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**Leg attachment and egg adhesion of  
the codling moth, *Cydia pomonella* (L.)  
(Lepidoptera: Tortricidae)  
to different surfaces**

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## *I dedicate my thesis*

*To my wonderful parents,  
who give me their best, inspiring me to give the world my best.*

*To Prof. Dr. Dr. C. P. W. Zebitz,  
who is interested in revealing some hidden secrets of *Cydia pomonella* and  
gave the original idea of this thesis.*

*To all, who are fascinated by the marvelous world of insects.*







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**The following cumulative PhD thesis comprises the following articles:**

<sup>1</sup>AL BITAR, L., VOIGT, D., ZEBITZ, C. P. W. & GORB, S. N. (2009) Tarsal morphology and attachment ability of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to smooth surfaces. *Journal of Insect Physiology* **55**(11), 1029-1038.

<sup>2</sup>AL BITAR, L., VOIGT, D., ZEBITZ, C. P. W. & GORB, S. N. (2010) Attachment ability of the codling moth *Cydia pomonella* L. to rough surfaces. *Journal of Insect Physiology* **56**(12), 1966-1972.

<sup>3</sup>AL BITAR, L., GORB, S. N., ZEBITZ, C. P. W. & VOIGT, D. (2012) Egg adhesion of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to various substrates: I. Leaf surfaces of different apple cultivars. *Arthropod-Plant-Interactions* **6**(3), 471-488.

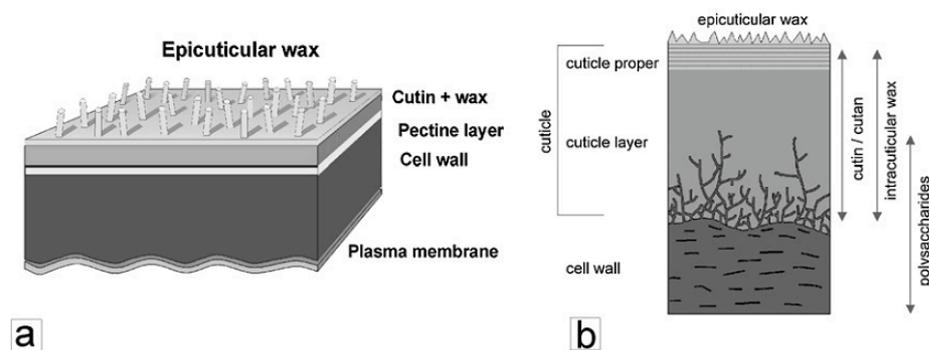
<sup>4</sup>AL BITAR, L., GORB, S. N., ZEBITZ, C. P. W. & VOIGT, D. (2014) Egg adhesion of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to various substrates: II. Fruit surfaces of different apple cultivars. *Arthropod-Plant-Interactions* **8**(1), 57-77.



# 1. General introduction

## 1.1. Plant surface structures and their diversity

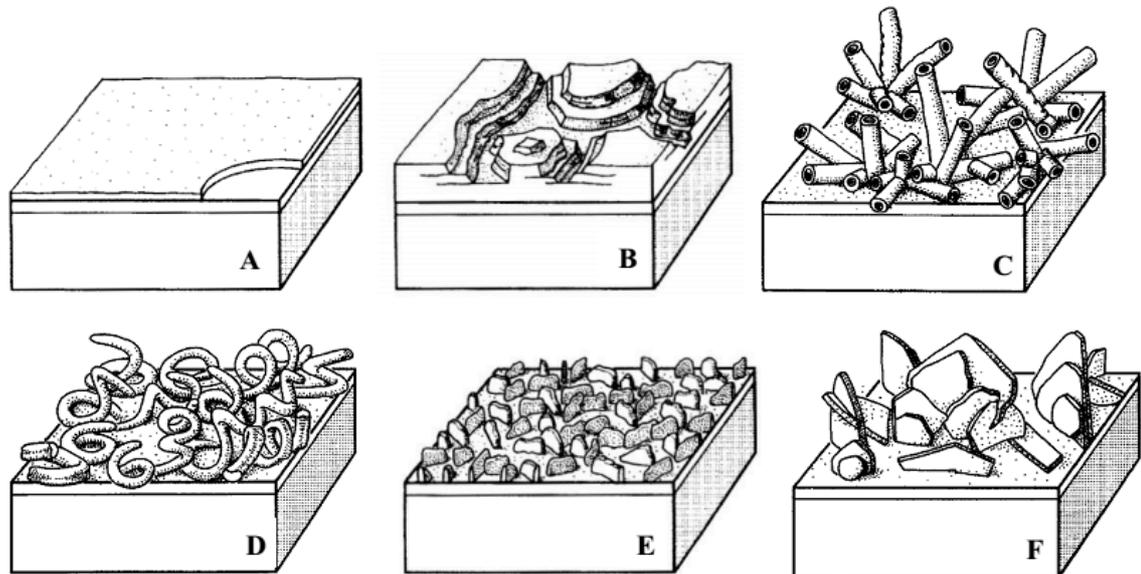
The epidermis of all aerial primary tissues (e.g. leaves, fruits, stems) of vascular plants are covered by a continuous extracellular membrane with striking physical and chemical properties, the cuticle, which serves as a protective, multifunctional interface between them and the environment (Jeffree 1986; Bargel et al. 2006; Riederer 2006). The plant cuticle consists mainly of two main components: cutin (insoluble polymer) and waxes (soluble lipids), with a tremendous diversity in composition and structure (Jeffree 1986; Bargel et al. 2006; Jeffree 2006; Koch et al. 2008).



**Figure 1.** Simplified models of the stratification of the structure of plant cuticles and their major components, (a) (modified by Koch et al. 2008 after W. Barthlott), (b) (modified by Bargel et al. 2006 after P. J. Holloway 1994).

From a morphological point of view, the cuticle membrane has a layered structure, which differs among plant species (Jeffree 1986, 2006). In general, three main layers can be noticed (Fig 1): (1) a thin outer layer called the cuticle proper, (2) a thick inner layer called the cuticle layer, and (3) a pectine-rich layer attaching the cuticle proper and the cuticle layer to the periclinal cellulose walls of the epidermal cells (Fig. 1a) (Jeffree 1986; Bargel et al. 2006; Koch et al. 2009). However, pectine does not arrange as a layer in all plant species (Fig 1b) (Koch et al. 2008). In most plant species, the cuticle is covered by a complex mixture of lipids called the epicuticular waxes (Jeffree 1986; Barthlott et al. 1998) (Fig. 1). There are 23 epicuticular wax types classified according to Barthlott et al. 1998, including thin two-dimensional wax films (2-

D waxes, up to 0.5  $\mu\text{m}$  thickness), thicker layers or crusts (0.5–10  $\mu\text{m}$  thickness), and epicuticular wax crystals. Epicuticular wax crystals are three-dimensional micro- and nanoprojections (3-D waxes), emerging from an underlying wax film, with characteristic shape, size, and orientation towards the surface (Fig. 1a, Fig. 2). Their most common types are plates, platelets, tubules, filaments, and rodlets (Fig. 2) (Barthlott et al. 1998).



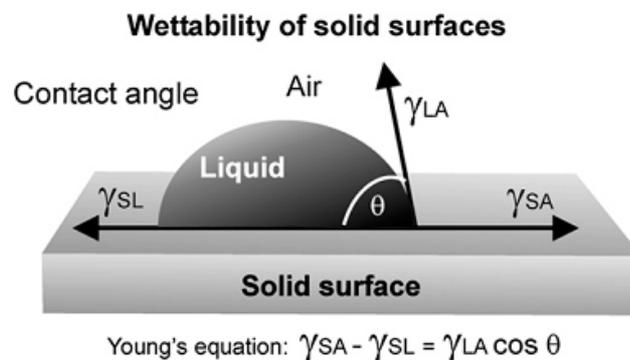
**Figure 2.** Schematic drawings of the most prominent types of epicuticular wax deposits: (A) smooth layers; (B) fissured (cracked) layers, (C) noncosanol-tubules; (D) coiled rodlets; (E) platelets; (F) plates (modified by Al Bitar after Barthlott et al. 1998).

Plant surfaces (plant cuticles and their epicuticular waxes) exhibit extraordinary diversity in structure and morphology, either amongst plant species, crop cultivars, organs of the same plant, and even during the organ ontogeny (e.g. Jeffree 1986; Barthlott et al. 1998; Koch et al. 2008). A comprehensive overview on the diversity of plant surface microstructures and their morphology had been given by Koch et al. 2008. They classified plant surface structuring into three main categories. (1) Plant surface structuring originates from the primary shape and curvature (i.e. flat, convex, or concave) of single epidermal cells and their surface structures, such as unicellular trichomes, papillae, 3-D epicuticular wax crystals, and surface foldings. (2) Plant surface structuring arises from hierarchical structures of single epidermal cells, such as a convex epidermal cell with cuticular foldings or 3-D epicuticular wax crystals on its surface. (3) Plant surface structuring occurs due to multicellular surface structures, such as glands and multicellular trichomes (i.e. glandular and non-glandular hairs). These surface microstructures

play crucial roles in the interaction between the plant surface and its biotic and non-biotic environment. Some of their main functional aspects are: surface hydrophobicity, transport barrier, mechanical properties, protection against harmful radiation, reduction of surface temperature, decreasing the adhesion of particles, pathogen spores, and insect legs and eggs, and many other functions (e.g. [Jeffree 1986](#); [Bargel et al. 2006](#); [Riederer 2006](#); [Koch et al. 2009](#)).

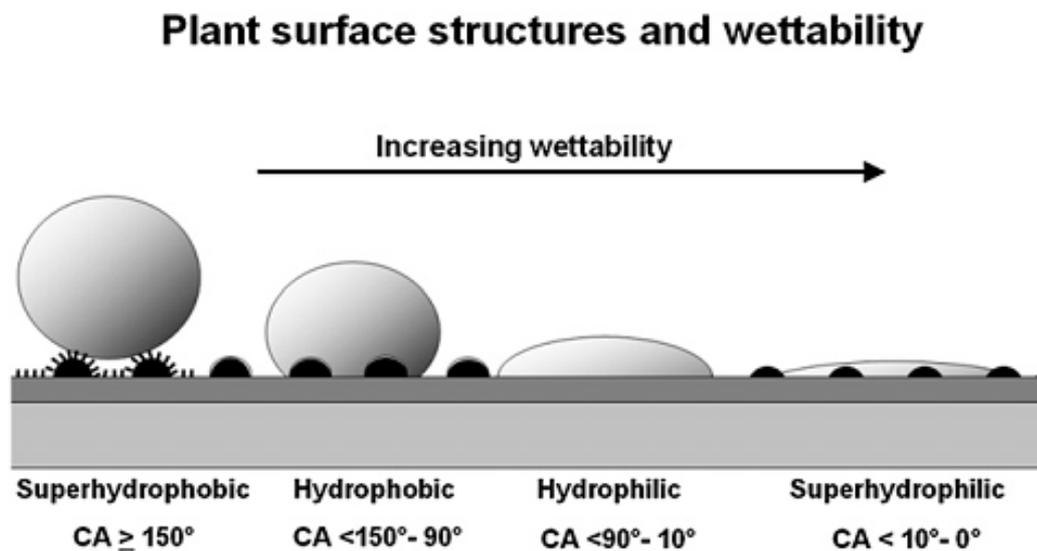
## 1.2. Plant surface structures and their wetting behaviour

Wetting process describes how a liquid droplet comes into contact with a solid surface in a surrounding medium (e.g. air). The wetting behaviour of surfaces can be determined by measurement of the contact angle (CA) of a liquid. A static CA of a liquid droplet on a given surface is determined by the interfacial surface tensions (molecular forces) at the boundaries between the involved liquid (L), solid surface (S) and the surrounding vapor (A), as shown by Young's equation in [Fig. 3](#) ([Koch et al. 2008](#)). Thus, wetting depends on the free surface energy (FSE, the ratio between the energy necessary for the enlargement of the surface and the gain of energy due to adsorption), in addition to other factors, such as surface roughness, and surface cleanliness ([Bhushan and Jung 2006](#); [Koch et al. 2008](#)). The wetting behaviour of solid surfaces can be distinguished into four classes as defined by their static CA: superhydrophilic ( $CA < 10^\circ$ - $0^\circ$ ), hydrophilic ( $CA < 90^\circ$ - $10^\circ$ ), hydrophobic ( $CA < 150^\circ$ - $90^\circ$ ), and superhydrophobic ( $CA \geq 150^\circ$ ) ([Koch et al. 2008](#)).



**Fig. 3** Wetting of a solid surface with a liquid (e.g. water droplet), with air as the surrounding medium.  $\gamma_{LA}$ ,  $\gamma_{LS}$  and  $\gamma_{SA}$  are the interfacial tensions at the boundaries between liquid (L), solid (S), and air (A), which determine the CA of an applied water droplet and are described by Young's equation (after [Koch et al. 2008](#)).

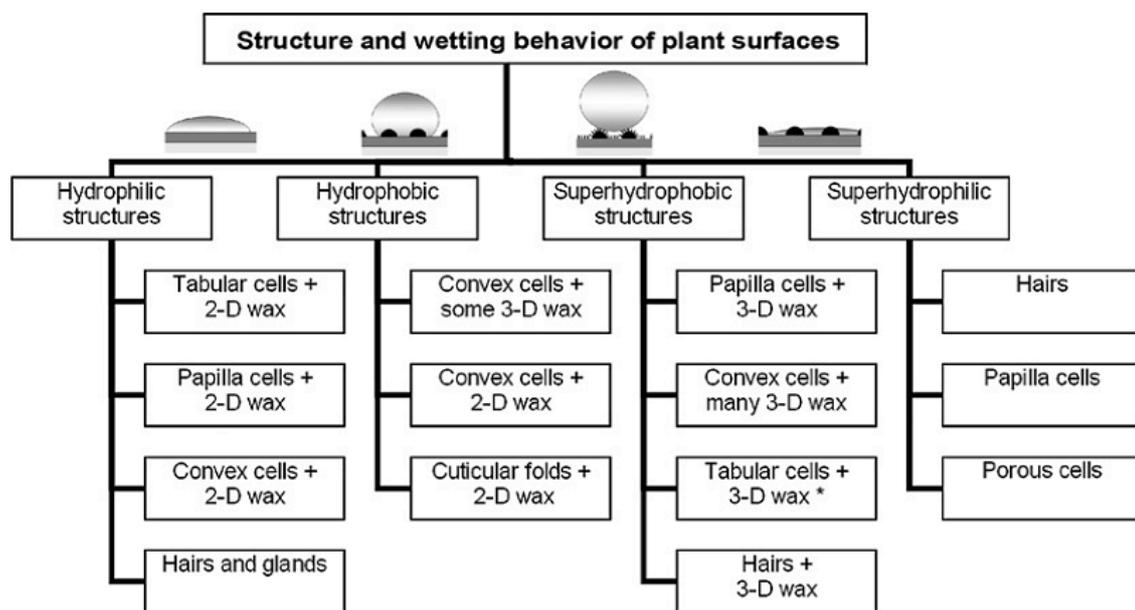
In general, the plant surface is a hydrophobic material due to its hydrophobic waxy nature. However, some structural, chemical, and biological modifications can cause remarkable changes in its wetting behaviour. Roughness of the plant surface plays a key role in the surface wettability (Barthlott and Neinhuis 1997; Koch et al. 2008). Thus, a considerable amplification of surface wettability could be induced by the shape and sculpture of epidermis cells, and their surface structures (such as trichomes, papillae, 3-D waxes, and surface foldings) (Neinhuis and Barthlott 1997; Koch et al. 2008), which is demonstrated in both Fig. 4 and Fig. 5. In other words, increasing the surface roughness causes a hydrophilic smooth surface getting more hydrophilic and a hydrophobic surface getting more hydrophobic (Fig. 4 and Fig. 5) (Koch et al. 2008). For example, a given hydrophobic plant surface consists of convex epidermis cells and is structured with a low amount of 3-D waxes can become superhydrophobic by possessing a high dense coverage of 3-D waxes on it (Fig. 5). Conversely, the surface wettability will increase by any erosion of these 3-D waxes by environmental impacts or other possible causes (Neinhuis and Barthlott 1997).



