

Plant distribution and the temperature coefficient of metabolism

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ABSTRACT

The spatial distribution of a plant species is limited by the range of climatic conditions to which the species can adapt. Temperature is one of the most significant determinants of plant distribution, but except for the effects of lethal limits, little is known about physiological changes in responses to differences in environmental temperature. In this study, temperature coefficients of non-photosynthetic metabolism have been determined in the normal environmental temperature range for selected annual and perennial plants. Distinct differences were found in the temperature coefficient of metabolism of woody perennial plants from high latitudes and high elevations and closely related low-latitude and low-elevation plants. Low-latitude and low-elevation woody perennials have Arrhenius temperature coefficients for metabolism that are larger than those for congeneric high-latitude and high-elevation plants. The Arrhenius temperature coefficient is not rapidly adapted to new environments. A simple function was developed relating Arrhenius temperature coefficient to latitude and elevation for accessions of three, woody, perennial species complexes of plants collected from a wide geographic range but grown in common gardens. Within these taxa, plants that experience broader ranges of temperature during growth in their native habitat have smaller temperature coefficients. Temperature coefficients also varied with growth stage or season. No similar relationship was found for annuals and herbaceous perennials. For the plants tested, Arrhenius temperature coefficients are high during early spring growth, but shift to lower values later in the season. The shift in Arrhenius temperature coefficients occurs early in the season for southern and low-elevation plants and progressively later for plants from further north or higher elevation. The changes in Arrhenius temperature coefficients result largely from increases in plant metabolic rates at lower temperatures while little change occurs in the rates at higher temperatures. Altering the temperature dependence of the control of metabolic rate is apparently an important means of response to climate change.

Key-words: plant distribution; respiration; activation energy; temperature coefficient.

INTRODUCTION

Explanation of the species richness gradient from low to high latitudes and elevations is one of the current outstanding problems in biology (Pianka 1966; Janzen 1967; Rohde 1992; Stevens 1992). Hypotheses to explain the observed geographical gradient of species diversity from tropics to high latitude and from low to high elevation are commonly framed in terms of the gradient of conditions faced across the range of environments these organisms experience (Rapoport 1982). Smaller numbers of organisms can adapt to the broad range of climatic conditions experienced at higher latitudes and elevations than to the narrower range of conditions at lower latitudes and elevations. However, little progress has been made in defining what physiological changes are expressed within the organisms that allow them to prosper in their respective climatic conditions.

Plant and animal distributions are rarely controlled by a single physical or biotic parameter, but are mediated by complex interactions (Harper 1977; Brown & Gibson 1983; Tilman 1988). However, one of the strongest determinants of geographical distribution is temperature (Pianka 1966; Fukai & Silsby 1977; Pollock 1990). This includes the temperature extremes experienced within a given area, lengths of growing seasons with favourable temperatures, and rates and magnitudes of daily changes in temperature. High and low temperature extremes define geographic limits for survival and reproductive capability and plants usually have high and low temperature tolerance limits that reflect adaptation to their native habitats (Stevens 1989). In addition, plant metabolism must adapt continuously to temperature change within the permissive range. Every biological process depends on a series of consecutive and linked reactions, each characterized by its own temperature coefficient. Regulatory controls must adjust to differential effects of temperature on a multitude of complex processes that must be stringently controlled to maintain balanced reaction rates over the range of temperatures encountered. These control processes have almost certainly been selected by evolutionary pressures to maxi-

mize competitive ability to grow and propagate within a given environment. Thus, we hypothesize that the temperature coefficient of metabolism is related to a plant's growth rate.

The focus of this study is to define how metabolic activity is related to native environment in the temperature range between the limits of stability. Growth performance in this permissive temperature range determines properties such as rates of biomass production, yields, ability to compete within the plant community, and how rapidly plants can shift or expand their range in response to climatic changes. To define plant responses to temperature, measurement of integrated whole plant responses is required. Since measurement of growth itself is difficult, of limited accuracy, and uninformative during dormant periods, determination of rates of integrated metabolic processes such as photosynthesis and respiration are commonly used as surrogates. In this study, we have employed heat conduction calorimetry to make measurements of plant metabolic heat rate as a function of temperature (Criddle *et al.* 1991).

Plants from a single species or taxon collected from widely diverse latitudes and elevations and grown in a common garden for up to 10 years were used to establish the relation between the Arrhenius temperature coefficient of metabolic heat rate and a latitude-elevation function.

MATERIALS AND METHODS

Metabolic heat rate measurements were done with a Hart Scientific model 7707 heat conduction differential scanning calorimeter. Scanning calorimetric measurements followed the procedures of Hansen & Criddle (1990). Isothermal heat rate measurements were as described by Criddle *et al.* (1988). Approximately 100 mg of cuttings of meristematic or leaf tissue samples were placed in the calorimeter ampules with sufficient air volume to provide required oxygen. Heat rate measurements were initially made at 25 °C. Then the temperature was changed (at a rate of 99 °Ch⁻¹) for additional heat rate measurements. Most measurements were taken at 5° intervals from 25 to 5 °C, then activity was remeasured at 25 °C to determine any activity loss during the metabolic rate measurements at lower temperatures. When metabolic rate did not return to the original value at 25 °C, estimates of heat rates at any time during the experiment were obtained by linear interpolation between initial and final measurements at 25 °C. Metabolic heat rates were in the range of 100–300 μW, and were measured with an accuracy of +5 μW. Temperature measurements had an accuracy of +0.02 °C. The measured heat rate is equal to the metabolic heat rate in μW, i.e. μJ s⁻¹. The data collected are metabolic heat rates at various temperatures.

The Arrhenius equation is currently the best means available for describing temperature dependence of metabolic rates (Johnson, Eyring & Stover 1974). Because of the complexity of the integrated metabolic reactions and the

lack of experimental control over metabolic variables, several assumptions are implied by analysis of the data in this way. The Arrhenius equation is:

$$k = Ae^{-E/RT} \quad (1)$$

where k is the rate constant, E is the activation energy, R is the gas constant, and T is absolute temperature. The general rate law is

$$\text{rate} = kf(C_1, C_2, \dots) \quad (2)$$

where f(C₁, C₂, ...) is a function of concentrations of metabolic intermediates. Substituting Eqn 1 into Eqn 2 gives Eqn 3.

$$\text{rate} = Ae^{-E/RT} f(C_1, C_2, \dots) \quad (3)$$

Multiplying both sides of this equation by ΔH for the process gives

$$q = Ae^{-E/RT} f(C_1, C_2, \dots) (-ΔH) \quad (4)$$

where q is the heat rate. If we now assume that ΔH for the process is constant over the temperature range of interest, assume further that the function of concentrations is constant for a plant in a controlled metabolic state, and take the natural logarithm, Eqn 4 reduces to Eqn 5,

$$\ln q = \ln C - μ/T \quad (5)$$

where C is a constant and μ = E/R. Using the nomenclature of Johnson *et al.* (1974), μ is the Arrhenius temperature coefficient, taking into consideration the above assumptions, and has units of kelvins (K). Note the use of μ eliminates the units of moles commonly employed with E measurements, making it more appropriate for description of complex biological systems.

