

# Oviposition Site Selection of the Codling Moth (Lepidoptera: Tortricidae) and its Consequences for Egg and Neonate Performance

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**ABSTRACT** The codling moth *Cydia pomonella* (L.) is a worldwide pest of pome fruit. A better understanding of oviposition site selection by this insect would help management of this pest in orchards. Oviposition site selection of codling moth was assessed by manipulative experiments and field survey. In addition, the temperatures of different sites were recorded. Neonate infestation and egg hatching were tested to evaluate the consequences of oviposition site selection. The percentage of eggs laid on the shady side of apple clusters was significantly higher than on the sunny side. However, this was not influenced by leaf surface turning. Percentage of eggs on upper and lower leaf surfaces was significantly influenced by leaf surface turning. Percentage of eggs on the lower leaf surface was significantly higher than turned lower leaf surface (~41.1% higher) and significantly higher (~35.5%) on the turned upper leaf surface than upper leaf surfaces. There was no significant difference in neonate infestation between leaves and fruit, as well as between the upper and lower leaf surfaces. Number of eggs hatching on the shady side of clusters was significantly higher than on the sunny side (56.3% higher). In both the manipulative experiment and field survey, codling moths did not choose the sites with the highest mean temperature, but chose sites suitable for egg development and hatching. This indicates that in the field codling moth, oviposition site selection is not strictly thermophilous, but they look for the lower leaf surface on the shady side, which benefits the offspring.

**KEY WORDS** oviposition, site selection, temperature, offspring performance, codling moth

Oviposition site selection is an important aspect of lepidopteran reproduction. Female selection of the oviposition site is crucial for egg survival and neonate performance (Renwick and Chew 1994). The preference–performance hypothesis (Thompson 1988) predicts that females should prefer to lay eggs in locations that enhance the performance of their offspring. The codling moth *Cydia pomonella* (L.) (Lepidoptera, Tortricidae), a key pest of apples (*Malus* spp.), has a global distribution (Barnes 1991). Codling moth eggs are laid singly, and after hatching, neonate larvae penetrate the fruit and then cause damage. Because codling moth neonate larvae are not very mobile (Jackson 1982), female moth oviposition site selection is crucial for egg hatching and neonate survival. Therefore, a study of oviposition site selection of codling moths and its consequence for eggs and neonates performance could provide a better understanding of codling moth reproduction.

This, in turn, could help improve application of ovicide and integrated management (such as tree thinning and guard line building) to increase the mortality of eggs and neonates larvae.

Studies on codling moth oviposition sites have yielded different results (Geier 1963, Wood 1965, Jackson 1979, Blomefield et al. 1997, Borchert et al. 2004, Du et al. 2012, Wei et al. 2012, Al Bitar et al. 2014). In particular variations in the proportion of eggs on different sites (upper leaf surface, lower leaf surface, and fruit) and egg distribution in relation to canopy aspect (south, north, east, or west facing) have been found. In some studies (Geier 1963, Jackson 1979), most eggs were not oviposited on fruit but on the leaves ~10 cm from the fruit. Oviposition site selection was considered to be related to the physical properties of different sites. The order of egg adhesive force on different sites was fruit > lower leaf surface > leaf upper the preferred oviposition site (Al Bitar et al. 2012, 2014). In a laboratory experiment, temperature influenced female codling moth behavior. Codling moth females even deposited eggs at temperatures greater than the levels suitable for their progeny (Kuhrt et al. 2006). However, different temperature gradients had a significantly different influence on codling moth egg development (Aghdam et al. 2009, Liu et al. 2012). Moreover, it was found that female codling moths lay eggs when the temperature was >35°C or <15°C (Blomefield and Giliomee 2011, Liu et al. 2012). Zalucki et al (2002)

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point out that the mortality in the egg and first-instar neonate stage of Lepidoptera were high (~41 and 54%, respectively). It was considered to be caused by plant traits, wind and rain, microclimate, and predator. However, direct field experiment studies to clarify the causes of egg and neonate mortality are rare. Therefore, the study on oviposition site selection of codling moths and the consequences for egg and neonate performance in the field is needed to provide knowledge for pest management.