**Fig. 4** A schematic demonstration of some possible surface structuring of plant surfaces, and their wetting behaviour, showing the four classes of surface wettability, defined by their static CA (after Koch et al. 2008).

Wetting behaviour of the plant surface is of great biological importance. For example, hydrophobic and superhydrophobic plant surfaces are dry and kept clean (self-cleaning mechanism) not only from contamination by particles and dust (Barthlott and Neinhuis 1997), but also from pathogenic microorganisms (Carver and Gurr 2006; Leveau 2006). Surface

hydrophobicity also affected insect-plant interaction. From one hand insect eggs and legs are generally less adhered on hydrophobic and superhydrophobic waxy surfaces (e.g. [Stork 1980](#); [Riedel et al. 2003](#); [Müller and Riederer 2005](#); [Gorb and Gorb 2006, 2009](#); [Voigt and Gorb 2010](#)), but better attached on hydrophilic surfaces such as flower petals ([Koch et al. 2008](#)). From the other hand, water droplets on the plant surface can affect the microclimate on the plant surface and also could be an important source of water for some insects living on or visiting the plant surface ([Müller and Riederer 2005](#)).



**Fig. 5** A summary showing the four classes of plant surface wettability presented in Fig. 4, and the possible structural characteristics of epidermis cells, and their surface microstructure combinations (after [Koch et al. 2008](#)).

### 1.3. The effects of plant surfaces on insects

Insects seek plant surfaces not only to feed on the tissues, but also as sites for living, resting, shelter, mating, and oviposition on or in them ([Southwood 1986](#); [Schoonhoven et al. 2005](#); [Müller 2006](#)). Therefore, success and efficiency in their activities are seriously affected by the physical and chemical characteristics of plant surfaces they live on ([Southwood 1986](#); [Eigenbrode and Espelie 1995](#); [Müller and Riederer 2005](#); [Schoonhoven et al. 2005](#)). According to the comprehensive review of [Southwood \(1986\)](#), the effects of plant surfaces on insects can be divided into three main headings: (1) effects at a distance, (2) direct and indirect contact effects,

and (3) effects when the insect penetrates the plant surface. Most important effects of plant surface microstructures on insects are summarized in [Fig.6](#).

### ***Effects at a distance***

Some plant surface structures, such as trichomes or 3-D epicuticular waxes, owing to their morphological features (e.g. shape, dimensions, density, orientation) and some volatile compounds emanating from them, are known to offer visual and chemical cues used by phytophagous insects for host detection at a certain distance from it ([Prokopy and Owens 1983](#); [Southwood 1986](#); [Schoonhoven et al. 2005](#)).

### ***Direct contact effects***

In the “contact phase”, plant surface structures (epicuticular wax crystals and trichomes) are considered as a direct defense strategy against many herbivorous insects, which affects insect-plant interactions directly in several possible ways ([Schoonhoven et al. 2005](#); [Southwood 1986](#)). (1) A dense coverage of epicuticular wax crystals on a given plant surface is known to reduce not only the attachment ability of many herbivorous insects ([Stork 1980](#); [Jeffree 1986](#); [Southwood 1986](#); [Eigenbrode and Espelie 1995](#); [Gorb and Gorb 2002, 2006b](#); [Gaume et al. 2004](#); [Müller and Riederer 2005](#)), but also the adhesion of their eggs on them ([Müller 2006](#); [Voigt and Gorb 2010](#)). (2) Plant trichomes, depending on their function and features (e.g. shape, density, length, orientation), could impede movement of some herbivorous insects, especially those of small size ([Smith et al. 1975](#); [Jackson and Harwood 1980](#); [Schoonhoven et al. 2005](#)), impale their cuticle leading to wounding and death (by hooked trichomes) ([Johnson 1953](#); [Pillemer and Tingey 1978](#)), or even have some physiological and behavioural effects on them (by exudates from some glandular trichomes) ([Jeffree 1986](#); [Southwood 1986](#); [Romeis et al. 1998](#); [Schoonhoven et al. 2005](#)).

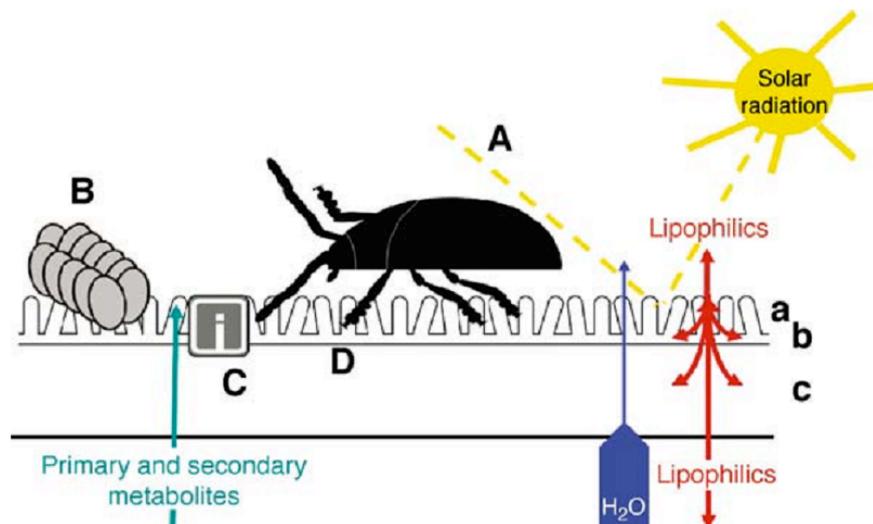
In addition, surface structures (3-D waxes, trichomes, folds, leaf veins, edges, cavities), and the chemical compounds present at their surface (e.g. epicuticular wax compounds, primary and secondary metabolites located on them, and also chemicals produced by insects and other microorganisms) are valuable cues used by herbivorous insects for host recognition and acceptance. They may act as repellents, deterrents or stimulants and mediate insect feeding and oviposition behaviours ([Southwood 1986](#); [Eigenbrode and Espelie 1995](#); [Müller and Riederer 2005](#); [Schoonhoven et al. 2005](#); [Müller 2006](#)).

### *Indirect contact effects*

The physical and chemical nature of the plant surface could also affect herbivorous insects in several indirect ways: (1) positive or adverse effect on the abundance and effectiveness of their natural predators and parasitoids (Southwood 1986; Eigenbrode and Espelie 1995; Eigenbrode and Castagnola 1996; Romeis et al. 1999; Eigenbrode 2004; Schoonhoven et al. 2005; Voigt et al. 2007), (2) effect on their pick-up of pathogens, and uptake of pesticides (Southwood 1986), (3) effect on the microclimate conditions around them (especially for small insects living on the surface), influencing significantly their physiology (such as temperature and water balance) (Willmer 1986; Schoonhoven et al. 2005) and many other possible indirect effects.

### *Effects when penetrating the surface*

Plant trichomes and cuticle toughness could serve as a mechanical barrier, limiting the accessibility of some insects and first instar larvae to reach the tissues within to feed on. Some herbivorous insects, owing to their probing bites, get important cues for host acceptance through the chemicals emanating from the tissues within (Southwood 1986).

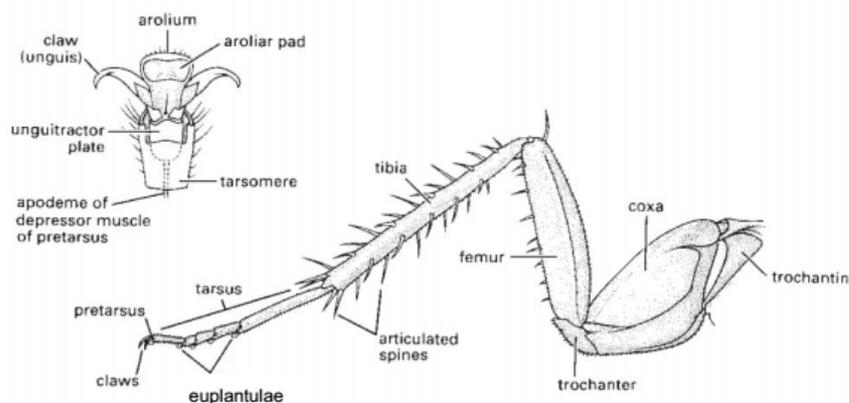


**Fig. 6** A schematic summary of the most important effects of plant surface microstructures on insects. (A) Microstructures affect as visual cues; (B) they affect the adhesion degree of insect eggs to the plant surface; (C) they give insects many important physical and chemical cues (water and other primary and secondary metabolites diffuse in different degrees through the cuticular layer, formed by epicuticular wax crystals) used for host recognition and acceptance by insects; (D) they affect attachment ability of insect legs to the plant surface and their locomotion on it; (a) epicuticular wax crystals; (b) the epicuticular wax film; and (c) cutin and intracuticular waxes (after Müller and Riederer 2005).

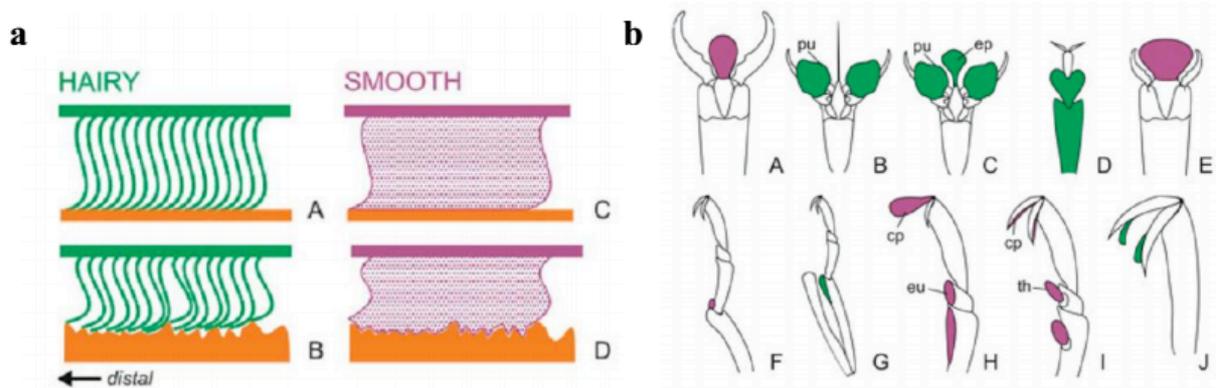
## 1.4. Attachment devices of insect legs

As shown previously, due to their physical and chemical characteristics, the epicuticular wax crystals could reduce the attachment ability of many herbivorous insects to the plant surface as a defense strategy before damage occurs, or for catching insects (as in carnivorous plants) (e.g. [Stork 1980](#); [Eigenbrode and Espelie 1995](#); [Gorb and Gorb 2002, 2006](#); [Gaume et al. 2004](#)). However, some insects have evolved various adaptive attachment devices, enabling them to overcome the previous difficulty and maintain their foothold on the diverse surfaces in their habitat ([Gorb 2001](#); [Beutel and Gorb 2001](#)) ([Fig. 7](#) and [Fig. 8b](#)).

Most insects are provided with a pair of lateral pretarsal claws ([Fig. 7](#) and [Fig. 8b](#)), supporting interlocking on structured surfaces with roughness larger than the claw tip diameter ([Dai et al. 2002](#)). Moreover, insects possess highly specialized adhesive structures, which may be located on different parts of their legs, such as claws, pretarsus, tarsomeres, tarsal apex, or tibia ([Beutel and Gorb 2001](#)) ([Fig. 7](#) and [Fig. 8b](#)). Despite these adhesive devices are widely diverse among insect species and orders in their location, ultrastructure and function, they are in general based on two main mechanisms: smooth flexible pads and hairy surfaces ([Gorb 2001](#); [Beutel and Gorb 2001](#)). Owing to their flexible nature, both types of adhesive devices are highly adapted providing the maximal contact area with a given surface regardless of its microstructures ([Fig. 8a](#)) ([Gorb et al. 2000](#); [Gorb 2001](#); [Beutel and Gorb 2001](#)).



**Fig. 7** Main parts of a hind leg of the cockroach *Periplaneta americana* L. (Blattodea: Blattidae), with enlargement of the ventral surface of the pretarsus and the last tarsomere. The following leg attachment devices can be noticed: the pretarsal claws (interlocking device), the euplantulae (smooth adhesive devices) and the arolium (a smooth adhesive device) (modified by Al Bitar after [Gullan and Cranston 2010](#)).



**Fig. 8** A scheme indicating the two main action mechanisms of insect adhesive devices in (a) and examples of their diversity (coloured areas) in (b). In both (a) and (b), green colour refers to hairy adhesive system, and pink colour refers to smooth adhesive system. Adhesive structures of both systems adapt well to smooth (A and C in a) and structured surfaces (B and D in a). In (b): (A) arolium, (B) pulvilli (smooth or hairy) (pu), (C) empodial pulvillus, (D) hairy adhesive soles of tarsomeres, (E) eversible pretarsal bladder, (F) eversible structure between tibia and tarsus, (G) fossula spongiosa, (H) euplantulae (eu); claw pad (cp), (I) tarsal thorns transformed into adhesive structures (th), claw pad (cp), (J) adhesive claw setae, (after [Beutel and Gorb 2001](#), [Gorb 2005](#)).

Hairy adhesive structures contain a lot of cuticular protuberances on their surfaces ([Gorb 2001](#)). They are common in some insect orders such as Diptera, Dermaptera and Coleoptera, however they vary in their type and size among these orders ([Gorb 2001](#); [Beutel and Gorb 2001](#)). Smooth adhesive pads appear smooth under the light microscope; however ultrastructural studies revealed that their cuticle has microfolds varying in their patterns according to the insect order ([Beutel and Gorb 2001](#)). The arolium as an example belongs to the smooth adhesive type of attachment pads. It is a median hollow lobe on pretarsi of most representatives of Hymenoptera, Mecoptera, Lepidoptera, Plecoptera, Caelifera, Phasmatodea, and Blattodea ([Fig. 7 above and Fig 8bA](#)) ([Beutel and Gorb 2001](#)). Another example is the euplantula on the ventral side of one or more tarsomeres, which is common in the larger species of Plecoptera, and most representatives of Blattodea, Mantodea, Caelifera, Phasmatodea; Notoptera ([Fig. 7 and Fig 8bH](#)) ([Beutel and Gorb 2001](#)). Attachment of these smooth adhesive pads to different plant surfaces depends to a large extent on their deformability and the softness of their pad materials ([Gorb et al. 2000](#); [Jiao et al. 2000](#)).

