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UPTAKE, EXCRETION AND RESPIRATION OF SUCROSE AND AMINO ACIDS BY THE PEA APHID *ACYRTHOSIPHON PISUM*

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Summary

Ingestion, excretion and respiration in aphids were studied using artificial diets labelled with radioactive sucrose or amino acids. The rate of ingestion of a 25 % w/v sucrose diet was 12.4 nl mg^{-1} h^{-1} and the honeydew excretion rate was 5.3 nl mg^{-1} h^{-1}, about 43 % of the volume ingested during the same period. The concentration of sugars in the honeydew was equivalent to 0.53 mol l^{-1} sucrose and 69 % of the sucrose ingested was assimilated. The amino acid concentration of honeydew was 24.6 mmol l^{-1} and 94 % of the ingested amino acids were assimilated. Respiration was measured by collecting respired $^{14}CO_2$ using a chamber which allowed the aphids to feed during the experiments on ^{14}C-labelled artificial diets. While feeding on a 25 % w/v sucrose diet, sucrose was respired at the rate of 1.32×10^{-6} mmol mg^{-1} h^{-1}, equivalent to 0.354 μl O_2 mg^{-1} h^{-1}, which was 14.6 % of the rate of ingestion. There was no evidence that reducing the dietary sucrose concentration from 22 to 11 % w/v had any effect on the rate at which sucrose was respired. Amino acids were respired at a rate of 0.14×10^{-6} mmol mg^{-1} h^{-1}, which was 6.4 % of the rate of ingestion. Dietary sucrose was oxidised in preference to amino acids.

Key words: *Acyrthosiphon pisum*, amino acids, aphid, excretion rate, feeding rate, respiration, sucrose.

Introduction

Aphids have piercing mouthparts (stylets) with which they are able to feed by taking sap directly from the sieve tubes of plants. Amino acids are extracted and excess sugars and water are excreted in the honeydew. The sucrose concentration of phloem sap varies between 0.5 and 30 % w/v (Auclair, 1963; Canny, 1973; Dixon, 1975; Srivastava, 1987), depending on species, plant parts, time of day and season (Moorby, 1981). Amino acid concentrations are similarly very variable and, although high levels (4.5–26.7 % w/v) have been recorded (Barlow and Randolph, 1978; Weibull, 1988), they usually lie below 1 % w/v (Zimmerman, 1960; Auclair, 1963). It is the presence of large quantities of sucrose and the osmotic problems this entails that have been perceived as an important disadvantage to feeding on phloem sap (Kennedy and Fosbrooke, 1973; Dixon, 1975). In artificial diets, the sucrose concentration is often higher than that normally encountered in plants. The pea aphid *Acyrthosiphon pisum*, for example, is thought to perform best on an artificial diet containing 35 % w/v sucrose (Srivastava and Auclair, 1971).

The overriding dominance of sucrose in phloem sap and synthetic diets makes it the obvious candidate for the main respiratory substrate. It has, however, been suggested that aphids utilise amino acids as their predominant energy source (Llewellyn, 1972; Dixon, 1973; Llewellyn and Qureshi, 1979; Van Hook *et al.* 1980). Ehrhardt (1962), however, estimated a respiratory quotient (RQ) of 1.0 for *Megoura viciae* taken directly from the food plant, as did Kunkel and Hertel (1975) for *Myzus persicae* feeding on an artificial diet, suggesting that under the conditions of their experiments carbohydrate was being respired.

A. pisum appears to have a high sucrose demand, producing a relatively dilute honeydew (Mittler, 1987). Mittler and Meikle (1991) found that *A. pisum* retained as much as 94–97, 66 or 36 % of the dietary sucrose when feeding on synthetic diets containing 10, 30 or 40 % w/v sucrose respectively. Randolph *et al.* (1975) claimed that an average of 34 % of the ingested energy was used in respiration by adult *A. pisum* apterae, feeding on peas, with a peak of 53 % being used at the onset of reproduction. Indeed, the energy released as a consequence of respiration during the life cycle of *A. pisum* was at least twice that of seven other species listed by Llewellyn (1987).