The objective of this study was to test oviposition site selection of codling moths under field conditions. Female oviposition site selection was also tested under experimental conditions to support the field survey. Microhabitat temperature was recorded to supply additional information on oviposition site selection and egg development. Egg survival and neonate performance at different oviposition sites was studied to evaluate the effect of site by direct experiment.

### Materials and Methods

**Orchard and Insect.** The study was conducted in an unmanaged apple orchard (4.2 ha) with 'Golden Delicious' and 'Red Delicious' in Inner Mongolia, Aka League, Qinggele, in 2014 (46° 17'4" N, 105° 50'37" E). Codling moth infestation in the orchard was heavy (average apple infestation percentage more than 46% in 2013). All of the experimental larvae were collected from a black cloth band tied to trees in the field. After collection, male and female larvae were distinguished and placed into plastic boxes with corrugated paper for pupating. To obtain fresh eggs and neonate larvae, codling moth pupae were placed in transparent plastic bottles (height: 15 cm; diameter: 6 cm) covered with nylon net (40 mesh) for mating and oviposition. Each bottle contained 10 males and 10 females. Humidity in the plastic bottle was maintained by wet cotton (the condition of the bottle was as follows: 22–28°C, 60–80% humidity, and photoperiod of 16:8 [L:D] h).

**Manipulative Experiment.** When the collected pupae were about to eclose, 10 of each sex were placed into nylon mesh bags (30 by 20 cm, 40 mesh), and then each bag was tied to one uninfested fruit cluster for mating and oviposition. To test the effect of canopy aspect on oviposition selection, nylon bags with codling moths were tied to either north- or south-facing fruit clusters (replication:  $n = 17$  per aspect). At the same time, the leaf surfaces of a group of north- and south-facing clusters (replication: south  $n = 11$ , north  $n = 12$ ) were turned (upper and lower leaf surfaces exchanged) to test the influence of leaf surface on oviposition selection. To make sure the leaf surfaces of clusters had turned, we picked the cluster in which most of the leaves were naturally growing into upper and lower surface-facing side exchanged, and then cut off the leaves that had not turned. Generally, there were at least five leaves on the cluster for experiment. During the observation, the number of eggs on each oviposition site (fruit, upper leaf surface, and lower leaf surface) and clusters in the sun (abaxial to the ground facing the sun) or shade (abaxial to the sun facing the ground) were recorded. The experi-

ment was started on 1 July and ended on 6 September 2014. We tried to have 20 bags in each treatment. However, codling moths died or did not oviposit in some of the bags because of rain (once a hail).

**Field Survey.** The field survey was conducted from 16 May to 2 September 2014 once a week. For each canopy aspect (north and south) in each week, 150 fruit clusters were randomly surveyed. During the survey, eggs on every cluster site (upper leaf side, lower leaf side, and fruit) were assessed for the presence of codling moth oviposition. The percentage of fruit infestation was recorded during the survey. Apples were not removed to avoid any bias in infestation. A 60× pocket lens was used to observe the eggs.

**Temperature Data.** Temperatures of fruit (abaxial to the ground, facing the sun), upper leaf surface (abaxial to the ground, facing the sun), and lower surface (abaxial to the sun, facing the ground) from the north- and south-facing tree side were recorded by an iButton (DS1921G, Maxim Integrated Products, San Jose, CA) stuck on the surface. Each site had three iButtons. The recording interval was 1 h for each iButton. Recordings commenced on 30 May at 1800 hours and ended on 2 September at 2300 hours. Each iButton was covered with a rubber film for water proofing. Codling moths are nocturnal, active from dusk to dawn (Weissling and Knight 1996, Witzgall et al. 1999, Wei et al. 2014), and adult codling moth behavior could be influenced by temperature (Kuhrt et al. 2006). Therefore, we extracted temperature data between 1900 to 0700 hours to evaluate the influence of temperature on oviposition site selection.

