AN ABSTRACT OF THE THESIS OF

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Title: A COMPUTER SIMULATION MODEL OF SEASONAL TRANSPIRATION IN DOUGLAS-FIR BASED ON A MODEL OF STOMATAL RESISTANCE

Abstract approved: Signature redacted for privacy.
R. H. Waring

Four study sites were selected along an altitudinal gradient on Mt. Ashland in the Siskiyou Mountains of southern Oregon. The altitudinal gradient roughly corresponded to a gradient in temperature and water availability ranging from very hot and dry to cool and moist. Air and soil temperatures were continuously measured on each of the plots by recording thermographs. Periodic measurements of atmospheric humidity were taken on each plot, and daily humidity data taken by the U.S. Forest Service were also used. The environmental data were used to develop a mathematical model of daily changes in vapor concentration gradient.

Measurements of diurnal patterns of xylem water potential (plant moisture stress) in young Douglas-fir trees (Pseudotsuga menziesii (Mirb.) Franco) were made at intervals throughout the

summers of 1969 and 1970, using the pressure bomb technique. Xylem water potential was found to be at a maximum value before dawn, and would decrease to approximately -15 atm during the day, then recover to a maximum level the following night. This maximum value of xylem water potential is believed to roughly correspond to soil water potential over the entire root zone. The maximum, or pre-dawn, xylem water potential values gradually decreased throughout the rainless summers, from -3 to -5 atm in the spring to values ranging from -12 to -28 atm in September depending on location. The seasonal decrease in pre-dawn xylem water potential was described mathematically by an exponential function.

Relative stomatal aperture was estimated by a stomatal infiltration technique. The relationship of relative stomatal aperture values to stomatal resistance was determined, where the log of stomatal resistance was found to be directly proportional to the pressure required to infiltrate the stomatal pores.

The stomata of Douglas-fir were found to be open at night in the spring, but were fully closed at night during the months of July through September. Stomatal opening during the summer months was triggered only by actual sunrise--the pre-dawn diffuse light had no effect. It was suggested that nocturnal stomatal behavior may be influenced by phenological changes. The stomata tended to open to some maximum aperture in the morning, then would remain at that aperture or would close to

a greater or lesser extent throughout the day. The rate of diurnal stomatal closure appeared to be related in some manner to pre-dawn plant moisture stress and other factors. When the soil was fully hydrated, the stomata would remain at the maximum aperture throughout the day. Later in the season, as soil moisture availability decreased (reflected in higher pre-dawn plant moisture stress), the stomata would tend to close: slowly when under moderate moisture stress, faster when under severe stress. The daily maximum stomatal aperture was found to be correlated with pre-dawn plant moisture stress. Stomatal behavior of Douglas-fir was found to be unaffected by soil temperatures greater than $2^{\circ}C$.

The observations on stomatal behavior were described mathematically. The models of vapor concentration deficit and stomatal behavior were incorporated into a digital computer simulation model of seasonal transpiration in Douglas-fir. Applications of the model in forestry and plant ecology are described.

A Computer Simulation Model of Seasonal Transpiration in Douglas-fir Based on a Model of Stomatal Resistance

by

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A COMPUTER SIMULATION MODEL OF SEASONAL TRANSPIRATION IN DOUGLAS-FIR BASED ON A MODEL OF STOMATAL RESISTANCE

I. INTRODUCTION

Plant ecologists have long recognized that plant growth and distribution is largely dependent upon environmental influences both past and present. Further, the correspondence between plant communities and the environment is thought so strong that inferences about environment can be made from comparative studies of plant communities. Most plant species have limits of tolerance to environmental extremes and are specially adapted to live within those limits. Therefore, if two plant communities were very similar in composition, the plant ecologist would suspect that the two communities exist under similar environmental conditions.

Unfortunately, the plant ecologist has not had the methodology to accurately assess the environmental variables operating on a given plant community. He has, therefore, been forced to describe the environment of interest in relative terms: A is drier than B, C is wetter than D, from physiographic comparisons. The vegetational distribution itself was used as an index useful in comparing ecosystems, based on the knowledge that plants are highly sensitive to environmental conditions and tend to grow where all the environmental influences are within the limits of tolerance. A methodology which

would allow the ecologist to quantify the range of tolerance of plant species to environment, would enable him to better explain plant growth and distribution in terms of measurable environmental variables, and in turn, to assess the degree and significance of environmental change brought about by perturbation.

Because a plant community is a complex system involving transfer of energy and matter as well as information, the interactions within the system have been poorly understood. The advent of systems modeling provides the ecologist with a potential method for understanding the complexities of an ecosystem. An ecosystem model can be devised which is analogous to the real system and which can be used as an aid in understanding the real system. The type and complexity of the model depend upon the ultimate goals of the investigator, the extent of the system as he perceives it, and the degree of resolution required to provide results in keeping with the investigator's goals. In other words, a real system as perceived and defined by the observer is reduced to a more abstract form, which is the model of the system. Given a realistic model (i. e., one which behaves in a manner similar to the behavior of the real system), a great deal can be learned about the system which previously would have been obscured by the complexity of the system.

Individual processes can also be modeled as a system. Photosynthesis, for example, is a complex system involving the conversion

of incoming energy and the use of this energy to transform water and carbon dioxide to sugars. Thus, photosynthesis could be modeled as a function of the various factors which affect the state of the system and the rate of change within the system. Photosynthesis would require a complex model but if such a model were available, it could be very useful as a means of understanding plant growth and distribution since relative growth and seed production are keys for survival. Because processes such as photosynthesis are so highly coupled to the plant's environment, a system model of a plant process as a function of the environment could provide an excellent tool for quantitatively describing the environment as it is sensed by the plant. Thus, seasonal trends in transpiration or photosynthesis could be used as an index to environment; different ecosystems could be compared using the model of plant processes and the differences between them could be determined in a comparatively precise manner.

Whereas most people would agree that knowledge of plant response to environmental variables would provide much insight into solutions of fundamental problems of plant ecology, the acquisition of such data is both costly and difficult. Thus, continuous collection of transpiration and photosynthetic data has limited utility for the plant ecologist because of the difficulty of acquiring representative data. However, realistic models based on such data could ultimately be of great utility to the field ecologist.

In simulation, data are generated which are analogous to data which would be observed in a real system operating under conditions similar to the conditions described by the model. As stated above, the degree of resolution of the model is determined by the needs of the researcher. The data generated by the model can be used as if they were obtained by observation of the real system, within the limits of the model.

The choice of simulation of analytical techniques depends upon the type and complexity of the models. If the analytical solution of the model is impossible or extremely difficult, or if the system cannot be modeled with a set of equations for which analytical solutions can be obtained, then the system can be studied using simulation techniques.

In cases where it is possible to actually measure the quantities in the system of interest, but where the acquisition of data is difficult or expensive, the necessary data can be simulated. Simulation models can provide much insight into the system, suggesting future priorities in research resulting from knowledge obtained from a sensitivity analysis of the model. In short, simulation techniques can be used to provide data which are not readily available or easily analyzed, and the model can be used as a predictive tool and as a means of investigating the relative importance of certain factors affecting the system.

In this thesis, environmental variables affecting transpiration and related plant responses are expressed mathematically and developed into a computer simulation model. By analyzing both

environmental and plant responses, the simulation model can identify the major environmental-plant interactions and indicate how these interactions control selection of the vegetation growing under different situations. Because the process of transpiration is affected by stomatal behavior, the model incorporates a model of stomatal behavior in response to environmental factors. In view of the fact that photosynthesis is also affected by stomatal behavior, the process of photosynthesis could be studied with a modification of the model presented in this thesis.

II. REVIEW OF RELATED LITERATURE

Transpiration

Transpiration, as mentioned in the introduction, is a plant process which is affected by both plant and environmental variables. In particular, transpiration is affected by a number of factors, among them (1) stomatal aperture and leaf morphology, (2) temperature of both air and leaf, (3) water vapor content of the air, (4) water status of the plant, (5) soil water availability. Not all of the above listed factors are independent. As will be demonstrated below, the factors of greatest importance are (1) temperature, (2) vapor content of the air, and (3) stomatal resistance.

In a very real sense, plants act as a water transport column from the soil to the atmosphere. Water is absorbed at the root level, translocated through the stem to the leaves, and is lost from the leaves through an evaporative process known as transpiration. This water flux through the plant could be described in terms of the following relation:

$$\frac{d\phi}{dt} = F(U, S, T) \qquad \text{Eq. 1}$$

where:

$d\phi$ = water flux through the plant

T = transpiration of water from the leaves

U = uptake through the roots

S = storage of water within the plant

Under normal conditions, the diurnal transpiration rate exceeds the uptake rate, inducing a stress in the plant which is indicated by a diurnal decrease in plant water potential (increase in plant moisture stress). At night, when transpiration is low or non-existent, uptake is then much greater than transpiration and the plant recovers from the diurnal water stress. It should be emphasized, however, that the rate of water uptake and transpiration are not independent. That is, a high transpiration rate increases water stress in the plant, expressed in negative water potential, which in turn increases the rate of uptake (Slatyer, 1967). Conversely, a high water uptake rate has an effect of increasing transpiration rate.

The general relationship of transpiration rate to plant and environmental factors is described in equation 2:

$$\frac{dT}{dt} = \frac{c_w - c_a}{R} \qquad \text{Eq. 2}$$

where:

$\frac{dT}{dt}$ = transpiration rate, g $cm^{-2} sec^{-1}$

c_a = concentration of vapor in the air, g cm^{-3}

c_w = concentration of vapor in the leaf, g cm^{-3}

R = resistance of water flux, sec cm^{-1}

This relation was first proposed by van den Honert (1948) and subsequently elaborated by Gaastra (1959), Slatyer (1967), Jarvis

and Slatyer (1970) and a number of other workers.

As indicated in Eq. 2, the environmental and plant variables are expressed in terms of vapor concentration and plant resistances. Thus, most of the important environmental factors affecting transpiration (e.g., temperature and humidity) are expressed in the numerator of Eq. 2. The effects of light (apart from the effect of light on leaf temperature), plant moisture stress, uptake rates, and various other plant factors are included in the resistance term in the denominator. R is actually the sum of all the resistances to transpiration as suggested by Eq. 3:

$$R = r_a + \frac{(r_s + r_m)\, r_c}{r_s + r_m + r_c} = r_a + r_l \qquad \text{Eq. 3}$$

where:

r_a = boundary layer resistance

r_s = stomatal resistance

r_c = cuticular resistance

r_m = mesophyll resistance

r_l = leaf resistance

all expressed in sec cm^{-1} (Gaastra, 1959; van Bavel et al., 1965; Slatyer, 1966, 1967; Ehrler and van Bavel, 1968; Gale and Poljakoff-Mayber, 1968; Hunt, 1968; Balasubramaniam and Willis, 1969; Jarvis and Slatyer, 1970). The resistance to water flux will be discussed in greater detail below.

In summary, transpiration is a phenomenon driven by the

gradient of vapor concentration between the leaves and the air and mitigated by the resistance of the plant and atmosphere to this water flux.

Stomatal Behavior

As described above, transpiration as well as photosynthesis are mediated directly by stomatal aperture. This is generally expressed in the form of stomatal resistance, which is the resistance to flux of CO_2 and H_2O as they pass through the stomatal pore. Stomatal pores are formed by two modified epidermal cells which lie in juxtaposition with concave surfaces facing each other. These cells, called guard cells, are directly effected by their hydration (Meyer and Anderson, 1952; Heath, 1959; Ketellapper, 1959, 1963; Levitt, 1967; Meidner and Mansfield, 1968). When the guard cells become fully turgid, the thickened concave wall becomes more concave, thus increasing the distance between the two concave surfaces, resulting in a wider stomatal pore and a reduction of stomatal resistance.

As discussed above, stomates have been shown to be important controllers of transpiration rate (Loftfield, 1921; van den Honert, 1948; Bange, 1953; Stålfelt, 1955; Kuiper, 1961; Meidner, 1965; Slatyer, 1967; Meidner and Mansfield, 1968; and many others). Transpiration rate is directly proportional to stomatal aperture as suggested by Eq. 2. Ehlig and Gardner (1964) questioned this

relationship, suggesting that transpiration is reduced only when stomatal aperture is very small. However, it may be that large boundary layer resistances in their experiments obscured the effect of stomatal resistance. The majority of workers in this field believe that stomatal resistance is an important controller of transpiration rate (Gayle and Poljakoff-Mayber, 1968; Hunt, 1968; Balasubramaniam and Willis, 1969, and many others); Slatyer (1967) and Ehrler and van Bavel (1968) show that the relationships expressed in Eq. 2 above are consistent with the data. It must be emphasized, however, that the resistance terms in Eq. 2 are sums of the many resistances in the plant, and, as is sometimes the case, a large resistance in one area may obscure the effects of others. This is pointed out by Bange (1953) and Slatyer (1967) who showed a distinct difference in stomatal effects on transpiration rate between leaves in still air and leaves in moving air. In the latter case, stomatal influence on transpiration rate is much more linear as the boundary layer resistance is removed.

The actual mechanism of stomatal movement has been subject to considerable controversy over the last few decades. Heath (1959) adhered to the classical view that stomatal opening is caused by an increase of turgor in the guard cells. But turgor loss in epidermal cells during incipient desiccation could also result in temporary stomatal opening because of release of pressure on the guard cells (Stålfelt, 1961). In any case, stomatal movement is in response to

turgor changes in the guard cells. The cause of these changes is subject to considerable controversy. Mechanisms of guard cell movement are discussed in Heath (1959), Ketellapper (1963), Zelitch (1965, 1967), Meidner and Mansfield (1968). Levitt (1967) points out four principal older hypotheses: (1) active absorption of water, (2) passive absorption of solutes followed by passive absorption of water, (3) active absorption of solute followed by passive absorption of water, and (4) formation of solutes in the cell followed by passive absorption of water. Until recently, (4) was the most popular hypothesis and a large amount of research was conducted in order to define a mechanism which would account for the observed phenomenon of stomatal behavior. Levitt throughly reviews the various hypotheses and present arguments as to why the fourth hypothesis is the most consistent. He further proposed a mechanism which would account for most of the observed stomatal responses. In Levitt's hypothesis, polysaccharides exist in the guard cells when the stomates are closed. The polysaccharides are then converted to sugars which result in an influx of water into the guard cell and cause stomatal opening. The changes from polysaccharides to sugars are moderated, or controlled, by the concentration of organic acids in the leaf.

Recently, hypothesis (3) has come into favor. Some workers observed that stomatal behavior seems to be affected by the nutrition of the plant. Woestmann (1942) reported that potassium ions induced

an increase in volume of epidermal cells and was associated with greater water uptake than was Ca^{++}. He proposed that K^+ causes an increase in water binding ability of the colloids thus allowing the plant to absorb more water. Kosmat (1953), Amer (1954), and Fujiwara and Iida (1955) found that a deficit in potassium seemed to inhibit stomatal control. The importance of potassium on stomatal behavior has been further demonstrated by Humble and Hsiao (1969) and Sawhney and Zelitch (1969) who showed that a direct accumulation of K^+ was associated with light activated opening in stomata. Humble and Hsiao floated strips of epidermis on 10 mM KCl and KNO_3. The stomata opened when exposed to light, subsequently closed in darkness, then reopened when illuminated again. This light activation effect was specifically associated with K^+ or Rb^+ ion influx. Other monovalent ions such as Na^+ were able to induce stomatal opening in the light but only at concentrations 100 times as great as that of K^+ or Rb^+. Influx of labelled Rb^+ was associated with stomatal opening and efflux of the ion was associated with stomatal closure. Humble and Hsiao concluded that since the stomates behaved normally in CO_2-free atmosphere and since movement of K^+ and Rb^+ was directly associated with stomatal movement, light triggers active uptake of K^+ which results in stomatal opening. This would also rule out the effects of CO_2 concentration on stomatal movement except perhaps as a secondary interaction.

Sawhney and Zelitch (1969) measured the concentration of K^+ directly in guard cells and concluded that the concentration of K^+ in the cells was sufficient to induce an influx of water in response to the osmotic gradient. This influx of water would cause stomatal opening.

In summary, there are a number of factors which control or affect stomatal movement: light, vapor pressure deficit (Raschke and Kühl, 1969), temperature, water potential of the plant, and potassium nutrition. The relative sensitivity of various plant species to each of the factors mentioned above is not clear. Nor is it certain that all plants have an identical mechanism of stomatal movement. It is conceivable that angiosperms may differ from gymnosperms in some mechanisms of stomatal movement.

Ecological Implications

As a summary of the factors affecting stomatal behavior and transpiration, the simple diagrams of Figures 1 and 2 are useful. Figure 1 illustrates stomatal behavior and Figure 2 illustrates water flux through the plant.

As illustrated in Figure 1, stomata may be in two states, open or closed. The rate of movement and the final aperture is controlled by water potential, ψ, potassium availability, K^+, light, L, and temperature, T. These controllers are symbolized by circles. The broken lines represent transfer of information, in this case,

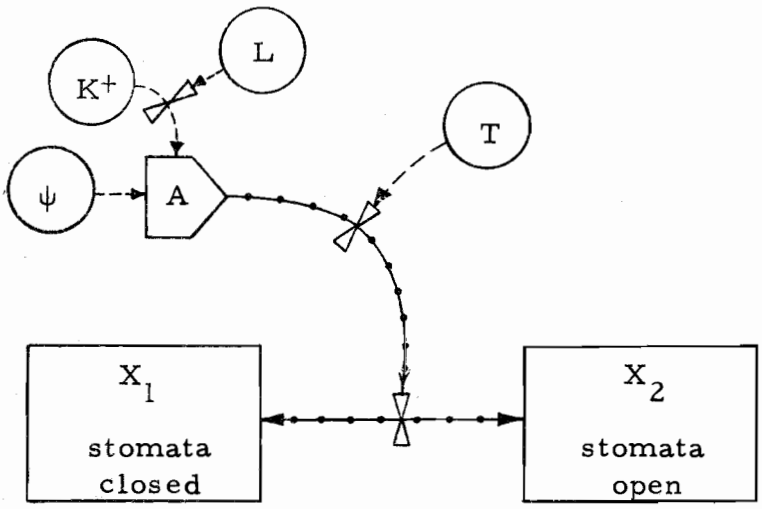


Figure 1. Schematic diagram of stomatal behavior. The circles represent controlling variables, the tag represents an integration, the butterfly represents a rate determining valve. The broken lines represent information transfer, the solid lines with dots represent decisions (in this case, change of state). Symbols after Forrester (1961).

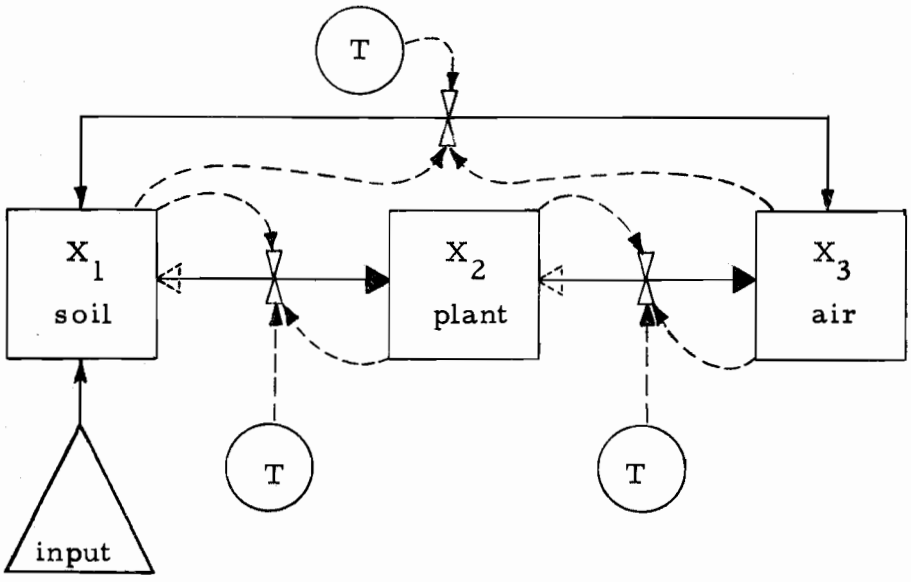


Figure 2. Schematic diagram of water flux through the plant. The compartments represent concentration of water in the soil, plant, and air; the circles represent control variables; the dashed lines represent concentration effects; the butterfly valves represent rate controls, the solid lines represent matter transfer.

information concerning the extent and timing of stomatal opening. This is modeled in Figure 1 as being controlled by K^+, ψ, and L. Temperature controls the rate of stomatal movement, and in special circumstances acts as a threshold below which stomata are closed (Reed, 1968). Rate controls are symbolized by butterfly valves on the arrows, tag "A" represents an integration. The solid lines with dots represent decisions (here, the decision to open or close stomata and determination of the extent of opening). The symbols are after Forrester (1961).

Thus, light operates as an off-on switch, leaf temperature as a rate controller. Water potential is seen to be the driving variable which determines the actual width of the stomatal pore, and K^+ movement as the mechanism triggering stomatal movement as it is itself triggered by light. It is possible that the relative importance of a given factor may be different at different times of the year, e.g., well hydrated soils and a low transpiration demand in the spring may allow water potential to override the closing effect of darkness, thus resulting in open stomata at night.

Water flux from the soil through the plant to the atmosphere can also be modeled by a schematic diagram (Figure 2). Water enters the soil (input), and moves into the other compartments via the solid arrows. Thus, the solid lines represent transfer of matter, the compartments (X_i) represent the concentrations of water in the soil

(X_1), plant (X_2), and atmosphere (X_3), respectively. The butterflies represent control valves, while the broken lines represent effect of concentration on the rate of water movement.

Thus, it can be seen that the movement of water from the soil to the plant is influenced by soil temperature and the concentrations of water in the soil and the plant (usually expressed as ψ_{soil} and ψ_{plant}). In reality, other factors would be necessary to completely describe water movement from soil to roots and into the roots. The dotted arrowheads indicate possible but unlikely transfer of water in the indicated direction. While it is conceptually possible that water can be transferred from the air to the leaves and from the roots to the soil, this occurs only under very special circumstances (Breazeale et al., 1950; Slatyer, 1956). These special circumstances probably are most uncommon in the field.

Likewise, water flux from the plant to the surrounding atmosphere is also affected by temperature and the quantity of water in the plant and atmosphere. The compartment X_3 is, in this case, taken to represent the air immediately surrounding the plant.

Flow rate equations can be substituted for the butterfly valves on the solid lines connecting the compartments. Thus, changes in water quantity in each compartment can be expressed as a system of differential equations where flux coefficients would be required for each compartment. Research would be necessary to determine the

actual functional relationships of these various flow rates. The system of equations given in Table 1 represents one approach that could be taken to convert the diagram of Figure 2 into a system of differential equations which could be solved.

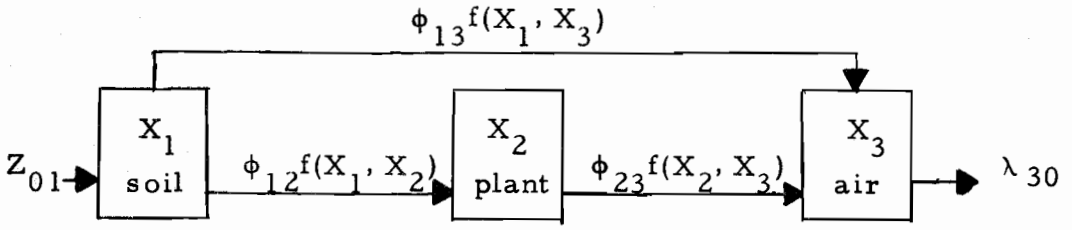
This model suggests an interesting research problem. However, it is only the relation between X_3 and X_2 that is of interest in this thesis. That is not to say that the effect of soil moisture on plant moisture content is ignored, but that part of the model is subsumed into ψ_{plant} which is modeled from empirical data.