Aphids spend the greater part of their time feeding, and free access to food is, therefore, desirable when attempting to measure their respiration rate. Fluctuations in respiration and possibly in the RQ can be expected when aphids are deprived of food or generally disturbed by the use of conventional respirometers, and the values may not be representative of aphids feeding on the host plant. The highly specialised nature of the diet, however, makes it very difficult to create the

necessary conditions which would allow feeding, and in few previous studies (see Table 2) has any attempt been made to provide food or to correct for the effect of removing the aphids from their host. Van Hook *et al.* (1980) placed aphids on small pieces of leaf and subtracted the oxygen consumption obtained from similar pieces of leaf to obtain the respiration rate of the aphid. They could find no difference between the oxygen consumption of aphids on pieces of leaf or damp filter paper and used the latter during their experiments. Llewellyn and Hargreaves (1984) measured the respiration of *Macrosiphum euphorbiae* on an artificial diet developed specially for *Dysaphis devecta* and, although the aphids had been offered the diet for approximately 12 h before the experiment, it is unlikely that, after such a short time, they would have been feeding normally on their own diet, let alone one formulated for another species. Kunkel and Hertel (1975) measured the oxygen consumption of aphids, *Myzus persicae*, which had been reared on a synthetic diet and were given access to food during the experiments.

In the present study, the ingestion, excretion and respiration of sugars and amino acids by *A. pisum*, continuously feeding on artificial diets, has been investigated using radioactively labelled substrates. For the first time, it has been possible to relate quantitatively these processes in an aphid.

Materials and methods

Diet and rearing of aphids

Experiments were carried out on the pea aphid *Acyrthosiphon pisum* Harris. It was found that adults taken directly from plants fed only intermittently and appeared very restless when offered an artificial diet, often dying soon after removal from the plant. For this reason, diet-reared aphids were chosen for all the experiments. The aphids used throughout were pre-reproductive, apterous adults, between 11 and 13 days old, which had been reared from birth on an artificial diet containing 25 % w/v (0.73 mol l^{-1}) sucrose, and kept at 20 °C, 16 h light:8 h dark. The mean mass of adult apterae reared on artificial diet was 1.76±0.04 mg (S.E.M., *N*=32). The diet was *Diet a* described by Kunkel (1977) after Mittler and Koski (1976). The total amino acid concentration in the diet was 176 mmol l^{-1}. Filtered diet (0.2 μm Acrodisc syringe filter; Gelman Sciences, USA) was presented to aphids in sachets made by stretching two layers of Nescofilm (Nippon Shoji Kaisha Ltd, Osaka, Japan) across the end of a small section of Perspex tubing. The Nescofilm was sterilised in absolute ethanol before use and the preparation of sachets was carried out in a clean-air station. Adult aphids reared on bean (*Vicia faba*) at 15 °C, 16 h light:8 h dark, were placed onto new diet sachets for approximately 24 h and the resultant offspring, which appeared quite settled, reared to adulthood. Sachets were renewed every 3 days. During experiments, the diet was labelled with [U-^{14}C]sucrose (Amersham International; CFB146), giving an activity in the diet of approximately 0.8 kBq μl^{-1} or with U-^{14}C-labelled amino acids mixture (Amersham International; CFB25) to give a similar activity.

