Diffusivity of Carbon Dioxide through the Skin and Flesh of ‘Russet Burbank’ Potato Tubers

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Abstract. The diffusion coefficient of CO₂ in ‘Russet Burbank’ potato (Solanum tuberosum L.) tubers was determined under steady-state conditions at 10 and 27°C. The data showed that the skin is the main barrier to gas diffusion, with an average diffusion coefficient of 6.57 × 10⁻⁷ and 7.61 × 10⁻⁷ cm s⁻¹ at 10 and 27°C, respectively. The flesh also presents an appreciable barrier to gas diffusion. The average diffusion coefficient of CO₂ in the flesh was 2.00 × 10⁻⁴ and 2.24 × 10⁻⁴ cm s⁻¹ at 10 and 27°C, respectively. Under regular storage conditions, the tuber is well aerated and the concentration of O₂ at the center of the tuber is sufficient to maintain aerobic respiration.

The diffusion of O₂ into the internal atmosphere of potato tubers has been the subject of considerable investigation because of concerns regarding its effects on sprouting (Banks and Kays, 1988; Bründle, 1968; Burton, 1950; Woolley, 1962). The intercellular spaces of potato tubers are small (Burton, 1950; Woolley, 1962), a fact that should appreciably limit the diffusion of gases to the center of the tuber. However, it was shown previously that, at regular storage temperatures, the intercellular spaces contain sufficient O₂ concentrations because of low respiratory activity (Burton, 1950; James, 1953; Solomos and Latties, 1975). Under adverse conditions of temperature and soil moisture, however, a partial anoxic environment may prevail at the center of the tuber.

In previous work, the diffusivities of gases through the skin and flesh were determined separately (Banks and Kays, 1988; Burton, 1950; Woolley, 1962). The permeability of gases through the flesh has been carried out in tissue segments. Because of the well-known effects of wounding on the rate of O₂ uptake and the flooding of the intercellular spaces of the cut surfaces (Latties, 1978; Woolley, 1962), this method may introduce uncertainties concerning the accuracy of gas diffusivities through the flesh.

In the present work, we have estimated the diffusivity of CO₂ in the skin and flesh of ‘Russet Burbank’ potato tubers. To ascertain the validity of the results, we determined the diffusion coefficient of CO₂ at two temperatures and used the results at one temperature to calculate either respiration or internal CO₂ concentration at the second temperature.

Materials and Methods

‘Russet Burbank’ potato tubers were purchased from the local supermarket, washed, and stored at 10°C for 24 h. Tubers were selected whose geometry most closely conformed to that of a cylinder, i.e., each tuber had a diameter that was uniform along its length. Despite these precautions, however, it was not easy to find tubers with an ideal cylindrical shape.

Determining skin thickness. Skin (phellem) thickness was determined by preparing thin slices of the tuber using a sharp razor.
blade. The slice, which included the skin, was mounted on a glass slide and washed several times with deionized water to remove the loose starch. Skin thickness was measured using a Diphot-TMD inverted microscope (Nikon, Image Systems, Columbia, Md.) equipped with a reticle built into the eyepiece (Klarmann and Rulings, Manchester, N.H.) and a camera. About 60 measurements were made on four slices taken from random locations on the tuber surface.

Determining the diffusion coefficient of CO₂. Previous work has shown that gas exchange in fruit and other bulky organs can be approximated by Fick’s first law of diffusion (Burg and Burg, 1965). This law states that the flux of a gas, diffusing normal to a barrier, depends on the diffusion coefficient, concentration gradient, and area (Crank, 1970; Jacobs, 1967):

\[ J = \frac{D dC}{dx} \frac{A}{h} \]  

where \( J \) (\( \mu \text{mol} \cdot \text{s}^{-1} \)) is the flux of the gas through the organ; \( A \) (cm\(^2\)) is the area of the barrier; \( D \) (cm\(^2\)·s\(^{-1}\)) is the diffusion coefficient; and \( \frac{dC}{dx} \) (\( \mu \text{mol} \cdot \text{cm}^{-2} \cdot \text{cm}^{-1} \)) is the concentration gradient with distance. To determine \( D \), \( \frac{dC}{dx} \) must first be calculated.

In Eq. [1], \( \frac{dC}{dx} \) frequently is replaced by \( \frac{\Delta C}{\Delta x} \). This replacement is permissible only if the change in concentration is linear with distance and if the barrier is either a metabolically inert plane or a hollow spherical shell (Jacobs, 1967; Nobel, 1983; Solomos, 1987). The concentration gradient is determined by solving Fick’s equation for the second law of diffusion (Crank, 1970; Jacobs, 1967).

