Plant Physiol. (1988) 86, 124–128
0032-0889/88/86/0124/05/$01.00/0

Oyxgen and Temperature Effects on Soybean Seed Coat Respiration Rates

Received for publication April 10, 1987 and in revised form September 11, 1987

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ABSTRACT

Soybean (*Glycine max* (L.) Merr) seed coat respiration rates in response to changing O_2 concentration and temperature were examined experimentally and with a mathematical analysis. The experimental observations showed seed coat respiration rates were sensitive to O_2 concentration below 0.25 micromole O_2 cm^{-3}. There was a steady decline in respiration rates from the saturating O_2 concentration down to about 0 to 0.03 micromole O_2 per cubic centimeter. Seed coat respiration rates were found to change linearly with temperature between 8 and 28°C. The explanation for these results was sought by examining the diffusion of O_2 into the vascular bundles of the soybean seed coat. Differential equations describing O_2 uptake in two distinct zones of the vascular bundle were solved. The outer zone was assumed to be O_2 saturated and respiration proceeded at a constant rate per unit volume. The inner zone was assumed to have respiration rates which were linearly dependent on O_2 concentration. The solution of this mathematical model showed considerable similarity with the experimental results. Respiration rates were predicted to saturate at about 0.31 micromole O_2 per cubic centimeter and to decrease curvilinearly below that concentration. While the mathematical model predicted an exponential response in respiration rate to temperature, it was found that the exponential response is difficult to distinguish from a linear response in the temperature range studied experimentally. Consequently, both the experimental and theoretical studies showed the importance of O_2 diffusion into soybean seed coat vascular bundles as a potential restriction on respiration rates. In particular, it was suggested that increases in the total length of the vascular bundles in the soybean seed coat was the major option for increasing the total respiratory capability.

Mitochondrial respiration is fully saturated at oxygen partial pressures (pO_2) less than 0.02 pO_2, or less than 10% of ambient, for a range of biological situations (17). Yet, several studies have shown intact soybean seeds are responsive to pO_2 well above the saturation pO_2 for mitochondrial respiration. Gale (5) found a linear increase in soybean seed respiration rates as the pO_2 was increased from 0.08 to 0.21. In long-term exposures of soybean shoots to 0.15 pO_2, Quebedeaux and Hardy (9) found seed yields to be only 60% of the yields of those plants maintained at ambient pO_2. Decreases in pO_2 to 0.10 and 0.05 in their study resulted in very little seed production. Similarly, Sinclair *et al.* (11) found in long-term exposures of only the developing soybean pods to altered pO_2 that the individual seed growth rate was decreased at 0.10 pO_2 relative to ambient and supra-ambient pO_2 treatments.

A probable site of this apparent O_2 sensitivity in developing soybean seeds is the seed coat. Thorne (16) showed that isolated embryos actually were fairly O_2 insensitive since sucrose uptake rates by embryos under anaerobic conditions were still 68 to 77% of ambient rates. Thorne also found from examination of ^{14}C-photosynthate distribution patterns in pods attached to plants whose leaves were previously fed $^{14}CO_2$, that import into the cotyledons did not occur under anaerobic conditions. All the photosynthate under the anaerobic condition remained in the pod walls and seed coats. These results indicate that O_2 is required to sustain photosynthate transport from the seed coat to the cotyledon. These O_2 responses in soybean seeds led Sinclair *et al.* (11) to speculate that an O_2 diffusion barrier exists in seed coats which isolates a rate-limiting respiratory process from atmospheric pO_2.

A second set of evidence that indicates a physical process may constrain seed growth is derived from temperature response data. Dungey and Pinfield (3) found a linear response in respiration rate of intact *Acer pseudoplatanus* (L.) seeds to temperature changes between 10 and 35°C. Similar results were obtained with attached soybean pods by Spaeth and Sinclair (12) who found linear changes in respiration rate between 7 and 22°C. Thorne (16) found that photosynthate accumulation in soybean seeds was linearly dependent on temperature between 15 and 35°C. The linear rather than exponential response observed in all these studies is generally assumed to be indicative of processes limited by physical mechanisms as opposed to biochemical processes.

