Plant Architecture, Hail Nets and Thermal Behaviour Influencing Developmental Rate and Modelling of the Codling Moth

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Abstract

Changes of plant architecture result in a considerable alteration of the microclimate within orchard trees with effects on insect pest development. Consequently, such changes require adjustments in modelling phenology. Thermoregulation by choice of preferred sites within the habitat also influences insects' body temperature and thus development. We investigated how tree shape of apple trees (high stem/dwarf) and the use of hail nets influence solar radiation and temperature within the habitats of a key pest in apple – the codling moth (*Cydia pomonella* L.). Furthermore, we examined whether distinct codling moth stages perform thermoregulation behaviour. Plant architecture parameters (leaf area index and global site factor), radiation intensity, and habitat temperatures were quantified in high stem and dwarf apple trees. Air temperature was assessed within the canopy, and surface temperature was determined on tree bark and apple fruits. Results from dwarf trees compare to high-stem trees as follows: The lower leaf area index of dwarf trees resulted in a higher radiation energy transmission. Air temperature within the canopy of dwarf trees was higher during daytime and lower at night. Surface temperature of bark was generally higher, while that of apple fruits was higher on sunny days, but cooler on overcast days. Hail nets reduced radiation intensity and air temperature within the canopy. The thermal response of mobile stages of the codling moth was examined in temperature gradient experiments. Feeding larvae preferred apple regions with higher temperatures, while mature larvae showed no temperature preference in cocooning sites. Adult moths responded negatively thermotactic, but females strongly preferred areas with higher temperatures as oviposition sites. The impact of plant architecture and hail nets on the developmental rate and seasonal cycle of *C. pomonella* is discussed.

INTRODUCTION

The codling moth, *Cydia pomonella* L., is the major pest insect in apple orchards worldwide (Dorn et al., 1999). Its integrated management strongly relies on the precise prediction of the appearance of susceptible stages. Prediction models are commonly based on temperature dependent developmental rates. Nevertheless, they often show a timing discrepancy between simulation results and observations, particularly for the later generations, which is likely caused by differences between air temperatures used to drive the models and microenvironmental temperatures experienced by developing individuals (Shaffer and Gold, 1985; Blago and De Berardinis, 1991; Blago, 1992).

Microclimate in apple trees, in particular radiation and temperature regime, is modified by plant architecture and hail nets. Furthermore, plant architecture of apple trees changed in the last few decades in tree shape from traditional high-stem trees to dwarf trees. However, only little is known about the effects of plant architecture and hail nets on pest insect development or even on the microclimatic factors within the pest's habitats. Differences in habitat temperatures may cause differences in body temperature (T_b) and hence lead to differences in developmental rates. Furthermore, insects can influence their T_b by behavioural or physiological thermoregulation (Heinrich, 1981; Heinrich, 1993). The probably most common and most effective mechanism of behavioural thermoregulation in insects is microhabitat selection (May, 1979; Casey, 1981), i.e. the short-term selection of thermally favoured microclimates, especially of sunny or shaded substrates. The mobile stages should be able to select favoured temperatures in their thermally heterogeneous environment (Jermy, 1964; Thorpe, 1974; Graf et al., 2001) to regulate their body temperature. However, behavioural thermoregulation of codling moth stages has never been investigated systematically.

In the present study the consequences for radiation regime and temperature of changing plant architecture and hail nets were characterised in codling moth habitats. Furthermore, the thermoregulation behaviour was assessed for mobile codling moth stages. Finally, the combined impact of plant architecture and hail nets as well as the thermoregulation behaviour on the development and the seasonal population cycle of the codling moth is discussed.

MATERIALS AND METHODS

Studies on orchard microclimate were carried out in 2002 in a commercial apple orchard with dwarf trees and in a traditional apple orchard with high-stem trees in northern Switzerland, near Böttstein, Kanton Aargau, at 436 m a.s.l. The high-stem apple orchard is situated about 500 m south-east of the dwarf apple orchard. The plant architecture and microclimate measurements were randomly assigned in high-stem trees of different varieties ('Gravensteiner', 'Renette', 'Berner Rose') and in 'Golden Delicious' spindle trees that were either protected with hail nets or unprotected. The black hail nets were closed from mid May until the beginning of November in 2002.

Measurements of Plant Architecture and Potential Irradiation

To characterise plant architecture of high-stem and dwarf trees, leaf area index (LAI) and global site factor (GSF) were determined in different heights using hemispherical photography (HemiView, Delta-T Devices Ltd., Cambridge, U.K.). For comparable results between high-stem and dwarf trees, the photographs were taken in 0.5-m steps from the treetop downwards (5 samples per height, site, and day). The sampling was conducted during the entire vegetation period, from March to December approximately in two-week intervals.

