* at fifth larval instar (L5) established with the biophysical model of Schoolfield et al. (1981) using experimental data of Baumgartner and Severini (1987) and the lethal temperature threshold given in Pincebourde et al. (2007). Portions of the development rate curve used during simulations for two periods with contrasting climatic conditions, May 2000 and July 2100, are shown by a *dashed line* and a *line* respectively (see Fig. 3)

change. The biophysical model was implemented with an explicit spatial representation of the canopy architecture, which is defined here as the 3-D coordinates and orientation angles of leaves. Simulations were performed using six 3-D apple tree virtual mock-ups representing six real trees from two different orchards (Table 1). The architecture of these trees, located in Centre de Fougères of Agroscope Changins-Wädenswil ACW research station, Switzerland, was digitised according to the method given in Sinoquet et al. (1998, 2009). Thereafter, each 3-D mock-up was built using the shoot scale method of Sonohat et al. (2006). The two orchards ($N = 3$ trees for each orchard) differed in their architectural managements during tree development (Sinoquet et al. 2007). In the two orchards, apple trees were subjected to one of these training regimes (see Table 1): (1) vertical axis ("V", a central axis tree bearing fruiting branches); (2) drilling ("D", a three scaffold branches tree); and (3) Ycare ("Y"; a two scaffold branches tree). In the first orchard, training systems were applied as vegetative shoots were pruned ("pruned" in Table 1). In the second orchard this training system was not strictly applied and the vegetative shoots were not pruned ("unpruned" in Table 1). Within the two virtual orchards, the row orientation was north-south, inter-row distance was 4 m, with interplant distance on the row equal to 1.25 m for vertical axis ("V") and drilling ("D"), and 1 m for Ycare ("Y") training systems.

Climatic scenario

Predicted meteorological data during the 21st century for the city of Avignon in France (43.94°N, 4.80°W) were used as input climatic variables (see Table 2). Daily data were provided courtesy of the AGROCLIM database (http://
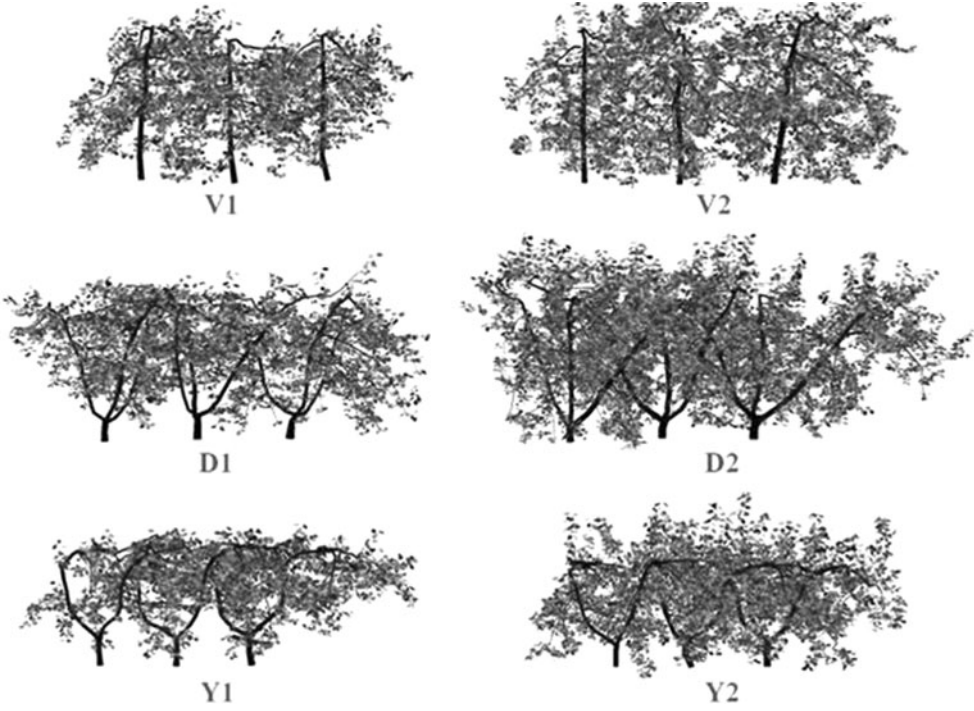
www.avignon.inra.fr/les_recherches__1/liste_des_unites/agroclim) through the CLIMATOR project (Brisson and Levrault 2010). To get realistic climatic data, daily input data were based upon the A1B SRES scenario (a medium emission climate change scenario) according to the IPCC (2007) and resulted from a coupled atmosphere–ocean model (ARPEGE model, Gibelin and Déqué 2003) for the atmospheric large scale computations coupled with the downscaling method of Boé et al. (2006) to provide data at a local scale. To give a relevant trend of the fifth larval instar of *P. blancardella* development related to climate variation, 5 years were used: 2000, 2025, 2050, 2075 and 2100. According to actual occurrence periods of *P. blancardella* instar of in Avignon (see supplementary figures, Fig. S1), selected starting dates for simulations were May 6, June 11, July 22, and September 11 for each year, denoted as May, June, July and September periods, respectively. This method was used to assess the impact of climate change on each generation within a year. Hourly meteorological data used for the simulations were computed from daily meteorological data assuming sinusoidal changes in air temperature and radiations (related to the sun's course during daytime). Relative humidity and wind velocity were set constant during each day but these factors differed among periods and years (Table 2). The atmospheric CO_2 concentration was set constant at an annual scale but increased from 2000 to 2100 (Table 2).

