Latitudinal trends in the responses of growth respiration and maintenance respiration to temperature in the beach pea, *Lathyrus japonicus*

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The response of dark respiration to temperature was measured for populations of *Lathyrus japonicus* collected from 39–56° N latitude. Carbon loss in dark respiration increases with latitude at all temperatures. This increased respiratory activity is attributable to concomitant increases in both the growth and maintenance components of total dark respiration. The possible adaptive significance of these respiratory responses is discussed.


Les changements dans les taux de respiration à l’obscurité en fonction de la température ont été analysés chez six populations de *Lathyrus japonicus* échantillonnées le long d’un gradient latitudinal (39–56° N) dans l’est de l’Amérique du Nord. La perte de carbone attribuable à la respiration à l’obscurité augmente avec la latitude à toutes les températures. L’augmentation de l’activité respiratoire est due aux composantes de croissance et du maintien qui participent à la respiration à l’obscurité. La signification adaptative de ces réponses respiratoires est discutée.

**Introduction**

The functional and adaptive significance of greater respiratory rates in plant populations from colder habitats remains to be established despite the long history of experimental evidence supporting this latitudinal and elevational trend (Wager 1941; Scholander and Kanwisher 1959; Bjorkman 1966; Stewart and Bannister 1974; Tieszen and Wieland 1975). The recent partitioning of plant respiration into two components (McCree 1970; Thornley 1970), one associated with growth of new tissues and the other with maintenance of existing tissues, can help explain this trend in total respiration. The greater rates of total respiratory carbon loss in more northern or higher elevation plant populations may be attributable to higher maintenance costs or to selection for more rapid growth rates.

The widely distributed herbaceous perennial, *Lathyrus japonicus* Willd. (Leguminosae), is a good species with which to examine latitudinal trends in these respiratory activities. *Lathyrus japonicus* primarily colonizes maritime dunes but also occurs along the sandy shores of large freshwater lakes (Hitchcock 1952; Lamoureux and Grandtner 1977). In eastern North America the species ranges from about 39–58° N latitude (Hitchcock 1952). We have therefore studied the respiratory responses to temperature for populations of *L. japonicus* from 39–56° N latitudes to determine the partitioning of respiratory activity in this species over its latitudinal range.
Methods

We collected rhizomes from six populations (Table 1) of *L. japonicus* for experimental study and grew them under greenhouse conditions. Each latitudinal site is represented by plants grown from rhizomes collected in single, extensive colonies; it is likely that only a single clone was collected at each site. The plants had been maintained in growth chambers for over 18 months at the time this experiment was initiated. For these experiments new plants were established from freshly harvested rhizomes. The plants received supplemental lighting on a 16-h photoperiod and ambient air temperatures fluctuated between 15–23°C. Plants were kept well watered and were fertilized regularly with Hoagland's solution.

Carbon dioxide efflux was measured in an open-system of infrared gas analysis (Sestak et al. 1971). Chamber air was rapidly circulated by a squirrel-cage fan; tissue temperatures were maintained by fluid circulating in a heat exchanger in the chamber base. The terminal 10 cm of vegetative shoots were enclosed in the chamber to assay respiratory activity at different temperatures; the remainder of the plant was at about 25°C. The experimental plants were all assayed within a 3-week period beginning when the plants had grown 2 months in the greenhouse. No plants began to reproduce before the completion of the experiments. Tissue temperatures were measured with 3 CuCl temperature couples pressed to the underside of the leaves. Respiration rates were determined at tissue temperatures from 4–36°C in approximately 5° steps. The plant was kept at a temperature until a stable respiration rate was attained, usually 15–30 min. Both the order in which individual plants were assayed and the order of exposure to the test temperatures were randomized. This randomization avoids introducing any spurious respiratory trends due to slight differences in plant age or to delayed responses to particular temperatures. Respiratory rates are expressed per gram dry weight of shoot tissue.

Total respiration was partitioned into its growth and maintenance components following the method of McCree (1974). Preliminary experiments at 20°C on *Lathyrus* showed a steady decline in respiration for 36 h after darkening followed by low but essentially constant CO₂ efflux. The same pattern of respiration after darkening has been reported for a number of agricultural species (McCree 1974; Moldau and Karolin 1977; Jones et al. 1978; Ryle et al. 1976). Using 14C-labelled assimilates, the exponentially declining respiratory rates in maize and barley have been shown to consist of two distinct components: (1) a rapid efflux with a half-life of 4–8 h associated with biosynthesis and (2) a slower efflux with half-life 26–120 h associated with maintenance (Ryle et al. 1976). Maintenance respiration, *Rₚ*, in *L. japonicus* was thus operationally defined as the respiration rate after 48 h in continuous darkness. Total dark respiration, *Rₜ*, was measured on plants darkened as the experiment began. Growth respiration, *Rₙ*, was taken as the difference of maintenance and total respiration: *Rₜ* = *Rₚ* + *Rₙ*.