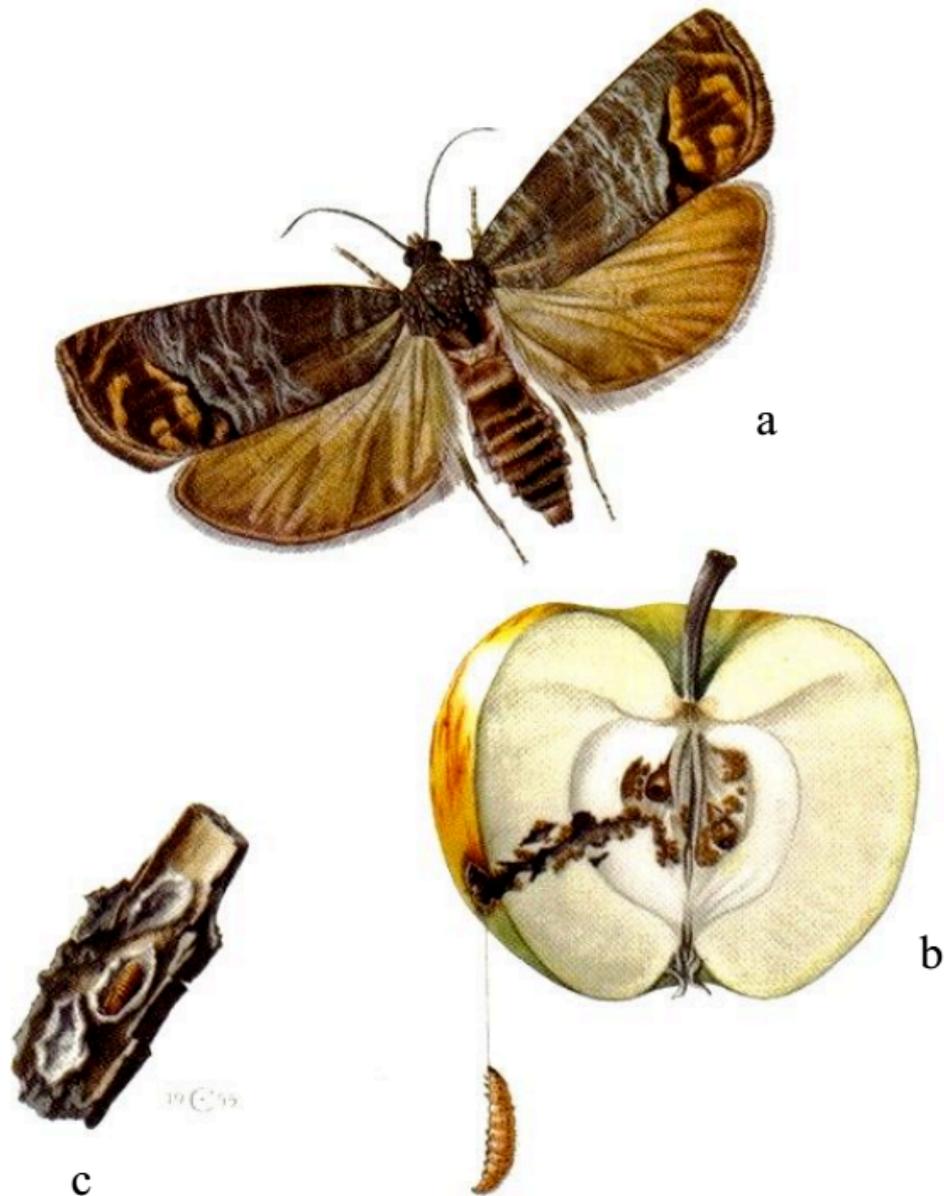
Many studies revealed fluid secretions in the attachment systems of both hairy ([Walker et al. 1985](#); [Ishii 1987](#)), and smooth adhesive pads of many insect species ([Roth and Willis, 1952](#); [Lees and Hardie 1988](#); [Dixon et al. 1990](#); [Jiao et al. 2000](#); [Vötsch et al. 2002](#); [Drechsler and](#)

Federle 2006; Scholz et al. 2008). It has been suggested that this secretion is transported from the epidermis to the epicuticle surface of the adhesive pads through thin canals found in some insect species (e.g. in cockroaches (Arnold 1974) and in locusts (Schwarz and Gorb 2003)), whereas they are not detected in other insects (e.g. in the stick insect *Carausius morosus* (Sinéty) (Scholz et al. 2008)). This secretion was considered to play a crucial role in enhancing the attachment ability of insect pads especially on rough surfaces, by maximizing the contact area (Drechsler and Federle 2006).

### 1.5. The codling moth *Cydia pomonella* L.

*Cydia pomonella* (L.) (Tortricidae, Olethreutinae: Grapholitini), the codling moth, is referred commonly in older literature to as *Carpocapsa pomonella* (L.) or *Laspeyresia pomonella* (L.). Recently, "*Cydia*" has been found to be the correct generic name for this moth (Brown 1979; Wearing et al. 2001; Brown 2006). The common name "codling moth" was given to this moth by Wilkes in 1747 in his book "The English Moths and Butterflies", referring to the elongated, greenish English cooking apples, which were known as "Codling" (Barnes 1991). The adults have brownish grey forewings with several light gray and copper stripes, whereas the hind wings are pale grey with fringed borders. It has a wingspan ranging from 12 to 18 mm and about 10 mm long when wings are folded in a rest position (Fig. 9). Males are smaller than females.

The codling moth is a key pest of domestic apples (*Malus domestica* Borkh.), its most favourite host plants, around the world except Japan and Korea (Barnes 1991). Although its close association with domestic apples, pears (*Pyrus communis* L.), quince (*Cydonia oblonga* Miller), and walnuts (*Juglans regia* L.) are also known to be additional preferred host plants (Barnes, 1991). Occasionally, it also could be found in some stone fruits such as plums (*Prunus domestica* L. and *Prunus salicina* Lindl.), apricots (*Prunus armeniaca* L.), peaches, (*Prunus persica* (L.) Batsch), nectarines, (*Prunus persica* var. *nucipersica* (Suckow) C.K. Schneid), and soft-shelled varieties of almonds (*Prunus amygdalus* Batsch) (Yokoyama and Miller 1988; Curtis et al. 1990; Barnes 1991). The codling moth is well known to discriminate not only between host plant species (e.g. Hagley et al. 1980; Curtis et al. 1990; Barnes 1991), but also between cultivars of the same species (e.g. Olson 1977; Hagley et al. 1980; Plourde et al. 1985; Blomefield et al. 1997; Marti 2001).

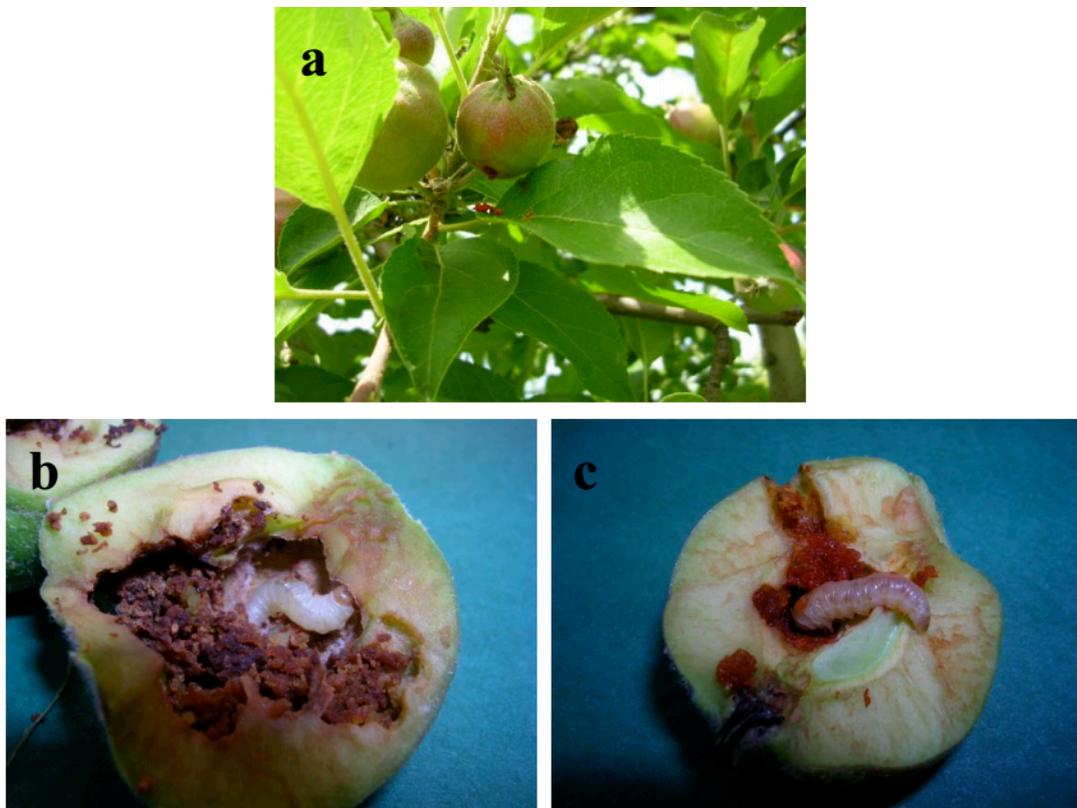


**Figure 9.** Scheme indicating: (a) the codling moth adult, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), (b) a damaged apple fruit due to a codling moth larva fed on its seeds, and later the mature larvae leaves the fruit and drops by a silken sting, searching for a proper place to either pupate or to enter diapause, (c) a codling moth pupa in the bark of a tree (slightly modified by Al Bitar, after a drawing by [Claus Caspari 1955](#), and printed in Germany, for "Mitteleuropäische Insekten").

In apple orchards, the codling moth has one generation in cooler climates, two generations in southern Middle Europe, and even three to four generations in warmer climates ([Audemard 1991](#); [Shel'Deshova 1967](#)). Generally, when the orchards left without control, a severe crop damage of 80-100% could be expected especially where two or more generations can occur ([Geier 1963](#)). This damage is owing to the larvae (5 instars), which bore deep into apple fruits

feeding on the flesh, and the developing seeds (Fig. 9b and Fig. 10). Mature larvae leave their fruits (Fig.9b), searching for dry, safe places to either pupate (Fig.9c) or to enter diapause.

Generally, most activities (such as flight, calling, mating and oviposition) of adult moths occur within or around sunset period, and less often shortly following sunrise, depending on several ecological factors such as light intensity, humidity, temperature, and air movement (Borden 1931). Mating occurs on plant surfaces, where the male first aligns parallel to the female, inserting its coupling organs and then moves to an opposite position (Borden 1931). Oviposition can set on 6-15 hours after mating (Howell 1991).



**Figure 10.** Samples of young apple fruits damaged by codling moth larvae of the first generation. (a) A young apple fruit with frass produced by a codling moth larva; (b) and (c) the inner sides of damaged young fruits, where the larvae can be seen boring within (Images by Al Bitar, L.).

Codling moth neonates are vulnerable and limited in their mobility (Fig. 11), and have to locate and penetrate into their food source (the fruit) within a few hours (Jackson and Harwood 1980; Jackson 1982). Therefore, their survival depends to a large degree on the choices made by the ovipositing females for the proper host plant and the proper oviposition sites (on or very close to the fruits, Geier 1963; Renwick and Chew 1994; Blomefield et al. 1997; Marti 2001). Here, these

oviposition choices are strongly affected by microclimate factors, and several signals emanating from the host plant foliage and fruits including visual stimuli, volatiles, surface kairomones and allomones, surface texture, and possibly other cues (e.g. Jackson 1979; Hagley et al. 1980; Plourde et al. 1985; Thiery et al. 1995; Yan et al. 1999; Marti 2001; Lombarkia and Derridj 2002; Witzgall et al. 2005).



**Figure 11.** Eggs and first instar larvae of the codling moth on the surface of an apple fruit: (a) two eggs of different developmental stages; (b) a neonate larva starts penetrating the fruit surface; (c) another neonate larva still exploring the fruit surface (image by Al Bitar, L.).

Egg distribution in the field vary through the season depending mainly on the host plants species, cultivar characteristics, and the phenological plant stage corresponding with the abundance of the gravid females. In apple orchards, at the beginning of the growing season, eggs are deposited on leaves adjoining to the trichome-covered young fruits (Hall 1929; Borden 1931; Geier 1963; Jackson 1979). The leaf side favoured for oviposition (upper, lower leaf surface or both of them) may differ considerably between apple cultivars (Wood 1965; Hagley et al. 1980; Plourde et al. 1985; Blomefield et al. 1997). Later in the growing season, the majority of eggs of the second and the third generations are laid directly on the fruits (e.g. Hall 1929; Blomefield et al. 1997; Borchert et al. 2004), which became larger and have lost their trichomes.

Having selected a suitable oviposition surface, the codling moth female begins brushing this surface with its ovipositor, and within very few seconds the egg appears as an oval, flat shiny disc and turns later to a milky white colour. Then immediately, the female moth moves or flies away (Borden 1931). Therefore, under field conditions, the eggs are singly laid and well distributed, and only occasionally two or more eggs on the same leaf or fruit can be found (Borden 1931; Geier 1963; Wood 1965; Jackson 1979).

## 1.6. Thesis Objectives

Through one hundred years of rich researches on the codling moth, a wealth of knowledge has been collected focusing mainly on its behaviour, ecology, chemoeology, damage, and many possible control techniques. However, many aspects of insect-plant-relationship of this important pest, especially those mediated by the physical characteristics of the plant surface are still largely unknown.

Given that codling moths live on widely different surfaces provided by their host plants, among them the gravid females prefer smooth and less hairy surfaces as oviposition sites (Westgard et al. 1976; Olson 1977; Hagley et al. 1980; Plourde et al. 1985; Curtis et al. 1990; Barnes 1991; Marti 2001; and own observations). The reasons for this preference are still uncovered. Therefore, we were motivated through the studies of this thesis to investigate the effect of structural and physicochemical characteristics of the surface on the attachment ability of legs and eggs of the codling moth, which could be responsible for the surface preference of their ovipositing females. Two main objectives were considered:

(1) The attachment performance of the codling moth adults on substrates varying in their surface characteristics (roughness and physicochemical), combined with a morphological study of the pretarsal attachment devices of adults of both sexes (studies 1 and 2).

(2) The egg adhesion of the codling moth to different leaf and fruit surfaces of the domestic apple (studies 3 and 4), combined with morphological and physicochemical properties of the tested plant surfaces to evaluate their role in the egg adhesion.







## 2. Attachment ability of the codling moth

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### 2.1. Tarsal morphology and attachment ability to smooth surfaces<sup>1</sup>

#### Abstract

Despite several studies on the attachment ability of different insect taxa, little is known about this phenomenon in adult Lepidoptera. In this study we combined morphological and experimental analyses of tarsal adhesive devices and the attachment ability of the codling moth *Cydia pomonella* (L.) (Lepidoptera, Tortricidae) to smooth surfaces. Pretarsi of *C. pomonella* attach to smooth substrates by means of their smooth, flexible and well developed arolia. Using the centrifugal force measurement technique, friction forces of males and females were assessed on hydrophobic and hydrophilic glass surfaces. Adults of both sexes generated similar forces in spite of the noticeable difference in their body masses. That is why males showed significantly higher safety factors (attachment force divided by body weight) compared to those of females. Hydrophobicity of the substrate had no considerable effect on friction forces. For females, friction forces (sliding parallel to the substrate plane) were compared with adhesive forces (pulling off perpendicularly from the substrate plane) measured on Plexiglas surfaces. It can be concluded that the attachment system of *C. pomonella* is rather robust against physico-chemical properties of the substrate and is able to achieve a very good attachment on vertical and horizontal substrata.

