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Reprinted from Ecology
Vol. 55, No. 1, Winter 1974
pp. 62-72
Made in the United States of America

COUPLING OF ENVIRONMENT TO PLANT RESPONSE: A SIMULATION MODEL OF TRANSPIRATION¹

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Abstract. A low-resolution simulation model of transpiration was developed and run, with data from field studies in southwestern Oregon. The output of the model served as a means of relating environmental variables to plant response. This relation was used to define an ordinate which, in conjunction with previously developed ecosystem ordinates, proved helpful for comparing ecosystems, predicting community composition and, in special cases, growth. The data requirements of the model are modest; we deliberately developed a model that can be used on data obtained from field studies where electric power is unavailable and use of sophisticated instrumentation is impossible. The model requires inputs of air and soil temperature, atmospheric humidity, seasonal plant water potential (expressed as plant moisture stress, the absolute value of plant water potential), and a model of stomatal behavior. Where it was impossible to obtain accurate data, stochastic models were used to provide the necessary input.

The model simulated both potential and actual transpiration, the ratio of which is the most valuable single index of the seasonal moisture regime. Where no measurable stomatal control was exerted by Douglas-fir, the ratio was 1.0, indicating that adequate water was available to meet the transpiration demand. The ratio approached 0.3 on the drier locations. Significant changes in vegetation and growth were associated with this index.

Key words: *Atmospheric humidity; conifers; ecosystem ordination; environment; models; simulation; stomatal behavior; temperature; transpiration; water potential.*

INTRODUCTION

The current ecosystem modeling effort of the International Biological Program is directed toward mechanistic "state variable" models. These models attempt to describe ecosystem structure and behavior as a set of state variables (compartments) and their relations with other compartments. Thus, for example, we can describe an ecosystem with a carbon-flow model where the state variables are carbon concentrations in a given segment of the ecosystem, i.e., leaves, stems, roots, consumers, and so on. The flow from one compartment to another is usually expressed as a time function, representing some process such as growth, photosynthesis, or death. Considerable effort is being expended to develop realistic process models for use in mechanistic state-variable models.

Overton (1972) argues that it is also worthwhile to take a holistic view of an ecosystem; that is, study the behavior of an ecosystem taken as a whole, not only as a collection of separate subsystems. This report suggests a strategy of studying ecosystem behavior as a *complete entity*, and demonstrates the value of such an approach.

¹ Paper 813, Forest Research Laboratory, School of Forestry, Oregon State University; contribution 6 from the Coniferous Forest Biome IBP. Manuscript received June 27, 1972; accepted May 19, 1973.

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THEORETICAL CONSIDERATIONS

Plant ecologists have long recognized that plant growth and distribution are largely dependent upon environmental influences, both past and present. In fact, the correspondence between plant communities and their environment is thought to be so strong that inferences about environment can be made from comparative studies of plant communities. Thus, when two plant communities are very similar in composition, we often can assume that they exist under similar environments.

Several major studies of plant communities have focused upon interpreting environment (Ellenberg 1950, Loucks 1962, Whittaker 1967, Bakuzis 1969). By observing plant distribution over a range of conditions representing gradients in moisture, temperature, light, and soil fertility, they were able to select sensitive species and use their overlapping ranges to assess environments. Whittaker and Loucks each quantified physiography, classifying ecosystems by elevation, potential incident radiation, and soil characteristics. Such gradients were basically descriptive or relied upon idealized climatological models, because the gradients were assumed to be too complex to be measured directly (Whittaker 1961, 1967, Whittaker and Niering 1965); however, their assumptions about temperature or moisture were rarely substantiated by measurement (Haase 1970).

The problem of defining and describing environment has been addressed critically by Mason and Langenheim (1957). By semantic logic, they con-

cluded that environment and organism are inseparable and cannot be studied independently. A similar philosophy is implicit in general systems theory (Klir 1969). As an extension of this philosophy, *environment* can be defined as an *n*-dimensional matrix space *E* with ordinates (axes) Θ , which is the set of all possible environmental ordinates: $\Theta = \{\theta_1, \theta_2, \dots, \theta_n\}$. The individual ordinate, θ_i , can be defined in many ways, most simply as a physical environmental variable, such as air temperature, i.e., $\theta_i = T_{air}$. Such simple definitions have limited use, so ecologists have attempted to define θ_i in a more meaningful way; hence the "complex gradients" of Whittaker (1967). If we define θ_i as a plant response to environmental stimuli, we can develop ordinates consistent with the ideas of Mason and Langenheim (1957). Thus

$$\theta_i = R(\mathbf{H}, \mathbf{B}) \quad (1)$$

where $\mathbf{H}$ is a set of physical environmental variables $\mathbf{H} = \{\eta_1, \eta_2, \dots, \eta_n\}$, and $\mathbf{B}$ is a set of parameters $\mathbf{B} = \{\beta_1, \beta_2, \dots, \beta_n\}$ that denote organism response to $\mathbf{H}$.

The physical variables $\eta_1, \eta_2, \dots, \eta_n$ are such things as light intensity, temperature, atmospheric humidity, and time. We can also define η_i as a function of other factors. For example, it may be convenient to define soil water potential as a physical variable, while it is clearly a function of rainfall, soil type, etc. Now $\mathbf{B}$ may be an empty set, as where θ_i is defined as a simple physical variable. In such a case, that particular ordinate will provide no information about an organism's response to the physical variable. Equation (1) also applies to complex plant process (physiological) models.

The set of all ecosystems is $\mathcal{E}$, where $\mathcal{E} = \{e_1, e_2, \dots, e_n\}$. Each ecosystem is a point or locus in the environment space *E*. The point e_i (Θ) is given by the values of the ordinates Θ characteristic of the given ecosystem: $e_i(\Theta) = (\theta_1, \theta_2, \dots, \theta_n)$, where the value of θ_i is determined by the values of the physical variables and the organism response, given in equation (1).