The objective of this research was to examine the hypothesis that O_2 availability in soybean seed coats is controlled by a diffusion process which may be a limiting step regulating seed growth rate. Experimental evidence was obtained by measuring the respiration response of isolated soybean seed coats to changes in pO_2 and temperature. Both sets of experimental data were consistent with the possibility that a diffusion process limits seed respiration. Subsequently, a mathematical analysis was undertaken to determine if seed coat anatomy was consistent with the existence of a diffusion barrier to O_2. The mathematical solution for O_2 flux in vascular bundles from partial differential equations confirmed a potential limitation on respiration rates as a consequence of O_2 diffusion processes.

MATERIALS AND METHODS

Seeds were collected from field-grown soybean plants, cultivar Kirby, immediately preceeding measurements of seed coat respiration. The plants were grown in field plots at Gainesville, FL, and the seeds were collected between 23 September and 5 October 1986. After bringing the harvested pods to the laboratory, only developing seeds were selected which were 10 × 7 × 3 mm and consequently had not reached full expansion. The seed coats were obtained by dissecting the seed between the two cotyledons and gently removing the two seed coat halves.

Fresh seed coats from 12 seeds were grouped together and used to measure respiration rates. The seed coats were put into a 31

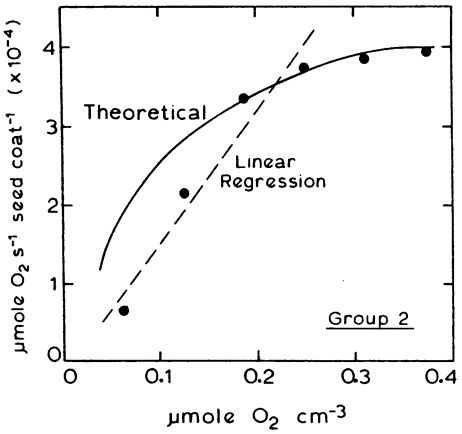

FIG. 1. Seed coat respiration rates as a function of oxygen concentration as determined experimentally (●) and theoretically (*solid line*).

ml glass vial which was filled with 5 mM MES solution adjusted to pH 6.0 and continuously stirred. The vial containing the seed coats was placed in a temperature-regulated water bath. During the measurements of the O_2 response the temperature was held constant at 26°C. Prior to measuring respiration rate by O_2 depletion in the solution, a fixed O_2 concentration was established by bubbling a gas mixture through the measurement solution until a constant concentration was achieved. The pO_2 of the gas mixture (O_2:N_2) was usually varied between 0.05 and 0.50 pO_2. The O_2 concentration in the solution was measured with a Clark-style oxygen electrode (Diamond Electro-Tech, Inc., Ann Arbor, MI[1]). Once a constant O_2 concentration was achieved the bubbling was stopped and the disappearance of O_2 from the solution was recorded during the following 5 to 7 min. Usually no more than 90 min were required to measure the response characteristics of a set of seed coats. Within the 90-min period no change in respiration rate under fixed conditions was observed.

The response to temperature was obtained by altering the temperature of the water bath in which the measurement container was placed. Temperatures were varied between 8 to 28°C. The O_2 concentration in the solution was maintained constant at 0.25 μmol cm^{-3} at all temperatures. Since O_2 solubility is temperature dependent, the pO_2 of the gas initially bubbled through the solution was altered with temperature.

RESULTS

The response of seed coat respiration to O_2 was measured on five groups of seed coats and found to be quite consistent among the groups. At less than about 0.25 μmol O_2 cm^{-3} respiration rate was found to decrease in response to decreasing O_2. For example, in Figure 1 are plotted the data for group 2 which illustrate the respiration rate below 0.25 μmol O_2 cm^{-3}. Above 0.25 μmol O_2 cm^{-3} little, if any, further increase in respiration rate was observed. The respiration rates observed at O_2 saturation agree with those reported for soybean seed coats by Guldan and Brun (6). Respiration rates were found to fall to zero between 0 and 0.03 μmol O_2 cm^{-3}.