The slope of a line through data plotted as the natural log of the heat rate versus the reciprocal of the kelvin temperature is equal to -μ. The intercept is ln C. μ and ln C values were determined by linear regression of data according to Eqn 5. Justification for the use of μ to describe complex biological systems is presented by Johnson *et al.* (1974).

Cuttings taken from plants growing in the field were placed in a test tube with 1/4 Hoagland's solution or water, and stored at 0–5 °C until heat measurements could be made. Barley (*Hordeum vulgare* L., var. CM72) root tips were collected from 4-d-old, dark-grown seedlings.

Greenhouse plants

Tomato (*Lycopersicum esculentum* Miller) leaf segments studied were small expanding leaves from greenhouse grown plants. Amaranth (*Amaranthus* L.) samples used were whole, small seedlings grown from seed obtained from Rodale Research Center, Kutztown, PA, USA, and grown in constant light at 22 °C (Saver 1976).

Studies with natural populations

For white fir (*Abies concolor* Lindley) and subalpine fir (*Abies lasiocarpa* Hooker), metabolic heat rate measure-

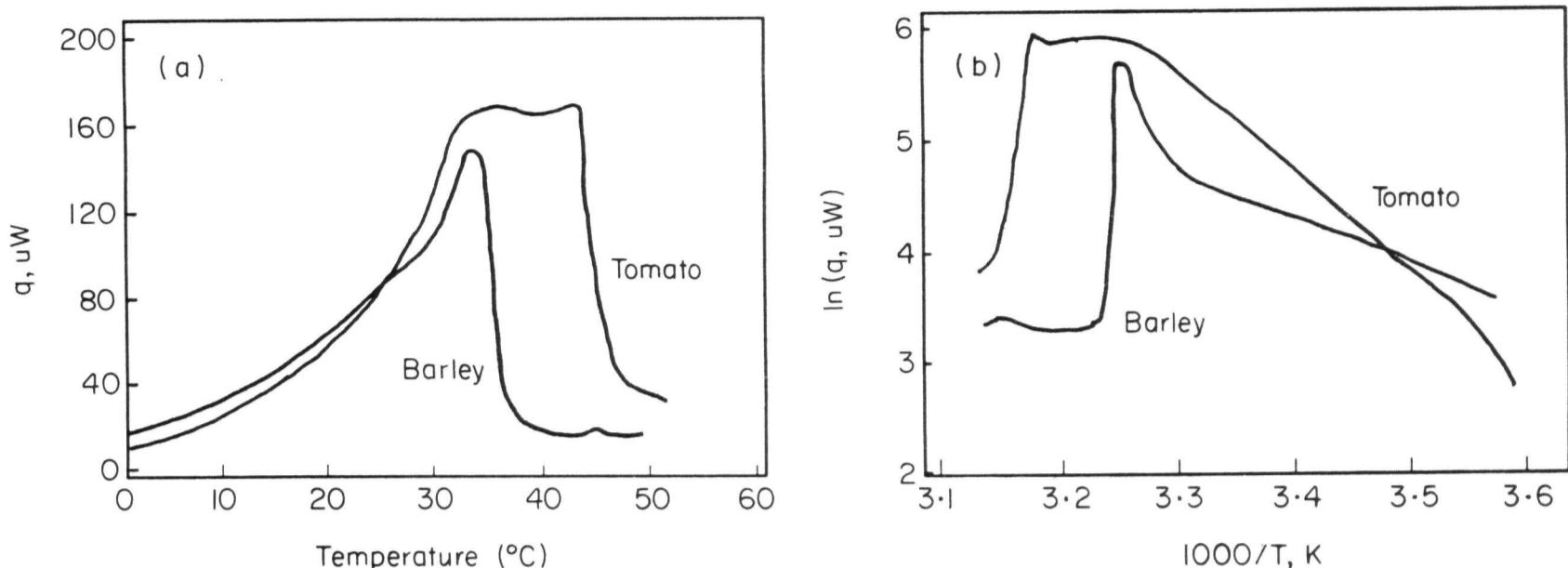


Figure 1. Differential scanning calorimetric determination of the metabolic heat rates (q) of tomato cells and barley root tips as a function of temperature determined by the procedures of Hansen & Criddle (1990): (a) metabolic rate versus Celcius temperature; (b) \ln metabolic heat rate versus $1000/T$, where T is in Kelvins.

ments were made using meristematic tissue from growing tips of branches. New leaves were used for chokecherry (*Prunus virginiana* Nelson, var. *melanocarpa*), sagebrush (*Artemesia tridentata* var. *tridentata* Nuttall for low elevation, and *Artemesia tridentata* var. *vaseyana* Nuttall for high elevation), Indian paintbrush (*Castilleja chromosa* Nelson for low elevation and *Castilleja miniata* Benth. for high elevation), bluebell (*Mertensia brevistyla* Watson for low elevation and *Mertensia ciliata* Don for high elevation), willow (*Salix exigua* Nuttall for low elevation and *Salix padifolia* Rydberg for high elevation), elderberry (*Sambucus caerulea* Nuttall for low elevation and *Sambucus racemosa* var. *microbotrys* Linnaeus for high elevation), groundsel (*Senecio integerrimus* Nuttall at low elevation and *Senecio serra* Hooker at high elevation), and gooseberry (*Ribes montigenum* McClatchie) for high elevation and golden currant (*Ribes aureum* Pushs.) for low elevation. Disks, cut with a punch from young expanding leaves, were used for the southern magnolia, *Magnolia grandiflora* L., and northern magnolia, *Magnolia soulangiana* Lindley. Small expanding leaf segments were used for studies of the different grass (*Poa*) species. Nomenclature follows, for the most part, Welsh *et al.* (1987).

Plants grown in common gardens

Common garden, woody, perennial species were originally collected throughout the intermountain western USA, a predominantly mid-latitude, semi-desert, steppe region with a wide range of elevations and latitudes. A garden in Springville, UT, planted with 12 individual plants of each accession, grown *in situ* for 10 years at that site was the source of bitterbrush (*Purshia tridentata* Candolle), and the closely related cliffrose (*Cowania stansburiana* Torrey). *Purshia* may have been derived directly from *Cowania* (McArthur, Stutz & Sanderson 1983). Hendrickson (1986) and Welsh (1986) have reduced *Cowania* to synonymy with *Purshia*. Plants grown in this garden

had native habitats from central Arizona to northern Washington, and from 450 to 2600 m elevation. Measurements were made on two to three fully expanded leaves. Rabbitbrush (*Chrysothamnus nauseosus* (Tallas) Britt. plants belonging to nine subspecies from five states were growing in a garden in the Snow Field Station, Ephriam, UT, for 8 years (McArthur, Mayer & Weber 1987; Meyer, McArthur & Jorgensen 1989; Bhat *et al.* 1990). Metabolic heat rate measurements were made on one cm tips from fully expanded leaves (eight to 12) from two plants from each accession. Wyoming big sagebrush (*Artemesia tridentata*, ssp. *wyomingensis* Nuttall) with accessions from four states grown for 4 years in a garden at Springville, UT, were studied. Earlier uniform garden growth studies on some of these sagebrush populations have been reported (McArthur & Welch 1982; Welch & McArthur 1986). Two to three fully expanded leaves were used for metabolic heat rate measurements.