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<sup>1</sup>AL BITAR, L., VOIGT, D., ZEBITZ, C. P. W. & GORB, S. N. (2009) Tarsal morphology and attachment ability of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to smooth surfaces. *Journal of Insect Physiology* 55, 1029-1038. doi:10.1016/j.jinsphys.2009.07.008



## 2. Attachment ability of the codling moth

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### 2.2. Attachment ability to rough surfaces<sup>2</sup>

#### Abstract

Host plant surfaces of the codling moth, *Cydia pomonella* L. (Lepidoptera, Tortricidae), vary in microtopography, which can affect its attachment, locomotion, and oviposition behaviour. This study was performed to investigate the effect of surface roughness on the attachment ability of adult insects. Using a centrifugal force device, friction forces of both sexes were assessed on six epoxy resin substrates differing only in the dimensions of their surface asperities, ranging from 0  $\mu\text{m}$  to 12  $\mu\text{m}$ . Surface topography significantly affected friction forces. Maximal force was measured on the smooth substrate whereas minimal force was assessed on microrough substrates with 0.3  $\mu\text{m}$  and 1.0  $\mu\text{m}$  size of asperities. On the remaining rough substrates, friction forces were significantly higher but still lower than on the smooth substrate. Both sexes generated similar forces on the same substrate, in spite of the considerable difference in their body mass. Thus, it is expected that both sexes can attach effectively to differently structured plant substrates in their habitat. However, since smooth surfaces have been reported previously to be the most favorable substrates for ovipositing females of *C. pomonella*, it is possible that they use their attachment system to sense the substrate texture and prefer those substrates to which their arolia attach the best.

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<sup>2</sup>AL BITAR, L., VOIGT, D., ZEBITZ, C. P. W. & GORB, S. N. (2010) Attachment ability of the codling moth *Cydia pomonella* L. to rough surfaces. *Journal of Insect Physiology* **56**(12), 1966-1972.  
doi:10.1016/j.jinsphys.2010.08.021



## 3. Egg adhesion of the codling moth

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### 3.1. Egg adhesion to leaf surfaces of different apple cultivars<sup>3</sup>

#### Abstract

Codling moths, *Cydia pomonella* L. (Lepidoptera, Tortricidae), of the first generation deposit eggs on apple leaves in the vicinity of small fruits. The choice of the suitable oviposition sites and proper fixation of eggs are expected to be crucial factors for the survival of the offspring. In this study, we investigated egg adhesion of the codling moth to leaf surfaces of different cultivars of the domestic apple, *Malus domestica* Borkh., by measuring the pull-off force required to detach the eggs from leaves. Since surface features may influence insect egg adhesion, morphological and physico-chemical properties (wettability, free surface energy) of these leaf surfaces were analyzed. Furthermore, eggs and their adhesives covering leaf surfaces were visualized. Eggs on the smooth upper leaf surfaces of all tested cultivars required significantly similar pull-off forces to be detached, at a total average of 6.0 mN. Up to 2-3 times stronger pull-off forces had to be applied to detach eggs from trichome-covered lower leaves, and these forces differed significantly between cultivars. The role of leaf surface properties is discussed in the context of egg adhesion, oviposition site choice, female attachment, as well as neonate locomotion speed and survival. The obtained results shed light on the susceptibility of various apple cultivars and leaf surfaces to the infestation of apple trees by first generation codling moths.

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<sup>3</sup>AL BITAR, L., GORB, S. N., ZEBITZ, C. P. W. & VOIGT, D. (2012) Egg adhesion of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to various substrates: I. Leaf surfaces of different apple cultivars. *Arthropod-Plant-Interactions* **6**(3), 471-488. DOI 10.1007/s11829-012-9198-z



### 3. Egg adhesion of the codling moth

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#### 3.2. Egg adhesion to fruit surfaces of different apple cultivars <sup>4</sup>

##### Abstract

In the late growing season of apples, most eggs of the codling moth, *Cydia pomonella* L. (Lepidoptera, Tortricidae), of the second and third generations are deposited directly on fruits. The apple fruit surface is densely covered by three-dimensional micro- and nanoprojections, the epicuticular wax crystals, emerging from an underlying wax film. These epicuticular waxes render the apple fruit surface hydrophobic, which could affect the attachment of insect legs and eggs to it. A better survival of the codling moth offspring is expected to be ensured by the selection of suitable oviposition sites by females, as well as by a proper adhesion of deposited eggs to these sites. In this study, we investigated egg adhesion of the codling moth to the fruit surface of different cultivars of the domestic apple, *Malus domestica* Borkh., by measuring the pull-off force required to detach eggs from fruits. Since surface characteristics may influence insect egg adhesion, the information about morphological and physicochemical properties of the fruit surface is crucial for understanding oviposition site selection by females. In the present study, surface morphology, wettability, and free surface energy of the apple cultivars ‘Boskoop’, ‘Elstar’, ‘Golden Delicious’, ‘Jonica’, and ‘Topaz’ were analyzed. Eggs adhered tightly to the fruit surface of all apple cultivars tested: pull-off forces averaged 63.9 mN. These forces are four- to tenfold stronger than those previously measured on adaxial and abaxial leaf surfaces of the identical apple cultivars. The mechanisms used by the moth to fix its eggs on the waxy surface of apple fruits, and the influence of fruit surface properties on egg glue adhesion are discussed. Furthermore, the results are debated in the context of the oviposition site selection by females, and its role in offspring survival of the second and third generations of the codling moth.

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<sup>4</sup>AL BITAR, L., GORB, S. N., ZEBITZ, C. P. W. & VOIGT, D. (2014) Egg adhesion of the codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) to various substrates: II. Fruit surfaces of different apple cultivars. *Arthropod-Plant-Interactions* **8**(1), 57-77. DOI 10.1007/s11829-013-9288-6



## 4. General discussion

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Adults of *Cydia pomonella* live on host plant surfaces, which are largely variable in their structural, chemical, and physicochemical characteristics not only amongst plant species, but also amongst cultivars, plant parts (e.g. upper/lower leaf sides, fruits, flower petals, twigs, bark), and plant phenological stages (e.g. Bell 1937; Skene 1963; Faust and Shear 1972; Considine and Brown 1981; Belding et al. 1998; Verardo et al. 2003; Bringe et al. 2006; Lombarkia and Derridj 2008; Velásquez et al. 2011; Chapter 3 of this thesis). Environmental conditions and orchard management practices can also affect physical or chemical plant surface traits (e.g. Faust and Shear 1972; Hull et al. 1975; Proctor and Loughheed 1980; Peet 1992; Opara 1993, 2000; Wojcik et al. 1997; Gibert et al. 2007; Rinallo and Mori 1996; Creasy 1980; Knoche and Grimm 2008, Hunsche et al. 2010). These highly variable properties of the plant surface may profoundly affect directly and indirectly many aspects of insect–plant interaction, such as attachment, locomotion, oviposition site selection, egg adhesion, and also survival of adults and their offsprings (Southwood 1986; Eigenbrode and Espelie 1995; Müller and Riederer 2005; Schoonhoven et al. 2005; Müller 2006).

More attention was drawn to volatile and non-volatile chemicals at the host plant surface and the behavioral response of the codling moth towards them (e.g. Yan et al. 1999; Bengtsson et al. 2001; Ansebo 2004; Landolt and Guedot 2008; Lombarkia and Derridj 2008). Conversely, physical properties of the host plant surface of the codling moth has been given only little attention in the literature and still has not been investigated in depth they deserve, in spite of their importance in many of codling moth–plant interactions (e.g. oviposition site selection Hagley 1980; Olson 1977, neonate speed Jackson 1982; Unruh et al. 2000). Therefore, studies were undertaken in thesis to investigate the effect of structural and physicochemical characteristics of the substrate on two main insect–plant interactions: (1) the attachment ability of codling moth adults (Chapter 2) and (2) the egg adhesion (Chapter 3). Moreover, some important behaviour observations (from previous studies and ours) of the ovipositing females and neonates were discussed and analyzed according to the new emerging results of our studies.

## 4.1. Attachment ability of the codling moth

A proper attachment ability of codling moth adults to various surfaces of their host plants is considered to be one of the key factors of the insect success not merely for maintaining their foothold on the plant surface during resting, mating, and oviposition, but also to assess many important cues provided by the plant surface (texture, all chemicals at/in the plant surface) in order to accept or reject the surface as a potential host plant/an oviposition site. Therefore, we started our investigation of their attachment ability by a study of the tarsal morphology of male and female moths to know more about their attachment devices and their modifications.

### *Attachment devices of the codling moth*

No sexual dimorphism was noticed in the pretarsal morphology of *C. pomonella* (Paper 1), which can be explained by the fact that adults of both sexes have the same need for a proper attachment to the plant surface during their life activities.

The pretarsus of *C. pomonella* is equipped with two main complementary attachment devices enabling the insect leg to attach to a variety of surfaces ranging from smooth to really rough surfaces. (1) A pair of curved claws with a tip diameter about 1.2  $\mu\text{m}$ , supporting insect attachment to rough surfaces with projections which are larger enough than the claw tip diameter (Dai et al., 2002). (2) A well developed arolium (an adhesive pad belonging to the smooth type of the locomotory attachment devices of insects, Beutel and Gorb 2001), which is expected to be responsible for insect attachment not only to smooth surfaces but also to a variety of microsculptured surfaces (Gorb 2001; Beutel and Gorb 2001). The arolium cuticle has microfolds in form of grooves, running perpendicularly to the longitudinal axis of the pretarsus. Moreover, some secretion residues were noticed at the inflated surface of the arolium.

### *Attachment of the codling moth to smooth substrates*

Using the centrifugal device, our friction force data revealed an excellent attachment ability of the codling moth adults of both sexes to all smooth artificial substrates tested, regardless of their materials (glass, Plexiglas<sup>®</sup>, and polymerized Spurr resin) (Papers 1 and 2), their wettability (hydrophobic and hydrophilic glasses) (Paper 1), and also the position (horizontal or vertical, tested for females) (Paper 1). This excellent attachment ability was more

obvious in the second study ([Paper 2](#)) when friction forces were assessed on six substrates made of the same material (polymerized Spurr resin) differing only in the dimensions of their surface asperities. Indeed, on the smooth substrate, codling moth adults of both sexes generated the maximal friction forces, which varied significantly from those generated on all other rough substrates tested ([Paper 2](#)). Similar excellent attachment abilities to a variety of smooth artificial and natural substrates have been also reported previously for many insect species (e.g. [Stork 1980](#); [Edwards 1982](#); [Eigenbrode 1996](#); [Federle et al. 2000](#); [Gorb and Gorb 2002](#); [Voigt et al. 2008](#)). This excellent attachment ability to smooth substrates is related to the well developed arolia. On such smooth surfaces, there is no projection for the claws to interlock with. Therefore, they will slip off, letting the arolium establishing presumably the maximal contact area with the surface ([Federle et al. 2001](#); [Frantsevich and Gorb 2002](#); [2004](#); [Federle and Endlein 2004](#); [Endlein and Federle 2008](#)), generating the maximal friction force on it. Thus, we conclude that the attachment system of the codling moth adults is well adapted to smooth plant surfaces. Keeping in mind that smooth plant surfaces are not perfectly smooth, but they are characterized by various degrees of surface sculpturing. Here, the pad material properties (high flexibility and viscoelasticity) ([Gorb et al. 2000](#); [Jiao et al. 2000](#), [Gorb 2008](#)), and the pad fluid secretion are expected to enhance the attachment ability on such surfaces ([Drechsler and Federle 2006](#); [Gorb 2008](#)).

This amazing result explains why the ovipositing codling moth females prefer to oviposit on smooth surfaces, such as the upper leaf surface of apples, over the too hairy or rough surfaces (e.g. [Wood 1965](#); [Jackson 1979](#); [Hagley et al. 1980](#); [Plourde et al. 1985](#); [Blomefield et al. 1997](#); [Subinprasert and Svensson 1988](#); [Borchert et al. 2004](#); own unpublished observations). Thus, the gravid females choose surfaces on which they can maintain their foothold the best. This point is more complicated and is discussed in more details in a following section of the general discussion.

### ***Attachment of the codling moth to rough substrates***

Our study demonstrated that codling moth adults of both sexes were able to attach well to all rough substrates tested (epoxy resin substrates with a nominal asperity size of 0.3  $\mu\text{m}$ , 1  $\mu\text{m}$ , 3  $\mu\text{m}$ , 9  $\mu\text{m}$ , and 12  $\mu\text{m}$ ). However, their friction forces were significantly lower than on the smooth substrate (0  $\mu\text{m}$ ), where the maximal friction force was found ([Paper 2](#)). We think that, in spite of its viscoelastic material ([Gorb et al. 2000](#), [Gorb 2008](#)) and the presence of the pad fluid secretion ([Vötsch et al. 2002](#); [Federle et al. 2002](#), [Drechsler and Federle 2006](#); [Persson](#)

2007), the arolium surface is unable to adjust completely to the substrate profile as it is the case on the smooth substrate. Thus, a reduction occurs in both the intimate contact area between the arolium and the substrate, as well as in the friction forces, especially on the substrates with asperities of 0.3  $\mu\text{m}$  and 1.0  $\mu\text{m}$ . The dimension of epicuticular wax crystals and some microstructures on fruit and leaf surfaces of codling moth's host plants resembles surface asperities of the tested substrates (Skene 1963; Faust and Shear 1972; Paper 3, Paper 4), suggesting that adult moth attach successfully to rough surfaces in their habitat.

Although the friction forces of codling moth adults were reduced to a minimum on the roughness of 0.3-1.0  $\mu\text{m}$  (critical roughness), two main points were interesting to consider. First, friction forces generated by females on this critical roughness did not differ significantly from those on other rough substrates tested, conversely to those generated by male adults. Second, both sexes of the codling moth attach stronger to substrates with such critical roughness, compared to previously studied insects with both smooth and hairy adhesive pads; such as leaf beetles, flies, mirid bugs, stick insects (Gorb 2001; Peressadko and Gorb 2004; Voigt 2005; Scholz et al. 2008; Voigt et al. 2008). These nominal asperity sizes are corresponding well to the dimensions of minute epicuticular wax crystals which cover some host plant surfaces of *C. pomonella* (Paper 4). Such surfaces have been repeatedly reported to reduce the attachment ability of many insect species in their natural environment (e.g. Stork 1980; Eigenbrode et al 1996; Federle et al. 2000; Gorb and Gorb 2002; Eigenbrode 2004; Voigt et al. 2007; Gorb et al. 2008). Therefore, both points indicate that *C. pomonella* females are well adapted to attach properly to plant surfaces, such as the waxy surface of apple fruits, resembling the critical roughness of the artificial substrate tested (Paper 4).

