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WATER VAPOR INTAKE AND BODY WATER (3HOH) CLEARANCE
IN THE HOUSEMITE GLYCYPHAGUS DOMESTICUS

BY

H. SEETHALER, W. KNÜLLE and T. L. DEVINE

INTRODUCTION

The body water dynamics of the tyroglyphid mite Glycyphagus domesticus (De Geer) is of interest because this mite is one of the few arthropods that do not, even in the adult stage, have a tracheal system and the associated contributions to the body water dynamics. This mite does, however, absorb water from vapor of a relative humidity as low as 75 % or slightly less (Seethaler, 1974).

The effective distribution of water in the body and the kinetics of supply and loss processes were established, and rate constants were then determined for water loss to dry air at each of several temperatures, and with different degrees of air turbulence, and to air of 15°C at each of several relative humidities.

METHODS

Mites were reared on baker's yeast in 75 % r.h. at 15°C. Cultures were isolated by setting the trays in liquid paraffin within a larger closed container. Females having 18 to 22 μg fresh weight, containing 15 to 18 μg of water, were selected for experiments, and cleaned with soft camel-hair brushes. Groups of 10 to 15 individuals were placed without food in a cage of glass tubing closed at either end with aluminum wire gauze. These were held for 96 hours at 15°C in 98 % r.h. prior to tests in dry air, or in 95 % r.h. 3HOH before tests of water supply and loss rates. During this time egestion, egg laying and body water turnover were essentially completed while 5 to 6 μg of solids were cleared from the body. The concentration of 3HOH in the saturated solution of KNO₃ was adjusted to result in some 1 000 cpm/individual at the end of exposure. Adult mites survived for two weeks while fasting in these conditions; the period is thought to be limited by their stored energy reserves.

For tests of water supply and loss, each of 50 to 80 3HOH labelled mites were placed in a cage of the type used in labelling. No anesthetic was used with these mites. The test animals were then exposed to a test atmosphere in 800 ml glass jars that also contained a large volume of a saturated salt solution which maintained the desired relative humidity (as tabulated by

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2. Institut für Angewandte Zoologie, Freie Universität Berlin, Haderslebener Str. 9, D 1000 Berlin 41.

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WINSTON & BATES, 1960) and absorbed the $^3\text{HOOH}$ cleared from the mites. Air in the chamber was stirred slowly to speed the equilibration of relative humidity and the removal of $^3\text{HOOH}$ from the cages. Effective removal of the cleared tritium was established in that an unlabelled mite held in a cage with a labelled mite acquired not the slightest trace of tritium. The test chambers were maintained in an incubator to within 1°C of the desired temperature. After each of several periods of exposure, 5 to 10 mites were removed and the surviving individuals were each weighed to ± 0.1 µg. Essentially all of the body water and tritium were extracted by placing the body in 1 ml methanol in a liquid scintillation counting vial for 4 days. The body was then removed (with the loss of less than 1% of the tritium), dried, and weighed again. The

![Graph](image-url)
final weight did not differ appreciably from that of vacuum dried replicate individuals. Scintillator solution was added to the methanol in each vial and the tritium was assayed. The counting characteristics were so uniform among samples that count rates could be compared directly (16 cpm background and 0.38 counts/disintegration).

Tests of weight loss to dry air differed in that unlabelled individuals were used and that the mites surviving test exposure were weighed in a group, rather than individually. Vacuum dry weight was determined for many of these. Compressed air was directed through a series of three flasks of silica-gel and then over the test animals. Test cages were constructed by drilling holes of 5 mm diameter in a plexiglass plate 2 mm thick and closing these with aluminum wire gauze which had about 50% open space. The average velocity of the air stream was calculated from the measured volume flow and the area of flow through the cages. Temperature and relative humidity were monitored with a "Humitemp" meter (Phys-Chem Research Co.) and continuously recorded.

Because the mites selected for tests were of such uniform size, the amounts of water and tritium could be compared directly. Values of individual tritium content, or in general terms, the displacement of tritium content from the steady-state value approached, were plotted on a logarithmic scale against a linear scale of time, as is the general approach to the analysis of turnover and variation in open material systems (Crank, 1964; Shipley & Clark, 1972). The time dependence of body water mass was analyzed in a similar manner. The dynamic characteristics and arguments for their analysis are readily established from the test data.