Simulations

For the periods chosen during the 21st century (5 years × 4 dates) and the six-tree configurations, a database of 120 scenarios was analysed. For each simulation, half of leaves potentially available for herbivory by the leaf miners was assumed to be occupied by a single *P. blancardella* mine. Mined leaves were uniformly distributed within the 3-D tree crowns corresponding to the natural distribution of this species in orchards (Pincebourde 2005; Pincebourde et al. 2007). The time step used for computation was 1 h. Each simulation ended when all L5 instar larvae finished their development (and entered in the pupal stage) or had died (see Fig. 1).

Statistical analysis

Statistica 7.0 (StatSoft Inc., Tulsa, USA) was used for the statistical analysis. The Kruskall–Wallis ANOVA test was used to compare the development time for the six scenarios at the annual and multi-annual scales. Furthermore, a homogeneity test was used to compare the mortality of larvae at both annual and multi-annual scales. The significance thresholds were deemed as significant ($p \leq 0.05$), highly significant ($p \leq 0.01$) or very highly significant ($p \leq 0.001$).

Table 1 Characteristics of 3-D apple tree mocks up of real orchards used in simulations

Scene	Training	Tree architecture	Total foliar surface (m²)	Crown volume (m³)	Leaves number	Foliar density (m²/m³)	Crown height (m)
V1	Pruned	Vertical axis	24.09	9.04	11,517	2.66	2.67
D1		Drilling	29.12	11.98	14,579	2.43	2.8
Y1		Ycare	23.62	7.53	11,001	3.14	2.06
V2	Unpruned	Vertical axis	43.68	12.28	22,246	3.56	2.96
D2		Drilling	62.84	18.63	31,059	3.37	3.3
Y2		Ycare	37.63	10.02	20,004	3.76	2.85

Results

Spatio-temporal dynamics of body temperatures at the tree scale

The biophysical model simulated body temperatures of caterpillars with a time step of 1 h. The model simulated a high variability in body temperature both in time and space at the within-tree scale. As an example, Fig. 3a, b shows change of body temperature (T_{body}) distribution over time for two contrasted periods in terms of development time and mortality: May 2000 and July 2100. Comparisons with air temperature dynamics, optimal development rate temperature and lethal temperature are also highlighted. For the two periods, T_{body} of *P. blancardella* caterpillars closely followed the sinusoidal changes in air temperature with a spatial dispersion around air temperature values changing during each day. Spatial dispersion reflected the within tree crown spatial variance of body temperatures

(e.g. shaded versus sunlit mines). It was highest at midday and lowest at midnight. In May 2000, however, a majority of caterpillars experienced T_{body} ranging from 2.7 to 28.6 °C, which is below the optimal temperature (Fig. 3a). In contrast, during the first days of July in the year 2100, T_{body} fluctuates markedly including the range between optimal and lethal temperatures, since it is modelled to vary from 19.6 to 42 °C (Fig. 3b).

