

Leaf Resistance Responses in
Selected Conifers Interpreted
with a Model Stimulating Transpiration
by
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The resistance of a leaf to molecular gaseous diffusion is an important physiological response. Control of leaf resistance enables a plant to control its transpired water loss and regulates photosynthesis.

Four study sites representing a gradient in available moisture and evaporative demand, were chosen in western

Oregon for the study of leaf resistance responses in five conifers. The conifers included Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis*, Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), noble fir (*Abies procera*, Rehd.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr). Study areas were located at a coastal site,

in the interior Coast range, at mid elevation in the west central Cascades, and in the western Siskiyou near Oregon Caves. Environments could be characterized respectively as mild and moist, hot and dry, cool and moist, and warm and dry in reference to temperature and evaporative demand.

Leaf resistance measurements were made during the period August 8 - September 24, 1972, with a modified aspirated diffusion porometer. Leaf resistance response was correlated with predawn plant moisture stress, absolute humidity deficit, and temperature. In both Douglas-fir and grand fir leaf resistance response was closely correlated with predawn plant moisture stress. As plant moisture stress increased from 4 - 18 atm, leaf resistances rose from 5 - 300 sec cm⁻¹. Leaf resistance in western hemlock ranged from 12 - 100 sec cm⁻¹ but was not closely correlated to any of the measured environmental variables. Noble fir and Sitka spruce showed little control of transpiration by leaf resistance over the range of environments measured.

Leaf resistance measurements were compared to an indirect estimate of stomatal aperture obtained by a pressure infiltration test. The comparison proved poor on all species. One possible cause was that leaf resistance measurements were restricted to current foliage which are more sensitive and variable than the older foliage normally selected for the infiltration test. Under extreme evaporative demand Douglas-fir and grand fir exhibited leaf resistances ranging from 300 - 1,200 sec cm⁻¹. Infiltration tests indicated stomata were still partially open suggesting that stomatal resistance

was not the cause of these extremely high leaf resistances. Rather it appears that mesophyll resistance may play an important role in reducing transpiration during times of high evaporative stress.

From the knowledge of leaf resistance responses, a simulation model of transpiration was constructed. Plant moisture stress estimated by soil water status was used to control leaf resistance. Simulation runs were made for an 80 meter tree, a 10.4 hectare watershed, and a 2 meter tree. Results from the 80 meter tree simulation indicated the importance of the hydrostatic gradient in stomatal control. From the 2 meter tree simulation the importance of water storage in sapwood for meeting daily transpiration demand was emphasized.

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LEAF RESISTANCE RESPONSES IN
SELECTED CONIFERS INTERPRETED
WITH A MODEL SIMULATING TRANSPIRATION

INTRODUCTION

The ability of different conifers to control transpired water loss is a primary physiological factor affecting their competitive ability in the Pacific Northwest, characterized by a normally dry growing season. Consequently scientists have attempted to quantify this ability and compare different tree species with respect to their capacity to control transpiration. Reed (1971) developed a simulation model for Douglas-fir that predicted potential transpiration for a tree given ambient temperature, humidity and predawn plant moisture stress. From the estimate of potential transpiration and input of stomatal control the model computed actual transpiration by the tree on a daily basis. Reed showed that the ratio of actual/potential transpiration provided an excellent integration of total water status of the plant; combining the effects of supply and demand with control of water by the tree. Waring et al., (1972) incorporated this model into their environmental grid for classifying coniferous forest ecosystems. The authors emphasized the importance of stomatal response to environmental stimuli because of its control of both carbon dioxide

and water vapor exchange. The general equation for transpiration is:

$$\frac{dT}{dt} = \frac{c_w - c_a}{R} \quad \frac{dT}{dt} = \text{transpiration rate, } g \text{ cm}^{-2} \text{ sec}^{-1}$$

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

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

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

Eq. 1

This simple equation was first formulated by van den Honert (1948) and more recently elaborated by Slatyer (1967). All environmental and physical factors have only indirect influence on the transpiration rate as shown in Equation 1 except absolute humidity deficit, $(c_w - c_a)$, the physical driving force and resistance (R) . Resistance, (R) , to transpiration has a number of components as shown in Equation 2.

$$R = r_a + r_l + (r_s + r_m) \frac{r_s + r_m + r_c}{r_c}$$

Eq. 2

r_a = boundary layer resistance

r_l = leaf resistance

r_s = stomatal resistance

r_c = cuticular resistance

r_m = mesophyll resistance

All resistance terms are in sec cm^{-1} . Equation 2

was first proposed by Gastra (1959). Boundary layer resistance, r_a , is a function of atmospheric turbulent mixing at the leaf surface whose principle component is wind velocity. Literature estimates of r_a in broad-leaved plants range from 0.05 - 3.0 sec cm⁻¹ (Slatyer, 1967; Hunt, 1968). Due to the narrow morphology of conifer needles, boundary layer resistances are generally below 0.5 sec cm⁻¹ and are considered negligible at any local windspeed over 100 cm sec⁻¹ (Gates, 1965). I ignored the boundary layer component allowing resistance to be treated entirely as a function of leaf resistance. Equation 2 is now reduced to

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

An analogy of Ohm's Law developed by Gastra (1959) allows Equation 3 to be written as

$$\frac{1}{R} = \frac{1}{r_l} = \frac{1}{(r_s + r_m)} + \frac{1}{r_c} \quad \text{Eq. 4}$$

This follows because r_s and r_m represent water flow in series while r_s and r_c represent parallel pathways of water flux. Jarvis and Slatyer (1970) reported mesophyll resistances of 0.4 - 4.0 sec cm⁻¹ in extremely desiccated cotton leaves. They concluded that mesophyll resistance is normally small. Under conditions when it may

increase the total leaf resistance increases far more through increased stomatal resistance. Measurements of cuticular resistance, r_c , in conifers are high, on the order of $200 - 300 \text{ sec cm}^{-1}$ (Slatyer, 1967). Since r_c is high ($\frac{r_c}{r_s}$ is small), and is a parallel pathway of water movement with stomatal resistance, it becomes unimportant except at high stomatal resistance values. This means leaf resistance, under normal circumstances, is controlled primarily by stomatal resistance.

This line of reasoning has led to estimating leaf resistance by measuring stomatal aperture. The aspirated diffusion porometer employed in this study does not require these assumptions because leaf resistance is measured directly. The porometer measures transpiration resistance as an undifferentiated summation as indicated in Equation 5.

$$R = r_l = f(r_s, r_m, r_c) \quad \text{Eq. 5}$$

This eliminates the necessity of attempting to discount r_m and r_c , and in fact under certain conditions allows one to measure these factors.

Returning to the original transpiration equation,

$$\frac{dT}{dt} = \frac{R}{c_w - c_a} \quad \text{Eq. 1}$$

the porometer measures $\frac{dT}{dt}$ with a humidity sensor and standardizes the numerator c_w and c_a , allowing one to calculate R given chamber temperature and leaf surface area. This relation was derived rigorously by Turner and Parlange (1970) and will be further discussed later. Although Equation 1 does not indicate it, a number of factors may influence transpiration indirectly. Among these potential factors may be (1) root soil water supply, (2) plant water status, (3) humidity or absolute humidity deficit from the leaf surface to the air, (4) leaf, air and soil temperature, (5) wind velocity, (6) radiation, and (7) resistances to water flux. This thesis attempts to quantify the effects some of these potential factors have on the denominator of the transpiration equation, resistance, R , since this is the only term that the plant can control. Factors (1) and (2) root soil water supply and plant status were jointly assessed by measurement of predawn plant moisture stress. Ambient humidity was measured to determine the effect on R . Air temperature was measured, and leaf temperature assumed similar to ambient. Soil temperature has been found to be influential on transpiration below 5°C (Reed, 1971; Benecke, 1972; Havarnek, 1972). Soil temperatures were greater than 5°C throughout the period of data collection. During measurements the needles were subject to a con-

stant mixing produced by a small electric fan within the porometer chamber.

Lacking suitable instrumentation radiation was not measured, so an attempt was made to standardize its effects. This will be discussed later. Resistances, including stomatal resistance (r_s), mesophyll resistance (r_m), and cuticular resistance (r_c), were measured as total leaf resistance (R_l), using an aspirated diffusion porometer. Summarizing, predawn plant moisture stress, ambient humidity and air temperature were measured concurrently with leaf resistance in an attempt to relate these environmental factors with response of the leaf resistance components r_s , r_m and r_c affecting R_l in transpiration Equation 1.

STUDY AREAS

Four areas were selected in western Oregon to encompass a range of environmental condition and forest composition, (see Fig. 1 and Table 1). All were in recent clearcuts occupied by healthy regeneration

1 - 3 m tall.

One area near the coast represented environments with low potential transpiration and optimal soil water throughout the growing season. The specific study site selected was on the Cascade Head Experimental Forest at 300 m elevation with a southwest aspect and slope of

about 20 percent. Rainfall averages 225 cm yr⁻¹ with a mean July maximum of 20°C and mean January minimum of 3°C reflecting the influence of the coastal fog belt.

The soil is an Astoria silty clay of the reddish brown latosol suborder of the great soil groups. Franklin and Dryness (1969) classify this area in the *Picea sitchensis* Zone of vegetation ecotypes. Principle

tree species include *Picea sitchensis*, *Tsuga heterophylla*, *Thuja plicata* with occasional *Pseudotsuga menziesii* and *Abies grandis*. Species investigated were *Picea sitchensis*, *Tsuga heterophylla* and *Pseudotsuga menziesii*.

A second area was selected at McDonald Forest in the interior Coast Range just northwest of Corvallis.

Map of Oregon showing location of the four study sites. (1, Cascade Head Experimental Forest; 2, McDonald Forest; 3, H. J. Andrews Experimental Forest; 4, Western Siskiyou.)

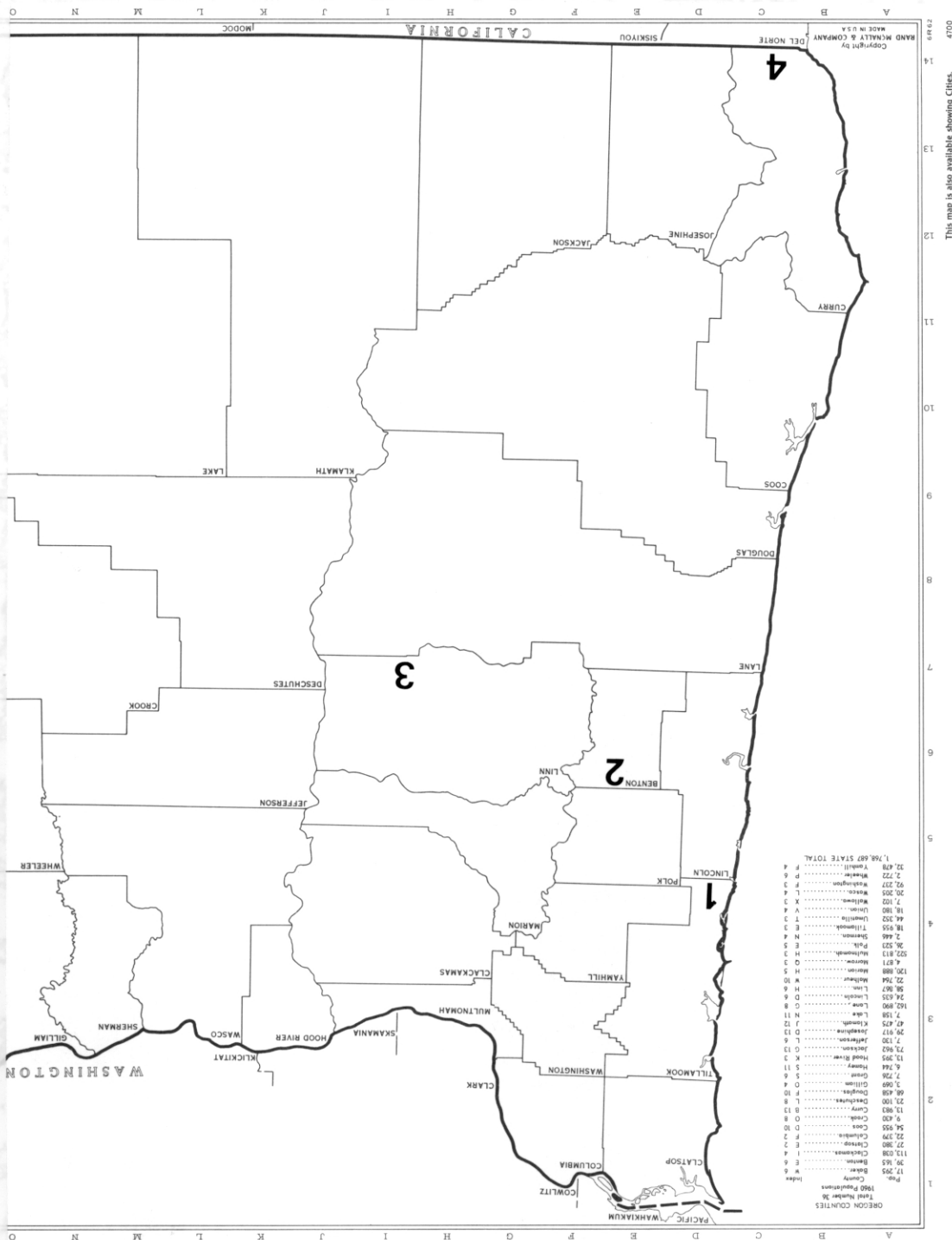


Table 1. Site characterization by plant response indices.

Site	Evaporative Demand ¹	PMS Index ²	Temperature Growth Index ³
Cascade Head	Low	5	67
Western Siskiyou	Med. high	15	60
McDonald Forest	High	20	89
H. J. Andrews	Medium	12	55

¹A relative comparison of the sites with respect to potential transpiration, a function of temperature and humidity.

²Plant Moisture Stress (PMS) is expressed in atm and represents predawn measurements on reference conifers near the end of the summer dry season.

³The Temperature-Growth Index reflects the potential for Douglas-fir seedling growth as a function of air and soil temperature throughout the growing season. A higher number indicates a site with higher growth potential.