As discussed by Kramer (1963), plant growth is controlled directly by plant water stress and only indirectly by soil water stress. Since plant water stress depends on the relative rates of water absorption and water loss, it is not safe to assume that a given degree of soil water stress will always be accompanied by an equivalent degree of plant water stress. Kramer concluded that plant moisture stress must be measured directly in research on the effect of water supply on plant growth and plant processes. Kramer and Brix (1965) point out that

> . . . we cannot make reliable assumptions concerning the degree of water stress existing in plants from soil moisture data or estimates of evapotranspiration. The only safe procedure is to measure the water stress of the plant by some direct method (p. 207).

In summary, transpiration is a plant process which is controlled by environmental demands and the ability of the plant to respond to

Table 1. System of differential equations represented by Figure 2.



ϕ_{ij} = coefficients of transfer

Z_{01} = input, g cm^{-3} t^{-1}

λ_{30} = output, g cm^{-3} t^{-1}

X_i = concentration of water in compartments, g cm^{-3}

Equations

$$\frac{dX_1}{dt} = \phi Z_{01} - \phi_{13}f(X_1, X_3) - \phi_{12}f(X_1, X_2)$$

$$\frac{dX_2}{dt} = \phi_{12}f(X_1, X_2) - \phi_{23}f(X_2, X_3)$$

$$\frac{dX_3}{dt} = \phi_{13}f(X_1, X_3) + \phi_{23}f(X_2, X_3) - \lambda_{30}$$

the demands. Plants lose water as a response to the difference in vapor concentration between the intercellular spaces in the leaves and the air. This difference in concentration of vapor is a function of temperature of the leaf and air, and the amount of water vapor in the leaf and air. Plants have defenses against water loss which are called resistances to water-loss. Plant resistance is affected by the soil moisture status, the plant moisture status, stomatal behavior, and morphological characteristics. Thus, the process of transpiration is affected directly or indirectly by temperature, atmospheric and internal vapor pressures, soil water status, plant moisture status, light, mineral nutrition, and so on. A working model of transpiration could be used to help solve one of the greatest problems in plant ecology: how to classify an environment.

Beginning with the theories of Clements and his associates, American plant ecologists have recognized the importance of environment on plant growth and associations (Clements, 1936; Weaver and Clements, 1938; Cain, 1939). The early ecologists observed that plants were adapted to survive in certain climates, and the theories of Clements held that given a sufficient length of time under a steady state climate, all plant communities would tend toward a climax association. This stable climax association would be characteristic of the steady state climate. Unfortunately for Clements, climatic variables were difficult or impossible to measure in the field, so

classical ecology was primarily concerned with describing plant associations themselves with less effort made to interpret these associations in terms of the actual environment.

While subsequent schools of plant ecology disputed much of Clements' theory, they continued to utilize the same basic approach pioneered by Clements and his colleagues (Langford and Buell, 1969). That is, they continued to emphasize vegetational comparisons, only secondarily interpreting differences in community composition and structure in relation to environmental gradients, as for example, the Wisconsin school (Curtis and McIntosh, 1951).

Whittaker (1967) reversed the emphasis by attempting first to classify environments along "complex" gradients of moisture and temperature, then interpreting vegetational mozaics in terms of these gradients. Whittaker stated

> . . . gradient analysis has changed the concept of vegetation as much as research on the genetic basis of variation and evolution has changed the concept of plant species. . . the change involved shift of emphasis from classification of the object of study to analysis of kinds of degrees of relationships among these objects (p. 343).

In gradient analysis, vegetation samples are arranged and studied according to known magnitudes or indices of positions along an environmental gradient which is accepted as a basis of study. This commonly includes a transect along a single "complex" gradient, usually in elevation, moisture, soil type, or temperature. The

population of species, according to Whittaker, form bell-shaped binomial curves along these gradients.

Because complex gradients are difficult to measure directly, they are usually correlated with physiography. Whittaker, for example, assumed that along an elevational gradient, a difference in temperature occurs and thus elevation is an index to a temperature (Whittaker, 1961, 1967).

Waring and his co-workers departed from physiographic indices and measured more directly some environmental gradients (Waring and Major, 1964; Waring and Cleary, 1967; Cleary and Waring, 1969; Waring, 1969). The distribution of plant communities as well as individual species are interpreted in terms of these measurements. Thus, Waring and his associates were able to predict the occurrence of various species in terms of their tolerance to extremes of moisture and temperature. The measured variables are similar to those employed in physiological studies and provide a step toward understanding environmental selection in an operational sense.

In Waring's approach to classifying environment, indices are developed which assess the environment in terms of the plant's response to a given environmental factor. For example, water status is measured in the plant with no attempt to measure soil water status, because of the aforementioned difficulty in relating soil moisture stress to that in the plant. Thus, the environment must be linked to

observable plant responses such as growth, death, nutrient content, water stress, photosynthesis, and transpiration.

At the present time, only two indices have been used: a temperature index (Cleary and Waring, 1969) and pre-dawn plant moisture stress measured at the end of the growing season. These indices were used in classifying ecosystems in the Siskiyou Mountains of southern Oregon, and predicting the composition of associated plant communities (Waring, 1969). Unfortunately, these indices were simplified to the extent that their applicability was limited to areas with rather Mediterranean climates, exemplified by summer drought. Indices which could be more generally used are required for employment of Waring's approach in other areas.

A system of measuring a plant process such as transpiration would be useful in an environmental classification system such as the one described above. An ecosystem could be classified according to its atmospheric transpiration demand, and the plants' transpiration in response to the demand. Thus, the environmental variables affecting transpiration would be measured as they are sensed by the plant and as they influence a plant process. As mentioned in the introduction, such measurement is not practical for most ecological research; therefore, a simulation model must be used. The output from such a model could be used in place of actual data in the

classification of ecosystems. It is to this end that the research in this thesis is directed.

III. FIELD METHODS

Introduction

The review above dealt with the fundamental theory of transpiration and stomatal behavior and the ecological implications of transpiration. I pointed out in the review that measurements of transpiration would be useful in ecosystem classification and that the difficulty in obtaining such data could be alleviated by simulation of the data. Therefore, one of the goals of this study was to develop biologically sound models of plant resistance and transpiration.

To these ends, it was necessary to obtain measurements of climatic and plant variables in the field. Because the atmospheric demand for transpiration is expressed in terms of vapor concentration gradient between the leaf and the air it was necessary to measure temperature and vapor pressure throughout the growing season in the field.

Transpiration is mediated by plant resistance, and the most important element of plant resistance is stomatal resistance. Therefore, it was necessary to measure stomatal aperture and the factors which affect stomatal behavior. The data used for the model in this thesis were gathered in the Siskiyou Mountains of southwestern Oregon (Lat. 42^{o}N, Long. 123^{o}W).

Table 2. Physiography and forest types characterizing study plots.

Plot	Slope (%)	Aspect	Elevation (m)	Vegetation type	Parent material
3	45	N	793	DF, BO, PP	Granitic
8	40	SW	1280	PP, DF	"
23	10	N	1402	ES, DF, WF	"
1	25	W	1493	WF, PP, DF	"

WF = White fir (Abies concolor Lindl. & Gord.)

DF = Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)

PP = Ponderosa pine (Pinus ponderosa Dougl.)

BO = Black oak (Quercus kelloggii Newb.)

ES = Engelmann spruce (Picea engelmannii (Parry) Engelm.)

Plot Descriptions

The field research was conducted on Mt. Ashland near the eastern limits of the Siskiyou Mountains in Oregon. Mt. Ashland has an elevation in excess of 2150 m (7000 ft), and roads give access to all parts of the mountain. Plots were selected along the Ashland Loop Road which traverses the Ashland watershed. These plots represent gradients in temperature and moisture. The principal characteristics of the plots are summarized in Table 2.

The lowest plot, Plot 3, is hot and dry, dominated by Douglas-fir (Pseudotsuga menziesii) and black oak (Quercus kelloggii). Although Plot 8 was higher than Plot 3, it is also very hot, usually recording the highest air temperatures of the four plots due to its southern exposure. Plot 8 is dominated by Ponderosa pine (Pinus ponderosa). Plot 23 was on the opposite side of the watershed, facing due north and is dominated by a relic stand of Engelmann spruce (Picea engelmanii) which survives in the cool and moist environment along a small creek. Plot 1, the highest of the plots, is within about 150 m of the upper altitude limit for Douglas-fir in this area. Analysis of the temperature patterns on all the plots indicates that the average day temperatures on Plots 8 and 1 were not greatly different from those of Plot 3, but differences in soil temperatures and soil water availability did exist. Plot 23, of course, was cooler in both

average air temperatures and soil temperatures.

The soil of Mt. Ashland is coarse and sandy, derived from granite, and has very poor water retention capacity. The climate is hot and arid in summer, cold in winter (although winter temperatures rarely fall below -12°C).

Field Measurements

Measurements of Stomatal Behavior

Because the guard cells and stomatal pore of most coniferous species are commonly found at the bottom of a pit which is often occluded by a waxy substance, conifer stomatal aperture cannot be directly measured. Stomatal aperture can be estimated by porometric techniques or by an infiltration technique (Fry and Walker, 1967). In the latter technique, a single needle of coniferous species is inserted into a chamber containing a 50% ethanol-water solution. Pressure is applied to the solution which is then forced through the stomatal pores. The pressure required for infiltration is inversely proportional to the pore width. An infiltration pressure (INF) of approximately 0.1 atm corresponds to open stomata, a pressure of 2.0 atm corresponds to closed stomata (Fry and Walker, 1967).

Fry and Walker derived the hypothetical equation below:

$$\text{Stomatal aperture} = 2R_2 = \frac{2\gamma}{\Delta P - (\frac{\gamma}{R_1})} \qquad \text{Eq. 4}$$

where:

R_1 = length of stomate, cm

γ = surface tension, 50% ethanol, dynes

ΔP = infiltration pressure (INF), dynes

$2R_2$ = width of the stomate, cm

Eq. 4 describes a hyperbola.

The actual relationship between infiltration pressure and stomatal aperture is not known, owing to the difficulty of directly measuring stomatal aperture in coniferous species. Fry and Walker's equation may be realistic for this relationship as it seems to agree with the data. Some of the results of this study support the findings of Fry and Walker.

The apparatus used in this study for measurement of INF is illustrated in Figure 3. The complete system consists of an infiltration chamber, a pressure gauge and a binocular dissecting microscope. Tygon tubing connects the pressure gauge to a small nitrogen tank. The pressure was controlled with a 0-100 lb/sq in regulator. The entire system is portable and is similar to that developed by Fry and Walker (1967).

The needle chamber (Figure 4) was cut from 1/2-in plexiglas, separated by a membrane made from a rubber contraceptive device.

Figure 3. Photograph of apparatus used for estimation of relative stomatal aperture (after Fry and Walker, 1967).

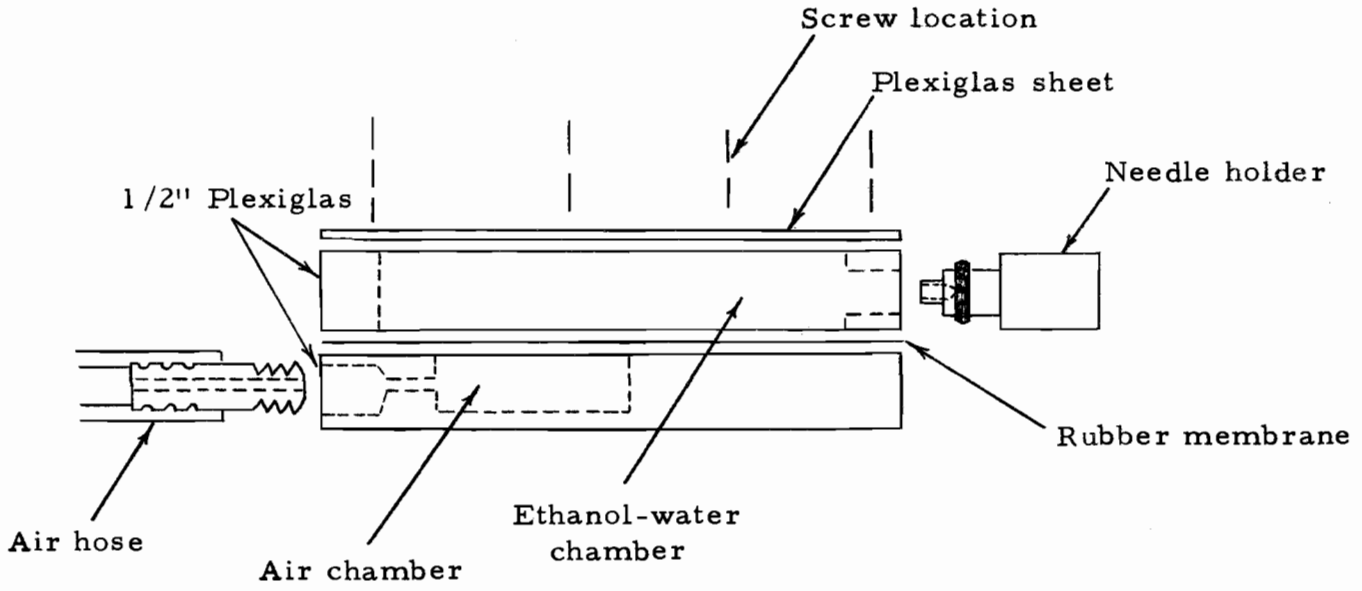


Figure 4. Pressure infiltration chamber, modified from Fry and Walker (1967). Description in text.

The two halves of the chamber were sealed with DuPont transparent silicone-rubber-bathtub sealer, and were screwed together. The needle holder was machined from a brass rod and equipped with an O-ring seal.

The measurement procedure consists of placing a needle in the chamber, then applying pressure until the stomatal pores show evidence of infiltration by the liquid in the chamber. A conifer needle to be tested was detached from the tree, the detached end quickly dipped into silicone grease or melted grafting wax, then placed in the needle holder (Figure 4). The needle holder with the needle is thrust into the plexiglass chamber filled with 50% ethanol solution; the chamber is then placed under the microscope and nitrogen under pressure is introduced into the chamber which forces the liquid through the stomatal pores. As the liquid passes through the pores, light reflects from the air-water interface within the sub-stomatal cavity. Thus, at the point of infiltration, a large number of tiny sparkles of light appeared. The pressure at which the majority of the pores are infiltrated is read from the guage: this value is stomatal infiltration pressure, INF.

Three Douglas-fir trees of 1 to 2 m in height were selected on each plot for study. Stomatal infiltration pressure was observed before dawn and at intervals throughout the day. For these observations, one-year-old needles were collected from all around the tree in order

to exclude bias due to sample location. Each sample consisted of four to six needles, placed in a plastic petri dish which had a piece of wet filter paper glued to the top. Needles could be kept in this petri dish without stomatal change for at least the three minutes required for making the readings (Fry and Walker, 1967). The stomatal infiltration pressure of each needle was determined and the value recorded. One-year-old needles were selected because it was found that they had a more uniform response and were often more healthy than older needles. Current foliage was too small and succulent for use during the first part of the season, so they were not used as sample material.

Measurement of Plant Moisture Stress
(Xylem Water Potential)

Plant moisture stress was measured directly in this study using the pressure bomb technique described by Scholander et al. (1965) and Waring and Cleary (1968). A twig is severed from a tree and quickly placed in a stainless-steel chamber, with the cut end protruding through an airtight rubber seal. As nitrogen is forced into the chamber under pressure, water is forced back to the cut surface of the stem from whence it had receded when the water column was broken. The pressure required to force the water back to the cut surface is believed to be very close to actual water potential in the plant (Boyer, 1967). We call this pressure PMS or plant moisture

stress instead of water potential because PMS is an estimate of water potential. PMS is expressed in negative atmospheres and should closely approximate xylem water potential.

The instrument used in this study was portable, mounted on a back pack, and could be carried into the plots where PMS was measured periodically throughout the day. Pre-dawn readings were taken, followed by additional readings throughout the day. Pre-dawn PMS is the least moisture stress to which the plant is subjected throughout the day. This is a value reached after a night of recovery from the preceding day's water loss. This recovery is possible because of reduced transpiration during the night concurrent with continued uptake of water. This minimum value may, in some cases, be close to soil water potential for the entire root system and is therefore indicative of the extent of soil water status.

Measurement of Temperature and Relative Humidity

Temperature is, of course, a highly important weather variable and a study coupling plant responses to the environment cannot be made without temperature records. Fortunately, temperature is also one of the easiest of environmental measurements to obtain. In this study, continuous records of air temperature (1 m above the forest floor) and soil temperature (30 cm below the forest floor) were

obtained with Partlow Circular recording thermographs, after Cleary and Waring (1968) and Waring (1969).

These thermographs have a 30-day circular chart with a temperature range from -40 to 150°F. The continuous temperature traces were digitized using a CALCOMP digitizer program which provided maximum temperatures, minimum temperatures, average day temperatures, and average night temperatures, as well as a daily record of soil temperatures. The differences between maximum diurnal air temperature and the minimum nocturnal air temperature were also printed out, which provided an index called day-type found helpful for modeling. A temperature difference of less than 10°F was a type 1 day, 10 to 20°F was a type 2 day, and greater than 20°F was a type 3 day. These day-type indices are related to amount of cloud cover during a given day because cloud cover depresses the difference between daily maximum and nightly minimum temperatures.

Relative humidity was measured in the field with an Assmann-type mercury and glass wet bulb-dry bulb psychrometer. This instrument was used in 1970 only, during the period that stomatal infiltration pressure readings were being taken.

Additional relative humidity data were provided by the U.S. Forest Service, Rogue River National Forest. Wet bulb-dry bulb readings were taken throughout the months of June through September

at a site in the Ashland watershed. These data were used for modeling, for want of continuous data on the plots.

IV. FIELD EXPERIMENTS AND RESULTS

Experimental Procedures

It was decided that field measurements of plant variables would be restricted to three trees on each plot. These young Douglas-fir trees of approximately 1 to 2 m in height were identified with plastic marking tape at each plot. The trees grew under a range of light conditions reflected by within-site differences in terminal growth (Table 3).

To determine when cambial activities ceased, the technique described by Brown and Wadziki (1969) was used. In this procedure, insect mounting pins are inserted into each of the experimental trees at intervals in time. Each pin was thrust through an aluminum tag on which was marked the tree number and date. At the end of the growing season the pins and wood samples in which the pins were embedded were cut out of the trees. They were then sectioned, mounted on microscope slides, and examined for evidence of cambial activity by Mr. Allen Doerksen, microtechnician, School of Forestry. If the pin had been inserted through dividing cambium, scar tissue would have developed from that point on. This can easily be detected from a microscopic preparation and the date of cessation of cambial activity can be determined between two successive insertions of the pins. This is because no scar tissue develops after cambial division stops.

Table 3. Height and leader elongation of experimental trees of the research plots, Mt. Ashland.

Plot	Tree no.	Height (cm)	Leader elongation (cm)		Date of cessation of cambial growth
		1968	1969	1970	1970
1	1	142	5.1	7.6	By 22 Sept.
	2	79	8.9	20.3	"
	3	178	3.5	6.4	"
3	1	140	10.1	24.1	By 2 Sept.
	2	150	10.1	20.3	By 20 Aug.
	3	137	10.1	25.4	"
8	1	249	30.5	40.6	-
	2	130	16.5	22.9	By 22 Sept.
	3	142	11.4	22.9	By 2 Sept.
23	1	144	6.5	6.5	By 2 Sept.
	2	117	2.5	3.8	By 22 Sept.
	3	183	1.3	1.3	By 2 Sept.

Note: Because of late spring, leader elongation growth in 1971 had not stopped in time for such measurements to be included in this thesis.

In summary, then, three trees approximately similar in size but growing under different light regimes were selected on each plot, and leader elongation and cambial growth was measured on each tree. Other physiological and environmental measurements were made on and around each tree throughout the summer.

Patterns of Plant Moisture Stress in the Field

Field studies were begun in the summer of 1969 and continued through the summer of 1970. Plant variables were measured only during the summer months, but temperature was recorded through the winter. The winter data were not used in the modeling.

Plant moisture stress, stomatal infiltration pressure, and psychrometric data were recorded during each summer field trip. Insect mounting pins with a dated label were inserted through the cambium of the study trees on each plot. Temperature was continuously recorded and the data were analyzed at convenient intervals.

During each field trip, two or more plots would be studied intensively, while on the remaining plots only pre-dawn PMS and INF at 0800 to 1000 hours were taken. At first, in 1969, attempts were made to follow diurnal PMS and INF on all plots, but this practice was abandoned when some patterns of stomatal behavior became clear. The practice of intensively studying only two plots per trip was a somewhat gradual development.

On the intensively studied plots, PMS, and stomatal infiltration pressure, INF, were observed on the study trees beginning before dawn and continuing throughout the day. Typical data are presented in Figure 5. The circles represent the sample mean stomatal infiltration pressures of single trees from Plots 1 (mixed conifer type), and 3 (oak type). The triangles represent PMS taken at the same time that the stomatal infiltration pressure data were being taken. Note that the stomata were closed before dawn then opened to a maximum between 0800 and 1000 hours. The maximum stomatal aperture of the tree on Plot 3 (oak type) was less than that of the tree on Plot 1 (mixed conifer type), and the pre-dawn plant moisture stress of Plot 3 was greater than that of Plot 1. The maximum daily PMS for each plot was not greatly different. The data in Figure 5 are typical of PMS patterns for Douglas-fir on a sunny day (Waring and Cleary, 1967), provided that the pre-dawn PMS is less than approximately 15 atm.

The values of pre-dawn PMS tended to increase throughout the summer due to the lack of rain for most of the summer months. The rate of soil water loss (as indicated by an increase in pre-dawn PMS) is different for each plot, but the trends were similar for all plots. The pre-dawn PMS in Douglas-fir on Plots 3 and 1 (oak type and mixed conifer type) are illustrated in Figure 6. The points represent the mean value of the three trees on the site, and the smooth curve is a

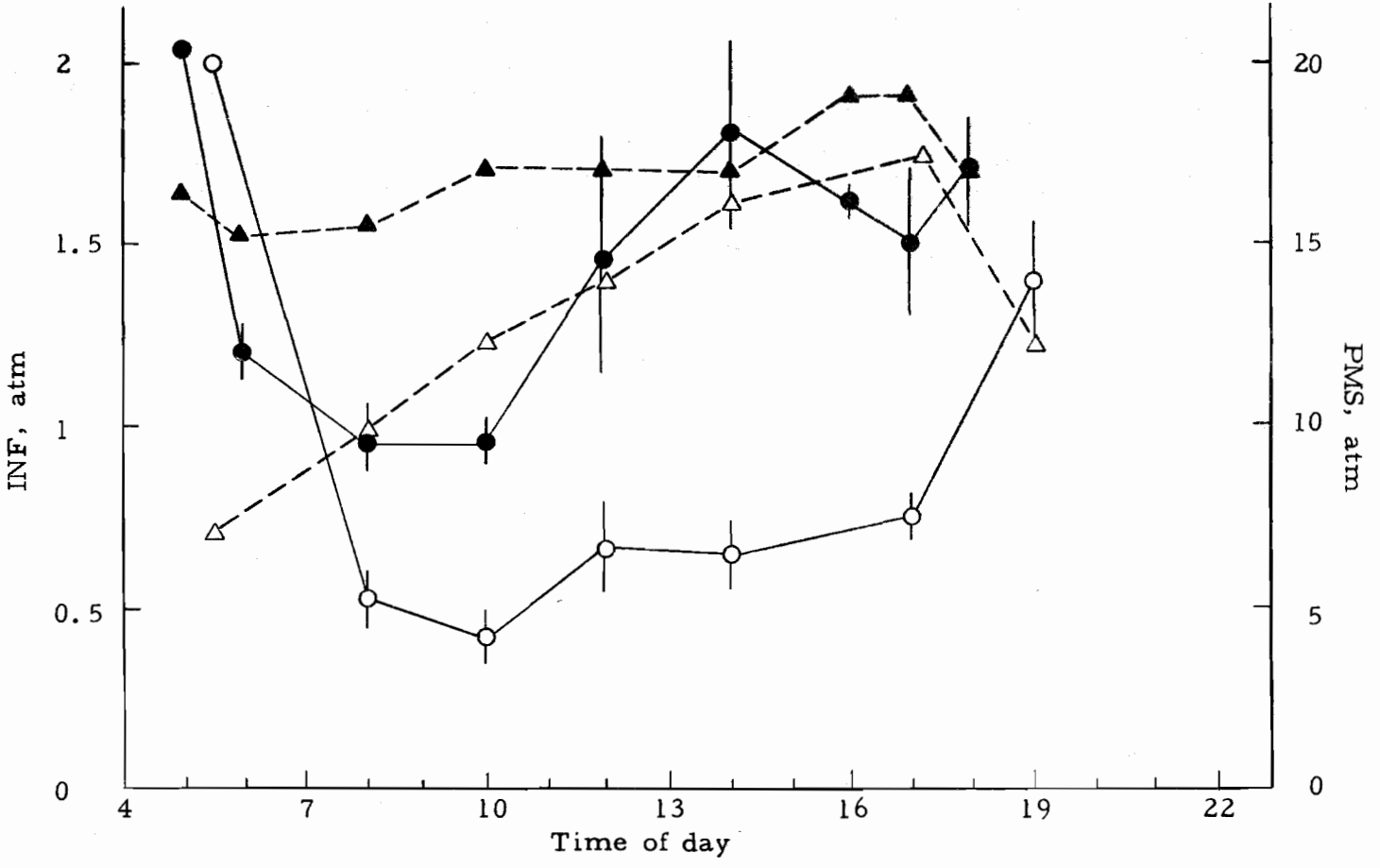


Figure 5. Stomatal infiltration pressure, INF, of tree no. 1, Plot 1, O, and tree no. 1, Plot 3, ●; plant moisture stress of the same tree on Plot 1, Δ, and Plot 3, ▲; for the dates of 5 and 6 August, respectively. Sunrise at 0530, sunset at 1900. The vertical lines from the INF points represent the 95% confidence intervals of the sample means.