The data gathered for the responses of respiration to temperature in the diverse populations of *L. japonicus* were analyzed by stepwise multiple linear regression (Draper and Smith 1966) and plotted as contour graphs. The total dark respiratory flux, *Rₜ*, was best described by the equation:

\[ \ln (Rₜ + 1) = 0.0253467 + 0.0003997L + 0.574789 \]

where *T* is tissue temperature in degrees Celsius and *L* is latitude of origin in decimal degrees. The absolute value of *Rₜ* + 1 was chosen as dependent variable to avoid trying to take the logarithm of negative or zero values. This equation had an *r²* = 0.73. The maintenance respiratory flux, *Rₚ*, was best described by the equation:

\[ |Rₚ| = 0.003028T² + 0.00219L² + 0.649118 \]

Table 1. Origin and thermal regime of the sampled *Lathyrus japonicus* populations

<table>
<thead>
<tr>
<th>Locality</th>
<th>Frost-free period, days</th>
<th>Mean temperature of hottest month, °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great Egg Harbor, New Jersey, 39°20' N, 74°35' W</td>
<td>185</td>
<td>26.1</td>
</tr>
<tr>
<td>Cape Cod, Massachusetts, 41°55' N, 70°15' W</td>
<td>180</td>
<td>25.5</td>
</tr>
<tr>
<td>Epoufette Beach, Michigan, 46°05' N, 85°05' W</td>
<td>120</td>
<td>27.6</td>
</tr>
<tr>
<td>Témiscamingue, Québec, 47°10' N, 79°10' W</td>
<td>115</td>
<td>25.1</td>
</tr>
<tr>
<td>Rivière Moisie, Québec, 50°20' N, 66°08' W</td>
<td>110</td>
<td>16.8</td>
</tr>
<tr>
<td>Poste de la Grande Baleine, Québec, 55°50' N, 77°80' W</td>
<td>80</td>
<td>15.1</td>
</tr>
</tbody>
</table>


This equation had an *r²* = 0.60. Graphs of the residuals against the predicted dependent variable and against the independent variables (Draper and Smith 1966) indicated both models gave unbiased and satisfactory estimations of the respiratory flux; examples of these residual plots appear in Fig. 1. From two to six and in most cases four replicates were used to determine the respiratory responses to temperature in each population. Maintenance respiration was measured 205 times at temperatures from 5 to 36°C; total respiration was measured 176 times at

![Fig. 1. Plots of the residuals against the estimated respiratory flux for total dark respiration (A) and for maintenance respiration (B). Note that the absolute value of the respiratory flux was actually estimated and thus appears on the abscissa.](image-url)
temperatures from 4 to 36°C. The origins of sampled populations range from 39 to 56° N latitudes (Table 1). The regression equations can only be used to make valid predictions of respiratory flux within these limits of temperature and latitude.

Multiple linear regression is particularly appropriate for description of multidimensional biological response data (Menke 1973; Mead and Pike 1975). A biological response controlled by interacting factors such as tissue temperature and the plant's latitude of origin can be effectively displayed using contour graphs plotted from a fitted regression equation. These contour graphs, like the familiar contour maps to which they are analogous, clearly show the rate of a response for any combination of the controlling factors. More important the graphs show how quickly the response changes with changes in the controlling factors. This latter aspect of a biological response cannot be effectively illustrated by any other graphic method. In examining contour graphs special attention should accordingly be given to the orientation and spacing of the contour lines. Closely spaced lines indicate rapid changes in response with changes in the controlling factors. Contour lines parallel to an axis indicate that the factor scaled on that axis has no effect on the response. Similarly, contour lines oriented diagonally illustrate an interacting control of both factors on the response. If the axes are scaled similarly, the axis to which the contour lines are more nearly perpendicular represents the factor with the greater effect on the response. The accuracy of this graphical representation of multidimensional biological response data of course requires both sound underlying experimental design and careful data analysis.

Results and discussion

More northerly populations of L. japonicus have higher rates of total respiration; this trend is more marked as tissue temperature increases (Fig. 2). Since the diverse populations sampled were all grown in a common greenhouse environment, this latitudinal trend reflects genetic differences in the populations. These results give firm support to generalizations based on earlier studies which had measured respiration only at fewer temperatures and latitudes of origin (Wager 1941; Scholander and Kanwisher 1959; Bjorkman 1966; Stewart and Bannister 1974; Tieszen and Wieland 1975). This pattern of variation in the response of total respiration to temperature and latitude of population origin is affected by increases in both growth and maintenance respiratory activity (Fig. 3).

Maintenance respiration in L. japonicus increases with temperature (Fig. 3A) as reported in

![Fig. 2](image-url) Fig. 2. Total dark respiration of greenhouse-grown L. japonicus as a function of tissue temperature and the latitude of population origin. Respiration is expressed as milligrams CO_2 per gram per hour.

![Fig. 3](image-url) Fig. 3. Maintenance respiration (A) and growth respiration (B) of greenhouse-grown L. japonicus as a function of tissue temperature and the latitude of population origin. Respiration is expressed as milligrams CO_2 per gram per hour.
studies on crop plants (Jones et al. 1978; Ryle et al. 1976). This increased maintenance respiration at higher temperatures primarily arises from the energetic demands of stimulated protein turnover and, to a lesser degree, active ion fluxes (Penning de Vries 1975). Maintenance respiration increases most markedly with latitude at low temperatures but shows some increase even at 35°C. This increased maintenance respiration in northern populations, particularly at low temperatures, may reflect greater energy investment in nutrient uptake (Chapin 1974).

At low temperatures growth respiration is little affected by latitude, but above 15°C growth respiration increases sharply with latitude (Fig. 3B). Growth respiration increases with temperature but never attained very high rates in these experiments. Since rates of growth respiration are proportional to gross photosynthesis (Sestak et al. 1971; Moldau and Karolin 1977), the relatively low overall rates observed can be explained by the light-limited greenhouse environment regimes. Assuming the observed trends also hold under brighter light, the latitudinal increase in growth respiration may be explained by natural selection favoring faster growing individuals. The ability to grow rapidly during brief warm spells would be particularly advantageous in the shorter growing seasons typical of more northerly populations (cf. Table 1).

These data for L. japonicus demonstrate that respiratory carbon losses increase with latitude over a broad range of tissue temperatures. This increase is attributable to concomitant changes in growth respiration and maintenance respiration which may be of adaptive advantage. The partitioning of respiratory activity into its functional components and further assessment of their adaptive significance should receive greater attention by physiological plant ecologists.

Acknowledgement

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