Uptake and excretion rates

Feeding and excretion rates were measured in groups of up to five aphids fed for 24 h on diets labelled with radioactive amino acids, under the same environmental conditions as those under which they were reared (20 °C and a 16 h day length). The honeydew was collected on filter paper discs placed directly below the feeding aphids. At the end of the feeding period, the aphids were crushed in 1 ml of NCS tissue solubilizer (Amersham International) and, after steeping for at least 24 h, when only decolorised cuticle remained undissolved, 10 ml of Picofluor-15 scintillation solution (Packard Instrument Company) was added and the activity in counts per minute (cts min^{-1}) of the sample measured by β-scintillation counting (Packard Tricarb 300). The filter paper discs holding the honeydew were treated in exactly the same way. The level of activity in the diet was estimated from three 1 μl samples in 10 ml of scintillation solution and 1 ml of tissue solubilizer. The background sample consisted of an unlabelled aphid dissolved in 1 ml of tissue solubilizer and 10 ml of scintillation solution. The inclusion of a relatively large proportion of tissue solvent meant that differences in quenching characteristics between samples were trivial. To calculate the volume of diet that had been ingested, the total cts min^{-1}, of aphids plus honeydew, was divided by the cts min^{-1} μl^{-1} of the diet. A correction was made by estimating the quantity of amino acids lost by respiration during the time of the experiment. The rate of excretion of honeydew could not be determined directly with sufficient accuracy by collection of honeydew samples owing to problems of collection and evaporation. However, the cts min^{-1} μl^{-1} honeydew could be determined. The volume of honeydew is then the cts min^{-1} excreted divided by the cts min^{-1} μl^{-1} honeydew.

Concentration of amino acids and sugars in honeydew

Honeydew was collected from groups of adult apterae during the last 6 h of a 72 h feeding period on 25 % w/v sucrose diet containing ^{14}C-labelled amino acids. To minimise evaporation, the honeydew was allowed to fall into a Repelcote (Hopkin and Williams, UK) -treated watch glass containing 1 ml of hexadecane. Sample volume was estimated by measuring the distance it flowed up a 1 μl microcapillary (Microcap). Samples, together with approximately 200 μl of water which had been used to wash out the receptacle, were added to 10 ml of scintillation solution and counted. Samples of the diet were also counted. The concentration of amino acids was then calculated as (cts min^{-1} μl^{-1} honeydew)/(cts min^{-1} mol^{-1} amino acids). The concentration of sugars in the honeydew, expressed in sucrose equivalents, was determined in a similar way after feeding on 25 % w/v sucrose diet containing ^{14}C-labelled sucrose.

Respiration rate

The respiration rate was determined by collecting the $^{14}CO_2$ produced by aphids feeding on radioactively labelled diet. Rilling and Steffan (1972) have used this method to study the

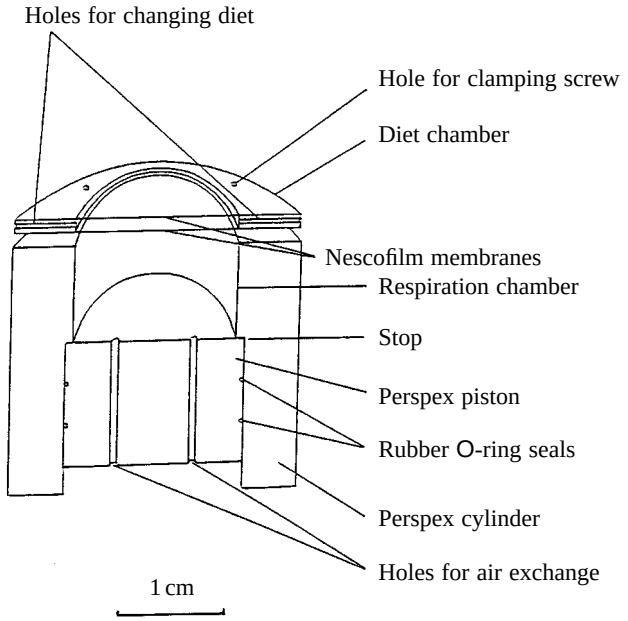

Fig. 1. A diagram of the respiration and diet chambers in half section before clamping. Scale is approximate.

CO_2 output of a phylloxerid, continuously feeding on ^{14}C-labelled sucrose. A similar method has also been used to study CO_2 output by the cockroach (Croghan *et al.* 1995; Noble-Nesbitt *et al.* 1995).

The respirometer used in the present study (Fig. 1) consisted of a small Perspex chamber sealed at the base by a Perspex piston fitting against a stop to give a volume of 1767 mm^3, and sealed at the top by the diet chamber. The diet chamber consisted of a Perspex ring, separating two layers of Nescofilm giving an approximate volume of 260 μl. The diet chamber was clamped to the top of the respiration chamber using a washer and retaining screws (not shown). The diet chamber could be filled *via* two holes drilled in the sides, parallel with the plane of the ring, using a peristaltic pump (Gilson). The same method could be used to change the diet during an experiment. Using a peristaltic pump (Gilson), air was drawn through the chamber, *via* two holes drilled in the piston, at the rate of 1 ml min^{-1}. The theoretical time constant (chamber volume/flow rate) for the chamber was 1.8 min.