Because it is defined as an organism's response to environmental stimuli, θ_i can be species-specific. The ordinate then becomes

$$\theta_{ij} = R(\mathbf{H}, \mathbf{B}_j) \quad (2)$$

where *j* is the *j*th species. This step greatly complicates our ordination system; therefore it is necessary to use a reference species on which to define θ_{ij} . The reference species must occur in most of the ecosystems in a given geographical area, thus insuring that θ_{ij} will be of sufficient resolution to separate a given ecosystem point in *E*-space from another. For example, in the northwestern United States, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) occurs throughout the region. Therefore, for classifying

forested ecosystems, the response of Douglas-fir to environmental stimuli will be useful even when extrapolated to forest areas where Douglas-fir does not occur. Western desert environments represent an environmental extreme, however, where there is no graduated response of Douglas-fir, thus rendering $\theta_{i,DF}$ meaningless as an ordinate for desert ecosystems. Here it may be necessary to use another species response, for example, sagebrush (*Artemisia tridentata* Nutt.). This step could be considered as an extension of $\theta_{i,DF}$ and is analogous to a logarithmic scale where more resolution is needed as we move down the scale.

Waring (1969) and his colleagues have attempted to define environmental ordinates that would conform to equation (1). Waring and Cleary (1967), for example, measured water stress (which is a function of water availability and plant factors) over a broad range of environments and found that in the droughty Siskiyou Mountains there were distinct differences in end-of-season plant moisture stress among the various ecosystems. Cleary and Waring (1969) interpreted temperature as it influenced dry-matter production. From laboratory studies, they developed an index for potential growth of Douglas-fir as a function of air and soil temperature.

Waring (1969) used end-of-season plant moisture stress and the temperature index to give two ordinates of *E*-space. Each ecosystem was a point at an intersection of $\theta_{i,DF}$, plant water stress, and $\theta_{2,DF}$, temperature index defined on Douglas-fir: $e_i(\Theta) = (\theta_{i,DF}, \theta_{2,DF})$. Waring observed that certain plant species occurred only in certain ranges of $\theta_{i,DF}$ and $\theta_{2,DF}$. Thus by measuring $\theta_{i,DF}$ he could predict community composition and conversely, could predict $e_i(\Theta)$ from community composition.

This two-dimensional ordination was successful in southern Oregon because temperature and moisture are limiting. Other factors become limiting in other locales, necessitating the use of more ordinates to resolve ecosystem differences. Further, the end-of-season plant moisture stress is obviously a weak ordinate; the seasonal pattern of stress is far more important. In addition, plant moisture stress affects growth; thus plant moisture stress per se can fall into the stimulus category, symbolized by η , not θ .

Transpiration is a plant process affected by temperature, atmospheric humidity, and plant factors, including plant moisture stress. We felt that seasonal transpiration rates could give us a new stimulus-response ordinate that would fit the relation of equation (1). Because transpiration is not easy to measure, particularly over a long growing season, we therefore decided to simulate it. A realistic simulation of transpiration requires a reasonable mathematical model; unfortunately, most physiological models of plant processes (Waggoner and Reif-

TABLE 1. Physiography and forest types characterizing study plots

Plot	Slope (%)	Aspect	Elevation (m)	Vegetation type ^a	Parent material
3	45	N	793	DF, BO, PP	granitic
8	40	SW	1,280	PP, DF	"
23	10	N	1,402	ES, DF, WF	"
1	25	W	1,493	WF, PP, DF	"

^a WF = white fir (*Abies concolor* Lindl. & Gord.), DF = Douglas-fir (*Pseudotsuga menziesii* [Milib.] Franco), PP = ponderosa pine (*Pinus ponderosa* Dougl.), BO = black oak (*Quercus kelloggii* Newb.), ES = Engelmann spruce (*Picea engelmannii* [Parry] Engelm.).

snyder 1968) are of high resolution and require input data impossible to obtain in the field, particularly over widely scattered sites. Consequently, if the ecologist is to use simulation as a tool, the model, in addition to being reasonable, must be one for which the input data can be obtained. Similar process models can serve to develop other ecosystem ordinates.

We developed a low-resolution leaf-level simulation of transpiration in the field. This model was based on stomatal behavior studies of Douglas-fir and on several years of field-temperature and moisture-stress data collected at 25 separate study plots in the Siskiyou Mountains of southwestern Oregon, latitude 42° N, longitude 123° W.

METHODS

Of the 25 study plots in the Siskiyou Mountains (Waring 1969), four were selected for intensive study to provide data for the modeling. These four plots were situated along an elevational gradient on Mt. Ashland and represented extremes in temperature and availability of soil moisture. Although the lowest of the plots (793 m) was the driest, it was not the hottest, and the highest plot (1,493 m) was intermediate in both temperature and moisture availability, which demonstrated that elevation can be misleading when used alone as an index to temperature and moisture gradients. The physiography and forest types characterizing the study plots are listed in Table 1. The plot numbers are the original ones assigned by Waring (1969).

Three Douglas-fir saplings (1–2 m tall) were selected on each plot for physiological measurements. The moisture status of the individual trees was assessed by means of the pressure bomb technique, which estimates xylem water potential (Scholander et al. 1965, Boyer 1967, Waring and Cleary 1967). Because water potential has units of negative atmospheres, we found it convenient to express water potential as plant moisture stress PMS, which equals the absolute value of plant water potential, thus having units of positive atmospheres. These measure-

ments were made throughout the summers of 1969 and 1970. As pointed out by Waring (1969), the plant moisture stress was least in the hours just before dawn. If nocturnal transpiration is negligible, predawn PMS should approach soil water stress over the entire rooting zone, or at least approach an equilibrium state. Therefore PMS was measured before dawn and at intervals throughout the day.

Stomatal aperture was estimated by the infiltration technique described by Fry and Walker (1967). Here, a 50% ethanol-water solution is forced through the stomatal pores; the pressure required for infiltration is inversely proportional to stomatal aperture, thus directly proportional to stomatal resistance (Jarvis 1971). Stomatal infiltration pressure readings (INF) were taken concurrently with the pressure-bomb readings of plant moisture stress. During the summer of 1970, we also measured atmospheric humidity with an Assmann-type spring-driven mercury and glass psychrometer.

Cleary and Waring (1969) measured air temperature at 20 cm above ground level; however, because we used 1–2 m saplings as references to the community, we preferred sensors at 1 m above ground even though this step introduces error when temperature data is measured both at 1 m and at 20 cm.

The air and soil temperatures measured at 1 m above and 20 cm below the forest floor were recorded continuously on Partlow model TRH spring-driven 30-day thermographs. The recorded temperature traces were digitized by computer and the daily maximum, minimum, and average temperature were printed out. Daily measurements of relative humidity taken at 1300 h by the USDA Forest Service in the same watershed were used for modeling purposes. The temperature data are available from 1966, relative humidity data from 1967.