To verify further the decline in seed coat respiration rates with O_2, for each set of seed coats linear regression analysis was performed on the data obtained between 0.05 and 0.25 μmol O_2 cm^{-3}. In all cases, seed coat respiration rates were found to be very responsive to changes in O_2 (Table I). Also, among the five sets of seed coats there was a high consistency in the magnitude of the O_2 response as evidenced by the slopes presented in Table I. The mean O_2 response was 1.4×10^{-3} (μmol O_2 s^{-1} seed $coat^{-1}$)/(μmol O_2 cm^{-3}).

Table I. *Slope of Seed Coat Respiration Rate vs O_2 Concentration between 0.05 and 0.25 μmol cm^{-3}*

Group No.	Seed Coat	μmol O_2 s^{-1} Seed $Coat^{-1}$ / μmol O_2 cm^{-3}	r
	mg		
1	6.2	1.4×10^{-3}	0.92
2	6.5	1.7×10^{-3}	0.97
3	6.4	1.3×10^{-3}	0.73
4	9.6	1.7×10^{-3}	0.97
5	7.0	1.1×10^{-3}	0.99

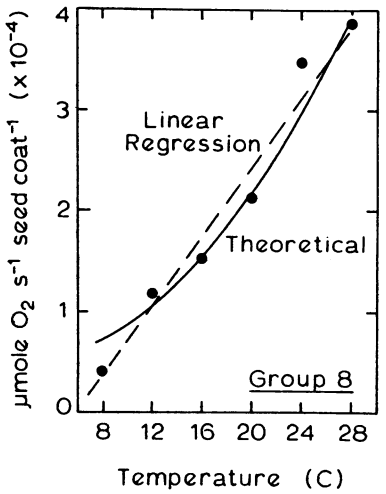

FIG. 2. Seed coat respiration rates as a function of temperature as determined experimentally (●) and theoretically from exponential temperature-response model (*solid line*).

Table II. *Slope of Seed Coat Respiration Rate vs. Temperature Between 8 and 28°C*

Group No.	Seed Coat	μmol O_2 s^{-1} Seed $Coat^{-1}$ / °C	r
	mg		
6	6.8	2.1×10^{-5}	0.98
7	7.3	1.3×10^{-5}	0.98
8	6.9	1.7×10^{-5}	0.98

Seed coat respiration rates in response to temperature were measured on three groups of seed coats. The temperature response was linear over the entire range of 8 to 28°C as illustrated by the data plotted in Figure 2 from Group 8. Linear regression analysis of the data from each set of seed coats resulted in quite high correlation coefficients between respiration rate and temperature (Table II), although there was variability in the slope of this relationship.

MATHEMATICAL ANALYSIS OF SEED COAT RESPIRATION

The experimental results obtained in this study are consistent with the suggestion of a diffusion limitation to seed coat respiration. Respiration rates were responsive to pO_2 levels that are substantially greater than what is usually required to saturate mitochondria. Also, seed coat respiration rates were found to be linearly responsive to changes in temperature. In this section, a

[1] Mention of company names or commercial products does not imply recommendation or endorsement by the United States Department of Agriculture over others not mentioned.

mathematical analysis is done on O_2 diffusion in the seed coat to assess from a theoretical viewpoint the potential importance of such a physical constraint on respiration rate.

Fortunately, soybean seed coat anatomy has been well documented (1, 15). It appears O_2 may be able to freely diffuse in the bulk seed coat. Oyxgen can be readily exchanged with the surrounding atmosphere via the micropyle and probably through the seed coat epidermis. In the protocol used in these experiments, the removal of the seed coat from the embryo would further facilitate O_2 diffusion into the seed coat by exposing its interior surface. Once O_2 is inside the seed coat, the large airspaces of the hypodermal layer and aerenchyma tissue would allow O_2 to diffuse readily in the gaseous phase throughout the seed coat. There is no obvious, major barrier for O_2 diffusion restricting entry into the seed coat.