In order to collect the respired $^{14}CO_2$, air drawn from the chamber was bubbled through a hypodermic needle into a mixture of 10 ml of scintillation solution and 1 ml of NCS tissue solubiliser (a highly alkaline solution) contained in a Pettenkofer tube (a slanting 10 ml glass pipette). By having two pipettes in series, it was demonstrated that the first pipette collected approximately 99.7 % of the $^{14}CO_2$. The collecting fluid could be rapidly changed during an experiment, without interrupting the flow of air through the chamber.

At the start of an experiment, three adults were put onto the Nescofilm membrane at the top of the respiration chamber, which was immediately sealed with the piston. The diet chamber was then filled with radioactively labelled diet, and the collection of $^{14}CO_2$ started. The absorbant was changed every hour and the amount of $^{14}CO_2$ taken up was determined. To replace the diet during an experiment, approximately 900 μl of fresh diet was pumped through the diet chamber. When a final mixture of half the original sucrose concentration was required, the fresh diet consisted of 450 μl of the original labelled diet plus an equal volume of unlabelled sucrose-free diet. All experiments were carried out at 20 °C, 16 h light:8 h dark.

The volume of oxygen consumed by aphids to convert sucrose to CO_2 during respiration was calculated in the following way:

moles sucrose respired = (cts min^{-1} $^{14}CO_2$)/(cts min^{-1} mol^{-1} sucrose);

moles CO_2 produced = moles sucrose respired × 12;

litres oxygen consumed = moles CO_2 × 22.4 (molar volume at STP).

This defines the respiration of sucrose.

A similar calculation was used to determine the rate of respiration of amino acids. The diet contains 20 amino acids with a total concentration of 176 mmol l^{-1}. The individual amino acids are labelled to varying degrees and it is thus difficult to make exact calculations. For the purposes of this study, it was assumed that the amino acids in the diet were labelled equally or were assimilated, occurred in the haemolymph and honeydew and respired in the same proportions as they are present in the diet. Then:

moles amino acids respired = (cts min^{-1} $^{14}CO_2$)/(cts min^{-1} mol^{-1} amino acids).

The data are expressed as the mean ± S.E.M. Rates are given per aphid or per milligram of aphid.

Results

Uptake and excretion

The measured feeding rate was 0.52±0.03 μl $aphid^{-1}$ day^{-1} (N=7) or 12.4±0.79 nl mg^{-1} h^{-1}. This includes the addition of 0.8 nl mg^{-1} h^{-1} which was the volume of diet containing the 0.14×10^{-6} mmol amino acids mg^{-1} h^{-1} respired during the same period (see below). Some amino acids undoubtedly do occur in aphid saliva (Miles, 1987), but the very small amounts likely to be involved were not considered to be of significance for the purposes of this experiment. When aphids fed on artificial diet containing ^{14}C-labelled sucrose were transferred to unlabelled diet for 3 h, no radioactivity was found to be regurgitated.

The amino acid contents of two samples of honeydew (each obtained from several aphids) were 24.7 mmol l^{-1} and 24.4 mmol l^{-1}. There is evidence to show that proteins very seldom occur in honeydew (Auclair, 1963; Klingauf, 1987). The mean rate of honeydew excretion was 0.22±0.03 μl $aphid^{-1}$ day^{-1} (N=7) or 5.3±0.5 nl mg^{-1} h^{-1}, which was about 43 % of the volume ingested during the same