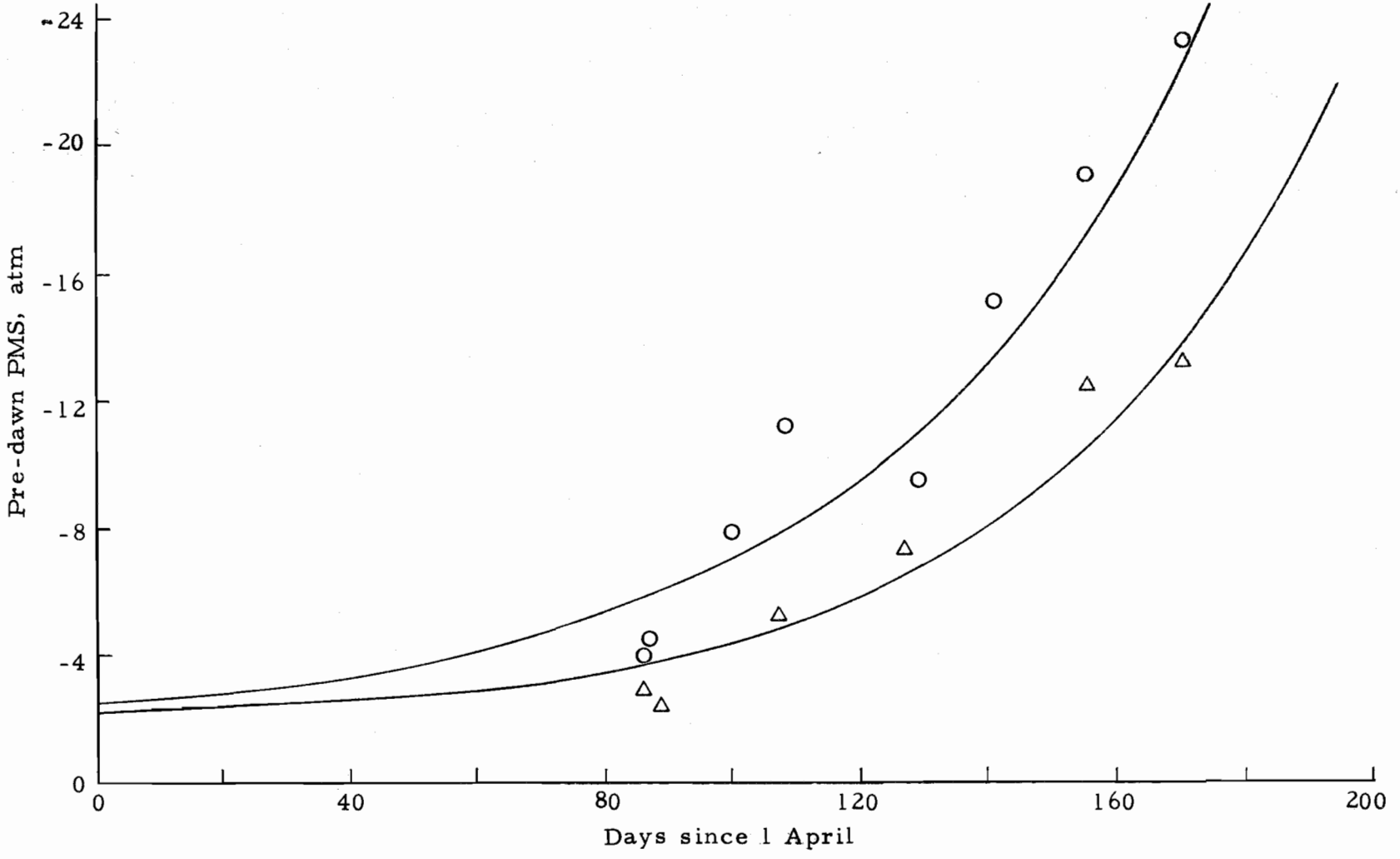


Figure 6. Pre-dawn plant moisture stress, PMS, of Plot 3, O (oak type), and Plot 1, Δ (mixed conifer type), plotted as a function of time. Time zero is 1 April, 1969.

non-linear least-squares fit to the data in the form:

$$-Y = \beta_1 + (\beta_2 - \beta_1)e^{\beta_3 t} \qquad \text{Eq. 5}$$

where

$-Y$ = mean pre-dawn PMS, atm

t = days since 1 April

The first parameter in the equation, β_1, is set to 2.0 atm. This is the asymptote of the function, and 2 atm is the lowest pre-dawn PMS ever observed in the Siskiyou study area. The second term $(\beta_2 - \beta_1)$ in the model consists of the t, Y intercept, and $e^{\beta_3 t}$ is the exponential growth term. This function was used in the simulation model to generate PMS. Values of the estimated parameters for the years 1968-1970 are listed in Table 8 (p. 89).

Stomatal Behavior in the Field

The stomatal behavior depicted in Figure 5 is typical. The stomata were closed at night, would open to some maximum value during the day, then would close at sunset. It was significant that the stomata would not respond to the pre-dawn light, but would open only after the sun came over the horizon. They tended to close in late evening shadow, particularly during the late summer months. Other conifers growing on the plots exhibited similar stomatal behavior. Thus, the stomatal response of all conifers seemed to be similar, at least in this locale.

Night closure of stomata was observed during the months of July through September. Observations in June suggest that the stomata were at least partly open at night during the spring and early summer. Unfortunately, insufficient data were collected in the early spring to fully explain this behavior. It would seem possible that phenology or soil moisture availability would have an effect on night opening of stomata in these species.

The diurnal stomatal behavior is not completely understood. The stomates usually opened to some minimum value, then would either remain at that value throughout the day or would close slightly (Figure 5 and Table 4). The data in Table 4 were taken from the field work of the summers of 1969 and 1970. The variable ΔINF is the difference between the mean INF readings no earlier than 1/2 hour after sunrise and no later than 1/2 hour before sunset. That is:

$$\Delta INF = INF_2 - INF_1$$

ΔINF was then divided by the time difference, Δt. This ratio is the slope of a line connecting the two means. The values of the slopes range from -0.050 to 0.11.

The slopes calculated from the means are not the same as slopes computed from regression analysis of the raw data. The slopes used in the model were calculated from the means because the mean of a given sample was used for all other modeling, but it was necessary to know at what point the slope becomes significant. Seven regression

Table 4. Diurnal change in stomatal infiltration pressure, measured as the difference between the mean INF_1 (no earlier than 1/2 hour after sunrise) and INF_2 (no later than 1/2 hour before sunset).

Plot	Date	Pre-dawn PMS (atm)	ΔINF (atm)	Δt (hr)	$\frac{\Delta INF}{\Delta t}$	Est. slope (b_1)	t Value	df
3	6-26-69	4.6	0.05	7.0	0.007			
1	6-28-69	2.5	0.06	8.0	0.008			
1	7-16-69	5.4	0.18	8.0	0.023	.024	6.02**	82
3	7-17-69	11.3	0.08	3.5	0.023			
8	7-18-69	7.0	-0.01	4.5	-0.002			
1	8- 5-69	7.4	0.33	9.0	0.037	0.047	8.98**	87
8	8- 6-69	7.1	0.32	9.0	0.036			
3	8- 7-69	15.6	0.63	9.0	0.070	0.093	8.98**	70
8	8-20-69	9.4	0.04	5.0	0.008	0.019	4.66*	52
23	8-20-69	5.4	0.20	4.0	0.050			
3	9- 2-69	19.3	0.32	5.75	0.056			
8	9- 2-69	12.7	0.01	6.0	0.002			
3	6-24-70	7.5	0.07	10.5	0.007			
3	7-15-70	10.0	-0.02	2.5	-0.008			
23	7-16-70	6.0	0.01	5.5	0.002			
8	7-28-70	7.2	0.30	4.75	0.063			
1	7-29-70	7.0	0.14	6.0	0.024			
3	8-19-70	20.8	0.51	7.5	0.068			
1	8-20-70	11.6	0.06	6.0	0.010	0.006	0.647 NS	34
3	9- 1-70	25.0	0.41	8.0	0.051	0.060	5.83**	46
1	9- 2-70	13.9	0.16	5.25	0.030			
1	9-22-70	15.9	-0.26	5.25	-0.050			
3	9-22-70	22.4	0.62	5.5	0.11	0.089	6.45**	34

**Significant at 99% level. *Significant at 95% level.

analyses were run on diurnal stomatal infiltration pressure data (indicated in Table 4). The data to be analyzed were selected on the basis of slope (ranging from large to small slope), number of sample periods during the day, and length of time from the first to the last sample period (Δt).

The regression model used was:

$$Y = \beta_0 + \beta_1 t + \epsilon \qquad \text{Eq. 6}$$

where

Y = INF

t = time

ϵ = random error, NID (o, σ^2)

If the slope is statistically significant, that is, if the observed rate of stomatal closure during the day is significant, β_1 in the model will exceed the critical value of Student's $t_{.025,\ d.f.}$ listed in a table of t. That is, we are testing the hypothesis that the slope of the regression line, β_1, is equal to zero:

$$Ho: \ \beta_1 = \beta_{10} = 0$$

$$Ha: \ \beta_1 \neq \beta_{10}$$

The estimates of the regression parameters, b_i, and their t values are listed in Table 4. The double asterisk indicates significance at P = 0.99, the single asterisk indicates significance at P = 0.95 (example in Figure 5, p. 40).

From this analysis, it would appear that if the estimated slope

(b_1) is greater than 0.01 atm hr^{-1}, the change in INF is statistically significant. This statement can be made because the sample variance is fairly constant. The biological significance of the change varies with the degree of initial and final aperture. An INF value of 1.5 atm represents stomata about 90% closed, while an INF value of 0.1 atm corresponds to fully open stomata. Therefore, a change of 0.2 atm, while statistically equally significant, has a very different biological significance because of the curvilinear relation between INF and stomatal aperture (Eq. 4).

Some of the variance might have been due to changes in vapor pressure deficit during the day, as VPD had been shown to affect stomata of Zea mays (Raschke and Kühl, 1969). Accordingly, some of the data were analyzed by a multiple regression technique, where INF was regressed on time and VPD. These results are shown in Table 5.

The data presented in Table 5 are inconclusive. They simply indicate that when stomata tend to close during the day, this closure can be correlated with vapor pressure deficit and time. If the stomatal aperture remains constant throughout the day, stomatal behavior is uncorrelated with VPD or time. It is possible that small changes in stomatal aperture may be a result of changes in VPD, but this cannot be verified from my data.

Two of the regressions of diurnal INF values are plotted in Figure 7. In addition to the diurnal stomatal behavior, one sees that

Table 5. Regressions of diurnal stomatal infiltration pressure (INF) on time (used in Table 4) and on time and VPD. (See Figure 7.)

Plot	Date	b_o	Variable	b_i (coefficient)	Student's t	Regression (R^2)	df	Regression (F)
1	7-16-69	0.389	X_1	0.024	6.02**	0.307		
1	8- 5-69	0.412	X_1	0.047	8.98**	0.484		
3	8- 7-69	0.969	X_1	0.093	8.98**	0.535		
8	8-20-69	0.516	X_1	0.019	2.16*	0.082		
1	8-20-70	0.752	X_1	0.006	0.65	0.012		
3	9- 1-70	1.167	X_1	0.060	5.83**	0.425		
3	9-22-70	1.363	X_1	0.089	6.45**	0.550		
			Multiple Regressions					
1	7-29-70	0.662	X_2	0.006	0.897	0.041		
			X_1	-0.006	- .309	0.044	33	0.76
3	9-22-70	1.266	X_2	.025	4.79**	0.677		
			X_1	.037	3.81*	0.756	45	69.7**
3	9- 1-70	0.867	X_2	0.062	1.91	0.479		
			X_1	-0.072	-1.03	0.492	45	21.7**
23	7-20-70	1.97	X_2	-0.063	-2.32	0.141		
			X_1	-0.012	-0.56	0.149	32	2.808

Y = INF
X_1 = time
X_2 = VPD

*Significant at the 95% level.
**Significant at the 99% level.

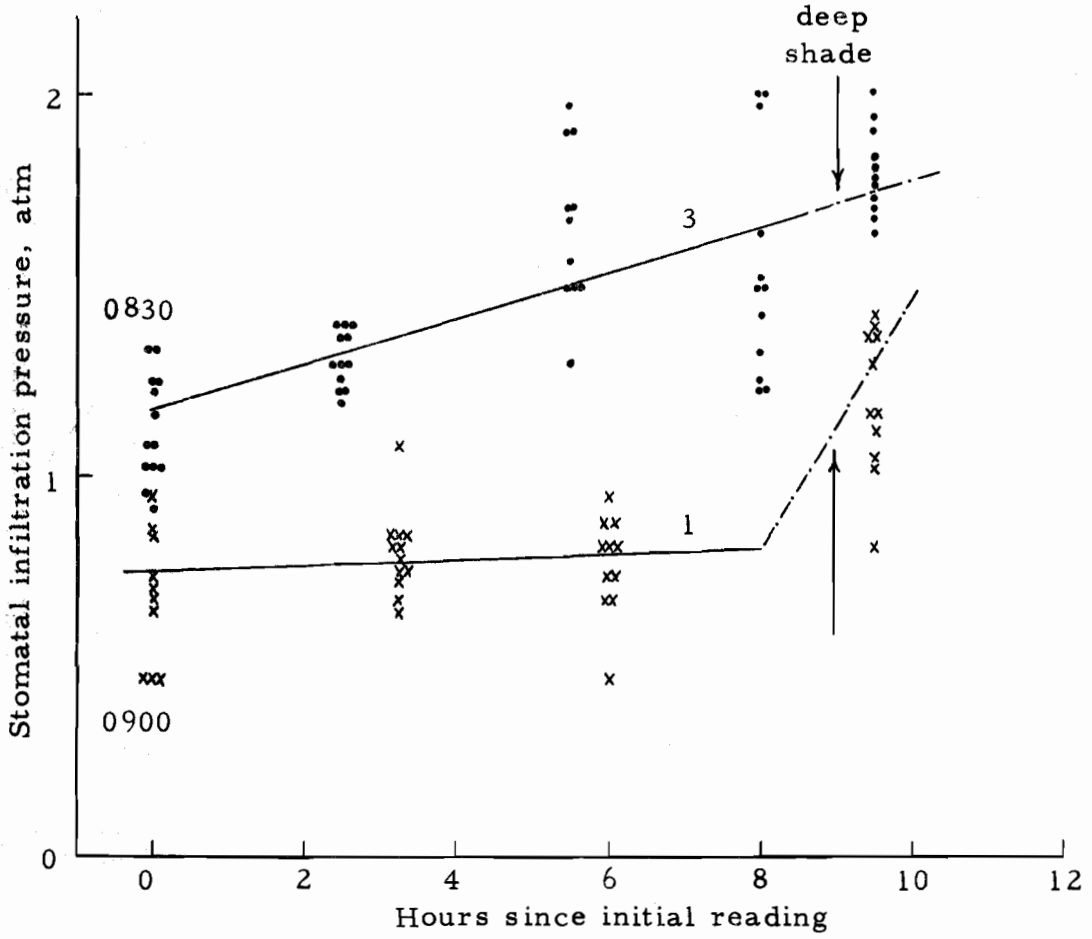


Figure 7. Diurnal variation in stomatal infiltration pressure. Each point represents the stomatal infiltration pressure of a single needle: the dots from Plot 3 (oak type), 1 Sept. 1970; the x's from Plot 1 (mixed conifer type), 20 Aug. 1970. The regression analysis data in Table 5. Points beyond dotted line not used in regression analysis due to proximity of sunset. Pre-dawn PMS: Plot 3 - 25 atm; Plot 1 - 11.6 atm.

the minimum INF value increases as the plant is subjected to a higher pre-dawn PMS. This is also indicated in Figure 5. This suggests that minimum INF is correlated with pre-dawn PMS. Because the diurnal INF was uncorrelated with diurnal PMS, a causal relationship between pre-dawn PMS and minimum stomatal aperture is suggested. A greater pre-dawn PMS is associated with a greater minimum INF. Therefore, a regression analysis was run on all the minimum INF data from all plots against the appropriate pre-dawn PMS (Figure 8). The minimum INF value usually occurred between 0800 and 1000 each day. Note that there is a rather large variance, but the R^2 for this regression was 0.55 and the F value was 71.66, which is highly significant (at the 99% level). An examination of the residuals suggests that the curve is slightly curvilinear, but an attempt to fit these data to the quadratic function $Y = \beta_0 + \beta_1 X + \beta_2 X^2$ was not successful. The quadratic term in this model was non-significant.

These observations are consistent with the dependence of guard cell turgor on water potential in the plant. If the plant were under water stress, the guard cells would simply not be hydrated to the same extent as if the plant were under low stress.

To summarize the field observations it can be stated that:

1. Pre-dawn PMS tended to increase throughout the summer as a result of long periods without rain. The rate and

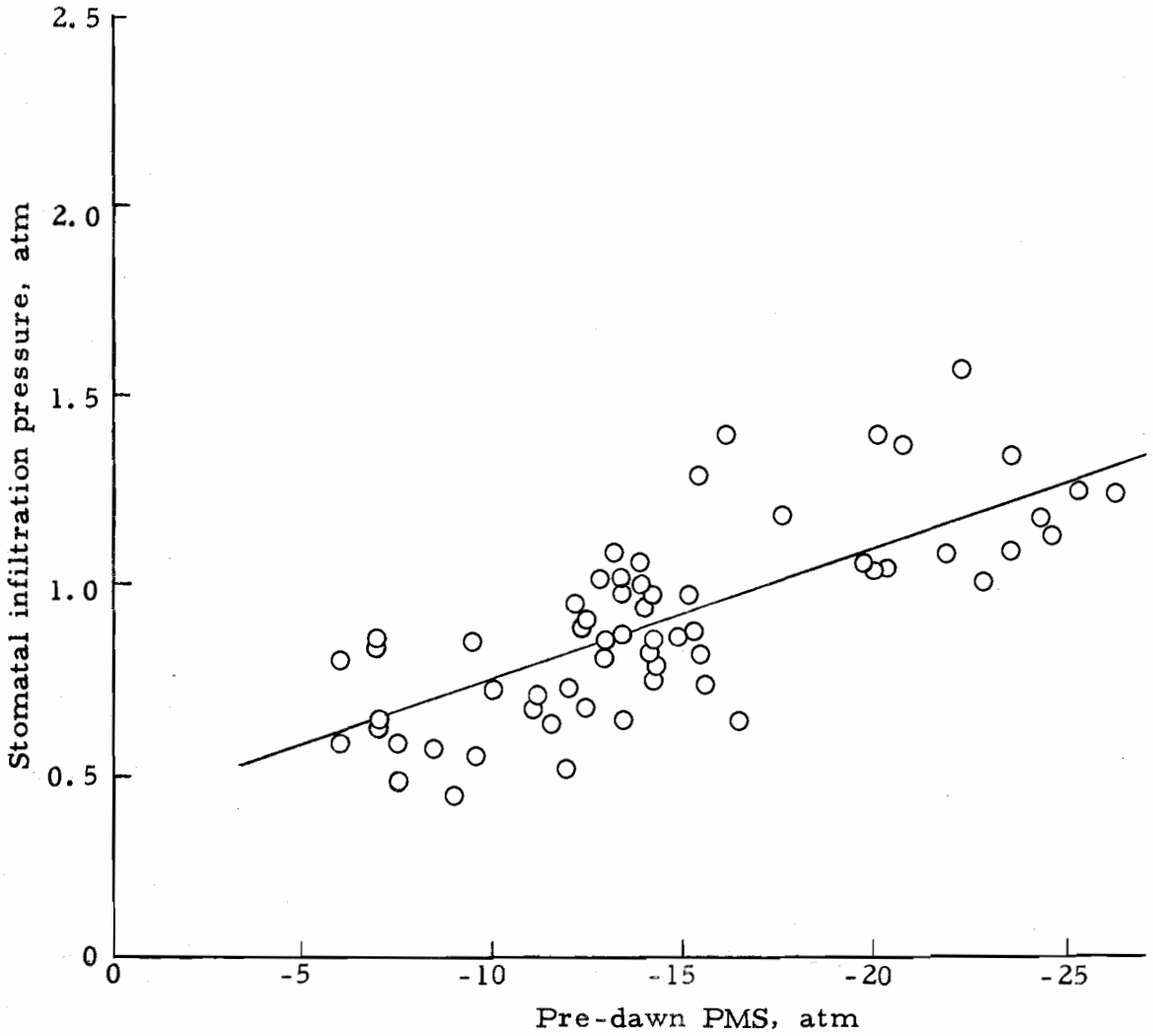


Figure 8. Minimum daily stomatal infiltration pressure from all plots as a function of the corresponding minimum plant moisture stress, PMS. Each point represents the mean INF value of the three trees on the respective plot corresponding to the mean PMS of the three trees. The regression equation is: $Y = 0.40 + 0.033X$; $R^2 = 0.55$; $F = 71.78^{**}$.

magnitude of desiccation was different for each plot, but the same general relation held.

2. Stomata of Douglas-fir and other conifers were closed at night except in spring and opened to some maximum aperture (usually between the hours of 0800 and 1000).

3. Stomatal behavior during the day cannot be completely explained from the data available. In general, however, except under conditions of very low pre-dawn plant moisture stress, stomatal aperture increases from dawn to 0800-1000 where a maximum aperture is reached. The behavior after 1000 hours probably depends upon a number of interrelated factors: plant moisture stress, transpiration rate, temperature, and vapor pressure gradient. For whatever reason, stomatal aperture may remain constant, increase slightly, or decrease after 1000 hours.

