

# Discontinuous carbon dioxide release in the German cockroach, *Blattella germanica* (Dictyoptera: Blattellidae), and its effect on respiratory transpiration

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## Abstract

The discontinuous gas exchange cycle (DGC) was described in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae) for the first time. Also, the effect of the DGC on water loss was investigated. The CO<sub>2</sub> emission pattern in both insecticide resistant and susceptible *B. germanica* varied with temperature. At 10, 15, and 20 °C the pattern was discontinuous. Cycle frequency increased at 25 and 30 °C, and at 35 °C the pattern became cyclic. In most DGCs, there was no clear distinction between the closed and flutter phases in both strains thus data for these phases were combined and analyzed as the interburst phase. The probability that *B. germanica* would breath discontinuously varied with temperature. Most cockroaches (62.8%) displayed DGCs at 10 °C, therefore measurement of metabolic rate and water loss was carried out at this temperature. Using repeated measures of analysis of variance, the interburst and burst  $\dot{V}_{CO_2}$  (ml h<sup>-1</sup>) were not significantly different between the two strains. The variability in CO<sub>2</sub> emission during the interburst and burst phases over time was not significantly different from cycle to cycle or between strains. Overall metabolic rate during the entire recording was not significantly different between both strains. There was a significant difference in the duration of the interburst and burst phases between the strains. The susceptible strain had significantly longer interburst and burst phase durations during a complete DGC than the resistant strain. The interburst and burst phase durations were 5.01 ± 0.19 and 6.21 ± 0.13 min, respectively, for the resistant strain, whereas the durations were 7.16 ± 0.37 and 6.73 ± 0.17 min, respectively, for the susceptible strain. This resulted in a DGC of significantly longer duration (13.89 ± 0.44 min) in the susceptible strain compared with the resistant strain (11.23 ± 0.26 min). The duration of the interburst phase was significantly different from the open phase duration in the resistant strain such that during a single DGC lasting ~11.23 min, 43.5% consisted of the interburst phase while the burst phase made up 56.5% of the cycle. The cuticular permeability at 10 °C and 0% RH was 2.26 μg cm<sup>-2</sup> h<sup>-1</sup> mmHg<sup>-1</sup> for the resistant strain and 3.42 μg cm<sup>-2</sup> h<sup>-1</sup> mmHg<sup>-1</sup> for the susceptible strain. In both strains, cuticular transpiration accounted for ~95% of total water loss. The significantly longer duration of the interburst phase of the susceptible strain was not important in reducing water loss.

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## 1. Introduction

It is becoming increasingly clear that gas exchange in many quiescent adult terrestrial insects is discontinuous

(see Kestler, 1985; Slama, 1988; Lighton, 1994). A typical discontinuous gas exchange cycle (DGC) begins with a closed-spiracle phase, when little external gas exchange takes place. This is followed by a fluttering-spiracle phase where the spiracles open and close rapidly enabling gases to pass through by convection and diffusion, and finally an open-spiracle phase during which accumulated CO<sub>2</sub> escapes from the tracheal

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system to the surrounding environment (Lighton, 1996). In some insects, DGC is reported to conserve body water (Kestler, 1985; Hadley, 1994; Lighton, 1996), as a result of reduced respiratory water loss during the closed phase, and low water loss during the flutter phase (Lighton, 1996).

In insects that exhibit DGC, it is possible to determine the significance of the discontinuous gas exchange pattern in water conservation since water lost during the open phase (burst) (cuticular and respiratory loss) can be separated from loss during the closed and flutter phases (interburst; cuticular loss) (Hadley, 1994). Even though cuticular transpiration is greatly reduced by lipids associated with the epicuticle, the cuticle is still considered the primary water-efflux path because of the large surface area-to-volume ratio of insects (Hadley, 1986, 1989). Regulation of cutaneous water loss is critical for small insects such as the German cockroach, *Blattella germanica* (L.) because of their small size (<15 mm long) and large surface area-to-volume ratio.