For a metabolically active cylinder under steady-state conditions, Fick’s equation for the second law of diffusion is (Crank, 1970; Hill, 1928; Jacobs, 1967):

\[ v = \frac{C_u - C_i}{r_i - r_o} \frac{2D}{h} \]  

where \( v \) (\( \mu \text{mol} \cdot \text{cm}^{-3} \cdot \text{s}^{-1} \)) is the specific rate of CO₂ production, \( r \) (cm) is the radius, and \( D \) (cm\(^2\)·s\(^{-1}\)) is the diffusion coefficient.

The skin of the potato tuber is treated as a hollow metabolically inert cylindrical shell, with \( r_o \) and \( r_i \) being the outside and inside radii of the cylindrical shell, respectively. The flux of CO₂ through such a cylindrical shell is given by Crank (1970):

\[ J = \frac{D}{h} \left( \frac{C_u - C_i}{r_i - r_o} \right) \]  

where \( h \) (cm) is the length of the cylinder; \( C_o \) and \( C_{ou} \) are the concentrations of CO₂ in (\( \mu \text{mol} \cdot \text{cm}^{-3} \)) under the skin and in the external ambient atmospheres, respectively; and \( r_i \) and \( r_o \) (cm) are the outside and inside radii of the cylindrical shell. In other words, \( r_o - r_i \) is the thickness of the skin.

It should be kept in mind that the above equations are only an approximation because the geometrical shape of the tuber is not a perfect cylinder and that the diffusion takes place through a perforated cylindrical shell and not the whole surface.

The diffusivity of the flesh of ‘Russet Burbank’ tubers is calculated by treating the tuber as a metabolically active solid cylinder. The concentration of CO₂ along the radius of the tuber is obtained from the solution of Eq. [4] (Hill, 1928):

\[ \frac{1}{r} \frac{d}{dr} \left( r^2 \frac{dC_i}{dr} \right) = 4D \frac{dC_i}{dr} \]  

where \( r_i \) (cm) is the inside radius of the tuber and \( C_u \) (\( \mu \text{mol} \cdot \text{cm}^{-3} \)) is the concentration of CO₂ under the skin.

Thus, assuming that the rate of CO₂ evolution is uniform throughout the cylinder, the concentration of CO₂ at the center, \( r = 0 \), of the tuber is

\[ C_o = \frac{C_{ou} - C_i}{r_i} \]

Results

The accurate determination of gas diffusivity through the tuber critically depends on the precision of gas analyses along the radius of the tuber. Previous techniques for determining the gas composition in the intercellular spaces are not suitable for routine analyses involving several tubers (Solomos, 1987). The present method allows multiple sampling of the same tuber over several days. It is expected that, with time, the gas in the needle (\( \approx 200 \text{ mm}^3 \)) will be in equilibrium with that of the tissue (Burg and Burg, 1965). Previous work indicated that, in apples, the internal pressure is similar to that of the ambient atmosphere (Hulme, 1951). Since O₂

Table 1. Partial pressures of O₂ and CO₂ at the center of the tuber.$

| Tuber | O₂     | CO₂   | CO₂ + O₂ | DIF (%) |
|-------|--------|-------|----------|---------|
| 1     | 16.07 (0.60) | 4.47 (0.05) | 20.54 | 97.27 |
| 2     | 16.23 (2.35) | 3.42 (0.19) | 19.65 | 92.61 |
| 3     | 16.69 (1.14) | 3.58 (0.46) | 20.27 | 95.52 |
| 4     | 16.66 (0.14) | 5.16 (0.24) | 21.82 | 102.83 |
| 5     | 16.53 (0.46) | 4.25 (0.31) | 20.78 | 97.94 |
| 6     | 14.70 (1.42) | 4.18 (0.06) | 18.88 | 88.98 |
| 7     | 16.59 (1.81) | 4.35 (0.26) | 20.94 | 98.75 |
| 1     | 10.27 (0.27) | 9.65 (0.77) | 19.92 | 93.88 |
| 2     | 10.54 (0.53) | 8.12 (0.24) | 18.66 | 87.90 |
| 3     | 12.40 (1.32) | 9.03 (1.33) | 21.43 | 100.99 |
| 4     | 10.07 (1.52) | 8.73 (0.44) | 18.80 | 88.62 |
| 5     | 11.34 (1.68) | 9.02 (0.29) | 20.36 | 95.97 |
| 6     | 9.47 (0.61) | 8.91 (0.59) | 18.83 | 86.60 |
| 7     | 12.08 (0.62) | 8.67 (0.53) | 20.75 | 97.77 |

$The values of the internal partial pressures of O₂ and CO₂ are the average of four and five measurements of 18C and 26C, respectively. The number in parenthesis = SD.