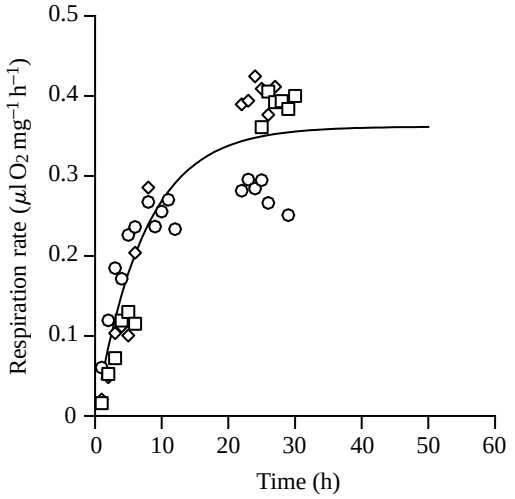

Fig. 2. The combined results of three experiments (indicated by different symbols) measuring the rate of respiration of [U-^{14}C]sucrose by groups of three adult *Acyrthosiphon pisum* apterae, feeding on artificial diet containing 25 % w/v sucrose. The results are calculated as equivalent O_2 uptake. The line was fitted to the data of the three experiments using equation 1.

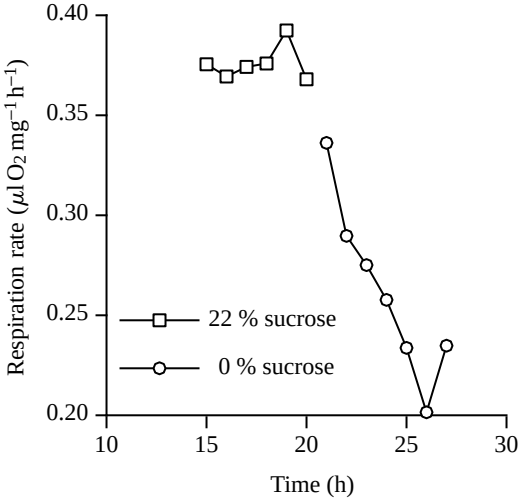

Fig. 3. The rate of respiration of sucrose by a group of three adult *Acyrthosiphon pisum* apterae, feeding on artificial diet which was changed from 22 to 0 % w/v sucrose. The results are calculated as equivalent O_2 uptake.

period. The rate at which amino acids were excreted was 0.13×10^{-6} mmol mg^{-1} h^{-1}, which was 6 % of the amino acids ingested in the same period and indicates that 94 % were assimilated.

The concentration of sugars in the honeydew, expressed as sucrose equivalent, was 0.53±0.01 mol l^{-1} (*N*=4). The rate of excretion, expressed as sucrose, was 2.81×10^{-6} mmol mg^{-1} h^{-1}, which was 31 % of the ingested sucrose in the same period and indicates that 69 % was assimilated.

Sucrose and amino acid respiration

From three experiments, in which the diet contained 25 % w/v sucrose, it is apparent that sucrose was rapidly assimilated by the aphids and utilised as a source of energy in respiration (Fig. 2). The rate of production of $^{14}CO_2$ rapidly increased during the first few hours of feeding, indicating the labelling of the metabolic pool, before it levelled to a more or less constant rate that was used to calculate the respiration rate. The mean rate at which adult apterae, feeding on a 25 % w/v sucrose diet, utilised sucrose for respiration was 1.317×10^{-6} ± 0.15×10^{-6} mmol mg^{-1} h^{-1}. This corresponds to 0.354 ±0.04 μl O_2 mg^{-1} h^{-1}.

Fig. 3 shows the effect of depriving aphids of sucrose on the rate of respiration of sucrose. From the time at which sucrose was excluded from the diet, there was a rapid fall in the rate of output of $^{14}CO_2$ and the calculated rate of oxygen consumption dropped from 0.376 to 0.202 μl mg^{-1} h^{-1} after 6 h, a fall of 46.3 %. Three experiments were performed (Fig. 4), during which a diet (22 % sucrose w/v) was exchanged for one of half the original sucrose concentration but at the same specific activity. The respiration rates were very variable, with no evidence of any effect of the dietary sucrose concentration.

