

Active Tracheal Ventilation and its Metabolic Cost in the Large Pine Weevil, *Hylobius abietis* (L.) (Coleoptera: Curculionidae)

IVAR SIBUL¹*, AARE KUUSIK², ANNE LUIK² AND ANGELA PLOOMP

¹*Institute of Forestry and Rural Engineering, Estonian University of Life Sciences, Kreutzwaldi St. 5, 51014 Tartu, Estonia; e-mail: ivar.sibul@emu.ee, tel. +372 7 313 156*

²*Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi St. 1, 51014 Tartu, Estonia*

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Abstract

The large pine weevil, *Hylobius abietis* (L.) is the major damaging insect pest in reforestation areas in coniferous forests in Europe. New control methods require detailed knowledge of the ecology, behaviour and also physiology of the pest. A study of respiration pattern was conducted to determine the metabolic cost of active ventilation in adults of the large pine weevil, *Hylobius abietis*. A volumetric-manometric respirometer was used in parallel with an infrared opto-cardiograph to record muscular contractions together with gas exchange patterns.

In the dry insect chamber, *i.e.* in the dehydrated conditions the pine weevil displayed discontinuous gas exchange cycles (DGCs). Most of the DGCs were of CFV (Closed-Flutter-Ventilation) type, where bursts of carbon dioxide release (V phase) were ventilated by abdominal pumping movements. However, about 10% of the bursts in each individual were not ventilated. In the ventilated cycle the burst volume (VCO₂) was about 20% greater than that of the non-ventilated cycle, suggesting a significant metabolic effect of pumping movements.

A minority (ca 10%) of dehydrated individuals exhibited DGCs of CFO (O=open) type, where pumping movements were lacking, and in these individuals the level of metabolic rate was about 20% lower than in weevils characterised by CFV cycles. The CFO cycles in *H. abietis* were considered as an exceptional and unfavourable event. Nevertheless, the results suggested that in individuals of *H. abietis* showing complete tonic immobility (CFO cycles) the levels of the true standard metabolic rate (SMR) were measured.

DGCs recorded by means of flow through method *i.e.* by infrared gas analyzer (IRGA), were usually recognized as signs about the existing standard metabolic rate in an insect. Our results indicated that DGCs appearing in dry air in pine weevils are a sign of standard metabolic rate only in case of CFO cycles, where muscular contractions are absent. In weevils showing CFV cycles cannot be measured the level of standard metabolic rate due to the vigour active ventilation by means of abdominal pumping movements. Thus, IRGA cannot be regarded as an universal method to differentiate the active and standard metabolic rates. Moreover, in parallel with respirometer must be used an actographic device, to record all body movements including abdominal pumping movements.

Key words: CFO and CFV cycles, discontinuous gas exchange cycles, DGC, *Hylobius abietis*, large pine weevil, standard metabolic rate

Introduction

The pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae), is one of the most important pests of temperate conifer forestry in Europe, particularly in Scandinavia and Baltic (Leather *et al.* 1999, Långström and Day 2004). Both larvae and adults feed on the bark of conifer species, but only adult feeding on seedlings is economically important. If plants are not protected, most of planted seedlings may be lost. Chemical control measures have been used to reduce the damage caused by *H. abietis*. Restrictions on the use of chem-

ical insecticides in forests in many countries have stimulated the experiments with alternative control methods against this forest pest (Luik *et al.* 2000, Sibul *et al.* 2002, 2005). At the same time, application of new control methods and introduction of biological insecticides require profound knowledge of the ecology, behaviour and physiology of forest pest insects (Merville *et al.* 1998, Sibul *et al.* 1999). Estimation of the physiological state (*e.g.* standard metabolic rate) of harmful insects is therefore an inevitable task.

Control levels in insect respirometry, known as resting or standard metabolic rate (SMR), are ordinari-

ly determined in an atmosphere saturated with water vapour on animals which are deprived of food, and are, insofar as possible, motionless (Keister and Buck 1974). The SMR is also defined as a value measured at a particular temperature when the insect is quiet, inactive, is not digesting a meal, nor exposed to any stress (Withers 1992). However, in a quiet, inactive and externally immobile insect, especially in coleopterous adults, vigorous abdominal pumping movements may occur under the elytra. Active ventilating with pumping movements is a specific mode of respiration in many insects (rev. by Miller 1974, 1981, Mill 1985, Nation 2002, Chown and Nicolson 2004). The major users of metabolic energy are the muscles. However, there is almost nothing known about the metabolic cost of the obligatory pumping movements in externally immobile beetles.