$Percentage DIF refers to the percentage difference between the expected and observed sum of the internal partial pressures of CO₂ and O₂.
Table 2. Partial pressures* of CO₂ in kPa at the center and under the skin of potato tubers held at 10 and 27°C (Expt. 1).

| Tuber | Fresh wt (g) | Fresh Respiration rate (µl CO₂/g per h) | kPa at center at 10°C | 27°C | kPa under skin at 10°C | 27°C | Respiration rate (µl CO₂/g per h) | 10°C | 27°C |
|-------|--------------|----------------------------------------|-----------------------|------|------------------------|------|-------------------------------|------|------|
| 1     | 363.7        | ±0.30                                  | 2.63 ± 0.30           | 7.21 ± 0.96 | 1.74 ± 0.25           | 4.75 ± 0.64 | 2.29 ± 0.05 | 6.83 ± 0.03 |
| 2     | 301.4        | ±0.22                                  | 2.31 ± 0.22           | 5.59 ± 0.71 | 1.71 ± 0.26           | 3.55 ± 0.76 | 2.25 ± 0.05 | 6.58 ± 0.03 |
| 3     | 304.5        | ±0.28                                  | 2.86 ± 0.28           | 8.16 ± 1.89 | 2.23 ± 0.34           | 6.64 ± 0.01 | 2.58 ± 0.25 | 7.21 ± 0.03 |
| 4     | 281.8        | ±0.21                                  | 2.29 ± 0.21           | 6.15 ± 1.49 | 1.83 ± 0.27           | 4.69 ± 1.18 | 2.15 ± 0.05 | 6.94 ± 0.03 |
| 5     | 285.9        | ±0.30                                  | 2.22 ± 0.30           | 6.31 ± 1.21 | 1.79 ± 0.30           | 4.67 ± 0.80 | 2.25 ± 0.05 | 6.84 ± 0.03 |
| 6     | 285.0        | ±0.33                                  | 3.70 ± 0.33           | 9.05 ± 0.95 | 3.07 ± 0.43           | 7.42 ± 1.29 | 2.50 ± 0.05 | 7.00 ± 0.03 |
| 7     | 294.0        | ±0.40                                  | 2.70 ± 0.40           | 7.43 ± 0.75 | 2.31 ± 0.36           | 6.75 ± 0.54 | 2.59 ± 0.05 | 7.25 ± 0.03 |
| 8     | 291.5        | ±0.34                                  | 2.49 ± 0.34           | 7.33 ± 1.72 | 1.77 ± 0.26           | 5.26 ± 0.74 | 2.76 ± 0.05 | 7.74 ± 0.03 |
| Average |             |                                        | 2.62 ± 0.30           | 7.15 ± 0.64 | 2.06 ± 0.30           | 5.44 ± 0.74 | 2.42 ± 0.05 | 7.05 ± 0.03 |

*The tubers were kept at the indicated temperatures and 50 µl air was removed three times daily. Respiration rate was determined under static conditions as described in material and methods.

Each number represents the average of eight measurements at 27°C and 15 measurements at 10°C (± SD).

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The diffusion of gases from the cell to the ambient atmosphere involves three barriers: cell membranes and walls, intercellular spaces, and the skin. The gas diffusivity through the first barrier is not known. It is fair to state that gases diffuse readily through biological membranes (Nobel, 1983). However, hydrated walls may in theory pose some resistance to gas diffusion (Chevillotte, 1973). Experimental evidence indicates that the diffusion of gases through bulky plant organs occurs in gaseous channels (Burg and Burg, 1965; Solomos, 1987). Simple calculations showed that, in apples, the presence of aqueous diffusion barriers drastically curtailed the internal concentration of O$_2$ (Solomos, 1987). More importantly, it was shown that the diffusivities of CO$_2$ and C$_2$H$_4$ in apples were inversely related, as expected from the ideal gas law, to the external total pressure (Burg and Burg, 1965). The existence of continuous gaseous channels in potato tubers is supported by previous microscopic observations where the intercellular spaces, 10 to 15 $\mu$m in diameter, are interconnected with narrow capillary tubes 3 $\mu$m in diameter (Woolley, 1962).