Climate change effects on developmental rate

Mean and maximal body temperatures were computed from spatio-temporal values and are shown in Fig. 4a. Mean values were calculated by averaging spatio-temporal data of all *P. blancardella* caterpillars and all tree scenes. Maximal body temperatures were computed by averaging the maximal body temperature reached for each tree scene (i.e. six values per date). Simulations predicted an increase in mean body temperature during May throughout the

Table 2 Predicted meteorological data during the 21st century for the city of Avignon (43.94°N, 4.80°W) used to simulate the development rate and the mortality of *P. Blancardella*

Years	Month	T_{min} (°C)	T_{max} (°C)	T_{avg} (°C)	RG (J cm^2)	HR (%)	Wind (m s^{-1})	CO$_2$ (Pa)
2000	May	9.8	20.6	15.2	2,384.7	52.5	3.2	38
	June	13.7	26.1	19.9	2,720.5	52.2	2.6	
	July	19.3	32.3	25.8	2,322.9	61.1	1.6	
	September	13.4	26.3	19.9	1,756.0	64.6	1.7	
2025	May	11.4	25.9	18.7	2,403.5	58.1	1.5	43
	June	18.0	27.6	22.8	2,574.9	64.2	2.0	
	July	18.8	31.1	24.9	2,522.4	60.4	2.4	
	September	14.5	26.2	20.4	1,618.5	71.7	1.9	
2050	May	12.2	22.6	17.3	2,298.0	67.9	2.3	54
	June	17.0	26.4	21.7	2,696.2	63.7	3.4	
	July	21.0	33.4	27.2	2,468.1	62.9	2.2	
	September	17.8	28.1	22.9	1,440.6	71.1	1.3	
2075	May	15.3	28.1	21.8	2,339.9	58.3	2.3	62
	June	17.0	24.5	20.8	2,379.7	71.5	2.2	
	July	24.3	35.5	29.9	2,317.9	63.6	1.4	
	September	17.7	29.6	23.6	1,631.4	62.5	1.1	
2100	May	14.0	27.1	20.6	2,600.4	46.2	3.4	69
	June	20.4	30.0	25.2	2,793.6	53.5	3.3	
	July	24.1	36.8	30.4	2,636.3	51.1	2.0	
	September	18.8	28.5	23.6	1,669.8	64.4	1.9	

T_{min} minimal air temperature, T_{max} maximal air temperature, T_{avg} averaged air temperature, *RG* averaged global radiation, *RH* air relative humidity, *Wind* averaged wind speed, *CO$_2$* atmospheric CO$_2$ concentration during a given period
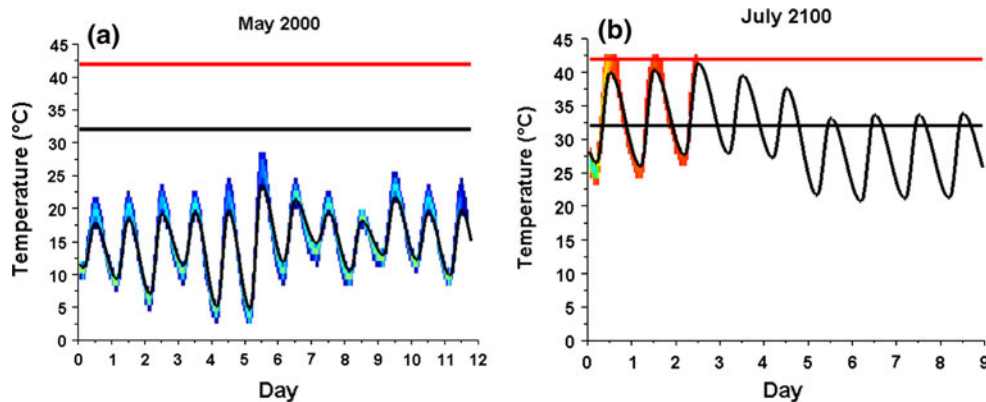