The important environmental features found here were a limiting to conifer growth before the end of the normal growing season. The area selected was at 600 m elevation on a 20 percent slope with a southeastern aspect. Rainfall averages 100 cm annually with only 5 percent falling during the growing season. July maximum temperatures average 28°C and coupled with the absence of summer rainfall result in a relatively severe drought potential. Mean January minimum temperatures are near 0°C. The soils in the area are derived from Tye sandstone. Franklin and Dryness (1969) characterize this area as part of the Interior Valley (Pinus-Quercus-Pseudotsuga) Zone. They further describe it as an

Acer circinatum-Gaultheria shallon, Corylus californica-Holodiscus conifer subtype. The dominate tree species is Pseudotsuga menziesii joined occasionally by Abies grandis, Acer macrophyllum, and Cornus nuttallii.

Measurements were taken on Pseudotsuga menziesii and Abies grandis.

In the west central Cascades on the H. J. Andrews Experimental Forest, a higher elevation site with moderate potential transpiration demand and moderate soil water availability was selected. The elevation of the site was 1,000 m with a western aspect on a slope of

less than 5 percent. Precipitation averages 180 cm yr⁻¹ with a snowpack that reaches 1 - 3 m during the winter. The mean July maximum temperature is 25°C with a mean January minimum of -5°C. The soil type is brown Podzol. This site is in the Abies amabilis Zone of Franklin and Dryness (1969). Primary tree species include Abies amabilis, Tsuga heterophylla, Pseudotsuga menziesii, Abies procera, Thuja plicata and Pinus monticola with scattered Abies grandis and Picea engelmannii. Species sampled were Pseudotsuga menziesii, Tsuga heterophylla, Abies procera and Abies grandis.

The fourth and least frequently sampled site was in the western Siskiyou of southwestern Oregon. The elevation was 1,000 m, with an eastern aspect on a 20 percent slope. Precipitation averages 120 cm annually including moderate snowpacks up to 2 m depth. Mean July maximum temperatures are 27°C and mean January minimum is -2°C. The soil type at the site is brown Podzol but considerable soil type variation occurs in this region. This site is part of the Abies concolor Zone of Franklin and Dryness (1969). Abies concolor and Pseudotsuga menziesii are the most common tree species. Since this rather narrow zone is bordered on its lower limits by the Mixed-Conifer Zone and upper limits by the Abies magnifica shastensis Zone a great number of other tree

species can be found on this site. Included are Pinus ponderosa, Pinus lambertiana, Pinus monticola, Abies magnifica var. shastensis, Libocedrus decurrens and relic Picea breweriana. All these eight species were present on my study site with the exception of Libocedrus decurrens. The other seven species were marked for sampling. Unfortunately due to adverse weather during two of the three trips to this site the sample size for species on this site was not sufficient for statistical analysis. Consequently I will report only some general results of measurement there.

Since the work of Fry and Walker (1967), the stomatal infiltrometer has been the standard field instrument in the Northwest for measuring stomatal response in conifers. With this method, a needle is inserted into a chamber containing a 50 percent ethanol-water solution. Pressure is then applied to the solution until surface tension at the stomatal pore is overcome, and the solution is forced into the stomatal cavity. The pressure required for infiltration is inversely proportional to the pore diameter by a nonlinear function. Infiltration pressures around 0.1 atm indicate open stomata and readings of 2.0 atm correspond to closed stomata. Unfortunately, the stomatal infiltrometer has a number of theoretical and practical problems associated with it. Of greatest significance is that the infiltrometer produces only an indication of stomatal aperture not an absolute measure. Beyond that it relates only indirectly to actual leaf resistance, the quantitative link to transpiration. In making estimates of infiltration a subjective judgement is required to assess exactly when a majority of stomata have been infiltrated. Samples are restricted to individual needles so a large number of

Stomatal Infiltrometer

METHODS

determinations may be involved. Finally, this technique was developed on Douglas-fir but has been found less satisfactory on other species with differing stomatal geometry.

Aspirated Diffusion Porometer

The publication of Turner et al., (1969) introduced a new form of diffusion porometer. Unlike previous

diffusion porometers, (van Bavel et al., 1965; Kanemasu et al., 1969) this porometer is not limited for use only on broadleaf plants in theory or design. The aspirated diffusion porometer (Fig. 2) consists of a chamber drilled from a block of acrylic plastic, with a lithium chloride humidity sensor and a bead thermistor (A) mounted inside. A fan (B), driven by a small motor (D), circulates air within the chamber. A plunger (C), filled with silica gel dessicant can be alternately entered or withdrawn from the chamber. An electrical

connector (J), links the sensor with a meter. A change in relative humidity in the chamber causes a change in conductivity in the sensor. The conductivity change is rectified and the resultant electrical resistance shown by the meter in microamperes. Power is supplied to the meter circuit by two 6.75 volt d.c. mercury batteries connected in series and to the fan motor by two 1.35

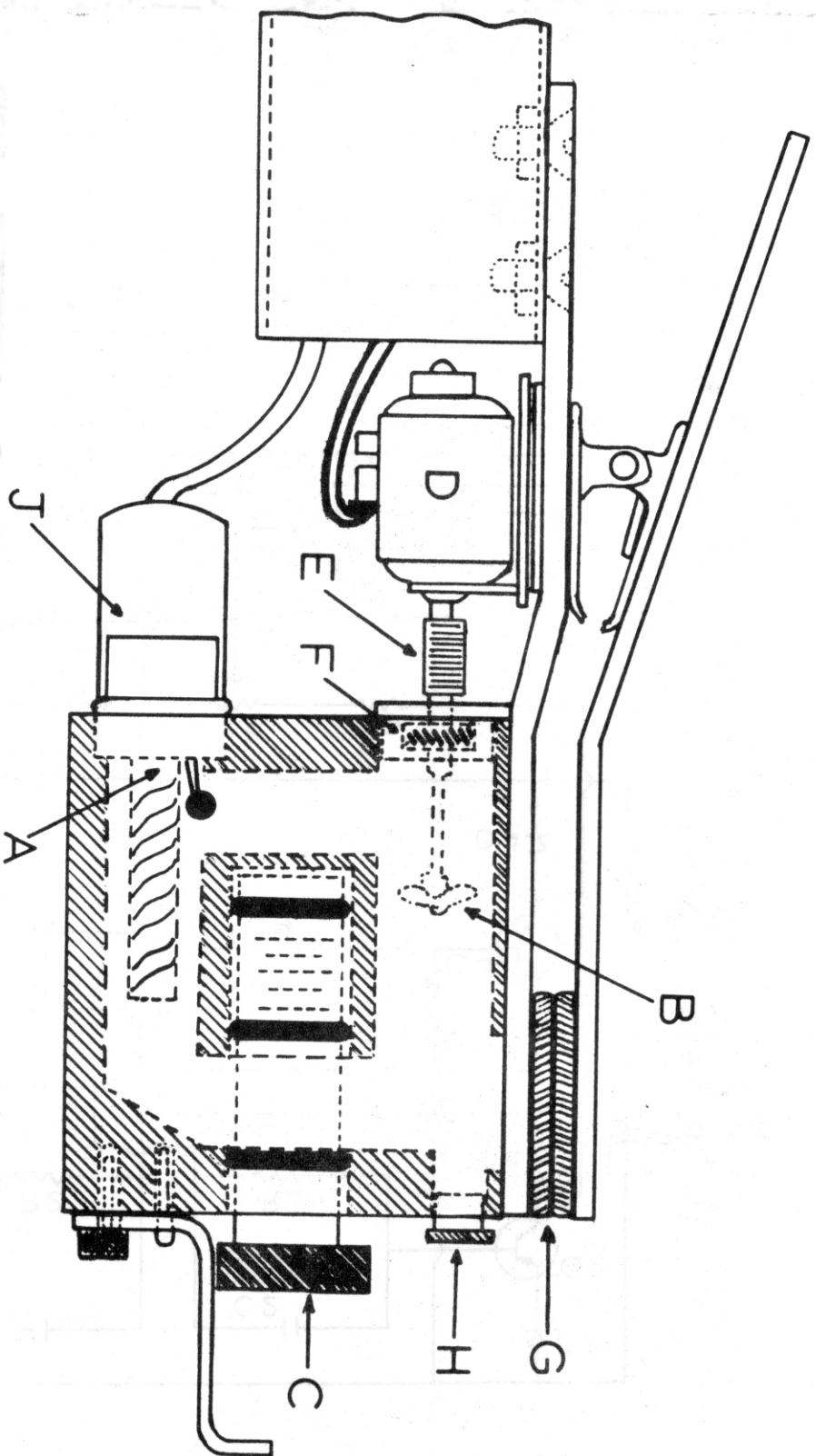


Figure 2. Side view of porometer (full scale). A, Humidity sensor and bead thermometer; B, fan; C, plunger containing desiccant; D, motor; E, rubber stopper coupling; F, sealed bearing; G, closed cell sponge rubber; H, port; J, electrical connector (Turner et al., 1969).

volt d.c. mercury batteries in series.

A porometer as described by Turner et al., (1969) was purchased from Wrenn Inst. Co. I then made the following modifications (Fig. 3). First the clamp and sponge rubber were removed and the port enlarged slightly to permit needle access. Next a split rubber stopper was wrapped around the intact stem of the twig and then inserted tightly into the port. Sealing putty in the split stopper prevented leaks between the stem and stopper. The chamber and meter were mounted on a camera tripod with a small shading umbrella to facilitate field use. Initial calibration curves supplied by the manufacturer were found inadequate. Recalibration was made in the laboratory by passing air of known humidity through the chamber at a fixed flow rate and plotting a curve of air humidity versus microampere output of the lithium chloride hygrometer.

Operation of the modified porometer required first, that the tripod on which the porometer was supported be in proximity of the branch tip to be sampled (Fig. 3). Next needles were peeled from the branch 4 - 8 cm behind the tip to prepare the stem for seating in the split rubber stopper. It was critical to mount this rubber stopper in such a way that water vapor leakage from these fresh needle scars did not enter the chamber. This left

Figure 3. Photograph of modified aspirated diffusion
porometer in operation on a conifer branch
tip.

approximately 4 cm of branch tip and 7 - 15 needles to be inserted into the porometer chamber. Once needles were inserted and the chamber sealed, the plunger was drawn up, introducing the silica gel dessicant into the chamber, and the fan was switched on. After the meter dropped scale readings to between 2.5 - 3.0, the plunger was pushed in, removing the dessicant from the chamber. The meter reading increased as humidity in the chamber increased due to transpiration by the needles. The time required for the meter needle to scan from 4.0 - 6.0 or 4.0 - 5.0 microamperes was recorded with a stopwatch. The temperature within the chamber was then recorded by switching the meter to the thermistor circuit. The reading was then complete and the needles removed from the chamber and retained for determining leaf surface area. Morrow and Slatyer (1971) suggested a number of storage and warm-up procedures for diffusion porometers which followed. These included storage and transportation in a sealed low humidity ice chest, shading the chamber to prevent temperature buildup, and beginning each sampling period by running the meter from 1.0 to 10.0 several times to sensitize the lithium chloride sensor. As operated this aspirated diffusion porometer has a number of advantages over the stomatal infiltrometer. First, it measures leaf resistance directly (not stomatal

aperture) by an equation to be discussed later, based on metered objective units. Second, it integrates response of 7 - 15 needles at one time. Third, leaf resistance is measured while the needles are intact on the tree. Finally it is lighter in weight and thus more portable than the infiltrometer. This present model of porometer has a number of disadvantages, some of which can be overcome by engineering. It measures only branch tips and new foliage and the chamber doesn't allow for many needles without seriously impeding chamber air circulation. The lithium chloride sensor doesn't function well below 10°C. Also the presence of any dew or free water on the needle or stem surface will invalidate readings. Any leakage from the chamber, particularly around the stem and stopper port will increase error as leaf resistance increases. Such leakage will normally lead to erroneously low leaf resistance values. Finally the porometer doesn't measure leaf resistance at ambient humidity but places the needles into an artificial environment of 25 - 30 percent relative humidity. The problem of chamber leakage and the artificial environment is minimized by keeping scan times to below 60 seconds by either using the shorter 4.0 - 5.0 scale range when necessary or by increasing, up to a limit, the number of needles inserted in the chamber.

Needle Surface Area Determination

As indicated earlier the leaf resistance measurements require accurate determination of leaf surface area. Thompson and Leyton (1971) developed a method whereby the needles are coated with an adhesive, weighed, covered with a monolayer of glass beads over the sticky needle surface and then reweighed. The regression of weight increase to surface area covered is then computed. This method was calibrated with squares of paper of known surface area by Reed (1971) who reported an $R^2 = .99$ for the regression between surface area of paper and increase in weight of the monolayer. For this study branch tips were stored after removal from the chamber in small sealed vials. After 1 - 2 days in the vials the needles lost sufficient water to reduce weighing fluctuations. The branch tips were then removed from the vials, dipped twice in 1:7 Scotch Spray mounting adhesive-benzene solution and allowed to dry by evaporating the benzene. The sample was weighed, rolled in a petri dish filled with 0.1 mm diameter beads and then reweighed. At this point a correction was made for glass-bead coverage of non-transpiring surfaces such as the stem and bud. The correction estimate was based on average surface area of a number of defoliated branch tips of each species. The

initial and corrected final weight were recorded and the difference, divided by the calibration coefficient 14.5 mg cm^{-2} , was the computed leaf surface area for that sample.

The adhesive-glass bead method is faster and more reliable than conventional length-width needle measurement techniques. However, it has a number of shortcomings. First, the calibration constant of mg weight cm^{-2} surface area is excessively sensitive to the type of paper or surface used for calibration. Consequently

variability between species may be expected. There is a rather fine balance between an adhesive solution concentrated enough to not allow bare spots on the needle surface but not so concentrated that glue clumps on the surface. In my study some error was still introduced

by glass-bead adhesion on bud and stem surface despite my approximate correction factors. Also clumps of beads often formed at the needle-petiole-stem corner. The

later two problems could have been solved by stripping the needles off the stem beforehand, but the large number of needles involved in my study made that alternative undesirable.