Actual solar radiation intensity (radiation flux density, Wm^{-2}) within the tree canopies was randomly measured with a pyranometer (Kipp & Zonen, Delft, The Netherlands). For comparable results between high-stem and dwarf trees, the radiation intensity was sampled in 0.5-m steps from the treetop downwards. Samplings were conducted on sunny days around noon (local noon ± 90 min), once per month from April to October (5 samples per height, site, and day).

Air temperature within the canopy (T_c) was measured with shielded thermistors (Campbell Scientific, Logan, U.K.) throughout the season. The thermistors were installed in one of the high-stem trees as well in a hail-protected and unprotected dwarf tree row. T_c was measured at 1-minute intervals and 10-minute averages were recorded by CR10 data-loggers (Campbell Scientific, Logan, U.K.).

Surface temperatures of bark and apple fruits on their north- and south-facing side were measured on selected clear sunny and overcast days with type T thermocouple probes (Physitemp Instruments, Clifton, New Jersey, USA). For comparable results

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between high-stem and dwarf trees, the habitat temperatures were sampled in 0.5-m steps from the treetop downwards (5 samples per height, site, and day). Temperatures of bark and apple fruits were measured around noon (local noon ± max. 90 min).

All habitat temperatures were analysed with a reference to the standard air temperature (T_s) measured 2 m above ground by a standard agro-weather station (Lufft, Mess- und Regeltechnik GmbH, Fellbach, Germany) at the dwarf apple orchard.

Temperature Gradient Experiment

1. Feeding Larvae. Apple fruits on dwarf trees were heated from one side using infrared lamps. The surface temperature of apple fruits was measured on the side exposed to IR-illumination (0° to illumination – $T_{0°}$) as well as on the opposite side (180° to illumination – $T_{180°}$), with a Thermocouple (Type BT-1, Physitemp Instruments, Clifton, New Jersey, USA). The temperature difference between both sides ($\Delta T = T_{0°} - T_{180°}$) ranged between 2° and 9°C (n = 66, mean ± SD: 4.8 ± 1.5°C). The apples were infested with newly hatched larvae placed on top of the apples at the vertical axis between the irradiated and the shaded apple hemispheres. After 25 days the apples were harvested. After harvest, the apples were cut horizontally into 5 mm thin slices and photographed with a digital camera. The areas of larvae's cavities were calculated with Scion Image software program (Version 1.6, Scion Corporation, Frederick, Maryland, USA) and summed up separately for the both apple hemispheres ($A_{0°}$, $A_{180°}$). The area index was calculated as the proportion of cavity area in the illuminated hemisphere relative to the total cavity area: $A_{0°} / (A_{0°} + A_{180°})$.

2. Fifth-instar Larvae. The temperature gradient setup for fifth-instar larvae consisted of a transparent polystyrene cylinder (300 mm long, 60 mm diameter). A corrugated cardboard strip was offered as cocooning shelter. The temperature gradient was generated with IR-lamps (PAR38, 100 W, Philips, Roosendaal, The Netherlands) and ranged from 9 to 29°C. A control experiment was carried out in a climate chamber with LD 16:8 h, day: 24°C, night: 18°C, 60% RH. The larvae were tested individually for their preference of cocooning sites in the temperature gradient and in the control. The location of each larva was assessed at the beginning of the experiment and after 24 h.

3. Adult Moths. The temperature gradient apparatus for adult moths consisted of a rectangular plexiglass arena (50 x 6.5 x 6.5 cm). Peltier elements (Minco Pe-127-20-35, Minco EC, Niederuzwil, Switzerland) were fixed along the sides of the arena to cool and heat the arena as needed. The experiments were run in a climate chamber at 15°C. The temperature in the apparatus ranged from 15 to 27°C. Relative humidity in the arena during experiments was not controlled. A control experiment was conducted in the arena at 18°C and 60% RH. The moths were tested individually for 20 minutes within 3 hours before day (light on). Moth's location was permanently recorded with the Observer program (Version 3.0, Noldus Information Technology b.v., Wageningen, The Netherlands).

4. Ovipositing Females. The temperature gradient setup for oviposition consisted of a transparent polystyrene cylinder (300 mm long, 60 mm diameter). The cylinders were lined with transparent plastic as substrate for oviposition. The temperature gradient was generated with IR-lamps (PAR38, 100 W, Philips, Roosendaal, The Netherlands) and ranged from 15 to 32°C. A control experiment was carried out at 24°C. Newly emerged females were mated for 24 h prior to the experiments and afterwards individually tested. After 24 h in the temperature gradient or in the control all eggs on the transparent plastic were counted.