Fig. 3 Predicted temporal dynamics of *P. blancardella* body temperature (T_{body}) for two periods with contrasting climatic conditions, May 2000 and July 2100, versus time (**a** and **b** respectively) and compared to air temperature dynamics (*black curve*), optimal development rate temperature (*black line*) and lethal temperature (*red line*). Day scales were set to fit the maximal time of caterpillar development obtained for each period: 12 and 9 days for May 2000 and July 2100, respectively

century, from 15 °C in 2000 to 19.8 °C in 2100 (Fig. 4a). By contrast, the increase in mean body temperature was less important during the other periods so that the higher mean body temperature reached in July every year remained relatively constant throughout the century (from 25.8 °C in 2000 to 26.5 °C in 2100). The same trend was found for the maximal body temperature. The lowest

values, predicted in May, increased from 28.5 °C in 2000 to 34.6 °C in 2100. Highest values (predicted for July) were close to the lethal temperature threshold of 42 °C in 2025 and 2050, and this threshold was reached in 2000, 2075 and 2100 (Fig. 4a).

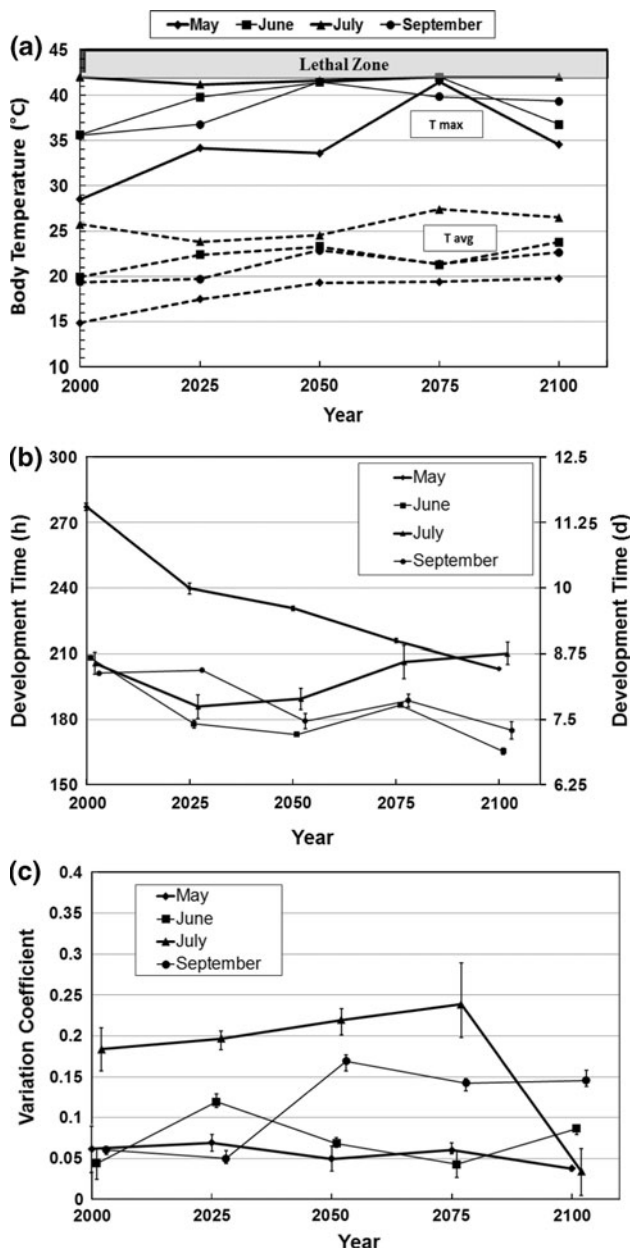The developmental time response of *P. blancardella* caterpillars, excluding dead larvae, was predicted to vary

