

## A Simulation Model of Plant Water Relations and Production in the Alpine Tundra, Colorado\*

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**Summary.** A model to predict the daily courses of leaf resistance, leaf water potential, transpiration, leaf temperature and net photosynthesis based on soil-plant-atmosphere continuum and energy budget concepts is presented. The principle water relations parameters required by the model are the minimum leaf resistance, the response curves of leaf resistance to light, temperature, and leaf water potential, and the relationship between leaf water potential and water deficit. Predictions of the effects of changes in soil water potential on the daily patterns of leaf resistance, leaf water potential, leaf temperature, and net photosynthesis in an alpine climate are examined. The model was tested using data from two alpine species, *Bistorta bistortoides* and *Caltha leptosepala*, that exhibited different daily leaf resistance and leaf water potential patterns as water stress developed. Agreement was found between predicted and observed patterns. Differences in the daily courses between the species are shown to be due to differences in the physiological parameters. The relevance of the daily leaf resistance patterns is discussed in the context of drought adaptability.

### Introduction

The concept of water movement in a soil-plant-atmosphere continuum (SPAC) along a series of gradients and impeded by a series of resistances was proposed by van den Honert (1948). More recently, refinements in concepts have led to the formation of more complex SPAC models (e.g., Cowan, 1965; Philip, 1966). These models, drawn as electrical analogues, attempt to explain the regulation of water movement from the soil through the plant and into the atmosphere by plant organs and physical variables. However, only segments of these models have been tested because of the great difficulty in simultaneously measuring all of the parameters needed to test the entire model.

On an ecological level one is interested not only in understanding the factors influencing water loss, but also in those factors which will influence carbon gain. Mathematical models to predict primary production have been developed for agricultural systems (Monsi and Saeki, 1953; Davidson and Philip, 1958; de Wit, 1965; Duncan *et al.*, 1967). These models have calculated primary production based on solar radiation, foliage distribution, and leaf angle, and have generally

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neglected the role of leaf resistance and internal water relations on production. Recent models developed by Miller (1972) for mangroves and Miller and Tieszen (1972) for the arctic tundra included the effects of leaf temperature and leaf resistance on photosynthesis and attempted to incorporate the effects of light and water stress on leaf resistance. However, feedback controls relating leaf resistances, water loss, water content, water uptake, and leaf temperature, were not included.

The purposes of this study were: 1) to construct a model describing the mechanisms of water transport in the SPAC, water loss regulation, and photosynthesis over a 24-hr period on an ecological level, and 2) to compare the predicted daily courses of leaf resistance and leaf water potential with field observations of water loss and internal plant water status. The model was constructed and tested for single leaves, but could be implemented into entire canopy models.

The model has been used to simulate the responses of two alpine herbaceous species, *Bistorta bistortoides* (Pursh) Small and *Caltha leptosepala* D.C., during non-drought and drought conditions. Data on the physiological parameters necessary for the model and the daily courses of physiological processes for both species were collected in the Colorado alpine tundra during the summer of 1972 and have been summarized by Ehleringer and Miller (1975) and Moore *et al.* (1975). Their field studies took place on Niwot Ridge (40° 02' N, 105° 33' W), above the University of Colorado Mountain Research Station at 3500 m. Parameter measurements of physiological relationships for both species were collected in the field independently of the daily course observations. A brief summary of the physiological ecology of these two species as published elsewhere follows to assist in the interpretation of the simulation results.

Both *Bistorta bistortoides* and *Caltha leptosepala* are common broad leaved herbaceous species attaining heights of 5 to 8 cm during a growing season. *Caltha* is restricted to marshy, wet meadows which receive runoff from snow accumulation areas. *Bistorta* occurs occasionally on these wet meadows but primarily on dry, snow free meadows and slopes. Through the course of the 1972 growing season significant differences developed between the morning and noon leaf resistances and leaf water potentials between non stress ( $\Psi_{\text{soil}} = -0.5$  bars) and water stress conditions ( $\Psi_{\text{soil}} = -5$  bars) (Table 1). These changes in soil water potentials occurred between the beginning of the growing season (early June) and midseason (late July). As shown in Table 1 there was no apparent increase in the leaf resistance values through the day in either of the species during the early part of the season. Leaf water potentials remained fairly high, never decreasing below  $-5.0$  bars. However, by mid-July water stress had set in and leaf resistances were higher. *Caltha* on the wet meadow site showed a midday increase in leaf resistance, but this feature was not seen in *Bistorta* from the dry meadow site. Leaf water potentials reached lower minima, typically down to  $-13.0$  and  $-15.0$  bars for *Bistorta* and *Caltha*, respectively. Three daily leaf resistance patterns were exhibited by *Bistorta* and *Caltha* through the season. Fig. 1, although idealized, demonstrates the salient features of these leaf resistance patterns. Numerical values for these curves may be found in Table 1. Curve A represents the daily pattern of both species in the early, non-stress part of the

