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Plant Transpiration at High Elevations: Theory, Field Measurements, and Comparisons with Desert Plants

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Summary. The influence of elevational changes on plant transpiration was evaluated using leaf energy balance equations and well-known elevational changes in the physical parameters that influence water vapor diffusion. Simulated transpirational fluxes for large leaves with low and high stomatal resistances to water vapor diffusion were compared to small leaves with identical stomatal resistances at elevations ranging from sea level to 4 km. The specific influence of various air temperature lapse rates was also tested. Validation of the simulated results was accomplished by comparing actual field measurements taken at a low elevation (300 m) desert site with similar measurements for a high elevation (2,560 m) mountain research site. Close agreement was observed between predicted and measured values of transpiration for the environmental and leaf parameters tested.

Substantial increases in solar irradiation and the diffusion coefficient for water vapor in air (D_{wv}) occurred with increasing elevation, while air and leaf temperatures, the water vapor concentration difference between the leaf and air, longwave irradiation, and the thermal conductivity coefficient for heat in air decreased with increasing elevation. These changes resulted in temperatures for sunlit leaves that were further above air temperature at higher elevations, especially for large leaves. For large leaves with low stomatal resistances, transpirational fluxes for low-elevation desert plants were close to those predicted for high-elevation plants even though the sunlit leaf temperatures of these mountain plants were over 10° C cooler. Simulating conditions with a low air temperature lapse rate ($0.003° \mathrm{C\,m^{-1}}$ and $0.004° \mathrm{C\,m^{-1}}$) resulted in predicted transpirational fluxes that were greater than those calculated for the desert site. Transpiration for smaller leaves decreased with elevation for all lapse rates tested ($0.003° \mathrm{C\,m^{-1}}$ to $0.010° \mathrm{C\,m^{-1}}$). However, transpirational fluxes at higher elevations were considerably greater than expected for all leaves, especially larger leaves, due to the strong influence of increased solar heating and a greater D_{wv}. These

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results are discussed in terms of similarities in leaf structure and plant habit observed among low-elevation desert plants and high-elevation alpine and subalpine plants.

Introduction

Plants libing at high elevations often have morphological features which are similar in many respects to desert plants (Went, 1953; Billings and Mooney, 1968; Walter, 1973). These features include dwarf shrubby or herbaceous habits, small leaves and reproductive structures, thick cuticles, and often a dense pubescence. Even the abundant montane and subalpine conifers have small needle-like leaves that are similar to the leaves or photosynthetic stems characteristic of the evergreen shrubs or trees (green leaves or stems) of the hot deserts of the southwestern U.S. such as *Bebbia*, *Cercidium*, *Dalea*, *Hoffmannseggia*, *Hymenoclea*, *Larrea*, *Peucephyllum*, and *Tamarisk*. Although reductions in leaf size have been shown to increase water conservation in desert plants (Gates, 1968; Smith and Nobel, 1977a, b; Smith, 1978), very little information exists regarding the effects of leaf size on the water relations of high elevation plants. To our knowledge there has been no comprehensive attempt to clarify the general biophysical indluences of higher elevations on plant transpiration, even though reference is often made to the environmental similarities between high elevation habitats and those of the lower elevation deserts. Moreover, these biophysical similarities may have contributed to the close phylogenetic relationship that appears to exist among certain desert and alpine plants (Went, 1953; Billings and Mooney, 1968).

Previous investigators have considered the effects of high elevations (low barometric pressures) om photosynthesis, recognizing that low partial pressures of CO_2 would act to decrease the diffusion rate of CO_2 into the leaf by lowering the concentration gradient from the air to the leaf (Billings et al., 1961; Mooney et al., 1966). However, subsequent work has shown that substantial increases in the diffusion coefficient for CO_2 in air (D_{CO_2}) at low atmospheric pressures may nearly compensate for the low ambient CO_2 concentrations under isothermal conditions (Gale, 1972, 1973). Even when one includes the effect of the dry adiabatic change in air temperature with elevation ($0.010° \mathrm{C\,m^{-1}}$), which would tend to decrease D_{CO_2}, a much smaller decrease in CO_2 uptake would occur than that expected when considering only the lower CO_2 volume concentrations at high elevations and not the substantial influence of pressure on D_{CO_2}.

In contrast to the diffusion of CO_2 into a leaf at low ambient pressures, water vapor diffusion from the leaf into the air would be expected to increase with elevation due to a corresponding increase in the diffusion coefficient for water vapor in air (D_{wv}) at lower atmospheric pressures (Grafts et al., 1949). Gale (1973) provided experimental evidence that a substantial increase in transpiration occurred for *Zea mays* and *Phaseolus vulgaris* with decreasing barometric pressure. However, his experiments were conducted under isothermal conditions which did not include an evaluation of the effects of air temperature lapse rates or the many other environmental, biophysical parameters which change markedly with elevation and may strongly influence transpiration rates.