**Offspring Performance.** To assess offspring performance, the success of egg hatching and neonate larval infestation was tested. To examine egg hatching success, transparent plastic bottles with eggs were placed on a south-facing branch (i.e., exposed to the sunshine,  $n = 3$ ) and the shady side of the canopy (i.e., not exposed to the sunshine,  $n = 3$ ). The numbers of hatched and unhatched eggs were counted. To examine neonate infestation, freshly hatched larvae were placed on fruit, and the upper and lower surfaces of leaves. All neonate larvae were placed within 10 cm of fruit. The number of fruit infested and uninfested with larvae was counted. For codling moth, the Briere-2 (1) model was considered to be suitable for describing the development rate (Aghdam et al. 2009). Therefore, using the Briere-2 model, we used temperature data to calculate the development rate at different sites. The different parameters of the model (1) are described by Aghdam et al. (2009).

$$r = aT(T - T_1)(T_2 - T)^{1/m} \quad (1)$$

Where  $r$  is developmental rate.  $T$  (°C) is temperature measured by iButton.  $T_1$  (°C) is the lower temperature threshold.  $T_2$  (°C) is the upper temperature threshold.  $a = 26.34 \times 10^5$ ,  $m = 4.0547$ .

**Statistical Analysis.** For oviposition site selection, egg numbers were calculated as the percentage of eggs laid by females on the different oviposition sites.

Percentage of infestation and number of eggs deposited by females in north- and south-facing canopies were calculated. When appropriate, the data were checked for normality and homoscedasticity, and percentage of eggs were arcsine square root-transformed before performing analysis of variance using oviposition site as an independent fixed factor. The Student–Newman–Keuls method was used to compare the means of accumulative temperature, development rate, and percentage of eggs on different oviposition sites. The data on infestation percentage and number of eggs deposited by females in north- and south-facing canopies did not fulfill the assumptions of parametric statistics. Therefore, a Mann–Whitney rank sum test was used for analysis. To analyze egg hatching frequency and success frequency of neonate larvae infestation, a chi-square test was used. All statistical analyses were performed with R (R 3.0.2, R Core Team 2013, Vienna, Austria).

**Results**

**Oviposition Selection.** In the manipulative experiment and field survey, for both canopy aspects, the percentage of eggs on the shady side of leaves was significantly greater than on the sunny side of leaves regardless of the leaf surface turning treatment. The percentage of eggs on the shady and sunny side of the south aspect was ~22–26% greater than the north aspect (Table 1; Fig. 1). In the field survey, the percentage of eggs on the shady and sunny side of the south aspect was ~21% greater than the north aspect (Table 1; Fig. 2).

In the manipulative experiment and field survey, the percentage of eggs on different oviposition sites was significantly different on both south- and north-facing canopies. Percentage of eggs on the leaf surface was significantly higher than on fruit of both south- and north-facing canopies (Table 2). However, in the manipulative experiment, the percentage of eggs on the lower leaf surface was significantly higher than the upper leaf surface (~36% higher). In the north-facing canopy, there was no significant difference between the lower and upper leaf surfaces. Leaf surface turning had a significant influence on percentage of eggs on the leaf surface in the south-facing canopy. Percentage of eggs on the lower leaf surface was significantly higher than the turned lower leaf surface (~41% higher), and the turned upper leaf surface was significantly higher than the upper leaf surface (~36% higher; Table 2;

Fig. 1). In the field survey, the percentage of eggs on the leaf surface was significantly higher than fruit in both the south- and north-facing canopies. The percentage of eggs on the lower leaf surface was significantly higher than the upper leaf surface in both canopy aspects (Table 2; Fig. 2).