The one region where O_2 diffusion may be restricted is within the vascular bundles. Within the soybean seed coat the vascular bundles form an extensive reticulate venation system throughout a layer of parenchyma cells. The vascular bundles are spaced approximately 100 μm apart and consist of a tightly packed group of cells including sieve tubes, companion cells and vascular parenchyma (15). These cells are interconnected by abundant plasmodesmata (15), and very few, if any air spaces, exist in the vascular bundles. Since the phloem unloading apparently occurs within the vascular bundles (15) and unloading is a respiratory-dependent process, a major site for seed coat respiration would be in the vascular bundles. The O_2 required for respiration must, therefore, diffuse through the liquid phase of the vascular bundle so that the low O_2 diffusion coefficient in liquids may well limit seed coat respiration rates. To analyze this possibility, a mathematical solution for O_2 diffusion in the vascular bundles was sought.

Derivation. An approach was used similar to that of Collis-George and Melville (2) for modeling O_2 diffusion into an entire seed. The vascular bundle was modeled as a cylinder comprised of two concentric zones responding differently to O_2 (Fig. 3). The outer zone was assumed to have O_2 concentrations sufficiently high to saturate the O_2 consumption mechanisms. In the inner zone it was assumed that O_2 concentrations were less than the saturating concentration and within this zone the O_2 consumption rate was proportional to O_2 concentration.

Mathematically, the differential equation for the outer zone is,

$$D\left[\partial^2 c/\partial r^2 + \frac{1}{r}\,\partial c/\partial r\right] = q$$

where:

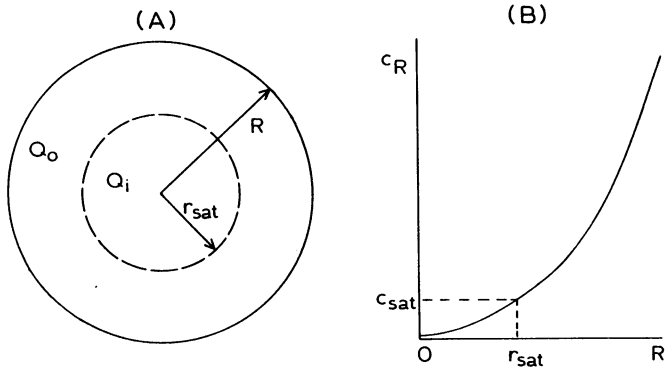

FIG. 3. (A) Diagrammatic representation of two zones of oxygen consumption in vascular bundle. (B) Plot of theoretical O_2 concentration as a function of radius from center of vascular bundle.

D = diffusion coefficient of O_2 in cytoplasm ($cm^2\ s^{-1}$),
c = O_2 concentration ($\mu mol\ cm^{-3}$),
r = radius (cm),
q = saturated O_2 consumption rate per unit volume ($\mu mol\ cm^{-3}\ s^{-1}$).

The solution of Equation 1 for O_2 concentration in the outer coaxial cyclinder with an outer radius R, an inner radius r_{sat} where respiration is just O_2 saturated, and an O_2 concentration at the external surface of c_R is

$$c = c_R - \frac{q}{4D}(R^2 - r^2) - \frac{\ln(r/R)}{\ln(r_{sat}/R)} \cdot [q/4D(R^2 - r_{sat}^2) + (c_R - c_{sat})]. \quad (2)$$

In those situations where r_{sat} is much less than R

$$c \approx c_R - q/4D(R^2 - r^2). \quad (3)$$

The total O_2 consumption in the outer zone, Q_0 ($\mu mol\ s^{-1}$), with saturated O_2 concentration is

$$Q_0 = \int_{r_{sat}}^{R} 2\pi r L q\, dr = \pi L q(R^2 - r_{sat}^2), \quad (4)$$

where:

L = total length of vascular bundles in the seed coat (cm),
r_{sat} = cylinder radius where O_2 concentration is at the threshold concentration for saturation (cm).