The specific purpose of this investigation was to develop an analytical framework for determining the biophysical effects of high elevation on plant transpiration and elucidate potential avenues for plant adaptation. Comparisons were made between measurements on low-elevation desert and high-elevation mountain plants to evaluate possible similarities in the environmental demands on transpiration. The analysis employed standard leaf energy balance equations which incorporated empirical relationships for elevational changes in parameters which are known to strongly influence plant transpiration. These parameters included variations in the amount of incoming solar and longwave irradiation, air temperature, air water vapor concentration, and changes in the transfer coefficients for water vapor and heat in air with increases in elevation. In addition, the influence of leaf size and stomatal resistance on transpiration was determined under desert and mountain conditions. Computer simulations of plant transpiration were compared to actual field measurements taken at a desert and a mountain research site to provide an empirical validation between predicted results and those actually measured in the field. Differences in plant adaptive strategies for water conservation are discussed based on differences in the physical factors influencing transpiration between desert and mountain habitats.

Material and Methods

A simulation model was developed to evaluate the influence of high elevation on transpirational flux from plant leaves with identical stomatal resistances to water vapor diffusion and energy balance properties. Hypothetically large leaves were simulated using boundary layer thicknesses (δ) of 0.2 cm compared to small leaves where δ was equal to 0.02 cm (Nobel, 1974). Validations of these simulated results were accomplished by comparing transpirational fluxes measured at a low elevation desert site and a high elevation mountain site for plant species with large or small leaves and relatively high ($6\,\mathrm{s\,cm^{-1}}$) and low ($2\,\mathrm{s\,cm^{-1}}$) stomatal resistances. The accuracy of the simulated environmental conditions was tested by comparing field microclimatic measurements at both sites with the values mathematically predicted using the relationships described below (Eqs. 2 through 7). Sensitivity tests were conducted within the simulation model to determine the quantitative importance of variations in the air temperature lapse rate, stomatal resistance, and leaf size with increases in elevation.

Leaf transpirational flux can be quantified using Fick's first law for diffusion or Ohm's law analogy for electrical circuits (Nobel, 1974) where

$$J_{\mathrm{wv}} = D_{\mathrm{wv}} \frac{\Delta C_{\mathrm{wv}}}{\Delta X} = \frac{\Delta C_{\mathrm{wv}}}{R_{\mathrm{wv}}^{\mathrm{tot}}} \tag{1}$$

and J_{wv} is the transpiration rate per unit leaf area, D_{wv} is the diffusion coefficient for water vapor in air, ΔC_{wv} is the water vapor concentration difference between the air inside the mesophyll air space and the ambient air surrounding the leaf, ΔX is the length of the diffusion pathway, and $R_{\mathrm{wv}}^{\mathrm{tot}}$ is the total resistance to water vapor diffusion along ΔX. $R_{\mathrm{wv}}^{\mathrm{tot}}$ may be divided into series resistances of the leaf (intercellular air space and stomatal) and the boundary air layer (δ) next to the leaf surface (R_{wv}^{bl}), plus the resistance of the epidermis which is a parallel pathway with the stomatal resistance.

The diffusion coefficient for water vapor in air (D_{wv}) was varied with temperature and ambient pressure as follows (Boynton and Brattain, 1929):

$$D_{wv} = D_{wv}^{0} \left(\frac{T}{T^{0}}\right)^{m} \left(\frac{P^{0}}{P}\right) \tag{2}$$

where D_{wv}^{0} is the diffusion coefficient at T^{0} equal to 273.15° K and P^{0} equal to 1,013.25 mb (1 mb$=10^{2}$ Pascals), m equals 1.75 for water vapor in air, T is air temperature in °K, and P is atmospheric pressure in mb. Elevation can be converted to ambient pressures using Vitkevich's (1968) relation:

$$Z = 18{,}400\,(1+0.00366)\left(\frac{T^{0}+T}{2}\right) \log\left(\frac{P^{0}}{P}\right) \tag{3}$$

where Z is the elevation in meters.

The amount of water vapor in air at saturation was approximated using the relation (Saucier, 1955),

$$e_{s} = 6.11\ [10^{at/(t+b)}] \tag{4}$$

where e_{s} is the saturation vapor pressure of water in air in *mb*, t is air temperature in °C, a equals 7.5 and b equals 237.3.