Many insects exhibit discontinuous gas exchange cycles (DGCs), which means that carbon dioxide is periodically released in bursts, and O_2 uptake is often cyclic. Classical "cyclic CO_2 release" (rev. by Miller 1974, 1981, Kestler 1971, 1985, Slama 1988, 1994, Lighton 1994, 1996, Chown and Nicolson 2004) is caused by the sequence of facultative constriction (C), flutter (F) and open (O) periods of the spiracles in (C)FO cycles (Schneiderman 1960) or in (C)FV cycles (Kestler 1971). In the CFV cycles classical discontinuous ventilation (V =pumping) with only short expiratory and inspiratory opening replaces the O period. Kestler (2003) proposed using DGC as a synonym for (C)FB (B=burst) with four respiratory movements patterns of the CFO or FO and CFV or FV type. Most adults of the dangerous forest pest, the large pine weevil (*Hylobius abietis*) exhibit pumping movements during the bursts of carbon dioxide in the CFV cycles, while these movements are externally invisible (Sibul *et al.* 2004a,b).

Discontinuous gas exchange cycles are thought to be the mechanism for restriction of water loss (hygric theory of DGCs origin) (rev. by Kestler 1985, Lighton 1996), but some other theories also exist (rev. by Chown *et al.* 2006).

It is usually believed that insects displaying DGCs can be measured at resting or standard metabolic rate because during the DGCs the insect is inactive and immobile, while activity commonly abolishes the cyclic gas exchange (Chown 2002, Chown and Nicolson 2004). According to Chown and Gaston (1999), flow-through CO_2 respirometry is revolutionizing results by allowing careful separation of resting (or standard) and active metabolic rates. However, the metabolic cost of the pumping movements during the (C)FV cycles has not yet been studied.

The aim of the present investigation was to measure the metabolic cost of active ventilation due to the pumping movements in the (C)FV cycles of *H. abietis*.

Materials and methods

Insects

The *H. abietis* adults were collected in May–June 2006 from ground pitfall traps in a freshly cut area in the forest district of R pina, Southern Estonia (latitude 58°09' N, longitude 27°08' E, altitude 55 m a.s.l.), where beetles were very abundant (Sibul 2000). After collection, the weevils were kept in groups of ten in glass jars with moistened moss in a refrigerator at 2–3 °C. Water and fresh Scots pine (*Pinus sylvestris* L.) twigs were added to the jars as needed. Prior to the experiments weevils were transferred to ambient laboratory conditions (25 °C, 60% RH and a photoperiod of L14:D10) for 48 h, while weevils kept without water and food are referred to as dehydrated. Only healthy, medium-sized individuals were accepted as experimental insects. The body mass of the weevils used in the experiments ranged from 200 to 230 mg. All measurements were performed at 25 °C.

Closed system respirometry

The method used was a continuously oxygen-compensating differential volumetric-manometric closed system respirometer (CC-dvmCSR), detail described earlier (Tartes *et al.* 1999, 2000, 2002, Vanatoa *et al.* 2006), referred to as a closed system respirometer. The respirometer allowed simultaneous recording of metabolic rate, discrete carbon dioxide releases (bursts), rapid intakes of air into the tracheae in microcycles, and abdominal pumping movements. The respirometer ensures continuous replacement of consumed oxygen with electrolytically produced oxygen. The insect itself plays an active role in this self-regulating system. The extreme sensitivity of the CC-dvmCSR method is based on the fact that it keeps the product of volume and pressure changes (energy) in the general gas law constant by compensating the energetic measurements by a molar change of O_2 during CO_2 absorption (Kestler pers. comm.).

The respirograms display the rates of electrolytically generated oxygen, which are indicated on the graphs as " FO_2 (ml h⁻¹)". The respirometer recorded the air pressure changes in the insect chamber, caused by the body volume changes due to the pumping abdominal movements of the insect. Carbon dioxide bursts are not measured but only indicated on the respirograms as clear downward peaks lasting several minutes.