The respirometer was also used for measuring the rate of respiration of amino acids by collecting $^{14}CO_2$ from aphids feeding on a diet containing ^{14}C-labelled amino acids. Fig. 5 shows that aphids can utilise amino acids as a source of energy. The rate of respiration of amino acids after 24 h is 0.14×10^{-6} ± 0.02×10^{-6} mmol mg^{-1} h^{-1} (*N*=3).

Discussion

Several authors have measured the feeding rate of adult *A. pisum* apterae on various artificial diets (Table 1) and, although

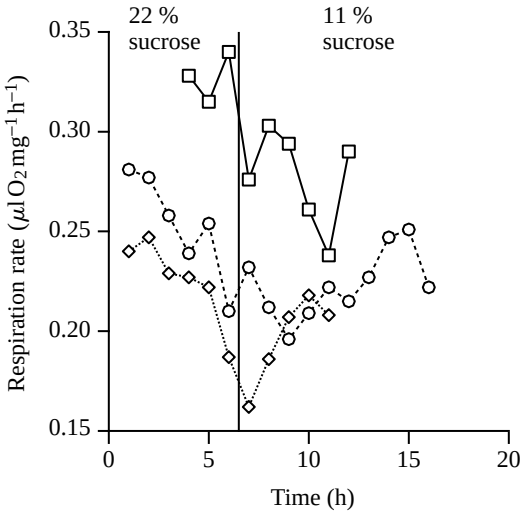

Fig. 4. The effect of the concentration of sucrose in the diet on the respiration of sucrose by adult *Acyrthosiphon pisum* apterae. During each of three experiments (indicated by different symbols), the concentration of sucrose in the diet was halved from 22 to 11 % w/v. The results are calculated as equivalent O_2 uptake. The aphids had been feeding on labelled 22 % sucrose diet for approximately 16 h before sampling began at time zero.

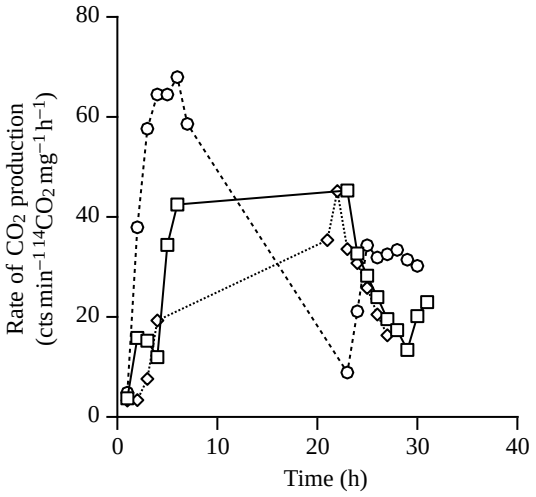

Fig. 5. The rate of production of $^{14}CO_2$ by three groups of three adult *Acyrthosiphon pisum* apterae, feeding on artificial diet containing 25 % w/v sucrose and U-^{14}C-labelled amino acids. The results of three experiments (indicated by different symbols) are presented.

the rate of ingestion obtained in this study is in the same range, it should be remembered that diet composition is known to influence ingestion rate (Mittler, 1967; Srivastava and Auclair, 1971, 1974). Nevertheless, the use of radioactively labelled amino acids, with a correction for respiratory loss, is a useful means of assessing diet uptake. Unlike inulin (Wright *et al.* 1985), for example, amino acids are a part of the normal diet and 94 % of the amino acids are assimilated, with relatively small losses by respiration and probably insignificant losses in the saliva. The technique could, however, be improved if, for instance, a single labelled amino acid that is almost entirely retained by the aphid was used.