After completing measurements for this study a short project was undertaken to compare the adhesive-glass bead method with an optical planimeter for determining

In this study plant moisture stress was measured using the pressure chamber technique described by Scho-lander *et al.*, (1965) and modified by Waring and Cleary (1967). A twig is cut from the tip of a branch and placed in a chamber with the excised end protruding through a rubber stopper. The chamber is sealed and nitrogen gas forced into it from a pressurized tank. When the twig is

Pressure Bomb

The optical planimeter consists of a transparent plate where the needle samples are placed and a light focused down upon the plate. A photoelectric cell beneath the plate records the loss of impinged light due to shadows of the needles, which by calibration can be calculated to surface area. The optical planimeter requires that the needles be stripped from the stem and laid flat on the plate without overlapping. Since the shadow is only a 2 dimensional representation of the needles a 3 dimensional correction factor based on cross sectional geometry must be computed for each species. Initial comparisons showed the optical planimeter produced equal accuracy and superior precision to the glass bead-adhesive technique on samples suited to both techniques. A more comprehensive comparison is currently being undertaken and will be published at a later time.

severed, water under tension, recedes from the cross-sectional cut surface of the stem and is forced back to that surface by a certain positive pressure. This pressure, called plant moisture stress, is an indication although not a direct measure of xylem water potential (Boyer, 1967). Ritchie and Hinkley (1971) showed that pressure chamber water potential estimates for stems were often significantly more negative than leaf water potentials. This they attributed to water filling non-xylem cells during the pressure chamber measurement, consequently there is some variability among species depending on their stem anatomy. This error is minimized at highest water potentials which commonly occur in a tree just before sunrise. Predawn moisture stress measurements also give the best estimate of soil water stress, since measurements during daylight reflect both soil water supply and leaf transpiration demand. Plant moisture stress on study trees was measured either the night before or the night after leaf resistance measurements.

Sling Psychrometer

Relative humidity was measured at two hour intervals during leaf resistance sampling using a Bacharach sling psychrometer. Wet and dry bulb temperatures were

recorded for use in calculating absolute humidity deficits,
the primary driving force of transpiration.

SAMPLING

At each of the four study areas two trees of each species present were selected for study and tagged. All trees on each area were within 20 m of each other to minimize chance of soil or other environmental differences. Each tree selected was 1 - 2 m tall, healthy in appearance and growing uncrowded relative to its associates. This size of tree was chosen because it was convenient for sampling, more sensitive than larger trees to environmental fluctuations, yet well enough established to represent competitive adaptability to the site better than seedlings still struggling to survive.

Field sampling took place from June 25 - September 18, 1972, at approximately two week intervals rotating from one area to another. Because an important environmental parameter, radiation, was not being measured, I attempted to standardize this factor by sampling only from 10:00a.m. to 4:00p.m. on clear days, and only on branches on the sunlit side of the tree. Due to porometer design restrictions, I sampled only fully expanded, first year needles at the tips of branches. Since porometer measurements necessitate subsequent branch tip excision for leaf surface area analysis, only one sample was taken from each tree at each two hour sample period to conserve foliage unless there were broken needles or other evidence of a faulty

reading. Preliminary testing had also shown the porometer to be capable of reproducing results to $\pm .3$ sec or about 1 - 3 percent. Stomatal infiltration pressures were taken on four needles immediately adjacent to the porometer sample within three minutes of the porometer measurement, and the average of the four infiltration pressures recorded. All field data were recorded on a large sheet partitioned to correspond to an IBM computer punch card of 80 columns. Data were recorded by a specific Format so that the field sheets could be directly punched onto cards, entered into the Oregon State CDC-3300 computer and analyzed. Data recorded included (1) a site code number, (2) Month/Day/Year, (3) Pacific Standard Time, (4) Dry bulb temperature, (5) Wet bulb temperature, (6) Genus-species-number, (7) Porometer scale range, (8) thermistor reading, (9) Scan time, (10) infiltration pressure, (11) minimum plant moisture stress, and (12) initial and final weights from surface area determination.

DATA ANALYSIS

Preliminary analysis calculated leaf resistance, R_L , from the input values on file. Turner and Parlange (1970) did a rigorous and thorough calibration of this model of ventilated diffusion porometer. Their work resulted in the following equation for calculation of leaf resistance.

$$r_s = \left\{ At / \ln \left[\frac{(C_\infty - C_0)}{(C_\infty - C_t)} \right] \left[V_s + V_c \right] \right\} - r_p \quad \text{Eq. 6}$$

A = surface area of needles exposed in chamber

t = scantime of microamp meter from scale correspond-

ing to $C_0 - C_t$

ln = natural logarithm of...

C_∞ = relative humidity at saturation in chamber

C_0 = relative humidity at beginning of scantime

C_t = relative humidity at end of scantime

V_s = effective volume of sensor, H_2O capacity

V_c = volume of chamber, H_2O capacity

r_p = porometer inertia resistance

This equation incorporated into a Fortran program written by Dr. Paul Waggoner and supplied with the instrument. After a number of minor changes were made to adapt this program to our computer system I introduced a number of modifications and extra computations. First I made a

sequence for computation of leaf surface area of each successive sample since the original program was built for broadleaves with a standard surface area. Next a number of numerical corrections were found to be necessary in the calibration data arrays.

Subsequent additions were made to the program tailoring it to my own study. I arranged the program, with each computation for a sample to printout; site, date, time, genus-species and number, scale range, thermometer reading, scanline and leaf resistance. Also printed out were stomatal infiltration pressure (INF) in lb in.⁻² and predawn plant moisture stress (PMS) in atmospheres. From inputs of wet and dry bulb sling psychrometer readings I had calculated and printed ambient temperature (T), saturation vapor pressure, vapor pressure deficit and absolute humidity the stomatal cavity to have an absolute humidity of saturation at ambient air temperature.

This basic computational output was filed on magnetic tape at the OSU Computer Center. The files were then used in the Oregon State Statistical Analysis Program Library. First I made standard 2 dimensional plots for each tree species of R_1 vs. PMS, R_1 vs. ABSHD, R_1 vs. INF and R_1 vs. T. On reviewing these plots a transformation $\ln(R_1)$ vs. PMS was made on Douglas-fir and grand fir all-sites data. A

stepwise multiple linear regression with analysis of variance and correlation coefficients was run for each species on SIPS (Statistical Interactive Programming System). Multiple regression equations were developed with R_1 as dependent variable and PMS, ABSHD, and T as independent variables. Between site variation was analyzed by also calculating Douglas-fir and grand fir data on the H. J. Andrews site and McDonald Forest separately.

RESULTS

Leaf Resistance

A summary of the stepwise multiple regression of predawn plant moisture stress (PMS), absolute humidity deficit (ABSHD), and ambient temperature (T) on leaf resistance is given in Table 2. Included also is the sample size, final coefficient of multiple determination, the highest F-value attained along with the step it was attained at and the tabular F-value required to meet a 99 percent confidence level. A number of general observations can be made. First, PMS was the primary independent variable in all except two regressions. Second, all regression equations were significant at the 99 percent confidence level. Third, the F-value, indicative of the variation about the regression line, was always highest on the first or second step of the regression. The regression equation has its greatest significance and predictive capacity at the step where the R^2 and F-value are simultaneously maximized.

Leaf resistance in Douglas-fir appeared to be controlled primarily by predawn plant moisture stress over the range in PMS measured, from 4.8 - 17.7 atm. Temperature ranging from 11°C - 37°C and absolute humidity deficit which ranged from $2.48 - 36.08 \times 10^{-6} \text{ gm cm}^{-3}$ together

Table 2. Stepwise multiple linear regression of the three measured variables on leaf resistance.

Y	Variable Entered			Total R ²	Highest F-value (step)	F Table (99% CL)	Sample Size
	X ₁	X ₂	X ₃				
<u>Douglas-fir</u>							
All sites	ln(R ₁)	PMS	T	.56	(1) 68.15	6.98	76
McDonald Forest	R ₁	PMS	ABSHD	.81	(2) 59.00	5.53	28
H. J. Andrews	R ₁	PMS	T	.52	(2) 7.57	6.36	17
<u>Grand fir</u>							
All sites	ln(R ₁)	PMS	ABSHD	.92	(2) 226.19	5.20	41
McDonald Forest	R ₁	PMS	ABSHD	.85	(2) 51.04	5.72	24
H. J. Andrews	R ₁	ABSHD	PMS	.68	(1) 21.25	8.68	16
<u>Western hemlock</u>							
	R ₁	PMS	T	.53	(2) 20.65	5.23	39
<u>Noble fir</u>	R ₁	ABSHD	T	.41	(1) 10.80	5.93	21

R_l = leaf resistance

PMS = predawn plant moisture stress

ABSHD = absolute humidity deficit from leaf surface to air

T = ambient temperature

accounted for less than 20 percent in the variation of leaf resistance. The regression for McDonald Forest site Douglas-fir alone showed an $R^2 = .81$ for $\ln(R_L)$ as a function of PMS and ABSHD. This significant increase in R^2 over the total Douglas-fir $R^2 = .56$ probably reflects the genetic variability of the species. The regression of Andrews site Douglas-fir was weak, possibly because the range in environmental and physiological variables was small, as was the sample size.

The graph of R_L vs. PMS (Fig. 4) for Douglas-fir appeared to follow an exponential growth type curve with an asymptote at around 18 - 20 atm. Although I have no data for confirmation, I would expect that curve to flatten out at a leaf resistance corresponding to complete stomatal closure and cuticular resistance around 250 - 300 sec cm^{-1} . This would produce a sigmoid type curve and was the type of curve used in my transpiration simulation. It is interesting that the range of PMS 18 - 20 atm where leaf resistance approaches cuticular resistance is similar to the PMS range where Waring (1969) found cambial division to cease in Douglas-fir.

The graph of R_L vs. PMS for Douglas-fir (Fig. 4) may be indicative of phenotypic variation between McDonald Forest and H. J. Andrews Douglas-fir. The majority of points above PMS of 10 atm were contributed by the

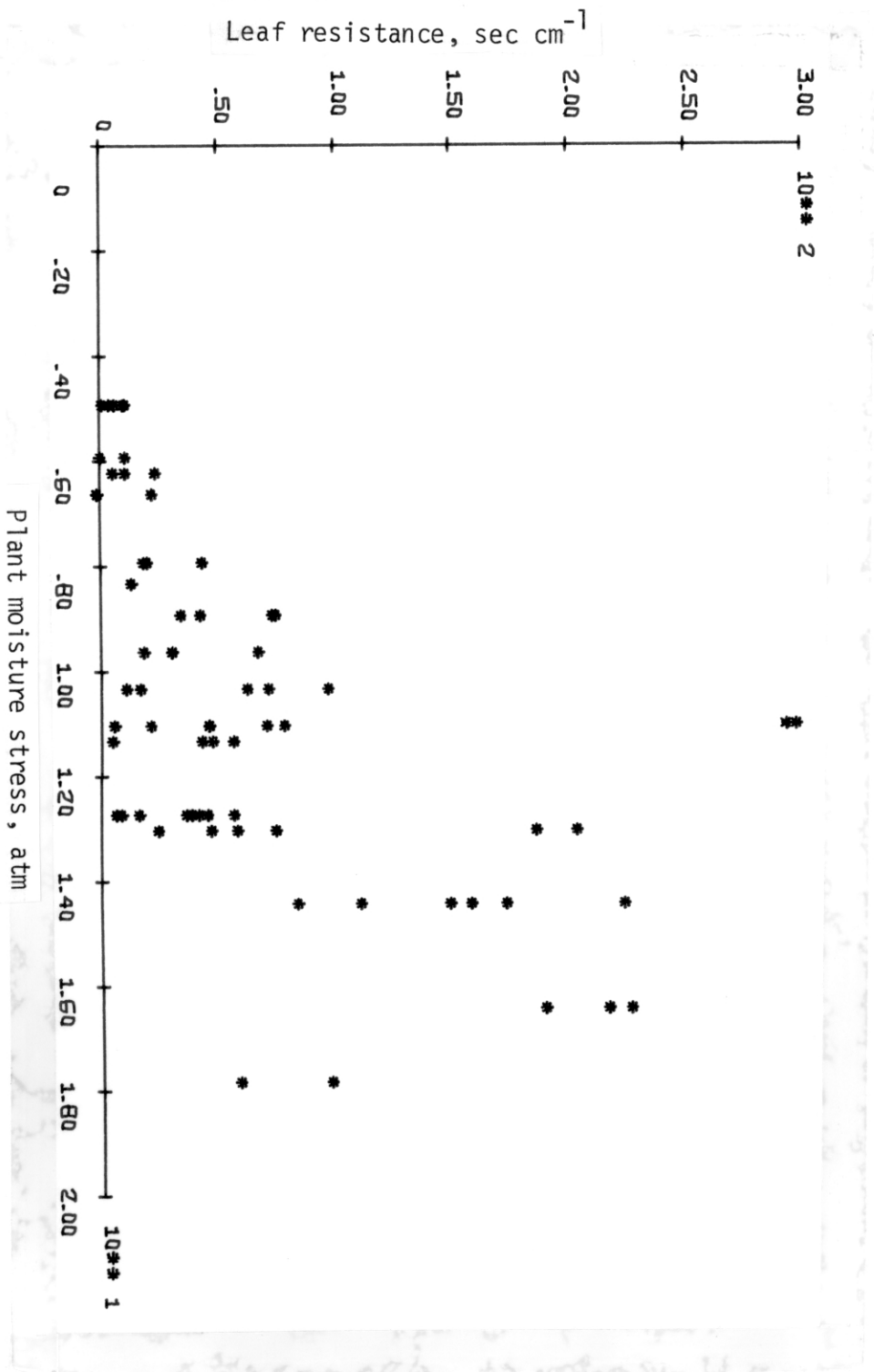
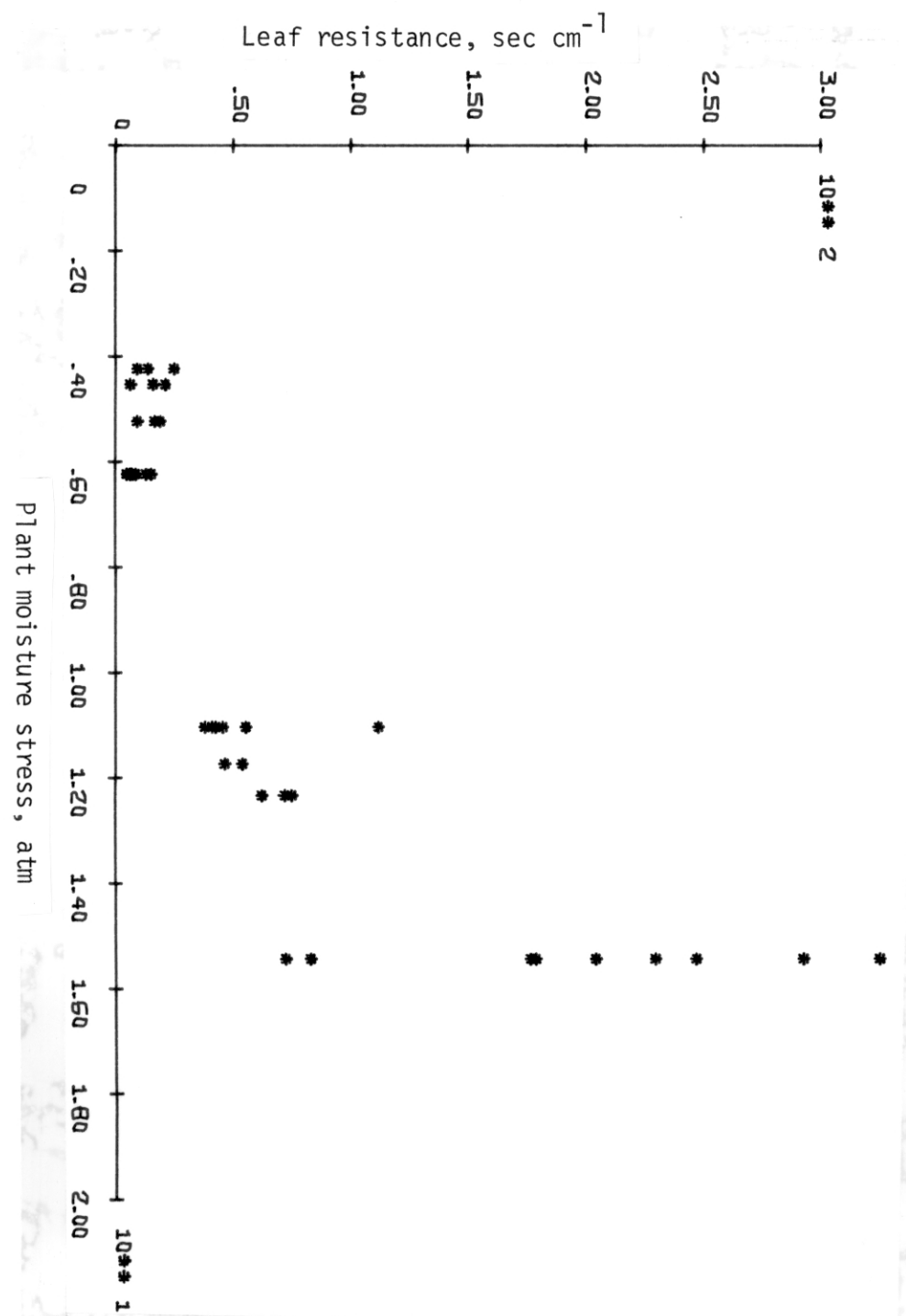