We used dry potassium hydroxide and a dry insect chamber (about 15% RH). The humidity (RH%) and temperature inside the insect chamber was controlled using the Humidity and Temperature Display Instrument for digital HygroClip probes (HygroPalm, Rotronic Company).

Flow-through respirometry

An infrared gas analyser (Infralyt-4, VEB, Junkalor, Dessau) adapted for entomological research was used to record the bursts of carbon dioxide release. This flow-through respirometer was calibrated at different flow rates by means of calibration gases (Trägergase, VEB, Junkalor, Dessau), with gas injection. Air flow rate was commonly 3.6 l per h. The rate of carbon dioxide release was measured (V_{CO_2} ml h⁻¹).

IR actography

The closed system respirometry and flow-through respirometry were combined with an infrared optical device referred to as infrared actograph. This device was commonly used as an insect IR cardiograph (Hetz *et al.* 1999, Kuusik *et al.* 2001) or optocardiographic method (Slama 2003). Two IR-emitting diodes (TSA6203) were placed on one side of the insect chamber, and two IR sensor diodes (BP104) were placed on the opposite side. The light from the IR-diode was modulated by the abdominal contractions. The level of output voltage reflected the vigour of the muscular contractions of the insect.

Data acquisition and statistics

Computerised data acquisition and analysis were performed using an analog-to-digital converter and TestPoint software with 10 Hz sampling rate (DAS 1401, Keithley-Metrabyte). The mean metabolic rate was automatically calculated by averaging data over a period involving at least 12 cycles of gas exchange. Means, standard deviations and the number of observations (N) are reported. Tests were performed using a statistic package StatSoft ver. 5.6, Inc/USA. Means were compared using Student's t-test.

Results

Metabolic cost of pumping movement in discontinuous gas exchange

During the first two hours after measurements were begun, most (88%, N=100) of the *H. abietis* dehydrated individuals displayed continuous abdominal pumping; this respiration mode was then transformed into discontinuous gas exchange cycles of the CFV type, which means that during the bursts of carbon dioxide release the abdominal pumping movements were recorded (Figures 1,2 and 3). However, in some individuals, about 10% of the DGCs were not ventilated by pumping movements (Figure 1). The simultaneous recording of the flow-through CO₂ respirometer and infrared actograph showed that the peaks due to bursts of carbon dioxide which were not ventilated by pumping movements were significantly shorter than peaks due to bursts which were actively ventilated (Figure 1). Thus each individual displayed both the

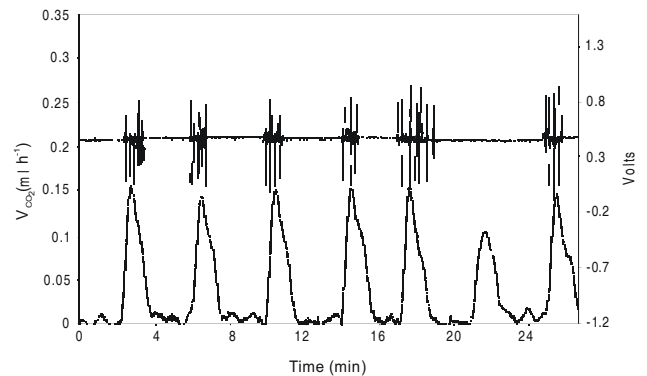


Figure 1. A flow-through CO₂ respirometry recording (lower trace, V_{CO_2} ml h⁻¹) of discontinuous gas exchange cycles of (C)FV type in adult *Hyobius abietis*. Upper trace is a synchronous recording of IR actograph. Note that one burst of carbon dioxide release is not ventilated by abdominal pumping movements