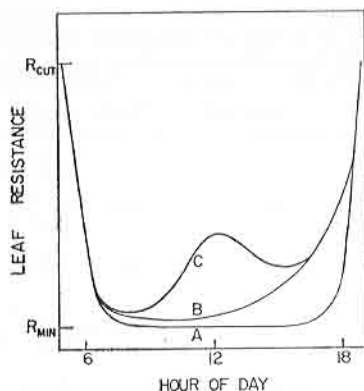


Fig. 1. Idealized daily leaf resistance patterns exhibited by *Bistorta* and *Caltha* early in the season (A) and by *Bistorta* (B) and *Caltha* (C) at midseason

Table 1. Representative leaf resistances and leaf water potentials of *Bistorta* and *Caltha* on Niwot Ridge, Colorado, during the summer of 1972 (adapted from Ehleringer, 1973)

	<i>Bistorta</i>		<i>Caltha</i>	
	Range	Mean	Range	Mean
<i>Early season</i> ( $\psi_s = -0.5$ )				
Leaf resistance (sec cm <sup>-1</sup> )				
Morning	1.4-1.8	1.6	1.9-2.4	2.2
Noon	1.4-1.8	1.6	2.0-2.4	2.2
Leaf water potential (bars)				
Dawn		-1		-0.5
Noon	-4 to -6	-5	-2 to -4	-4
<i>Midseason</i> ( $\psi_s = -5$ )				
Leaf resistance (sec cm <sup>-1</sup> )				
Morning	1.7-2.3	2.1	2.2-4.0	3.1
Noon	1.8-2.5	2.3	4.0-8.0	6.0
Leaf water potential (bars)				
Dawn		-5		-4
Noon	-9 to -14	-13	-8 to -15	-14

season. Curve B represents the pattern exhibited by *Bistorta* and curve C by *Caltha* during the water stress part of the season.

Data for parameters necessary to the model were collected in the field independent of the seasonal and daily course observations. Curves describing the relationships between the leaf water potential and relative saturation deficit for *Bistorta* and *Caltha* indicated that *Caltha* showed more mesic tendencies than *Bistorta*. This is seen in the differences between the initial slopes ( $m_1$ ) of the two curves and in the low breakpoint ( $bp$ ) of the *Caltha* curve (Table 2). Plots of the relationship between leaf resistance and water potential also indicated that

Table 2. Physiological input parameters used in the stimulations for *Bistorta* and *Caltha*. Parameter values are derived from data of Ehleringer and Miller (1975) and Moore *et al.* (1975) by methods described in the text

Parameter	Symbol	Units	<i>Bistorta</i>	<i>Caltha</i>
Water relations:				
Describes shape of leaf resistance-light curve	$a_1$	sec	30	30 <sup>a</sup>
Describes shape of leaf resistance-light curve	$a_2$	cm	1	1 <sup>a</sup>
Sensitivity of leaf resistance to light intensity	$a_3$	mW cm <sup>-2</sup>	$7 \times 10^4$	$7 \times 10^4$ <sup>a</sup>
Sensitivity of leaf resistance to temperature	$a_6$	sec cm <sup>-1</sup> °C <sup>-2</sup>	$1 \times 10^{-5}$	$1 \times 10^{-5}$ <sup>a</sup>
Leaf water potential at three times minimum leaf resistance	$A$	bars	-14	-14
Leaf water potential at stomatal closure	$B$	bars	-22	-17
Turgid weight specific leaf density	$D_l$	g cm <sup>-2</sup>	0.030	0.027
Minimum leaf resistance	$r_{\min}$	sec cm <sup>-1</sup>	1.2	1.8
Initial RSD $\times \psi_l$ slope	$m_1$	bars % <sup>-1</sup>	-0.8	-0.5
Second RSD $\times \psi_l$ slope	$m_2$	bars % <sup>-1</sup>	—	-5.0
Breaking point between RSD $\times \psi_l$ slopes	$bp$	%	—	10
Leaf temperature for minimum leaf resistance	$T_{r\min}$	°C	25	25 <sup>a</sup>
Net photosynthesis:				
CO <sub>2</sub> concentration in air	$C_a$	ppm	300	300
CO <sub>2</sub> concentration at chloroplasts	$C_{chl}$	ppm	0	0
Minimum mesophyll resistance	$r'_{\text{mes}}$	sec cm <sup>-1</sup>	13.2	13.2 <sup>a</sup>
Describes light sensitivity of mesophyll resistance	$K_2$	sec cm <sup>-1</sup>	120	120 <sup>a</sup>
Describes light sensitivity of mesophyll resistance	$K_3$	cm <sup>-2</sup> mW <sup>-1</sup>	0.031	0.031 <sup>a</sup>

<sup>a</sup> These values are the same as for *Bistorta* since actual photosynthesis data were not reported by Moore *et al.* (1975).