On very rough substrates with asperities greater than 12  $\mu\text{m}$ , such as large microcracks on the fruit surfaces, leaf trichomes and tree bark (Papers 3 and 4), the claws are expected to be responsible for attachment (Betz 2002; Dai et al. 2002; Voigt et al. 2007, 2008). Thus, owing to their well adaptable arolium and claws, codling moth adults are capable to attach well to variable smooth and rough surfaces in their habitat.

### ***Effect of physicochemical substrate properties on attachment of the codling moth***

Owing to their wide variation in the structure and the chemical composition, host plant surfaces of *C. pomonella* are considerably variable in their physicochemical characteristics (e.g. Holloway 1969; Leece 1976; Velásquez et al. 2011; Chapter 3 of this thesis), which may strongly affect their attachment ability and locomotion on these surfaces (e.g. Gorb and Gorb

2006, 2009). Our study showed clearly that the attachment system of adult moths of both sexes is rather robust against physicochemical characteristics of the substrate. Since their friction forces measured on the hydrophilic glass (CA of  $39.2^\circ$ ) did not differ significantly than those found on the hydrophobic silanized glass (CA of  $108.5^\circ$ ) (Paper 1). Presumably, this may be related to the aroliar fluid secretion (lipid nano-droplets dispersed in an aqueous liquid), with its possible affinity to hydrophobic and hydrophilic substrates (Vötsch et al. 2002). Previous studies have demonstrated that insects with smooth adhesive pads are able to attach to hydrophobic surfaces, such as wax (Roth and Willis 1952) and silanized glass (Dixon et al. 1990) and to hydrophilic substrate as well (Gorb and Gorb 2004).

#### *Attachment to horizontal and vertical substrates*

Gravid females of the codling moth are known to oviposit on both horizontal and vertical surfaces (leaf sides, fruit, and smooth artificial surfaces) (own observations). Moreover, surfaces positioned vertically or horizontally and facing upwards are sometimes much preferred for oviposition (own observations), especially on apple cultivars with too hairy lower leaf surface (as ‘Red Delicious’) (Marti 2001). Therefore females must be able to attach successfully to both positions. Our study demonstrated that codling moth females achieved very good attachment ability to the smooth Plexiglas<sup>®</sup> substrate in both positions: horizontally (friction forces were 11 times their own body weight), and vertically (adhesion forces were 7 times their own body weight). Similar experiments have been done on glass with blowflies, *Calliphora vomitoria* L. (with a hairy attachment system), showing even more contrasting attachment ability (Walker et al. 1985). Their friction forces were 28.1 times their own body weight in the horizontal position; and their adhesion forces were 3.4 times their own body weight in the vertical position (Walker et al. 1985).

## **4.2. Egg adhesion of the codling moth**

In many insect species, such as *C. pomonella* and many other lepidopterans, the neonates are vulnerable and limited in their mobility; therefore the selection of a suitable oviposition site by females (on or very near to the larval food source) is a crucial issue for survival of their offsprings (Singer et al. 1988; Thompson 1988; Renwick 1989; Renwick and Chew 1994). Besides, we think that a proper egg adhesion to oviposition sites reduces the probability of egg

loss due to abrasion and other mechanical stresses and also ensures indirectly a better survival of the neonates. If the eggs are detached from the oviposition sites, the hatching neonate larvae will have a long, hard travel to reach the fruit where they will feed, and may suffer from high mortality due to starvation, desiccation, unfavorable weather conditions, or predation (Jackson and Harwood 1980; Jackson 1982).

Very little is known in the literature about the mechanisms by which insect eggs adhere to the plant surface (Betz 2010; Voigt and Gorb 2010), and how surface characteristics can affect the adhesion strength of insect eggs (Fordyce and Nice 2003; Voigt and Gorb 2010). Studies of Chapter 3 of this thesis add new information not only about the effect of plant surface characteristics on the egg adhesion of the codling moth, but also in the context of oviposition site selection and the offspring survival.

#### ***Adhesion of *C. pomonella* eggs to different apple leaf surfaces***

In the third study of this thesis, data on pull-off forces of *C. pomonella* eggs revealed that eggs on the upper leaf sides of the tested cultivars were easily detached, requiring significantly similar pull-off forces (total average of 6.0 mN). It seems that the smooth surface and the low FSE (21.8-28.7 mN\*m<sup>-1</sup>) of this leaf side do not promote a strong adhesion, because they may reduce the contact area of the egg glue with the leaf surface. Since free surface energy between two contacting bodies could affect their adhesion by capillary interactions (Johnson et al. 1971; Israelachvili 1992).

Whereas on the lower leaf side of all tested cultivars, two main points could be noticed. (1) Eggs were tighter adhered requiring up to three times stronger pull-off forces (total average of 17.1 mN) than those required for eggs on upper leaf sides to detach. On this leaf side, the dense coverage by filamentous trichomes, combined with dispersed wax crystals (in some cultivars), and corrugations in form of stomata and cuticle foldings lead to an increase of the contact area between the egg glue and the leaf surface, enhancing attachment strength of eggs. Moreover, the physicochemical characteristics (CAs of water were 96°-120° and FSE values of 23.8-42.7 mN\*m<sup>-1</sup>) could also promote adhesion. (2) In contrast to the upper leaf side, pull-off forces assessed on the lower leaf side differed significantly between apple cultivars. Here, on the lower leaf side of 'Golden Delicious', which showed the lowest trichome density and the lowest FSE value of all considered lower leaf surfaces, eggs were adhered weaker than on the lower leaf surfaces of the other tested cultivars.

### ***Adhesion of C. pomonella eggs to different apple fruit surfaces***

Our ultrastructural examination of the different apple fruit surfaces revealed that they were characterized by (1) microcracks varying considerably in their characteristics (length, depth, and distribution pattern) between cultivars and also between sections of the same fruit, and (2) an irregular dispersion of superimposed 3-D epicuticular wax crystals in form of plates, platelets, and tiny transitional crystal forms (the latter found only on ‘Jonica’ and ‘Topaz’). These structured, waxy surfaces were water repellent (CAs of water were  $89^{\circ}$ - $113^{\circ}$ ) and exhibited low FSE values ( $19.2$ - $30.3 \text{ mN}\cdot\text{m}^{-1}$ ) with low polar components. Such structural and physicochemical characteristics of a given substrate have been previously shown to have anti-adhesive properties (e.g. [Neinhuis and Barthlott 1997](#); [Scholz 2009](#); [Koch 2010](#); [Voigt and Gorb 2010](#)). Therefore, apple fruit surfaces might be a challenge for insects to glue their eggs on them. Interestingly, our data of pull-off forces revealed that eggs of *C. pomonella* were indeed tightly cemented to apple fruit surfaces of all apple cultivars tested (total average of  $63.9 \text{ mN}$ ). These forces are 4-10 fold stronger than those previously measured on upper and lower leaf surfaces of the identical apple cultivars. We explain this strong egg adhesion on the apple fruit surface in three essential points. (1) The egg adhesive of *C. pomonella* is assumed to be of a surfactant-like nature ([Voigt and Gorb 2010](#)) and has a high protein content ([Burkhart et al. 1999](#); [Li et al. 2008](#); [Betz 2010](#)), which helps to overcome the unwettability of the surface and to establish an intimate contact area with it. (2) Likely, the egg glue is specialized to waxy plant surfaces such as apple fruits. And (3) roughness seems to be an important parameter supporting the formation of strong adhesive bonds between the egg glue and plant surface ([Uehara and Sakurai 2002](#); [Santos et al. 2005](#)). Here, the roughness level on apple fruits, due to the presence of microcracks and 3-D epicuticular wax crystals, was higher than that observed on both the smooth upper surface and the hairy lower leaf surface of apple leaves. This will increase the contact area of the egg glue with the fruit surface, resulting in a strong egg adhesion to it.

It is worth to note that *C. pomonella* eggs adhered stronger on the upper and middle fruit sections of all cultivars tested, than on the lower section. The high microcrack abundance on these sections in comparison with the lower section could be responsible for this better adhesion. Interestingly, pull-off forces measured on the lower section of ‘Golden Delicious’ (in total average of  $28.0 \text{ mN}$ ) were significantly lower than most of those obtained on the most tested fruit surfaces. This may be related to the less microcracked surface and the low FSE values that characterize this section. However, these characteristics were found also in other fruit surfaces tested, and caused a higher egg adhesion. Therefore, we assume that the lower fruit section of

‘Golden Delicious’ must possess a particular feature that weakens the egg adhesion. This may be attributed to a defensive response strategy (such as neoplasm formation) of fruit cuticles against egg deposition, in order to get rid of the eggs before being damaged by hatched larvae (Hilker and Meiners 2002). A previous study of Yokoyama et al. (1990) showed that the fruit cuticle of different host plant species was slightly thicker in areas beneath the moth eggs compared to those without eggs. However, these cuticle differences were considerable only in peaches. Further studies on this cultivar would shed light on this assumed defense response.

### 4.3 Plant surface characteristics and oviposition site selection

#### *Oviposition preference for smooth surfaces versus hairy ones*

In Lepidoptera, texture of the plant surface is known to be involved in the surface evaluation as ovipositional sites. However, this is expected to be more crucial for night active species (such as *C. pomonella*) than the diurnal ones (butterflies) (Renwick and Chew 1994). Some moth species oviposit preferentially on hairy or rough substrates (Ramaswamy et al. 1987; Ramaswamy 1988). Conversely, gravid females of *C. pomonella* exhibit a strong oviposition preference for smooth plant surfaces (e.g. the smooth upper side of apple leaves early in the season) and avoid oviposition on hairy surfaces of their host plants, such as in apples (young fruits and hairy lower leaf surfaces of some cultivars Geier 1963; Wood 1965; Jackson 1979; Hagley et al. 1980; Marti 2001; own observations), walnuts (hairy young nutlets Olson 1977), quinces (young fruits and hairy lower leaf surfaces reviewed by Barnes 1991), peach (hairy fruits Hagley et al. 1980; Yokoyama and Miller 1988; Curtis et al. 1990), and almonds (hairy-shelled fruits of most varieties reviewed by Barnes 1991). Additionally, the presence of long wax threads on the upper side of pear leaves was suggested by Hagley et al. (1980) to be responsible for egg laying avoidance on this leaf side (Westigard et al. 1976; Marti 2001). Moreover, codling moth females, also known to oviposit preferably on smooth artificial surfaces (e.g. glass, cellophane or polythene sheets) and to avoid the rough ones (e.g. foam rubber), which is a main point in the design of oviposition arenas for rearing and experiments in the laboratory (e.g. Curtis et al. 1990; Bathon et al. 1991; own experience). In spite of all these previous studies and observations, the reason for this oviposition preference and avoidance for variable surfaces is still unknown.

This oviposition avoidance of too hairy or rough surfaces could be explained in different ways. (1) Ovipositing females of *C. pomonella* prefer surfaces on which they can maintain successfully their foothold during oviposition as confirmed by [Chapter 2](#). The smooth adhesive devices (arolia) on pretarsi of the adults are well adapted for smooth surfaces, supporting the maximal attachment ability of their legs to all smooth surfaces tested. Whereas on rough substrates with surface asperities ranging 0.1-12  $\mu\text{m}$ , their attachment ability was significantly reduced due to an expected decrease in the real contact area between their arolia and the surface. On rougher surfaces than 12  $\mu\text{m}$ , such as the hairy lower leaf side of apple (whose trichome diameter ranged between 15  $\mu\text{m}$  and 22  $\mu\text{m}$ , [Paper 3](#)), the arolia cannot be used, and the claws are expected to be the sole responsible attachment device. Here, characteristics of trichomes and other surface structures (density, size, shape, orientation, exudates) largely affect the roughness level of the plant surface, which act as an oviposition deterrent due to the reduced ability of females to adhere to this surface during oviposition. This explanation is also valid for understanding similar oviposition preference for smooth (artificial and natural) versus rough surfaces which was reported for other tortricid moths such as the light brown apple moth, *Epiphyas postvittana* (Walker) ([Foster et al. 1997](#)). Interestingly, the recent comparative morphological study on pretarsal structures of ditrysian Lepidoptera of [Fänger \(2010\)](#) and the literature review within revealed clearly that the arolium is well developed in most taxa. Whereas, in several groups (all Papilionidae, some Hepialidae, certain Tineidae, some cossids, some Pieridae, some Nymphalidae, in a few Sphingidae, and Limoniidae), the arolium is absent or strongly reduced and some species have other pretarsal modifications. According to our explanation above and to these similarities or variation in the pretarsal structures of adults of different taxa of ditrysian Lepidoptera, we expect not only variable attachment abilities of these lepidopterans but also possible different oviposition preferences. Our study was the first which examined the attachment ability of a lepidopteran insect species. Therefore, similar studies on attachment abilities of other lepidopteran taxa to different surfaces could help to explain many of their behavioural features.

(2) Codling moth females oviposit in places where their vulnerable neonates have the potentially best performance in attachment and crawling. Therefore, oviposition on smooth surfaces supports shortening the travel time of neonates from the hatching sites towards the fruits, in contrast to densely hairy surfaces which would impede their locomotion and lengthening their travel time, as confirmed by [Jackson \(1982\)](#). He found that the locomotion speed of *C. pomonella* neonates was greater on smooth substrates than on rough bark or pubescent leaf pedicels. Moreover, the crawling speed of *C. pomonella* neonates was

significantly reduced by powdery Kaolin particle coverage on apple shoots in comparison to the speed on intact natural shoots (Unruh et al. 2000). Similarly, hairy cotton surfaces were found to confuse neonates of the pink bollworm, *Pectinophora gossypiella* (Saunders), and greatly impeded their movement (Smith et al. 1975). Interestingly, larvae of the chrysomelid *Altica subplicata* LeConte were found to fall off hairy leaves more quickly than smooth ones under various wind conditions, making the authors to suggest that their fleshy adhesive pads are more effective on smooth surfaces (Gannon et al. 1994).

And (3) Oviposition on the smooth upper leaf side could protect egg of the first generation from their potential predators which are abundant and efficient in this time on the hairy lower leaf side (Subinprasert and Svensson 1988).

### ***Oviposition preference for ridges on smooth surfaces***

Another pronounced surface texture characteristic has been observed to influence *C. pomonella* oviposition. Single ridges or grooves on a given smooth surface (such as secondary leaf veins on the upper leaf sides, wounds, scratches, microcracks on the fruit surfaces, and also ridges and grooves on artificial smooth surfaces) stimulate the gravid females to deposit her eggs on or very close to them (own observations). A similar behaviour was also observed by Foster et al. (1997) for the tortricid moth *E. postvittana*. They found that smooth models with a raised wax ridge on their surfaces stimulated more eggs to be laid on them compared to models without a ridge. They suggested that these wax ridges increase the oviposition probability of a landing gravid female on the model (within close proximity to the ridge). Likewise, Kanno and Harris (2000) demonstrated that grooves on the plant surface were observed to be an important physical feature stimulating egg laying of females of the Hessian flies, *Mayetiola destructor* (Say). Interestingly, in their study, groove depth appeared to be correlated with egg numbers on the plant surface. Because a positive linear relationship was found when mean groove depths for the six molded models (vinyl silicone molds having the physical features of the upper and lower leaf surfaces of the six grasses) were plotted against the mean percentages of eggs on real plants, however no relationship was found for the groove widths (Kanno and Harris 2000).