Except for samples collected from one black spruce (*Picea mariana* Britton) in Alaska, samples from black spruce and tamarack (*Larix laricina* Koch) were obtained from trees collected at various locations in northeastern North America and grown in a Forestry Canada plot near Fredericton, New Brunswick. Redwood (*Sequoia sempervirens* Endlicher and *Sequoia gigantum* Buchholz) trees sampled are growing in the University of California, Davis, CA, arboretum. Metabolic heat rate measurements of these trees were made using meristematic tissue from growing tips of branches.

RESULTS

Figure 1a shows metabolic heat rate measured as a function of temperature by scanning calorimetry for barley, a cold-climate plant, and tomato, a warm-climate plant. These two curves are typical examples of high and low latitude plant responses to temperature. These data, showing actual activity profiles (of what is so often hypothesized in

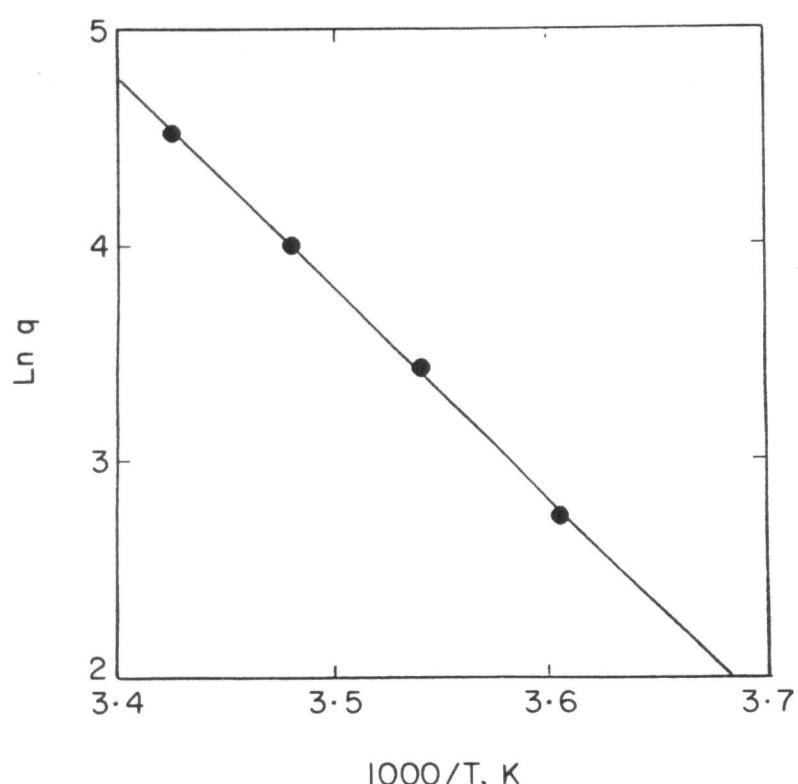


Figure 2. Illustration of isothermal calorimetric data collected for determination of Arrhenius temperature coefficients: an Arrhenius plot of metabolic heat rates measured for tamarack meristem tissue.

discussions of plant temperature response models) demonstrates two important points.

Firstly, the metabolic heat rate responses to limiting temperatures are obvious and largely what may be predicted from knowledge of growth habits of these two species. Barley metabolism rapidly decreases to near zero above 34 °C. Tomato activity plateaus at 32 °C and then decreases to near zero above 44 °C. Thus, the metabolic heat rate accurately reflects the high temperature stability of tomato as being 4–8 °C greater than that of barley. Additionally, considering the Arrhenius plots of these data (Fig. 1b), there are distinct differences at low temperatures. Below about 11 °C ($1000/T = 3.51$), tomato metabolism decreases rather abruptly with further decrease in temperature. This change in slope is typical of chilling-sensitive plants (Criddle *et al.* 1988). Barley metabolism continues with nearly constant μ down to near zero degrees.

Secondly, as no extended region of the Arrhenius plot is precisely linear, there are no extended temperature ranges where the activity conforms precisely to the Arrhenius equation. Therefore, reported values of μ must include the temperature range studied, and comparisons of μ values for different plants should be made only when measurements are examined in overlapping temperature ranges.

Isothermal rather than scanning calorimetry was employed to measure metabolic heat rates at several temperatures to obtain μ values because this method is more accurate for this purpose. Figure 2 is an Arrhenius plot showing the type of data obtained in such studies. The slope of the plot of the natural log of the heat rate against reciprocal Kelvin temperature is equal to $-\mu$. The fit of the data to a straight line demonstrates adherence to the Arrhenius relationship for tamarack in this temperature range. Such plots differ markedly for different plant species.

Table 1 gives μ values obtained for several pairs of woody plants from higher and lower latitudes and for pairs of closely related species of woody plants from high- and low-elevation habitats. All plants from high latitudes or elevations had μ values lower than their low latitude or elevation congeners. While the standard errors in these μ values are large because of within-sample population variation, and thus the significance of the differences between some individual pairs of plants is small, the conclusion that differences exist between high and low elevation, or high and low latitude samples remains highly significant ($P < 0.01$) when pooled data are considered. Thus, μ for a given species or for plants within a species is a function of both the elevation and latitude of the native habitat. No similar relationship holds for comparisons among genera; for example, the high elevation gooseberry has a value of μ larger than many of the species from low elevation.

The magnolia, spruce, tamarack and redwood plants tested had different geographical origins, but plant pairs used in this study (with the exception of an Alaskan black spruce) were raised for >5 years in common gardens. Thus, not only are the values of μ different, but they are genotypic. All these measurements were made during the month of June.

Table 2 shows results of similar studies on related pairs of herbaceous perennials. No relationship was found between μ values and geographic origin. Similar studies of μ made on laboratory-grown seedlings of amaranth (a widely distributed annual) from different geographical origins, showed no relation between μ and geographic origin (Table 3).

To define more clearly the nature of the dependence of μ on elevation and latitude, woody plant species complexes sharing genomes, collected from wide geographical areas but grown in common gardens, were examined. Three different species complexes were studied: bitterbrush; rabbitbrush; and sagebrush. The collection sites for each of the plants tested are shown in Table 4. Table 4 also presents μ values determined on plant materials collected from 6 to 18 June for each of the bitterbrush/cliffrose accessions. These values may be used to relate the slopes of the individual curves in Fig. 3a to the accessions.

Results of measurements of metabolic rates of the bitterbrush/cliffrose accessions tested are presented in Fig. 3a as Arrhenius plots. The differences in slopes (i.e. differing values of μ) for bitterbrush plants from different accessions result primarily from differences in metabolic rates at low, rather than at high temperatures. The lines of these Arrhenius plots of metabolic rates for tissue from this taxon cross near 25 °C. Thus, all plants have approximately the same specific metabolic heat rates in $\mu\text{W g}^{-1}$ tissue in the temperature range around 25 °C, but rates differ markedly at lower temperatures. The temperature at which all plants of this species have the same metabolic rate per milligram of tissue is referred to as the isokinetic temperature. For bitterbrush, the isokinetic temperature around 25 °C is above the average environmental temperature

Plant	Latitude (°N)	μ (K ± SE ³)	Temperature range (°C)
Northern Magnolia, <i>M. soulangiana</i>	unknown	5500 ± 800	15–35
Southern Magnolia, <i>M. grandiflora</i>	unknown	7500 ± 500	15–35
Black spruce, AK <i>Picea mariana</i>	68	4800 ± 400	4–19
Black spruce	58	7100 ± 600	4–19
Black spruce	46	8400 ± 600	4–19
Tamarack, <i>Larix laricina</i>	48	7400 ± 500	4–19
Tamarack	43	8400 ± 600	4–19

¹Each group of plants tested was grown in common gardens for >5 year except the Alaskan Black Spruce.