*Bistorta* was more drought adapted than *Caltha* since complete stomatal closure occurred at -17 bars in *Caltha*, but at -22 bars in *Bistorta*. The parameter values to describe the net photosynthetic relationships of *Bistorta* were derived from Moore *et al.* (1975). They reported that *Bistorta* peak photosynthetic rates were almost 9 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> and that the optimum leaf temperature for photosynthesis was 20° C. Photosynthetic response curves of *Caltha* were assumed

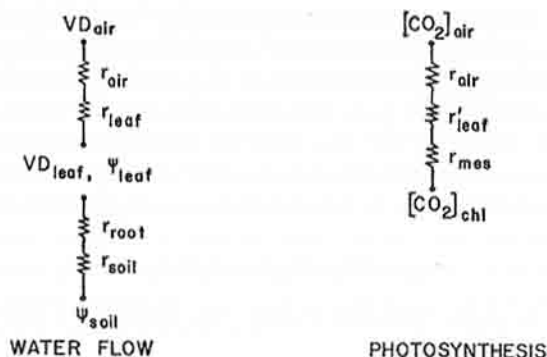


Fig. 2. Electrical analogues for water flow through the plant and photosynthesis as used in the model

to be similar to those measured for *Bistorta*, since measurements were not made in that study. This will suffice for the purposes of this paper as we are more interested in the relative and not absolute changes in the photosynthetic rate. Other water relations and photosynthetic parameters for these two species to be used in the simulations are also summarized in Table 2.

### The Model

The model calculates the effects of the soil moisture content and micro-meteorological parameters on the plant water status, on water flux through the plant, on leaf temperature and on net photosynthesis. Hourly values of solar radiation, air temperature, wind speed, vapor density of the air and the water potential of the soil are required as forcing functions. The model then simulates the daily course of transpiration, net photosynthesis, leaf temperature, leaf resistance, and internal plant water status. The major interest of this paper was the synthesis of information on plant water relations; the estimates of net photosynthesis and production are only relative as the experimental data needed are not complete.

### Photosynthesis

The rate of net photosynthesis is considered in an Ohm's Law analogy as being directly related to a potential gradient, which is the  $\text{CO}_2$  concentration gradient between the outside air and the site of carboxylation, and inversely related to a series of resistances between the outside air and the carboxylation site (Fig. 2), including the laminar boundary layer resistance, leaf resistance, and internal mesophyll resistance (Gaastra, 1963). The more detailed analyses of the internal resistances (*e.g.*, Waggoner, 1969; Chartier *et al.*, 1970) could not be followed because of inadequate data. All resistances are physical except for the mesophyll resistance, which combines both a physical and biochemical resistance. Mathematically net photosynthesis is expressed as

$$P_N = \frac{k_1(C_a - C_{chl})}{r_a + 1.56r_l + r_{mes}} \quad (1)$$

where  $P_N$  is the net photosynthetic rate in  $\text{mg dm}^{-2} \text{hr}^{-1}$ ,  $C_a$  is the carbon dioxide concentration in the outside air in  $\text{g cm}^{-3}$ ,  $C_{\text{chl}}$  is the carbon dioxide concentration in the chloroplast just after carboxylation in  $\text{g cm}^{-3}$ ,  $r_a$  is the laminar boundary layer resistance in  $\text{sec cm}^{-1}$ ,  $r_l$  is the leaf resistance to water loss in  $\text{sec cm}^{-1}$ , 1.56 corrects the resistance for the different diffusion coefficients of water and  $\text{CO}_2$ ,  $r_{\text{mes}}$  is the mesophyll resistance in  $\text{sec cm}^{-1}$ , and  $k_1$  converts units.

The mesophyll resistance is calculated from net photosynthesis light curves by the equation

$$r_{\text{mes}} = (C_a - C_{\text{chl}})k_1 / P_N - r_a - 1.56r_l \quad (2)$$

The resulting mesophyll resistance values were fitted by a least squares method to the equation

$$r_{\text{mes}} = r'_{\text{mes}} + k_2 e^{-k_3 S} \quad (3)$$

where  $r'_{\text{mes}}$  is the calculated mesophyll resistance at light saturation and optimum photosynthetic temperature in  $\text{sec cm}^{-1}$ ,  $k_2$  and  $k_3$  are calculated coefficients related to the shape of the net photosynthesis light curve, and  $S$  is the absorbed solar radiation in  $\text{mW cm}^{-2}$ .

Eq. (1) describes net photosynthesis in the light at optimum temperature. At other temperatures photosynthesis is decreased and this decrease is described as

$$P_{NT} = b_0 + b_1 T + b_2 T^2 \quad (4)$$

where  $P_{NT}$  is the net photosynthetic rate corrected for temperature effects and  $b_0$ ,  $b_1$ , and  $b_2$  are coefficients for the regression describing the relationship of net photosynthesis to leaf temperature. The values of  $b_0$ ,  $b_1$ , and  $b_2$  used in these simulations are 0.5041, 0.0479, and  $-0.0012$ , respectively, and are derived from data for *Bistorta* from Moore *et al.* (1975).

### Transpiration

Water movement through the plant is also treated as an Ohm's Law analogy (van den Honert, 1948; Cowan, 1965). For the water movement through the plant, potential gradients between the leaf and the soil and between the leaf and the outside air were considered (Fig. 2). Transpiration is directly related to the vapor density gradient and inversely related to the leaf and laminar boundary layer resistances to water vapor diffusion by the equation (Lee and Gates, 1964)

$$E = \frac{60(q_{s,T_l} - q_a)}{r_l + r_a} \quad (5)$$

where  $E$  is the transpiration rate in  $\text{g cm}^{-2} \text{min}^{-1}$ ,  $q_{s,T_l}$  is the saturation vapor density at leaf temperature in  $\text{g cm}^{-3}$ ,  $q_a$  is the vapor density of the air in  $\text{g cm}^{-3}$  and  $r_l$  and  $r_a$  are the leaf and boundary layer resistances in  $\text{sec cm}^{-1}$ .