Auclair (1965) measured the honeydew excretion rate of apterous adult *A. pisum* as 0.3 μl aphid^{-1} day^{-1}, when fed a synthetic diet containing 35 % w/v sucrose. Mittler and Meikle (1991) estimated the rate on a 35 % w/v sucrose diet to be about 0.36 μl aphid^{-1} day^{-1} and about 0.65 μl aphid^{-1} day^{-1} on a 25 % w/v sucrose diet. The rate of excretion, like that of uptake, is greatly affected by environmental conditions and the composition of the diet (Mittler, 1958; Mittler and Meikle, 1991; Auclair, 1963) and one might, therefore, expect a good deal of variation between the published figures. It should, nevertheless, be remembered that the excretion rate measured in the present study (0.22 μl aphid^{-1} day^{-1}) has been calculated using an estimate of the amino acid concentration of honeydew, a figure which might also be expected to vary. The 57 % difference in volume between ingestion and excretion must represent uptake from the gut lumen, balancing loss by evaporation from the surface of the aphid and from the tracheal system. There is a similar difference (approximately 60 %) between the uptake rate estimated by Srivastava and Auclair (1974) (see Table 1) and the excretion rate measured by Auclair (1965) on similar diets. Thus, it is invalid to use excretion rate to estimate ingestion rate.

Adult apterae of *A. pisum* were found to utilise O_2 for the respiration of sucrose at the rate of 0.354±0.04 μl mg^{-1} h^{-1}, while feeding on artificial diet containing 25 % w/v sucrose. This figure is lower than most values presented in Table 2, although it is comparable with values for the similarly sized *M. viciae*. As sucrose is assimilated from the gut, it enters a carbon pool in the body of the aphid, from which it is metabolised and ultimately released as CO_2. As ^{14}C enters the aphid, it appears as $^{14}CO_2$ in increasing amounts until the entire pool is labelled. For a one-compartment model, the rate of production of $^{14}CO_2$ (Q_t) would be defined by the function:

$$Q_t = Q_\infty(1 - e^{-t/\tau}), \quad (1)$$

where Q_∞ is the final rate of $^{14}CO_2$ production, expressed as μl O_2 mg^{-1} h^{-1}, t is time (h) and τ is the time constant or turnover time (h) of the pool. The curve in Fig. 2 represents the combined results of the three experiments, where the sucrose concentration in the diet was 25 % w/v. The model fits the data well, with a time constant of 7.35 h. The size of the carbon pool in terms of sucrose, can be calculated from

$$A = Q\tau, \quad (2)$$

where A is the pool size (mol sucrose mg^{-1}) and Q is the rate of sucrose respiration (mol sucrose mg^{-1} h^{-1}). The pool size for an aphid feeding on a 25 % w/v sucrose diet was 4.37×10^{-3} mg sucrose equivalent mg^{-1}, which, at a rate of utilisation through respiration of 0.45×10^{-3} mg mg^{-1} h^{-1}, is equivalent to a 10 h supply. When the dietary sucrose was reduced to zero, the sucrose respiration fell rapidly, as expected (Fig. 3).

Table 1. *Estimates of the feeding rate of adult* Acyrthosiphon pisum *apterae on artificial diets*

Diet (% w/v)		Temperature	Volume ingested	
Amino acids	Sucrose	(°C)	(μl aphid^{-1} day^{-1})	Reference
2.5	35	21	0.74	Srivastava and Auclair (1974)
0.0	35	21	0.15	Srivastava and Auclair (1974)
3.6	29.2	21	≈0.45	Rahbe *et al.* (1988)
*	≈29	15	0.71–0.86	Sasaki *et al.* (1991)
2.5	25	20	0.52	Present study

*Value not given.

Table 2. *The respiration rates of various species of aphid*

Species	Morphology	RQ	Respiration rate (μl O_2 mg^{-1} h^{-1})	Temperature °C	Reference
Acyrthosiphon pisum	Apterae?	1.0	1.83*	20	Randolph *et al*. (1975)
	Apterae		0.354	20	Present study
Drepanosiphum platanoides	Alatae		2.21	18	
			2.54†	20	Dixon (1973)
Eucallipterus tiliae			2.21	15	
	Alatae		3.12†	20	Dixon (1973)
Macrosiphum liriodendri	Apterae	0.82	1.17*	20	Van Hook *et al*. (1980)
Megoura viciae	Apterae?	1.0	1.63	22	Ehrhardt (1962)
			0.407†	20	Ehrhardt (1962)
M. viciae	Apterae?	0.82	0.349		Llewellyn and Qureshi (1979)
Myzus persicae	Apterae		1.84	20	Kunkel and Hertel (1975)

*Converted from dry mass to live mass assuming dry mass is 20 % of wet mass (Brough, 1987).
†Oxygen consumption recalculated for 20 °C using Q_{10} = 2 (Erhardt, 1962; Van Hook *et al*. 1980)
RQ, respiratory quotient.