In view of the above evidence concerning the nature of the diffusion channels, the observed decrease in the diffusivity of CO$_2$ through the flesh and skin from its value in air could be attributed, in part, to the tortuosity of the diffusion path but mainly to the decrease in the gaseous spaces available to gas diffusion. Woolley (1962) calculated that only 1/1000 of the total flesh surface is available to gas diffusion. Burton (1950) concluded from measurements of gas flow through potato tissue cylinders that only 0.5% of the cross-sectional surface area was available to gas flow. Based on these observations, Burton (1950) calculated that the diffusion coefficient of O$_2$ in the flesh was 2.94 $\times$ 10$^{-6}$ ml·cm$^{-2}$·s$^{-1}$. However, deducing diffusion coefficients from gas flow measurements requires a somewhat precise knowledge of the geometry of the capillaries because, according to Poiseuille’s law of viscous flow through capillary tubes in response to pressure differential, the flow is proportional to the fourth power of the radius (Siau, 1984), whereas, the diffusion coefficient is proportional to the second power of the radius. In addition, it is questionable whether the resistance to gas flow is uniform throughout the tissue because the intercellular spaces adjacent to cut surfaces may be water-injected (Woolley, 1962). Similarly, the decrease in the diffusivity of CO$_2$ in the skin is due to the fact that only a small fraction of the skin is permeable to gases (Burton, 1950).

The present data agree in that the diffusion channels for CO$_2$ are gaseous in nature. For instance, it is expected that the ratio of the CO$_2$ fluxes at 27 over 10C should equal the product of 1.123 $\times$ (ACO$_2^{27}$/ACO$_2^{10}$), where 1.123 is the theoretical value of D$_{CO_2}^{10}$/D$_{CO_2}^{27}$ (Jost, 1960). It may be concluded from data in Table 2 that the average value of J$_{27}/J_{10}$ is 3.226, whereas, the product 1.123 $\times$ (ACO$_2^{27}$/ACO$_2^{10}$) is 3.257. Furthermore, we calculated the diffusion coefficient in the flesh from the observed value at 27C. This value, along with the observed specific rates of CO$_2$ evolution, its concentration at the center, and radius of the tuber, were inserted in Eq. [5] to calculate the CO$_2$ concentration under the skin at 10C. The results of Table 4 indicate that the calculated values agree well with those observed. Furthermore, when the theoretical values of both D$_{CO_2}^{skin}$ and CO$_2$ concentration under the skin (Table 4), along with the dimensions of the tuber and CO$_2$ concentrations in the ambient atmosphere, were inserted in Eq. [3], the resultant CO$_2$ respiration rates were similar to those observed (Table 4). In view of the fact that CO$_2$ seems to diffuse in the skin through open gaseous pores, Eq. [3] should be multiplied by a number, L, denoting the fraction of the cylindrical surface available to gas diffusion. From the observed values of D$_{CO_2}^{10}$ at 10C and the known value of D$_{CO_2}^{10}$ (0.148 cm·s$^{-1}$), it is calculated that an average of 6.29 $\times$ 10$^{-4}$ of the total cylindrical surface is occupied by the open pores.

The results of Table 1 indicate that the sum of the internal partial pressures of CO$_2$ and O$_2$ is equal to that of the latter in the ambient atmosphere. Thus, the partial pressure of O$_2$ at each point along the radius would be equal to the difference between its partial pressure in the ambient atmosphere and the partial pressure of CO$_2$ at a particular point in the tuber. Figure 2 shows that the ‘Russet Burbank’ tuber is well aerated and the O$_2$ gradient between the

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### Table 3. Diffusion coefficient of CO$_2$ in the skin and flesh of tubers.