### Water Uptake

Water uptake from the soil to the leaf requires a water potential gradient between the leaf and the soil and is impeded by soil and root resistances. Thus,

$$W_{\text{up}} = 60(\psi_s - \psi_l) / (r_r + r_s) \quad (6)$$

where  $W_{up}$  is the rate of water uptake in  $\text{g cm}^{-2} \text{ leaf min}^{-1}$ ,  $\psi_s$  is the soil water potential in bars,  $\psi_l$  is the leaf water potential in bars, and  $r_s$  and  $r_r$  are the resistances to water transfer of the soil and roots, respectively, in  $\text{sec cm}^{-1} \text{ bar}^{-1}$ .

The soil resistance in this model is a function only of the soil water potential. As soil water potential decreases, soil hydraulic conductivity (inverse of soil resistance) will decrease logarithmically (Gardner, 1960). A first approximation to the soil resistance was made by calculating the soil resistance as the mean of the soil resistances at water potentials equal to the leaf water potential and at the bulk soil water potential. The rationale behind this is that there will be a gradient of soil water potentials extending from the root surface outward to a point where the soil water potential does not change appreciably during the course of a day. As an approximation to the resistance over this distance, the soil resistance was calculated as the mean of the resistances at the two extremes.

The root resistance was assumed to remain constant for lack of information and data on its functional relationships.

There will be some degree of error associated with the estimate of the root and soil resistances. Root resistance has been shown to decrease with increasing transpiration, but to assume a constant value at relatively low transpiration rates (Tinklin and Weatherley, 1966, 1968; Stoker and Weatherley, 1971). Root permeability has been shown to vary with temperature (Brouwer, 1953; Kuiper, 1961; Kramer, 1969), but soil temperatures in the root zone during the field study varied normally less than  $3^\circ \text{C}$  daily (Ehleringer, 1973). In the model, the ratio of root to leaf surface area is incorporated into the estimates of the root and soil resistances.

### *Relative Saturation Deficit*

The leaf relative saturation deficit is the leaf water content deficit relative to the fully turgid state. It is expressed as a percentage and is related to the transpiration and water uptake rates as

$$RSD_t = RSD_{t-1} + D_T^{-1} \int (E - W_{up}) dt \quad (7)$$

where  $RSD_t$  and  $RSD_{t-1}$  are the relative saturation deficits at time  $t$  and time  $t-1$  in per cent,  $D_T$  is the turgid weight specific leaf density in  $\text{g cm}^{-2}$ , and  $dt$  is the time interval. The relationship of leaf water potential to relative saturation deficit is calculated from field data. Single straight lines are frequently used to describe this relationship. However, occasionally two straight lines have been necessary (Ehlig and Gardner, 1964).

### *Leaf Resistance*

In this model the leaf resistance is assumed to be influenced by three variables: light intensity, leaf water potential, and leaf temperature. Curves describing the generalized effects of these variables on leaf resistance were derived by synthesizing published data from a number of plant species (*e.g.* Stålfelt, 1955, 1962; Kuiper, 1961; Zelitch, 1965; Slatyer, 1967; Berger, 1973). The general shapes of these relationships are shown in Fig. 3. The parameter values necessary to describe these curves were derived from field data. The direct effects of carbon dioxide and vapor density on leaf resistance were not considered in this model.



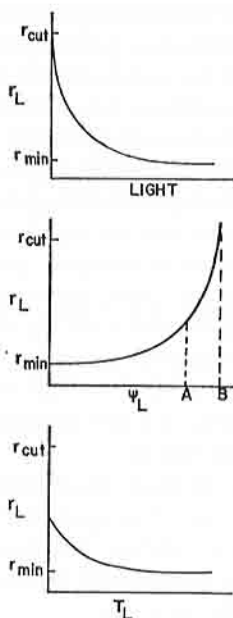


Fig. 3. Generalized relationships of leaf resistance to light intensity, leaf water potential, and leaf temperature as used in the model. See text for further explanation

Leaf resistance is thought of as decreasing from a maximum, the cuticular resistance ( $r_{cut}$ ), in response to increases in light intensity and leaf temperature. Conversely leaf resistance is thought to increase in response to water stress as measured by the leaf water potential. Complete stomatal closure occurs at the maximum tolerable water stress (B). Beyond this point incipient plasmolysis and leaf mortality may occur. In Fig. 3, the leaf water potential at three times the minimum leaf resistance is A. This point is necessary to describe the relationship mathematically.