RESULTS

For each of several test conditions, even in the non-steady-state, the graph of the body tritium content (A) on a logarithmic scale against time was a straight line (Eq. 1) from shortly after the beginning of test exposure; virtually all of the tritium was subject to clearance (A∞ = 0). The intercepts of regression on data according to Eq. 1b for each of 10 tests at 15°C were an average 0.99 of the observed initial values; evidently the rates of the tritium clearance processes adjusted within an hour to the test conditions, after which a constant fraction \( k = dA/A \, dt \) of the remaining tritium cleared each hour (Eq. 2). That each tritium atom had equal probability per hour \( k \) of leaving the body indicates a single well-mixed compartment of body water (i.e. of methanol extractable tritium and water).

\[
(A-A_\infty) = (A_0-A_\infty) \, e^{-kt} \quad 1a
\]

or

\[
\ln (A-A_\infty) = \ln (A_0-A_\infty) - kt \quad 1b
\]

\[
\frac{d}{dt} \ln A = \frac{dA}{A} \, dt = -k \quad \text{where } A_\infty = 0 \quad 2
\]

\[
(m-m_\infty) = (m_0-m_\infty) \, e^{-kt} \quad 3a
\]

or

\[
\ln (m-m_\infty) = \ln (m_0-m_\infty) - kt \quad 3b
\]

\[
\frac{d}{dt} \ln (m-m_\infty) = \frac{dm}{(m-m_\infty)} \, dt = -k \quad 4
\]

\[
m_+ = k \, m_\infty \quad 5
\]
The integrity of the tracer molecule ($^3$HOH) and the rates of tracer ($^3$H) transport and reaction relative to those of the traced material (H$_2$O) were established by comparing the time dependence of the displacement in amount of tracer from its steady-state value (A-A$_m$) to that of the body water mass (m-m$_\infty$). Such data from a system in the non-steady-state reflect the kinetics of the rate processes operating, as well as the distribution and mixing of tracer and material within the body. During exposure to dry air, the mean values of water mass and tritium content of the mites decreased at quite the same fractional rate (Eq's. 2 & 4) among samples taken at intervals of several hours. The lethal limit of water loss, the ""water reserves"", was consistently one-half of the initial mass of body water, whatever the test conditions. A steady-state value of body water mass (m$_\infty$) could be determined by inspection to fit Eq. 3b or by regression of m vs $e^{kt}$ according to Eq. 3a with values of $e^{kt}$ from tritium data; the remaining displacement of body water mass (m-m$_\infty$) declined in close parallel to that of tritium, and after a few hours in test conditions these declined by quite the same fraction each hour (k). Evidently the tritium absorbed by the mites from $^3$HOH vapor is an accurate tracer of body water turnover. The processes that contribute to water supply, as well as those of water and $^3$HOH clearance, adjusted rapidly to ambient conditions and then did not vary in time, because the regression intercepts of body water mass were an average of 1.02 of the observed initial values for 8 tests in dry air at 15°C and 1.00 for 5 tests in dry air at different temperatures. There was certainly no physiological regulation of water loss with respect to declining water reserves. The time dependence observed is typical of diffusion between a body that is small or has a rate limiting surface and physical surroundings that are maintained constant in time (Crank, 1964). As may be recognized in the derivative of the mass equation with respect to time (Eq. 4), this time dependence could result from a supply of water molecules at a constant rate (m$_+ = k$ m$_\infty$) concurrent with a clearance of body water at a differential rate (km). The rate constant for a change in the tracer content of the body (k) would also reflect any incorporation of tritium from water into other tissue components as well as any subsequent production from these labelled components of $^3$HOH or other methanol soluble labelled materials; these clearly involved little tritium and slow rates of turnover compared to the $^3$HOH in body water. The value of k, then, is essentially that of body water clearance. The value of the constant rate term (m$_+$) is the sum of the water intake from surroundings, the small rate of metabolic water production, and that of any processes having rates that do not vary with changes in body water mass (conceivably secretion or excretion). The latter, zero-order components of water loss would not alter the time dependence of the body water mass unless their rates exceed those of the supply processes; they are difficult to detect in less than very precise tracer data unless their rates are significant in comparison to those of the differential processes, but evidence of such a process was recognized in the variation of m$_+$ with relative humidity.