²Spruce and tamarack plants were collected from sites in Eastern Canada with elevations <700 meters.

³Standard error.

Table 1. (a) Arrhenius temperature coefficients of woody perennial plants from different latitudes^{1,2}

Plant	Elevation (m)	μ (K ± SE ³)	Temperature range (°C)
Sierra redwood, <i>Sequoia sempervirens</i>	1400	5000 ± 400	5–25
Coast redwood, <i>Sequoia gigantum</i>	100	8300 ± 800	5–25
Gooseberry, <i>Ribes montigenum</i>	3500	8800 ± 1000	4–19
Golden currant, <i>Ribes aureum</i>	1900	11000 ± 200	4–19
Mountain chokecherry, <i>Prunus virginiana</i>	3500	4500 ± 2600	5–20
Valley chokecherry, <i>Prunus virginiana</i>	1900	6100 ± 2400	5–20
Mountain willow, <i>Salix planifolia</i>	3500	3800 ± 1800	5–20
Valley willow, <i>Salix exigua</i>	1900	8200 ± 1600	5–20
Mountain sagebrush, <i>A. tridentata</i> var. <i>vaseyana</i>	3500	1400 ± 900	5–20
Valley sagebrush, <i>A. tridentata</i> var. <i>tridentata</i>	1900	5000 ± 1000	5–20
Subalpine fir, <i>Abies lasiocarpa</i>	3500	4500 ± 500	5–20
White fir, <i>Abies concolor</i>	1900	5500 ± 600	5–20

⁴Plants in this part of the study were all from 40 ± 1 °N latitude. Two to four plants were measured for each species.

Table 1. (b) Arrhenius temperature coefficients of woody perennial for high/low elevation comparisons⁴

encountered by this species during seasons of active growth.

Figure 3b presents these same data as a contour plot, relating latitude, elevation and μ . The contours link regions with common μ . This plot shows that the origins of plants studied from the bitterbrush common garden are widely distributed in latitudes and elevations, and demonstrates the gradient of decreasing μ as measurements are made from low elevation and latitude to higher elevation and latitude plants.

Figure 4 shows the relationship between μ values for individual bitterbrush plants and the geographical origin of the plants. μ is plotted as a function of elevation plus latitude. The function best fitting these data to a straight line was determined by multivariate least squares analysis to be:

$$\mu = 14.3 - [1.43 \text{ Elevation} + 0.122 \text{ latitude}]$$

(7)

where elevation is in kilometres and latitude is in degrees. The quantity in the brackets, providing the best-fit function of latitude and elevation for the horizontal axis for these bitterbrush accessions, is also used below to provide a fit of μ versus plant origin for rabbitbrush and sagebrush. The two coefficients have units of kiloKelvin per kilometre (kK km^{-1}) and kK degree^{-1} , respectively. The ratio of these two coefficients is 85 m degree^{-1} , i.e. an 85 m increase in elevation has an effect on plants equivalent to one degree increased latitude. The constant, 14.3 kK, is the extrapolated value of μ expected for bitterbrush plants adapted to conditions at the equator and sea level. While the significance of this extrapolated value is questionable, it is worth noting that μ values for tropical plants are commonly in this range (unpublished observations).

The absolute values measured for μ for individual bitterbrush plants changed as the growth season progressed.

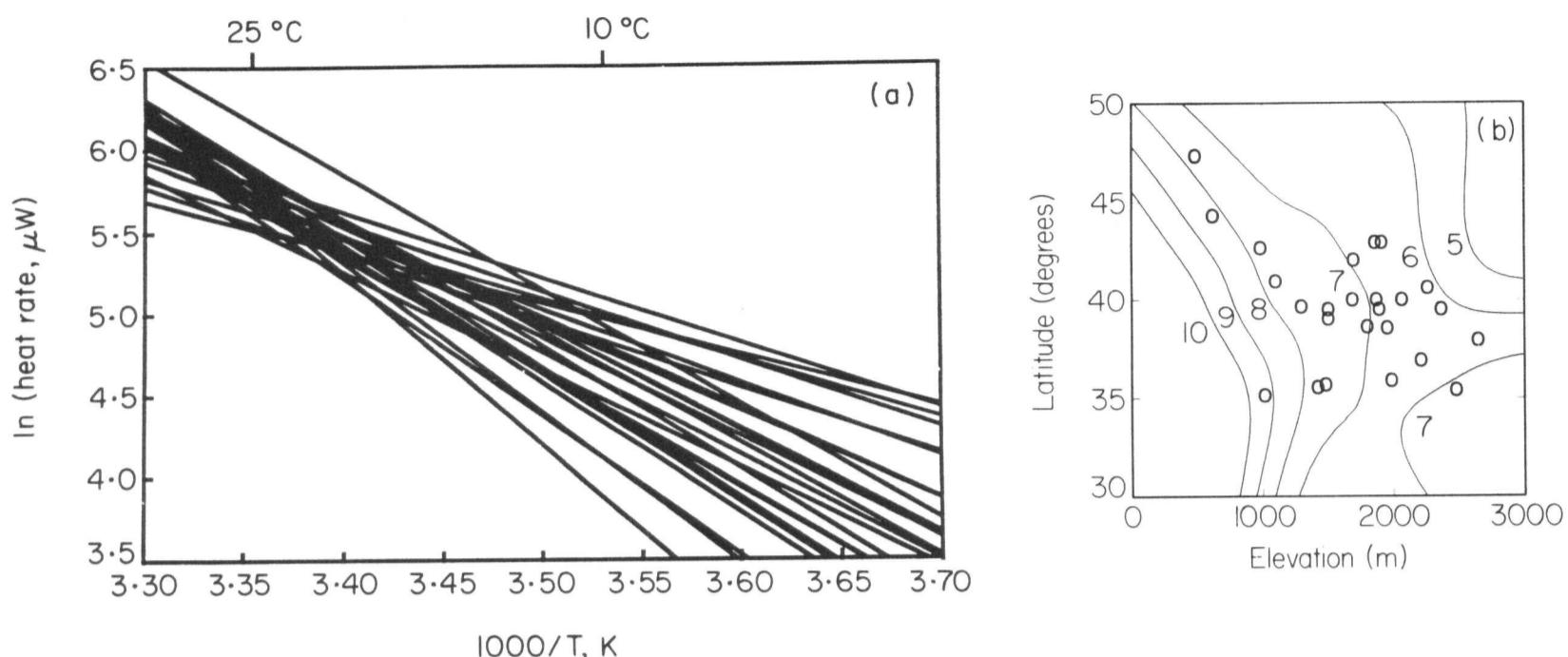


Figure 3. Temperature dependence of metabolic activities of bitterbrush and cliffrose accessions. (a) Arrhenius plots of metabolic activities of bitterbrush and cliffrose accessions. Data were collected as shown in Fig. 2 on samples of similar mass, and plotted as \ln (heat rate mg^{-1}) to illustrate intersection at a common temperature. Individual lines in this plot can be related to plants from different origins by comparing relative values of μ from Table 4a. (b) Values of μ obtained from plot (a) are presented as a contour plot to show relation of μ to geographic distribution of plant sources. Contour lines connect regions of common μ . Numerical values associated with each contour line represent the values of μ .