The O_2 concentration in the inner cylindrical zone, where O_2 consumption is linearly dependent on O_2 concentration, is defined by the following differential equation.

$$D\left[\partial^2 c/\partial r^2 + \frac{1}{r}\,\partial c/\partial r\right] = kc, \quad (5)$$

where k is the O_2 consumption rate coefficient (s^{-1}). The solution to Equation 5 as given by Roughton (10) a is

$$c = c_{sat}\frac{I_0(r\sqrt{k/D})}{I_0(r_{sat}\sqrt{k/D})}, \quad (6)$$

where:

c_{sat} = threshold O_2 concentration for saturation ($\mu mol\ cm^{-3}$),
$I_0(x)$ = Bessel function of the first kind, of zero order.

The total consumption in the inner zone (Q_i) is given by

$$Q_i = \int_0^{r_{sat}} 2\pi r L k c\, dr = \frac{2\pi L K c_{sat}}{I_0(r_{sat}\sqrt{k/d})}\int_0^{r_{sat}} r I_0(r\sqrt{k/d})\, dr, \quad (7)$$
$$= 2\pi L\sqrt{kD}\, c_{sat} r_{sat}\frac{I_1(r_{sat}\sqrt{k/D})}{I_0(r_{sat}\sqrt{k/D})}.$$

where I_1 is the Bessel function of the first kind, of first order.

The total O_2 consumption can be predicted by summing Equations 4 and 7. That is,

$$Q = Q_0 + Q_i. \quad (8)$$

To evaluate Equation 8, the value of several parameters for the seed coat vascular system must be estimated. The radius of the vascular bundles (R) is about 15×10^{-4} cm (15). From the bundle spacing and area of the seed coat, the total length of the vascular bundle system is estimated to be roughly 100 cm. The value of q was calculated from the experimental observations of O_2 consumption at saturated concentrations and from the estimated volume of the vascular bundles ($\pi R^2 L = 7 \times 10^{-4}$ cm^3) to be approximately 0.5 μmol O_2 cm^{-3} s^{-1}. From the analysis of mitochondrial respiration by Wilson *et al.* (17) it appears c_{sat} is no greater than about 0.03 μmol cm^{-3} and k is no greater than about 3 s^{-1}. The value of D for O_2 in the cytoplasm was assumed to be about an order of magnitude less than that in water due to the greater viscosity and tortuosity of diffusion in cytoplasm, or 1×10^{-6} cm^2 s^{-1}.

Calculations of Q_0 and Q_i were done with varying values of r_{sat}. These calculations showed that except for very large values of r_{sat} ($r_{sat}/R > 0.8$) the value of Q_0 was always considerably greater than Q_i (Table III). That is, only under those circumstances when the external O_2 concentration (c_R) was very low so that r_{sat} becomes large, did the respiration in the interior zone account for a substantial fraction of the respiration estimate.

Implications. The above analysis can be used to predict the external O_2 concentration (c_R) at which saturation of seed coat respiration might be expected. Equation 3 can be rearranged and solved for the situation where no inner zone exists, that is r_{sat} exactly equals zero.

$$c_R = c_{sat} + \frac{qR^2}{4D}. \tag{9}$$

From the previously assumed values for the variables on the right-hand side, the value of c_R when the entire vascular bundle is O_2 saturated is calculated to be 0.31 μmol cm^{-3}. This predicted value is slightly greater than the experimentally observed saturation value at or above 0.25 μmol cm^{-3} at 26°C.