RESULTS

With respect to plant architecture, tree shape significantly influenced the leaf area index (repeated-measures ANOVA: $F_{1, 65} = 4.64$, $P = 0.035$) as well as the global site factor (RM ANOVA: $F_{1, 65} = 5.65$, $P = 0.020$). However, tree shape did not significantly influence actual radiation intensity within the canopy (RM ANOVA: $F_{1, 90}$

$= 3.48$, $P = 0.066$). Hail nets had no significant effect on LAI (RM ANOVA: $F_{1, 40} = 0.509$, $P = 0.48$) or on GSF (RM ANOVA: $F_{1, 40} = 0.103$, $P = 0.75$). However, they significantly affected the radiation intensity in dwarf trees (RM ANOVA: $F_{1, 90} = 5.28$, $P = 0.024$) causing the largest reduction in the upper strata.

Habitat Temperature

Season-long measurements yielded temperatures for the canopy as the habitat for adult codling moths, the bark as habitat for late larvae and pupae, and the apple fruit as the habitat for the larvae:

On sunny days, tree shape significantly affected air temperature within the canopy (T_c) during daytime (9:00-17:00 h), leading to higher T_c in dwarf trees than in high-stem trees. The largest temperature differences occurred in the afternoon (14:00-15:00 h), when T_c in dwarf trees exceeded that in high-stem trees (Fig. 1a). During this time these temperature differences averaged for the whole season by 1.0°C. On cloudy days during daytime, T_c did not differ significantly between dwarf and high-stem trees (RM ANOVA throughout the season: $P > 0.05$). Air temperatures at night (21:00-5:00 h) were significantly lower in the dwarf trees than in the high-stem trees, independent of weather conditions. Hail nets clearly affected air temperature within the canopy on sunny days during the daytime, leading to T_c under hail nets up to 0.8°C lower compared to that in unprotected dwarf trees. This temperature deficit showed two peaks: before noon (8:00-10:00 h) and after noon (13:00-16:00 h) (Fig. 1b). On cloudy days, there was no significant effect of hail nets on T_c and hail nets did not alter air temperatures at night (RM ANOVA throughout the season: $P > 0.05$).

Surface temperature of bark was significantly higher in dwarf trees than in high-stem trees on both sunny days (RM ANOVA: $F_{1, 134} = 84.7$, $P < 0.001$) and overcast days (RM ANOVA: $F_{1, 146} = 14.5$, $P < 0.001$). On overcast days, the mean temperature difference amounted to 0.2°C, while on sunny days, this temperature difference changed with the exposure and the progress of season. On the shaded north-facing side bark temperature was on average 1.6°C and on the irradiated south-facing side it was on average 0.3°C higher in dwarf trees than in high-stem trees (Fig. 2). Hail nets did not significantly influence bark temperature at noon on sunny days (RM ANOVA: $F_{1, 70} = 0.124$, P = 0.726), while they reduced bark temperature on overcast days by approximately 0.3°C (RM ANOVA: $F_{1, 74} = 82.0$, P < 0.001).

The tree shape significantly influenced the surface temperature of apple fruits on sunny days (RM ANOVA: $F_{1, 370} = 558.9$, $P < 0.001$) as well as on overcast days (RM ANOVA: $F_{1, 438} = 213.3$, $P < 0.001$; Fig. 2). On sunny days, apples in dwarf trees were 2.8°C warmer on their south-facing surface and 1.8°C warmer on their north-facing surface than apples in high-stem trees. On overcast days, the surface temperature of apples was constantly 0.6°C lower in dwarf trees than in high-stem trees, whereas exposition did not have any influence, either. Hail nets had no significant effect on surface temperature of apple fruits, neither on sunny days (RM ANOVA: $F_{1, 218} = 0.306$, $P = 0.58$) nor on overcast days (RM ANOVA: $F_{1, 300} = 1.44$, $P = 0.230$).

Thermal Response of the Codling Moth

The feeding larvae built larger cavities in the 'warmer' apple hemispheres than in the 'cooler' apple hemispheres (mean area index = 0.64 ± 0.03, one-sample t-Test: $t = 4.15$, $P < 0.001$). The proportion of cavities in the warmer apple hemisphere, i.e. arcsine-squareroot transformed area index, increased with increasing temperature at the illuminated apple surface $T_{0°}$ (Pearson's correlation: $r = 0.376$, $P = 0.002$). The (transformed) area index also increased with increasing temperature difference between both apple sides ΔT (Pearson's correlation: $r = 0.276$, $P = 0.025$).