**Mean Temperature, Accumulative Development Rate, and Percentage of Eggs at Different Oviposition Sites.** In the field survey, mean temperatures (1900 to 0700 hours) were significantly different between oviposition sites. The highest temperatures were on north-facing fruit and lowest were on south-facing fruit. Accumulative development rate was significantly different between different oviposition sites. The highest accumulative development rates were on north-facing fruit and lowest on north-facing upper leaf surfaces. Percentages of eggs oviposited were significantly different between different oviposition sites. The highest percentage of eggs was on the south-facing lower leaf surfaces, and lowest on south-facing fruit. Percentage of eggs on south-facing lower leaf surfaces, north-facing lower leaf surfaces, and north-facing upper leaf surfaces were significantly higher than other sites. The mean temperatures from 1900 to 0700 hours at the three sites were between  $19.18 \pm 0.17^\circ\text{C}$  and  $18.71 \pm 0.16^\circ\text{C}$  (Table 3).

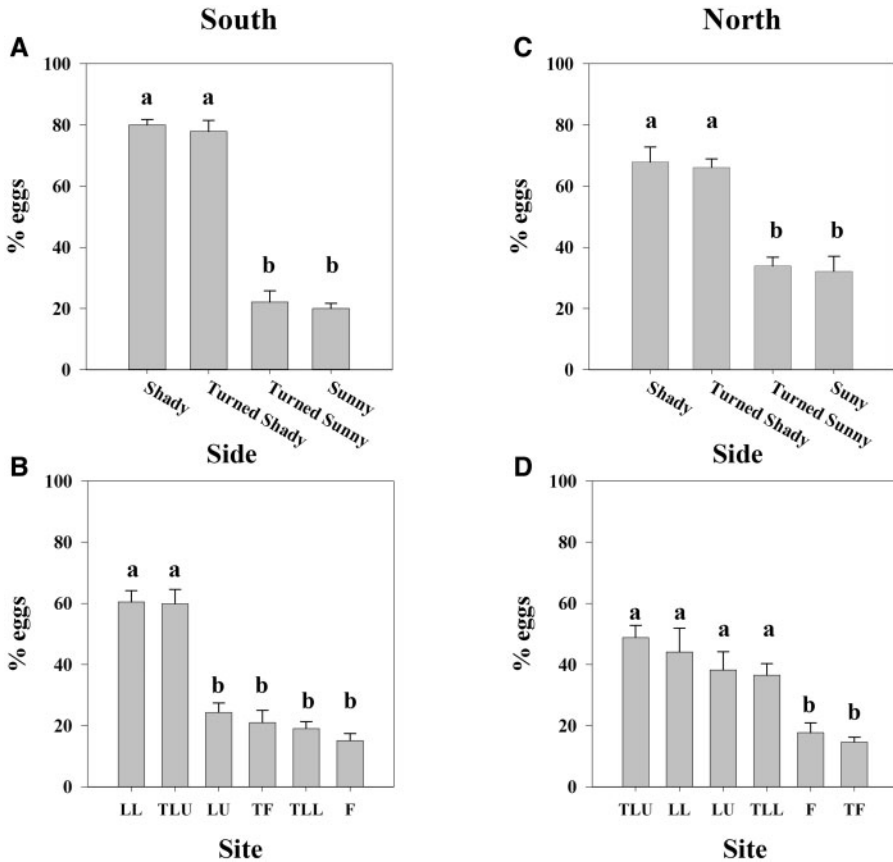
In the manipulative experiment, mean temperatures during 1900 to 0700 hours were significantly different between different oviposition sites. The highest temperatures were on north-facing fruit and lowest on south-facing upper leaf surfaces. The mean temperature from 1900 to 0700 hours at the two sites was between  $19.19 \pm 0.19^\circ\text{C}$  and  $18.59 \pm 0.29^\circ\text{C}$ . Accumulative development rate was significantly different between different oviposition sites. The highest accumulative development rate was on north-facing fruit and lowest on north-facing upper leaf surfaces. Percentage of eggs was significantly different between different oviposition sites. The highest percentage of eggs was on south-facing lower leaf surfaces and the lowest on south-facing fruit. Percentage of eggs on south-facing lower leaf surfaces and north-facing lower leaf surfaces were the two highest values among the six sites (Table 3).