I was unable to obtain sufficient data to resolve the question of causal factors of this behavior. The rates of change in stomatal aperture, expressed as change in INF per hour (from Table 4), for three ranges of pre-dawn plant moisture stress are listed in in Table 6.

4. Maximum stomatal aperture (minimum INF) was correlated with pre-dawn plant moisture stress (PPMS).

Table 6. Rates of change of stomatal aperture from not less than 1/2 hour after dawn to not more than 1/2 hour before sunset grouped according to the pre-dawn moisture stress (PPMS) values. Data from Table 4.

Pre-dawn PMS (atm)	PPMS $\leq$ 5	5 $\leq$ PPMS $\leq$ 15	15 < PPMS
Rate of change in stomatal aperture (ΔINF hr^{-1})	.007	.023	.070
	.008	-.002	.056
		.037	.068
		.036	.051
		.050	-.050
		.007	.110
		.002	
		.063	
		.024	
Mean rate of change	.0075	.020	.051

V. LABORATORY EXPERIMENTS AND RESULTS

Estimation of Stomatal Resistance in Douglas-fir

Introduction and Rationale

In order to calculate transpiration from Eq. 2 of the review section, it is necessary to have some method of estimating stomatal resistance. Because stomatal resistance is a function of stomatal aperture, it is possible to obtain a functional relationship between stomatal infiltration pressure (INF) and stomatal resistance. The rationale for the determination of this relationship is described below.

Transpiration can be generally described by equation 2 (Slatyer, 1967; Jarvis and Slatyer, 1970).

$$\frac{d\tau}{dt} = \frac{c_w - c_a}{R} \qquad \text{Eq. 2}$$

where

$\frac{d\tau}{dt}$ = transpiration rate, g cm^{-2} sec^{-1}

c_w = vapor concentration in leaf, g cm^{-3}

c_a = vapor concentration in air, g cm^{-3}

R = resistance to water flux, sec cm^{-1}

The resistance to transpiration, R, can be broken down into component parts:

$$R = r_a + r_l \qquad \text{Eq. 7}$$

where r_l is leaf resistance and r_a is atmospheric or boundary layer resistance. Bange (1953) pointed out that a high boundary layer resistance tends to obscure the effect of the leaf resistance but if r_a is negligible, stomatal resistance has a linear effect on transpiration. This effect becomes non-linear very quickly if r_a is important. This view was supported by Ehlig and Gardner (1964) who thought that r_l would be negligible if r_a were large and if stomates were wide open. They concluded that stomatal control is important only when the stomata are mostly closed.

Few authors agree with this view.

There are several methods of estimating boundary layer resistance, r_a. The most common method is to use wet filter paper cut in the shape of a leaf. This technique was used by Gale and Poljakoff-Mayber (1968), Jarvis and Slayter (1970) and others. Hunt (1968) derived boundary layer resistance from an energy balance relationship and obtained values of much smaller magnitude than those estimated by the "classical" approach. Literature estimates of boundary layer resistances range from 0.1 to 3 sec cm^{-1} for most leaves (Slatyer, 1967), to Hunt's values of 0.05 to 0.13 sec cm^{-1}.

Although in the previous paragraph I have treated leaf resistance to be essentially equivalent to stomatal resistance, this is not the case. Leaf resistance is another composite term and can be broken down as follows:

$$\frac{1}{r_l} = \frac{1}{r_s} + \frac{1}{r_c} = \frac{1}{(r_s + r_m)} + \frac{1}{r_c} \qquad \text{Eq. 8}$$

where

r_l = leaf resistance, sec cm^{-1}

r_s = stomatal resistance

r_c = cuticular resistance

r_m = mesophyll resistance

Mesophyll resistance (r_m) has been interpreted to be a result of one of two possible mechanisms (Jarvis and Slatyer, 1970). The first is development of high resistance to evaporation from the cell walls due to incipient drying. In incipient drying, the water on the surface of the cell wall retreats into the cell wall, thereby removing the free evaporating surface. The other postulated mechanism is that a substantial depression of vapor pressure at the evaporating surface is developed because of solute accumulation. Slatyer (1966) states that incipient drying appears improbable because of the high permeability of the water pathway through the walls of the leaf cells and also because of the small void sizes in the interfibrillar spaces of the cell walls. Significant vapor pressure depression also seems improbable partly because the relative high rate of water exchange between cells tends to prevent the development of steep local gradients of leaf water potential. Further, a very high concentration of solute is required to reduce the vapor pressure of a liquid more than a few percent.

Jarvis and Slatyer (1970) measured mesophyll resistance in

cotton and their values range from 0.4 sec cm^{-1} to approximately 4 sec cm^{-1} when the leaf is extremely desiccated. Therefore, mesophyll resistance is negligible in cases of considerable drought because stomatal resistance (r_s) is much greater, indeed, approaching infinity. In the case of well watered plant material, r_m may be significant but still contributes only a small part to the total leaf resistance. Therefore, for the purpose of this research, mesophyll resistance is considered to be negligible or at least subsumed into the error of the estimates of stomatal resistance.

Having eliminated r_m, our equation for total leaf resistance (R) reduces to equation 9:

$$R = r_a + \frac{r_s r_c}{r_s + r_c} \qquad \text{Eq. 9}$$

If, as according to Hunt, boundary layer resistance is very small, or if the leaf under consideration is aspirated to such an extent that the vapor boundary layer is removed, transpiration then reduces to two terms as expressed in equation 10:

$$R = \frac{r_s r_c}{r_s + r_c} \qquad \text{Eq. 10}$$

But r_s and r_c represent two parallel pathways of water flow. That is, water simultaneously moves through the cuticle and through the stomates. Therefore, Gaastra (1959) and most other workers since (Slayter, 1967) have used an analogy to Ohm's law to solve for stomatal resistance if r_a is eliminated and r_c is known:

$$\frac{1}{R} = \frac{1}{r_s} + \frac{1}{r_c} \qquad \text{Eq. 11}$$

This can then be solved for stomatal resistance where

$$\frac{1}{r_s} = \frac{1}{R} - \frac{1}{r_c} \qquad \text{Eq. 12}$$

By solving our original Eq. 2 for R, given measurements of T and $c_w - c_a$, leaf resistance can be easily calculated. Then, if cuticular resistance were known, stomatal resistance at a given time can be calculated by solving Eq. 12.

Experiments and Results

Using this rationale, an experiment was designed to provide the functional relationship between infiltration pressure, INF, and stomatal resistance. If it were possible to set up an experiment where transpiration and infiltration pressures could be measured at intervals throughout an experiment concurrently with vapor concentration measurements, the desired relationship between infiltration pressure and stomatal resistance could be obtained.

Surface Area Determinations. As is implied in Eq. 2 of the literature review, transpiration is expressed in g cm^{-2} sec^{-1}. Thus, surface area of leaves must be measured in order to use Eq. 2. The surface area-dry weight ratio of our Douglas-fir needles was estimated by the technique described by Thompson and Leyton (1971).

Leaves were coated with a tacky adhesive and subsequently covered with a monolayer of small glass beads. The weight of the needle was taken before and after treatment, and the added weight of the uniform layer of glass beads is directly proportional to the needle surface area. The technique I used was modified slightly from that described by Thompson and Leyton.

The adhesive solution was made up by diluting 3M Scotch spray mounting adhesive with benzene. This adhesive is available only in an aerosol spray form; it was necessary to spray the adhesive into 100 ml of benzene until the total volume equaled 110 ml. The needles were weighed, then dipped twice in the adhesive solution; the second dip after a sufficient delay to allow the benzene to evaporate. After the adhesive completely covered the needle, it was then dipped into a pile of the small glass beads and reweighed. The needles were weighed to $\pm$ 0.1 mg on a Mettler balance.

The technique was calibrated by cutting graph paper into a series of squares of 1 to 32 cm^2 in area. The squares of paper were weighed, then coated with the glass beads and reweighed. The change in weight as a function of surface area is depicted in Figure 9. This regression had an excellent agreement with that obtained by Thompson and Leyton where a theoretical maximum would be approximately 15 mg cm^{-2}.

For the actual estimation of surface area, a technique similar to

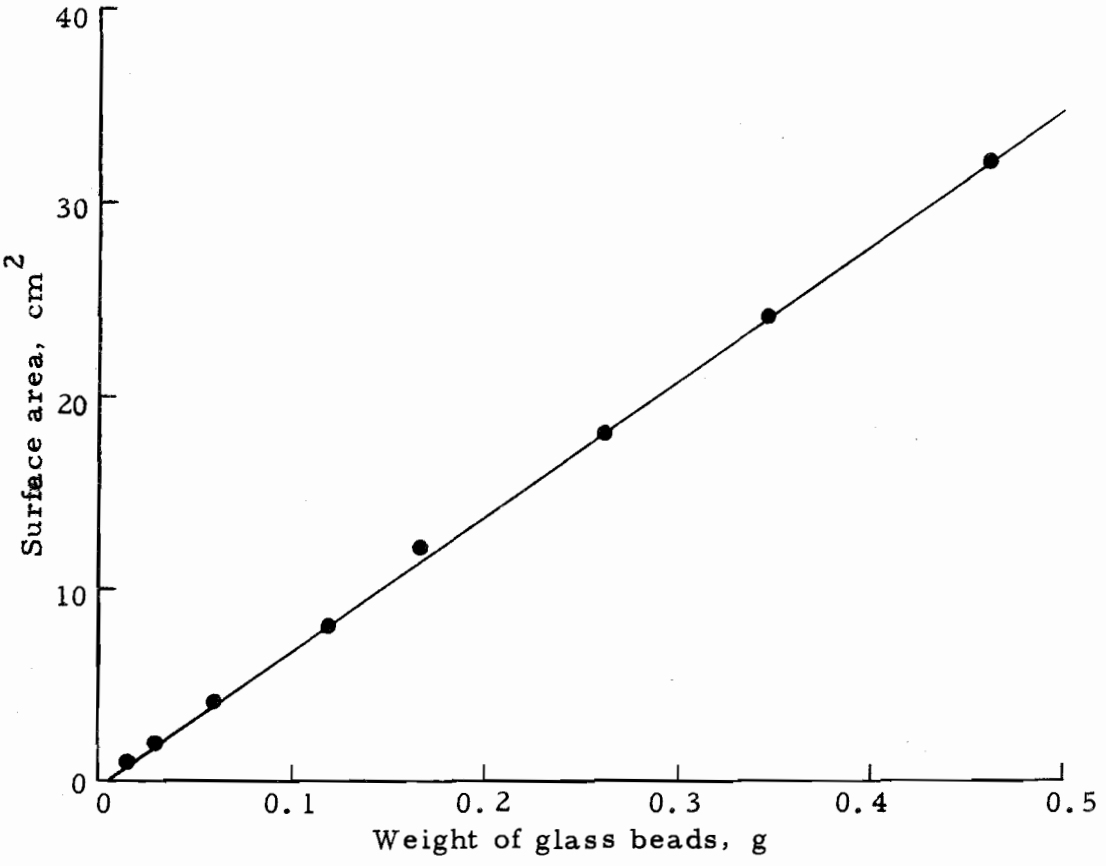


Figure 9. Calibration of the Thompson and Leyton technique for estimating surface area by covering an object with tiny glass beads. Surface area of squares of graph paper regressed on weight of glass beads covering the paper on both sides. Regression equation: $Y = -.04 + 69.01X$; $R^2 = 0.999$.

that used in calibration was used. A number of dry needles were placed in an ice tray where the first chamber contained two needles, the second, 3, the third, 5, the fourth, 10, and so on. The needles in each chamber would be treated as described above. The relation of dry weight to surface area was determined by linear regression (Figure 10). The R^2 of this regression was always greater than 0.99. The ratio of surface area to dry weight varied from seedling to seedling, ranging from 131 $cm^2 g^{-1}$ to 188 $cm^2 g^{-1}$. The surface area to dry weight ratio was determined for every seedling used in the laboratory experiment.

Experimental Estimation of Stomatal Resistance. Five potted Douglas-fir seedlings, four of a Siskiyou seed source and one from an unknown seed source, were selected and brought into the weighing room and placed on a table under normal room light. They had been well watered one day prior to being brought inside. The top of one of the shoots was then cut off and was immediately weighed on a Mettler balance, accurate to 0.1 mg. The branch was then placed on a rack in a vertical position in the direct path of a high-speed fan. A sample of three needles was taken just prior to the first weighing. The stomatal infiltration pressure (INF) of this sample was measured; this value was considered to be the INF at time zero. The branch was then reweighed at intervals ranging from 5 minutes at the outset to 30 minutes toward the end of the experiment. The branch was weighed,

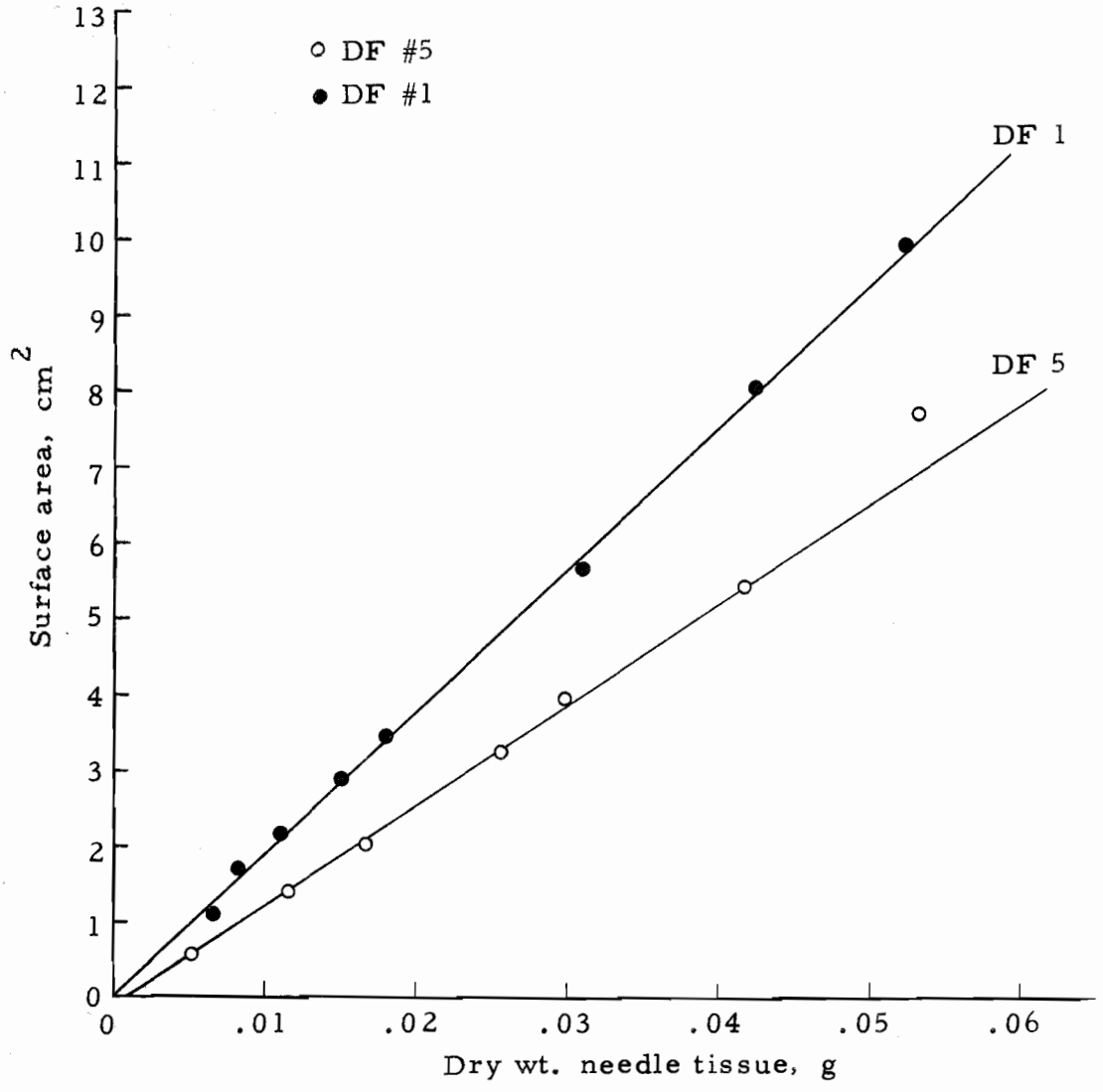


Figure 10. Surface area of needles from two different Douglas-fir seedlings as functions of dry weight of the needles. Surface area estimated by the Thompson and Leyton technique. Regression equations: for Douglas-fir #1 - $Y = -0.007 + 188.2X$; $R^2 = 0.99$; for Douglas-fir #5 - $Y = -0.11 + 133.13X$; $R^2 = 0.99$.

then three needles were removed and the branch immediately re-weighed. The branch was then quickly placed back under the fan and the INF of the sampled needles was determined. The interval between the first and second weighings was usually less than 30 seconds. The second weighing was necessary in order to correct for weight loss due to needle sampling. The sampled needles were held in a plastic petri dish until the weighing was completed; INF was determined immediately after. At the same time, the wet and dry bulb temperatures were read from an Assmann mercury and glass psychrometer. This process was repeated for each of the five seedlings. The weight data were corrected for needle loss due to sampling and the results expressed as amount of water lost per unit time.

The infiltration pressure at time t was recorded along with the wet bulb-dry bulb temperatures. After the experiment was completed, the sampled needles were placed in small glass bottles marked as to sample number and placed in the drying oven at 70 ^{o}C. The remainder of the branch was also dried in the oven and the weight of the needle samples and total branch were determined.

After the dry weights were determined for the samples and for the total amount of remaining tissue, the surface area to dry weight ratio was determined as described in the methods section. The final transpiration results were then expressed in grams water lost per dm^2 of leaf tissue per minute, and vapor concentration gradient was

expressed in g cm^{-3}. Transpiration, in mg dm^{-2} min^{-1}, was plotted against time. A curve was fitted through the data points using the non-linear least squares curve fitting program. The model used was:

$$Y = \beta_0 + \beta_1 e^{-\beta_2 t} \qquad \text{Eq. 13}$$

This model fit the data quite well in most cases as is illustrated in Figure 11. The transpiration rate at the asymptote, estimated by b_0, was used as an estimate of cuticular transpiration. This, in turn, was used to calculate cuticular resistance.

The conversion of the psychrometric data to vapor concentration was accomplished by first computing vapor pressure in millibars from values given in the Smithsonian Meterological Tables (1966, Table 94). The vapor pressure within the leaf is assumed to be saturation vapor pressure at leaf temperature (Slayter, 1967). This value for saturation vapor pressure is simply taken from Table 94. The values of saturation vapor pressure (e_s) and atmospheric vapor pressure (e_a) were converted to absolute humidity with the formula from Slayter (1967):

$$C = \frac{18\, k e_i}{RT} = \frac{2.17 \times 10^{-4} e}{T} \qquad \text{Eq. 14}$$

where

R = gas constant, erg $mole^{-1}$ deg^{-1}

T = temperature, ^{o}K

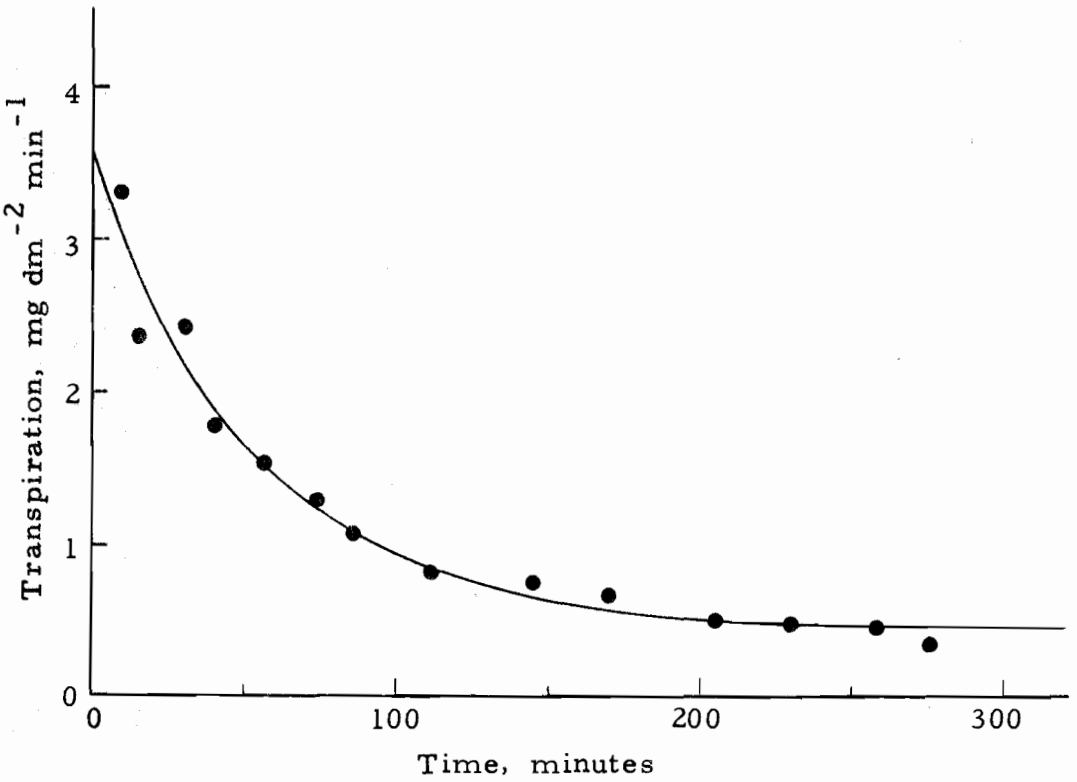


Figure 11. Transpiration from the severed seedling, Douglas-fir #1 (DF #1), as a function of time. Time was measured from the point of severing. Smooth curve fit to the data by least squares estimation. Equation of the curve:

$$Y = 0.452 + 3.00e^{-1.779t}$$

e_i = vapor pressure, mb

k = constant to convert e to dyne cm^{-2}

This calculation was used to calculate c_a and c_w where c_a is the vapor concentration of the air and c_w is the vapor concentration within the leaf. A FORTRAN program was written to read all the data from the experiment, solve the various equations, and print out R, r_s, r_c, ΔC and transpiration rate, T.

A regression analysis of stomatal resistance (r_s) on the corresponding infiltration pressure readings was used to develop the relation of r_s with INF depicted in Figure 12. The regression line is given by Eq. 15:

$$\text{Log}_{10} r_s = -0.088 + 1.39\ \text{INF} \qquad \text{Eq. 15}$$

where

r_s = stomatal resistance, sec cm^{-1}

INF = stomatal infiltration pressure, atm

This regression had an R^2 of 0.93 with an F value of 413.3 which is highly significant (99% level).