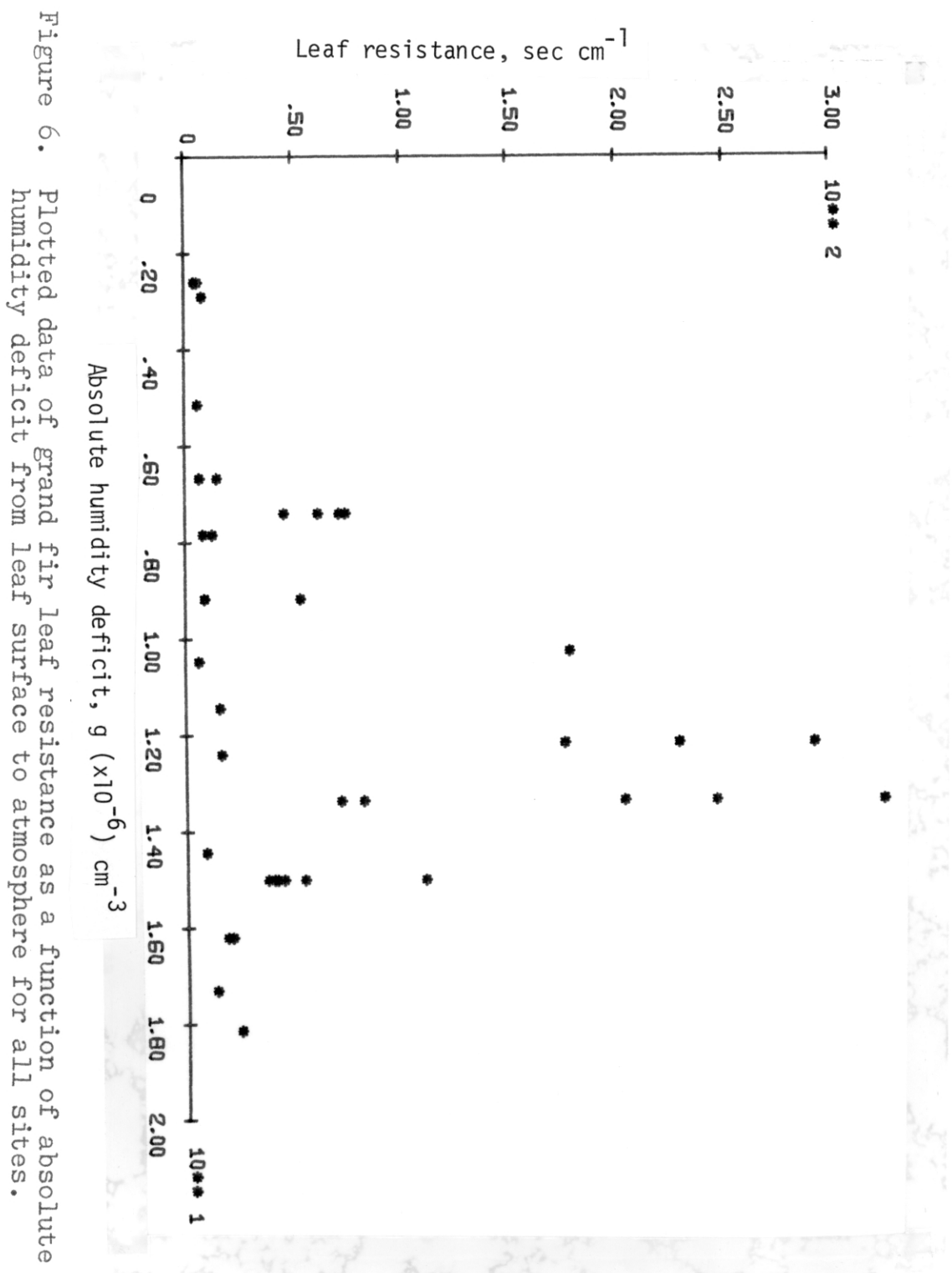
Figure 4. Plotted data of Douglas-fir leaf resistance as a function of predawn plant moisture stress for all sites.

Figure 5. Plotted data of grand fir leaf resistance as a function of predawn plant moisture stress for all sites.



McDonald Forest trees while those below are from H. J. Andrews. The graph could be interpreted in two sections. First would be a response rate of around 7 sec cm^{-1} atm^{-1} corresponding to H. J. Andrews Douglas-fir. Second, the McDonald Forest response curve would be expected to taper off to some minimum R_L . Also at some PMS above 15 atm the H. J. Andrews trees would probably exhibit a rapid increase of R_L . Dr. Don Zobel (pers. comm.) has encountered similar stomatal responses in grand fir as measured by the infiltrometer, where an eastern phenotype on the H. J. Andrews responded differently to PMS than a western phenotype. In the midrange of PMS 5 - 15 atm these two different response rates may be more accurate for the respective site.

Grand fir exhibited similar behavior to that in response to PMS (Fig. 5) of Douglas-fir but with less total variation. The stepwise regression for all grand fir was highly significant with an $R^2 = .92$ using the natural logarithm of leaf resistance as dependent variable. Again analysis of the Andrews site alone produced a weak regression. Also regression for the Andrews site entered ABSHD first instead of PMS, and carried an $R^2 = .56$. For the McDonald Forest site the regression of R_L vs. ABSHD had an $R^2 = .57$. The pooled data for R_L vs. ABSHD is shown in Figure 6. Douglas-fir had an all sites $R^2 = .26$ for



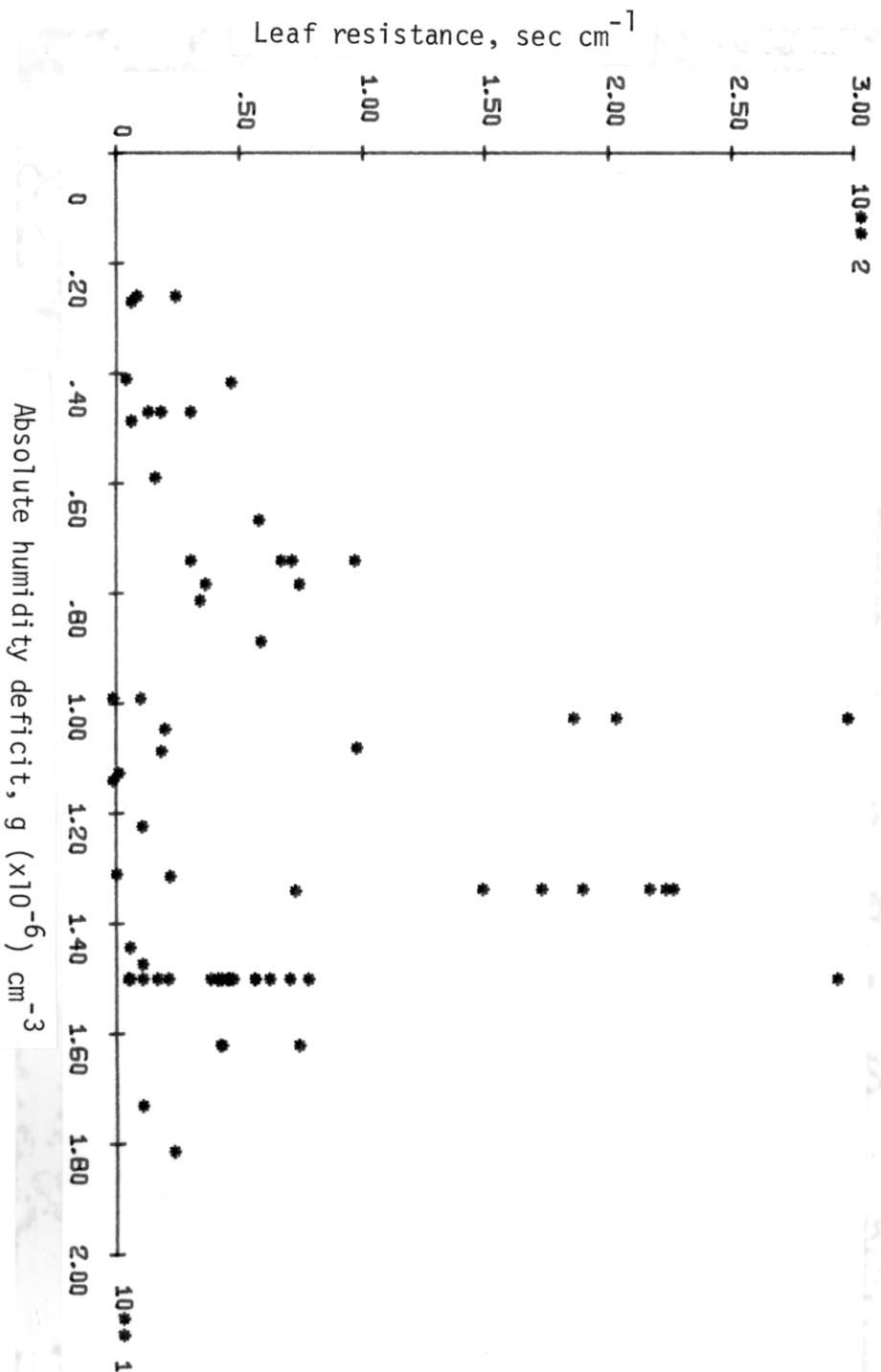
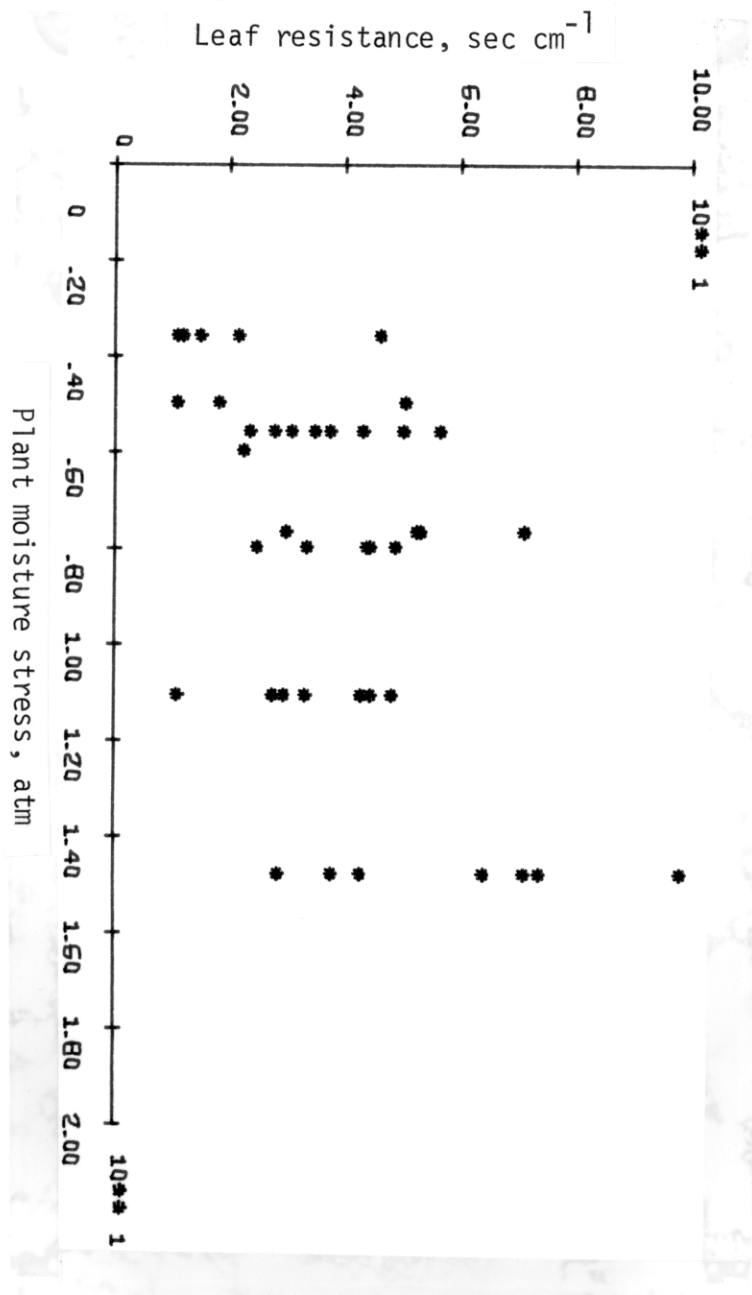


Figure 7. Plotted data of Douglas-fir leaf resistance as a function of absolute humidity deficit from leaf surface to atmosphere for all sites.