We compared the mean number of eggs on south- and north-facing canopies in both the field survey and manipulative experiment. There were no significant differences between south and north canopies in the field survey and manipulative experiment. A comparison of

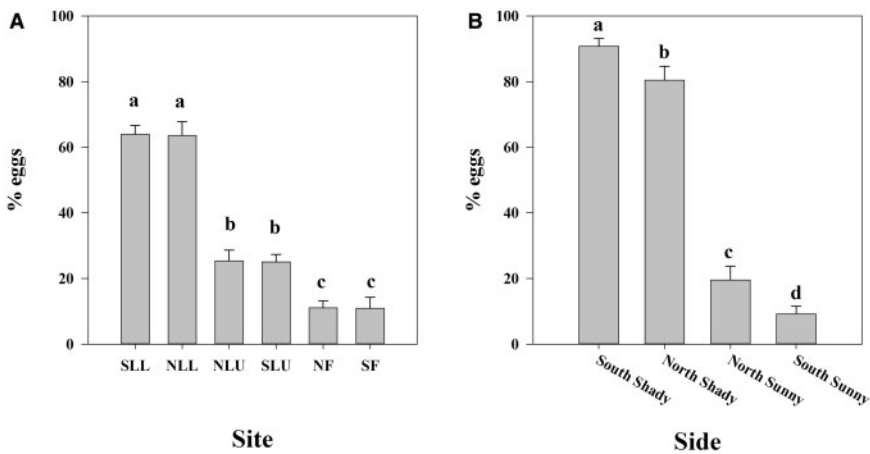
**Table 1. Effect of leaf surface turning on percentage of eggs on different cluster sides (sunny and shady) on north- and south-facing canopies**

Experiment	Canopy aspect	n	Percentage of eggs on different sides (%)				ANOVA
			Sunny	Turned sunny	Shady	Turned shady	
ME	South	1,262	20.0 ± 1.7b	22.1 ± 3.6b	80.0 ± 1.7a	77.9 ± 3.6a	$F_{3,55} = 182.667; P < 0.001$
	North	1,696	32.1 ± 4.9b	33.9 ± 2.8b	67.9 ± 4.9a	66.1 ± 2.8a	
FS	South	1,029	9.2 ± 2.4d	–	90.8 ± 2.4a	–	$F_{3,35} = 114.366; P < 0.001$
	North	925	19.5 ± 4.2c	–	80.5 ± 4.2b	–	

Data expressed as mean ± SE. Different letters in a row indicate significant differences ( $P < 0.05$ , one-way ANOVA). ME, manipulative experiment; FS, field survey.



**Fig. 1.** Effect of leaf surface turning on percentage of eggs on different cluster sides (A and C), sunny and shady, and different oviposition sites (B and D); LL, lower leaf surface; LU, upper leaf surface; F, fruit; TLU, turned upper leaf surface; TLL, turned lower leaf surface; TF, turned fruit) on north and south canopy aspects. Data expressed as mean  $\pm$  SE. Different letters above the bars indicate significant differences ( $P < 0.05$ , one-way ANOVA).