There were several assumptions made in this experiment: (1) boundary layer resistance was negligible. This is reasonable since the air velocity across the needle was very high throughout the course of the experiment. (2) It was assumed that leaf temperature equaled air temperature. This again was reasonable since the light intensity of the room was relatively low, and the needles aspirated. Under

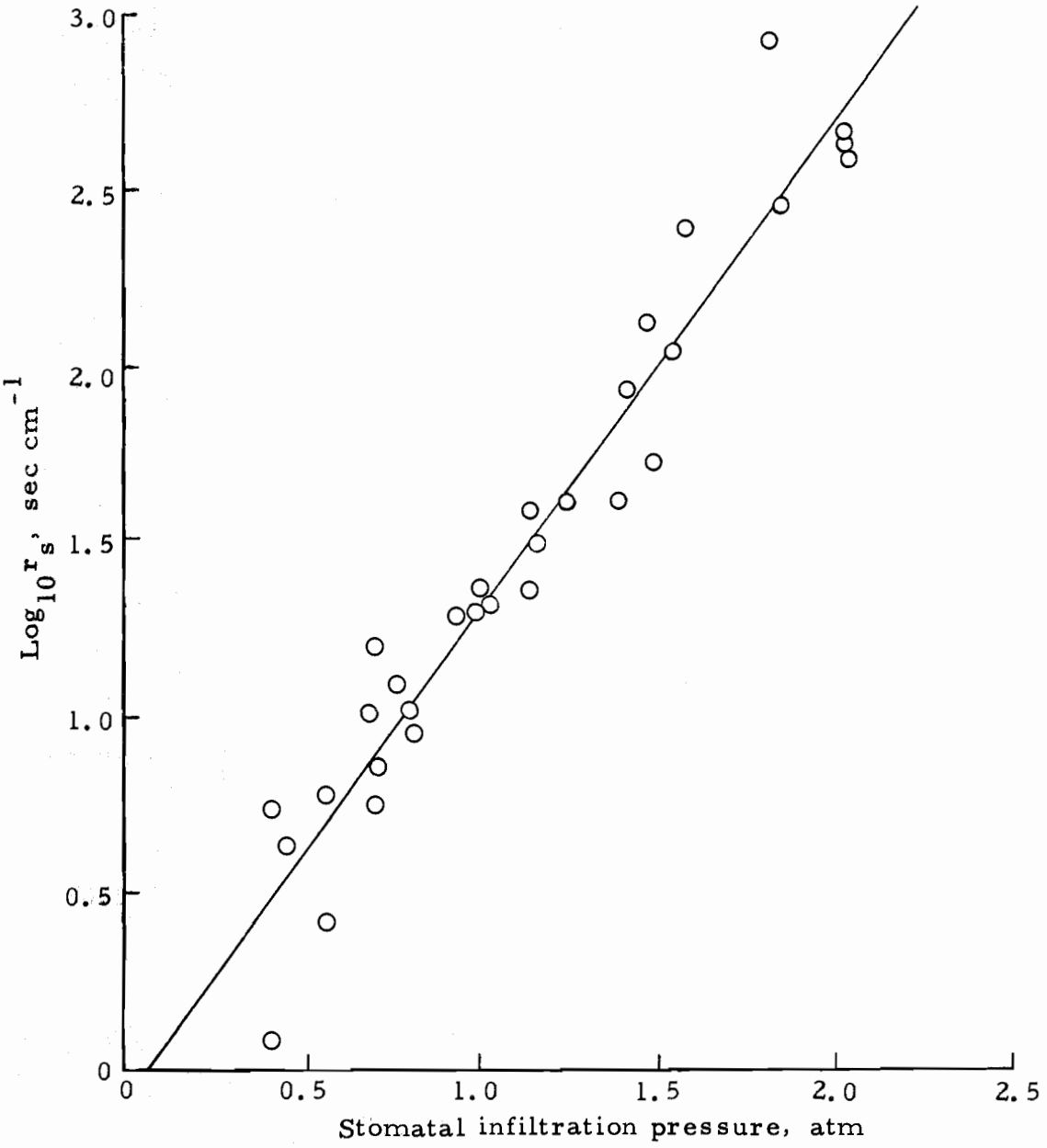


Figure 12. Stomatal resistance of Douglas-fir as a function of stomatal infiltration pressure. Equation:

$$\log_{10} Y = -0.088 + 1.39X;\ R^2 = 0.93;\ F = 413.3^{**}.$$

those conditions the difference in temperature between the leaf and air should be negligible. It is possible that during periods of high transpiration rate leaf temperatures may have been slightly lower than air temperatures. This would cause the calculated values of ΔC to be low. It is doubtful, however, that the difference in temperature was sufficiently great to introduce a great deal of error in the calculation of ΔC. It is more likely that the greatest source of error lies in the measurement of wet and dry bulb temperatures with the Assmann psychrometer. (3) Experimental conditions alone had no effect on the stomatal aperture. This was supported by the fact that INF of the uncut seedlings measured periodically throughout the experiment did not change. (4) The asymptotic transpiration rate represents cuticular transpiration and, therefore, could be used in the calculation of cuticular resistance.

This last assumption was probably the principle source of error in this experiment because sampling the needles left leaf scars. On a small branch, particularly at very low transpiration rates, water loss through the leaf scars could be significant. This would result in erroneously high transpiration rates which, in turn, would result in an erroneously low calculation of r_c. In our experiments, r_c ranged from 28 to 74 sec cm^{-1}. These values, when compared with values in the literature appear to be low. However, it must be noted that these seedlings were not well hardened off; the needles were unusually soft.

Allen Drew (personal communication) measured cuticular transpiration in Douglas-fir with the stomatal side of the needle coated with silicone grease and calculated r_c values of 300 sec cm^{-1}. This value seems high since Slatyer (1967) reports that typical values of r_c range from less than 20 sec cm^{-1} for shade plants to about 200 sec cm^{-1} for xerophytes. The calculated values of stomatal resistance for this experiment were reasonable, so I believe that the error was fairly small (10-20%).

In order to test the idea that our calculated values of r_c are too low due to leaf scar transpiration, another seedling from the Siskiyou source, labeled DF6, and a branch from a Douglas-fir tree growing outside the lab, labeled DF7, were brought into the weight room. The experiment was carried out exactly as described above except that no needles were sampled for infiltration pressure measurement. The transpiration data were again expressed in g cm^{-2} min^{-1} and the asymptotic transpiration rate was used in the calculation of cuticular resistance. The value calculated for r_c of DF6 was 43 sec cm^{-1} and the calculated value for DF7 was 132 sec cm^{-1}. These values seem reasonable in light of the ranges of r_c cited by Slatyer (1967). The cuticular resistance of Douglas-fir in the Siskiyous is assumed to be 150 sec cm^{-1} for modeling purposes.

During the laboratory experiments, stomatal closure began almost immediately after the branches were excised. This was not

expected because the field data indicate that stomatal aperature is independent of diurnal fluctuations of PMS. The observation raised the question as to whether the excised twigs were excessively dehydrated. Therefore, at the conclusion of the experiment the cut branch was immediately placed in a pressure bomb and the plant moisture stress determined. In no case did the plant moisture stress exceed 28 atm.

Effect of Soil Temperature on Douglas-fir Stomata

Introduction

Kramer (1942) observed that a large variety of plant species exhibited a marked reduction in transpiration rate as the temperature of the soil was reduced. Cox and Boersma (1967) controlled soil moisture stress and soil temperature while air temperature, vapor pressure gradient, light intensity and wind speed were all held constant. They reported a marked depression in transpiration rate of clover associated with a reduction of soil temperature. In the ranges of soil temperature from 10 to 26.7°C, transpiration rate was reduced over the lower ranges but approached an asymptotic value at approximately 21°C. Transpiration was reduced as temperature was lowered and soil moisture stress increased from 0.35 to 1.30 atm. They also showed that stomatal aperture was reduced by a decrease

in soil temperature, and by an increase in soil moisture stress. Unfortunately, they did not investigate this effect at higher soil moisture stresses. The SMS range of approximately 0.3 to 1.3 atm is very low, especially when Slatyer (1957) pointed out that permanent wilting point for tomato was 20 atm soil moisture stress, and PWP for cotton was 48 atm soil moisture stress.

Babalola, Boersma and Youngberg (1968) showed that transpiration of Monterrey pine was also affected by soil temperature. They controlled soil temperature (10 to 16°C) and soil water potential (-0.35 to -1.30 atm). Transpiration decreased with a decrease in soil water potential and with a decrease in soil temperature from 26 to 10°C. Kuiper (1964) reported that bean roots grown at 17°C absorbed more water than roots grown at 24°C when subjected to low soil temperatures. Slatyer (1967) suggests that these differences may be due to different membrane characteristics. Again, these plants were not subject to high soil moisture stress.

House and Jarvis (1968) observing tritiated water uptake in corn roots found that there is a definite rate determining step: flux across the membrane in living roots. They found that this flux was greater at 25°C than at 5°C.

The major problem with all the above cited papers is that in every case, soil moisture stress was very low. Uptake is a function of diffusion across the root membrane which is dependent upon both

temperature and soil water potential. This temperature dependency could therefore be easily masked by soil moisture stress. This statement is supported by Anderson and McNaughton (1971) who found that water status due to low temperature is not an important factor in the field. They reported that neither transpiration nor photosynthesis of several species was reduced at 3°C under the conditions of their observations.

The effect of soil temperature on water uptake in nature is probably limited to periods of high soil water availability and low temperatures (e.g., early spring). Obviously, soil temperature can have a significant indirect effect on plant water status and growth as it affects root growth.

Experiments and Results

Although none of my field work was conducted at a time when soil temperature was less than 10°C, I wished to ascertain the effect of soil temperature on stomatal behavior for modeling purposes. Accordingly, six Douglas-fir seedlings of about 20 cm in height were placed in a specially constructed growth chamber containing an insulated root bath. The seedlings were left in this chamber for three weeks under a 12-hour photoperiod and a temperature regime of 13°C during the day, and 8°C at night. Radiant energy, as measured by a Kipp solarimeter, was 0.15 cal cm^{-2} sec^{-1} at seedling height.

After the acclimation time of three weeks, the soil temperatures of all seedlings were adjusted downward. Four of the seedlings had root temperatures of $0^{\circ}C$. The other two had root temperatures slightly higher. Throughout the next three days, air temperature, soil temperature, and vapor pressure deficit were all measured. The root temperature was varied from $0^{\circ}C$ to about $8^{\circ}C$. Stomatal infiltration pressure readings were taken concurrently with acquisition of environmental data. A quadratic regression model of the form

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_1^2 \qquad \text{Eq. 16}$$

where Y = INF, X_1 = soil temperature, was fit to the pooled data from all six seedlings with an R^2 of 0.23.

These data were also analyzed separately because it was apparent that some of the seedlings were responding somewhat differently from the others. Therefore, the data for seedlings #1 and #2, seedlings #3 and #4, and seedlings #5 and #6 were analyzed separately. The data for seedlings #1 and #2 are illustrated in Figure 13. The fitted equations and results of the analysis are listed in Table 7.

Table 7. Regression analysis of effects of soil temperature on stomatal behavior of Douglas-fir seedlings. Model used: Eq. 16.

Seedling no.	Regression equation	R^2	Regression F level	d.f.
1, 2	$Y = 1.01 - 0.202X + 0.023X^2$	0.547	27.7**	2, 46
3, 4	$Y = 1.49 - 0.202X + 0.023X^2$	0.247	8.17**	2, 51
5, 6	$Y = 1.27 - 0.145X + 0.010X^2$	0.145	4.73*	2, 56

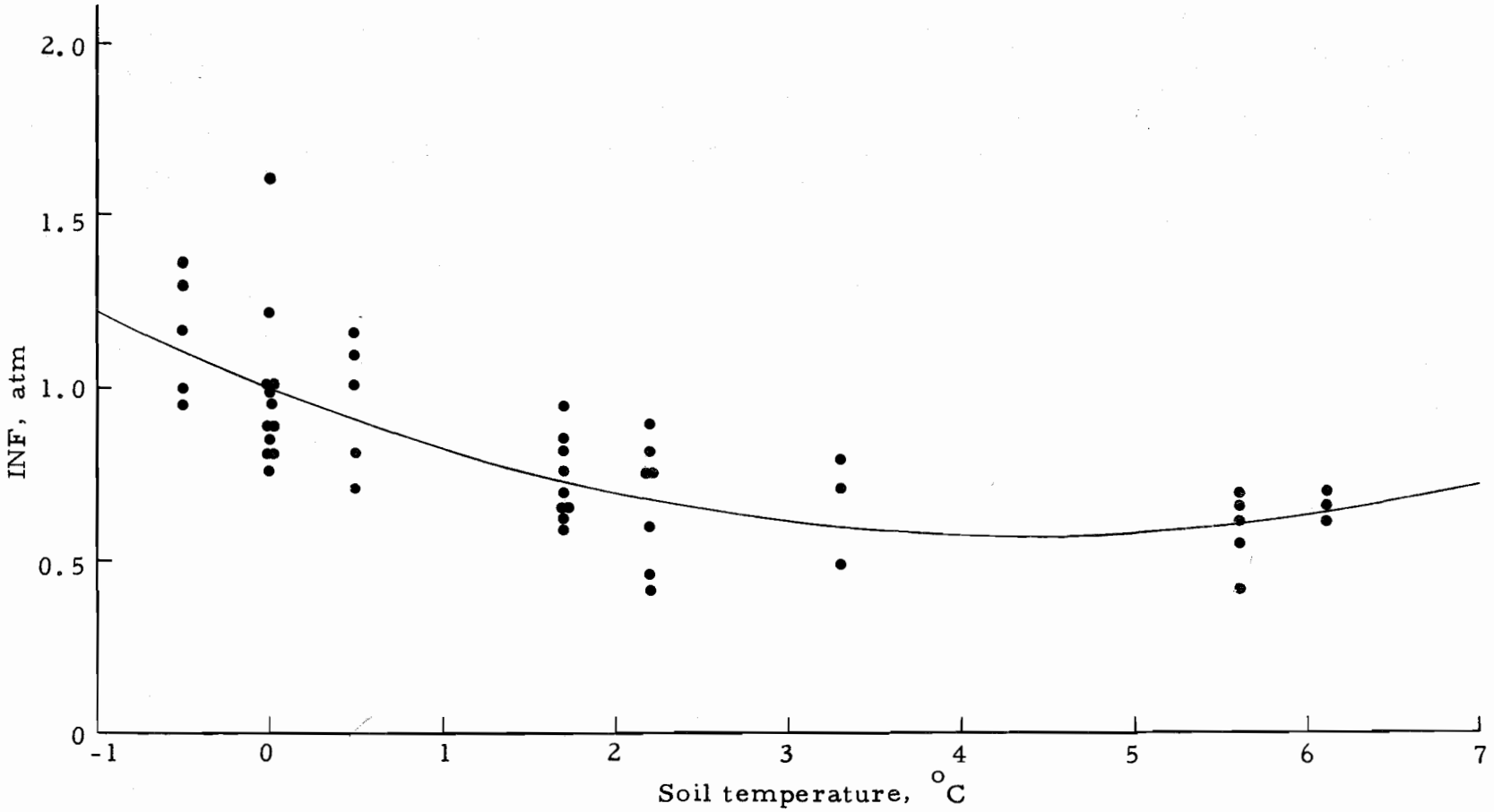


Figure 13. Effect of soil temperature on INF (stomatal infiltration pressure) of two potted Douglas-fir seedlings in a growth chamber. Root temperature was varied, air temperature varied slightly. Equation of curve: $Y = 1.01 - 0.202X + 0.023X^2$; $R^2 = 0.547$; $F = 27.7^{**}$.

Examination of the plotted curve of Figure 13 indicates that under the conditions of this experiment, stomatal aperture is probably unaffected by soil temperature above 2°C. This was also reflected in the data for the other four seedlings. The interaction between soil temperature, soil moisture status, transpiration rates and vapor pressure as they affect stomatal behavior were not studied in great detail.

A multiple regression of INF on PMS, VPD, air and soil temperature showed a significant correlation only between soil temperature and INF. The soil moisture stress was not measured, but night-time PMS values ranged from -7 to -10 atm on the last day of the experiment. These values would approximate soil moisture stress if nocturnal transpiration were negligible. The stomata of the seedlings in the chamber closed at night, but there was a positive vapor pressure deficit within the chamber at all times, so nocturnal transpiration was possible at least to some extent. It is probable that soil moisture stress exceeded 5 atm, which may have obscured the effect of soil temperature on stomatal aperture.

The effect of low soil temperature on stomatal behavior was ignored in the modeling because of its small importance in late spring and summer in southern Oregon.

VI. SIMULATION STUDIES

Introduction

As described above, ecologists have long attempted to characterize environment in terms of environmental effects on plant communities. Until recently, interpretation of environmental data in terms of plant response was not possible in field research. The vegetation was described but most relationships with the environment were inferred. With the advent of new techniques, ecological classification systems have evolved based upon measurements of environmental and coupled plant response (Waring, 1969).

As discussed in the introduction, simulation offers a means whereby data can be generated in cases where acquisition of actual data is exceedingly difficult or impossible. If structurally and mathematically sound models are used, the simulated data can help explain how different systems respond to various stimuli.

There are several approaches possible in modeling a plant process such as transpiration or photosynthesis. The brief review below outlines some of them.

Woo (1964) developed an analog simulation model of transpiration processes which included a stomatal control mechanism. He did not attempt to simulate weather in the field. Zahner and Stage (1966) used the Thornthwaite potential evapotranspiration equations and

attempted to obtain an evaluation of plant moisture stress from environmental data. These were used in regressions to obtain predictions of tree growth. Botkin (1969) used a step-wise multiple regression analysis of photosynthesis as a function of temperature and radiation, based on data from a single leaf. His equation entailed the use of linear, quadratic and cross-product terms in a multiple regression model and obtained fair agreement with real data taken subsequently from different leaves in an oak stand.

Idso and Baker (1968) used an energy balance approach based on that of Gates (1965) and Idso and Baker (1967). Photosynthesis was calculated as a function of temperature and light; they measured relative humidity, wind velocity, and air temperature at the height of the soybean crop and used these data to derive a model depicting the varying energy environment and its effects on photosynthesis, with reasonable results.

Rozenzweig (1968) modified Thornthwaite's evapotranspiration model to estimate the difference between potential and expected transpiration for a number of plots. He obtained a relationship between the "annual active evapotranspiration" and the net above-ground productivity.

Waggoner and Reifsnyder (1968) and Waggoner et al. (1969) utilized quite sophisticated energy budget models to simulate evaporation, sensible heat exchange, vapor pressure, and temperature at

various levels within a canopy. Their models required as input: distribution of absorption of net radiation throughout the canopy, air temperature and vapor pressure at the top and floor of the canopy, and several other variables including leaf size and stomatal resistance.

From the brief review given above, it can be seen that modeling plant processes can be undertaken from a variety of approaches, ranging from mechanistic to purely associative. The selection of approach should be determined by the goals of the modeler. The complex models utilizing the energy budget approach have considerable theoretical validity and serve as excellent tests of theories of the fundamental nature of energy exchange, but the highly sophisticated measurements required for acquisition of the necessary data preclude the use of such models for most ecological research. Further, such models cannot be readily applied to mountainous terrain with a complex canopy.

On the other hand, models such as the one by Botkin (1969) are severely limited by their empirical nature which makes extrapolation beyond the data quite hazardous. In some cases, however, such a model can be of considerable utility, as long as the user can be reasonably confident that the model is valid under the conditions for which it is being applied.

Most of the models described above have a common element: the attempt to develop a functional model of a complex system. Even

the empirical model of Botkin expresses photosynthesis as a function of several variables and includes crossproduct terms which account for some of the interactions of the external variables affecting the system. It is necessary to account for such interactions because, as Bertalanffy (1968) points out, a system is more than the sum of its parts.

This concept has not received total acceptance in science, particularly in biology. This failure to recognize the importance of interactions as they affect a system has contributed considerably to confusion in the literature of science. Much of the controversy concerning the relative effects of the various factors influencing stomatal behavior is due to failure to recognize the important fact that stomata behave as a system and must be considered as such.

If a process is a function of several variables, e.g.,

$$\mathcal{T} = f(T, e, \psi) \qquad \text{Eq. 17}$$

where

$\mathcal{T}$ = transpiration

e = vapor pressure of the air

ψ = water potential of the leaf

T = temperature

then it should, if possible, be solved analytically. It has been popular recently to present a model such as Eq. 17, and by differentiation obtain:

$$\frac{dT}{dt} = \left[\frac{\partial T}{\partial T}\right]_{e,\psi} dT + \left[\frac{\partial T}{\partial e}\right]_{T,\psi} de + \left[\frac{\partial T}{\partial \psi}\right]_{T,e} d\psi \qquad \text{Eq. 18}$$

(Cleary, 1970; Hinckley, 1971). Eq. 18 presents some difficulties: (1) the solution could be very difficult, and (2) the model assumes that the variables are independent. It would be preferable to express the relation of Eq. 17 as a system of differential equations similar to those of Table 1, which would accommodate the interactions of the terms which are not independent.

I chose a simpler approach. Eq. 2 is an accepted equation for transpiration in terms of the atmospheric demand and the plant responses. The interactions of T and e of Eq. 17 are incorporated into the numerator of Eq. 2 and the effects of ψ are subsumed into the resistance term in the denominator of Eq. 2. Thus,

$$\frac{dT}{dt} = \frac{c_w - c_a}{R} = \frac{\Delta c}{R}$$

where

$\Delta c = c_w - c_a$ = vapor concentration in the leaf minus the vapor concentration in the air, g cm^{-3}

R = plant resistance to transpiration, sec cm^{-1}

$\frac{dT}{dt}$ = transpiration rate

satifies the dual requirements of biological and mathematical reality.

Description of the Simulation Program

A digital computer program was written in FORTRAN IV and run on the CDC 3500 computer on the Oregon State University campus. It performed one iteration each "day," during which it generated all the necessary variables to compute transpiration for that "day." At the end of each "month," the daily transpiration values, the daily values of the other variables, and bi-weekly and monthly transpiration totals were printed out. The program also simulates potential transpiration, defined as transpiration expected if the stomata were fully open, and the difference between the potential transpiration and the "actual" transpiration. These latter values were printed out with the rest of the data.

There are two versions of the program: one which generates all the data it needs, and one which reads the temperature data from a file. For the former, temperature data were generated by random selection from a Normal (μ, σ) distribution generated around the expected temperature for the given month and day-type.[1] The expected temperature is the estimate of the parameter μ, with a standard deviation, σ. The random selection procedure involves the generation of a sequence of uniform random numbers which are then used to generate a normal distribution about the expected value. The

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[1] Day type is described on page 34.

uniform random numbers, $0 < RN < 1$, were generated by a standard pseudorandom number routine provided through the courtesy of Carole Settles of the Department of Statistics, Oregon State University. The Normal (μ, σ) distribution was generated by use of a routine described in Nailer et al. (1967). Five years of temperature records were analyzed in developing the probabilistic model of temperature.

The second version of the program simply reads actual temperature data from thermograph records which have been placed in disk storage. These data were taken from the records of daily maximum temperature for each plot for the period of 1 April through 30 September, 1968 and 1970, and were used in the program to generate a value of maximum vapor pressure deficit, VPD_m.

The output from the second version will be discussed in this thesis; this output corresponds to actual temperature data and are therefore more meaningful in explaining the differences between 1969 and 1970. The probabilistic temperature model of the first version could be used for predictive purposes but was not used because of insufficient funds.

The program is relatively short for a simulation model, normally requiring 30-45 seconds of computer time for simulation of transpiration on four plots for a six-month period (732 iterations).

Derivation of the Transpiration Model

Basic Model of Transpiration

Given Eq. 2

$$\frac{d\tau}{dt} = \frac{\Delta C}{R} = \Delta C \frac{1}{R}$$

letting

$$\frac{1}{R} = \frac{1}{r_s} + \frac{1}{r_c}$$

then

$$\frac{d\tau}{dt} = \Delta C\left(\frac{1}{r_s} + \frac{1}{r_c}\right) = \Delta C\left(\frac{1}{r_s} + \epsilon\right) \qquad \text{Eq. 19}$$

because r_c is a constant.

Derivation of Time Function of ΔC

Equation 19 can be solved for daily transpiration by integration if ΔC and the resistance term can be mathematically described as functions of time.

Because vapor pressure gradient, hence ΔC, is a function of temperature, the time course of diurnal 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 plots suggests that a quadratic function should suffice for a model of daily time course of ΔC. Hence:

$$\Delta C = \beta + \gamma t - \delta t^2 \qquad \text{Eq. 20}$$

The constants β, γ, and δ must be determined for each day. This can easily be done if the daily maximum and the value for β is known. During early spring and in areas reaching dewpoint at night, $\beta = 0$. At the time of maximum ΔC, the derivative of Eq. 20 equals 0. Therefore, by differentiating Eq. 20 with respect to t we get

$$\frac{d\Delta C}{dt} = \gamma - 2\delta t = 0 \text{ at } \Delta C_{max}$$

solving for δ, we have

$$\delta = \frac{\gamma}{2t_m} \qquad \text{Eq. 21}$$

By substitution into Eq. 20, we get

$$\gamma = \frac{2\Delta C_m - \beta}{t_m} \qquad \text{Eq. 22}$$

where ΔC_m and t_m are maximum ΔC and time of maximum ΔC, respectively.