A possible explanation for this behaviour is that these structures could increase egg attachment to the smooth surface (Müller 2006). Our observations and results of the third study of this thesis (Paper 3) confirm this explanation. Since *C. pomonella* eggs adhere 2-3 times better to the hairy, structured lower side of apple leaves than to the favored smooth upper side. Secondary leaf veins (likewise, for grooves and edges on a given smooth surface) provide certain

roughness leading to an increased contact area between the egg adhesive and the plant surface, resulting in stronger egg adhesion. Therefore for a gravid female, depositing eggs on or in the vicinity of secondary leaf veins of the upper leaf side will increase their adhesion and get simultaneously the benefits of these smooth surfaces (as shown above). Here also the flat shape of the *C. pomonella* eggs play an important role in reducing their exposure to weathering and increasing their survival on such smooth surfaces.

### ***Oviposition on the fruit surface***

We assume that females' selection for apple fruit surfaces as oviposition sites lately in the growing season reflects in many ways a maternal care for the best survival and performance of their offspring of the second and third generations.

(1) Oviposition on the fruit surface ensures that eggs are tightly fixed (Paper 4), and lessen their dislodgement through weathering till hatching of the larvae (ca. 4-25 days, depending on temperature and other weather conditions (Wood 1965; Aghdam et al. 2009; Blomefield and Giliomee 2009). Moreover, the preferred oviposition sites on apple fruits (both upper and middle sections of apple fruits) were associated also with stronger egg adhesion forces compared with the less preferred lower fruit section (Paper 4).

(2) Laying *C. pomonella* eggs directly on apple fruits ensures maximizing the survival rate of the vulnerable neonate larvae, because they are already on their food source (the apple fruit) and do not have to travel searching for it. Moreover, the presence of microcracks, wounds, or other irregularities on the fruit surface could facilitate neonate penetration into the fruit, increasing their survival probability (Marti 2001).

And (3) oviposition on fruits could be a mechanism to avoid predation for both eggs and neonate larvae, since the predation rate on *C. pomonella* eggs was significantly reduced lately in the season compared with the earlier period (Subinprasert and Svensson 1988). This could be related to the role of epicuticular wax crystals of the fruit skin in reducing the attachment and the foraging efficiency of many predatory insects (Eigenbrode et al. 1996; Eigenbrode et al. 1998; Eigenbrode and Kabalo 1999; Eigenbrode 2004). Whereas, we expected that *C. pomonella* females are well adapted to attach successfully while oviposition on such waxy surfaces (Paper 2). Because female arolia are adapted to attach effectively on microrough surfaces with asperities of 0.3-12  $\mu\text{m}$  (Paper 2), corresponding well to those of epicuticular wax crystals on the fruit skin (0.1-5.6  $\mu\text{m}$ , for transitional crystal forms, plates and platelets, Paper 4). On rough cracked fruit surfaces with larger asperities, like the fruit surface of cv. 'Boskoop', the claws are expected to be used to establish the proper attachment (Paper 2).

In conclusion, for oviposition decisions of the codling moth females, information about the physical features of the plant surface can be just as important or more important as information about the chemical features.



## 5. Summary

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Adults of the codling moth, *Cydia pomonella* L. (Lepidoptera, Tortricidae), live on host plant surfaces, differing considerably in their structural, chemical, and physicochemical characteristics according to host plant species, cultivar, plant organ (e.g. upper/lower leaf sides, fruits), phenological stage, environmental conditions, and orchard management practices. This large, variable world provided by plant surfaces can profoundly affect directly and indirectly many aspects of insect–plant interactions, such as attachment, locomotion, oviposition site selection, egg adhesion, and also survival of adults and their offsprings. Despite their importance, little attention has been given to the structural and wetting properties of the codling moth’s host plant surface and their effect on insect–plant interactions of this important pest. Therefore, studies in this thesis were undertaken to investigate the effect of structural and physicochemical characteristics of the substrate on two main codling moth–plant interactions: (1) the attachment ability of adults, and (2) the adhesion of their eggs.

The first part of this thesis was performed to (1) analyze tarsal morphology of male and female *C. pomonella* to know more about their pretarsal attachment devices, and (2) to investigate their attachment ability on a variety of smooth and rough substrates, using a centrifugal force device. On all smooth artificial substrates tested, both sexes of *C. pomonella* adults achieved excellent attachment ability, by means of their smooth, flexible and well developed arolia. Hydrophobicity of the substrate had no considerable effect on friction forces. *Cydia pomonella* females showed a very good attachment ability to the smooth Plexiglas<sup>®</sup> substrate in both positions: horizontally (friction forces were 11 times their own body weight), and vertically (adhesion forces were 7 times their own body weight). Thus, it can be concluded that the attachment system of *C. pomonella* is rather robust against physicochemical properties of the substrate and is able to achieve a very good attachment on vertical and horizontal plant surfaces.

Results on the epoxy resin substrates (six substrates made of polymerized Spurr resin, differing only in surface asperity size: 0  $\mu\text{m}$ , 0.3  $\mu\text{m}$ , 1  $\mu\text{m}$ , 3  $\mu\text{m}$ , 9  $\mu\text{m}$ , and 12  $\mu\text{m}$ ) revealed that the attachment ability of both sexes was significantly affected by surface roughness. Maximal friction force was measured on the smooth substrate whereas minimal friction force was assessed on microrough substrates with 0.3  $\mu\text{m}$  and 1.0  $\mu\text{m}$  size of asperities. On the remaining rough substrates, friction forces were significantly higher but still lower than on the smooth substrate. It is worth to note that both sexes generated similar friction forces on the same substrate (for all smooth or rough substrates tested), in spite of the considerable difference in

their body mass, suggesting that both sexes attach effectively to variable rough plant surfaces in their habitat. However, since smooth surfaces have been reported previously to be the most favorable substrates for ovipositing females of *C. pomonella*, it is possible that they use their attachment system to sense the substrate texture and prefer those substrates to which their arolia attach the best.

A better survival of the codling moth offspring is assumed to be ensured by the selection of suitable oviposition sites by females, as well as by a proper adhesion of deposited eggs to these sites. In apple orchards, eggs of the first generation of the codling moth are laid on leaf surfaces in the vicinity to small fruits, later in the growing season, most eggs are deposited directly on fruits. In the second part of this thesis, egg adhesion of the codling moth to different leaf and fruit surfaces of the domestic apple, *Malus domestica* Borkh., was investigated by measuring the pull-off force required to detach the eggs from the plant surface. Morphological and physicochemical properties (wettability, free surface energy) of the tested plant surfaces were analyzed to evaluate their role in egg adhesion. Furthermore, eggs and their adhesives covering leaf or fruit surfaces were visualized. Eggs on the smooth upper leaf sides of the tested cultivars were easily detached, requiring similar pull-off forces (total average of 6.0 mN). Up to 2-3 times stronger pull-off forces had to be applied to detach eggs from the trichome-covered lower leaf side (total average of 17.1 mN), and these forces differed significantly between cultivars, owing mainly to different trichome covered areas. Whereas on the waxy fruit surface of all apple cultivars tested, eggs were very tightly adhered, and required 4-10 fold stronger pull-off forces than those previously measured on upper and lower leaf surfaces of the identical apple cultivars (total average of 63.9 mN). *Cydia pomonella* eggs adhered stronger on the upper and middle fruit sections of all cultivars tested, than on the lower section.

The influence of plant surface properties on egg adhesion, as well as the mechanisms used by the moth to overcome the presumable anti-adhesive properties of apple fruit surfaces, were discussed. Additionally, the results were debated in the context of the oviposition site selection, female attachment, as well as offspring survival of the first, second and third generations of the codling moth.



## 6. Zusammenfassung

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Nach dem Schlupf leben die Adulten des Apfelwicklers, *Cydia pomonella* L. (Lepidoptera, Tortricidae), auf ihren Wirtspflanzen, die sich je nach Wirtspflanzenart, Sorte, Pflanzenorgan (Blattober- und unterseiten, Früchte) und phänologischem Stadium der Pflanzen beträchtlich in ihrer morphologischen, physikalischen und physikochemischen Oberflächenbeschaffenheit unterscheiden. Diese Oberflächeneigenschaften können ihrerseits wiederum von Umwelteinflüssen und der Kulturführung der Apfelanlagen beeinflusst werden. Diese durch Pflanzenoberflächen geschaffene heterogene Umwelt kann direkt und indirekt tiefgreifend das Insekt-Pflanze-Verhältnis bestimmen und sich auf die Anhaftung an Oberflächen, Fortbewegung, Wahl des Eiablageplatzes, Haftung der Eier am Substrat und das Überleben von Adulten und Larven auswirken. Trotz der wichtigen Rolle, die die Oberflächen im Leben der adulten Apfelwickler einnimmt, fanden sie in der wissenschaftlichen Betrachtung ihrer strukturellen und physikochemischen Eigenschaften und deren Einfluß auf die Insekt-Pflanze-Interaktionen wenig Beachtung. Daher wurden in dieser Arbeit Untersuchungen unternommen, um deren Effekt auf zwei Aspekte der Apfelwickler-Wirtspflanze-Beziehung näher zu beschreiben: (1) die Anhaftungsfähigkeit der Adulten und (2) die Haftung der Eier an unterschiedlichen Substraten.

Der erste Abschnitt der Untersuchungen befaßt sich (1) mit der Analyse der Tarsen-Morphologie von *C. pomonella* Männchen und Weibchen, um die an der Anhaftung beteiligten Feinstrukturen zu charakterisieren und (2) mit der Ermittlung der Haftfähigkeit der Tiere auf unterschiedlichen glatten und rauhen Substraten. Mit einem Zentrifugalkrafttester wurde die Reibungskraft von Männchen und Weibchen auf hydrophoben und hydrophilen Glasoberflächen gemessen. Es zeigte sich, dass Adulte beider Geschlechter, unabhängig ihres signifikant unterschiedlichen Körpergewichtes, durch ihre gut ausgebildeten glatten, flexiblen Aroliae ähnlich starke Haftkräfte generierten. Die hydrophobe Eigenschaft des Substrats hatte keinen merklichen Einfluss auf die Reibungskraft beider Geschlechter. *Cydia pomonella*-Weibchen zeigten sowohl in horizontaler Position (die Reibungskraft betrug das 11-fache des Körpergewichtes) als auch in vertikaler Position (die Adhäsionskraft betrug das 7-fache des Körpergewichtes) sehr gute Haftungsfähigkeit. Aus den Ergebnissen kann geschlossen werden, dass *C. pomonella* über ein robustes Haftsysteem verfügt, welches den Adulten über sehr unterschiedliche physikochemische Substrateigenschaften hinweg dienlich ist und ihnen ein hohes Adhäsions-Reibungsverhältnis und damit sicheren Halt auch in vertikaler Position bietet.

Die Haftungsfähigkeit auf rauhen Oberflächen wurde an Epoxidharz-Substraten (Spurr) mit definierter Rauigkeit (0  $\mu\text{m}$ , 0,3  $\mu\text{m}$ , 1  $\mu\text{m}$ , 3  $\mu\text{m}$ , 9  $\mu\text{m}$ , und 12  $\mu\text{m}$ ) ermittelt. Die Ergebnisse zeigten, daß die Haftungsfähigkeit beider Geschlechter signifikant durch die Oberflächenrauigkeit beeinflusst wurde. Maximale Reibungskraft ergab sich auf der glatten Fläche (0  $\mu\text{m}$ ), während auf Rauigkeiten von 0,3 bis 12  $\mu\text{m}$  nur minimale Reibungskraft erzielt wurde. Obwohl sich die Geschlechter in ihrem Körpergewicht deutlich unterscheiden, generierten Männchen und Weibchen doch gleiche Reibungskräfte auf glatten und rauhen Substraten und zeigten so, daß sie wirkungsvoll auf verschiedenen rauhen Substraten ihres Habitates anhaften können. Da aber von Weibchen für die Eiablage glatte gegenüber rauhen Oberflächen bevorzugt wurden (eigene Vorversuche) wird vermutet, daß eiablagebereite Weibchen die morphologischen Haftungssysteme (Aroliae) zur Prüfung der Oberflächenbeschaffenheit benutzt werden, um einen geeigneten Eiablageplatz zu finden.

Es darf vermutet werden, daß die bessere Anhaftung an glatten Oberflächen die Überlebenswahrscheinlichkeit der Eier und der daraus schlüpfenden Larven erhöht. Die Eier der ersten Generation des Apfelwicklers werden von den Weibchen auf den Blättern in der Nähe junger Apfelfrüchte abgelegt, während die Eiablage der zweiten Generation später in der Vegetationsperiode direkt auf der Fruchtoberfläche erfolgt. Daher wurde im zweiten experimentellen Abschnitt dieser Arbeit die Haftung der Apfelwicklereier auf unterschiedlichen Oberflächen von Blättern und Früchten von fünf verschiedenen Apfelsorten untersucht. Hierfür wurde die aufzuwendende Kraft (pull-off force) gemessen, um die von Weibchen auf Blattober- und unterseiten sowie auf drei verschiedenen Abschnitten von Apfelfrüchten abgelegten von der jeweiligen Oberfläche zu entfernen.

Morphologische und physikochemische Eigenschaften, wie Benetzbarkeit und freie Oberflächenenergie, der getesteten Pflanzenoberflächen wurden analysiert, um ihre Bedeutung für die Eiadhäsion zu bewerten. Außerdem wurden die von den Eiern und ihrem Eikitt bedeckte Fläche erfaßt und in die Bewertung mit einbezogen. Auf der Blattoberfläche abgelegte Eier benötigten nur geringe Kraft, um sie von der Fläche abziehen wobei keine Sortenunterschiede zu verzeichnen waren (Mittelwert gesamt: 6,0 mN). 2-3-fach höhere Kräfte waren dagegen nötig, um die Eier von den trichombedeckten Blattunterseiten abziehen (Mittelwert gesamt: 17,1 mN), wobei signifikante Sortenunterschiede auftraten. Diese waren durchweg auf die unterschiedlichen von den Trichomen bedeckte Fläche der Blattunterseiten zurückzuführen. Auf den mit Wachs bedeckten Fruchtoberflächen aller Apfelsorten waren die Eier wesentlich stärker befestigt und benötigten 4-10-fach höheren Kraftaufwand als bei den Blattoberflächen um sie

von der Fruchtoberfläche zu entfernen Mittelwert gesamt: 63,9 mN). Auf den einzelnen Fruchtabschnitten war die Haftung an den oberen und den mittleren Fruchtabschnitt stärker als die an dem unteren Fruchtabschnitt.

Der Einfluß der Oberflächeneigenschaften von Apfelblättern und -früchten auf die Adulten und Eier des Apfelwicklers sowie die unterliegenden Mechanismen, anti-adhäsive Eigenschaften der Fruchtoberflächen zu überwinden werden im Kontext mit der Wahl des Eiablageplatzes und der Überlebenswahrscheinlichkeit der Erstlarven der ersten, zweiten und dritten Apfelwicklergeneration diskutiert.