The effects of factors affecting leaf resistance are assumed to be additive. Thus, leaf resistance to water loss ( $r_l$ ) is related to solar radiation, leaf temperature, and leaf water potential by the following equation:

$$r_l = r_{min} + [a_1/(a_2 + a_3S)] + [f(T)] + [-\psi_l/(a_4 - a_5\psi_l)] \quad (8)$$

where  $r_{min}$  is the minimum leaf resistance,  $a_1$ ,  $a_2$ , and  $a_3$  are constants describing the shape of the leaf resistance-light curve,  $a_4$  and  $a_5$  are constants related to the shape of the leaf resistance-leaf water potential curve,  $S$  is the solar radiation and  $f(T)$  is the effect of leaf temperature on leaf resistance. It should be noted that the cuticular resistance ( $r_{cut}$ ) can be expressed as

$$r_{cut} = r_{min} + a_1/a_2 \quad (9)$$

and that  $a_3$  describes the sensitivity of the leaf resistance to light intensity. The constants  $a_1$ ,  $a_2$ , and  $a_3$  are derived by fitting that portion of Eq. (8) to data on leaf resistance and solar radiation. The temperature effect on leaf resistance,



$f(T)$ , describes the decrease in leaf resistance as leaf temperature increases up to a minimum resistance temperature,  $T_{r_{\min}}$ . There is no further decrease in leaf resistance due to leaf temperature above  $T_{r_{\min}}$ . The equation describing this relationship is

$$f(T) = a_6(T_{r_{\min}} - T_l)^2 \quad (10)$$

but if  $T_l > T_{r_{\min}}$ ,  $f(T) = 0$ . The constant  $a_6$  is empirically derived. The constants  $a_4$  and  $a_5$  determine the shape of the leaf resistance-leaf water potential curve. The value of  $a_4$  can be calculated as:

$$a_4 = \frac{AB}{2r_{\min}(B-A)} \quad (11)$$

and  $a_5$  as:

$$a_5 = a_4/B.$$

Data to determine relationships of light, temperature, and leaf water potential to leaf resistance came from various techniques. A Siemans cuvette system operated in the field was used by Moore *et al.* (1975) to determine the effects of light and temperature on leaf resistance. Data for the relationship between leaf resistance and leaf water potential were collected in the field using a porometer over the span of several days during hours in which light intensity and temperature were not limiting (Ehleringer and Miller, 1975).

Calculations of the water relations in the model begin with the calculation of the relative saturation deficit, based on the transpiration and water uptake rates of the previous period. Leaf water potentials are then calculated, followed by the leaf resistance calculations. The water uptake rate is calculated after the leaf resistance and the transpiration rate is calculated last. The model proceeds on a minute-by-minute basis calculating the values of each of the variables.

Leaf temperatures are calculated by solving the leaf energy budget equation as developed by Gates (1965, 1968). The energy budget is solved by a linear approximation method (Miller, 1972).

An annotated copy of this model in FORTRAN is available upon request.

### Simulations

Two days representing the average environmental conditions during the end of June or the beginning of July when soil water potentials are high (early season) and during late July or early August when soil water potentials are low (mid-season) were simulated. The input microclimatic data were based on field measurements collected in 1972 by Ehleringer (1973), but the daily courses of solar radiation and air temperatures were smoothed (Fig. 4). Air temperatures ranged between 4° and 22° C during the day. Solar radiation varied sinusoidally through the day, reaching a maximum of 79 mW cm<sup>-2</sup> at noon. The vapor density of the air and the wind speed were both constant at 5 g m<sup>-3</sup> and 250 cm sec<sup>-1</sup>, respectively. The same microclimatic data were used in the simulations of both days in an effort to reduce the variability and aid in the interpretation of the results of the simulations. The input soil water potentials were -0.5 bars and -5 bars for early and mid-season, respectively, and were based on the dawn

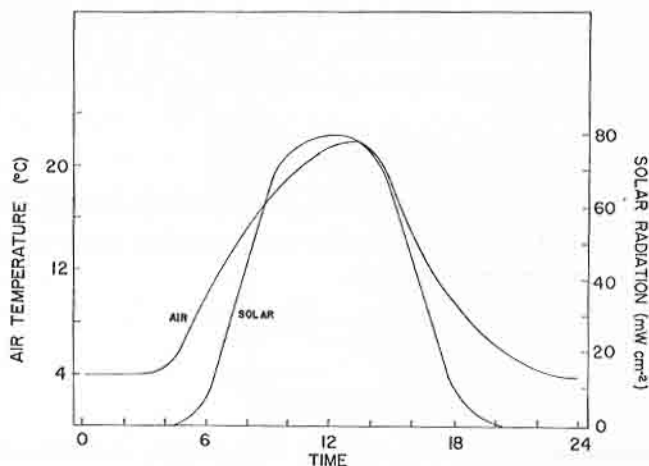


Fig. 4. Daily courses of air temperature ( $^{\circ}\text{C}$ ) and solar radiation ( $\text{mW cm}^{-2}$ ) used in all of the simulations

water potential measurements of *Bistorta* and *Caltha* collected by Ehleringer and Miller (1975). The model simulated the physiological activities of single leaves oriented due south and at a leaf angle of  $45^{\circ}$  degrees. For each of the two days, simulations were run for *Bistorta* and *Caltha*.

Simulation results for *Bistorta* early in the season showed that leaf resistances decreased in the morning to a value of  $1.6 \text{ sec cm}^{-1}$  and remained at this value through the day, increasing at the end of the day as solar radiation decreased (Fig. 5A). For comparison purposes refer to the summarized field data of leaf resistances and leaf water potentials in Table 1. Leaf water potentials decreased through the morning hours attaining a minimum of  $-5.3$  bars. Leaf temperatures closely tracked ambient air temperatures and reached a maximum of  $22.6^{\circ}\text{C}$  at 1400. Predicted photosynthesis closely followed solar radiation through the day, but leveled off at midday when leaf temperatures exceeded the optimum photosynthetic temperature. There was no decrease in net photosynthesis by increasing leaf resistances. Unfortunately there are no actual field observations of leaf temperatures and net photosynthesis to compare with the simulations.