Table 2. Arrhenius temperature coefficients of herbaceous perennials from different elevations^{1,2,3}

Plant	μ (K)
Alpine ⁴ bluebell, <i>Mertensia ciliata</i>	3300 ± 800
Valley bluebell, <i>Mertensia brevistylle</i>	3400 ± 600
Alpine elderberry, <i>Sambucus racemosa</i>	6700 ± 900
Valley elderberry, <i>Sambucus caerulea</i>	6100 ± 500
Alpine bluegrass, <i>Poa</i> spp.	7000 ± 600
Valley bluegrass, <i>Poa</i> spp.	5000 ± 400
Alpine paintbrush, <i>Castilleja miniata</i>	5800 ± 300
Valley Paintbrush, <i>Castilleja chromosa</i>	7000 ± 1200
Alpine groundsel, <i>Senecio serra</i>	5400 ± 800
Valley groundsel, <i>Senecio integerrimus</i>	5200 ± 400

¹The temperature range for all these studies was 5–25 °C.

²Plants in this study were collected between 40 and 41 °N latitude.

³Elderberry (*Sambucus* spp.) is included in this table because it acts as a herbaceous perennial in activation energy and the pithy, woody stems of the high elevation plants behave in a herbaceous manner; for example, freeze back annually or semiannually. The low elevation plants do not freeze.

⁴Alpine elevations are in the range 3300–3500 m. Valley species were collected near 1700 m elevation.

Samples collected during the early spring flush of leaf growth yielded μ values that were high, but changing daily to lower values (Table 5). Arrhenius plots, developed using early and later season metabolic rate measurements for a single bitterbrush plant, gave lines that again intersected at a common point to give an isokinetic temperature near 25 °C (Fig. 5). Once again, it is clear that this intersection of lines is generated by seasonal changes in metabolic activities at low, rather than at high temperatures. Similar seasonal changes in temperature dependence of

metabolism were observed for all seven bitterbrush plants examined in this fashion.

Not all plants of a given taxon undergo the change to lower μ at the same time of year. The change for the more southerly occurring cliffrose plants preceded changes in its more northern bitterbrush relative (Table 5, and similar results shown in Fig. 7 for sagebrush). Moreover, both bitterbrush and cliffrose accessions with more southern and low elevation origins also generally changed to lower μ values earlier in the growing season than more northern and high elevation accessions.

Studies of metabolic rates of rabbitbrush at different

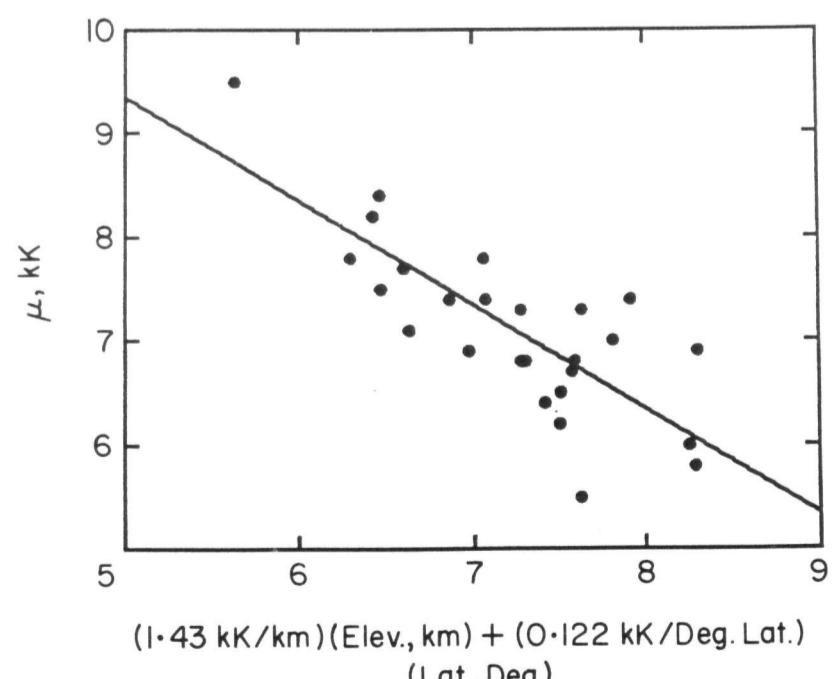


Figure 4. Arrhenius temperature coefficients of bitterbrush and cliffrose accessions plotted as a function of latitude and elevation of plant origin. The function of latitude and elevation used is an empirically derived expression to produce the best fit of the data to a straight line.

Species	Origin ¹	Climate	μ (K ²)
<i>A. hybridis</i>	Nigeria	Dry tropical	9500 ³
<i>A. hybridis</i>	West Pakistan	Dry tropical	9500
<i>A. caudatus</i>	Cusco, Peru	Mountain, chill	5600
<i>A. caudatus</i>	South Lorenzo, Bolivia	Mountain, chill	8900
<i>A. caudatus</i>	Ayacucho, Peru	Mountain, chill	6600
<i>A. hypochondriacus</i>	Janla, Nepal	Warm, subtropical	6800
<i>A. hypochondriacus</i>	?	Warm, subtropical	7100
<i>A. hypochondriacus</i>	Mexico	Warm, subtropical	7800
<i>A. cruentus</i>	Benin (Africa)	Temperate and subtropical	7400

Table 3. Arrhenius temperature coefficients of *Amaranthus*

¹Amaranth species originated in the highlands of tropical and subtropical America but are now widely grown and naturalized in other areas (Saver 1976).

²Measurements on four samples from each provenance gave an average standard error of ± 600 K.

³Measurements of μ were all done over a 5–25 °C temperature range.

temperatures yielded a family of intersecting lines for different subspecies in an Arrhenius type plot similar to that for bitterbrush (Fig. 3a). The resulting curves intersect with values of metabolic heat near 1.5 $\mu\text{W g}^{-1}$ and at an isokinetic temperature near 28–30 °C as shown in Fig. 6a. In this study, leaf tip tissues from two separate rabbitbrush plants from each accession were examined to determine intra-accessional variability. These pairs are plotted in Fig. 6b as open and closed circles showing μ versus the same elevation plus latitude function developed for bitterbrush. Regression lines fit to each set of data have virtually the same slope and similar intercepts. This establishes not only that bitterbrush and rabbitbrush have similar relations between μ and plant origin, but also that a significant portion of the scatter in fit of the data in these plots is due to individual variability among plants of a given accession.