## 7. References (for chapters 1 and 4)

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- Aghdam, H.R., Fathipour, Y., Radjabi, G., Rezapanah, M., 2009. Temperature-dependent development and temperature thresholds of codling moth (Lepidoptera: Tortricidae) in Iran. *Environmental Entomology* 38: 885–895.
- Ansebo, L., Coracini, M.D.A., Bengtsson, M., Liblikas, I., Ramírez, M., Borg-Karlson A-K, Tasin, M., Witzgall, P., 2004. Antennal and behavioural response of codling moth, *Cydia pomonella* to plant volatiles. *Journal of Applied Entomology* 128: 488–493.
- Arnold, J.W., 1974. Adaptive features on the tarsi of cockroaches (Insecta: Dictyoptera). *International Journal of Insect Morphology and Embryology* 3: 317–334.
- Audemard, H., 1991. Population dynamics of the codling moth. In: Van der Geest, L.P.S., Evenhuis, H.H. (eds) *Tortricid pests: Their biology, natural enemies and control*. Elsevier, Amsterdam, pp 329–338.
- Bargel, H. Koch, K., Cerman, Z., Neinhuis, C. 2006. Structure-function relationships of the plant cuticle and cuticular waxes - A smart material? *Functional Plant Biology* 33:893–910.
- Barnes, M.M., 1991. Codling moth occurrence, host race formation, and damage. In: Van der Geest, L.P.S., Evenhuis, H.H. (eds) *Tortricid pests: Their biology, natural enemies and control*. Elsevier, Amsterdam, pp 313–327.
- Barthlott, W., Neinhuis, C., 1997. Purity of the sacred lotus, or escape from contamination in biological surfaces. *Planta* 202: 1–8.
- Barthlott, W., Neinhuis, C., Cutler, D., Ditsch, F., Meusel, I., Theisen, I., Wilhelmi, H., 1998. Classification and terminology of plant epicuticular waxes. *Botanical Journal of the Linnean Society* 126: 237–260.
- Bathon, H., Singh, P., Clare, G.K., 1991. Rearing methods. In: van der Geest, L.P.S., Evenhuis, H.H. (eds) *Tortricid pests: Their biology, natural enemies and control*. Elsevier, Amsterdam, pp 283–293.
- Belding, R.D., Blankenship, S.M., Young, E., Leidy, R.B., 1998. Composition and variability of epicuticular waxes in apple cultivars. *Journal of the American Society for Horticultural Science* 123: 348–356.
- Bell, H.P., 1937. The protective layers of the apple. *Canadian Journal of research* 15: 391–402.

- Bengtsson, M., Bäckman, A.C., Liblikas, I., Ramirez, M.I., Borg-Karlson, A.K., Ansebo, L., Anderson, P., Löfqvist, J., Witzgall, P., 2001. Plant odor analysis of apple: Antennal response of codling moth females to apple volatiles during phenological development. *Journal of Agricultural and Food Chemistry* 49: 3736–3741.
- Betz, O., 2002. Performance and adaptive value of tarsal morphology in rove beetles of the genus *Stenus* (Coleoptera, Staphylinidae). *Journal of Experimental Biology* 205: 1097–1113.
- Betz, O., 2010. Adhesive exocrine glands in insects: morphology, ultrastructure, and adhesive secretion. In: Byern, J., Grunwald, I. (eds) *Biological adhesive systems from nature to technical and medical application*. Springer, Wien, pp 111–152.
- Beutel, R., Gorb, S.N., 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. *Journal of Zoological Systematics and Evolutionary Research* 39: 177–207.
- Bhushan, B., Jung, Y.C., 2006. Micro- and nanoscale characterization of hydrophobic and hydrophilic leaf surfaces. *Nanotechnology* 17: 2758–2772.
- Blomefield, T.L., Pringle, K.L., Sadie, A., 1997. Field observations on oviposition of codling moth, *Cydia pomonella* (Linnaeus) (Lepidoptera: Olethreutidae), in an unsprayed apple orchard in South Africa. *African Entomology* 5: 319–336.
- Blomefield, T.L., Giliomee, J.H., 2009. Development rates of the embryonic and immature stages of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), at constant and fluctuating temperatures. *African Entomology* 17: 183–191.
- Borchert, D.M., Stinner, R.E., Walgenbach, J.F., Kennedy, G.G., 2004. Oriental fruit moth (Lepidoptera: Tortricidae) phenology and management with Methoxyfenozide in North Carolina Apples. *Journal of Economic Entomology* 97: 1353–1364.
- Borden, A.D., 1931. Some field observations on codling moth behavior. *Journal of Economic Entomology* 24: 1137–1145.
- Bringe, K., Schumacher, C.F.A., Schmitz-Eiberger, M., Steiner, U., Oerke, E.C., 2006. Ontogenetic variation in chemical and physical characteristics of adaxial apple leaf surfaces. *Phytochemistry* 67: 161–170.
- Brown, R., 1979. The Valid Generic and Tribal Names for the Codling Moth, *Cydia pomonella* (Olethreutinae: Tortricidae). *Annals of the Entomological Society of America* 72: 565–567.
- Brown, J.W., 2006. Scientific names of pest species in Tortricidae (Lepidoptera) frequently cited erroneously in the entomological literature. *American Entomologist* 52: 182–189.

- Burkhart, C.N., Stankiewicz, B.A., Pchalek, I., Kruge, M.A., Burkhart, C.G., 1999. Molecular composition of the louse sheath. *Journal of Parasitology* 85: 559–561.
- Carver, T.L.W., Gurr, S.J., 2006. Filamentous fungi on plant surfaces. In: Riederer, M., Müller, C. (eds) *Biology of plant cuticle*. Blackwell Publishing, Oxford, pp 368–397.
- Considine, J.A., Brown, K.C., 1981. Physical aspects of fruit growth: Theoretical analysis of distribution of surface growth forces in fruit in relation to cracking and splitting. *Plant Physiology* 68: 371–376.
- Creasy, L.L., 1980. The correlation of weather parameters with russet of 'Golden Delicious' apples under orchard conditions. *Journal of the American Society for Horticultural Science* 105: 735–738.
- Curtis, C.E., Tebbets, J.S., Clark, J.D., 1990. Ovipositional behavior of the codling moth (Lepidoptera: Tortricidae) on stone fruits in the field and an improved oviposition cage for use in the laboratory. *Journal of Economic Entomology* 83: 131–134.
- Dai, Z., Gorb, S.N., Schwarz, U., 2002. Roughness-dependent friction force of the tarsal claw system in the beetle *Pachnoda marginata* (Coleoptera, Scarabaeidae). *Journal of Experimental Biology* 205: 2479–2488.
- Dixon, A.F.G., Croghan, P.C., Gowing, R.P., 1990. The mechanism by which aphids adhere to smooth surfaces. *Journal of Experimental Biology* 152: 243–253.
- Drechsler, P., Federle, W., 2006. Biomechanics of smooth adhesive pads in insects: influence of tarsal secretion on attachment performance. *Journal of Comparative Physiology A* 192: 1213–1222.
- Edwards, P.B., 1982: Do waxes on juvenile eucalyptus leaves provide protection from grazing insects? *Australian Journal of Ecology* 7: 347–352.
- Eigenbrode, S.D., 1996. Plant surface waxes and insect behaviour. In: Kerstiens, G., (ed.) *Plant Cuticles: an integrated functional approach*, BIOS, Oxford, pp. 201–222.
- Eigenbrode, S.D., Castagnola, T., Roux, M.-B., Steljes, L., 1996. Mobility of three generalist predators is greater on cabbage with glossy leaf wax than on cabbage with a wax bloom. *Entomologia Experimentalis et Applicata* 81: 335–343.
- Eigenbrode, S.D., 2004. The effects of plant epicuticular waxy blooms on attachment and effectiveness of predatory insects. *Arthropod Structure & Development* 33: 91–102.
- Eigenbrode, S.D., Espelie, K.E., 1995. Effects of plant epicuticular lipids on insect herbivores. *Annual Review of Entomology* 40: 171–194.

- Eigenbrode, S.D., Kabalo, N.N., 1999. Effects of *Brassica oleracea* waxblooms on predation and attachment by *Hippodamia convergens*. *Entomologia Experimentalis et Applicata* 91: 125–130.
- Eigenbrode, S.D., White, C., Rohde, M., Simon, C.J., 1998. Behavior and effectiveness of adult *Hippodamia convergens* (Coleoptera: Coccinellidae) as a predator of *Acyrtosiphon pisum* (Homoptera: Aphididae) on a wax mutant of *Pisum sativum*. *Environmental Entomology* 27: 902–909.
- Endlein, T., Federle, W., 2008. Walking on smooth or rough ground: passive control of pretarsal attachment in ants. *Journal of Comparative Physiology A* 194: 49–60.
- Faust, M., Shear, C.B., 1972. Fine structure of the fruit surface of three apple cultivars. *Journal of the American Society for Horticultural Science* 97: 351–355.
- Fänger, H., 2010. Comparative morphological study of pretarsal structures of ditrysian Lepidoptera, with some phylogenetic implications. *Entomologische Zeitschrift, Stuttgart* 120: 15–23.
- Federle, W., Endlein, T., 2004. Locomotion and adhesion: dynamic control of adhesive surface contact in ants. *Arthropod Structure and Development* 33: 67–75.
- Federle, W., Rohrseitz, K., Hölldobler, B., 2000. Attachment forces of ants measured with a centrifuge: better ‘wax-runners’ have a poorer attachment to a smooth surface. *Journal of Experimental Biology* 203: 505–512.
- Federle, W., Brainerd, E.L., McMahon, T.A., Hölldobler, B., 2001. Biomechanics of the movable pretarsal adhesive organ in ants and bees. *Proceedings of the National Academy of Sciences Online (US)* 98: 6215–6220.
- Federle, W., Riehle, M., Curtis, A.S.G., Full, R.J., 2002. An integrative study of insect adhesion: mechanics and wet adhesion of pretarsal pads in ants. *Integrative and Comparative Biology* 42: 1100–1106.
- Fordyce, J.A., Nice, C.C., 2003. Variation in butterfly egg adhesion: adaptation to local host plant senescence characteristics? *Ecology Letters* 6: 23–27
- Foster, S.P., Howard, A.J., Harris, M.O., 1997. The influence of tactile and other non-chemical factors on the ovipositional responses of the generalist herbivore *Epiphyas postvittana*. *Entomologia Experimentalis et Applicata* 83: 147–159.
- Frantsevich, L.I., Gorb, S.N., 2002. Arcus as a tensegrity structure in the arolium of wasps (Hymenoptera: Vespidae). *Zoology* 105: 225–237.

- Frantsevich, L.I., Gorb, S.N., 2004. Structure and mechanics of the tarsal chain in the hornet, *Vespa crabro* (Hymenoptera: Vespidae): implications on the attachment mechanism. *Arthropod Structure and Development* 33: 77–89.
- Gannon, A.J., Bach, C.E., Walker, G.K., 1994. Feeding patterns and attachment ability of *Altica subplicata* (Coleoptera: Chrysomelidae) on sand-dune willow. *Great Lakes Entomologist* 27: 89-101.
- Gaume, L., Perret, P., Gorb, E., Gorb, S., Labat, J.-J., Rowe, N., 2004. How do plant waxes cause flies to slide? Experimental tests of wax-based trapping mechanisms in three pitfall carnivorous plants. *Arthropod Structure and Development* 33: 103–111.
- Geier, P.W., 1963. The life history of codling moth *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) in the Australian Capital Territory. *Australian Journal of Zoology* 11: 323–367.
- Gibert, C., Chadœuf, J., Vercambre, G., Génard, M., Lescourret, F., 2007. Cuticular cracking on nectarine fruit surface: spatial distribution and development in relation to irrigation and thinning. *Journal of the American Society for Horticultural Science* 132: 583–591.
- Gorb, E.V., Gorb, S.N., 2002. Attachment ability of the beetle *Chrysolina fastuosa* on various plant surfaces. *Entomologia Experimentalis et Applicata* 105: 13–28.
- Gorb, E.V., Gorb, S.N., 2006. Physicochemical properties of functional surfaces in pitchers of the carnivorous plant *Nepenthes alata* Blanco (Nepenthaceae). *Plant Biology* 8: 841–848.
- Gorb, E.V., Gorb, S.N., 2009. Effect of surface topography and chemistry of *Rumex obtusifolius* leaves on the attachment of the beetle *Gastrophysa viridula*. *Entomologia Experimentalis et Applicata* 130: 222–228.
- Gorb, E., Voigt, D., Eigenbrode, S.D., Gorb, S., 2008. Attachment force of the beetle *Cryptolaemus montrouzieri* (Coleoptera, Coccinellidae) on leaflet surfaces of mutants of the pea *Pisum sativum* (Fabaceae) with regular and reduced wax coverage. *Arthropod-Plant Interactions* 2: 247–259.
- Gorb, S.N., 2001. Attachment devices of insect cuticle. Kluwer Academic Publishers, Dordrecht.
- Gorb, S.N., 2005. Uncovering insect stickiness: structure and properties of hairy attachment devices. *American Entomologist* 51: 31–35.
- Gorb, S.N., 2008. Smooth attachment devices in insects: functional morphology and biomechanics. *Advanced Insect Physiology* 34: 81–115.
- Gorb, S.N., Gorb, E.V., 2004. Ontogenesis of the attachment ability in the bug *Coreus marginatus* (Heteroptera, Insecta). *Journal of Experimental Biology* 207: 2917–2924.

- Gorb, S.N., Jiao, Y., Scherge, M., 2000. Ultrastructural, architectural and mechanical properties of attachment pads in *Tettigonia viridissima* (Orthoptera, Tettigoniidae). *Journal of Comparative Physiology A* 186: 821–831.
- Gullan, P.J., Cranston, P.S., (eds.) 2010. *The insects - an outline of entomology*, Blackwell.
- Hagley, E.A.C., Bronskill, J.F., Ford, E.J., 1980. Effect of the physical nature of leaf and fruit surfaces on oviposition by the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). *Canadian Entomologist* 112: 503–510.
- Hall, J.A., 1929. Six years' study of the life history and habits of the codling moth (*Carpocapsa pomonella* L.). Book 59th Annual Report Entomological Society of Ontario 1928. pp. 96–105.
- Hilker, M., Meiners, T., 2002. Induction of plant responses towards oviposition and feeding of herbivorous arthropods: a comparison. *Entomologia Experimentalis et Applicata* 104: 181–192.
- Holloway, P.J., 1969. The effects of superficial wax on leaf wettability. *Annals of Applied Biology* 63: 145–153.
- Howell, J.M., 1991. Reproductive biology. In: van der Geest, L.P.S., Evenhuis, H.H. (Eds.), *Tortricid pests: Their biology, natural enemies and control*. Elsevier, Amsterdam, pp. 157–174.
- Hull, H.M., Morton, H.L., Wharrie, J.R., 1975. Environmental influences on cuticle development and resultant foliar penetration. *Botanical Review* 41: 421–452.
- Hunsche, M., Blanke, M.M., Noga, G., 2010. Does the microclimate under hail nets influence micromorphological characteristics of apple leaves and cuticles? *Journal of Plant Physiology* 167: 974–980.
- Ishii, S., 1987. Adhesion of a leaf feeding ladybird *Epilachna vigintioctomaculata* (Coleoptera: Coccinellidae) on a vertically smooth surface. *Applied Entomology and Zoology* 22: 222–228.
- Israelachvili, J., 1992. *Intermolecular and surface forces*. London, UK: Academic Press.
- Jackson, D.M., 1979. Codling moth egg distribution on unmanaged apple trees. *Annals of the Entomological Society of America* 72: 361–368.
- Jackson, D.M., 1982. Searching behavior and survival of 1<sup>st</sup>-instar codling moths. *Annals of the Entomological Society of America* 75: 284–289.
- Jackson, D.M., Hardwood, R.E., 1980. Survival potential of first instars of the codling moth in laboratory experiments. *Annals of the Entomological Society of America* 73: 160–163.