We related stomatal infiltration pressure to stomatal resistance by measuring transpiration rates in the laboratory and calculating stomatal resistances. The five Douglas-fir seedlings used in this experiment were brought into the balance room under normal room light after being well watered the previous day. The top of a shoot was cut off and immediately weighed on a Mettler balance, accurate to 0.1 mg. The excised shoot was then placed on a rack in a vertical position in front of a high-speed fan. A sample of three needles was taken just before the first weighing. The stomatal infiltration pressure INF of this sample was measured; this value was considered to be infiltration pressure at time zero. The branch was reweighed at intervals ranging from 5 min at the outset to 30 min toward the end of the experiment. After each weighing, three needles were plucked from the branch for determination of INF and the branch was quickly reweighed. Thus the change in weight could be corrected for weight loss

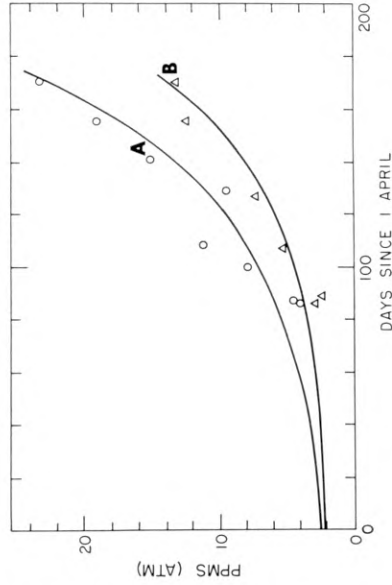


FIG. 1. Predawn plant moisture stress PMS of (A) plot 3 (oak type), and (B) plot 1 mixed conifer type, plotted as a function of time. Time zero is April 1, 1969.

The stomata of Douglas-fir typically close at night from July through September. Spot checks of other conifers suggested similar stomatal behavior, but they were not studied in detail. After sunrise, stomata opened to some maximal aperture, then either remained at that value throughout the day or closed to various degrees. Plant moisture stress during spring and early summer increased each day from the minimum value in the predawn darkness to approximately 15–18 atm at midday. In late summer, when soil water had been depleted, maximum PMS was even greater. Typical stomatal behavior and plant moisture stress values are illustrated in Fig. 2 with data from plots 1 and 3.

The stomata tended to be closed before dawn, then opened to a maximum between 0800 and 1000 h (Fig. 2). The maximum stomatal aperture of the tree on plot 3 (oak type) was less than that of the

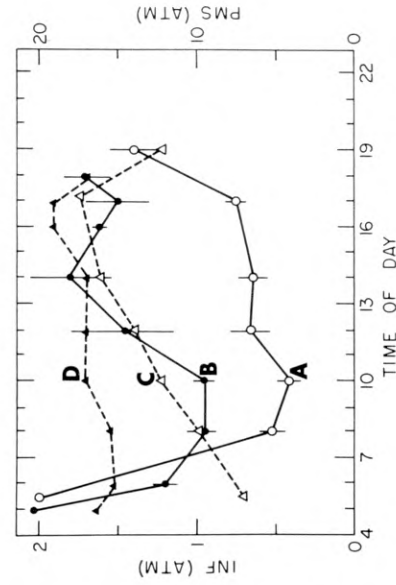


FIG. 2. Stomatal infiltration pressure INF of tree no. 1, plot 1 (A), and tree no. 1, plot 3 (B); plant moisture stress of the same trees in plot 1 (C), and plot 3 (D); for August 5 and 6, respectively. Sunrise at 0530, sunset at 1900 hr. The vertical lines from the INF points represent the 95% confidence intervals of the sample means.

EXPERIMENTAL RESULTS

Field results

Plant water stress PMS measured before dawn and throughout the day, as well as stomatal behavior, were measured on the plots during each field trip. The measurement period began approximately 2 h before dawn and ended after dark. In 1969, PMS and stomatal infiltration pressure were measured at intervals throughout the day on all plots during each field trip, requiring one day per plot. As stomatal behavior became better understood, fewer measurements were necessary, so two plots could be studied on a single day.

Predawn moisture stress PMS tended to increase throughout the summer because of general absence of rain in the region. The rate of soil water depletion differed from plot to plot, but the trends were similar. The increase in PMS on plots 1 and 3 is illustrated in Fig. 1. The solid curves are given by a nonlinear least-squares fit of an exponential function to the data. The function is asymptotic to 2 atm, the lowest PMS observed. The integral of this function over time could be useful as a moisture stress ordinate with units atm days where a transpiration simulation would be impractical.

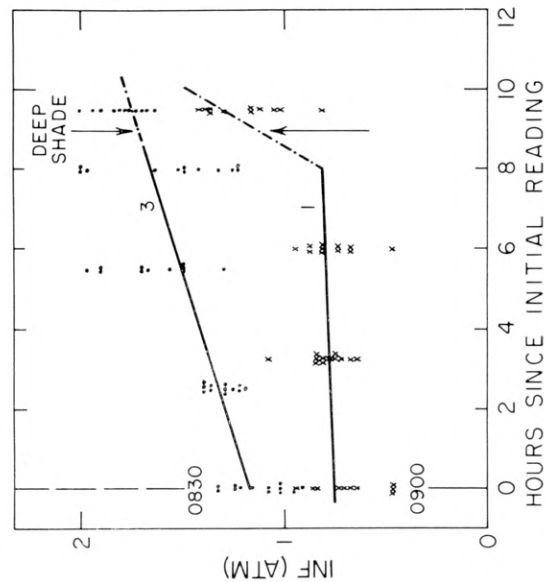


FIG. 3. Diurnal variation in stomatal infiltration pressure. Each point represents the stomatal infiltration pressure of a single needle; the dots are from plot 3 (oak type), September 1, 1970; the x's are from plot 1 (mixed conifer type), August 20, 1970. Points beyond dotted line were not used in regression analysis because of proximity of sunset. PPMS: plot 3, 2.5 atm; plot 1, 11.6 atm.

tree on plot 1 (mixed conifer type) while PPMS was greater on plot 3 than on plot 1, indicating drier soil. The maximum values of PMS for each plot were not greatly different. These data are typical of water-potential patterns for Douglas-fir on a sunny day (Waring and Cleary 1967), when PPMS is less than approximately 15 atm.

The stomatal behavior depicted in Fig. 1 is typical for middle and late summer, but the stomata do not close at night in spring when the soil is fully charged. In middle and late summer, when the stomata are completely closed at night, they respond only to direct sunlight and are unaffected by predawn diffuse light. They also begin to close at dusk.