Fig. 4 Climate change effects on L5 instar *P. blancardella* including all 3-D apple tree mock-ups of real orchards during the 21st century at the city of Avignon (France). **a** Predicted mean and maximal body temperatures, **b** mean development time and **c** coefficient of variation for development times. *Error bars* stand for tree structure variability i.e. differences of mean values with maximum and minimum values
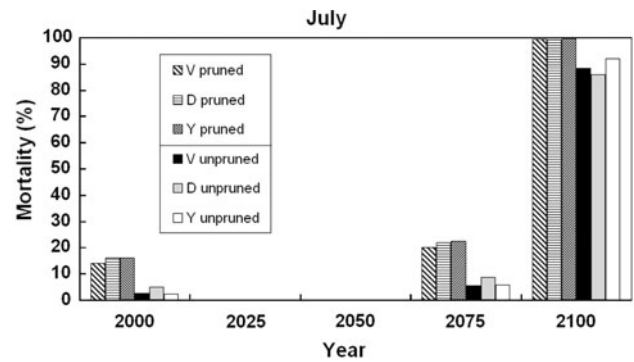

Fig. 5 Tree architecture effect on mortality of *P. blancardella* at L5 instar for six 3-D apple tree mock-ups of real orchards during July periods in the 21st century at the city of Avignon (France). No heat-related mortality was predicted during the other months (not shown)

markedly according to season and year (Fig. 4b). For May, simulations indicated a constant decrease in the development time of the L5 caterpillars from about 280 to 203 h during the century (Fig. 4b; Table S4). A decrease of the L5 caterpillar development time was also obtained for simulated periods in June and September, from 210 to 166 h (Fig. 4b; Table S5) and 201 to 173 h (Fig. 4b; Table S7), respectively. Contrary to other months, the development time of the L5 caterpillar predicted for July remained

nearly constant over the century from 202 to 205 h (Fig. 4b; Table S6).

We quantified the impact of climate change on the variance in development time at population level by calculating the coefficient of variation (CV: the ratio of the total interval to the median emergence time) of development times (Fig. 4c). The CV provides an indication of the level of synchronisation in larval performance. The CV for May was nearly constant and low over the century (i.e. 5 % of the mean). For June, CV values fluctuated from 3 to 12 % of the mean. For July, values were high and increased from 16 to 23 % of the mean from 2000 to 2075. Year 2100 was characterised by a strong decrease in the CV down to 3 % of the mean. For September, CV values exhibited an opposite trend with small values (nearly 5 % of the mean) for the years, 2000 and 2025, and with larger and nearly constant values (15 % of the mean) for the years, 2050, 2075 and 2100.

Tree architecture effects on development rate and heat-related mortality

For all years and months, *P. blancardella* development times were significantly different between pruned and unpruned trees (Tables S3) with shorter development time for May, similar development time for June and longer development time for July and September (Fig. 4b; Table S8). For each training considered (pruned and unpruned), the tree structure had, for some dates within the century, a significant effect on development times (Table S3). However, statistical analysis (Table S3) and mean time development values (Table S8) indicate that managing the tree structure has lower impact than pruning trees.

The mortality rate is defined as the ratio of the number of dead L5 caterpillars to the initial number of L5 caterpillars within the canopy. For each orchard scenario, simulations indicated no mortality for May, June and

September during the century (Tables S4, S5 and S7). In July, at the beginning of the century (i.e. the year 2000), between 2.5 and 16 % of the *P. blancardella* caterpillars died (Fig. 5). No mortality was simulated for the years 2025 and 2050. The mortality significantly increased at the end of the century—between the years 2075 (between 5 to 22 %) and 2100 (i.e. between 86 to 99.8 %) (Fig. 5; Table S6). In July, for each orchard scenario and at the annual scale, *P. blancardella* mortality was always significantly higher for pruned trees (Y1, D1 and V1) than for unpruned ones (Y2, D2 and V2) (Fig. 5; Table S3), with 12 % higher mortality for pruned orchards than for unpruned ones. For each training system, simulated differences between tree architectures (Y, D and V) were significant, with differences in mortality of about 6 %.

Although significant, the effect of tree architecture and training practice is relatively weak in comparison with the effect of climate change.

Discussion

Model validity and assumptions

The different models used in this study were shown in previous studies to be valid within a broad range of climatic data (i.e. air temperature and radiation level) (Sinoquet et al. 2001; Pincebourde and Casas 2006a). The combination of these several models into a single framework does not disproportionately increase the error of prediction. The largest error, 1 °C, obtained with the integrated model was in predicting the temperature within mines hit by direct sunlight (Pincebourde et al. 2007). Even so, more field measurements are still needed to broaden the range of climatic variables within which the biophysical model is shown to be valid and accurate.