Measurements on a third woody perennial, Wyoming big sagebrush, yielded similar results. Values of μ again show the same type of biogeographical distribution when plotted versus the elevation-latitude function (Fig. 7).

Again, values of μ changed as the growing season progressed, with the time of decrease being a function of latitude and elevation. This is demonstrated by considering first the open symbols (circles and triangles) in Fig. 7. The open symbols show data obtained on 28 June. These data show no correlation with elevation and latitude since some of the data were collected on plants that had gone through the characteristic seasonal change to lower μ while others had not. The solid circles represent data collected on 27 August. The data plotted as open and closed circles in Fig. 7 both fit the same latitude plus elevation relationship observed with bitterbrush and rabbitbrush.

The early season data (plotted as open triangles) fit Eqn 7, but with a different intercept. When four of these five samples were remeasured on 27 August (now plotted with solid circles), they did become part of the population fit by the common elevation plus latitude function. Plants with an elevation plus latitude function greater than eight on the scale of these plots are likely to encounter frost during any month of the year.

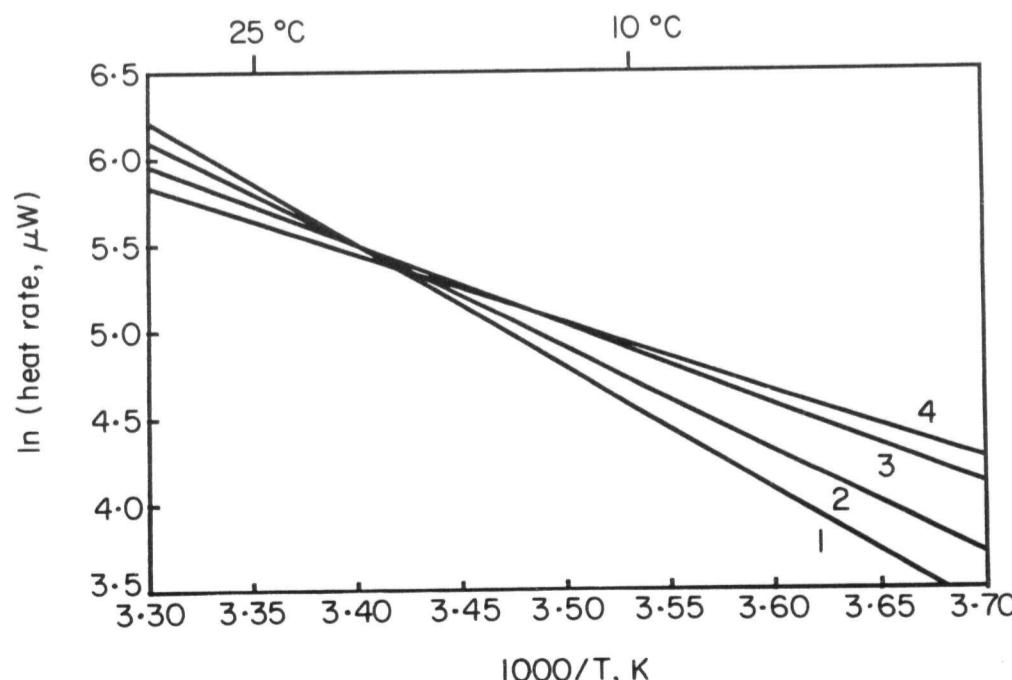


Figure 5. Arrhenius plots of metabolic rates of similar sized samples from a single plant from a single bitterbrush accession (Fairview, UT, 39° 38' latitude, 1950 m elevation) at different times in the growth season. Curves indicated 1 through 4 were obtained on 9 May, 4, 6 and 19 June in 1991, respectively.

Table 4. Plant collection sites

Species/location	Elevation (m)	Latitude ($^{\circ}$ N)	μ (K^{-1})
(a) Bitterbrush, <i>Purshia tridentata</i> , and cliffrose, <i>Cowania stansburiana</i>			
American Fork, UT	1550	39.7	7.4
Bell Rapids	950	42.8	7.7
Bishop, CA	1850	37.4	7.5
Blackfoot, ID	1400	43.2	7.3
Bryce, UT	2400	39.7	5.8
Dave Valley, NV	1950	38.7	6.2
Diamond Mt. UT	2300	40.6	6.0
Elko, NV	1700	40.0	6.8
Fairview, UT	1950	39.6	7.3
Hagarman, ID	900	42.3	8.2
Janesville, UT	1350	36.3	7.4
Kaibab, AZ	1900	34.8	6.9
Kyle Canyon	2150	36.3	6.5
Mono Lake, CA	2600	37.5	6.9
Montrose	1800	38.5	6.8
Nahahum, WA	450	40.0	7.7
Pioche, NV	1950	37.9	6.4
Point of Rocks, WY	2050	40.0	7.0
Prescott, AZ	1450	34.5	7.4
Preston, ID	1700	42.1	6.7
Santaquin, UT	1550	39.6	7.8
Service Creek, OR	650	44.9	8.2
Silver City, UT	1900	39.9	6.8
Soda Springs, ID	1900	42.6	7.4
Thoreau, NM	2350	35.0	7.3
Ventura, CA	1000	34.3	9.7
Weed, CA	1100	41.3	7.1
(b) Rabbitbrush, <i>Chrysothamnus nauseosus</i>			
Big Water, AZ	1360	37.1	5.7
Coral Pink Sand Dunes UT	1800	37.0	5.9
Ephriam, UT	2520	39.2	4.3
Halls Fork, UT	2060	40.2	4.0
Lancaster, CA	730	34.7	6.9
Mt Dell, UT	1790	40.7	5.2
Nephi Canyon UT	1780	39.7	4.3
Pt. of Rocks, NV	1400	36.8	6.9
Trout Creek, NV	1310	41.3	6.3
Terry, MT	740	46.8	6.5
Walker River, CA	2000	38.5	6.6
(c) Sagebrush, <i>Artemisia tridentata</i>			
Arco, ID	1645	45.0	
Brown's Park, UT	1710	40.8	
Daniel, WY	2225	42.8	
Dinosaur, CO	1750	40.2	
Fredonia, AZ	1710	36.9	
Glenn's Ferry, ID	950	43.0	
Gordon Creek, UT	2130	39.6	
Kemmerer, WY	2260	41.9	
Loa, UT	2200	38.4	
Oasis, NV	1780	41.0	
Rush Valley, UT	1650	40.3	
Squaw Butte, OR	1465	43.5	
Warren, MT	1370	45.1	

¹ Values measured 6-18 June.

DISCUSSION

The metabolic rates of plants are commonly assumed to double with every 10° increase in temperature (near 25°C), i.e. $Q10=2$ (James 1953; Atkin & day 1990). While recognition of differences in $Q10$ among plants is widespread, there is limited available information describing previous systematic studies of the relation of $Q10$ or μ to climate (temperature) adaptation. For plants from some woody species, our results establish a relationship between μ and the elevation and latitude at which a plant is native.