In the simulation model, β is set to zero for Plot 23; $\beta = 0.1\ \Delta C$ for all other plots as they seldom reach dewpoint at night in summer. It then remains to provide a value of ΔC_m each day and to solve Eq. 21 and 22 for δ and γ.

The time course of ΔC as calculated from the model and from observed humidity data taken on Plot 3, 15 July 1970 is compared in Figure 14.

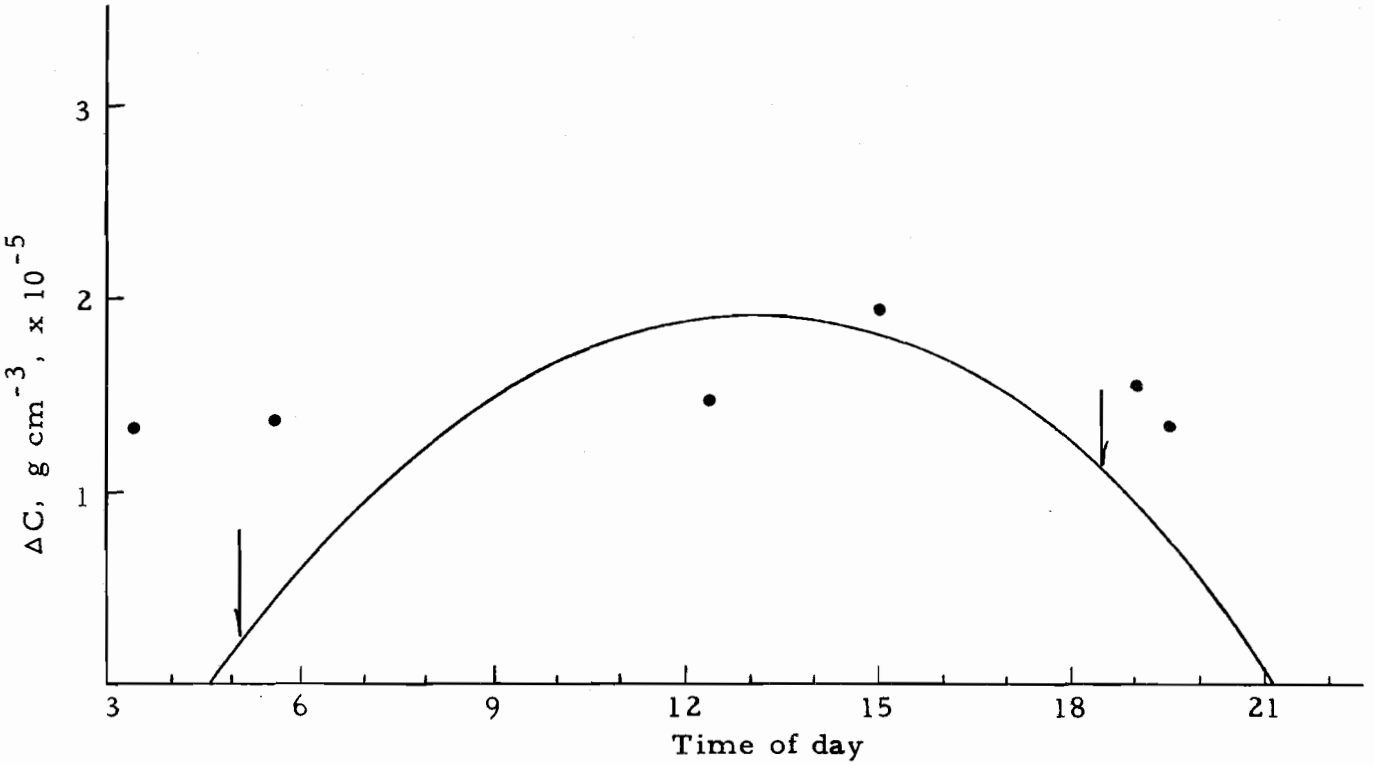

Figure 14. Vapor concentration deficit, ΔC, Plot 3 (oak type), 15 July 1970. Points represent measured ΔC, curve from Eq. 20, in text. Arrows represent sunrise and sunset respectively. (Example of greatest deviation from model.)

Derivation of the Stomatal Resistance Model

In order to solve Eq. 19, it is necessary to express stomatal resistance as a function of time. The field observations of stomatal behavior suggest that stomatal behavior can be modeled as increasing linearly with respect to time. By assuming that the time of maximum aperture is immediately after sunrise, stomatal infiltration pressure can be expressed as:

$$INF = INF_0 + \alpha t \qquad \text{Eq. 23}$$

where α = the change in infiltration pressure per second. By converting the rates of stomatal change listed in Table 6 (atm hr^{-1}) to atm sec^{-1} (letting ψ = PPMS), we have:[2]

$\alpha = 2.78 \times 10^{-7}$ atm sec^{-1} when $\psi \leq 5$ atm

$\alpha = 5.56 \times 10^{-6}$; $5 < \psi \leq 15$

$\alpha = 1.39 \times 10^{-5}$; $15 < \psi$.

The relation of stomatal resistance to INF is given by Eq. 15:

$$\log_{10} r_s = -0.088 + 1.39INF \qquad \text{Eq. 15}$$

letting X = INF and substituting Eq. 23 into Eq. 15, we have

$$\log_{10} r_s = -0.088 + 1.39X_0 + 1.39\alpha t \qquad \text{Eq. 23}$$

or

$$\log_{10} r_s = a' + b't \qquad \text{Eq. 24}$$

[2]The value given in Table 6 for $\psi < 5$ atm is .0075. Because this slope is nonsignificant, I used the value .001 in lieu of 0.0 because t appears alone in the denominator of the transpiration model.

where

$$a' = -.088 + 1.39X_0$$

$$b' = 1.39\alpha$$

converting Eq. 24 to natural logs,

$$\ln r_s = a + bt$$

where

$$a = 2.303\, a'$$

$$b = 2.303\, b'$$

taking the log of both sides

$$r_s = e^{a + bt} \qquad \text{Eq. 25}$$

or

$$r_s = e^{2.303[(-.088+1.39X_0) + 1.39\alpha t]}$$

Transpiration Model

By substituting Eq. 20 and 25 into Eq. 2 we get

$$\frac{dT}{dt} = (\beta + \gamma t - \delta t^2)\left(\frac{1}{e^{a+bt}} + \epsilon\right)$$

where

$$\epsilon = \frac{1}{r_c} = \frac{1}{150} = 6.67 \times 10^{-3}$$

By cross multiplying we have:

$$\frac{dT}{dt} = \frac{\beta}{e^{a+bt}} + \frac{\gamma t}{e^{a+bt}} - \frac{\delta t^2}{e^{a+bt}} + \epsilon\,\beta + \epsilon\,\gamma t - \epsilon\,\delta t^2$$

To solve:

$$\int_0^{\tau} d\tau = \frac{\beta}{e^a} \int_0^t e^{-bt} dt + \frac{\gamma}{e^a} \int_0^t te^{-bt} dt - \frac{\delta}{e^a} \int_0^t t^2 e^{-bt} + \ldots$$

$$+ \beta\epsilon \int_0^t dt + \epsilon\gamma \int_0^t tdt - \epsilon\delta \int_0^t t^2 dt \qquad \text{Eq. 26}$$

Integrating Eq. 26 we have

$$\tau = \frac{\beta}{e^a} A + \frac{\gamma}{e^a} B - \frac{\delta}{e^a} C + \epsilon\beta t + \frac{\epsilon\gamma t^2}{2} - \frac{\epsilon\delta t^3}{3} \qquad \text{Eq. 27}$$

where A, B, and C are the solutions to the respective integrals of Eq. 26:

$$A = \int_0^t e^{-bt} = \frac{1 - e^{-bt}}{b}$$

$$B = \int_0^t te^{-bt} = \frac{-e^{-bt}(bt+1)}{b^2} + \frac{1}{b^2}$$

$$C = \int_0^t t^2 e^{-bt} = \frac{e^{-bt}}{b^3} [b^2 t^2 - 2bt - 2] + \frac{2}{b^3}$$

Methods of solution of A, B, and C are presented in Appendix I.

Equation 27 is the model used in the program to calculate daily transpiration.

Potential transpiration is expected transpiration if the stomata remain fully open throughout the day. The model used for potential transpiration is:

$$\frac{dPTR}{dt} = (\beta + \gamma t - \delta t^2) \frac{1}{R}$$

where $R = 2 \text{ sec cm}^{-1}$, thus

$$\int_0^{PTR} PTR = .5 \int_0^t (\beta + \gamma t - \delta t^2) dt = .5[\beta t + \frac{1}{2} \gamma t^2 - \frac{1}{3} \delta t^3] \qquad \text{Eq. 28}$$

Other Models Used in Simulation

Generation of Plant Moisture Stress

The program simulates transpiration on a daily basis beginning 1 April. A value of pre-dawn plant moisture stress, PPMS, is generated each "day" for use in generating stomatal infiltration pressure, INF. PPMS is simply calculated from the appropriate equation obtained by fitting the model described on page 42(Eq. 5) to the PPMS data for each plot. A separate equation is used for each plot and year. The model used is

$$Y = \beta_1 + (\beta_2 - \beta_1) \exp(\beta_3 t) \qquad \text{Eq. 5}$$

The equations used in the simulation runs are listed in Table 8.

These equations represent idealized curves for PPMS and do not account for soil recharge due to rain. Minor soil recharge can occur in the summer in southern Oregon, introducing a small error in calculated PPMS. Considerably more error can be introduced when a severe late summer storm recharges the soil after a period of high drought. This could have the effect of reducing PPMS by ten or more

Table 8. Equations used to compute plant moisture stress (PMS) in the simulation runs.

Plot	Year	Equation
3 (oak type)	1968	$PMS = 2 + 3.04 \exp(0.0179t)$
	1969	$PMS = 2 + 0.70 \exp(0.0203t)$
	1970	$PMS_1 = 2 + 0.76 \exp(0.0225t)$ $t \leq 154$
	1970	$PMS_2 = 2 + 24.4 \exp(-0.045t)$ $t \geq 154$
1 (mixed conifer)	1968	$PMS = 2 + 1.52 \exp(0.0124t)$
	1969	$PMS = 2 + 0.285 \exp(0.0223t)$
	1970	$PMS_1 = 2 + 0.470 \exp(0.0214t)$ $t \leq 154$
	1970	$PMS_2 = 2 + 12.6 \exp(-0.045t)$ $t > 154$
8 (mixed conifer)	1968	$PMS = 2 + 3.68 \exp(0.0092t)$
	1969	$PMS = 2 + 0.47 \exp(0.0190t)$
	1970	$PMS_1 = 2 + 0.34 \exp(.0240t)$ $t \leq 154$
	1970	$PMS_2 = 2 + 14.5 \exp(-0.045t)$ $t > 154$
23 (Engelman spruce)	1968	$PMS = 2 + 1.31 \exp(0.0126t)$
	1969	$PMS = 2 + 0.10 \exp(0.0230t)$
	1970	$PMS_1 = 2 + 0.072 \exp(0.016t)$ $t \leq 154$
	1970	$PMS_2 = 2 + 8.7 \exp(-0.045t)$ $t > 154$

atm. Fortunately, such storms are exceedingly rare in the Siskiyou Mountains and did not occur during the period of my research.

The PPMS curves for 1970 differ from those of 1968 and 1969 because of the early arrival of fall rain and snow in the high elevations. Accordingly, a negative exponential decay model was used to compute PPMS after the first of September. It is not known how closely this model approximates the PPMS during the month of September because no data were available.

Generation of Stomatal Infiltration Pressure

As described in page 85, the minimum daily value of stomatal infiltration pressure, INF_0, is needed in the stomatal resistance model. Having generated PPMS, INF_0 is selected randomly from a Normal (μ, σ) distribution generated about the regression line described by Eq. 29 (this regression is discussed in detail in on page 80 and 81):

$$E(INF) = 0.40 + 0.033\ PPMS \qquad \text{Eq. 29}$$

Thus, Eq. 29 is the estimated value of μ, which had a standard deviation, s, of 0.1684. The procedure for selecting INF_0 is the same as that described in Section VI.

Generation of Vapor Pressure Deficit

Vapor pressure deficit is defined as $e_s - e_a$ where e_s is

saturation vapor pressure, in millibars, at a given temperature, and e_a is the vapor pressure of the air. Vapor pressure deficit, VPD, is an index of the evaporative potential of a water surface at the same temperature as the air. Thus, use of VPD as an index of potential transpiration can be a source of error if the leaf temperature is different from air temperature. Consequently, it is preferable to express the evaporative potential as vapor pressure gradient, VPG, where $VPG = e_{sl} - e_a$. E_{sl} is the saturation vapor pressure at the leaf temperature. However, it was not practical to model leaf temperature in this thesis, so I assumed that leaf temperature equals air temperature.

Because it was not possible to continuously record humidity on the research plots, it was necessary to use humidity data provided through the courtesy of the Rogue River National Forest, U.S. Forest Service. Three years of humidity data taken at 1300 (1:00 p.m.) during the months of June through September on the Ashland watershed were used to develop a model which could be used to generate VPD.

Because VPD is a function of temperature and vapor pressure, a regression analysis was run on the Forest Service data which provided an equation suitable for generating a value of VPD in the program. The regression model used was:

$$Y = \beta_0 + \beta_1 X + \beta_2 X^2 + \epsilon$$

where X is dry-bulb temperature and VPD is the corresponding value

of vapor pressure deficit calculated from the empirical data. The regression had an R^2 of 0.81 (the model accounts for 81% of the variance). The empirical data and the regression curve are illustrated in Figure 15.

Given the regression equation (Eq. 30), VPD was generated by the same procedure used to generate INF_0, where VPD_m is selected from a Normal (μ, σ) distribution, where μ is estimated by Eq. 30:

$$\mu \doteq E(VPD)_m = 0.484 + 0.020X + 0.031X^2 \qquad \text{Eq. 30}$$

and σ is estimated by the regression standard deviation, s = 3.254. In the program, $X = T_{max}$, the maximum temperature. This is reasonable because the empirical data were gathered at 1300 hours, which corresponds to the usual time of maximum temperature. Therefore, VPD_m as generated is assumed to be the maximum VPD.

VPD is then converted to ΔC_m, the maximum vapor concentration difference between the leaf and air by means of Eq. 14 (page 63).

Summary of the Simulation Model

The model is written in FORTRAN IV to simulate transpiration on a daily basis for a specified number of days. Version 2 generates a value of maximum temperature based on a probabilistic model, Version 3 reads actual temperature data obtained from thermograph records. The program counts the "days" and calculates a value of

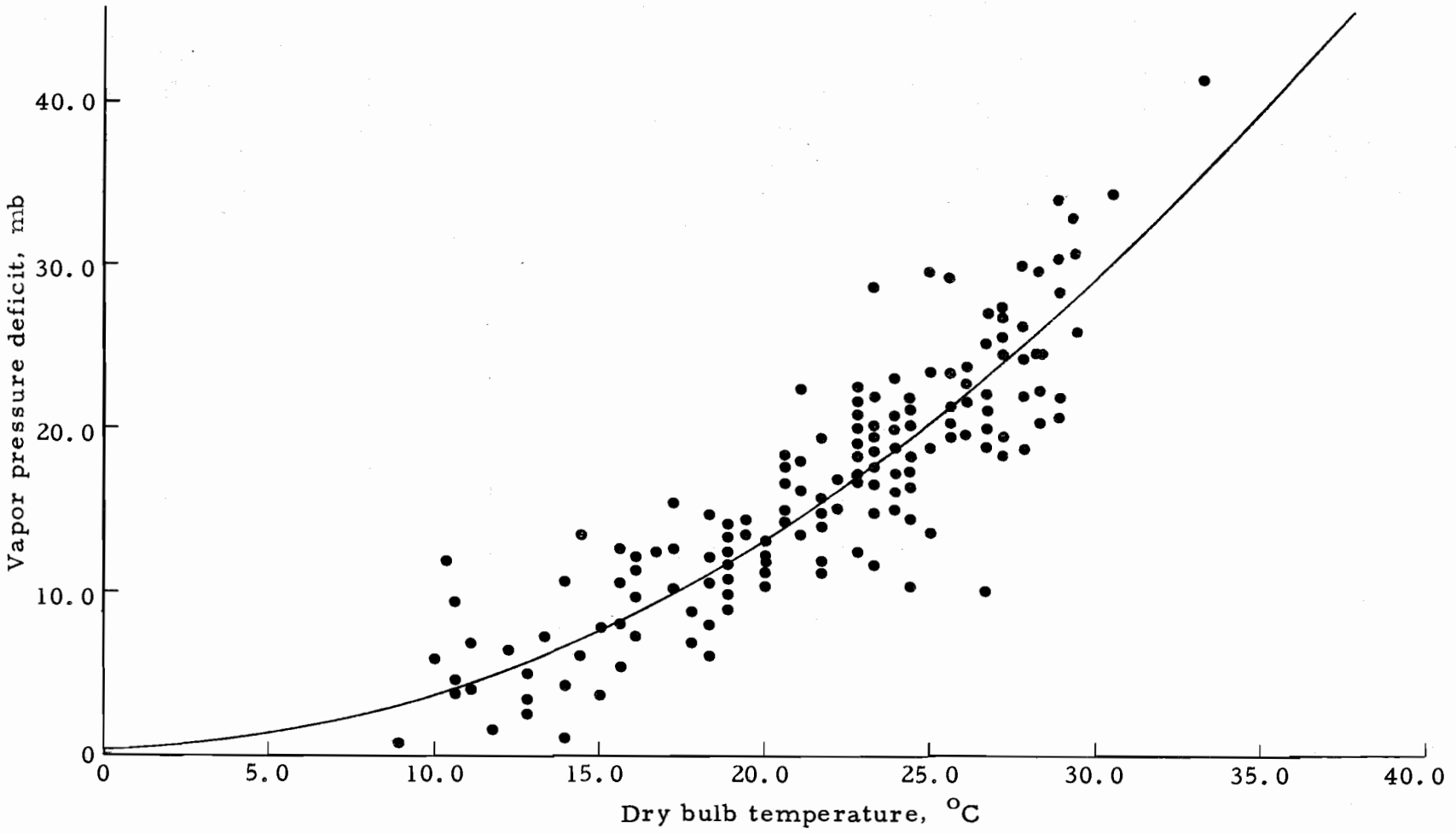

Figure 15. Vapor pressure deficit, VPD, as function of dry bulb temperature, TDB, in °C. Equation of curve: $Y = 0.484 + 0.020X + 0.031X^2$. Data from Ashland watershed, 1969, 1970.

pre-dawn plant moisture stress, PPMS, from one of the equations listed in Table 8.

Having calculated PPMS, the program next generates INF_0 which is used as a constant in the stomatal resistance model, Eq. 25. Given a temperature value, either by simulation or by reading the appropriate value produced, VPD_m, maximum vapor pressure deficit is generated. This value is converted to AC_m which is used to calculate the constants in Eq. 20.

The values of the variables needed to solve Eq. 27 have now been generated. The program then computes daily transpiration by solving Eq. 27, daily potential transpiration by solving Eq. 28, and the difference between the two. These data are stored in memory and are printed out at the end of each "month." After Eqs. 27 and 28 are solved, the algorithm is repeated for each day of the simulation. At the end of the specified time period, the algorithm is terminated.

Results of Simulations

Transpiration (TR) and potential transpiration (PTR) for the six-month period beginning 1 April was simulated by Version 3.5 of the simulation program. Data from thermograph records taken during the years of 1968 and 1970 were used as input. The simulated output is exemplified in Figures 16 and 17. The broken line represents PTR; the solid line, TR; the triangles represent Plot 3 (oak type) and circles

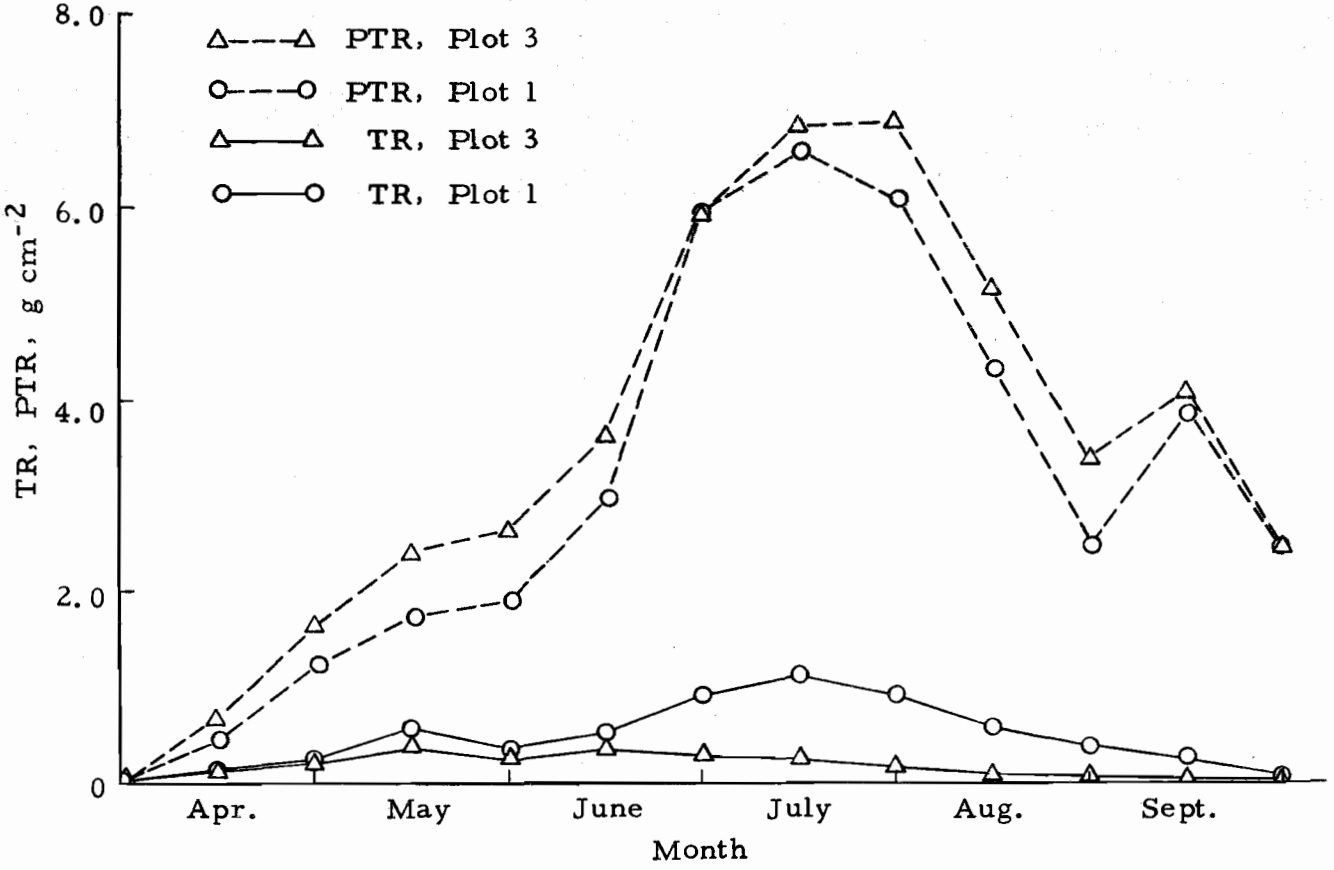

Figure 16. Potential, PTR, and "actual" transpiration, TR, simulated for Plots 1 and 3 (mixed conifer and oak type, respectively), 1968.