Simulated values for increases in solar irradiation with elevation were determined according to Becker and Boyd (1961) for 40 °N. latitude, where

$$\%\,Solar = 2.955 + 4.685\,(Z-1) - 0.225\,(Z-1)^{2} \tag{5}$$

and % *Solar* is the percent increase in solar irradiation with elevation Z in thousands of feet.

Longwave irradiation from a clear sky (IR_{sky}) was computed as a function of water vapor pressure (e) in millibars and air temperature in °K as in Goss and Brooks (1956), or

$$IR_{sky} = 0.66 + (0.039\sqrt{e})\,\sigma(T)^{4} \tag{6}$$

IR_{sky} is in cal cm^{-2} min^{-1} (1 cal cm^{-2} min^{-1} $=697$ W m^{-2}) and σ is the Stefan-Boltzmann constant (6.13×10^{-11} cal cm^{-2} min^{-1} °K^{-4}). Upward longwave irradiation from the soil surface (IR_{up}) was calculated for soil surface temperatures considered to be 20° C above air temperature for sunlit surfaces and 5° C above air temperature for shaded soils, based on actual field measurements taken in June, 1976 at the desert site and June, 1978 at the mountain site. Soil temperatures were converted to longwave irradiation values using the Stefan-Boltzmann equation and assuming a soil emissivity of 0.97 (Nobel, 1974, Campbell, 1977).

The thermal conductivity coefficient (k) was varied according to air temperature by the relation

$$k = 0.00001\,(t) + 0.00348 \tag{7}$$

where k is in cal cm^{-2} min^{-1} °C^{-1} (Montgomery, 1948). Air temperatures were varied with elevation ranging from the dry adiabatic lapse rate of 0.010° C m^{-1} to a much lower rate of 0.003° C m^{-1}. Estimates of actual lapse rates between the desert and mountain research sites were calculated according to long term weather station records (Ting, 1976; Rechard and Smith, 1972, respectively) with corrections for standard latitudinal differences of 0.055° C °latitude^{-1} (Munn, 1966). Mean maximum air temperatures were compared to give more accurate estimations of transpirational demands during midday. Relative humidities at solar noon were estimated to be about 20% based on the weather station records at both research sites for June ($\bar{X}=21 \pm 7\%$ and $20 \pm 11\%$ for the desert and mountain sites, respectively).

Field measurements of plant transpiration and microclimate were taken during June, 1976 at the Philip L. Boyd Deep Canyon Desert Research Center located near Palm Desert, California (116° 22′ W., 33° 39′ N., elevation 300 m) and during June, 1978 at the University of Wyoming Science Camp near Centennial, Wyoming (106° 10′ W., 41° 21′ N., elevation 2,560 m). Air, soil, and leaf temperatures were measured with fine-wire copper-constantan thermocouples, or an infrared field thermometer (Barnes Engineering Co. model 14-220-4). Leaf resistances to water vapor diffusion were determined with a diffusion resistance porometer (Lambda Instruments Corp. model LI-60) with calibrations adjusted for variations in ambient pressure with elevation. The water vapor concentrations of the air adjacent to individual leaves was determined using a dewpoint hygrometer (Cambridge model 880) and the air inside the leaf was considered saturated at the leaf temperature.

Standard leaf parameters used throughout this investigation were a leaf absorptance to solar irradiation of 0.60, an emissivity to longwave irradiation of 0.97, a perpendicular orientation to the sun's direct rays, and a full hemispherical exposure to the sky above. Individual plant species chosen for comparisons between theoretically predicted and measured parameters were selected according to similarities in leaf size, stomatal resistance, and leaf absorptance. All computer simulations and sensitivity tests were run on a Xerox Sigma 7 computer at the University of Wyoming Computer Center.

Results

The influences of increasing elevation on the biophysical factors that may strongly influence plant water loss are schematically shown in Fig. 1. Following Eqs. 2–7, the diffusion coefficient for water vapor in air (D_{wv}) increases with decreasing pressure, but decreases in response to the decrease in air temperature associated with increasing elevation (Eq. 2). Solar and longwave irradiation from the sky (IR_{sky}) typically increase and decrease, respectively, with elevation according to Eqs. 5 and 6. A decrease in air temperature leads to a decrease in the amount of water vapor in the air ($C^{\mathrm{a}}_{\mathrm{wv}}$) at the same relative humidity (Eq. 4), plus a decrease in the thermal conductivity of heat in air (k) according to Eq. 7. A decrease in k acts to raise leaf temperature (T_{leaf}), which increases the leaf-to-air water vapor concentration difference ΔC_{wv}. However, the relationships shown in Fig. 1 indicate that the net effect of these elevational changes in