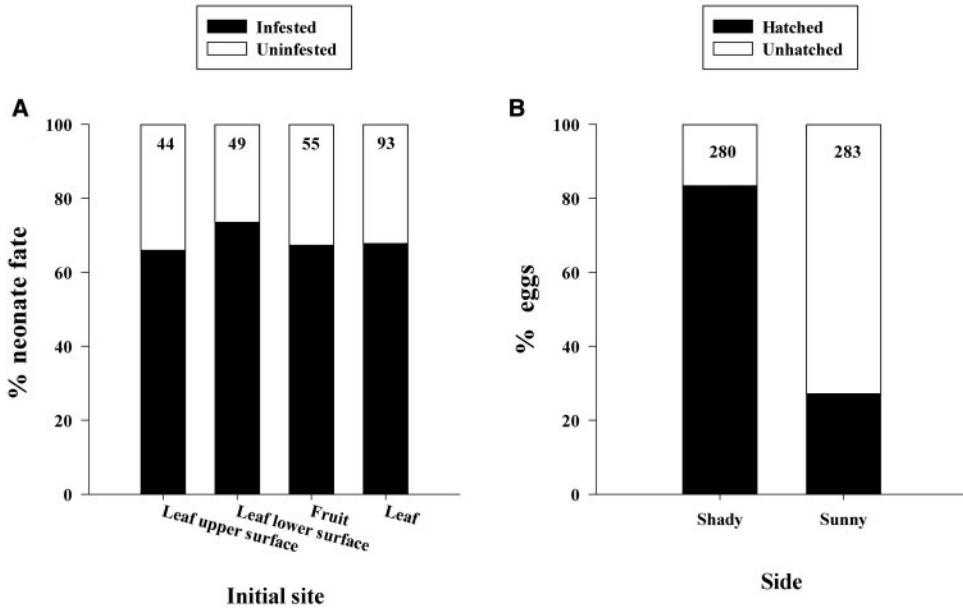


**Fig. 2.** Percentage of eggs on different sites (A) SLU, south upper leaf surface; SLL, south lower leaf surface; SF, south fruit; NLU, north upper leaf surface; NLL, north lower leaf surface; NF, north fruit; and different oviposition sides (B) on north- and south-facing canopy aspects in the field survey. Data expressed as mean  $\pm$  SE. Different letters above the bars indicate significant differences (one-way ANOVA,  $P < 0.05$ ).

**Table 2. Effect of leaf surface turning on percentage of eggs on different oviposition sites on north- and south-facing canopies**

Experiment	Canopy aspect	n	Percentage of eggs on different oviposition sites (%)						ANOVA
			Upper leaf surface	Turned upper leaf surface	Lower leaf surface	Turned lower leaf surface	Fruit	Turned fruit	
ME	South	1,262	24.4 ± 3.0b	59.9 ± 4.7a	60.5 ± 3.6a	19.1 ± 2.3b	15.1 ± 2.3b	21.0 ± 4.0b	$F_{5,71} = 8.469; P < 0.001$
	North	1,696	38.2 ± 6.0a	48.8 ± 4.0a	44.1 ± 7.8a	36.5 ± 3.7a	17.7 ± 3.2b	14.7 ± 1.6b	
FS	South	1,029	29.9 ± 1.5b	–	53.2 ± 1.6a	–	17.9 ± 2.8c	–	$F_{5,53} = 54.419; P < 0.001$
	North	925	29.9 ± 2.2b	–	53.1 ± 2.5a	–	18.7 ± 2.0c	–	

Data expressed as mean ± SE. Different letters in a row indicate significant differences ( $P < 0.05$ , one-way ANOVA). ME, manipulative experiment; FS, field survey.



**Fig. 3.** Infestation of codling moth neonates at different sites (A) and egg hatching success on different sides (B) (sample size for each category is on the bar).

the percentage fruit infestation between south- and north-facing canopies (field survey) revealed that there was no significant difference between south and north (Table 4).

**Egg Hatching and Neonate Performance.** The success of infestation was not significantly different between larvae placed on leaves and fruit ( $\chi^2 = 0.0151$ ,  $P = 0.902$ ; infestation rate: 67.7 and 67.3%, respectively; Fig. 3A). Infestation was not significantly different between larvae placed on upper and lower leaf surfaces ( $\chi^2 = 0.322$ ,  $P = 0.571$ ; infestation rate: 65.9 and 73.5%, respectively; Fig. 3A). Hatching success of eggs was significantly greater in eggs placed in the shade when compared with those in the sun ( $\chi^2 = 177.974$ ,  $P < 0.001$ ; hatching percentage: 83.4 and 27.1%, respectively; Fig. 3B).