The important observations and conclusions from the μ data are:

- (1) In all woody plants studied, southern members of pairs of closely related plants have higher μ than northern members, and low-elevation members have higher μ than high-elevation members.
- (2) While relative μ values among congeneric, woody, perennial plants are related to the latitude and elevation of plant origin, we could find no relation between the location of plant origin and absolute μ values.
- (3) For the woody plants studied, values of μ change during the growth season. Values start high in the early spring, then decrease and level during the summer. The time of occurrence of this change differs with accession and is related to elevation and latitude of plant origin, with low, southern changing before high and more northern. Earlier studies of $Q10$ through three years of growth of hinoki trees have shown a similar seasonal dependence (Hagihara & Hozumi 1991). Relatively high $Q10$ values (near 3) were noted in early spring, followed by an approximately linear decrease to about 1.5 during July and August and a return to higher values in the autumn.
- (4) Since all plants tested from the common garden plots were grown >4 (most for >10) years in the locally prevailing conditions, the differences in μ and times of changes in μ during the growing season must be genetically determined characteristics.
- (5) The elevation-latitude function describing μ is approximately the same for each of the woody, perennial species complexes studied. This similarity was established by plotting data from each species against the elevation-latitude function developed for bitterbrush. The ratio of the elevation and latitude coefficients suggests that an 85-m elevation increase has the same effect on the adaptation of μ to the environment as a 1° increase in latitude. This is remarkably similar to the common dictum that a 100-m increase in elevation is equivalent to a 1° increase in latitude with respect to changes in the mean atmospheric temperature (Raven *et al.* 1981).
- (6) No apparent relation exists between activation energies and geographic origins of the pairs of herbaceous perennials and annuals (Tables 2 & 3). Annuals and herbaceous perennials apparently respond to their environmental temperature regime in a fashion different from that of the woody perennials. The annuals

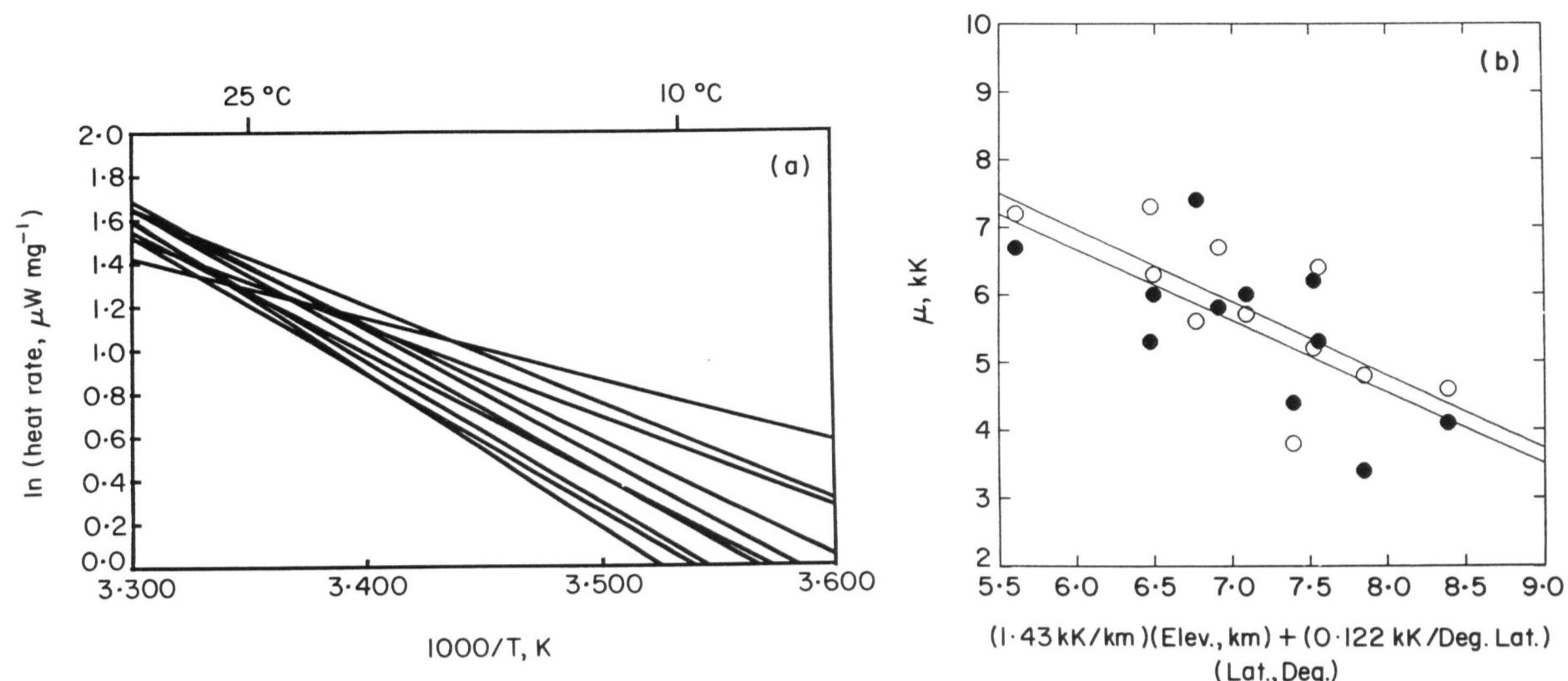


Figure 6. (a) Plots of \ln (specific metabolic heat rates; averaged for two plants for each accession) versus $1/T$ to determine the isokinetic temperature for rabbitbrush accessions. The relative slopes for individual plants in this plot can be related to plants from a given accession by comparison with the μ data listed in Table 4b. (b) Arrhenius temperature coefficients of various accessions of rabbitbrush as a function of latitude and elevation of origin. Two different plants were tested from each accession (indicated by open and filled circles at the same abscissa).

with their short growing seasons may simply adjust the time at which growth occurs to avoid large differences in growth climates, i.e. alpine annuals grow later in the summer than the valley annuals. The temperature ranges to which they are subject during their growth season may thus not be much different in different climatic zones.

Clearly, μ is an important determinant of relative metabolic and growth rates, and thus, can affect a plant's ability to compete with other plants in the environment.

Not only must the value of μ be matched to the climate at the growth site, the change in μ during early spring growth of perennials must also be matched to seasonal changes in the local climate. The climate: μ mismatch probably explains why bitterbrush plants collected from both the north and south ends of the range do not perform well in the common garden located near the latitude-elevation centre of the range in Provo, UT. Because plants cannot maintain their tissues at an optimum growth temperature, matching μ to the temperature profile experienced can be

Origin	Elevation (m)	Latitude ($^{\circ}$ N)	Date measured ¹	μ (K ²)
Prescott, AZ	1450	34.5	9 May	8300
			4 June	7400
Mono Lake, CA	2600	37.5	14 May	9700
			6 June	6900
Hagerman, ID	900	42.4	9 May	11400
			18 June	8200
Boise, ID	900	43.4	9 May	11500
			18 June	5600
Mt Dell, UT	1790	40.8	9 May	10000
			18 June	5500
Bishop, CA	1850	37.2	9 May	11300
			18 June	7500
Diamond Mtn, UT	2300	40.6	4 June	8500
			18 June	6000
Ventura, CA	1000	34.3	4 June	9700
			18 June	8700
Fairview, UT	1950	39.6	9 May	10100
			4 June	8100
			6 June	7300
			18 June	5400

Table 5. Change in Arrhenius temperature coefficient during spring development of bitterbrush (*Purshia tridentata*) and cliffrose (*Cowania stansburiana*)

¹Measured in 1991.