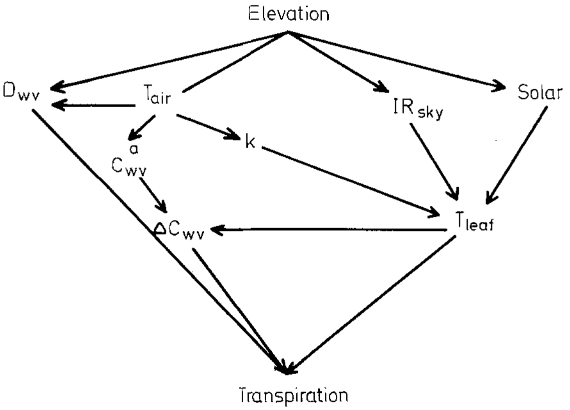

Fig. 1. Schematic representation of the influence of elevational increases on plant transpiration. D_{wv} is the diffusion coefficient for water vapor in air, T_{air} is air temperature, IR_{sky} and *Solar* are the amounts of downward infrared and total solar irradiation from a clear sky, C^a_{wv} is the H_2O vapor concentration of the air, k is the thermal conductivity of heat in air, ΔC_{wv} is the H_2O vapor concentration difference between the leaf and air, and T_{leaf} is the leaf temperature

transpiration are not intuitively predictable. The opposing influences of a lower atmospheric pressure and air temperature on D_{wv} and, thus, plant transpiration, is strongly dependent on the air temperature lapse rate of the area. Decreases in air temperature with elevation lead to decreases in C^a_{wv} which increase ΔC_{wv} and, therefore, transpiration (Eq. 1). However, the ultimate influence of elevation on T_{leaf} and, therefore, ΔC_{wv} is not obvious, but dependent on the combined effects of changes in T_{air}, k, IR_{sky}, and solar irradiation. In summary, although two of the three parameters influencing transpiration (according to Eq. 1) are known to be strongly affected by increases in elevation, the exact quantitative, or even qualitative, effects on plant transpiration are not known for these relatively familiar changes in environmental parameters with elevation.

Individual Changes in Physical Parameters with Elevation

Figure 2 shows the simulated changes in parameters that may strongly influence plant transpiration for an elevational range of from sea level (S.L.) to 4 km on June 21 at solar noon under clear skies, according to Eqs. 3–7. Predicted total solar irradiation at solar noon increased almost 40% from S.L. to 4 km with the most rapid change occurring from S.L. to about 2 km. Also, total solar irradiation measurements at solar noon around June 21 with clear skies at the desert and mountain sites were within 3% of the predicted values (849 vs. 870 W m^{-2}, desert site; 1,121 vs. 1,115 W m^{-2}, mountain site). Variations in longwave irradiation and air temperature showed a strong dependence on the air temperature lapse rate chosen, as well as elevational changes. Somewhat greater differences occurred in longwave irradiation between the simulated minimum and maximum lapse rates, compared to variations that resulted from elevational changes at a given lapse rare (Fig. 2). Field measurements of longwave irradiation and air temperatures indicated that the appropriate air temperature lapse rate for comparisons between the mountain and desert research sites, after correcting for differences in latitude (0.5° C °latitude^{-1}), was approximately 0.006° C m^{-1}. This estimated value for the air temperature lapse rate was