There was no evidence that reducing the dietary sucrose concentration from 22 % to 11 % w/v had any effect on the rate at which sucrose was respired (Fig. 4). Concentrations above 3.6 % w/v sucrose will contain more than is required for respiration alone. However, the level at which sucrose ceases to be the dominant energy source remains to be determined. Many of the respiration rates recorded in Table 2 are higher than the rate reported here. However, the present results were obtained using a respirometer that enabled the aphids to feed continuously, under conditions that must be more representative of the natural situation. If the higher respiration rates were correct, it would suggest that respiration of sucrose plays a very significant role in managing the osmotic problems resulting from the high sucrose concentration of the diet. However, the results reported here indicate that the rate of oxidation of sucrose is not greatly affected by changes in the sucrose concentration of the diet and that, on a 25 % w/v sucrose diet, only 14.6 % of the ingested sucrose is oxidised.

For an ingestion rate of 12.4 nl mg^{-1} h^{-1}, the rate of amino acid ingestion is 2.18×10^{-6} mmol mg^{-1} h^{-1} and the proportion respired is 6.4 %. This can be compared with the proportion for sucrose, which is 14.6 % of that ingested. A selectivity coefficient (*S*) can be defined as:

$$S = \frac{\text{moles amino acid respired}}{\text{moles amino acid in diet}} \times \frac{\text{moles sucrose in diet}}{\text{moles sucrose respired}} . \quad (3)$$

S is a measure of the degree to which amino acids are selected as the respiratory substrate in preference to sucrose. The selectivity coefficient was 0.44, showing that sucrose is preferentially utilised. If a coefficient were defined in terms of the quantities of amino acid or sucrose taken up from the gut, rather than the quantity ingested, selectivity would be even more apparent.

Ammonia and ammonium salts have been detected repeatedly in the honeydew of aphids (Lamb, 1959; Sidhu and Patton, 1970; Hussain *et al*. 1974; Whitehead *et al*. 1992), leading many (Lamb, 1959; Dixon, 1973, 1975; Kennedy and Fosbrooke, 1973) to the conclusion that aphids, like many aquatic invertebrates, excrete nitrogen in the form of ammonia. When calculating the available energy in the amino acid fraction of the diet, it was assumed, therefore, that ammonia was one of the products of respiration. Brafield and Llewellyn (1982) take the oxidation of 1 mol of amino acid to consume 4.6 mol of oxygen. From the rate of amino acid respiration of 0.14×10^{-6} mmol mg^{-1} h^{-1}, it is estimated that 0.0206×10^{-3} mg O_2 mg^{-1} h^{-1} are consumed. Assuming an oxycalorific coefficient (Brafield and Llewellyn, 1982) for protein of 13.36 J mg^{-1} O_2, when ammonia is the excretory product, this will yield 0.275×10^{-3} J. On a 25 % w/v sucrose diet, the oxidation of sucrose consumes oxygen at the rate of 0.354 μl mg^{-1} h^{-1}, which is equivalent to 0.506×10^{-3} mg O_2 mg^{-1} h^{-1}. The oxycalorific coefficient for carbohydrate is 14.76 J mg^{-1} O_2 and, therefore, 7.47×10^{-3} J are produced. This means that, in *A. pisum*, the energy produced from amino acids is only 3.6 % of the total for both substrates.

In this study on the aphid *A. pisum*, feeding on a high-sucrose diet, it has been shown that a small proportion of the ingested sucrose accounts for the bulk of the respiratory metabolism. Sucrose is preferentially used for respiration compared with amino acids, a high proportion of which are retained in the aphid body. In a subsequent paper (J. D. Rhodes, P. C. Croghan and A. F. G. Dixon, in preparation), the osmotic problems associated with the high sucrose concentration in the diet will be addressed.

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