R_1 vs. ABSHD (Fig. 7) and even lower correlations when sites were analyzed separately. This effect of humidity on grand fir may explain the response found between leaf resistance and infiltration pressure for that species. As will be discussed later, grand fir had the lowest of all four species tested on the regression of R_1 vs. INF, $R^2 = .01$. I am suspicious though, that the high R^2 may be statistical artifact. The sample points at R_1 above 200 sec cm^{-1} and medium ABSHD (Fig. 6) were all recorded on one day and distort the graph. On this day R_1 values above 450 sec cm^{-1} were recorded, indicating an abnormal leaf resistance.

Western hemlock produced the most puzzling data of the trees sampled (see Fig. 8, Fig. 9). The range in PMS measured was 3.4 - 14.6 atm, temperature varied from 11°C - 30°C and absolute humidity deficits from 2.48 - 18.02 $\times 10^{-6}$ g cm^{-3} . Even under mild conditions leaf resistance values were never below 11.5 sec cm^{-1} . For comparison minimum leaf resistances for Douglas-fir were 3.0 sec cm^{-1} and for grand fir 6.2 sec cm^{-1} . In terms of transpiration this would indicate that western hemlock has a maximum transpiration rate 2 - 3 times lower than Douglas-fir or grand fir. Equally interesting and of greater significance is that the maximum leaf resistance measured was 74.7 sec cm^{-1} except for one outlying point

Figure 8. Plotted data of western hemlock leaf resistance as a function of predawn plant moisture stress for all sites.



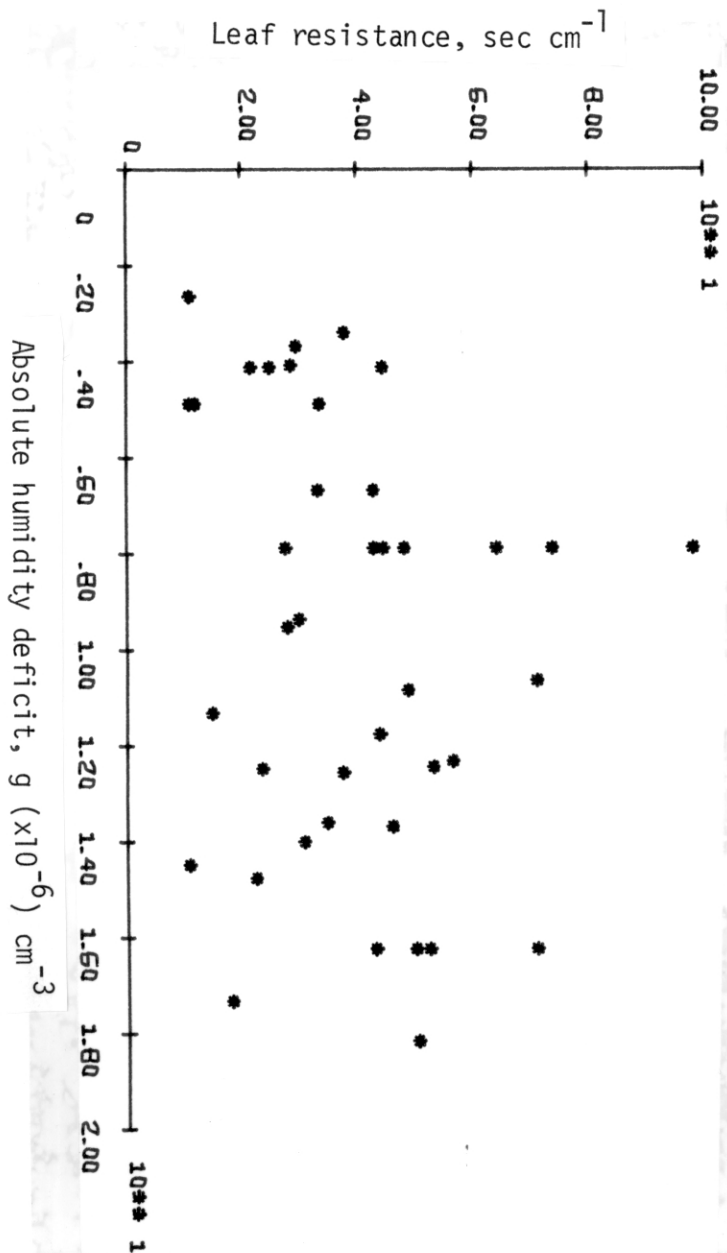


Figure 9. Plotted data of western hemlock leaf resistance as a function of absolute humidity deficit from leaf surface to atmosphere for all sites.

at 98.9 sec cm⁻¹. Admittedly none of the western hemlock measured was under extreme moisture stress but 14.6 atm is enough to produce leaf resistance of 150 - 250 sec cm⁻¹ in Douglas-fir.

The stepwise multiple regression for western hemlock, Table 2, showed PMS to be the primary independent variable but with a weak $R^2 = .24$. Addition of temperature increased the $R^2 = .53$ with an F-level = 5.23 for a 99 percent confidence level. A standard rule of thumb is that if the calculated F-level is less than four times greater than the tabular value, the regression even though significant, is not powerful enough to be used for predictive purposes. Neither of the two important independent variables PMS and T were correlated highly with R_1 when regressed separately and only when entered in a multiple regression could they attain the still weak $R^2 = .53$.

Over the environmental range measured, noble fir showed virtually no stomatal control. At a PMS of 14.6 atm four leaf resistance values averaged 10.5 sec cm⁻¹. Again this is compared to Douglas-fir which at this PMS would range from 150 - 250 sec cm⁻¹. As a result of this small range in leaf resistance the stepwise multiple regression in Table 2 was rather inconclusive. ABSHD was the only significant variable with an $R^2 = .35$. Addition of T and PMS was at the expense of lowering the F-level and increased

the R^2 to only .41.

Although the data for Sitka spruce were not sufficient for statistical analysis a number of general observations can be made. First, even after the extremely hot, dry summer of 1972, the highest predawn plant moisture stress measured was 4.4 atm. At the Cascade Head site only nine days recorded temperatures over 27°C during the period June 1 - October 1. The few leaf resistances measured taken ranged from 7.4 - 21.2 sec cm⁻¹. The highest leaf resistances were recorded during sampling on one of these days over 27°C. Since no range in PMS was recorded the only variables under consideration were Γ and ABSHD. Generally it appears that increasing Γ and ABSHD will increase leaf resistance over a very limited range of leaf resistance. Beardsell et al., (1972) have reported that Sitka spruce planted in Scotland have leaf resistances as low as 4 sec cm⁻¹ but that a vapor pressure gradient of less than 10 mb can cause a doubling even with saturated soils.

A number of measurements were made on a variety of species at the western Siskiyou site and will be briefly summarized. Five measurements on Brewer spruce at a PMS of 9 atm, 15°C and high humidity produced a leaf resistance range of 3.6 - 8.0 sec cm⁻¹. Ponderosa pine at a lower, drier site had a PMS = 15 atm and leaf resistances of

24.3 - 45.2 sec cm⁻¹. All these leaf resistance values, it should be emphasized, are for current foliage. Older needles are known to have higher leaf resistances (Waggoner and Turner, 1971).

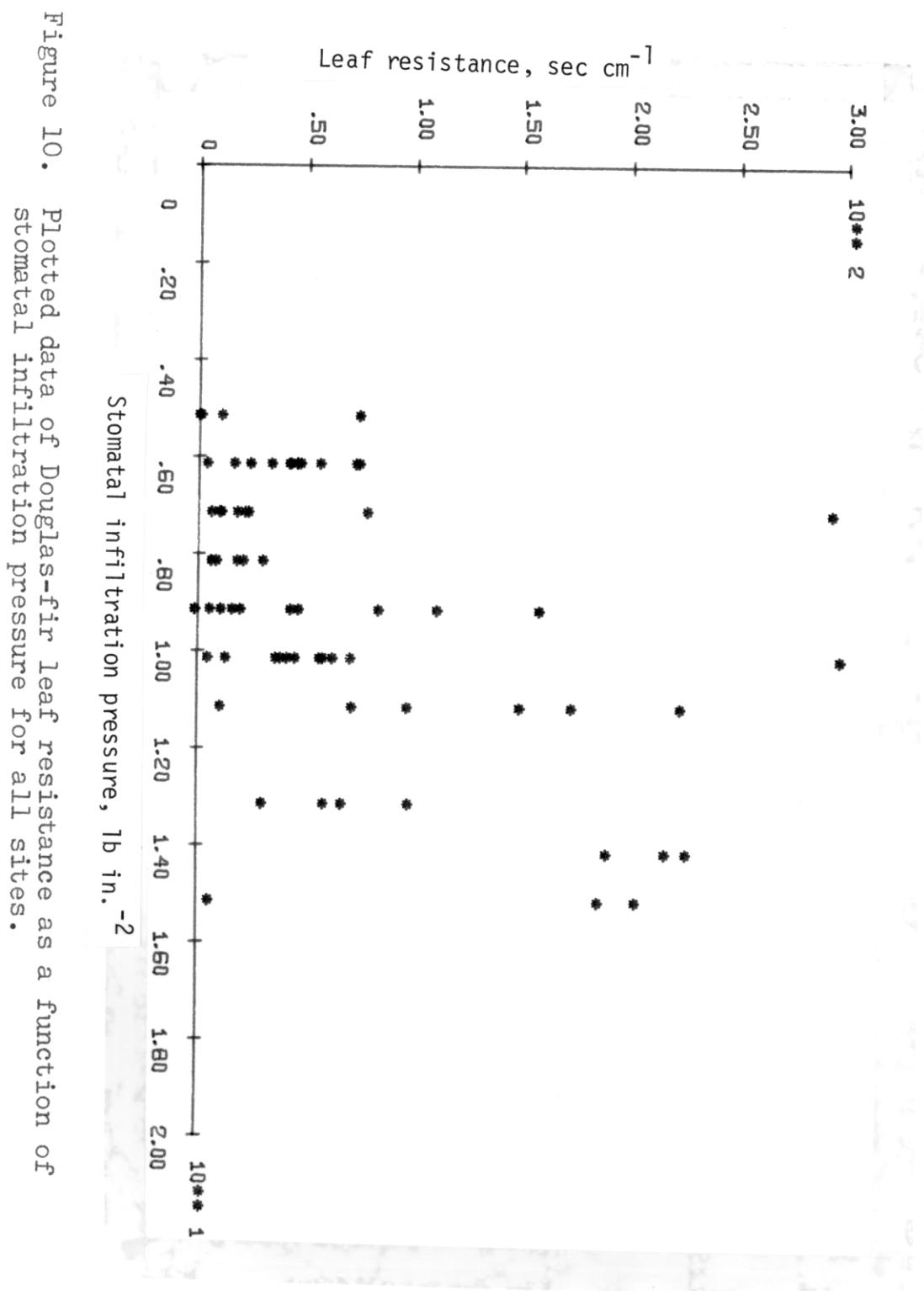
Infiltration Pressures

Due to the special significance of the stomatal infiltrometer in conifer research in the Northwest I wanted to analyze it separately. As presented in Table 3 the correlations of infiltration pressure on leaf resistance were extremely poor. The all sites regression for the data presented in Figure 10 for Douglas-fir had an $R^2 = .34$. For a range of infiltration pressures of 5 - 15 lb in.⁻². The regression for McDonald Forest alone improved the R^2 slightly to .48. There was effectively no correlation in grand fir between infiltration pressure and leaf resistance, shown in Figure 11. As stated before this may partially be a result of the heavy influence humidity appears to have on leaf resistance in grand fir. Possibly this is perpetuated by changes in mesophyll resistance. Some supporting data for this will be discussed shortly.

The regression for noble fir was confounded because noble fir is amphistomatous. Infiltration readings were either very low, 5 - 8 lb in.⁻² or very high, above 20 lb in.⁻². Perhaps on the upper side of the needle the

Table 3. Linear regression of stomatal infiltration pressure on leaf resistance.