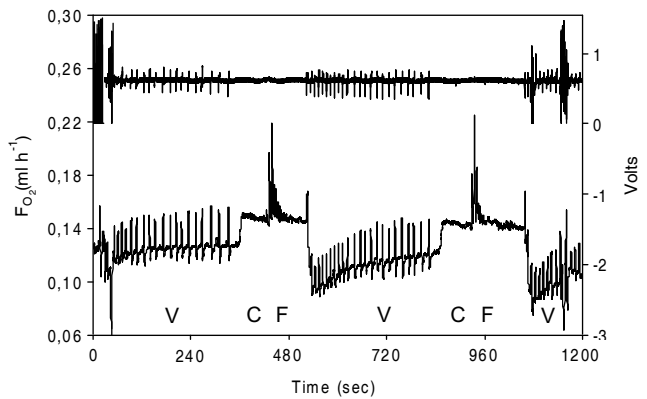


Figure 2. Discontinuous gas exchange cycles of CFV type demonstrating a long V (ventilation) period and micro-openings of the spiracles during the F period (upper trace), a recording of constant volume respirometer. The simultaneous recording of infrared actograph is seen on the upper trace (Volts)

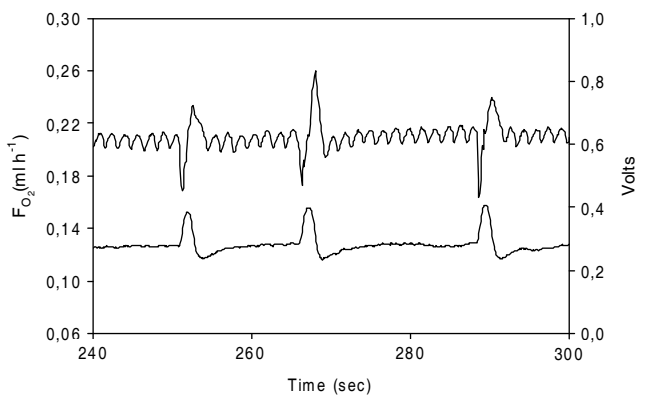


Figure 3. A detail of figure 2. Between pumping movements are recorded the signals due to heartbeats

CFV and CFO cycles of gas exchange. The calculated metabolic cost of the pumping movements contributed $20.5\% \pm 1.6\%$ (range 18.4% to 22.3%; N=30 individuals with 120 CFV and 14 CFO cycles) of total carbon dioxide release. The mean burst volume of the CFV cycle was significantly greater than that of the CFO cycle (Student's t-test; $t=4.77$, $df=9$; $P=0.00$; N=10 individuals 40 CFV and 10 CFO cycles) (see Table 1).

Table 1. Comparison of gas exchange parameters in CFV and CFO cycles of adult *Hylobius abietis* at 25° C

Variable	(C)FV cycle (N= 10 individuals)	(C)FO cycle (N=10 individuals)
Body mass (mg)	219±7.4	212±8.2*
FO ₂ (μl h ⁻¹)	44.3±6.6	36.5±4.7*
FO ₂ (μl g ⁻¹ h ⁻¹)	200.6±29.8	172.6±20.4
Burst volume (CO ₂ μl) ^a	3.29±0.28	2.57±0.36*
Burst frequency (mHz)	4.47±0.06	4.23±0.09
Burst frequency per h	15.2±0.86	14.9±0.75

* Asterisks indicate the significant ($P < 0.05$) differences between CFV and CFO cycles.

^a Burst volume was calculated in individuals displaying both types of cycles. See text for test results.

A minority of individuals (10%; n=100) displayed clear CFO cycles for at least 8–10 hours when pumping movements were lacking (Figure 4). The metabolic rate during the CFO cycles may be regarded as the real standard metabolic rate when no muscular activity was observed. Infrared actograph recorded 1–2 short periods of activity per two hours. These activity periods coincided only accidentally with the burst of CO₂. The activity periods were characterised by irregular muscular contractions (Figure 4). The obligatory pumping movements during the CO₂ bursts were very regular (Figures 2 and 3).

The comparison of individuals exhibiting CFV cycles with those which showed CFO cycles revealed that the level of metabolic rate in CFV cycles was significantly higher than in individuals with CFO cycles (Student's t-test; $t=2.59$, $df=23$, $P=0.016$; N=10 individuals each with 5–8 cycles) (see Table 1). The comparison was made between two series with similar body mass and similar frequencies of DGCs (see Table 1).

Commonly the V period in the CFV cycle contributed about 30% of the total cycle. There occurred individuals whose V periods in CFV cycles was about 60% of the total cycle; in these weevils the level of metabolic rate was 2–3 times higher than in the case of shorter V periods (Figure 2). The higher levels of metabolic rates were obviously due to vigorous pumping movements during the long V periods.