Like any modelling study, the approach we developed involves assumptions that need to be addressed. The first main approximation concerns the starting date of each of the four annual generations, which we assumed to be invariable throughout the century. The emergence of overwintering *P. blancardella* pupae depends strongly on temperature once the developmental threshold of about 5.2 °C has been reached (Baumgartner and Severini 1987). We can therefore reasonably expect the emergence date of overwintering individuals to advance significantly as a response to climate warming. Nevertheless, the bias of this assumption might be limited given that we report results for the development of the L5 instar, which occurs much later than first emergence. The temporal trends predicted by the model would not be affected either, but a shift in phenologies might influence the probability to meet extreme events like heat waves and lethal body

temperatures, with consequences for the predicted mortality rates.

The second main assumption of our modelling study is that the potential for acclimation and adaptation to gradually changing climatic conditions was not included. In the leaf miner system, a shift in the larval upper lethal temperature and a change in the apple stomatal properties, in response to the concomitant increased in temperature and CO_2 level, cannot be excluded. On the one hand, as the leaf miner experiences hotter, sub-lethal conditions, the developmental performance curve may change to greater resistance to high temperatures (Huey and Kingsolver 1993; Angilletta 2009) which would improve survival by the end of the century. On the other hand, the consequence of warming and atmospheric CO_2 enrichment on the plant would modify the response of stomatal conductance to daily weather variations. Stomatal conductance is expected to be lower on average in the future compared to current conditions (Ainsworth and Rogers 2007), resulting in an even warmer mine microclimate (but see below) and increased risk of mortality. The issue of the interactions in terms of survival will likely depend on the rates at which both insect thermal sensitivity and stomatal characteristics will adapt to changing conditions.

Manipulating tree architecture for pest management

Control of pests through tree architecture manipulation is sometimes viewed as a good alternative to the use of synthetic chemical insecticides in organic fruit production (Simon et al. 2006, 2007). The present study confirms that tree architectural characteristics significantly influence development time and mortality in *P. blancardella* caterpillars at the L5 instar. From a quantitative point of view, it appears that vegetative shoot pruning (or unpruning) has a larger impact than designing specific tree architectures (vertical axis, drilling and Ycare). Unpruned trees led to longer development time and lower mortality than pruned tree. The main reason for this is that an unpruned tree provides more shaded leaves within the tree crown (due to higher foliage density) leading to relatively cooler mines on average, whereas a tree's shape does not change many important responses. Even so, however, the effects of manipulating tree structure on the leafminer development and survival are relatively weak compared to the impact of the putative climate change.

Climate and leafminer performance

In accordance with the hypothesis suggesting an increase in the number of insect annual generations due to a warmer future climate (Volney and Fleming 2006; Lange 2008), our simulations suggest an overall decrease in the

development time of L5 caterpillars as climate is warming (Fig. 4b). From these simulations, it seems that climatic change would not affect insect development with the same intensity depending on the season within a year. Developmental time would be strongly shortened during May between the years 2000 and 2100, while developmental time would remain about the same during July periods. Such trends reveal the main importance of the temperature-dependent rate function used in insect development forecasting models. When a poikilotherm organism like the *P. blancardella* caterpillar is considered, the effect of the body temperature on the developmental rate is best modelled by a curvilinear curve (Schoolfield et al. 1981) that presents an optimum temperature above which development rate decreases sharply with increasing temperature. Most of the *P. blancardella* caterpillars experienced temperature above optimal temperature during July in the simulation period 2000–2010. As a consequence, their development time increased in contrast with the May period where body temperatures mainly changed by following the linear increasing part of the phenological curve leading to a decrease in development time.