In tests at 15°C, clearance rate constants ranged from 1.6 to 2.4 %/h in relative humidity from 0 to 70 %, but then increased toward 6 %/h in saturated vapor (Fig. 2). The steady-state mass of body water (m$_\infty$ in Eq. 3a) increased rather linearly with r.h. from — 3.5 µg in dry air to 4.5 µg in 79 % r.h.; these data extrapolate to 10 µg/h in saturated vapor, but the values actually increased to 15 µg in 80 % r.h. and toward 18 µg in saturated vapor, no doubt as a result of physiological absorption of vapor. Values of the constant rate term (m$_+$) calculated from these data (Eq. 5) increased from — 0.056 µg/h in dry air toward 0.15 µg/h in saturated vapor, but in fact increased rather linearly from 0.1 µg/h in 70 % r.h. to 1.0 µg/h in saturated vapor. The values of m$_+$ and m$_\infty$ in dry air are identified with the sum of metabolic water production and those loss processes having rates independent of mass and time (zero-order). The rate of metabolic water production can only be estimated as a zero-order process with a rate equal to 4 % of the
FIG. 2. — From tests of $^2$HOH labelled mites in air of 15°C at each of several values of relative humidity, the rate constants for tritium clearance ($k$), steady-state mass of body water approached ($m_\infty$), zero-order "supply" of water molecules ($\dot{m}_+$), and the "conductance ratio".
normal water supply, as in other arthropods of stored food products (Devine, 1978). The opposing, zero-order removal rates would then be as much as 0.1 µg/h or 0.6 %/h of 16 µg. Outward diffusion would then be estimated at 1.4 %/h of the total 2 %/h loss in air of low r.h. The increase of mω with r.h. over low to moderate relative humidities (Fig. 2) may be supposed to result from inward diffusion of water molecules; this component increased in proportion to both the rate constant for outward diffusion and the ambient r.h., from 0 in dry air to 0.16 µg/h in 70 % r.h. The process by which clearance increases with higher r.h. has not been determined; secretion and subsequent ingestion may be suspected since this is found in ticks (Rudolph & Knüll, 1974, 1978) and inferred for other Acaridei (Wharton & Furumizo, 1977; Wharton, 1978).

Vapor entry at a proportional rate would range from 0.32 µg/h in 80 % r.h. to 1.0 µg/h in saturated vapor, and higher as the activity of water in this component of clearance is reduced by the vapor absorbing mechanism. These rates of vapor entry, added to metabolic production and zero-order clearance, amount to water supply rates of 0.26 and 0.94 µg/h at 80 % and 100 % r.h. respectively; their differences from the observed values of mω estimate the rates of physiological absorption of vapor at from 0.14 µg/h in 80 % r.h. to 0.06 µg/h in saturated vapor. These values change considerably with the assumptions made for their resolution.

Movements of air over the body surface had no effect on the rate of body water clearance to dry air; the rate constants were 1.8 to 2.7 %/h in no appreciable correlation to flow of 0 to 10 liters/minute, or corresponding mean velocity of from 0 to 1.7 m/sec. This result is consistent with the diffusion of water between the body and the surroundings at a rate that is limited of the surface rather than by the surrounding air (Ramsay, 1935; Wigglesworth, 1945; Beament, 1961).

The increase with temperature in the rate constant for clearance to dry air was consistent with an Arrhenius coefficient of 13 kcal/mole in temperature below 25°C and 36 kcal/mole in higher temperatures; the Arrhenius coefficient for tabled values of vapor pressure is 10.6 kcal/mole. A temperature of 35°C or greater was lethal before substantial water loss occurred.

**DISCUSSION**

Isotopically labelled water affords evaluation of the body water budget and its dynamic characteristics in greater and more fundamental detail than has been accomplished by conventional analysis of weight change data.

The integrity of the tracer molecule and the similarity of its rate of transport relative to that of the unlabelled molecule was demonstrated again in *G. domesticus*, as for *L. echidnina* (Devine & Wharton, 1973) and *D. variabilis* (Knüll & Devine, 1972). But movement of the ³H in forms other than water or at a different rate than H₂O remains plausible and must be determined in each investigation.

The turnover and changes in amount of body water in *G. domesticus* were those of a single, well-mixed compartment, as was reported for other mites. The observed tolerance of *G. domesticus* to the loss of one-half the normal amount of its body water is not remarkable among terrestrial arthropods.