**Discussion**

In previous studies, Geier (1963) and Jackson (1979) found more eggs on the leaf than fruit and more eggs on upper leaf surface than lower leaf surface. Borchert et al. (2004) found more eggs on leaf than fruit at the

beginning of the growing season. However, it varied inversely by the end of the growing season. Lei Du et al. (2012) found more eggs on leaf than fruit and more eggs on lower leaf surface than on upper leaf surface. In our research, leaf surface turning had no significant influence on oviposition side (shady vs. sunny) selection. However, leaf surface turning had a significant influence on oviposition site (upper leaf surface and lower leaf surface). In the field survey, percentage of eggs on the shady side was significantly greater than the sunny side. This coincided with results from the manipulative experiment. The neonate performance test implied that once eggs were oviposited within 10 cm of the fruit neonate, infestation of fruit did not differ between leaves and fruit. Therefore, oviposition on leaves does not mean a reduction in neonate fruit infestation. In the egg-hatching experiment, egg-hatching success on the shady side was significantly higher than on the sunny side (56.3% higher). We also found that in the field, the shady side of clusters was favored by female codling moths. In the field, not all of the clusters upper surfaces of leaves were on the sunny side and lower surfaces of leaves on the shady side.

**Table 3. Comparison of mean temperature during 1900 to 0700 hours, accumulative development rate and percentage of eggs in the field survey and manipulative experiment**

Experiment	Parameter	n	Site						ANOVA
			SF	SLU	SLL	NF	NLU	NLL	
Field survey	Mean temperature during 1900 to 0700 hours (°C)	21,204	18.36 ± 0.02c	18.52 ± 0.16bc	18.71 ± 0.25abc	19.35 ± 0.08a	19.18 ± 0.17ab	18.71 ± 0.16abc	$F_{5,17} = 5.936; P = 0.005$
	Accumulative development rate (1/d)	39,150	11.89 ± 0.15c	12.40 ± 0.25b	12.88 ± 0.05ab	13.25 ± 0.07a	12.71 ± 0.09ab	13.12 ± 0.17a	$F_{5,17} = 11.837; P < 0.001$
Manipulative experiment	Percentage of eggs (%)	2,075	20.3 ± 5.0b	24.4 ± 2.6b	55.2 ± 5.1a	16.0 ± 5.6c	28.8 ± 4.4b	55.3 ± 4.6a	$F_{5,77} = 12.858; P < 0.001$
	Mean temperature during 1900 to 0700 hours (°C)	1,6416	18.25 ± 0.03c	16.84 ± 0.12d	18.59 ± 0.29c	19.33 ± 0.02b	20.21 ± 0.20a	19.19 ± 0.19b	$F_{5,17} = 44.326; P < 0.001$
	Accumulative development > rate (1/d)	30,420	8.85 ± 0.07c	9.49 ± 0.07b	9.80 ± 0.03b	10.15 ± 0.02a	9.66 ± 0.04b	10.02 ± 0.11a	$F_{5,17} = 52.861; P < 0.001$
	Percentage of eggs (%)	3,020	15.1 ± 2.3c	24.4 ± 3.0c	60.5 ± 3.6a	17.7 ± 3.2c	38.2 ± 6.0b	44.1 ± 7.8b	$F_{5,86} = 17.158; P < 0.001$

Data expressed as mean ± SE. Different letters in a row indicate significant differences ( $P < 0.05$ , Student–Newman–Keuls method test). SLU, south upper leaf surface; SLL, south lower leaf surface; SF, south fruit; NLU, north upper leaf surface; NLL, north lower leaf surface; NF, north fruit.

This varied during the growing season. For the fruit, either young fruit or mature fruit had greater chance of being exposed to sunshine because they are either upright in the center of the cluster, or hanging under the cluster. Therefore, the result of previous studies based on different sites (fruit, upper leaf surface, and lower leaf surface) could differ. A few studies have shown that the number of eggs on leaves was significantly greater than on fruit (Geier 1963; Jackson 1979; Lei Du 2012). There was no significant difference in the mean number of eggs between south- and north-facing canopies in both the manipulative experiment and field survey. Similarly, percentage of fruit infestation was not significantly different between south- and north-facing canopies. This result is similar to that of a previous study (Stoeckli et al. 2008).