In the early season *Caltha* simulations leaf resistances decreased in the morning to a minimum of  $2.1 \text{ sec cm}^{-1}$ , maintaining this value through the day (Fig. 5B). Leaf water potentials decreased through the morning and attained a minimum of  $-4.5$  bars. The maximum leaf temperature was  $23.2^{\circ}\text{C}$ , only  $1.2^{\circ}\text{C}$  above ambient. Photosynthesis closely followed solar radiation, but the absolute rate was somewhat more depressed in *Caltha* than in *Bistorta* because of the higher leaf resistances.

By midseason soil water potentials had decreased from  $-0.5$  bars to  $-5$  bars. With these decreases in soil water potential, the simulations predicted overall higher leaf resistances and lower leaf water potentials.

In the midseason simulations the leaf resistances of *Bistorta* attained a morning low of  $2.1 \text{ sec cm}^{-1}$ , which was followed by a midday value of  $2.3 \text{ sec cm}^{-1}$

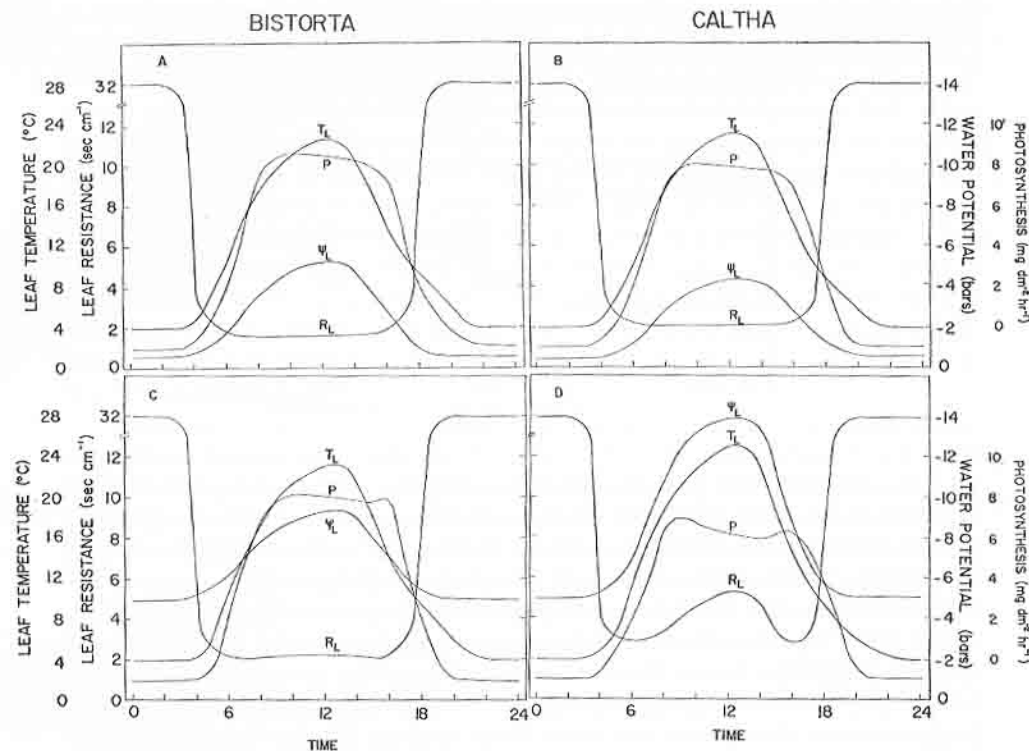


Fig. 5 A—D. Predicted daily courses of leaf temperature ( $T_L$ ), leaf resistance ( $R_L$ ), leaf water potential ( $\psi_L$ ), and net photosynthesis ( $P$ ) for *Bistorta* (A) and *Caltha* (B) early in the season when water stress is low and for *Bistorta* (C) and *Caltha* (D) at midseason when water stress is high

(Fig. 5C). Predicted leaf water potentials were much lower than values predicted for earlier in the season. The midday leaf water potential for *Bistorta* was  $-9.5$  bars. The maximum leaf temperature was  $23.6^{\circ}\text{C}$ , up one full degree because of the increased leaf resistances. The overall photosynthetic rate was decreased due to higher leaf resistances and the dip at midday was due to both higher leaf resistances and higher leaf temperatures.

The simulated daily leaf resistance pattern for *Caltha* at midseason is vastly different from any of the previous leaf resistance patterns. Predicted leaf resistances decreased to a minimum value of  $2.8 \text{ sec cm}^{-1}$  and then rose to a midday value of  $5.6 \text{ sec cm}^{-1}$ , before again decreasing in the midafternoon (Fig. 5D). Leaf water potentials decreased throughout the morning and attained a minimum of  $-14.0$  bars. The maximum leaf temperature was  $25.3^{\circ}\text{C}$ ,  $1.9^{\circ}\text{C}$  higher than predicted in the early season simulation. Predicted photosynthetic rates were likewise reduced. The overall decreased rate and specifically the midday depression in the predicted photosynthetic rate were due to both increased leaf resistances and higher leaf temperatures resulting from increased leaf resistances.