- Jeffree, C.E., 1986. The cuticle, epicuticular waxes and trichomes of plants, with reference to their structure, functions and evolution. In: Juniper, B.E., Southwood, S.R., (eds) *Insects and the plant surface*. Edward Arnold Publishers, London, pp 23–64.
- Jeffree, C. E., 2006. The fine structure of the plant cuticle. In: Riederer, M., Müller, C. (eds) *Biology of plant cuticle*. Blackwell Publishing, Oxford, pp 11–125.
- Jiao, Y., Gorb, S.N., Scherge, M., 2000. Adhesion measured on the attachment pads of *Tettigonia viridissima* (Orthoptera, Insecta). *Journal of Experimental Biology* 203:1887–1895.
- Johnson, B., 1953. The injurious effects of the hooked epidermal hairs of french beans (*Phaseolus vulgaris* L.) on *Aphis craccivora* Koch. *Bulletin of Entomological Research* 44:779–788.
- Johnson, K.L., Kendall, K., Roberts, A.D., 1971. Surface energy and the contact of elastic solids. *Proceedings of the Royal Society London A* 324: 301–313.
- Kanno, H., Harris, M.O., 2000. Leaf physical and chemical features influence selection of plant genotypes by Hessian fly. 26: 2335–2354.
- Knoche, M., Grimm, E., 2008. Surface moisture induces microcracks in the cuticle of ‘Golden Delicious’. *HortScience* 43:1929–1931.
- Koch, K., 2010. Design of hierarchically sculptured biological surfaces with anti-adhesive properties. *Functional Nanoscience*: 167–178.
- Koch, K., Bushan, B., Barthlott, W., 2008. Diversity of structure, morphology and wetting of plant surfaces. *Soft Matter* 4: 1943–1963.
- Koch, K., Bhushan, B., Barthlott, W., 2009. Multifunctional surface structures of plants: an inspiration for biomimetics. *Progress in Materials Science* 54: 137–178.
- Landolt, P.J., Guedot, C., 2008. Field attraction of codling moths (Lepidoptera: Tortricidae) to apple and pear fruit, and quantitation of Kairomones from attractive fruit. *Annals of the Entomological Society of America* 101: 675–681.
- Leece, D.R., 1976. Composition and ultrastructure of leaf cuticles from fruit trees, relative to differential foliar absorption. *Australian Journal of Plant Physiology* 3: 833–847.
- Lees, A.D., Hardie, J., 1988. The organs of adhesion in the aphid *Megoura viciae*. *Journal of Experimental Biology* 136: 209–228.
- Leveau, J. H. J., 2006. Microbial communities in the phyllosphere. In: Riederer, M., Müller. C., (eds) *Biology of plant cuticle*. Blackwell Publishing, Oxford, pp 334–367.

- Li, D., Huson, M.G., Graham, L.D., 2008. Proteinaceous adhesive secretions from insects, and in particular the egg attachment glue of *Opodiphthera* sp. moths. *Archives of Insect Biochemistry and Physiology* 69: 85–105.
- Lombarkia, N., Derridj, S., 2002. Incidence of apple fruit and leaf surface metabolites on *Cydia pomonella* oviposition. *Entomologia Experimentalis et Applicata* 104: 79–87.
- Lombarkia, N., Derridj S., 2008. Resistance of apple trees to *Cydia pomonella* egg-laying due to leaf surface metabolites. *Entomologia Experimentalis et Applicata* 128: 57–65.
- Marti, S.M., 2001. Host selection, reproductive biology, host-specific development and mortality of the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), in apple and pear. PhD. Thesis, Oregon State University, Corvallis, Oregon, United States.
- Müller, C., 2006. Plant-insect interactions on cuticular surface. In: Riederer, M., Müller, C., (eds) *Biology of plant cuticle*. Blackwell Publishing, Oxford, pp 398–422.
- Müller, C. Riederer, M. (2005) Plant surface properties in chemical ecology, *Journal of Chemical Ecology*. 31: 2621–2651.
- Neinhuis, C., Barthlott, W., 1997. Characterization and distribution of water-repellent, self-cleaning plant surfaces. *Annals of Botany* 79: 667–677.
- Olson, W.H., 1977. Walnut varieties differ in susceptibility to codling moth damage. *California Agriculture* 31: 14–15.
- Opara, U.L., 1993. A study on stem-end splitting in apples. PhD. Thesis, Massey University, New Zealand
- Opara, L.U., Hodson, A.J., Studman, C.J., 2000. Stem-end splitting and internal ring-cracking of 'Gala' apples as influenced by orchard management practices. *Journal of Horticultural Science and Biotechnology* 75: 465–469.
- Peet, M.M., 1992. Fruit cracking in tomato. *HortTechnology* 2: 216–223.
- Peressadko, A.G., Gorb, S.N., 2004. Surface profile and friction force generated by insects. In: Boblan, I. and Bannasch, R. (Eds.), *Proceedings of the First International Conference Bionik 2004*, Hannover, Germany, VDI Verlag, Düsseldorf, pp. 257–263.
- Persson, B.N.J., 2007. Wet adhesion with application to tree frog adhesive toe pads and tires. *Journal of Physics: Condensed Matter* 19, N376110 doi:10.1088/0953-8984/19/37/376110.
- Pillemer, E.A., Tingey, W.M., 1978. Hooked trichomes and resistance of *Phaseolus vulgaris* to *Empoasca fabae* (Harris). *Entomologia Experimentalis et Applicata* 24: 83–94.
- Plourde, D.F., Goonewardene, H.F., Kwolek, W.F., 1985. Pubescence as a factor in codling moth oviposition and fruit entry in five apple selections. *HortScience* 20: 82–83.

- Proctor, J.T.A., Lougheed, E.C., 1980. Cracking of Golden russet apples. *Canadian Plant Disease Survey* 60: 55–58.
- Prokopy, R.J., Owens, E.D., 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28: 337–64.
- Ramaswamy, S.B., 1988. Host finding by moths: sensory modalities and behaviours. *Journal of Insect Physiology* 34: 235–249.
- Ramaswamy, S.B., Ma, W.K., Baker, G.T., 1987. Sensory cues and receptors for oviposition by *Heliothis virescens*. *Entomologia Experimentalis et Applicata* 43: 159–168.
- Renwick, J.A.A., 1989. Chemical ecology of oviposition in phytophagous insects. *Experientia* 45: 223–228.
- Renwick, J.A.A., Chew, F.S., 1994. Oviposition behavior in Lepidoptera. *Annual Review of Entomology* 39: 377–400.
- Riedel, M., Eichner, A., Jetter, R., 2003. Slippery surfaces of carnivorous plants: composition of epicuticular wax crystals in *Nepenthes alata* Blanco pitchers. *Planta* 218: 87–97.
- Riederer, M., 2006. Introduction: biology of the plant cuticle. In: Riederer, M., Müller, C., (eds) *Biology of plant cuticle*. Blackwell Publishing, Oxford, pp 1–10.
- Rinallo, C., Mori, B., 1996. Damage in apple (*Malus domestica* Borkh) fruit exposed to different levels of rain acidity. *Journal of Horticultural Science* 71: 17–23.
- Romeis, J., Shanower, T.G., Zebitz, C.P.W., 1998. Physical and chemical plant characters inhibiting the searching behaviour of *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). *Entomologia Experimentalis et Applicata* 87: 275–284.
- Romeis, J., Shanower, T.G., Zebitz, C.P.W., 1999. Why *Trichogramma* (Hymenoptera: Trichogrammatidae) egg parasitoids of *Helicoverpa armigera* (Lepidoptera: Noctuidae) fail on chickpea. *Bulletin of Entomological Research* 89: 89–94.
- Roth, L.M., Willis, E.R., 1952. Tarsal structure and climbing ability of cockroaches. *Journal of Experimental Biology* 119: 483–517.
- Shel'Deshova, G.G., 1967. Ecological factors determining distribution of the codling moth, *Laspeyresia pomonella* L. (Lepidoptera: Tortricidae) in the northern and southern hemispheres. *Annual Review of Entomology* 46: 349–361.
- Santos, R., Gorb, S., Jamar, V., Flammang, P., 2005. Adhesion of echinoderm tube feet to rough surfaces. *The Journal of Experimental Biology* 208: 2555–2567.

- Scholz, I., 2009. Ultrastructure and functional morphology of adhesive organs and anti-adhesive plant surfaces. PhD Thesis, RWTH Aachen University, Aachen.
- Scholz, I., Baumgartner, W., Federle, W., 2008. Micromechanics of smooth adhesive organs in stick insects: pads are mechanically anisotropic and softer towards the adhesive surface *Journal of Comparative Physiology A* 194: 373–384.
- Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., 2005. *Insect-Plant Biology*. Oxford University Press, 421 pp.
- Schwarz, H., Gorb, S., 2003. Method of platinum–carbon coating of ultrathin sections for transmission and scanning electron microscopy: an application for study of biological composites. *Microscopic Research and Technology* 62: 218–224.
- Singer, M.C., Ng, D., Thomas, C.D., 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42: 977–985.
- Skene, D.S., 1963. The fine structure of apple, pear, and plum fruit surfaces, their changes during ripening, and their response to polishing. *Annals of Botany* 37: 581–587.
- Smith, R.L., Wilson, R.L., Wilson, F.D., 1975. Resistance of cotton plant hairs to mobility of first-instars of the pink bollworm. *Journal of Economic Entomology* 68: 679–683.
- Southwood, R., 1986. Plant surfaces and insects – an overview. In: Juniper, B., Southwood, R. (eds.), *Insects and the plant surface*. Edward Arnold Publishers, London, pp. 1–22.
- Stork, N.E., 1980. Role of waxblooms in preventing attachment to Brassicas by the mustard beetle, *Phaedon cochleariae*. *Entomologia Experimentalis et Applicata* 28: 100–107.
- Subinprasert, S., Svensson, B.W., 1988. Effects of predation on clutch size and egg dispersion in the codling moth *Laspeyresia pomonella*. *Ecological Entomology* 13: 87–94.
- Thiery, D., Gabel, B., Farkas, P., Jarry, M., 1995. Egg dispersion in codling moth: Influence of egg extract and of its fatty acid constituents. *Journal of Chemical Ecology* 21: 2015–2026.
- Thompson, J.N., 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata* 47: 3–14.
- Uehara, K., Sakurai, M., 2002. Bonding strength of adhesives and surface roughness of joined parts. *Journal of Materials Processing Technology* 127: 178–181.
- Unruh, T.R., Knight, A.L., Upton, J., Glenn, D.M., Puterka, G.J., 2000. Particle films for suppression of the codling moth (Lepidoptera: Tortricidae) in apple and pear orchards. *Journal of Economic Entomology* 93: 737–743.

- Velásquez, P., Skurtys, O., Enrione, J., Osorio, F., 2011. Evaluation of surface free energy of various fruit epicarps using acid-base and Zisman approaches. *Food Biophysics* 6: 349–358.
- Verardo, G., Pagani, E., Geatti, P., Martinuzzi, P., 2003. A thorough study of the surface wax of apple fruits. *Analytical and Bioanalytical Chemistry* 376: 659–667.
- Voigt, D., 2005. Untersuchungen zur Morphologie, Biologie und Ökologie der räuberischen Weichwanze *Dicyphus errans* Wolff (Heteroptera, Miridae, Bryocorinae). Dissertation. Technische Universität Dresden, Dresden, Germany, 185 pp., [http://deposit.d-nb.de/cgi-bin/dokserv?idn=978746090&dok\\_var=d1&dok\\_ext=pdf&filename=978746090.pdf](http://deposit.d-nb.de/cgi-bin/dokserv?idn=978746090&dok_var=d1&dok_ext=pdf&filename=978746090.pdf)
- Voigt, D., Gorb, S., 2010. Egg attachment of the asparagus beetle *Crioceris asparagi* to the crystalline waxy surface of *Asparagus officinalis*. *Proceedings of the Royal Society London B* 277: 895–903.
- Voigt, D., Gorb, E.V., Gorb, S.N., 2007. Plant surface-bug interactions: *Dicyphus errans* stalking along trichomes. *Arthropod-Plant Interactions* 1: 221–243.
- Voigt, D., Schuppert, J.M., Dattinger, S., Gorb, S.N., 2008. Sexual dimorphism in the attachment ability of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) to rough substrates. *Journal of Insect Physiology* 54: 765–776.
- Vötsch, W., Nicholson, G., Müller, R., Stierhof, Y.-D., Gorb, S.N., Schwarz, U., 2002. Chemical composition of the attachment pad secretion of the locust *Locusta migratoria*. *Insect Biochemistry and Molecular Biology* 32: 1605–1613.
- Walker, G., Yule, A.B., Ratcliffe, J., 1985. The adhesive organ of the blowfly, *Calliphora vomitoria*: A functional approach (Diptera: Calliphoridae). *Journal of Zoology London A* 205: 297–307.
- Wearing, C.H., Hansen, J.D., Whyte, C., Miller, C. E., Brown, J., 2001. The potential for spread of codling moth via commercial sweet cherry: a critical review and risk assessment. *Crop Protection* 20: 465–488.
- Westgard, P.H., Gentner, L.G., Butt, B.A., 1976. Codling moth: egg and first instar mortality on pear with special reference to varietal susceptibility. *Environmental Entomology* 5: 51–54.
- Willmer, P., 1986. Microclimatic effects on insects at the plant surface. In: *Insects and the plant surface*. Juniper, B., Southwood, T.R.E., (eds), Arnold, London. pp. 65–80.
- Witzgall, P., Ansebo, L., Yang, Z., Angeli, G., Sauphanor, B., Bengtsson, M., 2005. Plant volatiles affect oviposition by codling moths. *Chemoecology* 15: 77–83.

- Wojcik, P., Dyki, B., Cieslinski, G., 1997. Fine structure of the fruit surface of seven apple cultivars. *Journal of Fruit and Ornamental Plant Research* 5: 119–127.
- Wood, T.G., 1965. Field observations on flight and oviposition of codling moth (*Carpocapsa pomonella* L.) and mortality of eggs and first-instar larvae in an integrated control orchard. *New Zealand Journal of Agricultural Research* 8: 1043–1059.
- Yan, F., Bengtsson, M., Witzgall, P., 1999. Behavioral response of female codling moths, *Cydia pomonella*, to apple volatiles. *Journal of Chemical Ecology* 25: 1343–1351.
- Yokoyama, V.Y., Miller, G.T., 1988. Laboratory evaluations of codling moth (Lepidoptera: Tortricidae) oviposition on three species of stone fruit grown in California. *Journal of Economic Entomology* 81: 568–572.
- Yokoyama, V.Y., Miller, G.T., Hartsell, P.L., 1990. Evaluation of a methyl bromide quarantine treatment to control codling moth (Lepidoptera: Tortricidae) on nectarine cultivars proposed for export to Japan. *Journal of Economic Entomology* 83: 466–471.







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