Site	Regression Equation	R ²
<u>Douglas-fir</u>		
All sites	$y = -56.5 + 12.6x$	.34
McDonald Forest	$y = -83.5 + 17.2x$	.48
H. J. Andrews	$y = -73.0 - 4.6x$	.21
<u>Grand fir</u>		
All sites	$y = 206.1 - 5.95x$	.01
McDonald Forest	$y = 585.1 - 30.1x$	.07
H. J. Andrews	$y = 13.2 + 0.05x$	.00
<u>Western hemlock</u>		
Western hemlock	$y = 16.5 + 1.85x$	.15
<u>Noble fir</u>		
Noble fir	$y = 14.80 - 0.097x$	.02



stomata were closed and on the lower side open. This brings up the point that noble fir has twice the potential surface area for transpiration as the other conifers and may partially explain its low leaf resistance values.

Mesophyll Resistance

The maximum leaf resistance normally measured in conifers is in the 250 - 300 sec cm⁻¹ range. These values correspond to normal cuticular resistance with complete stomatal closure and theoretically infinite stomatal resistance (Slatyer, 1967). On September 1, 1972, I measured seven leaf resistances on three different Douglas-fir at McDonald Forest in the range of 550 - 1,200 sec cm⁻¹. Two measurements on two grand fir that same day yielded leaf resistances of 750 and 1,000 sec cm⁻¹. These measurements were taken between 2:00 - 3:00 p.m. and the temperature at this time was 37°C. The absolute humidity deficit was 36×10^{-6} g cm⁻³, more than twice the deficit of the next highest day in my data. In more comparable terms, it was 37°C with a relative humidity of 14 percent. The PMS range on these five trees was 14.3 - 16.3 atm. Their stomatal infiltration pressures ranged from 8 - 10 lb in.², indicating stomata at least half open. On September 12, measuring the same trees, three leaf resistance values on the Douglas-fir ranged from

380 - 550 sec cm^{-1} . Three grand fir readings were from 360 - 470 sec cm^{-1} . Environmental conditions were much milder that day. The temperature at 12:00 - 1:00 p.m. was 25°C and the absolute humidity deficit was only $12 \times 10^{-6} \text{ g cm}^{-3}$. The PMS range in the trees was 10.9 - 16.3 atm and stomatal infiltration pressures were from 10 - 15 lb in.⁻², still moderately open.

Under laboratory conditions Reed (1971) calculated the range of 8 - 15 lb in.⁻² infiltration pressure to be equivalent to 10 - 78 sec cm^{-1} . The only other resistance term in series with stomatal resistance is mesophyll resistance. I will not postulate any mechanism for these extreme leaf resistances but they obviously raise the question of incipient drying of the mesophyll tissues under extreme conditions. Fry (1965) found evidence for a cell wall resistance that increased under conditions of high absolute humidity deficit, low plant water content and open stomata. Transpiration experiments by Swank (1972) and Lopushinsky (1969) also suggested a resistance to water vapor diffusion of mesophyll or cell wall origin. It is possible these values are an artifact of the porometer. However these results are based on 15 measurements of five different trees on two separate days. On the first day ambient humidity was below porometer chamber humidity so any leakage of water vapor out of the chamber could

erroneously increase leaf resistance. I doubt however, that the chamber could leak that fast. Also the humidity on the second day was about 46 percent, considerably above the chamber humidity range of 25 - 30 percent. This phenomenon was not found at any other time during the summer but I do feel it to be a repeatable event that bears close study.

COMPUTER SIMULATION

To help interpret the importance of leaf resistance measurements on gas exchange processes I wrote a computer simulation model for water transport from the soil, through a tree to the atmosphere. With the same basic model structure transpiration in an 80 meter tree, a watershed, and a 2 meter tree were simulated. I will use the 2 meter tree as an example in the explanatory section. The prototype model was written in Dynamo II and is discussed by Waring et al., (1973). The final model was written in FLEX I, a computer processor for complex system modeling. It consists of a root water zone broken down into three compartments, a joint runoff/seepage sink for water in excess of what the soil root zone at field capacity can retain, a sapwood storage compartment and an atmospheric transpiration sink. A flow diagram of the model is presented in Figure 12. Water is the flux variable in the model, transpiration acts as a feedback driving force. The physiological control of transpiration is through leaf resistance which in turn is calculated from soil moisture status, reflected from plant moisture stress. For modeling purposes the rooting zone is defined to extend to a depth encompassing 90 percent of root biomass. In modeling the 2 meter tree, I assumed roots might normally reach a depth of at least one meter.

A second necessary assumption was the average horizontal rooting range. I assumed that a 2 meter tree with surrounding competition would have roots extending horizontally as far as the branches on an average (Wagenknecht, 1960). By measurement horizontal branch extension was found to average about one meter. Field capacity of a soil is defined as the total amount of water held in that soil at a soil moisture tension of .3 atm, and the lower limit extractable by plant roots is approached at 15 atm. The volume of water held between these two values is the storage capacity of the root zone. For the 2 meter tree, the rooting volume was $\pi \times \text{lm}(\text{radius}) \times \text{lm}(\text{depth})$. This represented a storage capacity of $4.5 \times 10^5 \text{ cm}^3$ of water (Harr, pers. comm.).¹ This was then partitioned 1:1:75:1.75 to approximate water held in a surface horizon layer (level A), a mid-root zone layer (level B) and lower root zone layer (level C) (Krygier, 1971).

Compartment 4 of the model structure is a joint runoff/seepage sink. Whenever precipitation input exceeds the field capacity of the soil rooting zone, the excess is dumped into this compartment & sink. No attempt is made to distinguish between seepage from any of the soil levels or runoff from the surface although the latter is a rare

¹Dr. Dennis Harr, data for Analysis of Ecosystem Program on H. J. Andrews Experimental Forest.

occurence on soils in the western Cascades and Coast Range. The sapwood water storage was estimated from measurement by assuming the standard 2 meter tree to have a base diameter of 8 cm. Assuming the stem to approximate a cone 2 m long and 8 cm in diameter the cone volume was determined. Ignoring bark this entire volume was defined as sapwood. The sapwood is known at saturation to contain a maximum of 200 percent of its weight in water which can be withdrawn down to approximately 100 percent of sapwood weight (Graham, 1964). Again choosing an operational definition the available sapwood storage capacity was defined as the difference from 200 - 100 percent by weight of water that can be taken or available sapwood water volume equals sapwood weight. Doley (1967) reported that the sapwood in Eucalyptus marginata acted as the reservoir for daily transpiration and was refilled at night. Clark and Gibbs (1957) also found a significant seasonal variation in the water content of sapwood in a number of Canadian forest trees. On older trees with established heartwood, the percentage of stem functioning as sapwood can be very different from one species to the next. This would need consideration if this model was built simulating large trees of different species.

The model considers the atmosphere as an infinite sink, compartment 6, for water transpired by the standard

2 meter tree. The components of transpiration for the model are $T = \frac{R}{ABSHD} (DL \times LA)$, where Resistance and Absolute Humidity Deficit are averaged for the day, $DL =$ Daylength and $LA =$ Leaf Surface Area. The general equation has been derived previously with the basic units of $g\ cm^{-2}\ sec^{-1}$. The physical driving force for water movement through a tree is the gradient in water vapor concentration from the leaf surface to the air, ABSHD. In terms of water potential gradients a relative humidity of 89.5 percent at 25°C is equivalent to -150 bars, considerably higher than the highest tolerable leaf water potentials of the hardest conifer. For this model running on a daily time resolution the basic equation must be multiplied by Daylength in seconds and estimated Leaf Surface Area for the standard 2 meter tree to compute transpiration per day for the tree. Leaf Surface Area was computed using a regression of sapwood crosssectional area on foliar biomass (Grier, pers. comm.). ABSHD is read in daily as a climatological variable leaving leaf resistance as the tree's controlling variable for regulating water loss. I have modeled leaf resistance to be entirely controlled by predawn plant moisture stress by the empirical relationship shown in Figure 13. My field data has shown PMS to be the primary controlling factor for leaf resistance response in grand fir and Douglas-fir, but it admittedly

Figure 13. Relationship between leaf resistance and predawn plant moisture stress in 2 meter tall Douglas-fir.

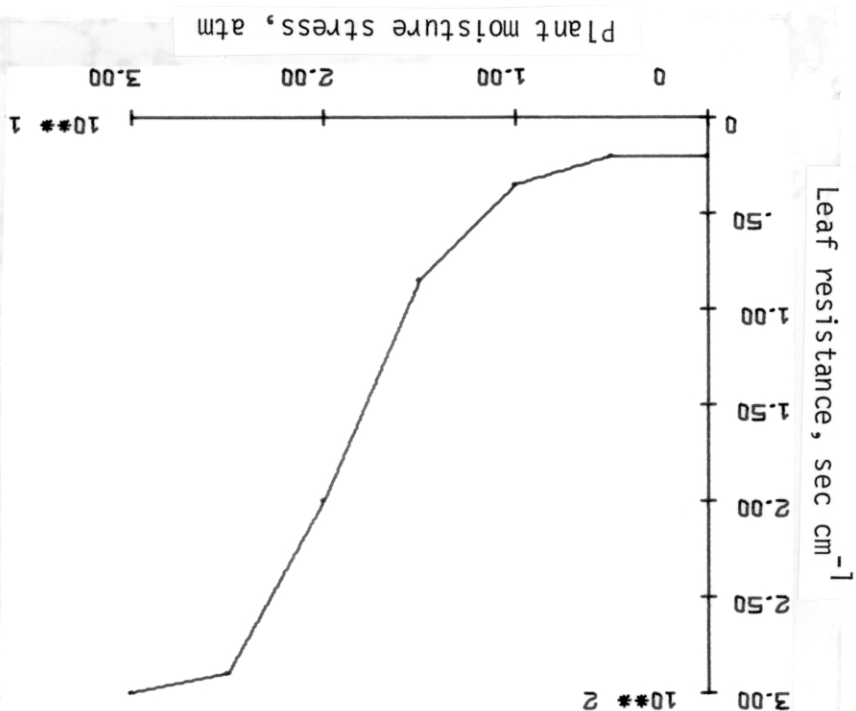
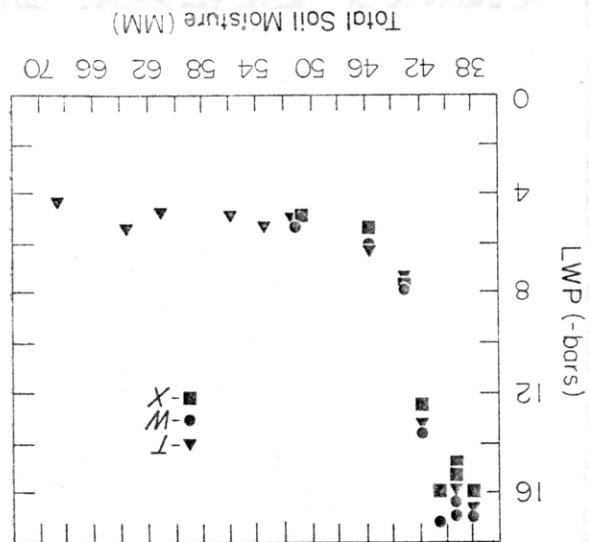


Figure 14. Determination of available water in soil by monitoring predawn water stress in *Pinus resinosa* (Sucoff, 1972).



is not the only control.

Sucoff (1972) showed the relationship coupling root zone water to plant moisture stress in 7 - 8 m *Pinus resinosa* (Fig. 14). For my purpose I translated units on the x-axis to remaining available water percentage. This allows the estimation of plant moisture stress based upon the fraction of remaining water below field capacity in the three soil levels according to this relationship. As long as more than 20 percent of the original soil water storage capacity is present plant moisture stress remains minimal, 2 atm plus 1 atm per 10 m in tree height for the hydrostatic gradient. Below 20 percent water content, a linear relationship was modeled so that at water storage of 0.0, plant moisture stress is 30 atm and subsequently leaf resistance is 300 sec cm⁻¹.

Soil level water uptake is modeled by a set of step-wise exponential drawdown curves (Krygier, 1971). Upon transpiration demand, the first level is used as sole water supply for the tree until level A water content is 20 percent. Woods (1965) found when injecting tritium into the soil that water uptake by oak trees from 0 - 30 cm depth was 38 times the volume taken up from 30 - 60 cm. The primary water demand then drops to level B, then level C with an exponentially decreasing residual coming from level A, B, etc., until they are empty. This water enters

the sapwood to recharge at least partially, what the sapwood has lost to daily transpiration. As water runs low in the soil levels, plant moisture stress increases, increasing leaf resistance and decreasing the transpiration demand.

Two threshold functions have been built into the model. First is a response to low soil temperature. Reed (1971) and Reed (1968) showed that new foliage on Douglas-fir will if root temperatures are lowered below 2°C. Havranek (1972) reported European larch and spruce to reduce transpiration by 50 percent at soil temperatures of 2°C compared to 15°C. I induced transpiration reduction in the model by increasing plant moisture stress linearly from 3 - 30 atm as soil temperature dropped from 5° to -2°C. In these cases PMS was calculated independently of the available soil water fraction. The second threshold function used was a complete transpiration shutdown when input absolute humidity deficit went above $30 \times 10^{-6} \text{ g cm}^{-3}$.

Ambient humidity is input as absolute humidity deficit from the saturated leaf to the air because this is the form needed for the transpiration equation. During my field studies I discovered Douglas-fir and grand fir with extreme leaf resistances above 1,000 sec cm^{-1} at ABSHD of $36 \times 10^{-6} \text{ g cm}^{-3}$ which would result in a negligible transpiration rate. This was discussed in detail elsewhere.

Consequently for modeling I added a simple on - off switch to the transpiration function. Whenever the input absolute humidity deficit exceeds $30 \times 10^{-6} \text{ g cm}^{-3}$ transpiration will automatically drop to 0. This threshold was never exceeded with the climatic data used to run these simulations.

Four environmental parameters were needed to run the model and are entered on a daily basis. These are average ambient humidity (or absolute humidity deficit), daylength, soil temperature and precipitation. A daily average of dewpoint, air and soil temperature and precipitation was available from the Andrews Climatological Station, Coniferous Biome, IBP, for a period from May 10 - October 27, 1972. From the dewpoint and air temperature data, an average absolute humidity deficit for the day is computed. A soil temperature and precipitation are input directly. A modified sine wave is used to compute seasonal daylength fluctuations for that period. Light is not entered as a variable. Transpiration is considered to proceed full force for the input daylength and cease at night.