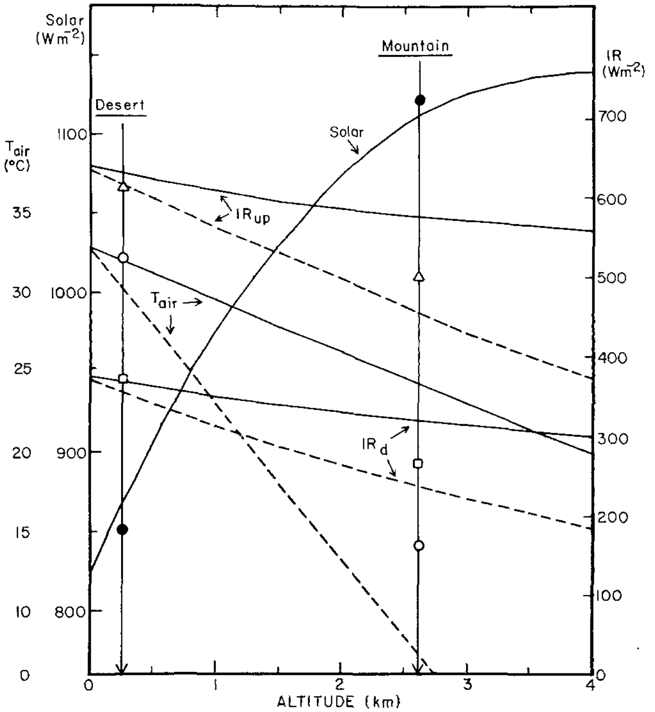

Fig. 2. Simulated variations in environmental parameters with increasing elevation for June 21 at solar noon. Changes in upward longwave irradiation from the ground (IR_{up}), longwave irradiation from the sky (IR_d), and air temperature (T_{air}) are plotted for air temperature lapse rates of 0.003° C m^{-1} (*solid lines*) and 0.010° C m^{-1} (*dashed lines*). Actual field measurements taken between June 19–23 at the desert and mountain research sites are also shown (Solar, —●; IR_{up}, —△; IR_d, —□; T_a, —○)

verified in the following section (Table 1) and used in subsequent calculations of plant transpiration at low and high elevations.

The calculated diffusion coefficient for water vapor in air (D_{wv}) changes markedly from S.L. to 4 km (Eq. 2). Simulating the lowest lapse rate of 0.003° C m^{-1} results in an increase in D_{wv} of about 45% (0.267 to 0.386 $cm^2 s^{-1}$) compared to an increase of almost 26% for a simulated lapse rate of 0.010° C m^{-1} (0.267 to 0.336 $cm^2 s^{-1}$). In contrast, the theoretical variation in the thermal conducticity coefficient (k) for heat in air with elevation is relatively small (Eq. 7). For the lowest lapse rate tested (0.003° C m^{-1}), k varies only about 4% from S.L. to 4 km (2.64 versus 2.55 W m^{-1} °C^{-1}) compared to about 12% (2.64 versus 2.36 W m^{-1} °C^{-1}) for the dry adiabatic lapse rate of 0.010° C m^{-1}.

Air Temperature Lapse Rates

Mean maximum daytime air temperatures were compared for the desert and mountain research sites from weather records collected within 0.5 miles of the research areas (Table 1). These values represent 13-year averages for the desert

Table 1. Air temperature lapse rates determined from monthly mean maximum air temperatures at the desert (elev. 300 m) and mountain (elev. 2,560 m) research sites from Ting (1976) and Rechard and Smith (1972), respectively. Adjusted lapse rates were calculated using a correction of 0.5° C per degree difference in latitude

Month	Mean maximum air temperatures (° C)		Non-adjusted lapse rate ($^{\circ}\mathrm{C\,m^{-1}}$)	Adjusted lapse rate ($^{\circ}\mathrm{C\,m^{-1}}$)
	Desert	Mountain		
May	31.2	11.1	0.0087	0.0071
June	35.4	19.4	0.0071	0.0054
July	38.3	22.8	0.0069	0.0052
August	37.7	23.9	0.0061	0.0044
$\bar{X}=$	35.7	19.3	0.0072	0.0055

(Ting, 1976) and 7-year averages for the mountain site (Rechard and Smith, 1972). Lapse rates for the spring and summer averaged about 0.006° C $\mathrm{m^{-1}}$ after adjustments of 0.5° C $^{\circ}\mathrm{latitude}^{-1}$ were made for the 7° 42′ difference in latitude between the two research sites. These months encompass the major summer growth period at the mountain research site, while May through June may also be a common period of substantial growth for a host of annual and perennial plants in the desert (Munn, 1974).

Plant Transpiration Parameters

The elevational parameters that influence plant transpiration according to Eq. 1 are plotted in Fig. 3 for the simulated large ($\delta = 0.20$ cm) and small ($\delta = 0.02$ cm) leaves, each with a low (2.0 s $\mathrm{cm^{-1}}$) and relatively high (6.0 s $\mathrm{cm^{-1}}$) stomatal resistances to water vapor diffusion. Predicted leaf temperatures were considerably higher than air temperature for the larger leaves at both stomatal resistances. However, a much greater maximum difference in leaf and air temperature occurred at 4 km than at S.L. (19.5° C versus 12.5° C). Simulated leaf temperatures for smaller leaves ($\delta = 0.02$ cm) were always within 3° C of air temperature at either stomatal resistance (Fig. 3). The smallest variation in leaf temperature with elevation occurred for small leaves (approx. 34° C at S.L. versus 12° C at 4 km) compared to large leaves (approx. 45.5° C at S.L. versus 28.5 at 4 km).