TABLE 2. Rates of change of stomatal aperture from not less than $\frac{1}{2}$ hr after dawn to not more than $\frac{1}{2}$ hr before sunset grouped according to the predawn moisture stress (PPMS) values

PPMS (atm)	PPMS ≤ 5	5 $\leq$ PPMS ≤ 15	PPMS > 15
Rate of change in stomatal infiltration pressure (Δ INF hr $^{-1}$)	0.007 ^a 0.008 ^a 0.037 0.036 0.050 0.007 0.002 0.063 0.024	0.023 0.002 0.056 0.068 0.051 -0.050 0.110	0.070 0.056 0.068 0.051 -0.050 0.110
Mean rate of change	0.0075 ^a	0.020	0.051

^a Not different from zero, statistically.

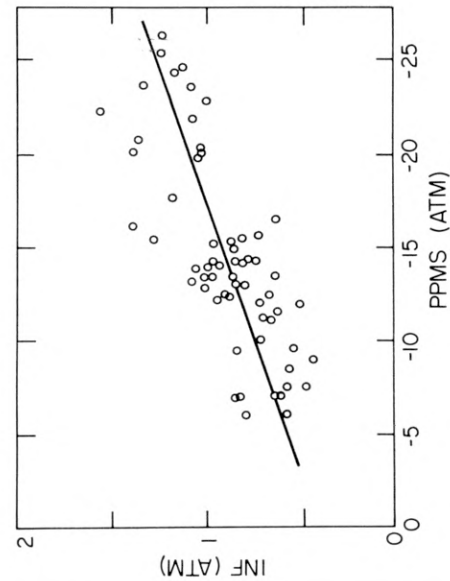


FIG. 4. Minimum daily stomatal infiltration pressure INF from all points as a function of the corresponding predawn plant moisture stress PPMS. Each point represents the mean INF value of the three trees on the respective plot corresponding to the mean PPMS of the three trees.

Even though the stomata are open at night in springtime, it is doubtful that the soil moisture status is the only factor influencing nocturnal stomatal behavior. Douglas-fir stomata on all plots were closed at night by the end of the elongation growth period (ca. July 1) in spite of great differences in PPMS. The importance of potassium nutrition in stomatal behavior (Humble and Hsiao 1969, Sawhney and Zelitch 1969) may account for this behavior as potassium levels in older foliage during the time of elongation growth may be low. Clearly, additional research is indicated.

Stomatal behavior during the daylight hours is also incompletely understood. The stomata usually opened to some maximum aperture, then remained at that value throughout the day or closed slightly (Fig. 3). The slope of the regression lines in Fig. 3 indicate the rate of change of the stomata. The slopes of a number of linear regressions of stomatal infiltration pressure on time are given in Table 2. These data suggest that when PPMS is low, the stomata remain at a maximum value throughout the day. A greater rate of change is associated with increased PPMS.

The maximum diurnal stomatal aperture is given by the intercept of the regressions depicted in Fig. 3 and Table 2. This maximum stomatal aperture was found to be correlated with PPMS (Fig. 4). The regression equation obtained from this analysis was $\text{INF} = 0.40 + 0.033 \text{ PPMS}$ ($R^2 = 0.55$, $F = 71.78^{**}$). This equation and the relations shown in Table 2 were used in the simulation to predict stomatal behavior as a function of water stress.

To summarize the field observations:

- 1) Predawn plant moisture stress PPMS tended to

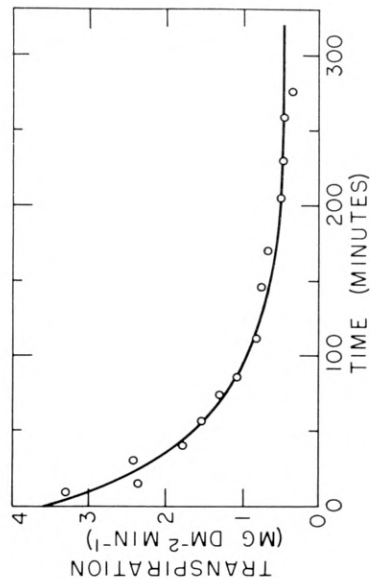


FIG. 5. Transpiration rate $d\tau/dt$ from the severed seedling, Douglas-fir no. 1 (DF 1), as a function of time. Time was measured from the point of severing. Smooth curve was fitted to the data by least-squares estimation.

increase exponentially throughout the summer. The rate and extent of depletion of soil moisture was characteristic of each plot.

- 2) Stomata of Douglas-fir as well as other conifers were closed at night in summer and early fall; they reached a maximum aperture between 0800 and 1000 hr. This maximum aperture was correlated with PPMS.

- 3) Diurnal stomatal behavior cannot be explained completely on the basis of data available. After achieving maximum aperture, the stomata either remained at that aperture, or closed to some extent. The rate of closure seemed to be affected by the extent of soil moisture depletion as indicated by increasing PPMS (Table 2), but only in a general way.

Laboratory results

Transpiration rates measured on cut branches from Douglas-fir seedlings were plotted against time and fit to a nonlinear regression model, $Y = \beta_1 + (\beta_2 - \beta_1) \exp(-\beta_3 t)$ giving transpiration at time t . The model fit the data well in most instances (Fig. 5).

Equation (3) gives transpiration rate as a function of vapor concentration deficit between the leaf mesophyll and the air ΔC , and the total leaf resistance to water flux Σr (Slatyer 1967):

$$\frac{d\tau}{dt} = \frac{\Delta C}{\Sigma r} \quad (3)$$

Setting equation (3) equal to the fitted regression model above, and solving for Σr gives

$$\Sigma r = \Delta C [\beta_1 + (\beta_2 - \beta_1) \exp(-\beta_3 t)]^{-1} \quad (4)$$