Table 3. Predicted daily totals of net photosynthesis and transpiration and  $T/P$  ratios from the four simulations. Units for net photosynthesis and transpiration are  $\text{mg dm}^{-2} \text{ day}^{-1}$  and  $\text{g dm}^{-2} \text{ day}^{-1}$ , respectively.  $T/P$  ratio is the ratio of the water lost as transpiration in grams per gram carbohydrate gained ( $\text{CH}_2\text{O}/\text{CO}_2 = 0.68$ )

	<i>Bistorta</i>	<i>Caltha</i>
Early season ( $\psi_s = -0.5$ )		
$P_{\text{net}}$	79.2	75.0
$E$	23.42	19.75
$T/P$ ratio	435	387
Midseason ( $\psi_s = -5$ )		
$P_{\text{net}}$	75.4	63.0
$E$	19.47	12.42
$T/P$ ratio	380	290

The predicted total carbon gain and transpiration in both species showed decreases under water stress, but there was an increase in the water use efficiency of both species under water stress (Table 3). The  $T/P$  ratio, a measure of water use efficiency, is the ratio of the total water lost as transpiration in grams to the total carbon dioxide fixed as carbohydrate in grams, assuming that  $\text{CH}_2\text{O}/\text{CO}_2$  equals 0.68. Note that the  $T/P$  ratio is a theoretical value and that it does not consider respiratory losses. Thus, it cannot be compared to water use efficiency values based on harvesting techniques. *Bistorta* had the highest predicted production rate during both non water stress ( $79.2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ day}^{-1}$ ) and water stress conditions ( $75.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ day}^{-1}$ ). However, *Caltha* was seen to have the greater water use efficiency under both conditions (387 and 290 for non water stress and water stress conditions). This was mainly because *Caltha* had a higher minimum leaf resistance.

Transpiration rates decreased dramatically between non-stress and water stress conditions in both species, while the decrease in net photosynthetic rates were much less. These results indicate that both species have higher water use efficiencies under conditions when water is limiting. Two factors contribute directly to the higher water use efficiencies. First, in the alpine tundra, temperatures are relatively low, and thus the slope of the saturation vapor density-temperature curve is small and as leaf temperatures rise leaf-air vapor density gradients will be likewise small. Secondly, the leaf resistance to carbon dioxide uptake is small with respect to the overall resistance to carbon dioxide transfer. Consequently, an increase in the leaf resistance will result in a sharp decrease in transpiration, yet with only a small reduction in net photosynthesis. In summary, it would appear from these simulations that under mild water stress the leaf resistance influence on the photosynthetic rate operates more to decrease production through increased leaf temperatures than by limiting gaseous diffusion.

### Discussion

There is agreement between the simulations (Fig. 5) and the field observations (Table 1) in all simulations for morning and midday values of leaf resistances

and leaf water potentials. The differences between predicted and average observed morning and midday leaf resistances are small, generally less than  $0.2 \text{ sec cm}^{-1}$  with the exception of the predicted midday *Caltha* leaf resistance at midseason which is  $1.0 \text{ sec cm}^{-1}$  from the observed mean. Predicted midday leaf water potentials are within 0.5 bars of observed means for the early season simulations and within 2.0 bars of the observed mean values for the midseason simulations.

While comparisons of these point values support predictions of the model, there are some discrepancies between the predicted and observed shapes of the daily leaf resistance curves during drought stress conditions (compare curves B and C of Fig. 1 with leaf resistances of Fig. 5). The shapes of the predicted leaf resistance patterns appear to follow the observed patterns in the predawn hours, but the predicted leaf resistances in the afternoon show a decrease not seen in the field observations.

Responsibility for these discrepancies in the model might lie in either of two simplifying assumptions made at the outset. First is that carbon dioxide and vapor density do not play a significant role in affecting stomatal aperture over the range of values experienced by the leaf through the day. The second is that endogenous or circadian rhythms do not play a significant role in affecting the values of any of the modelled parameters. None of these possibilities were tested in the field and thus cannot be ruled out. Carbon dioxide is known from many experiments to influence stomatal aperture. It is possible under water stress conditions that as the photosynthetic rate declines in the afternoon, internal carbon dioxide concentrations reach levels high enough to adversely affect the stomatal aperture. Vapor density has been shown to directly affect stomatal aperture in some plants independent of leaf water potential (Lange *et al.*, 1971; Schulze *et al.*, 1972a). This may possibly affect the leaf resistances as large vapor density gradients occur during the day. Similarly it is possible that endogenous rhythms may play a significant role in causing the stomatal closure in the late afternoon under water stress conditions. Meidner and Mansfield (1965) and Pallas *et al.* (1974) have shown that stomatal aperture may fluctuate on a daily cycle independent of external environmental parameters. Any of these possibilities might explain the discrepancies between the predicted and observed daily course of leaf resistances.