²Average error in two or three replicates of each sample was ± 675 K.

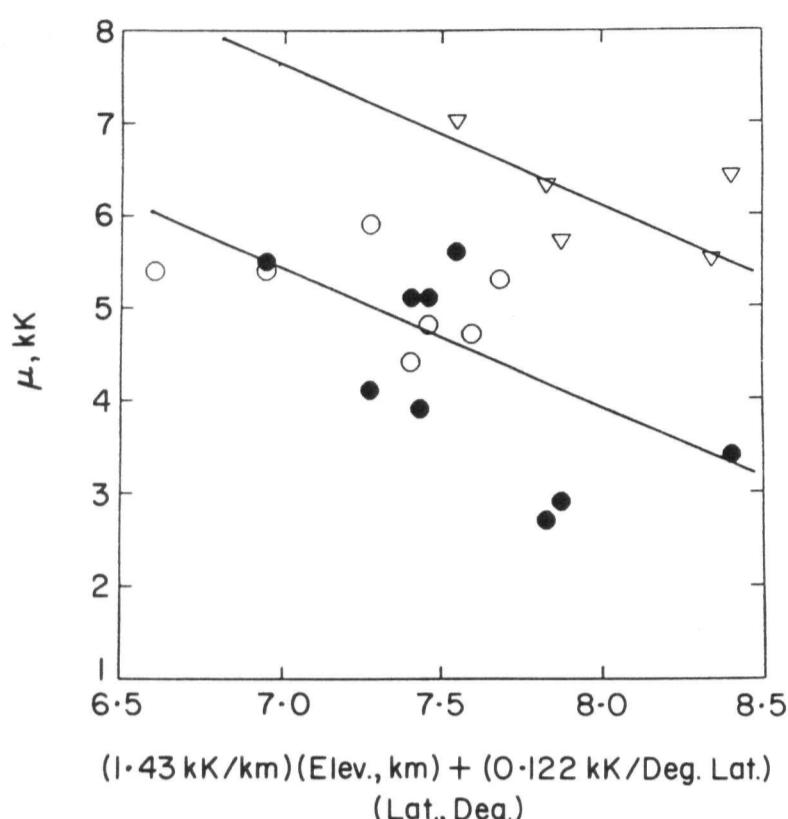


Figure 7. Arrhenius temperature coefficients for metabolism of various accessions of Wyoming big sagebrush as a function of latitude and elevation of origin on 28 June (open symbols), and on 27 August (closed circles). The two lines are plotted according to Eqn 7 with different intercepts for the open triangles and closed circles.

an important mechanism for optimizing economic growth rate (Stucki 1989; Westerhoff *et al.* 1983). Furthermore, because biomass accumulation is an exponential function of growth rate, a small difference in μ can have a very large effect on total plant growth (Amthor 1989).

Evaluation of the importance of high or low μ to plant growth is aided by consideration of Fig. 3a. Bitterbrush, rabbitbrush and sagebrush, plants spend the majority of their growing time at temperatures below the isokinetic temperature. At all temperatures below the isokinetic temperature, the metabolic rate (and thus total growth) is greater for those plants with lower μ values. At 10°C, for example, the metabolic rate gets larger by a factor of about 2 for a doubling of μ . Temperate and Arctic plants with their broad range of seasonal temperature exposures, relatively low average temperature, and large magnitude and rate of daily temperature variations would be expected to maximize relative growth rate by having low μ , relatively high activity near 0°C and an isokinetic temperature near the maximum limit of thermal stability.

The correlation of μ with latitude and elevation suggests that development of increasingly low μ values with increasing latitude and elevation increases the survival and competitiveness of bitterbrush, rabbitbrush and sagebrush plants. Data taken on the pairs of species from different climate zones suggests the observations on bitterbrush and rabbitbrush and sagebrush can be extended to a general statement that within a given competitive niche, μ is related to the latitude and elevation, among species as well as within a given species.

One possible reason for the evolutionary adaptation of low μ values as a rationale in development of high latitude

and high elevation plants is that wide variations of temperature will cause relatively small variations in metabolic rate. Limiting the temperature dependence of metabolic steps results in smaller changes in absolute and relative concentrations of intermediate metabolites. Since these concentrations must be regulated to maintain balanced metabolism, low activation energies can allow a smaller range of controls.

Possible reasons for high μ in the spring are less apparent. All three of the woody perennials studied in detail experience large spring temperature fluctuations with a continuing threat of freezing injury until early or even late summer over portions of their native region. Young, rapidly growing tissue is sensitive to freezing damage. Development of lower μ would then follow as danger of freezing passed. This could allow plants an effective means to extend their normal temperature (and geographical) range. The loss in overall growth in early spring due to temperature shutdown would be more than made up by avoiding tissue damage. With this rationale, the more southern and lower elevation plants would switch to the low μ form earlier in the year (as observed) as threat of freezing passes earlier.

Temperature dependencies of plants originating in subtropical and tropical environments would not necessarily benefit from these same rationales.

There are no compelling reasons to link μ and enzyme catalytic efficiency (i.e. interpretation in terms of activation energies of enzyme catalysed reactions) in these studies. Values of μ probably should be interpreted simply in terms of the temperature dependence of some controlling process. This could be a direct temperature effect on kinetics or a temperature effect on binding of regulator molecules. The observed linear \ln (heat rate) versus $1/T$ dependence applies equally well to both. The Arrhenius equation ($\ln k = \text{Constant} - E/RT$) and the van't Hoff equation [$\ln K_{\text{eq}} = \text{Constant} - (\Delta H/RT)$] describing a temperature induced shift in equilibria have the same form. These are indistinguishable without knowing details of the chemistry.

In addition to describing how temperature influences biogeographic patterns of plants, the discoveries reported here may have practical applications in the improvement of crop productivity. For crop plants with an isokinetic point above the average temperature of the environment, selection for a low μ may be a useful tool to increase growth rate. On the other hand, selection for a high μ may result in increased productivity of crops derived from a population with an isokinetic temperature below the average environmental temperature.

The experiments reported on plants of a given species with different geographical origins, but grown in common gardens, indicate that μ is a genetically defined plant property, and therefore, may be a candidate for molecular genetic manipulation. The fact that μ values differ quite widely among plants within a given species also suggests the possibility of selection for this characteristic to extend ranges of plant growth. The differing values of μ across the

geographic range suggest that μ and the maximum or minimum temperature limits for stability combine to determine growth range. The response to temperature extremes generally determines viability of a plant in a particular environment in a yes/no fashion. The temperature dependence of metabolism acts in a more subtle fashion through competition, both inter- and intraspecies. Without exceeding temperature limits, a plant can still experience deleterious effects of moving across a range. The mismatching of μ to climate may explain why north to south plantings are frequently not successful, even within known temperature extreme limits. The requirement that μ and climate be matched for good performance also has consequences in a plant's ability to migrate and compete in communities during periods of climate change, even if temperature limits for growth and reproduction are not exceeded.

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