Fifth-instar larvae preferred to hide at either end of the cardboard arena in the temperature gradient (χ^2–test, males: $\chi^2 = 34.5$, df = 4, $P < 0.001$; females: $\chi^2 = 38.2$, df = 4, $P < 0.001$) providing average temperatures of 12.8° and 26.8°C. Also in the control,

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most fifth instar larvae hid at either end of the cardboard avoiding the centre (χ^2–test for deviation from start distribution, males: $\chi^2 = 21.3$, df = 4, $P < 0.001$; females: $\chi^2 = 31.9$, df = 4, $P < 0.001$).

Adult unmated male and female moths preferred the cooler temperature zones in the temperature gradient after 20 minutes (χ^2–test, males: $N = 35$, $\chi^2 = 12.9$, df = 4, $P = 0.012$; females: $N = 35$, $\chi^2 = 32.9$, df = 4, $P < 0.001$). The behaviour of male and female moths in the temperature gradient differed significantly from that in the control under constant temperature (χ^2–test: males: $\chi^2 = 63.1$, df = 4, $P < 0.001$; females: $\chi^2 = 63.4$, df = 4, $P < 0.001$). In the control, female moths were equally distributed, while male moths settled more frequently in sector 4.

Females laid the eggs preferably in the warmest zone in the temperature gradient with a mean temperature of 29°C (Friedman-test: $N = 28$, $\chi^2 = 60.4$, df = 4, $P < 0.001$). In the control (constant temperature) the distribution of eggs is bimodal (Friedman-test: $N = 29$, $\chi^2 = 27.9$, df = 4, $P < 0.001$) with two peaks at both ends of the arena.

DISCUSSION

In conclusion, the present study shows that plant architecture significantly influences radiation energy transmission and temperatures in habitats of the codling moth. Comparing the two tree shapes studied, the leaf area index as a parameter of plant architecture is reduced in dwarf trees, leading to a higher global site factor and consequently to a higher actual radiation energy transmission in dwarf trees. Hence, daytime temperatures in the different habitats of the codling moth are higher in dwarf trees than in high-stem trees. Radiant heating and cooling are considered the main impact factors leading to temperature differences in insect habitats (Wellington, 1950). Here we can show that also daily fluctuations are more pronounced when the microhabitats receive higher radiation due to plant architecture. In a study of different apple cropping systems, slender spindle trees (height 2.3 m, spread 1.6 m) showed lower leaf areas and higher light levels than larger pyramid hedgerow trees (height 4.5 m, spread 4.5 m) (Ferree, 1989). Hail nets over dwarf trees reduce radiation energy transmission considerably, though they have no effect on LAI and GSF. They reduced air temperatures within the canopy during daytime, but not temperatures of tree bark and apple fruits. Hail nets have also been shown to reduce the actual radiation transmission in other apple cultures (reviewed by Mantinger, 2003).

The thermal response of the codling moth varied with the distinct stages. Feeding larvae preferred apple regions with higher temperatures, as they built larger cavities in the warmer apple hemispheres. Mature larvae, on the other hand, showed no temperature preference in cocooning sites. Unmated adult moths responded negatively thermotactic preferring cooler ambient temperatures. Mated females, however, clearly chose areas with higher temperatures as oviposition sites.

The differences in radiation regime and temperature of codling-moth habitats due to changes in plant architecture and the use of hail nets in apple orchards may have consequences for the development of the codling moth. As habitat temperatures in dwarf trees in our study generally exceed those in high-stem trees, in particular on sunny days, codling-moth development should be enhanced in dwarf trees. The differences in habitat temperatures are sufficiently large to be given serious consideration in prediction models, thereby improving the accuracy of forecasting the pest insect. Hail nets, on the other hand, may have a low or even negligible effect on the life cycle of the codling moth. The thermotactic codling-moth stages (feeding larvae in apples, ovipositing females) use their thermally heterogeneous habitats to manipulate their body temperature (or that of the eggs). The next step will be to incorporate temperature differences and thermoregulation behaviour in modelling codling moth development to estimate the impact of plant architecture, hail nets, and thermoregulation behaviour on the life cycle and hence population dynamics of *C. pomonella*.

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Wellington, W.G. 1950. Effects of radiation on the temperatures of insectan habitats. Sci. Agric. 30:209-234.