Both zero-order and first-order processes of body water clearance were identified in *G. domesticus* where only first-order processes were found to be significant in the other species, and only the dust mites had two distinct first-order components of body water clearance (Arlian & Wharton, 1974).
That in desiccating conditions the rate of water loss declines in a simple constant proportion to the remaining amount of body water (as RAMSAY noted in 1935) is a characteristic of diffusion from a body at a rate limited at the surface. Where the passage of water through the integumental water retaining devices is much slower than that through the surrounding air, it is not surprising that wind or air turbulence has little effect on the rate (RAMSAY, 1935; WIGGLESWORTH, 1945). The characteristic time dependence of water mass in such a system must be recognized and properly taken into account. It is not true that changes in the amount of water should proceed at a constant rate described by Ficks’ Law of diffusion; that consideration does not lead to a model of acceptable accuracy for the data reported, and physiological regulation
The variation of body water clearance (k) with relative humidity over the higher range is more pronounced in the data of *G. domesticus* than in data reported for other mites (reviewed by Wharton & Richards, 1978). This is conceivably related to the lower relative humidity, i.e. activity of water vapor, above which physiological absorption of vapor can proceed. Some clearance of body water through the vapor absorption mechanism would account for the increase of water loss rates with relative humidity that was not in constant proportion to the vapor pressure deficit. But it has not been excluded that the diffusion coefficient of water through the integumental barriers varies with its concentration, as occurs in numerous materials (Crank, 1964). It is particularly significant that this increase of body water clearance occurs in a species that has no tracheal system.

**SUMMARY**

The dynamics of body water in the fasting adult *G. domesticus* was that of a single compartment from which water was cleared by zero-order and first-order processes while water was supplied at a constant day-to-day rate. The clearance rate was not affected by air turbulence nor was it regulated with respect to the remaining body water reserve. Clearance rates increased with temperature according to the Arrhenius relation with a coefficient of 13 kcal/mole below 25°C and 36 kcal/mole at higher temperatures. In air of 15°C the first-order clearance increased with relative humidity towards 5.4 %/h in saturated vapor from 2 %/h in 70 % or lower r.h. while the zero-order clearance was at least 0.06 µg/h; water vapor diffused into the body at up to 0.23 µg/h in proportion to both the rate constant of first-order clearance and the relative humidity, and water was physiologically absorbed from air of 75 % or greater r.h. at mean rates from 0.14 µg/h in 80 % r.h. to 0.06 µg/h in saturated vapor while maintaining a steady-state mass. The zero-order clearance is the only feature that differs remarkably from the body water dynamics reported for mites that have a tracheal system, where *G. domesticus* does not.

**ZUSAMMENFASSUNG**

Die Dynamik des Körperwassers hungerner Adulter von *G. domesticus* entspricht der eines einzelnen Kompartments von dem Wasser durch Prozesse 0. Ordnung und 1. Ordnung abgegeben wird, während die Wasserzufuhr mit einer pro Tag konstanten Rate erfolgt. Die Clearance Rate wurde weder durch Luftbewegung noch in Beziehung zu den im Körper verbleibenden Wasserreserven reguliert. Die Clearance Rate stieg mit der Temperatur in Übereinstimmung mit der Arrhenius Beziehung mit einem Koeffizienten von 13 kcal/Mol unterhalb von 25°C und 36 kcal/Mol bei höheren Temperaturen. In Luft von 15°C nahm die Clearance Rate 1. Ordnung mit der relativen Feuchte zu, von 2 %/h in 70 % r.F. oder darunter auf 5.4 %/h in wasserdampfgesättigter Luft, während die Clearance Rate 0. Ordnung wenigstens 0.06 µg/h betrug. Wasserdampf diffundierte in den Körper bis zu 0.23 µg/h in Proportion sowohl zu der Ratenkonstante der Clearance 1. Ordnung als auch der relativen Feuchte, und Wasser wurde physiologisch aus der Luft mit einer r.F. von etwa 75 % oder höher mit durchschnittlichen Rates von 0.14 µg/h in 80 % r.F. bis zu 0.06 µg/h in wasserdampfgesättigter Luft bei Aufrechterhaltung einer steady-state Wassermasse aufgenommen. Die Clearance 0. Ordnung bei *G. domesticus*, die kein Tracheensystem besitzt, ist das einzige Charakteristikum, das wesentlich von der Körperwasser­dynamik von Milben mit einem Tracheensystem abweicht.
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