This general model structure has been adapted to three sets of simulation exercises. The first considered an 80 meter Douglas-fir at the H. J. Andrews Forest. Tritiated water experiments in June, 1972, were used to estimate transpiration rates and sapwood storage capacity. Leaf

area was estimated using the regression of sapwood cross-sectional area at DBH vs. foliage biomass (Grier, pers. comm.). Rooting zone H_2O capacity was estimated as water held in an area 1 m deep and 10 m in radius from the tree base. Transpiration for the 1972 growing season was simulated using the input environmental data.

A second simulation effort was made by attempting to estimate transpiration for Watershed 10 on the H. J. Andrews. The leaf area and sapwood were summed for all trees on the watershed to develop a stand "super-tree" model. Rooting zone water capacity for the entire watershed was taken from hydrologic data.

The third simulation effort was the standard 2 meter tree model used as an example in the explanation of the model structure. It was intended to be used to compare transpiration response differences using different leaf resistance control curves as indicated by my thesis data. This proved impossible as will be discussed later.

SIMULATION RESULTS

The transpiration simulation for the 80 meter tritiated water tree on the H. J. Andrews provided an opportunity to validate the model structure. The tritiated water experiment provided values for sapwood capacity and average daily transpiration for late June, which would otherwise have required estimation. The model was initially run with a set of constant climatic data representing a late June average. Average absolute humidity deficit was set at $7.0 \times 10^{-6} \text{ g cm}^{-3}$ and daylength at $5.76 \times 10^4 \text{ sec}$. From Kline (pers. comm.) the daily transpiration was known to be 530 l day^{-1} . The first simulation run, using an average minimum leaf resistance of 5 sec cm^{-1} , estimated transpiration at $4,185 \text{ l day}^{-1}$. This rate effectively emptied the soil water reservoir in 20 days. It quickly became obvious that a minimum of 40 sec cm^{-1} leaf resistance was necessary to simulate transpiration of 530 l day^{-1} . This drastic increase in leaf resistance can be justified on two counts. First, the minimum of 5 sec cm^{-1} was based on data obtained on new foliage. At least 70 - 80 percent of the foliage on an 80 meter tree can be expected to be anywhere from 1 - 6 years old. It has been shown that leaf resistances in red pine increase from 11 sec cm^{-1} in new needles to 22 - 28 sec cm^{-1} in 2 - 4 year old foliage (Waggoner and Turner, 1971).

Second, an 80 meter tree will have a hydrostatic gradient of 6 - 8 atm (Tobiesse et al., 1971). This will produce base PMS values of 9 - 11 atm on the upper portions of the tree. If PMS is a major controlling factor for leaf resistance response, needles on the upper limbs of the tree will be limited by this high PMS to leaf resistances considerably above 5 sec cm⁻¹. The effect of the hydrostatic gradient on leaf resistances needs study.

Based on these two justifications the average minimum leaf resistance was increased to 20 sec cm⁻¹ and a hydrostatic gradient of 1 atm per 10 meter tree height were incorporated into the model structure. Also at this time the 170 day climatic data file (running from May 10 - October 27, 1972) was added to replace the constant climatic data values. A simulation was then run for the period approximating the growing season for the summer of 1972. Simulation results showed a maximum transpiration rate attained on August 9 of 1,135 l. For the entire period transpiration was 66,000 l compared with the estimated soil water capacity of 47,000 l. The upper soil level A was depleted below 20 percent of capacity on July 5. Between May 10 and July 5 four rainfalls had occurred, on June 9 level A had been completely refilled. From July 5 - July 28 when no rainfall occurred, soil water level B was depleted to 20 percent of capacity. Rainfall during the

period from August 16 - August 18 refilled level A. All three levels were depleted below 20 percent of capacity by September 4. Transpiration was reduced by increased leaf resistance caused by the increased moisture stress over the period September 4 - September 19. Beginning September 19 rainfall was more frequent filling level A by September 21 and level B by September 25. Due to this rainfall, decreased daylength and decreasing average daily absolute humidity deficits, actual and potential transpiration was greatly lowered for the rest of the period ending October 27. No excess water was lost to runoff/seepage during the entire period though. The only runoff/seepage lost during the entire period was during the period May 20 - 26 where soil levels were still near capacity and heavy rainfall occurred. Throughout the summer season the sapwood level fluctuated according to the magnitude of the daily transpiration and subsequent recharge. The minimum sapwood level attained was about 75 percent of capacity and occurred occasionally throughout the period July 4 - September 4 corresponding to the period of highest transpiration demand. Before and after this period demand was low enough that virtual complete recharge was possible almost every night. On September 4, when reduction in transpiration began, the sapwood was able to recharge. After September 19 when the fall rain began, sapwood remained full to the end of the simulation period.

The goal of the transpiration simulation for the 80 meter tree was to examine the dynamics of the system throughout the summer. The second simulation run was a transpiration estimation for a 10.4 hectare watershed. Unlike the first model the purpose of this simulation was purely quantitative, to estimate total transpiration for the watershed over the period May 10 - October 27. In order to fit a watershed to this model a hypothetical "super-tree" was required. Since the watershed is an intensive study site for the Oregon IBP, Coniferous Forest Biome, many necessary data were available for parameter estimation. From hydrology subsystem data the soil water storage in the rooting zone analogous to levels A, B, and C was 3.3×10^7 l (Dr. Dennis Harr, pers. comm.). Dr. Chuck Grier provided an estimate of total sapwood storage for all trees on the watershed of 6.0×10^6 l of water. Also from Dr. Grier's biomass data total transpiring leaf surface area for all conifers was estimated as 2.7×10^{10} cm². Obviously the dynamics of modeling a watershed as a single tree are meaningless. No attempt will be made to rationalize this approach. The only result considered was the estimation of total transpiration.

A water balance for Watershed 10 provided a hydrologic estimate of plant transpiration. This was based on an average of 30 years climatic data supplied by the U.S.

Forest Service. By mass balance subtraction, Dr. Harr calculated that of the average 234 cm of precipitation impinging on the watershed, 51 cm or 5×10^7 l of water are lost to plant transpiration on an average year. The estimate generated by my simulation was 7×10^7 l for the 170 day modeling period during which time probably 90 percent of the yearly transpiration occurs. Remembering that the summer of 1972 was abnormally hot and dry, one would expect transpiration for that year to be somewhat above a 30 year average transpiration. It appears then, that although the model structure is not really suitable for handling a watershed it is capable of generating fairly accurate estimates of total transpiration over a long period of time.

My final modeling effort was an attempt to simulate transpiration in several species of conifers using the different leaf resistance response patterns found during my field research. Since my data were taken on 1 - 2 m trees I made the necessary parameter estimations on the basis of a hypothetical 2 meter tree as described earlier. Three representative response patterns were chosen for modeling. First was the Douglas-fir response, a sigmoid curve from 20 - 300 sec cm^{-1} as PMS went from 0 - 30 atm. This response was chosen to represent fairly drought hardy trees with good stomatal control. A western hemlock response was chosen to represent mesophytic trees with

only fair stomatal control. The response curve modeled was a linear increase in leaf resistance from 20 - 100 sec cm^{-1} as PMS went from 0 - 20 atm. Above 20 atm leaf resistance was 300 sec cm^{-1} . Finally a "no stomatal control" curve, typifying noble fir and Sitka spruce was modeled. Leaf resistance stayed at 20 sec cm^{-1} until PMS reached 20 atm; then was increased to 300 sec cm^{-1} . Again the models were run using the 170 day climatic data from the IBP Climatological Station on the H. J. Andrews Experimental Forest. In effect I was testing the adaptability in terms of transpiration control of these species to that site.

The 2 meter Douglas-fir simulation resulted in a total transpiration of 720 l for the period, compared to a total soil water capacity of 450 l. This ratio of total transpired water/soil water capacity of 1.6 is very similar to that ratio for the 80 meter tree of 1.4. In this simulation level A was depleted to below 20 percent capacity on June 4, then after a rain again on June 22. Level B was depleted by July 7. The total soil water supply dropped below 20 percent capacity on July 19 initiating progressive reduction of transpiration. During the period July 19 - August 16 transpiration was reduced by increasing leaf resistance brought on by increasing PMS. Actual transpiration dropped below 10 percent of potential

or demanded transpiration by the end of this period. After a brief reprieve resulting from rainfall on August 16 - 17, transpiration was again limited from August 24 - September 21. After September 21 recurring rainfalls recharged the soil water levels until at the end of the period, October 27, levels A and B were full and C 75 percent full. There is a very significant comparison to be made in the results of the 80 meter and 2 meter Douglas-fir. The 80 meter tree was subjected to a situation of reduced transpiration from September 4 - September 21, 17 days. The 2 meter tree by contrast had transpiration reduced from July 19 - August 16 and August 24 - September 21, a total of 54 days. One cause of this difference is the lower average minimum leaf resistance on the 2 meter tree due to lack of a hydrostatic gradient, a greater percentage of young needles and little self shading. Also the 2 meter tree has virtually no sapwood storage capacity. The sapwood water in the 80 meter tree is enough to run all transpiration for 5 - 10 days. The sapwood water in the 2 meter tree can be drained as much as three times in one day when transpiration is not being limited. The simulations of western hemlock and noble fir transpiration revealed an erroneous modeling assumption. On July 27 the three soil levels dropped below 20 percent

capacity. This caused the PMS to increase but since leaf resistance was not significantly affected by increasing PMS, transpiration was reduced only slightly. This resulted a demand greater than the supply and caused the sapwood compartment to empty to zero. Sapwood is the coupling between the soil and the leaves. When it computed a negative value and became non-functional, the leaves demanded a certain quantity of water for transpiration, the soil relinquished a certain amount based on PMS and remaining soil water volume, but this demand and supply were not coupled. The basic assumption was made when building the model structure on one day time resolution that the sapwood would have the capacity to provide one days transpiration and then would be recharged that night. This assumption is false on the 2 meter tree. At least two revisions appear to be appropriate. First the daily time step used for the 80 meter tree model is too long for the 2 meter tree model. Being a discrete model, the computer only makes adjustments in the status of each compartment once each day. When transpiration exceeds the capacity of the sapwood compartment, that compartment must be recharged during the day or within the iteration, which is impossible. In actuality the sapwood is continuously being recharged at all times and would not empty until water in the soil was exhausted. For modeling purposes

a basic rule must be that the time step is shorter than the depletion time for any compartment in a discrete model. Secondly an overriding transpiration control must be included for conditions when demanded transpiration rate continues to exceed the recharge rate emptying the sapwood on simulations where no stomatal control reduces transpiration. Either mesophyll resistance or wilting needles would slow transpiration. By definition the tree cannot transpire more water than it has supplied to it. This last correction illustrates another serious modeling error. PMS is obviously not the only control of leaf resistance but was necessary due to lack of data conclusively demonstrating other controls. When other leaf resistance controls are identified and quantified the overriding transpiration control now necessary will be replaced.

A number of other characteristics of the model require comment. For convenience the model assumes no transpiration at night. Usually absolute humidity deficits are low and stomata often are closed at night but this omission causes some loss of realism. The model also does not account for growth or death of needles or for seasonal changes in their characteristics. For simulations of short duration on yearly time scales these deficiencies may need consideration. Averaging leaf resistance response

For an entire crown is dangerous although necessary at this resolution level. A more realistic model must address itself to needle age, hydrostatic gradient effects, radiation and shadings. Temporal and spatial variations in leaf resistance responses in a crown should also be included. These corrections require a model of finer time resolution and data which at present are not available. Parameter estimation will remain a problem. Estimation of the soil rooting zone of a tree, the available sapwood capacity and the leaf surface area are particularly difficult. Also flow of water from unsaturated soil or seepage into the rooting zone was not considered in modeling of the soil water levels and flows. Finally the model is dependent upon the accuracy of climatic data used for input.

CONCLUSION

Douglas-fir and grand fir appeared to have good leaf resistance control to regulate transpired water loss. Increasing plant moisture stress was closely correlated with increasing leaf resistance in both species. Humidity

also seemed to have an effect on leaf resistance in grand fir but little in Douglas-fir except under extreme conditions. Results would have been more conclusive if the sampled trees had reached higher plant moisture stresses at least to 25 atm.

The most interesting aspect of the western hemlock data was the limited range of leaf resistances, 12 - 75 sec cm⁻¹. Sitka spruce needs to be studied on a site nearer its environmental limits. The Cascade Head site, which developed only 4 atm PMS at the end of the summer was not harsh enough to require transpiration control in 1972, so accurate conclusions cannot be drawn on stomatal control of Sitka spruce. Noble fir appeared to have no stomatal control up to 16 atm PMS and an ABSHD of 18.0 x 10⁻⁶ g cm⁻³. This lack of control could restrict it to higher elevation where the snowpack results in a shorter growing season and low PMS.

On all counts results would probably have been more conclusive if higher PMS had been attained by the sample trees. Also diurnal plant moisture stress data may

correlate well with diurnal leaf resistance response, particularly for western hemlock, which showed some control but largely from an unmeasured source. Radiation data may have been helpful since stomatal aperture response has been correlated with light (Reed, 1971).

Infiltration pressure data appeared much poorer than are probably warranted. The infiltrometer has been used in a number of other studies and produced meaningful data. A number of reasons may have caused problems here. First many studies use stomatal infiltration pressure in a relative sense and never attempt to correlate it to actual leaf resistance. Second, when attempts are made to correlate infiltration pressure and leaf resistance the methods used have been rather crude. Fry and Walker (1967) and

Reed (1971) described methods involving excision of twigs measurement of their weight loss in a controlled humidity room to estimate transpiration then measurement of infiltration pressure of needle samples. I have found branch excision to have an immediate effect on leaf resistance in all except very well watered trees. Leaf resistance increase will often begin within 60 seconds of excision, much faster than stomatal response time. Consequently any transpiration or leaf resistance measurement made on excised tissue does not accurately reflect the status of the intact tissue. Finally, by necessity of porometer

limitations I was forced to use only current needles on
 branch tips. It is well known that these needles are more
 sensitive and more variable than older needles. In fact
 it is for that reason that infiltration data are commonly
 taken on one-year old foliage. The limitation of the
 porometer to new foliage is a serious one. Until it can
 be alleviated by a different chamber design, the utility
 of the porometer is restricted. A null balance porometer
 described by Beardsell (1972) does not have this restriction
 and may prove of greater utility.