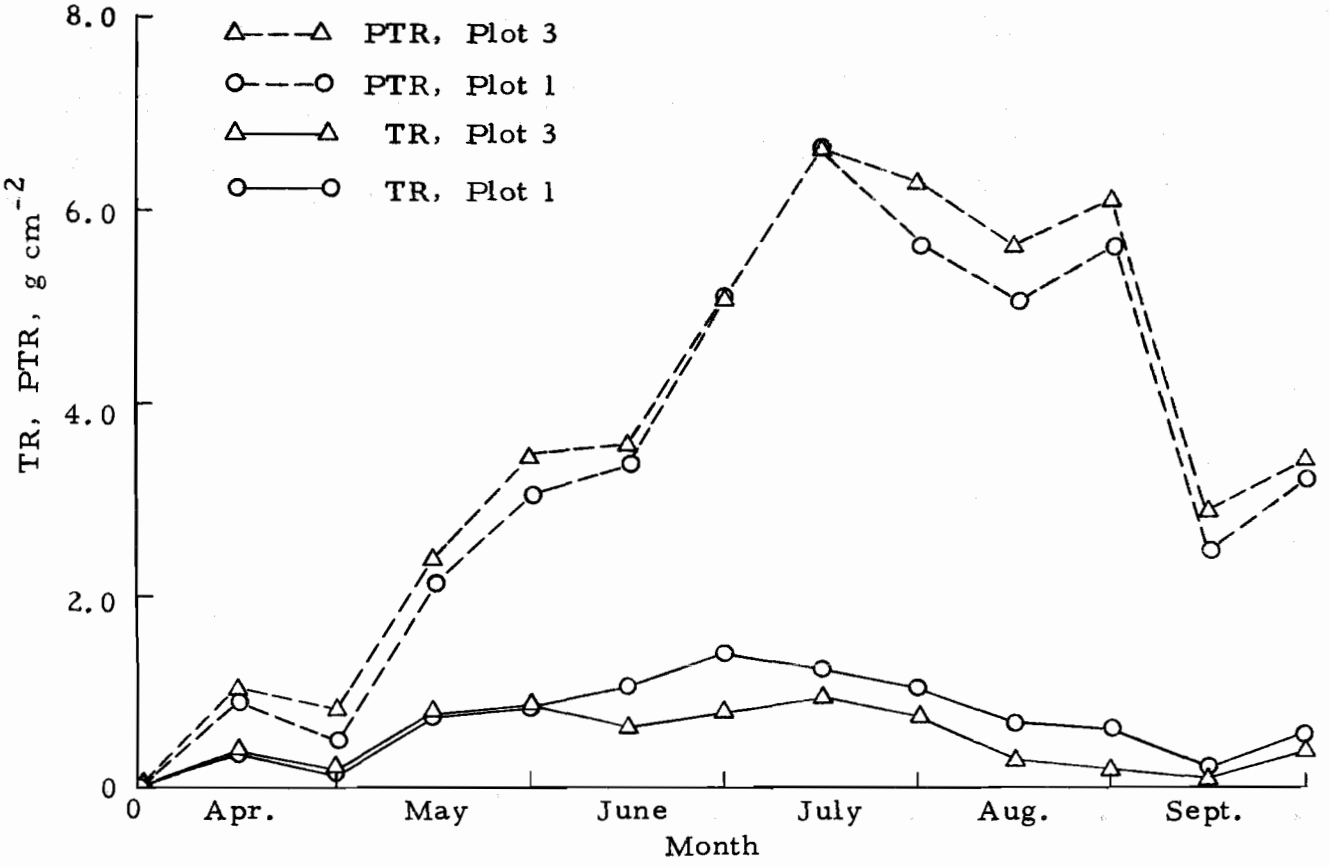

Figure 17. Potential, PTR, and "actual" transpiration, TR, simulated for Plots 1 and 3 (mixed conifer and oak type, respectively), 1970.

represent Plot 1 (mixed conifer). The data plotted in Figures 16 and 17 are from 1968 and 1970, respectively.

The difference between potential transpiration and "actual" transpiration is quite striking, particularly from June through September. These data illustrate the effect of stomatal control on transpiration and the relative importance of the two components of the transpiration model, the atmospheric demand and the plant resistance.

Two important facts are illustrated in Figures 16 and 17: (1) transpiration rates in the spring are limited primarily by the weather. The cool wet weather in the spring results in a low evaporative demand, hence low transpiration rates. It is at this time when plant growth and transpiration rate may not be correlated, because it is possible that photosynthesis may be near optimum at this time. However, the complex interaction between growth and photosynthesis is not fully understood so a correlation between photosynthesis and growth may also be nonsignificant. (2) Transpiration is limited by plant resistance in late summer, and is in the case of Plot 3, 1968, lower than spring transpiration even though the demand is three times as great (Figure 16, Plot 3).

Cumulative transpiration for the four plots during 1968 and 1970 is illustrated in Figures 18 and 19. The difference between the two years is striking: Seasonal cumulative transpiration on Plot 3 (oak

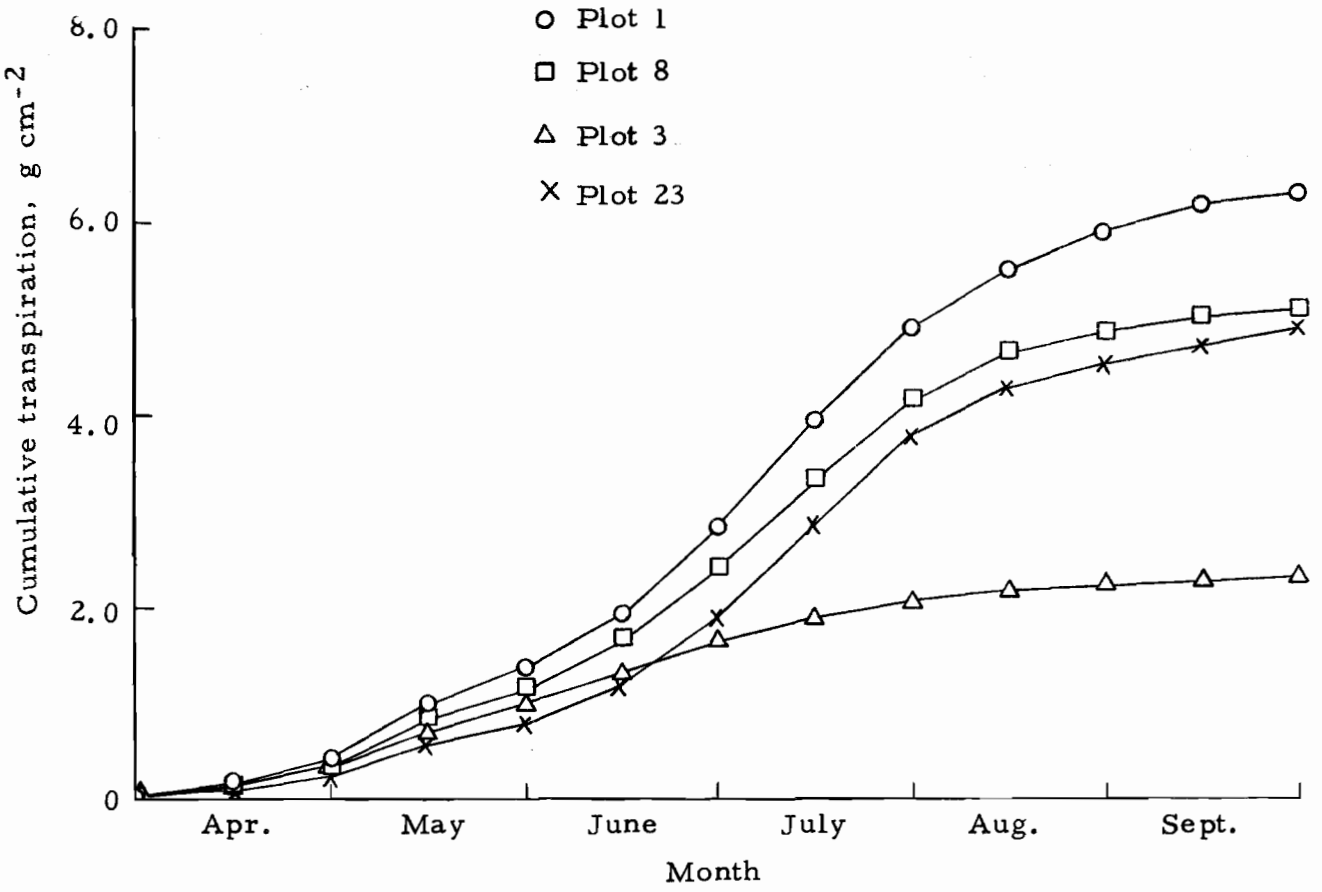

Figure 18. Simulated cumulative transpiration data for all plots on Mt. Ashland, 1968.

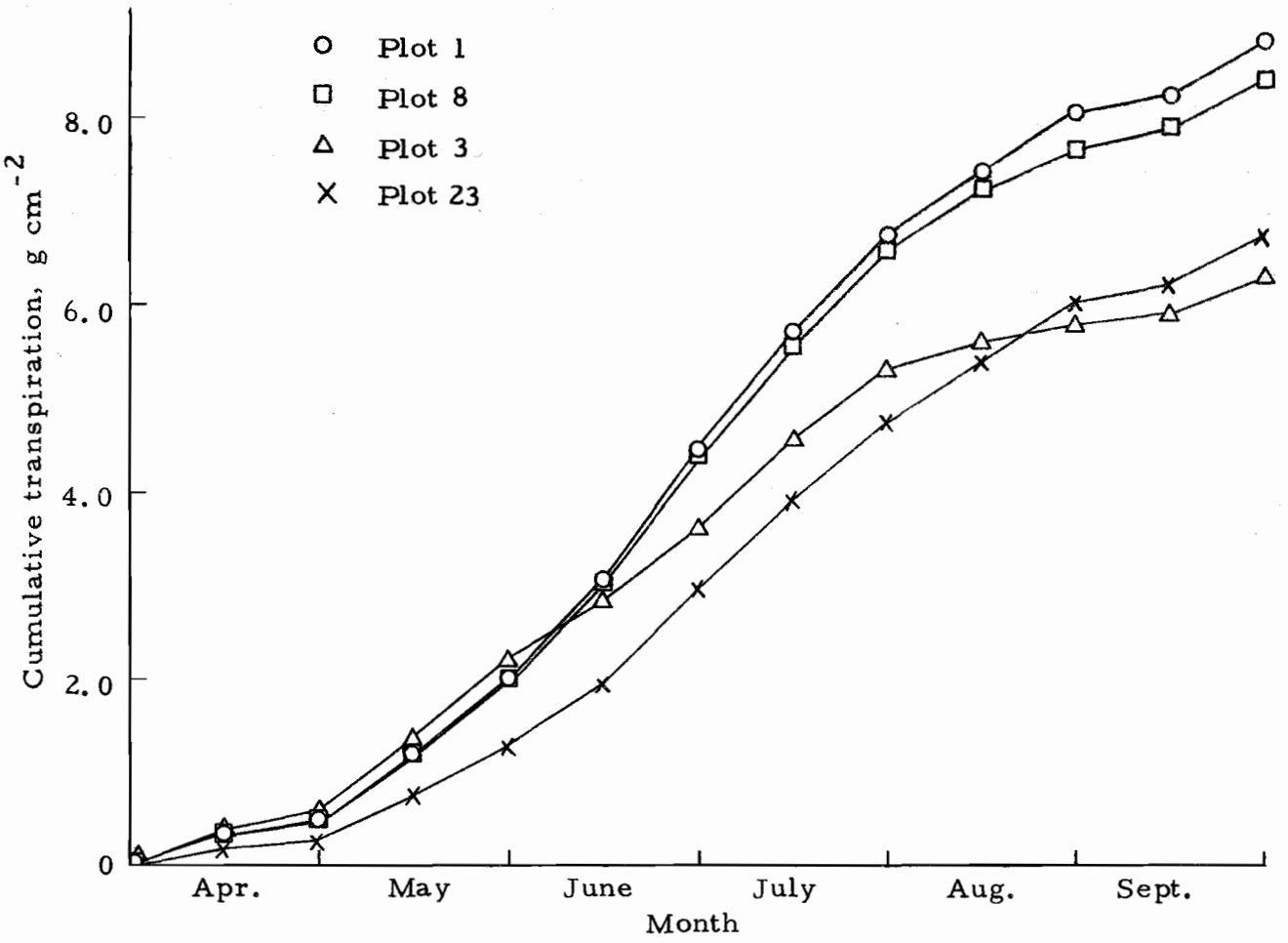

Figure 19. Simulated cumulative transpiration data for all plots on Mt. Ashland, 1970.

type) is only 1/3 that of 1970! The difference between the two years is less on other plots, but transpiration was considerably reduced on all plots in 1968. There could be three hypotheses explaining this difference: (1) 1968 was much cooler and wetter than 1970, thus reducing transpiration demand, (2) the plant resistance was greater in 1968 than 1970, which implies that stomatal resistance was greater, or (3) a combination of both.

The atmospheric demands can be assessed by examination of potential transpiration, PTR. From the data presented in Figures 16 and 17, it can be seen that PTR for the two years was not greatly different, which eliminates (1). The difference between the atmospheric demand for transpiration, PTR, and "actual" transpiration, TR, provides an index as to the environmental demand and the plant's response to the demand. Because PTR was not greatly different between the two years and TR in 1968 was much less, the difference must be the result of greater stomatal resistance in 1968. This difference becomes apparent when TR is divided by PTR.

The ratio ΔTR, or transpiration deficit (analogous to vapor pressure deficit), reflects the relative importance of the two major forces controlling plant transpiration: atmospheric demand and plant resistance. A ratio approaching unity reflects low demand or low resistance, or both; a ratio near zero indicates that plant resistance is the limiting factor. Thus, ΔTR, used in association with PTR,

Table 9. Monthly and seasonal totals of TR, PTR and ΔTR, 1968 and 1970. Units: g cm^{-2}.

		1968				1970			
		Plot				Plot			
		3	1	8	23	3	1	8	23
April	TR	.59	.91	.61	.74	.58	.46	.47	.28
	PTR	3.60	2.95	3.84	2.23	1.86	1.32	1.35	.84
	ΔTR	.164	.308	.159	.332	.312	.348	.348	.333
May	TR	.64	.95	.78	.54	1.64	1.54	1.48	.99
	PTR	5.03	3.56	5.46	1.85	5.84	5.08	4.80	3.37
	ΔTR	1.27	.267	.143	.292	.281	.303	.308	.294
June	TR	.66	1.46	1.25	1.09	1.40	2.47	2.40	1.69
	PTR	9.52	8.86	10.6	6.14	8.63	8.37	7.76	5.68
	ΔTR	.069	.165	.118	.178	.162	.295	.309	.298
July	TR	.43	2.07	1.74	1.89	1.69	2.28	2.16	1.78
	PTR	13.7	12.6	15.5	11.0	13.0	12.2	11.4	9.08
	ΔTR	.031	.164	.112	.172	.130	.187	.189	.196
Aug.	TR	.15	1.00	.70	.75	.50	1.30	1.13	1.28
	PTR	8.50	6.73	8.97	4.71	11.7	10.6	9.90	8.10
	ΔTR	.018	.148	.078	.159	.043	.123	.114	.158
Sept.	TR	.089	.41	.24	.37	.49	.79	.72	.74
	PTR	6.53	6.22	7.31	4.58	6.31	5.62	5.70	3.81
	ΔTR	.014	.066	.033	.081	.078	.141	.126	.194
Seasonal									
	TR	2.30	6.29	5.06	4.89	6.30	8.83	8.36	6.76
	PTR	45.7	39.5	50.5	29.2	47.3	43.2	40.9	30.9
	ΔTR	.050	.159	.100	.167	.133	.204	.204	.218

provides an excellent means of assessing atmospheric demand and plant capability to respond in a given ecosystem or time period. ΔTR for Plot 3 (oak type), 1968 and 1970, is illustrated in Figure 20. Note that ΔTR drops considerably as the dry season progresses indicating progressively increasing drought.

The use of this simulation model as a means of comparing ecosystems and years in terms of transpiration and demand is illustrated in Table 9 where TR, PTR, and ΔTR for the four study plots in 1968 and 1970 are compared. The ranking of the plots according to PTR and ΔTR from Table 9 is depicted in Table 10.

The relative ranking of Plot 8 (Ponderosa pine, Douglas-fir) changes from 1968 to 1970; this was totally unexpected and would suggest that climatic gradients can change from year to year. However, the 1970 ranking of Plot 8 is probably due to instrument error because the relative rankings of 1968 are supported by supplemental simulation runs based on 1966 temperature data.

Table 10. Ranking of the plots in terms of PTR and ΔTR.

Rank	1968		1970		1966	
	PTR	ΔTR	PTR	ΔTR	PTR	ΔTR
1	8	23	3	23	8	23
2	3	1	1	1, 8	3	1
3	1	8	8		1	8
4	23	3	23	3	23	3

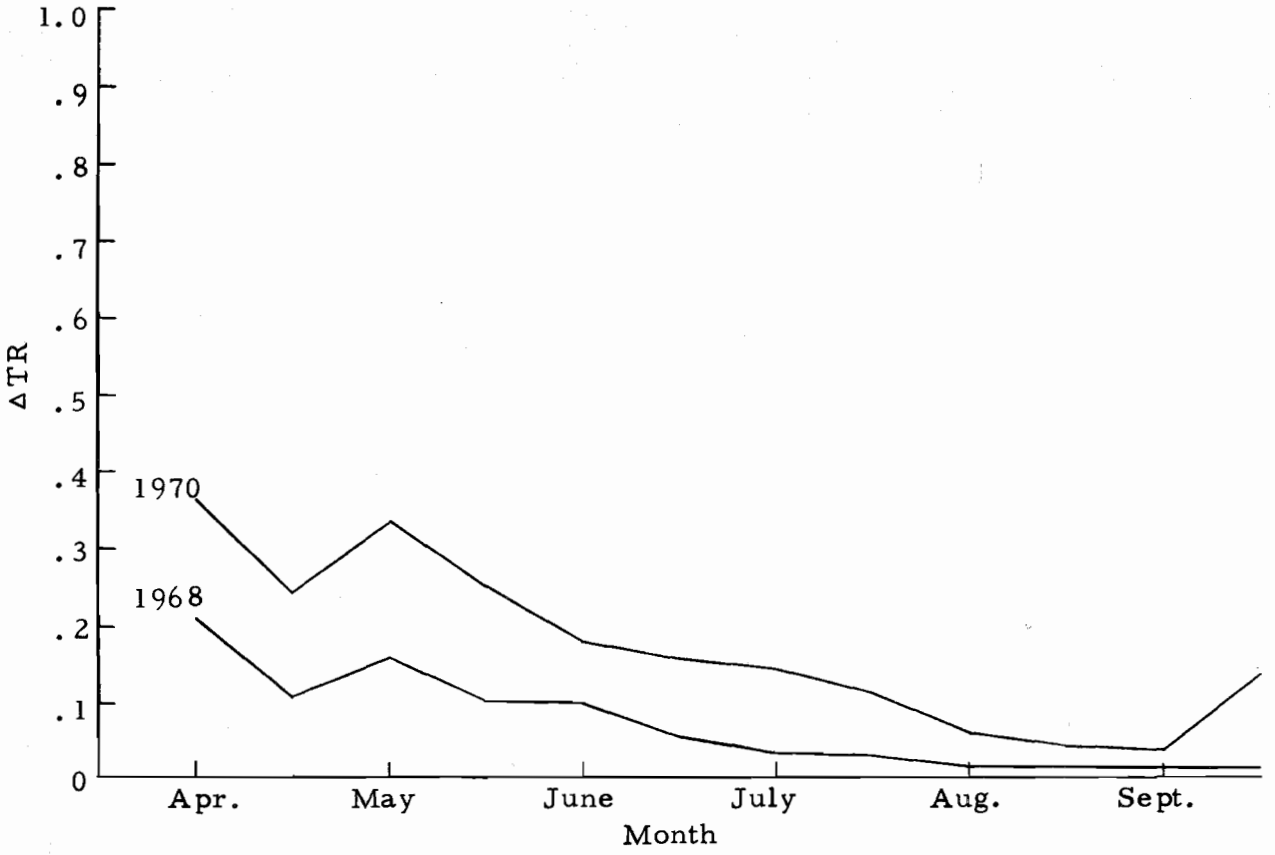

Figure 20. Simulated transpiration deficit, ΔTR, Plot 3, 1968 and 1970.

VIII. DISCUSSION

Discussion of the Models Used

There are several models used in the simulator which could be improved. These improvements would, for the most part, consist of refinements of the models themselves to better reflect nature, and could be made pending acquisition of more data.

Temperature

Temperature was modeled in a most simplistic manner: only the maximum daily temperature was used in the simulations. Leaf temperature was not modeled because of the highly complex nature of models predicting leaf temperature (e. g., Gates, 1968), and because of the enormous variation in leaf temperature in the field due to irregular occurrence of sunflecks, changing wind velocities, different transpiration rates at different times of year, etc. Thus, a seasonal transpiration simulation model of sufficient resolution to require a model of leaf temperature would in all probability be impractical for general ecological use. The data required to develop the model, and the extreme complexity of the model itself would preclude its general application.

In other simulation models, such as a model of photosynthesis, it would be necessary to model diurnal temperature patterns. This

could be done by means of a sinewave function or as a quadratic function.

Vapor Pressure

Because vapor pressure deficit, hence vapor concentration deficit (ΔC) is a function of temperature and the amount of water vapor in the air, the random generation of VPD from the regression depicted in Figure 15 gave reasonable values of maximum VPD. However, the model has several shortcomings. It is assumed throughout that the general shape of the diurnal course of ΔC is similar to that of Figure 14 regardless of magnitude of maximum ΔC, and does not take temperature fluctuations into account.

A second limitation of the model lies in its empirical nature: the prediction of maximum ΔC was based on a regression model of humidity data gathered in the area. Nothing is known about the accuracy of the measurements, and the validity of extrapolating the regression equation from the point of measurement to the study plots has not been established. Thus, microsite differences in VPD can only be predicted from differences in temperature, when using this model.

It is possible that, for the most part, atmospheric vapor concentration along an altitudinal transect of a forested mountain does not vary greatly; therefore, differences in vapor concentration deficit

would largely result from temperature differences. In any case, direct measurement of humidity data on the plots would be preferable, if possible.

Plant Moisture Stress

The functions used for generation of plant moisture stress values within the program were site specific. Pre-dawn PMS data are required which involves some effort on the part of the researcher. Further, these data may not always fit some simple function; it may be necessary to describe the curve in a numerical manner, or to break the data into segments which can be mathematically described. The use of plant moisture stress instead of soil moisture or some other variable, however, is simpler and more direct than trying to couple plant water potential to soil moisture. All of the factors affecting uptake of water are incorporated in the value of pre-dawn PMS. Kramer (1963) pointed out that the relation between soil moisture stress and plant moisture stress is not an exact one; therefore, it is important to measure and model plant moisture stress directly if one is attempting to model a plant process.

There is considerable variance about the smooth curves used in this model. It would be desirable to have more data in order to determine whether this variance is random. Further, brief summer showers may temporarily depress PPMS; summer storms may have a

profound effect. This is seldom a problem in the Siskiyou study area, but would have to be considered for a model in other areas. Even the rains of August 1968 seemed to have had little long term effect on the PMS of the plants because the coarse granitic soils have low water holding capacity. The principal effect seems to have been a reduction in transpirational demand.