Flutter period

During the flutter periods the constant volume respirometer recorded the very regular upward spikes (Figure 4) in the CFV and CFO cycles. One might think that these are muscular contractions, however, simultaneous recording of the infrared actograph proved

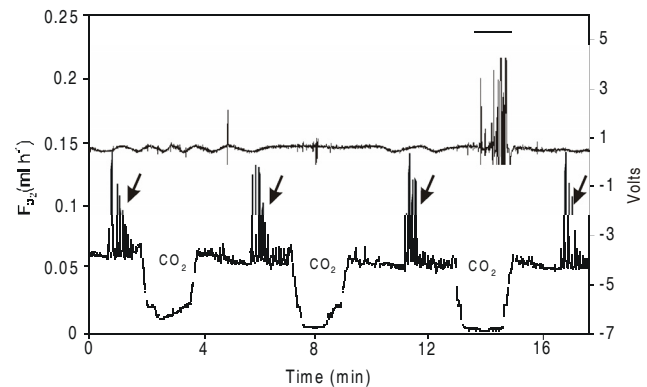


Figure 4. Discontinuous gas exchange cycles of (C)FO type in adult *H. abietis* recorded by constant volume respirometer (lower trace, FO₂ (ml h⁻¹)). Note that the abdominal pumping movements during the bursts of carbon dioxide release are absent (upper trace, recording of infrared actograph, Volts). A short period of activity is indicated by a horizontal line. The arrows on the lower trace indicate the micro-opening of the spiracles and miniature inspirations recorded during the F (flutter) periods

that no muscular contraction occurred during these spikes; they were caused by the micro-openings of the spiracles *i.e.* due to the miniature inspirations.

One period of miniature inspiration is known as the flutter phase of the DGC. Thus all three phases of DGC (closed=C, flutter=F, open=O) are well defined by the CC-dvmCSR respirometer (see Figures 2 and 4).

Discussion

The respirometry and IR actography revealed that adult *H. abietis* use the respiration mode of continuous ventilation by abdominal pumping and convective gas exchange cycles of CFV type. A similar respiration pattern was described in *Periplaneta americana* (see Kestler 1971). Active ventilation in dehydrated immobile weevils lasted maximally 1–2 hours, then transformed into discontinuous gas exchange cycles (DGCs), mostly of CFV type. Thus, active continuous ventilation seemed to be a precursor of discontinuous gas exchange cycles, as it was also described in adult *Leptinotarsa decemlineata* (Vanatoa *et al.* 2006). However, the results did not exclude the possibility that active continuous ventilation was a sign of apparatus stress (see Kestler 1991).

According to Duncan *et al.* (2002) a tenebrionid beetle displayed DGCs when dehydrated, and a con-

tinuous gas exchange pattern after being supplied with food and water.

In the weevils that displayed the CFV cycles, there occurred rare bursts of carbon dioxide release, which were not accompanied by abdominal pumpings. The calculated metabolic cost of pumping contributed about 20% of total emission of carbon dioxide during a burst.

In a small number of weevils were recorded clear CFO cycles without any pumping movements and the level of oxygen consumption was significantly lower in these weevils than in individuals of CFV cycles. According to Kestler (1985) the CFV cycles due to convective V periods are less water-consuming than diffusive (CFO) cycles. The replacement of diffusive O period by convective V period avoids the higher diffusion of water (Kestler 2003). The CFO cycles that were recorded in a minority of dehydrated *H. abietis* may be a sign of abnormality caused by factors that remain unknown. However, the results suggested that individuals with CFO cycles displayed the actual standard metabolic rate.

Obviously for adult Coleoptera is characteristic a relatively high expenditure of metabolic energy during the active ventilation. In contrast to these observations the active ventilation during the pupal stage of *Tenebrio molitor* (Coleoptera: Tenebrionidae) amounted only about 1% of the total energy used during the metamorphosis (Harak *et al.* 1996, 1998, Kuusik *et al.* 1994).