Fry (1965), Swank (1972) and Lopushinsky (1969) all
 found evidence of mesophyll resistance in Douglas-fir
 although none had absolute measurements. The measurement
 of 300 - 1,200 sec cm⁻¹ in Douglas-fir and grand fir are
 well beyond known cuticular resistances. Also infiltration
 pressures indicated stomata to be at least partly
 open. Even though the accuracy of the porometer is re-
 duced at these extremely high leaf resistances, I believe
 mesophyll resistance may have a role in transpiration
 reduction under certain conditions.

Only a more complete simulation model can generate
 answers, individual experiments can not adequately reflect
 coupled interactions. My model does suggest some inter-
 esting hypotheses and study problems. First it dramatically
 illustrated that average minimum leaf resistance for a

tree may be much higher than studies with seedlings has suggested. A 2 meter tree might have an average minimum resistance of 20 sec cm^{-1} and an 80 meter tree of 40 sec cm^{-1} . Second, if plant moisture stress does control leaf resistance, the hydrostatic gradient would cause a theoretical maximum in tree height. As a tree grew the increasing PMS on the upper limbs would cause new needles to maintain increasingly higher leaf resistances. Above a limit needles would have closed stomata and maximum leaf resistance as soon as the needles hardened off, if full development were possible in the first place. The comparison of 80 meter tree and 2 meter tree results show the importance of sapwood storage and higher leaf resistance in larger trees. If these results can be extrapolated to a new seedling with all current foliage, virtually no sapwood and a small rooting zone, the task of regeneration on a hot, dry clearcut is brought into greater perspective. In a purely modeling context it is rather disturbing to discover that a model adequate to describe transpiration functions in an 80 meter tree is totally inadequate for a 2 meter tree. This result is very important as modeling becomes more widespread. A model built for one purpose may be used by another person for a different purpose. The result generated may be wrong but to the person unfamiliar with the model, the errors may not be obvious.

Assuming a more adequate instrument will soon be available for measurement of leaf resistance without sampling restriction a number of research projects are needed. Spatial variability of leaf resistance of conifers in terms of height (hydraulic gradient), needle age and crown position require study. Diurnal and seasonal response patterns, related to important environmental and physical parameters are required. Extensive knowledge of leaf resistance patterns during the winter and at night are also lacking. Present modeling efforts in the fields of hydrology, nutrient cycling, primary productions and water relations are hampered by the lack of this knowledge. Since transpiration control is of such paramount importance in the distribution and competition of Pacific Northwest conifers, these would make worthwhile research projects.

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APPENDICES

FORTRAN program computing leaf resistance
from porometer inputs; also absolute humidity
deficit from sling psychrometer input.

APPENDIX I

```

PROGRAM PORO
COMMON/DATA/RPX(5),RY(5),VX(5),VY(5),CMX(7),CMY(7)
DATA ((RPX(1),1,5)=15.,20.,25.,30.,35.),
      ((RY(1),1,5)=1.50,1.50,1.50,1.50,1.50),
      ((VX(1),1,5)=15.,20.,25.,30.,35.),
      ((VY(1),1,5)=137.,110.,83.,56.,29.),
      ((CMX(1),1,7)=45.,51.,57.,63.,69.,75.,80.),
      ((CMY(1),1,7)=10.,15.,20.,25.,30.,35.,39.)
DIMENSION IDATE(3),ITEMP(2)
VC=29.0
IFLAG=0
100 READ (5,1) ISITE, IDATE, TIME, TDO, TWO, TREE, RM1, RM2, CM, TM,
      C INF, PMS, WTINIT, WTEND
1 FORMAT (11,X,3I2,X,14,2F3.0,X,A5,X,2F1.0,F3.0,F5.1,13,
      C F4.0,2F5.1)
IF (EOF(5)) CALL EXIT
5 FORMAT (11)
IF (IFLAG.EQ.0) WRITE (6,5)
IFLAG=1
AREA=(WTEND-WTINIT)/14.5
RM1=RM1*10.
RM2=RM2*10.
IF (TM.EQ.0.0) GO TO 100
C=F(CM,CMX,CMY,7)
RH0=H(RM1,RM2,C)
RHT=H(RM2,RM1,C)
RP=1.50
V=(-4.5*CM+367.0)+VC
RS=AREA*TM/V/ALOG((100.-RH0)/(100.-RHT))-RP
RM1=RM1/10.
RM2=RM2/10.
PMS=PMS/14.7
TD=.55*(TDO-32.)
TW=.55*(TWO-32.)
ESD=6.11*EXP((17.27*TD)/(TD+237.30))
ES=6.11*EXP((17.27*TW)/(TW+237.30))
E=ES-(6.6E-4)*1000.*(TD-TW)
VPD=ESD-E
TD=TD+273.16
ABSHD=((2.17E-4)*VPD/TD)*1.0E+6
WRITE(6,4) ISITE, IDATE, TIME, TDO, TWO, ESD, VPD, ABSHD, TREE,
1 RM1, RM2, CM, TM, INF, PMS, RS
4 FORMAT(14,2X,I2,-1,I2,-1,I2,15,2X,F2.0,X,F2.0,2X,
2 F5.2,X,F5.2,X,F5.2,2X,A5,F3.0,10,F2.0,
C F7.1,5X,F5.1,5X,I2,F5.1,F7.1)
GO TO 100
END

```

```

FUNCTION H(X,Y,C)
COMMON RPX(5),RY(5),VX(5),VY(5),CMX(7),CMY(7)
COMMON/DATA/R4(4),R5(4),R6(4),R7(4),TX(4)
DATA ((R4(1),1,4)=28.1,25.4,23.2,21.1),
1((R5(1),1,4)=29.6,26.8,24.5,22.3),
2((R6(1),1,4)=31.1,28.1,25.7,23.4),
3((R7(1),1,4)=34.9,31.7,29.2,26.8),
4((TX(1),1,4)=4.5,16.0,27.0,38.0)
IF (X .GE. 50.) GO TO 1
H=F(C,TX,R4,4)
IF (X .EQ. 40) GO TO 110
Z44=F(C,TX,R5,4)
H=H+(Z44-H)*(X-40.)/10.
GO TO 110
1 IF (X .GE. 60.) GO TO 2
H=F(C,TX,R5,4)
IF (X .EQ. 50.) GO TO 110
Z55=F(C,TX,R6,4)
H=H+(Z55-H)*(X-50.)/10.
GO TO 110
2 IF (X .EQ. 60.) H=F(C,TX,R6,4)
IF (X .EQ. 70.) H=F(C,TX,R7,4)
110 RETURN
END
FUNCTION F(X,XX,YY,N)
DIMENSION XX(7),YY(7)
Y=0.0
M=2
M1=M+1
I=M1
IF (X .LT. XX(1)) GO TO 33
DO 1 I=M1,N
DO 1 I=M1,N
IF (X .LT. XX(1)) GO TO 33
1 CONTINUE
GO TO 33
2 IF ((XX(1)-X) .LT. (X-XX(1-1))) I=I+1
33 M1=MAX0(I,M1)
M1=MIN0(N,M1)
M2=M1-M
DO 3 K=M2,M1
PKX=1.0
PKXK=1.0
DO 4 I=M2,M1
IF (1 .EQ. K) GO TO 4
PKX=(X-XX(1))*PKX
PKXK=(XX(K)-XX(1))*PKXK
4 CONTINUE
Y=YY(K)*PKX/PKXK + Y
3 CONTINUE
F=Y
RETURN
END

```

FLEX I components of model
simulating transpiration

APPENDIX II


```

FUNCTION F0101(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0101=B(6)
  IF (Z(1).LE.B(6))
    RETURN
  END
FUNCTION F0404(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0404=Z(1)-B(6)
  IF (Z(1).LE.B(6))
    RETURN
  END
FUNCTION F0102(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0102=X(1)-B(1)
  IF (X(1).LE.B(1))
    RETURN
  END
FUNCTION F0203(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0203=X(2)-B(2)
  IF (X(2).LE.B(2))
    RETURN
  END
FUNCTION F0304(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0304=X(3)-B(3)
  IF (X(3).LE.B(3))
    RETURN
  END
FUNCTION F0105(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0105=G(15)
  RETURN
END
FUNCTION F0205(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0205=G(16)
  RETURN
END
FUNCTION F0305(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0305=G(17)
  RETURN
END
FUNCTION F0506(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  F0506=G(18)
  RETURN
END

```

```

FUNCTION G01(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G01=(X(1)+X(2)+X(3))/(B(1)+B(2)+B(3))
RETURN
END
FUNCTION G02(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G02=X(1)/B(1)
RETURN
END
FUNCTION G03(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G03=X(2)/B(2)
RETURN
END
FUNCTION G04(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G04=X(3)/B(3)
RETURN
END
FUNCTION G05(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G05=B(9)
RETURN
END
FUNCTION G06(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G06=B(04)
IF (G(18).LE.B(4))
G06=G(18)
RETURN
END
FUNCTION G07(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G07=G(09)
IF (Z(4).LE.5.)
G07=G(08)
RETURN
END
FUNCTION G08(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G08=-3.85*Z(4)+22.3
IF (B(5).GT.10.)
G08=30-140*G(01)
IF (Z(4).LE.0.)
G08=30.
RETURN
END
FUNCTION G09(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G09=2+B(5)/10.
IF (G(01).LT..2)
G09=30-140*G(01)+B(5)/10.
RETURN
END

```

```

FUNCTION G10(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G10=0.
IF (G(02).GT..2)
RETURN
END
FUNCTION G11(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G11=0.
IF (G(03).GT..2)
RETURN
END
FUNCTION G12(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G12=0.
IF (G(04).GT..2)
RETURN
END
FUNCTION G15(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F1=X(1)-G(10)
FAC=G(06)-G(10)
G15=G(10)+FAC*EXP((FAC/F1)*((X(1)/B(1))-3.))
IF (G(06).LE.G(10))
RETURN
END
FUNCTION G16(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
FAC=G(06)-G(15)-G(11)
F1=X(2)-G(11)
G16=G(11)+FAC*EXP((FAC/F1)*((X(2)/B(2))-3.))
IF (G(06)-G(15).LE.G(11))
G16=G(06)-G(15)
RETURN
END
FUNCTION G17(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
FAC=G(06)-G(15)-G(12)
F1=X(3)-G(12)
G17=G(12)+FAC*EXP((FAC/F1)*((X(3)/B(3))-3.))
IF (G(06)-G(15).LE.G(12))
G17=G(06)-G(15)-G(16)
RETURN
END
FUNCTION G18(K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
A=G(07)
G18=Z(2)*B(8)*Z(3)/S1(A,B,Z)
IF (Z(2).GE.B(7))
RETURN
END

```

```

FUNCTION S1(G7,B,Z)
  DIMENSION B(1),Z(1),F(10),P(10)
  DATA ((F(1),I=1,9)=20.,20.,35.,85.,210.,290.,300.,
    P(1)=0.,
    DO 5 I=1,8
    P(I+1)=P(I)+5.
    DO 10 I=1,8
    IF(G7.LE.P(I)).OR.G7.GT.P(I+1)) GO TO 10
    IN=1
    GO TO 12
  10 CONTINUE
  WRITE(61,100) G7
  100 FORMAT(' ERROR IN INTERP S1--THE G7 VAL=',E10.3)
  CALL EXIT
  12 S1=F(IN)+((F(IN+1)-F(IN))/(P(IN+1)-P(IN)))*(G7-P(IN))
  RETURN
END

```

```

SUBROUTINE ZCOMP(K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
  READ(5,100)KD,TD,DP,PPT
  100 FORMAT(7X,13,4X,F3.0,10X,F3.0,9X,F5.2)
  IF(EOF(5))CALL EXIT
  Z(1)=PPT*3.1E+4
  Z(4)=10.0
  XK=KD-79.
  IF(XK.LT.0.)XK=286.+KD
  DHRS=3.5*(SIN(XK*.01721))+12.0
  Z(3)=DHRS*3600
  ESD=6.1078*EXP((17.269*TD)/(237.30+TD))
  ES=6.1078*EXP((17.269*DP)/(237.30+DP))
  VPD=ESD-ES
  TD=TD+273.16
  Z(2)=((217.0E-6*VPD)/TD)
  RETURN
END

```


XN(1)=1.0E+5
 XN(2)=1.75E+5
 XN(3)=1.75E+5
 XN(4)=0.0
 XN(5)=3.2E+3
 XN(6)=0.0
 INPUT=60

B(1)=1.0E+5
 B(2)=1.75E+5
 B(3)=1.75E+5
 B(4)=1.0E+5
 B(5)=1.0
 B(6)=5.0E+5
 B(7)=30.0E-6
 B(8)=3.5E+5
 B(9)=3.2E+3
 INPUT=60

LAG=1 LAGX()=1,2,3,4,5,6
 XDC ,1)=1.0E+5,1.75E+5,1.75E+5,0.,3.2E+3,0.
 TTYPRT=30
 YMAX=12
 TTY=Y(1) TTY=Y(3) TTY=Y(5) TTY=Y(9) TTY=Y(11)
 TTY=Y(2) TTY=Y(4) TTY=Y(6) TTY=Y(10) TTY=Y(12)
 LPRT=2 LPUN=6
 LP=Y(1) LP=Y(2) LP=Y(3) LP=Y(4) LP=Y(5)
 LP=Y(6) LP=Y(7) LP=Y(8) LP=Y(9) LP=Y(10)
 LP=Y(11) LP=Y(12)
 DPRT=1 DUMPLUN=10
 D=Y(1) D=Y(2) D=Y(3) D=Y(4) D=Y(5)
 D=Y(6) D=Y(7) D=Y(8) D=Y(9) D=Y(10)
 D=Y(11) D=Y(12)
 INPUT=60