Stomatal resistance was calculated by solving equation (5) (Slatyer 1967, Jarvis and Slatyer 1970) for stomatal resistance r_s :

$$\Sigma r = r_a + \frac{r_c(r_s + r_m)}{(r_s + r_m) + r_c} \quad (5)$$

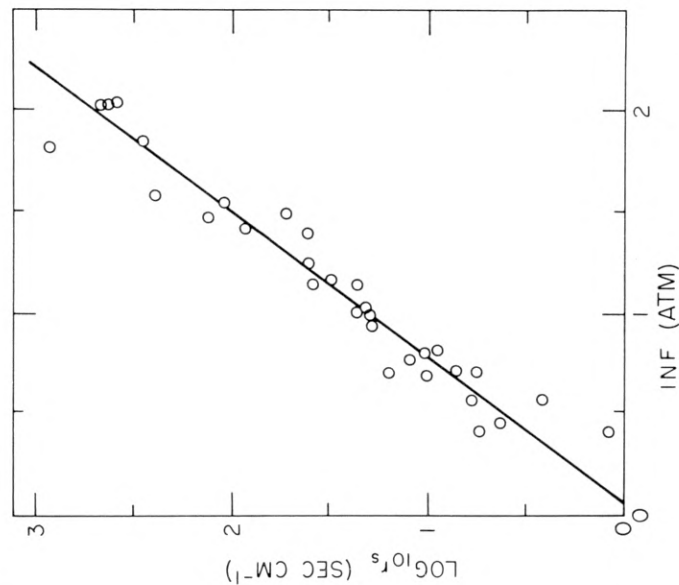


FIG. 6. Stomatal resistance r_s of Douglas-fir as a function of stomatal infiltration pressure.

where r_a = boundary layer resistance, r_s = stomatal resistance, r_m = mesophyll resistance, and r_c = cuticular resistance. The solution of equation (5) for r_s is simplified by elimination of boundary layer by means of the fan, and by assuming r_m is negligible (Jarvis and Slatyer 1970) except at very low Σr .

The asymptotic transpiration rate given by the estimated value of β_1 in the fitted model was considered to be cuticular transpiration and was used to calculate cuticular resistance r_c . The calculated values of r_s were then regressed on the corresponding values of stomatal infiltration pressure, giving the relation shown in Fig. 6. The regression analysis was run on pooled data from all five seedlings. The resulting equation (6) was used to calculate stomatal resistance as a function of stomatal infiltration pressure INF:

$$\log_{10} r_s = -0.088 + 1.39 \text{ INF} \quad (6)$$

A residual analysis of the regression supports the assumption that most of the experimental errors were random ($R^2 = 0.93$, $F = 413.3$), but some bias was introduced in the estimation of cuticular resistance. Values for cuticular resistance estimated from the asymptotic transpiration rate may be low because of water loss from leaf scars exposed during the experiment.

In a subsequent experiment where needle samples were not taken, cuticular transpiration was lower than that of seedlings from which needles had been removed for determination of INF. Cuticular resis-

tance values ranged from 28–74 sec cm⁻¹ for the sampled plants to 43–132 sec cm⁻¹ for branches with no needles removed. The seedlings used in this experiment were not hardened off; the needles were soft and flexible. The value of 132 sec cm⁻¹ was obtained from a tree near the laboratory, and is more consistent with the range of values for cuticular resistance cited by Slatyer (1967). Cuticular resistance of Douglas-fir in the dry Siskiyou Mountains was assumed to average 150 sec cm⁻¹.

The results of the soil temperature experiment were analyzed by regression analysis. Soil temperature, air temperature, and vapor pressure gradient were expressed as independent variables in a stepwise multiple regression analysis with stomatal infiltration pressure as the dependent variable. Under the conditions of the experiment, soil temperature had an influence upon stomatal response only below 2°C. None of the other factors influenced stomatal aperture significantly. Generally, elongation of new foliage does not occur in the field until soil temperature exceeds 2°C (Waring 1969). Later during the growing season, limiting soil water appears to mask any possible direct effect of soil temperature upon stomatal behavior. These observations agree with those of Anderson and McNaughton (1971), who found that low soil temperature had no effect on photosynthesis or transpiration of several alpine species.

In summary, field and laboratory observations were necessary to develop a model of stomatal behavior. Our study disclosed that predawn water potential influenced maximum stomatal aperture as well as the diurnal behavior of stomata. An empirical relation of stomatal infiltration pressure to stomatal resistance was established, and the effect of soil temperature on stomata was found to be minor. These observations were used to develop a low-resolution stochastic model of stomatal behavior of Douglas-fir in the field.

SIMULATION MODEL

Our goal was not to develop a detailed mechanistic model of transpiration as discussed by Waggoner and Reifsynder (1968) and Waggoner et al. (1969), but a realistic model with only limited requirements for data. Ecosystem comparisons were our immediate objective, and construction as well as further requirements of the model reflect this bias. The model, although not exact, should allow us to identify environmental ordinates useful for both comparative and predictive purposes because it would relate environmental variables to a plant response. Our reference organism was a hypothetical Douglas-fir, 2 m tall, with perfectly homogeneous foliage and no boundary layer resistance, growing in the understory of our ecosystems.

As discussed, transpiration was described in the literature of plant physiology (Slatyer 1967) by equation (3). Ignoring boundary layer resistance, equation (3) can be expanded to

$$\frac{d\tau}{dt} = \Delta C \left(\frac{1}{r_s} + \frac{1}{r_c} \right) = \Delta C \left(\frac{1}{r_s} + \epsilon \right), \quad (7)$$

where ΔC is vapor concentration gradient (g cm⁻³), τ is transpiration (g cm⁻²), r_s is stomatal resistance (sec cm⁻¹), and ϵ is the inverse of cuticular resistance, set to 1/150 sec cm⁻¹. Equation (7) can be solved by integration if ΔC and r_s can be expressed as functions of time.

Because vapor concentration gradient is a function of temperature, the daily time course of ΔC should parallel the time course of temperature. Examination of the temperature traces from the thermograph charts and the vapor pressure data taken on the various plots in 1970 suggests that a quadratic function of time should suffice for ΔC , the constants of which must be determined each day by the simulation based on input data. Substitution of a quadratic time function for ΔC into equation (7) gives

$$d\tau/dt = (\beta + \gamma t - \delta t^2)(1/r_s + \epsilon). \quad (8)$$

It still remains to express r_s as a time function.

By assuming that the rate of stomatal closure after achieving maximum aperture is a linear function of time (Table 2), we developed a model expressing daily stomatal behavior:

$$\text{INF} = \text{INF}_0 + \alpha t \quad (9)$$

where α is the change in infiltration pressure per second and INF_0 is the minimum stomatal infiltration pressure, assumed to be reached instantly after sunrise. It is also necessary to convert the rates of stomatal change listed in Table 2 (atmospheres per hour) to atmospheres per second, so that the units of α will agree with those of equation (8).