Our simulations also suggest that more than 80 % of the larvae would die each summer by the end of the century assuming no evolution or acclimation occurs. The main reason for this is that even if air temperature does not reach the lethal zone (temperature larger than 42 °C during 1 h (Pincebourde and Casas 2006a), body temperature does (see Figs. 3b, 4a). This situation occurs under particular climate conditions (e.g. high solar radiation, high air temperature, and/or low wind speed) that favoured high mine temperatures up to the lethal temperature threshold. Thus, in July 2075 and July 2100, the model showed that all surviving *P. blancardella* caterpillars (less than 20 % of the initial L5 instar caterpillar population depending on the tree scenario considered) were located in shaded leaves. The low variability in developmental times (i.e. low CV, Fig. 4c) emphasises the role of the canopy which, in this case, provided the remaining caterpillars with quasi-identical microhabitat conditions, inducing small variability in caterpillar development time. When taking into account the non-linear temperature-dependent development, the heterogeneity in microclimatic conditions at the canopy scale and the mortality rates, it is not obvious that a warmer future climate will lead to the expected explosion of pests, at least for endophytic ones, as examined here.

Biophysical modelling in plant–insect relationships

The biophysical modelling framework incorporates the effects of a concomitant increase in both air temperature and atmospheric CO_2, two key factors in the development

and phenology of insects (Bale et al. 2002; Stiling and Cornelissen 2007). The importance of these two factors has long been assessed separately without taking into account their interactive effects (Williams et al. 2000). Biophysical models are flexible enough to quantify the relative importance of the direct (e.g. temperature) and indirect effects (e.g. CO_2) on plant–insect systems. In the leafminer-apple relationship, CO_2 concentration influences the insect larvae thermal environment by causing stomata to close.

The mechanistic framework proposed here could be used to simulate the effects of a putative climate change on the developmental time of insects within plant canopies by considering the impacts on the microclimate. The biophysical model gives temperature predictions on an hourly basis, allowing estimation of the daily maximal body temperatures. These temperatures directly set the mortality rate, which cannot be predicted solely from daily mean body temperatures. In a context of climate change studies, forecasting with such temporal resolution (hour) is made possible thanks to the recent developments of weather model generators, such as the one used here (Brisson and Levrault 2010). In addition, the biophysical modelling approach establishes predictions at different spatial scales, linking global/regional climate to the microclimate of species in a tree canopy. This link is necessary, as the body temperature of an organism is usually non-linearly related to climate variables. The high spatial and temporal resolutions used in this study allowed elucidation of the mechanisms by which climate change may differentially affect leafminer survival according to season. Such biophysical modelling methodology offers highly promising avenues for the development of ecological forecasting in a global change context.

References

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising (CO_2): mechanisms and environmental interactions. Plant Cell Environ 30:258–270

Angilletta MJJ (2009) Thermal adaptation—a theoretical and empirical synthesis. Oxford University Press, Oxford

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer Brown VK, Butterfield J, Buse L, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperatures on insect herbivores. Glob Change Biol 8:1–16

Bauerle WL, Bowden JB, Mcleaod MF, Toler JE (2004) Modeling intra-crown and intra-canopy interactions in red maple:

assessment of light transfer on carbon dioxide and water vapor exchange. Tree Physiol 24:589–597

Baumgartner J, Severini M (1987) Microclimate and arthropod phenologies: the leaf miner *Phyllonorycter blancardella* F. (Lep.) as an example. In: Prodi F, Rossi F, Cristoferi F (eds) Proceedings of the international conference on agrometeorology. Fondazione Cesena Agricultura Publications, Cesena, pp 225–243

Boé J, Terray L, Habets F, Martin E (2006) A simple statistical-dynamical downscaling scheme based on weather types and conditional resampling. J Geophys Res 111:D23106. doi: 10.1029/2005JD006889

Brisson N, Levrault F (2010) Projet Climator—changement climatique, agriculture et forêt en France: simulations d'impacts sur les principales espèces (ed ADEME), ADEME édn., pp 334

Casas J, Djemai I (2002) Canopy architecture and multitrophic interactions. In: Tscharntke T, Hawkins BA (eds) Multitrophic interactions. Cambridge University Press, Cambridge, pp 174–196

Coakley SM, Scherm H, Chakraborty S (1999) Climate change and plant disease management. Annu Rev Phytopathol 37:399–426

Gates DM (1980) Biophysical ecology. Springer, New York

Gibelin AL, Déqué M (2003) Anthropogenic climate change over the Mediterranean region simulated by a global variable resolution model. Clim Dyn 20:327–339