To explain fully the experimental results, an important issue is whether the mathematical analysis indicates a respiration rate response to O_2 concentrations over the fairly broad range of pO_2 observed experimentally. An iterative procedure was employed to solve for Q at varying c_R using the parameters as defined previously. An initial estimate of Q_0 was arbitrarily chosen and the initial estimate of r_{sat} was estimated by rearranging Equation 4,

$$r_{sat} = \sqrt{R^2 - Q_0/\pi LQ}. \tag{10}$$

The next step in the iteration was to obtain an improved estimate of Q_0 from Equation 2,

$$\begin{aligned} Q_0 &= 2\pi RLD \left(\frac{dc}{dr}\right)_{r=R} \\ &= \frac{\pi Lq}{2}\left[2R^2 + \frac{(R^2 - r_{sat}^2)}{\ln(r_{sat}/R)}\right] \\ &\quad - 2\pi LD \frac{(c_R - c_{sat})}{\ln(r_{sat}/R)}. \end{aligned} \tag{11}$$

The iteration procedure of improved estimates of r_{sat} and Q_0 was continued until successive estimates of Q_0 agreed within 1%. Finally, an estimate for Q_i was obtained from the calculated r_{sat} using Equation 7.

The resulting estimates calculated from the above model for seed coat Q at various c_R are plotted in Figure 1. Interestingly, the mathematical result has features not too dissimilar to the experimental observations. At low O_2 concentrations the mathematical analysis yielded a curvilinear response in respiration to pO_2 up to a saturation value approximating the experimental results. The results from the mathematical analysis indicate a response function over the range of pO_2 that appears consistent with the experimental observations.

Table III. *Calculated Oxygen Flux Rates for Outer Zone (Q_0) and Inner Zone (Q_i) of Vascular Bundles at Varying Values for Radius of O_2 Saturation (r_{sat})*

$r_{sat/R}$	Q_0	Q_i
	μmol/s	
0	35.3×10^{-5}	0
0.2	33.9	0.2×10^{-5}
0.4	29.7	0.9
0.6	22.6	1.8
0.8	12.7	2.8
0.9	6.7	3.3
0.95	3.4	3.6
1.00	0	3.8

The experimental observation of a linear response in seed coat respiration to temperature can also be examined with the mathematical model. Since the O_2 concentration during the temperature response measurements was at or near saturation, there is assumed to be negligible O_2 consumption in an inner zone and the expression for flux given in Equation 4 can be simplified by assuming $r_{sat} \ll R^2$. Therefore,

$$Q = \pi LqR^2. \tag{12}$$

Assuming an exponential temperature response function for the biochemical processes that determine the value of q,

$$q = B \exp(-A/R'T), \tag{13}$$

where:

B = constant,
A = activation energy (kcal/mol),
R' = gas constant (kcal mol^{-1} K^{-1}),
T = temperature (K),

an exponential response in seed coat respiration is predicted. However, within the 20°C temperature range tested it is important to realize the difficulty in distinguishing between an exponential response and a linear response. For example, in Figure 2 a plot is also shown for the predicted response to seed coat temperature if the activation energy for respiration was as high as 15 kcal/mol. Lower activation energies would approach linearly even more closely. Consequently, the experimentally observed linear response to temperature is consistent with a high activation energy for the biochemical processes. An apparent linearity in temperature response does not exclude a biochemical origin as initially assumed.

DISCUSSION

Even though mitochondrial respiration is saturated at low pO_2, the experimental results showed soybean seed coat respiration was not saturated until external pO_2 was increased to levels above ambient. These results help to explain the respiration response to O_2 by whole soybean seeds (5), the inhibited unloading of labelled photosynthate from soybean seed coats under anaerobic conditions (16), and the inhibited soybean seed growth under subambient pO_2 (9, 11). These results all point toward a constraint on O_2 diffusion that restricts O_2 availability in the soybean seed coat. The seed coats were also found to have a linear response in respiration rate to temperature. These results confirmed the observed linear response of intact seeds to temperature (12, 16).

The mathematical derivation describing soybean seed coat respiration and the O_2 diffusion in the vascular bundles provides

a theoretical basis that affirms and allows further interpretation of the experimental results. The underlying assumption of the derivation was that respiration rate in the vascular bundle accounts for much of the seed coat respiration because the vascular bundle is the site of phloem unloading (15). Further, it was assumed that the anatomy of the vascular bundles was such that O_2 must diffuse in the bundle through the liquid cytoplasm of the cells. That is, it was assumed little or no airspace exists in the seed coat vascular bundles to facilitate O_2 diffusion. From these two assumptions concerning vascular bundle function and anatomy, the mathematical analysis was able to describe many of the observed features of seed coat respiration.