Overall, however, there appears to be good correlation between the patterns and values of leaf resistances and water potentials seen in the field for *Bistorta* and *Caltha* and those predicted by the model. This agreement forms preliminary support of the model. The following trends were both predicted by the model and observed in the field data:

- 1) In the beginning of the season there was no midday increase in leaf resistance in either *Bistorta* or *Caltha*.
- 2) In the middle of the season there was a midday increase in leaf resistance in *Caltha*, but not in *Bistorta*.
- 3) Leaf resistances were higher in both species later in the season.
- 4) The minimum leaf water potential and daily pattern of leaf water potentials for *Bistorta* and *Caltha* changed through the season, with diurnal fluctuations becoming larger at midseason.

5) The magnitude and daily pattern of leaf resistances of *Bistorta* and *Caltha* changed through the season.

Primary production in alpine tundra ecosystems is generally considered to be limited by the shortness of the season and not by drought stress, except for vegetation lying within snowbanks (Billings and Bliss, 1959; Billings and Mooney, 1968). The role of water stress operating through stomatal closure and higher leaf temperatures to limit production has not been examined. Billings and Mooney (1968) stated that "plants from moist sites . . . have little control over transpiration as compared with the more efficient water use of dry site plants". This implies that higher production rates might be expected in the wet site plants even as leaf water potentials decrease. Ehleringer and Miller (1975) found that wet site plants are capable of stomatal control though not as efficient as dry site plants. Results from these simulations predicted that both *Bistorta* and *Caltha* could respond to decreasing soil water potentials by reducing transpiration. As a consequence simulations predicted that net photosynthesis was somewhat reduced, but water use efficiency in both species was greatly enhanced. Previous experimental studies have demonstrated that the net photosynthetic rate decreased with soil moisture in alpine situations (Klikoff, 1965; Hillier, 1970; Kuramoto and Bliss, 1970). However, none of these studies pointed out that this reduction in net photosynthesis was due to both stomatal closure and higher leaf temperatures as was predicted by our modelling efforts. The simulations indicated that leaf resistances increased through the season in response to decreasing soil moisture, supporting the hypothesis that water may limit production in the alpine tundra.

The three daily leaf resistance patterns exhibited by *Bistorta* and *Caltha* through the season (Fig. 1) appear to be part of a general phenomenon also found in the results of many studies (*e.g.*, Rees, 1961; Lange *et al.*, 1969; Schulze *et al.*, 1972b, c; Harrison, 1971) and were also noticed by Stocker (1956). It is of significance that the daily leaf resistance patterns found in each of the species, irrespective of environment, represented differing degrees of water stress found in those environments. Consequently, it appears that upon examining a species within its native habitat pattern A of Fig. 1 would typically be observed at times when water was "relatively" abundant and pattern C at times of high water stress. The most important physiological parameter here determining these stomatal response patterns may be the relationship between leaf resistance and leaf water potential.

Hypothetically, a generalized leaf resistance—leaf water potential curve could be drawn and divided into three sections (Fig. 6). Each zone would represent a different level of leaf water stress and the range of each zone would be comparable to the range in leaf water potentials that might be experienced by a leaf on any one day. Zone A is a region of no water stress, zone B one of low water stress, and zone C one of high water stress. The daily course of leaf resistances to be predicted for plants occupying each of the three zones might correspond to the daily leaf resistance patterns shown in Fig. 1. This conclusion is not wholly supported by the results of our modelling efforts, but many of the qualitative features appear to be. Additionally, in studies by Rees (1961), Schulze *et al.*, (1972c) and Harrison (1971) it was found that under increasing water stress, species progressively displayed changes in the daily leaf resistance pattern,



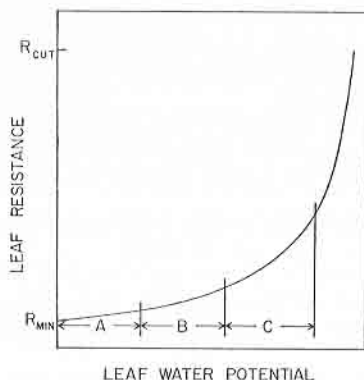


Fig. 6. Idealized leaf resistance-leaf water potential curve divided into three zones designating different levels of water stress. See text for explanation

beginning with pattern A and ending up with pattern C. Further, it can be expected that a species at the xeric end of its distribution will exhibit the daily leaf resistance pattern C more frequently and earlier in the season than members of the same species occupying more mesic sites. This has been confirmed by observations in the alpine tundra by Ehleringer (1973) and in the chaparral by Harrison (1971).

By integrating different physiological parameters into the model and assigning different values it is possible to predict the adaptive role of each parameter to modifying plant performance. In this way it is possible to examine the different physiological ways in which plants may adapt to their environment to maintain favorable water and carbon balances. Physiologically, it is through the daily course of leaf resistances that plants regulate the trade off between water loss and carbon gain in their respective environments and thus determine plant performance.

The use of the model as a tool describing the complex physiological relationships and environmental interactions contributes to our understanding of how different factors influence transpiration and net photosynthesis.

Results of these simulations when compared to actual field observations tend to support the relationships described by the model. As a consequence it is possible to better understand the adaptive significance of relationships within a species and the significance of differences between dissimilar species. But, moreover, it is hoped that the model may serve to point out some of the critical physiological relationships that should be measured if we are to get a better grasp of plant water relationships and an understanding of some of the physiological patterns that are seen in the field.

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