| Tuber | Skin (10$^{-6}$ cm·s$^{-1}$ at 10C) | D$_{CO_2}^{27}$/D$_{CO_2}^{10}$ | Flesh (10$^{-4}$ cm·s$^{-1}$ at 10C) | D$_{CO_2}^{27}$/D$_{CO_2}^{10}$ |
|-------|---------------------------------|-----------------------------|----------------------------------|-----------------------------|
| 1     | 7.16                            | 1.15                        | 1.67                             | 1.14                        |
| 2     | 6.73                            | 1.39                        | 2.17                             | 1.03                        |
| 3     | 6.03                            | 1.00                        | 2.63                             | 1.18                        |
| 4     | 6.04                            | 1.32                        | 2.68                             | 1.08                        |
| 5     | 6.37                            | 1.22                        | 2.30                             | 1.16                        |
| 6     | 4.19                            | 0.98                        | 3.65                             | 1.04                        |
| 7     | 5.56                            | 0.98                        | 2.01                             | 1.07                        |
| 8     | 7.79                            | 1.17                        | 2.50                             | 1.07                        |
| Average| 6.24                            |                             | 2.65                             |                             |

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### Table 4. Carbon dioxide concentration $^2$ (µmol·cm$^{-3}$) under the skin at 10C.

| Tuber | Observed | Calculated |
|-------|----------|------------|
| 1     | 0.740    | 0.712      |
| 2     | 0.728    | 0.700      |
| 3     | 0.961    | 0.932      |
| 4     | 0.776    | 0.747      |
| 5     | 0.759    | 0.730      |
| 6     | 1.304    | 1.280      |
| 7     | 0.982    | 0.950      |
| 8     | 0.742    | 0.710      |
| Average| 0.870    | 0.850      |

$^2$The CO$_2$ concentration under the skin at 10C was calculated by inserting a) the theoretical value of the diffusion coefficient at 10C, which was calculated from its observed value at 27C, and b) the observed specific rate of CO$_2$ evolution and CO$_2$ concentration in the center into Eq. [5]. The theoretical rates of respiration at 10C were calculated by inserting the calculated values at 10C of CO$_2$ concentration and D$_{CO_2}$ from observed values at 27C along with the dimensions of the tuber and CO$_2$ concentration in the ambient atmosphere into Eq. [3].
center and area under the skin is rather small, in contrast to that reported previously (Brändle, 1968). Also, Burton (1950) calculated a small O₂ gradient along the tuber. However, for large tubers and high temperatures, there may be an O₂ deficiency at the center of the tuber. We measured the CO₂ concentration of two breeding lines, B0234-4 and B0245-8, of the breeding program at the U.S. Dept. of Agriculture, Beltsville, Md. These tubers were rather spherical, with an average radius of 4.1 and 4.5 cm for B0234-U and B0245-8, respectively. It may be seen from the data of Table 5 that, at high temperatures, the center of the tissue may experience partial anaerobiosis. Incidentally, both lines showed extensive development of hollow heart abnormalities. It is not clear whether there is any correlation between levels of CO₂ or O₂ and the development of these abnormalities.

The present data indicate that gas diffusivities in the skin and flesh of potato tubers can be determined simultaneously. Furthermore, the diffusion channels are gaseous in nature and the skin is the main barrier to gas diffusion mainly because only a small portion of the cylindrical surface is available for gas exchange. However, the flesh also presents an appreciable diffusion barrier to gas exchange. Under normal storage conditions, the tuber is well aerated and the O₂ concentration at the center of the tuber is sufficient to maintain aerobic respiration because of the high affinity for O₂ of the cytochrome oxidase.

### Table 5. Partial pressure of CO₂ at the center of the tuber.

| Cultivar | Tuber Temp (°C) | kPa |
|----------|-----------------|-----|
| B0234-4  | 1 10            | 3.53 ± 0.37 |
|          | 2               | 3.77 ± 0.30 |
|          | 3               | 4.22 ± 0.10 |
|          | 4               | 3.95 ± 0.37 |
|          | 5 27            | 12.60 ± 0.18 |
|          | 6               | 15.23 ± 0.61 |
|          | 7               | 16.86 ± 0.13 |
|          | 8               | 14.88 ± 1.89 |
|          | 9               | 18.78 ± 1.36 |
|          | 10              | 15.23 ± 2.12 |
| B0245-8  | 1 10            | 2.77 ± 0.17 |
|          | 2               | 4.19 ± 0.25 |
|          | 3               | 3.37 ± 0.47 |
|          | 4               | 2.74 ± 0.56 |
|          | 5               | 4.56 ± 0.32 |
|          | 6 27            | 12.72 ± 0.70 |
|          | 7               | 17.40 ± 0.64 |
|          | 8               | 10.86 ± 0.45 |
|          | 9               | 15.37 ± 0.93 |

The values are the average of five readings (±SD).

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