Based on the mathematical analysis, it was concluded that under ambient pO_2 the vascular bundles are nearly saturated with O_2. Increases in O_2 around soybean seeds above ambient were predicted to result in only marginal increases in respiration rates as was observed in the seed coat respiration data. On the other hand, decreasing external O_2 concentrations below ambient was predicted to result in nonsaturated conditions in the vascular bundles. A decrease in seed coat respiration rate with O_2 was predicted (Fig. 1) in a manner similar to the experimental response. An approximately linear temperature response of seed coat respiration was also predicted (Fig. 2) from the mathematical analysis based on the expected biochemical respiration response to temperature.

One very interesting implication of the results presented here is the complimentary nature of the vascular bundle anatomy and ambient pO_2. The very dense packing of the vascular bundle cells with a large number of connecting plasmodesmata facilitates phloem unloading and photosynthate transport. The potential inhibition of respiration, and consequently unloading, by inadequate O_2 is alleviated by restricting the radius of the vascular bundle. Seed coat respiration is nearly O_2 saturated at ambient pO_2 with vascular bundles of radius approximately 15×10^{-4} cm. It is predicted that increasing vascular bundle diameter would not increase overall respiration rate because more of the bundle interior would become oxygen deficient. Similarly if the atmosphere pO_2 was lower than ambient, the vascular bundle would not be O_2 saturated and rates in phloem unloading would decrease.

Of course, alternative sites for unloading outside of the vascular bundles would greatly decrease the dependence of respiration rate on vascular bundle morphology. If gaseous pathways exist for oxygen diffusion to these alternative unloading sites, then dispersion of unloading would greatly decrease the potential inhibition of inadequate oyxgen. In fact, Offler and Patrick (8) concluded unloading in *Phaseolus vulgaris* L. seed coats occur throughout the branch parenchyma. Such a scheme would help to explain the high rates of unloading and seed growth in *P. vulgaris* even though the seed coat contains fewer vascular bundles than soybean.

Nevertheless, if the original assumptions of this analysis with soybean are valid, no biochemical options in soybean are apparent for increasing vascular bundle respiration and presumably phloem unloading rate at 26°C as used experimentally. While it certainly may be possible to speed the biochemical rate per unit volume, that is increase q, such an increase has little impact on overall vascular bundle respiration rate, Q. The effect of increasing q is to increase the respiratory activity of the outer zones of the vascular bundle, but this also decreases the volume of the exterior zone (r_{sat} increases). Increasing r_{sat} would stabilize the overall oxygen flux into the vascular bundle at approximately the original rate. Only if phloem unloading was made independent of aerobic respiration does it appear likely that phloem unloading could be significantly increased.

The one factor indicated by the mathematical analysis of soybean vascular bundles that significantly alters respiration rate per seed coat is the total length of the vascular bundles, L. The obvious conclusion for increasing soybean seed coat respiration is simply to increase the overall length of the vascular bundles. Either a greater density of vascular bundles or a larger seed coat is predicted to result in greater soybean respiration per seed coat. Not surprisingly then, the greatest individual seed growth rates in soybean are associated with those genotypes that develop the largest seed coats (4, 6, 14). Hanson (7) showed directly that the sucrose unloading rate from soybean seed coat was linearly related to the seed coat area. Unfortunately, the logical conclusion that genotypes with larger seed coats will produce the greatest seed yields per plant does not stand because of the great compensation in soybean that restricts the number of seeds set per plant when the individual seed size is large (13).

Acknowledgments—The author acknowledges the work done by Carolyn A. Randall in the preliminary development of the techniques for measuring seed coat respiration rates. The helpful discussions with P. Randall Weisz in the development of the mathematical analysis are also gratefully acknowledged.

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