



The growth on different stored legume species affects the profiles of cuticular hydrocarbon (CHC) in *Acanthoscelides obtectus* (Say)

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ABSTRACT

Acanthoscelides obtectus (Say) (Coleoptera: Chrysomelidae: Bruchinae) is a widespread pest of stored products from Fabaceae family. The evolution of this species is associated with common bean domestication and the ability to invade other hosts in storages. To analyze the role of diverse nutrition in the ability of insects to shift to another host species we tested the effects of nutrition history on composition of cuticular hydrocarbons (CHCs), the compounds that have various ecological and reproductive functions in insects. The study was performed on *A. obtectus* laboratory populations which were bred for 51 generations either on common bean, *Phaseolus vulgaris* (L.), or on chickpea, *Cicer arietinum* (L.), a novel and less suitable species for larval development. To obtain conclusions about short-term nutritional effects, we tested whether exposure of seed weevils to alternative hosts for just one generation might influence CHC composition. Gas chromatography and gas chromatography–mass spectrometry analyses were performed and compounds' relative abundances were computed from the corresponding GC-FID peak areas. A total of 21 compounds were identified, among which 38% showed significant abundance differences between selection regimes and for 33% of compounds short-term developmental effects were revealed. All except three compounds showed significant differences between genders. We hypothesized that long-term changes in quantitative levels of specific CHC compounds were the results of diverse selection pressures on weevils' metabolic pathways induced by chemically divergent hosts. However, long-term adaptations to host species did not influence the ability of *A. obtectus* to quickly respond to chemical specificities of novel hosts (i.e., short-term effects were significant) which could be one of the major reasons for the great expansiveness of this species. Differences in relative CHCs abundances between sexes implied their roles in chemical communication and mate recognition systems.

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1. Introduction

Acanthoscelides obtectus (Say) is a widespread pest of domesticated legumes. Although the common bean (*Phaseolus vulgaris* L.) is its primary plant host, this weevil is also capable of successfully completing development on other, suboptimal, plant species. Within the family Fabaceae there are several potential hosts: chickpea (*Cicer arietinum* L.), azuki bean (*Vigna angularis* Wild), green bean (*Vigna radiata* L.), broad bean (*Vicia faba* L.), yardlong bean (*Vigna unguiculata* L.) pigeon pea (*Cajanus indicus* L.), or common pea (*Pisum sativum* L.). According to Alvarez et al. (2005), *A. obtectus* originated in equatorial Andes and later invaded Mesoamerica, Europe and the whole world following the trade routes.

This species gained the ability to reproduce without diapause after domestication of common bean (Labeyrie, 1990) or even earlier as a consequence of evolution on the wild bean species *Phaseolus polyanthus* (Greenman) which produces seeds all year round (Alvarez et al., 2005). Certainly, this feature enabled *A. obtectus* to be highly competitive when invading stored products. On a global scale, damages to these stored legumes could reduce crops up to 30% (Cardona, 1989). Long-distance colonization events seem to be responsible for genetic divergence between well-marked clades of bruchid species, whereas fine-scale adaptation to host plants resulted in species radiation (Ehrlich and Raven, 1964). When a lineage of bruchids becomes adapted to a certain kind of host-plant, it may undergo evolutionary radiation onto other closely related plants (Alvarez et al., 2006). Adaptation to secondary metabolites characteristic of a group of closely related plant species allow a lineage of insects to radiate adaptively onto other host plants of this group. Basically, this host-shift should be the

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mechanism that enabled *A. obtectus* to expand its host range in storages with legume products all over the world.

During the past forty years, one particular group of chemical compounds that cover insects integument, 'cuticular hydrocarbons' (CHCs), has been distinguished as an important determinant of insect metabolism and biology, and, as such, this group of compounds became the subject of many studies dealing with evolutionary changes of insect populations (e.g., Howard and Blomquist, 2005; Blomquist and Bagnères, 2010; Menzel and Schmitt, 2012). An increasing number of papers in this field of research suggest that, besides various biological roles of CHCs which have been already discovered in arthropod species, many questions still remain unanswered. As has been indicated by Howard and Blomquist (2005) hydrocarbons may be simple in chemical terms, but the ways in which insects and other arthropods have evolved to use them for diverse biochemical, physiological, and semiochemical functions, such as prevention of desiccation and barriers to microorganisms, are far from simple.

Because they are part of a complex cuticular structure, one of the first recognized biological functions of CHCs was the control of water balance (Wigglesworth, 1933; Gibbs and Rajpurohit, 2010). Ecological roles of CHCs, reviewed in Howard and Blomquist (1982, 2005), covered a whole spectrum of functions: from recognition signals between individuals of the same and/or different species, gender and nestmate recognition, task-specific cues, dominant and fertility cues, and even chemical mimicry. It has been shown that patterns of CHC composition are species specific, suggesting that CHC profiles evolved in a context of specific abiotic factors (e.g., climate, van Wilgenburg et al., 2011), biotic interspecific interaction (e.g., parabiotic species, Menzel et al., 2008a) and internal biological characteristics of species (e.g., species and sex membership signals, Ayasse et al., 2001; communication and nestmate recognition, Martin and Drijfhout, 2009).