The constant volume respirometer used (CC-dvmC-SR) allowed us to clearly record the VC, CF and FV transitions. In 1985, Kestler showed that in large adult insects with their coordination of ventilation and spiracular control, tracheal pressure measurements clearly distinguish the named transitions. Pressure measurements are at least a useful adjunct to gas exchange measurements (Chown *et al.* 2006).

During the flutter (F) period of *H. abietis*, there occurred regular and discrete oxygen uptake volleys due to passive suction ventilation and diffusion in the short micro-openings of the spiracles. Thus earlier observations on flutter in *H. abietis* were supported (see Sibul *et al.* 2004a, 2006). A similar pattern of oxygen uptake during the flutter, *i.e.* passive suction ventilation, was also described in adult *Leptinotarsa decemlineata* (see Vanatoa *et al.* 2006). However, it was also claimed that beetles with thin, membranous tergites cannot develop negative endotracheal pressure and therefore are unable to create passive suction ventilation (see Lighton 1994). Nevertheless, Kestler (1985) recorded negative tracheal pressure in *Periplaneta americana* despite its very thin membranous tergites.

Physiological recordings of present study are linked with the behaviour of the *H. abietis*. Several authors (Havukkala and Selander 1976, Sibul *et al.* 1999) have shown that *H. abietis* is influenced by air humidity. Under the condition of high relative humidity weevils' movement is very active, while in lower relative humidity conditions it decreases significantly (Sibul *et al.* 1999).

Conclusions

In dry air discontinuous gas exchange cycles appeared in the large pine weevil, *Hylobius abietis*. The results of the present study revealed a significant metabolic cost of the pumping movements in the CFV cycles. We demonstrated that the true standard metabolic rate in the large pine weevil were recorded in the CFO cycles, where abdominal pumping movements were absent. At the same time the CFO cycles seemed to be the exceptional, abnormal and even disadvantageous events in the respiration of *H. abietis*.

During the flutter period, there always occurred regular and discrete O₂ uptake volleys, and thus O₂ uptake was measured due to passive suction ventilation and diffusion in the short micro-openings.

The constant volume electrolytic respirometry combined with infrared actography presented more information about the gas exchange of beetles than traditional flow-through respirometry.

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ПОТРЕБЛЕНИЕ ЭНЕРГИИ ПРИ АКТИВНОЙ ВЕНТИЛЯЦИИ ТРАХЕЙ У СОСНОВОГО ДОЛГОНОСИКА *HYLOBIUS ABIETIS* (L.) (*COLEOPTERA: CURCULIONIDAE*)

И. Сибул, А. Куузик, А. Луйк и А. Пломи

Резюме

У соснового долгоносика *Hylobius abietis* было изучено дыхание с целью выявления потребления энергии т.е. цена обмена активной вентиляции, проводимой насекомым при помощи сокращения брюшных мышц. Был использован манометрический респирометер постоянного объема, комбинированный с инфракрасным опто-кардиографом.

В сухом воздухе сосновый долгоносик продемонстрировал прерывистый газообмен с циклическим выделением углекислого газа, где „выхлопы“ этого газа сопровождались сокращением брюшных мышц. Однако примерно 10% из выхлопов углекислого газа не сопровождались сокращением мышц и в этом случае уровень дыхания был примерно на 20% ниже, чем при выхлопах, сопровождающихся активной вентиляцией.

Сравнивая потребление кислорода у долгоносиков с активной вентиляцией с долгоносиками, у которых активная вентиляция отсутствует, выяснилось, что у первой группы уровень дыхания был почти на 20% выше, чем у второй группы.

Контрольный уровень потребления кислорода насекомых известен как „стандартная скорость обмена“, измеряемый при полном мышечном покое. Обычно принято считать, что прерывистый газообмен, регистрируемый при помощи инфракрасного газоанализатора, свидетельствует о мышечном покое насекомого, поскольку при мышечной активности выхлопы углекислого газа исчезают т.е. газообмен становится непрерывным.

В настоящей работе на примере соснового долгоносика показано, что истинную стандартную скорость обмена необходимо измерять при отсутствии активной вентиляции трахей.

Следовательно, синхронно с записью дыхания необходима запись сокращений брюшных мышц проводимым актографом.

Ключевые слова: активная вентиляция трахей, *Hylobius abietis*, соснового долгоносика, прерывистый газообмен, стандартная скорость обмена