Helmuth B (1998) Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. Ecol Monogr 68:51–74

Huey RB, Kingsolver JG (1993) Evolution of resistance to high temperature in ectotherms. Am Nat 142:S21–S46

IPCC (2007) Contribution of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate Change. Core Writing Team. Pachauri RK, Reisinger A (eds), Geneva, pp 104

Jackson JE (1980) Light interception and utilization by orchard systems. Hortic Rev 2:208–267

Kingsolver JG (1983) Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. Ecology 64:534–545

Lange MA (2008) Assessing climate change impacts in the European north. Clim Change 87:7–34

Pangga IB, Hanan J, Chakraborty S (2011) Pathogen dynamics in a crop canopy and their evolution under changing climate. Plant Pathol 60:70–81

Pincebourde S (2005) Biophysique environnementale des insectes endophytes. PhD thesis, Université François Rabelais, Tours, pp 165

Pincebourde S, Casas J (2006a) Multitrophic biophysical budgets: thermal ecology of an intimate herbivore insect–plant interaction. Ecol Monogr 76:175–194

Pincebourde S, Casas J (2006b) Leaf miner-induced changes in leaf transmittance cause variations in insect respiration rates. J Insect Physiol 52:194–201

Pincebourde S, Sinoquet H, Combes D, Casas J (2007) Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. J Anim Ecol 76:424–438

Robinson TL, Lakso AN (1991) Bases of yield and production efficiency in apple orchard systems. J Am Soc Hortic Sci 116:188–194

Scherrer D, Korner C (2009) Infra-red thermometry of alpine landscapes challenges climatic warming projections. Glob Change Biol 16:2602–2613

Schoolfield RM, Sharpe PJH, Magnuson CE (1981) Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J Theor Biol 88:719–731

Simon S, Lauri PE, Brun L, Defrance H, Sauphanor B (2006) Does manipulation of fruit-tree architecture affect the development of pests and pathogens? A case study in an organic apple orchard. J Hortic Sci Biotechnol 81:765–773

Simon S, Sauphanor B, Lauri PE (2007) Control of fruit tree pests through manipulation of tree architecture. Pest Technol 1:33–37

Sinoquet H, Thanisawanyangkura S, Mabrouk H, Kasemsap P (1998) Characterization of the light environment in canopies using 3-D digitising and image processing. Ann Bot 82:203–212

Sinoquet H, Le Roux X, Adam B, Ameglio T, Daudet FA (2001) RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. Plant Cell Environ 24:395–406

Sinoquet H, Stephan J, Sonohat G, Lauri PE, Monney P (2007) Simple equations to estimate light interception by isolated trees from canopy structure features: assessment with 3-D digitized apple trees. New Phytol 175:94–106

Sinoquet H, Pincebourde S, Adam B, Donès N, Phattaralerphong J, Combes D, Ploquin P, Sangsing K, Kasemsap P, Thanisawany-angkura S, Groussier-Bout G, Casas J (2009) 3-D maps of tree canopy geometries at leaf scale. Ecology 90:283

Skirvin DJ (2004) Virtual plant models of predatory mite movement in complex plant canopies. Ecol Model 171:301–313

Sonohat G, Sinoquet H, Kulandaivelu V, Combes D, Lescourret F (2006) Three dimensional reconstruction of partially 3-D-digitalized peach tree canopies. Tree Physiol 26:337–351

Stiling P, Cornelissen T (2007) How does elevated carbon dioxide (CO_2) affect plant-herbivore interactions? A field experiment and meta-analysis of CO_2-mediated changes on plant chemistry and herbivore performance. Glob Change Biol 13:1–20

Volney WJA, Fleming RA (2006) Spruce budworm (*Choristoneura* spp.) biotype reaction to forest and climate characteristics. Glob Change Biol 13:1630–1643

Willaume M, Lauri PE, Sinoquet H (2004) Light interception in apple trees influenced by canopy architecture manipulation. Trees Struct Funct 18:705–713

Williams RS, Norby RJ, Lincoln DE (2000) Effects of elevated CO_2 and temperature-grown red and sugar maple on gypsy moth performance. Glob Change Biol 6:685–695