The water vapor concentration gradient from the leaf to the air (ΔC_{wv}) decreased significantly with elevation, especially for the simulated large leaf with high stomatal resistance (Fig. 3). The large leaves had the most rapid decreases in ΔC_{wv} at the higher elevations while small leaves had greater decreases in ΔC_{wv} at the lower elevations. For the large leaf with higher leaf resistance, ΔC_{wv} decreased about 52% (59.5 µg $\mathrm{cm^{-3}}$ at S.L. versus 28.5 µg $\mathrm{cm^{-3}}$ at 4 km) compared to a 68% decrease (29.1 versus 9.2 µg $\mathrm{cm^{-3}}$) for the small leaf with higher

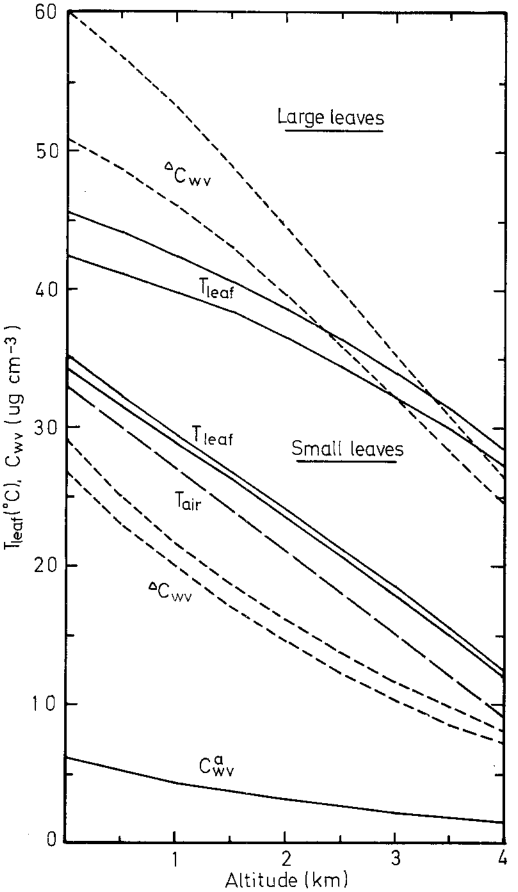

Fig. 3. Simulated variation in transpirational components with increases in elevation for large (δ $=0.2$ cm) and small ($\delta=0.02$ cm) leaves. ΔC_{wv} is the leaf-to-air water vapor difference (*dashed lines*), T_{leaf} is the leaf temperature (*solid lines*), T_{air} is air temperature, and C^{a}_{wv} is the water vapor content of the air. Each pair of curves for ΔC_{wv} and T_{leaf} are for a simulated high (6.0 s cm^{-1}) and low (2.0 s cm^{-1}) stomatal resistance to water vapor diffusion (upper curves in each pair represent higher resistance). The assumed lapse rate in air temperature was 0.006° C m^{-1}

leaf resistance. The water vapor concentration of the air, assuming 20% relative humidity, decreased 70% from S.L. to 4 km (6.1 to 1.8 µg cm^{-3}) reflecting the simulated decrease in air temperature of 0.006° C m^{-1}.

Simulated Plant Transpiration

Transpirational fluxes for large and small leaves with low and high stomatal resistances were plotted versus increases in elevation at various air temperature lapse rates (Fig. 4). Transpiration for the large leaves increased with elevation up to about 2.5 km for simulated lapse rates of 0.003° C m^{-1} and 0.004° C m^{-1}, and up