Stomatal Behavior

Stomatal behavior was modeled much as it was observed, except that nocturnal stomatal behavior was ignored. Thus, stomatal behavior was modeled as if the stomata were opened to the maximum aperture at sunrise, then began to close at a rate determined by the extent of plant water stress. Even in cases where the stomata were open at night, as in the spring, the error would be small because the vapor pressure deficit approaches zero. In the Siskiyou study area, during the period when nocturnal vapor pressure deficit is not low (e.g., late summer), the stomata of all the coniferous species in that locale remain closed throughout the night. Therefore, in either event, nocturnal transpiration would be negligible.

These observations of stomatal behavior are being corroborated by work now in progress in the Willamette Valley and the western Cascade Mountains (William Emmingham, personal communication).

The evidence that K^+ plays an important role in light induced

stomatal movement (Humble and Hsiao, 1969; Sawhney and Zelitch, 1969) could account for some of the difference between nocturnal stomatal behavior in the spring and summer. It is possible that high soil water availability coupled with high K^+ demand in expanding foliage results in a loss of stomatal control. Observations of nocturnal stomatal behavior in the Siskiyou study areas by Waring and Emmingham indicate that the stomata were remaining open at night through July in 1971. This was associated with an abnormally late spring and delayed budburst. These observations suggest that stomatal behavior may well be coupled with phenology, and suggests a new avenue of research in the study of stomatal behavior.

Applications of the Model

Although this model does couple environment to a plant process, it is admittedly of coarse resolution. Much of the variance was simply allowed to fall into the residuals with no attempt to isolate other factors which could account for a greater percentage of the variance. Nevertheless, this greatly simplifies the model. Such a model permits us to better understand the major operating variables and to focus upon a minimum of essential data.

This simulation also provides new indices of plant and environmental variables and suggests better means of relating environmental variables to differences in species composition and growth. Indices

of environment such as altitude, slope, aspect, latitude, mean summer temperature, temperature days, etc. have very little information about the actual environment sensed by the plant and are almost impossible to model in a realistic manner.

Transpiration demand (PTR), actual transpiration (TR), transpiration deficit (ΔTR), and another index I have termed Stress Index (SI, the integral of the PPMS function) provide far more information about the plant's operational environment than any other indices available, a goal identified as paramount in the ecological literature (Mason and Langenheim, 1954; Waring and Major, 1964).

The stress index (SI, moisture stress index) is obtained by integrating the functions of PPMS over time.

This integral could be used as a moisture stress index, which should have wider application than end of season PPMS used by Waring (1969). This would be particularly true if there were great variation in the seasonal moisture stress curves (here the integral would have to be approximated by a summation).

The functions of PPMS fitted in this simulation are of the form

$$Y = \beta_1 + (\beta_2 - \beta_1)^{\beta_3 t} \qquad \text{Eq. 26}$$

This function can be re-parameterized to

$$Y = a + be^{ct} \qquad \text{Eq. 27}$$

Integrating this function over time gives the stress index, SI:

$$SI = \int_0^t (a + b\, e^{ct})dt \qquad \text{Eq. 28}$$

Letting $x = ct$, then $dx = cdt$, implying that $dt = \frac{dx}{c}$,

$$SI = \int_0^t a\,dt + \frac{b}{c} \int_0^x e^x dx$$

$$SI = at + \frac{b}{c}(e^x - 1) \qquad \text{Eq. 29}$$

Substituting the original parameters of Eq. 26 into Eq. 29, we get

$$SI = \beta_1 t + \frac{(\beta_2 - \beta_1)}{\beta_3}(e^{\beta_3 t} - 1) \qquad \text{Eq. 30}$$

In the last part of the 1970 simulation it is necessary to integrate between the limits of 0 to 153 according to Eq. 30 (Figure 22) and from 154 to 183 according to Eq. 31:

$$SI = \beta_1 t + \frac{(\beta_2 - \beta_1)}{\beta_3}(1 - e^{-\beta_3 t}) \qquad \text{Eq. 31}$$

setting day 154 to zero, and 183 to 29 (i.e., integrating between the limits of 0 and 29). The stress index (SI) was evaluated for the years 1968-1970 (Table 12). Figures 21 and 22 illustrate the PMS curves used for plots 1 and 3, 1968 and 1970.

According to the data in Table 12, the stress index (SI) for Plot 3, 1968, was 1.9 times as great as SI for 1970. This difference can be attributed to a hot, dry early spring (Table 10) in 1968 and to the difference in snowpack during the preceding winter (Table 13) of

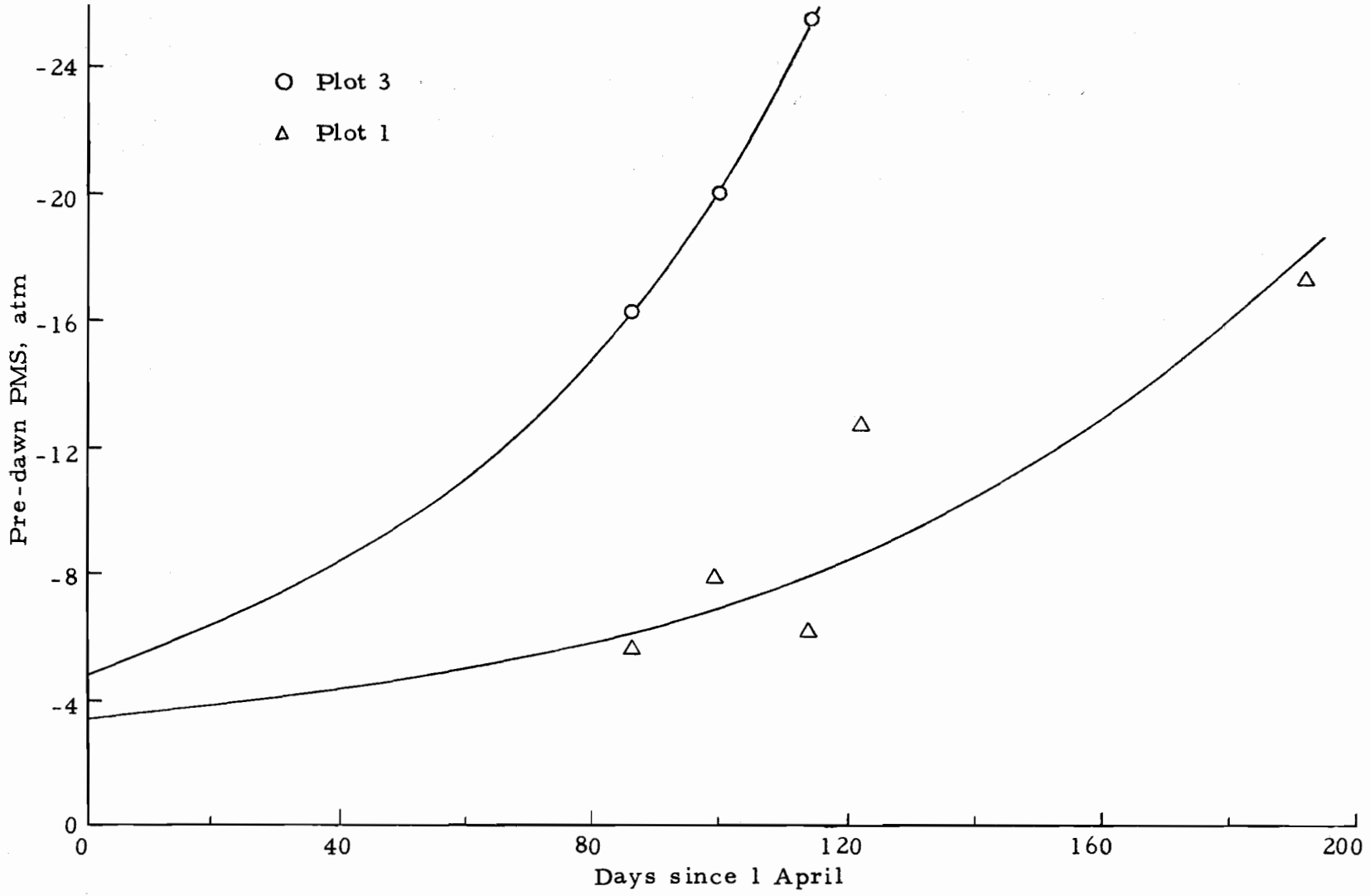

Figure 21. 1968 Pre-dawn xylem water potential (PPMS) of Plots 1 (mixed conifer type) and 3 (oak type) as a function of time.

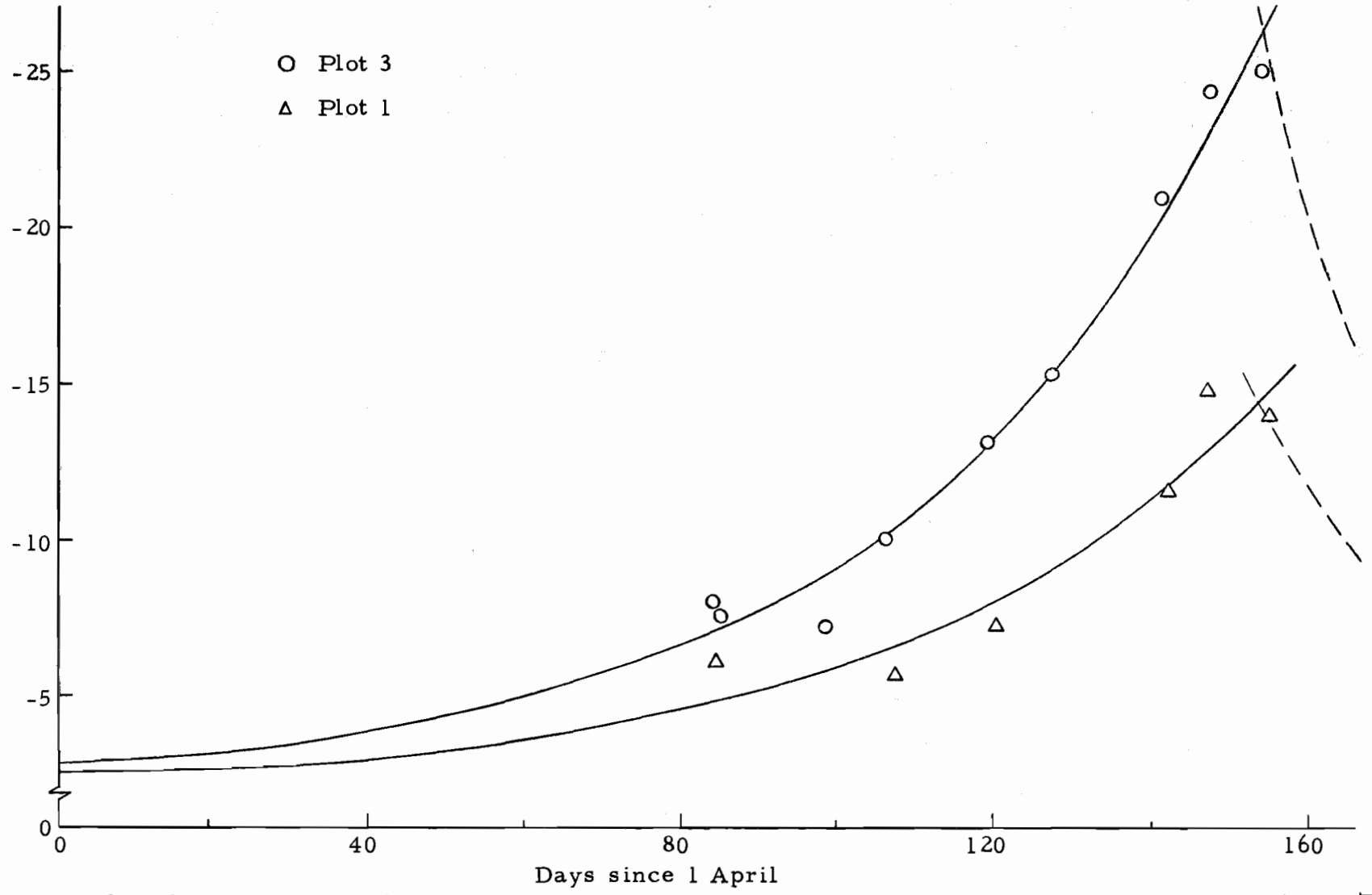

Figure 22. 1970 Pre-dawn xylem water potential (PPMS) of Plots 1 (mixed conifer type) and 3 (oak type) as a function of time.

1968 and 1970. This demonstrates how data in the form of Tables 9, 11 and 12 can be used to quantify a climatic-plant interrelation over various time intervals. Because plant responses are included in the indices, this approach could be very useful in plant ecology.

Use of this model coupled with a simulation of photosynthesis in the field could provide a great deal of useful information. Indeed, such data could be used in attempts to model growth as a function of the environment, and to ascertain the "biologic potential" of a given ecosystem. Because this model requires relatively modest data acquisition, it could be applied to different locales with a minimum of field study.

Development of a model for photosynthesis would require in addition to the transpiration simulation, a model of incident solar energy (400-700 nm band), a model of diurnal temperature, and a model of photosynthesis as a function of light, temperature, and the plant's resistances to CO_2 flux.

This latter model could be adapted from that developed by Webb (1971), who studied the CO_2 assimilation of red alder (Alnus rubra) in a specially constructed growth chamber. Beginning with the basic model

$$N.A._{CO_2} = F\ (\text{temp, light}) \qquad \text{Eq. 32}$$

he was able to develop a multiple non-linear regression model of the form

Table 11. Moisture stress index for Plots 3-23 on Mt. Ashland. Units are atm day.

Year	Plot number			
	3	1	8	23
1968	3414	1430	2114	1309
1969	1740	1109	1149	655
1970	1814	1144	1338	989

Table 12. February snow survey data, Mt. Ashland (U.S. Forest Service, Rogue River National Forest).

Date	Average snow depth (cm)	Average water content (cm)	Average density (%)
2-24-67	175	62	35.7
3- 1-68	137	59	42.8
2-27-69	279	93	33.0
3- 1-70	195	58	29.2

$$N.A. = \beta_0 + \beta_1 T + \left\{\beta_2 + \beta_3[(T - \beta_4)^2][1 - e^{\beta_5 L}]\right\} \qquad \text{Eq. 33}$$

which follows from Eq. 32 given Webb's derivation. The parameters in this model were estimated from empirical data using a non-linear regression program.

Webb's data were obtained from alder growing in a nutrient solution; the stomata were probably wide open throughout the course of the experiments. In order to use a model of this sort, it would be necessary to estimate the parameters for Douglas-fir, and to include a term accounting for stomatal resistance. Webb's model (represented as F(T, L) could easily be expanded by adding a term accounting for stomatal resistance and CO_2 concentration:

$$N.A. = \frac{F(T, L)\, H(CO_2)}{g(r_s)} \qquad \text{Eq. 34}$$

which follows from

$$\text{Net } CO_2 \text{ uptake} = \frac{C_{air} - C_{chl}}{\Sigma R} \qquad \text{Eq. 35}$$

where

C_{air} = concentration of CO_2 in the air

C_{chl} = concentration of CO_2 at the photosynthesizing surface

ΣR = sum of resistances to CO_2 flux

This equation is from Rabinowitch (1951) and Gaastra (1959).

Such a simulation model of photosynthesis and transpiration in one species could be used only as an index to environment and possibly

growth, but as such, it could provide considerable insight into the biologic potential of an ecosystem by evaluating the environment throughout the year.

The problem of coupling the processes of transpiration and photosynthesis to growth could be approached through simulation. Measurements of growth (as in Table 3) could be correlated with simulated transpiration and photosynthesis. Leader elongation in 1969 after the severe summer of 1968 was as little as 1/2 that of 1970. Because of the late spring in 1971, leader elongation data could not be obtained in time for inclusion in this thesis, but measurements in July, 1971 indicated that leader growth would be greater in 1971 than in 1970. These rates of leader elongation reflect the effects of weather during the current and preceding year. Therefore, a realistic simulation model of plant transpiration and photosynthesis could be extremely useful in interpretation of weather influences on plant growth and distribution.

By evaluating the environment throughout the year, a model could be developed which accounts for the coupling of the plant to its environment and makes predictions concerning plant growth and distribution. That is, the ecologist could classify the environment in terms of factors which are important to the plants, not simply conveniently measured arbitrary factors.

A system of environmental classification using a model of

transpiration and photosynthesis stems from the idea that plants sense five essential environmental factors: light, temperature, moisture, nutrition, and physical stress. These factors could be indexed in the following manner:

I. The environmental classification:

   a. Moisture availability, and temperature as a factor in transpiration would be indexed by ΔTR and PTR (transpiration deficit and potential transpiration) from a simulated model.

   b. Temperature as it affects growth would be indexed by the temperature index used by Cleary and Waring (1967).

   c. Nutrient levels could be assessed by measurements of certain nutrients as critical times of the year (Waring, personal communication).

   d. Mechanical stress could be assessed by an index of snowpack or animal browsing.

   e. Light index would result from output of photosynthesis simulation model.

II. Uses of the environmental classification system.

   a. The tolerance of various plant species could be defined in terms of the classification system outlined above. A system could be developed where an ecosystem could be

classified according to the presence of species of known tolerance to the above factors (after Waring, 1969).

b. The system could be used in the development of a growth model based on the plant responses to the environment described by the system above. This would probably be confined to a site-index type model for the present.

c. Ecosystems can be classified in the manner suggested above, then they could be compared one with another in an objective manner. Differences in growth, vegetation associations, and genotype could be related to the environment and these differences could be expressed in a meaningful manner.

d. Low resolution models of the type suggested above requiring little input of data could be of use in ecosystem modeling attempts by the International Biological Program, pending the development of more sophisticated models.

Some Examples of Use of the Environmental Classification System Based on the Simulation Model

The effects of various forestry practices on the environment can be assessed in terms of the changes in photosynthetic and transpiration potential, etc. These assessments can be used to predict the effects of clearcutting or a given degree of select cutting on the plant

community, and could be used as a guide in management decisions.

Similarly, the effects of extended periods of smoke, haze, and other atmospheric contaminants on forest ecosystems could be studied by comparison of homologous sites, one existing in an area of atmospheric pollution, the other in cleaner air. Having used the classification model to assess the similarities of the two ecosystems, differences as a response to the atmospheric contamination could be observable.

If the system were being used to classify an ecosystem where Douglas-fir does not grow, the system might have to be recalibrated for the dominant species if the environment is such that the model with respect to Douglas-fir is not sufficiently sensitive to resolve differences in climate, e.g., in the juniper dominated area of central Oregon. Likewise, the model may not be applicable for a deciduous forest in the east. However, as an index to environment, the differences between the eastern deciduous forests and the western coniferous forests could be assessed in terms of the model based on Douglas-fir response, even though the model would be inadequate for explaining species distribution in the eastern forests.

An estimation of total transpiration of a forest stand could be made by incorporation of a leaf area index, and some refinements in the model.

In conclusion, the uses of the environmental classification model could at last provide the plant ecologist with a means of

answering some of the questions asked by ecologists for many years, e.g., how can ecosystems be compared directly, in what way do plants respond to environment, and what could be expected following a perturbation of the ecosystem.

The system could prove to be very useful in forest management decisions, because an objective means of assessing the effects of the various logging practices and providing a predictive tool for reforestation has long been needed. If the range of tolerances of various sensitive species are known for the five indices in the model, the vegetational associations in the field could be assessed by foresters who could then use the model to make more valid inferences about the environment. These inferences could then be used as an aid in timber harvesting decisions.

Thus, the model has both practical and theoretical utility, and constitutes a potentially useful tool in plant ecology.

Validation of the Model

The accuracy of the model in predicting transpiration is not known. The data are reasonable, but no observations of transpiration were made during the research. As a means of checking the general plausability of the results, the highest rate of transpiration observed in the laboratory studies was extrapolated to give an estimate of seasonal transpiration comparable to transpiration observed in the

field. Transpiration rates observed in the laboratory were under conditions of modest atmospheric demand, but stomatal resistance was very low. The highest laboratory rate was 14.6×10^{-7} g cm^{-2} sec^{-1}. Multiplied by the number of seconds in 183 14-hour days gives a total of 13.4 g cm^{-2}. The greatest value obtained in the simulation was approximately 9 g cm^{-2}. Therefore, the simulated transpiration values are reasonable. The accuracy of the simulation is not known at this time. Some of the error in the model is random, e.g., error caused by changes in boundary layer resistance which was not estimated, but some of the error is probably due to bias. The magnitude and direction of the error cannot be assessed without comparison with actual data. However, it is believed that the error is acceptable within the objectives of the modeling effort. Further refinement is possible pending acquisition of additional data.

Recommendations for attempts to use the model would include bi-weekly measurement of plant moisture stress, and continuous measurements of temperature and humidity (if possible). In this way, some error due to inaccuracy of the models of PPMS and VPD could be reduced.

IX. CONCLUSIONS

1. Plant moisture stress of Douglas-fir, measured before dawn, increased progressively throughout the growing season, which could be described by an exponential function.
2. The stomata of Douglas-fir were open at night in the spring, but were fully closed at night during the months of July through September. Stomatal opening during the summer months was triggered only by actual sunrise--the pre-dawn diffuse light had no effect.
3. After sunrise, stomata tended to open to some maximum value after which stomatal aperture would remain at that value or would close to a greater or lesser extent. This behavior was apparently related to pre-dawn plant moisture stress and other factors.
4. The maximum diurnal stomatal aperture was found to be correlated with pre-dawn plant moisture stress and was unaffected by soil temperatures greater than $2^{o}C$.
5. The stomatal infiltration method of estimating relative stomatal aperture could be correlated with calculated values of stomatal resistance.
6. By means of mathematically describing stomatal behavior as observed in the field, and incorporating the model of stomatal

behavior with a mathematical model of atmospheric transpiration demand, a computer simulation model of seasonal transpiration in Douglas-fir was developed which has potential application in forestry and plant ecology.

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APPENDICES

APPENDIX I

Solution of Equation 27, The Model of Daily Transpiration

The model as described in the text is:

$$\frac{d\tau}{dt} = (\beta + \gamma t - \delta t^2)\left(\frac{1}{e^{a+bt}} + \epsilon\right)$$

Cross multiplying, we get

$$\frac{d\tau}{dt} = \frac{\beta}{e^{a+bt}} + \frac{\gamma t}{e^{a+bt}} - \frac{\delta t^2}{e^{a+bt}} + \epsilon\beta + \epsilon\gamma t - \epsilon\delta t^2$$

Thus

$$\int_0^\tau d\tau = \frac{\beta}{e^a}\int_0^t e^{-bt}dt + \frac{\gamma}{e^a}\int_0^t te^{-bt}dt - \frac{\delta}{e^a}\int_0^t t^2e^{-bt}dt \ldots$$

$$+ \beta\epsilon\int_0^t dt + \gamma\epsilon\int_0^t tdt - \delta\epsilon\int_0^t t^2dt$$

Integration gives

$$\tau = \frac{\beta}{e^a}A + \frac{\gamma}{e^a}B - \frac{\delta}{e^a}C + \epsilon\beta t + \frac{\epsilon\gamma t^2}{2} - \frac{\epsilon\delta t^3}{3}$$

where

$$A = \int_0^t e^{-bt}dt = \frac{1 - e^{-bt}}{b}$$

$$B = \int_0^t te^{-bt}dt = -\frac{\partial}{\partial b}\int_0^t e^{-bt}dt = -\frac{\partial}{\partial b}\left(\frac{1 - e^{-bt}}{b}\right)$$

By differentiation,

$$B = -\frac{e^{-bt}(bt+1)}{b^2} + \frac{1}{b^2}$$

$$C = \int_0^t t^2e^{-bt} = \frac{\partial^2}{\partial b^2}\int_0^t e^{-bt} = -\frac{\partial}{\partial b}B$$

$$C = -\frac{\partial}{\partial b}\left[-\frac{bte^{-bt}}{b^2} - \frac{e^{-bt}}{b^2} + \frac{1}{b^2}\right]$$

Therefore,

$$C = \frac{e^{-bt}}{b^3}\left[-b^2t^2 - 2bt - 2\right] + \frac{2}{b^3}$$