The relation of stomatal resistance to INF is given by equation (6), which is substituted into equation (9) and expressed in natural logs:

$$\ln r_s = 2.303(-0.088 + 1.39 \text{INF}_0 + 1.39 \alpha t) = a + bt, \quad (10)$$

where $a = 2.303(-0.088 + 1.39 \text{INF}_0)$ and $b = 2.303(1.39 \alpha)$. Taking the log of both sides, $r_s = \exp(a + bt)$, which is substituted into equation (8) gives

$$d\tau/dt = (\beta + \gamma t - \delta t^2)(1/\exp(a + bt) + \epsilon). \quad (11)$$

Solving equation (11) by integration gives us

$$\tau = (1/\epsilon^a)(\beta A + \gamma B - \delta C) + \epsilon(\beta + \gamma t/\delta^2/3), \quad (12)$$

where

$$A = \int_0^t e^{-bt} dt = (1 - e^{-bt})/b,$$

$$B = \int_0^t t e^{-bt} dt = 1/b^2 - e^{-bt}(bt + 1)/b^2,$$

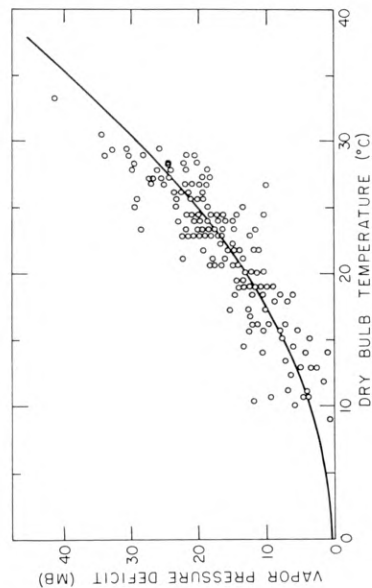


FIG. 7. Vapor pressure deficit VPD as a function of dry-bulb temperature in degrees C on Ashland watershed, 1969. Equation of curve: $\text{VPD} = 0.484 + 0.0207T + 0.031T^2$.

stochastic model incorporates the variance into the generated value, giving reasonable values of vapor pressure deficit (VPD). These generated values were taken to be maximum VPD (corresponding to maximum temperature) and were used to calculate maximum vapor concentration deficit ΔC . The constants β , γ , and δ were calculated for each iteration by the program. Having generated all the variables needed, the program simply solves equations (12) and (13), then repeats the process in the next iteration.

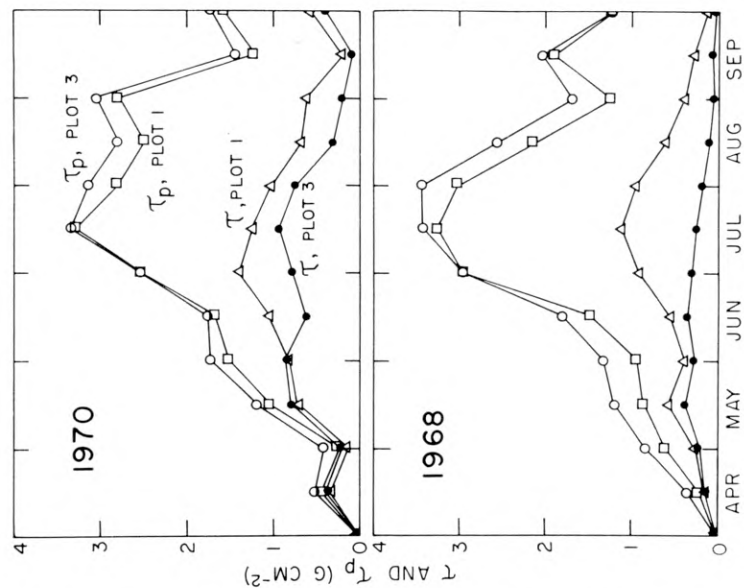


FIG. 8. Simulated transpiration for two plots on Mt. Ashland at 2-week intervals throughout the growing season in 1970 (top) and 1968 (bottom).

$$C = \int_0^t t^2 e^{-bt} dt = (e^{-bt}/b^3)(-b^2t^2 - 2bt - 2) + 2/b^3.$$

Equation (12) gives a value for daily transpiration in Douglas-fir when t equals number of seconds per day. Potential transpiration τ_p that transpiration expected if the stomata of Douglas-fir were fully open throughout the day and season, could be useful in assessing the atmospheric demand for transpiration. Potential transpiration is obtained by setting total resistance Σr to the minimum value observed, 4 sec cm⁻¹ and integrating equation (13):

$$\tau_p = \frac{1}{4} \int_0^t (\beta + \gamma t - \delta t^2) dt. \quad (13)$$

Given equations (12) and (13), τ and τ_p can be calculated given the following information: maximum vapor concentration gradients, predawn plant water potential (expressed as plant moisture stress, the absolute value of water potential), and day length in seconds. We simulated transpiration and potential transpiration for the 6-month period of April 1 and September 20.

A digital computer program was written in FORTRAN IV and run on the CDC 3300 computer on the Oregon State University campus. It performed one iteration each "day," during which it generated all of the necessary variables to solve equations (12) and (13). These values were stored as daily, monthly, and seasonal totals. There were two versions of the simulation program: one that generated all the necessary variables from stochastic models, and one that accepted temperature records for the period of interest. Both versions used the fitted equations described in Fig. 1 with parameters characteristic of each plot to generate idealized values of predawn plant moisture stress. Given a value of PPMS, the routine stochastically generated values of stomatal infiltration pressure INF by random selection from a normal (μ , σ) distribution about the regression line of Fig. 4, where μ = expected value of INF (from the regression equation) and σ = the standard deviation of the normal distribution of residuals. This value was INF_0 in the transpiration model.