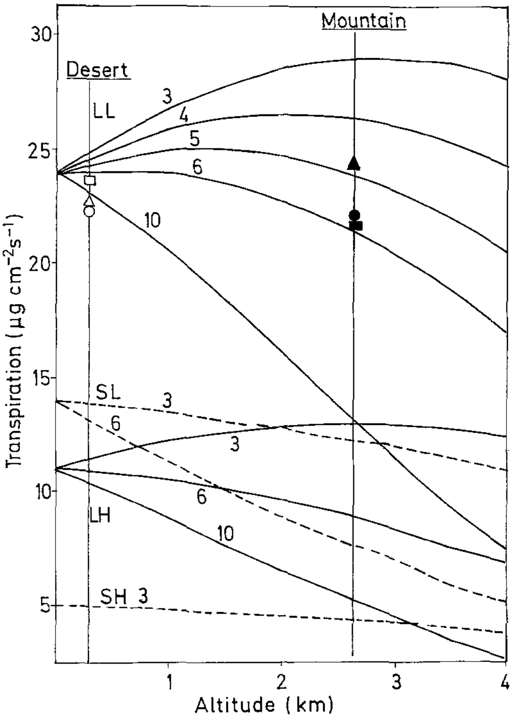

Fig. 4. Simulated transpiration with increasing elevation for large ($\delta = 0.2$ cm) and small ($\delta = 0.02$ cm) leaves with high (6.0 s cm^{-1}) and low (2.0 s cm^{-1}) stomatal resistances to water vapor diffusion (*LL*, large leaf with low resistance; *LH*, large leaf with high resistance; *SL*, small leaf with low resistance; *SH*, small leaf with high resistance). Indicated numbers within each group represent the simulated air temperature lapse rates, e.g. 3 represents 0.003° C m^{-1}. Symbols are for transpirational fluxes measured in the field for representative plants at the desert and mountain sites (*Encelia farinosa* and *Arnica cordifolia* △, ▲; *Hyptis emoryi* and *Mertensia viridus* □, ■; *Cucurbita palmata* and *Mimulus guttatus* ○, ●)

to about 1.5 km for lapse rates of 0.005° C m^{-1} and 0.006° C m^{-1}, but decreased rapidly with elevation for the dry adiabatic lapse rate of 0.010° C m^{-1}. Predicted transpiration was greater at the elevation of the mountain site compared to the desert site for lapse rates of lower than about 0.005° C m^{-1}. Higher elevations resulted in less transpiration as the lapse rate increased. Differences in predicted transpiration due to elevational changes at a given lapse rate were less than differences that resulted from the simulated variations in air temperature lapse rates (Fig. 4).

Simulated large leaves with a high stomatal resistance had much lower transpiration rates compared to large leaves with low stomatal resistance at all lapse rates tested (Fig. 4). Also, the percentage increase in transpirational flux with elevation was slightly greater for the large, high-resistance leaves than for the large leaves with the lower leaf resistance (a 73% versus 69% increase from S.L. to 4 km). For the dry adiabatic lapse rate of 0.010° C m^{-1}, large and small leaves had their most similar transpirational fluxes at an elevation of 4 km (7.5 versus 2.8 μg cm^{-2} s^{-1}, respectively) compared to a maximum difference of 23.9 versus 11.1 μg cm^{-2} s^{-1} which occurred at S.L. (Fig. 4).

Small leaves with low stomatal resistances had transpirational fluxes similar to large leaves with higher stomatal resistances, but had greater decreases in predicted transpiration with elevation than their large leaf counterparts, especially at elevations below 2 km (Fig. 4). A decrease in water loss of 8.5 $\mu g\,cm^{-2}\,s^{-1}$ occurred from S.L. to 4 km for the small leaf and 6.8 $\mu g\,cm^{-2}\,s^{-1}$ for the large leaf at the 0.003° C m^{-1} lapse rate, or a 61% reduction in transpiration for the small leaf compared to a 28% reduction for the large leaf. Variation in transpiration for the small leaf with a higher stomatal resistance was less, without any increase in transpirational flux with elevation, even at the lowest lapse rate tested (0.003° C m^{-1}).

Discussion

Plants growing at high elevations experience major changes in several environmental parameters that influence plant transpiration and photosynthesis, including the indirect effects of leaf temperature alterations and the more direct effects on the diffusion of CO_2 and H_2O vapor in air. The leaf temperatures simulated here show that the net effect of these elevational changes leads to substantially lower leaf temperatures, but with concurrent increases in leaf temperature over air temperature (Fig. 3). Thus, the heating effects due to a decrease in k and an increase in solar heating override the elevational decrease in longwave irradiation (Fig. 2). Apparently, for the hypothetical leaves treated here, a relatively large increase in D_{wv} with elevation does not increase transpirational cooling enough to offset the above heating effects. This is partially due to the contrasting effect of elevation on ΔC_{wv} (Fig. 3), whereby the decrease in ΔC_{wv} as a result of a much lower leaf temperature has a greater influence than the increase in ΔC_{wv} due to a lower air temperature and thus lower C^{a}_{wv} (Fig. 3 and Eq. 4). The relative heating effects due to a decrease in k compared to similar heating caused by an increase in solar irradiation becomes increasingly important for larger leaves, for which δ is thicker. A larger leaf in the sun has a larger portion of the total heat dissipation as conduction across δ.