*B. germanica* is a world wide household pest, which may harbor and transmit human disease-causing pathogens (Ramirez, 1989). Their body parts and feces are also potent allergens to sensitive people (Roberts, 1996). Pyrethroid insecticides are widely used for *B. germanica* control because of their effectiveness and low mammalian toxicity. However, control failures in some field populations have been reported as a result of the development of resistance (Cochran, 1989; Valles et al., 2000). Resistance levels generally decline in the absence of insecticide selection (Tabashnik et al., 1994; Rahardja and Whalon, 1995), and a decrease in resistance may be associated with increased biotic fitness (Tabashnik et al., 1994). Fitness can be observed as changes in survival rate, egg hatch, weight and metabolic rate (Groeters et al., 1994; Idris and Grafius, 1996; Hollingsworth et al., 1997; Dingha et al., 2004).

In cockroaches, the DGC pattern has been reported and described at 20 °C in the American cockroach, *Periplaneta americana* (L.) (Kestler, 1985, 1991; Machin et al., 1991), and *Perisphaeria* sp. (Marais and Chown, 2003). A cyclic O<sub>2</sub> consumption pattern was recorded from the tropical cockroach, *Blaberus giganteus* (L.) at 26.6 °C (Bartholomew and Lighton, 1985). The aim of this study was to describe the respiratory gas exchange patterns at different temperatures, investigate the effects of DGC on water loss, and determine if there are differences in the DGC characteristics between insecticide resistant and susceptible strains of *B. germanica*. To accomplish this, we conducted experiments to test two major hypotheses. First, we hypothesized that *B. germanica* would show a pronounced DGC only at lower temperatures and continuous cycling of CO<sub>2</sub> release at higher temperatures. Since increased temperature generally causes the metabolic rate to rise, the frequency of spiracular opening would increase at higher

temperatures (Chappell and Rogowitz, 2000). Therefore, DGCs would be more pronounced in insects at lower temperatures and cyclic at higher temperatures. For example, in some adult insects, such as the eucalyptus-boring beetle, *Phorocantha* spp. (Chappell and Rogowitz, 2000), the California grasshopper, *Melanoplus sanguinipes* (Rourke, 2000), *P. americana* (Kestler, 1985, 1991; Machin et al., 1991) and *Perisphaeria* sp. (Marais and Chown, 2003), DGC was not exhibited at higher temperatures, instead it was observed only at lower temperatures. Second, we hypothesized that genetically resistant *B. germanica* not exposed to insecticide for several generations would have similar metabolic rates and DGC characteristics as a susceptible strain. In addition, we hypothesized there would be no significant difference in water loss between the two strains.

## 2. Materials and methods

### 2.1. Cockroach strains

Two *B. germanica* strains were used in this study. ACY (American Cyanamid Co., Clifton, NY), is an insecticide susceptible strain that has been reared in the laboratory without exposure to insecticide for >40 years. The second is Apyr-R (Alabama, pyrethroid resistant); a resistant strain collected from an infested kitchen in Opelika, Lee County, Alabama, USA in 1999 after control failures with permethrin and deltamethrin. This strain was subsequently selected with permethrin and deltamethrin for several generations prior to this study (Wei et al., 2001; Pridgeon et al., 2002). Levels of resistance to permethrin and deltamethrin in Apyr-R were 97- and 480-fold, respectively, compared with the susceptible strain (Wei et al., 2001; Pridgeon et al., 2002). All cockroaches were reared at 25 ± 2 °C and 50 ± 10% RH, with photoperiod of 12L: 12D. Dry dog chow and water were supplied ad libitum.

### 2.2. Respirometry and metabolic rate measurement

We recorded patterns of CO<sub>2</sub> emission of individual adult male *B. germanica* at 5, 10, 15, 20, 25, 30, and 35 °C using flow through respirometry. Males were selected to avoid complications arising from the metabolic demands of oogenesis in females. To avoid stress (Kestler, 1991; Machin et al., 1991), cockroaches were allowed to crawl into a 3 cm × 1.0 cm transparent Tygon<sup>®</sup> tubing respirometer chamber which was then sealed at both ends with a rubber stopper and connected to the CO<sub>2</sub> and H<sub>2</sub>O analyzer. Cockroaches were acclimated in the respirometry chamber for ~1 h before recordings were initiated. This allowed for acclimation to the initial temperature and predesiccation to remove

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