Vapor concentration deficit ΔC likewise was generated by random selection from a normal distribution about a regression line, in this instance the relation of vapor pressure deficit to temperature. Vapor pressure deficit is defined as the difference between saturation vapor pressure at temperature T and the actual vapor pressure at that temperature. Because we had no continuous records of vapor pressure on our plots, an empirical approach was necessary. Three years of humidity data taken at 1300 hr by the USDA Forest Service near our research sites were used to obtain the necessary relation of temperature to vapor pressure deficit (Fig. 7, $R^2 = 0.81$, $F = 897$). Although there is considerable variance, the

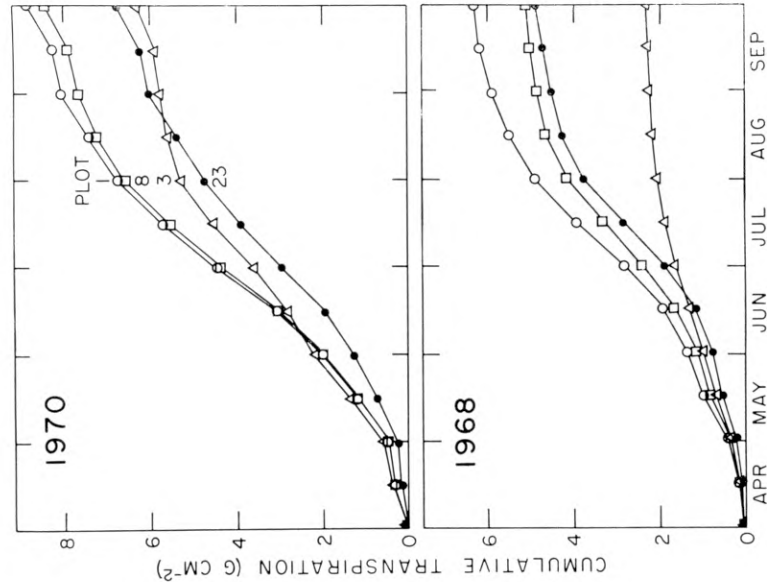


FIG. 9. Simulated cumulative transpiration for all plots on Mt. Ashland in 1970 (top) and 1968 (bottom).

RESULTS OF SIMULATIONS

Transpiration τ and potential transpiration τ_p for the 6-month period beginning April 1 were simulated for the years 1968 and 1970. Typical simulated output is shown in Fig. 8. The striking difference between potential and "actual" transpiration illustrates effects of stomatal control on transpiration and the relative importance of the two components of transpiration, atmospheric demand and plant resistance. Two important observations are also illustrated in Fig. 8: transpiration in the spring is limited primarily by the weather, i.e., the cool wet spring weather results in a low transpiration demand, hence low transpiration rates; and transpiration is limited by plant resistance in late summer. For example, in plot 3, 1968, late summer transpiration is less than spring transpiration even though the demand is three times as great.

Cumulative transpiration for the four plots during 1968 and 1970 is illustrated in Fig. 9. The impressive difference between the 2 years is attributable primarily to an unusually dry winter in 1968, when the maximum snowpack was 137 cm, compared to 195 cm in 1970. This resulted in low water availability. The difference in atmospheric demand between the 2 years is small, even though cloudy weather with

TABLE 3. τ_p , τ/τ_p , potential growth index PGI, and maximum height of Douglas-fir on each plot

Plot	τ_p	τ/τ_p	PGI	Maximum height (m)
1	13.5	0.58	74	44
2	12.2	0.51	62	42, 38, 47, 40
3	17.7	0.29	98	22, 24, 33, 24, 26, 25, 24
4	12.7	0.62	52	34, 40
5	16.5	0.40	70	23, 19
8	21.4	0.42	96	44
9	12.5	0.57	59	44, 49
10	10.3	0.46	52	15, 27
11	16.8	0.68	58	55
19	13.1	1.00	85	83, 81, 85, 84, 82

some rain in August 1968 reduced demand. The amount of rain was insufficient to recharge the soil.

It was impossible to validate the model by comparing its results with field measurements, but laboratory data can be extrapolated. The maximum transpiration rate shown in Fig. 4 is about $4 \text{ mg dm}^{-2} \text{ min}^{-1}$ which is equivalent to 36.0 mg cm^{-2} per 15 hr day. Multiplying by 180 days (the time span of the simulation) gives 6.5 g cm^{-2} . This agrees favorably with the simulated totals of $2\text{--}9 \text{ g cm}^{-2}$ over 180 days (Fig. 9), supporting our belief that the model is reasonable. Deviations from the extrapolated value can easily be explained by stomatal control and differences in evaporative demand.

The ratio of τ to τ_p provides an excellent environmental ordinate because it couples both atmospheric demand and the plant's ability to respond. Large differences exist between plots (Fig. 8), and the ratio of transpiration to potential transpiration characterizes the relative drought of the plots, while potential transpiration provides insight into the atmospheric conditions prevailing.

If the indexes τ_p and τ/τ_p are coupled realistically to plant response, there should be some correlation with growth. That is, a high value of τ_p and a low value of τ/τ_p should indicate an extreme environment, both hot and dry. A high value of τ_p and a ratio of τ/τ_p approaching unity indicates that, although the atmospheric demand is high, soil water is adequate. We would expect low productivity in the first instance and high productivity in the second.

The simulation was run for 14 additional plots that have Douglas-fir in the overstory. Temperature data for 1966 were used because the thermographs had been removed in 1968 from all but the four plots used in this study. The τ_p , τ/τ_p , potential growth index PGI (Cleary and Waring 1969), and maximum height of Douglas-fir on each plot are listed in Table 3. The maximum height was obtained on plots 3 and 19 by extrapolation of site class curves (King 1966). A stepwise multiple regression analysis was run on the data where $x_1 = \tau_p$, $x_2 = \tau/\tau_p$, $x_3 = \text{PGI}$, $x_4 = (\tau/\tau_p)^2$, $x_5 = \tau_p(\tau/\tau_p)$ and $x_6 = \text{PGI}(\tau/\tau_p)$.

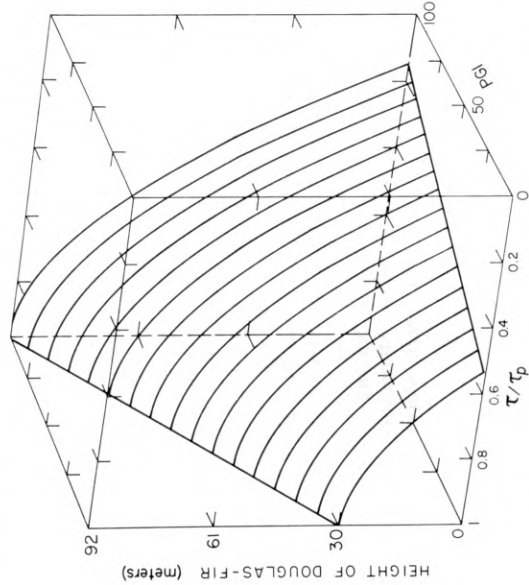


FIG. 10. Maximum height of Douglas-fir on 10 ecosystems of τ/τ_p and PGI. Data in Table 3.