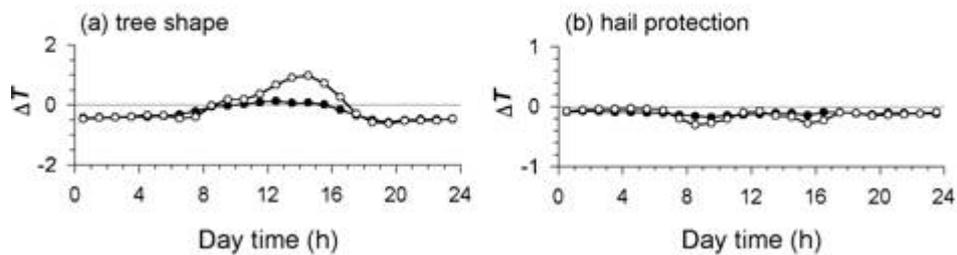Fig. 1. Mean differences in canopy-air temperature (ΔT) between dwarf and high-stem apple trees (a) and between dwarf apple trees with and without hail nets (b) for the season 2002. T_c is averaged for sunny days (open circles) and for cloudy days (filled circles). The zero-reference line indicates equal ΔT; $\Delta T > 0$ indicate higher temperatures in dwarf trees (a) or unprotected dwarf trees (b); $\Delta T < 0$ indicate higher temperatures in high-stem trees (a) or dwarf trees with hail nets (b).
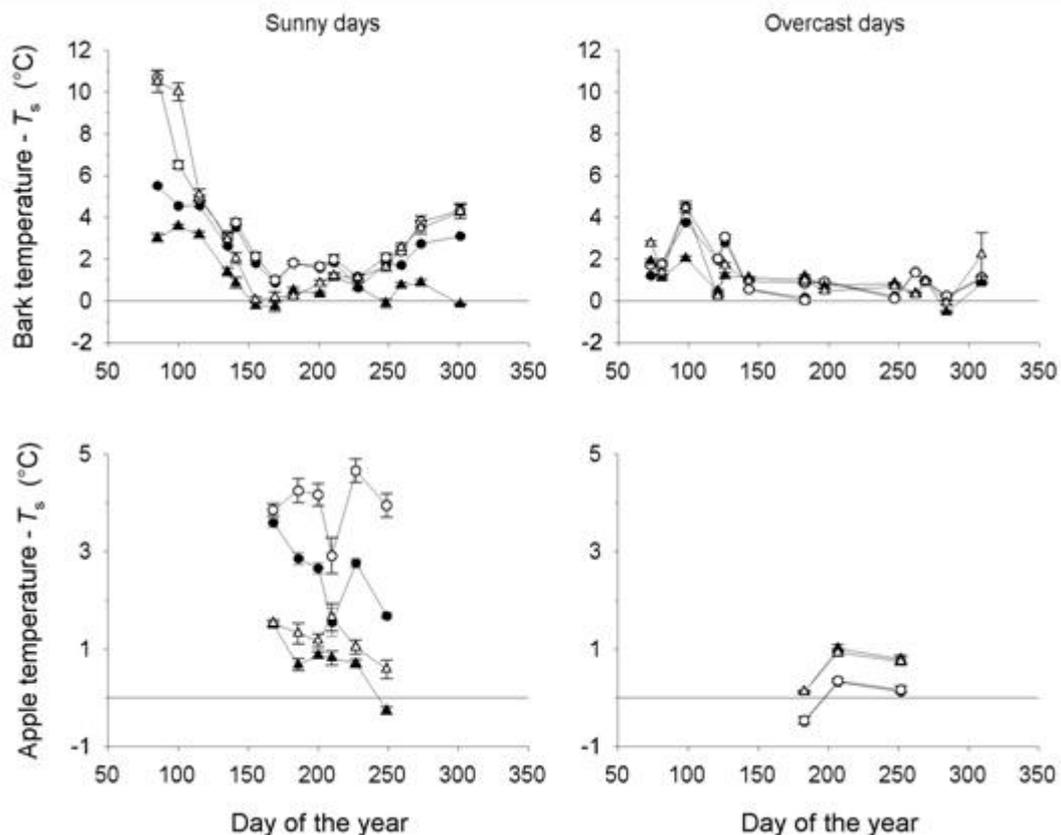

Fig. 2. Mean (± standard error) of the differences between bark-surface temperature (top) of apple trees and standard air temperature (T_s, measured 2 m above ground level) and between apple-surface temperature and T_s (bottom) on sunny and overcast days over the season. The temperature differences are averaged over the different heights in high-stem trees (north – filled, south – open triangles) and dwarf trees (north - filled, south – open circles).