The combined effect of having a leaf temperature that is further above air temperature and a greater D_{wv} with increasing elevation results in substantial increases in transpirational fluxes for an air temperature lapse rate of below about 0.005° C m^{-1} at elevations of less than about 2,500 m (Fig. 4). For higher lapse rates, predicted transpiration would decrease with increases in elevation, although these transpirational fluxes at higher elevations would still be relatively large, considering the much lower leaf temperatures at these elevations. For example, assuming a lapse rate in air temperature of 0.006° C m^{-1} and relative humidity of 20%, a large, low-resistance leaf at solar noon on June 21 at about 42° C would transpire about 24 $\mu g\,cm^{-2}\,s^{-1}$ at the low elevation desert site compared to 21.5 $\mu g\,cm^{-2}\,s^{-1}$ for a similar leaf at the mountain site with a leaf temperature of about 36° C (Fig. 4). Considering the exponential effect of temperature on the water vapor saturation of air, these transpiration rates are remarkably similar for a leaf temperature difference of 6° C. If all other diffusion characteristics were identical, the differences in these two leaf temperatures alone would generate concentration gradients in water vapor from the leaf to the air of about 59 $\mu g\,cm^{-3}$ at the mountain site, or an expected transpirational flux of almost 60% greater for plants at the low elevation, desert site for the same stomatal opening. However, with the enhanced influence on transpiration due to elevational effects (a greater D_{wv} and leaf temperature further above air temperature), predicted transpiration is only about 12% greater (24.0 versus 21.5 $\mu g\,cm^{-2}\,s^{-1}$) at the desert site than the mountain site (Fig. 4).

For a smaller leaf with low stomatal resistance, comparative differences in calculated transpirational fluxes between the desert and mountain sites are somewhat greater, 11.0 versus 8.9 $\mu g\,cm^{-2}\,s^{-1}$, resulting in a 24% increase at the desert site (Fig. 4). Assuming similar characteristics for diffusion, a 20% relative humidity, and considering only leaf and air temperatures, as above, the anticipated transpiration rate would be over 100% greater at the desert site (ΔC_{wv} equal to 31.0 $\mu g\,cm^{-3}$ versus 15.0 $\mu g\,cm^{-3}$). Thus, a smaller leaf (thinner δ) would have a considerable reduction in transpiration at both sites, but would also have a greater reduction in transpirational differences between a low and high-elevation site (100% to 24%) than the analogous reduction calculated for a larger leaf (60% to 12%). Increases in the air temperature lapse rate would lead to greater reductions in transpiration at higher elevations due to the increased importance of temperature on D_{wv} which would outweigh the contrasting effect of a lower atmospheric pressure on D_{wv} (Fig. 1). This would result in a smaller enhancement of transpiration and, thus, a greater disparity between high and low-elevation transpirational fluxes for leaves with similar stomatal resistances and energy balance properties.

Tranquillini (1976) reported that spruce twigs growing at 1,940 m had three times the transpiration rate of shoots growing at 1,000 m. Also, twigs of Krummholz spruce growing at 2,140 m had transpiration rates of over seven times those at 1,000 m. It was not determined if these differences in transpiration rates were due to differences in stomatal compared to cuticular resistances, or was a result of different microclimatic and diffusional characteristics of a higher elevation. However, there are reports of relatively high leaf temperatures for subalpine conifers that were considerably above air temperature during the winter and spring which, in combination with a low C^{a}_{wv}, led to leaf-to-air water vapor gradients nearly equal to mid-summer values (Michaelis, 1934; Tranquillini and Turner, 1961). Those data are similar to our simulated results when comparing ΔC_{wv} and T_{leaf} for desert and mountain plants during the summer (Figs. 3 and 4).

Other investigators have concluded that there is little difference between plant transpiration at higher elevations compared to low-elevation rates (Walter, 1973; Prutzer, 1961). In addition, Mooney et al. (1966) found that transpiration for *Polygonum bistortoides* phytometer plants growing at a lower elevation (1,829 m) was about twice that for plants growing at 2,438 m. Comparisons of the effects of elevation on transpiration are needed under more controlled experimental conditions (Gale, 1973) to elucidate the possible effects of microenvironmental differences between elevational sites that are not solely characteristic of elevational changes. The possibility exists that microclimatic variations may overshadow general elevational changes in climate to varying degrees. The extreme topographic variations associated with mountainous terrain may result in a wide range of microclimatic conditions of any given elevation (Billings and Mooney, 1968). However, microclimatic variations in ambient pressure would not be expected to occur and, thus, quantitative predictions concerning pressure changes an D_{wv} would still be valid. The results presented here show that plant transpiration at higher elevations may be potentially as severe as at low elevation desert sites, even though plant temperatures may be considerably lower. This may be especially true of high elevation areas near coastlines where isothermal lapse conditions prevail due to moist air masses and advective winds (Katznelson, 1956). Thus, the similar high transpirational fluxes calculated and measured for desert and mountain plants, which occur under quite different environmental conditions, provides evidence that morphological changes leading to increases in water-use efficiency could be equally advantageous in both habitats. These results may partially explain the similarities in plant structure and the close phylogenetic relationships among certain desert, alpine, and subalpine species.

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