The physical properties of different surfaces can influence oviposition site selection. Eggs on the upper leaf surface are more firmly fixed than on the lower leaf surface (Al Bitar et al. 2012, 2014). In the manipulative experiment, leaf surface turning significantly affected the percentage of eggs on the leaf surface (Fig. 1). In the south-facing canopy, turning the leaf surface decreased the percentage of eggs on the south-facing lower leaf surface from  $60.5 \pm 3.6$  to  $19.1 \pm 2.3\%$ , whereas eggs on the south upper leaf surface increased from  $24.4 \pm 3.0$  to  $59.9 \pm 4.7\%$ . Conversely, the percentage of eggs on the shady side was significantly higher than the sunny side, regardless of leaf surface turning. The neonate performance test showed no significant difference between upper and lower leaf surfaces in terms of neonate infestation success on fruit. Egg hatching success under shade was significantly greater than under sunny conditions. Thus, eggs oviposited on the shady side have the best chance for offspring survival. This indicates that in terms of codling moth oviposition site selection, shady versus sunny side is a more decisive factor than the physical properties of the surface.

As nocturnal insects, codling moths are considered thermophilous and lack the mechanism to avoid temperatures lethal to progeny development (Kuhrt et al. 2006, Notter-Hausmann and Dorn 2010). In our study, the mean temperatures of different oviposition sites were significantly different between 1900 and 0700 hours (Fig. 3). However, the sites with the highest mean temperature ( $19.35 \pm 0.08^\circ\text{C}$  and  $20.21 \pm 0.20^\circ\text{C}$  in field survey and manipulative experiment, respectively) did not have the highest percentage of eggs. The mean temperatures during 1900 to 0700 hours of sites that had a high percentage of eggs were between  $19.19 \pm 0.19^\circ\text{C}$  and  $18.59 \pm 0.29^\circ\text{C}$ . Furthermore, the order of accumulative development rate at different sites coincided with the percentage of eggs at different sites. In the manipulative experiment, the order of the accumulative development rate was north lower leaf surface (NLL) > south lower leaf surface (SLL) > north upper leaf surface (NLU) > south upper leaf surface (SLU). The order of percentage of eggs was NLL > SLL > NLU > SLU. In the field survey, the

**Table 4. Percentage of fruit infestation in the field survey, mean number of eggs in field survey and manipulative experiment from two canopy aspects (north and south)**

Parameter	n	North	South	Mann-Whitney rank sum test
Mean no. of eggs in field survey	2,075	73.7 ± 17.4	85.9 ± 15.7	T = 159.5, P = 0.427
Mean no. of eggs in manipulative experiment	3,020	70.7 ± 19.4	45.1 ± 7.9	T = 703.0, P = 0.222
Percentage of fruit infestation in field survey (%)	4,100	42.9 ± 8.5	52.1 ± 8.3	T = 155.0, P = 0.305

Data expressed as mean ± SE.

order of the accumulative development rate was  $NLL > SLL > NLU > SLU$ . The order of percentage of eggs was  $SLL > NLL > NLU > SLU$ . In previous study, temperature  $>35^{\circ}\text{C}$  was considered unsuitable for codling moth egg development (Aghdam et al. 2009; Liu et al. 2012). In our recording, the times of temperature exceeded  $35^{\circ}\text{C}$  on south upper leaf surface (sunny side) were  $\sim 114$  times. While south lower leaf surface (shady side) were  $\sim 80$  times during the monitoring period. The result in eggs hatching also showed that the egg-hatching success under shade was significantly greater than sunny conditions. This indicates that in the field, codling moths selected suitable oviposition sites for egg development that were not strictly thermophilous.

In conclusion, through manipulative experiments and field surveys, our results revealed that shady sites are favored by codling moths in the field for oviposition. However, there was no significant difference in the mean number of eggs and percentage infestation between north- and south-facing canopies. By means of a neonate performance test, an egg hatching test, and temperature records, we found that in the field, codling moths did not choose the sites with a high mean temperature, but choose sites suitable for egg development and hatching. Our results indicate that a trade-off in codling moth oviposition site selection may exist.

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