An analysis of variance table indicated that x_1 and x_5 were nonsignificant. The combined effect of τ/τ_p and PGI on growth is illustrated in Fig. 10. The regression had an R^2 of 0.95, $F = 148^{**}$, $SE = 3.27$. Note that the surface in Fig. 10 has been extrapolated beyond the data; height of Douglas-fir should drop to zero when PGI approaches zero.

Thus the variables τ/τ_p and PGI were correlated strongly with growth, but neither transpiration τ nor potential transpiration τ_p alone was important in predicting growth. We believe that these indexes have validity both as a descriptive tool and as a means of assessing the impact of certain environmental variables upon plant growth and response.

Limits of various species in terms of the new ecosystem index developed in this study were defined and used in an ecosystem classification (Waring et al. 1972). The new index added more predictive power to the system described by Waring (1969). The transpiration model is one means of using physiological process models as an ecological tool. The development of various additional ordinates will allow the ecologist to understand more completely factors influencing community structure and behavior.

ACKNOWLEDGMENTS

The humidity data were provided by the USDA Forest Service Fire Weather Sections of the Rogue River and Siskiyou National Forests. Steve Running, who helped in collecting the field data, deserves special thanks for his mathematical counsel. Fieldwork was supported from a McIntire-Stennis federal grant and the modeling effort by National Sciences Foundation grant no. GB-20963 to the Coniferous Forest Biome, Ecosystem Analysis Studies, U. S./International Biological Program.

LITERATURE CITED

- Anderson, J. E., and S. J. McNaughton. 1971. Effects of low soil temperatures on photosynthesis, transpiration, and leaf relative water content of montane plants. *Bull. Ecol. Soc. Am.* **52**: 31.
- Babalola, O., L. Boersma, and C. T. Youngberg. 1968. Photosynthesis and transpiration of Monterey pine seedlings as a function of soil water suction and soil temperature. *Plant Physiol.* **43**: 515-521.
- Bakuzis, E. V. 1969. Forestry viewed in an ecosystem perspective, p. 189-258. In B. M. Van Dyne [ed.], *The ecosystem concept in natural resource management*. Academic Press, New York. 383 p.
- Boyer, J. S. 1967. Leaf water potentials measured with a pressure chamber. *Plant Physiol.* **42**: 133-137.
- Cleary, B. D., and R. H. Waring. 1969. Temperature: Collection of data and its analysis for the interpretation of plant growth and distribution. *Can. J. Bot.* **47**: 167-173.
- Cox, L. M., and L. Boersma. 1967. Transpiration as a function of soil temperature and soil water stress. *Plant Physiol.* **42**: 550-556.
- Ellenberg, H. 1950. *Unkrautgemeinschaften als Zeiger fuer Klima und Boden*. Landwirtschaft. Pflanzensozologie. Bd. I. Ulmer, Stuttgart. 141 p.
- Fry, K. E., and R. B. Walker. 1967. A pressure infiltration method for estimating stomatal opening in conifers. *Ecology* **48**: 155-157.
- Haase, E. F. 1970. Environmental fluctuations on south-facing slopes in the Santa Catalina Mountains of Arizona. *Ecology* **51**: 959-974.
- Humble, G. D., and T. C. Hsiao. 1969. Specific requirements of K^+ for light-activated opening of stomata in epidermal strips. *Plant Physiol.* **44**: 230-234.
- Jarvis, P. G. 1971. The estimation of resistances to carbon dioxide transfer, p. 566-631. In Z. Sestak, J. Catsky, and P. G. Jarvis [ed.], *Plant photosynthetic production. Manual of methods*. W. Junk, The Hague. 818 p.
- Jarvis, P. G., and R. O. Slatyer. 1970. The role of the mesophyll cell wall in leaf transpiration. *Planta* **90**: 303-322.
- King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Pap. 8, Centralia, Wash.
- Klir, G. J. 1969. An approach to general systems theory. Van Nostrand Reinhold, New York. 323 p.
- Loucks, O. L. 1962. Ordinating forest communities by means of environmental scalars and phytosociological indices. *Ecol. Monogr.* **32**: 137-166.
- Mason, H. L., and J. H. Langenheim. 1957. Language analysis and the concept *Environment*. *Ecology* **38**: 325-340.
- Overton, W. S. 1972. Toward a general model structure for a forest ecosystem, p. 37-47. In J. F. Franklin, L. J. Dempster, and R. H. Waring [ed.], *Proceedings—Research on Coniferous Forest Ecosystems—A Symposium*, USDA For. Serv. Portland, Oregon. (U.S. Gov. Print. Off., Washington, D.C.) 322 p.
- Sawhney, G. L., and I. Zelitch. 1969. Direct determination of K^+ accumulation in guard cells in relation to stomatal movement in light. *Plant Physiol.* **44**: 1350-1354.
- Scholander, P. F., H. T. Hammel, D. Broadstreet, and E. Z. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* **148**: 339-346.
- Slatyer, R. O. 1966. Some physical aspects of internal

- control of leaf transpiration. *Agric. Meteorol.* **3**: 281-292.
- _____. 1967. Plant-water relationships. Academic Press, London and New York. 366 p.
- Thompson, F. B., and L. Leyton. 1971. Method for measuring the leaf surface area of complex shoots. *Nature* **227**: 572-573.
- Waggoner, P. E., G. M. Furnival, and W. E. Reifsnyder. 1969. Simulation of the microclimate in a forest. *For. Sci.* **15**: 37-45.
- Waggoner, P. E., and W. E. Reifsnyder. 1968. Simulation of the temperature, humidity, and evaporation profiles in a leaf canopy. *J. Appl. Meteorol.* **7**: 400-409.
- Waring, R. H. 1969. Forest plants of the eastern Siskiyou: Their environmental and vegetational distribution. *Northwest Sci.* **43**: 1-17.
- Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: Evaluation by pressure bomb. *Science* **155**: 1248-1254.
- Waring, R. H., K. L. Reed, and W. H. Emmingham. 1972. An environmental grid for classifying coniferous forest ecosystems, p. 79-91. *In* J. F. Franklin, L. J. Dempster, and R. H. Waring [ed.], *Proceedings—Research on Coniferous Forest Ecosystems—A Symposium*. USDA For. Serv., Portland, Oregon. (U.S. Gov. Print. Off., Washington, D.C.) 322 p.
- Whittaker, R. H. 1961. Vegetation history of the Pacific coast states and the "central" significance of the Klamath region. *Madroño* **16**: 5-23.
- _____. 1967. Gradient analysis of vegetation. *Biol. Rev.* **49**: 207-264.
- Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the south slope. *Ecology* **46**: 429-452.