In addition to their varied roles in survival, CHCs have important effects in reproductive behavior of insects. They can vary between genders both quantitatively and qualitatively. For example, in *Drosophila* one gender may have compounds that other gender does not have (e.g. Ginzl et al., 2003), or sexes could differ in the relative abundance of synthesized CHCs (e.g. Cobb and Ferveur, 1996). Some CHCs stimulate and others inhibit various aspects of sexual behavior, and both "major and minor components of the bouquet may be used both for intra and interspecific communication to influence mate choice and reinforce sexual isolation" (Ferveur, 2005, p. 291). In several studies, however, no differences between genders in CHC profiles were discovered (Howard et al., 2003; Howard and Baker, 2003).

Within species boundaries, CHC profiles are not rigid components of cuticular surface. As shown in many studies, both quantity and quality of 'CHC bouquet' can be influenced directly by environmental factors, such as temperature, and the food type that was available during insect development (Savarit and Ferveur, 2002; Stennett and Etges, 1997). Since mechanisms of excreting and presenting CHCs on the cuticular surface, as well as *de novo* synthetic pathways, may depend on chemical content of available resources, it is reasonable to assume that these plastic changes in CHC repertoire can alter the course of adaptations in specific environments (*sensu* Pigliucci, 2001). For example, Liang and Silverman (2000) have demonstrated that nutritional alterations change CHC profiles and influence recognition cues leading to aggressive behavior between colonies of Argentine ant. Blomquist and Bagnères (2010) speculate that changes in CHC profiles induced by food quality might enable herbivorous insects to shift from one to another plant host.

In this study we tested whether nutrition history (i.e., the acquisition of different plant hosts during development) could

change CHC profiles in *A. obtectus*. The experiment was performed on laboratory populations which were reared for 51 generations either on common bean, *P. vulgaris* (L.), the preferred host of this bean weevil, or on chickpea (*C. arietinum*, L.), a novel and less suitable host for larval development. These populations differ in several important life history traits as a consequence of selection associated with their host plants (Milanović et al., 1991; Tucić et al., 1996). If populations, raised for many generations on distinct hosts, differ in their CHC profiles, that would indicate diverse courses of specialization on these host species. On the other hand, if larvae are exposed to distinct hosts for just one generation, the differences in CHC profiles between weevils developed on their native and novel hosts reveal short-term plastic responses of metabolic and synthetic pathways to host identity. Here we tested whether populations specialized on one stored legume species varied in their sensitivity to another host. Also, considering results of previous studies on the reproductive roles of CHCs in insects, we analyzed the effects of diverse nutrition on CHC repertoire in males and females and, consequently, their possible influences on mate recognition systems in *A. obtectus*. Generally, the main goal of this study is to investigate the chemical consequences of short- and long-term experiences of the bean weevil on novel host since it is largely recognized that these processes are involved in host-range expansion of herbivorous insects. Taking into consideration the biological roles of CHCs in insects, there is a great economical significance in studying hydrocarbons because they demonstrate that changes and adaptations accompanied with host shift can happen in storages with multiple legume products.

2. Materials and methods

2.1. *Acanthoscelides obtectus* (Say)

The bean weevil, *A. obtectus* (Say) (Coleoptera: Chrysomelidae: Bruchinae) today presents an example of world wide pest of stored legumes. Individuals of this holometabolic insect are facultative aphagous in adult phase, and larvae are well adapted to dry seeds. This enables them to mate and complete their life cycle using only metabolic water and resources acquired during larval development. Mated females are stimulated to deposit eggs in the presence of seeds. The oviposition behavior of *A. obtectus* differs from that of other bruchids (Šešljija et al., 2009). Females usually do not attach their eggs onto a surface of beans, but scatter them among the seeds. Hatching larvae are motile and move among seeds before boring into them. Larval development and pupation are completed entirely within a single seed, and after approximately 30 days, adults emerge. Two hours after emerging from the seed, adults are capable to reproduce. This species is an excellent model system for a long-term laboratory evolution experiments because laboratory conditions resemble environments in legume storages.

2.2. Selection regimes, experimental procedures and rearing conditions

In this experiment we have used eight laboratory populations of *A. obtectus* four of which were maintained on a common bean *P. vulgaris* (hereafter referred to as the 'Phaseolus' or P selection regime) and four reared on chickpea *C. arietinum* (hereafter referred to as the 'Cicer' or C selection regime) for 51 generations (approximately four years). Although *Cicer* is less suitable host for this weevil, larval survival on chickpeas is satisfactory (Tucić et al., 1997).

Populations in both P and C selection regimes were established from a synthetic base (B) population that was obtained by mass mating weevils from three different storages of beans in the vicinity

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