

AN ABSTRACT OF THE THESIS OF

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Title: PHYSIOLOGICAL RESPONSES OF FOUR DOUGLAS-FIR
POPULATIONS IN THREE CONTRASTING FIELD
ENVIRONMENTS

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When trees from 16 populations of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco. var. menziesii) were grown at ten geographically diverse locations for seven years, those from a Vancouver Island source were among the top three for height growth on nine of the ten plantations (Rowe and Ching, 1974). In contrast, growth of a west central Oregon source consistently ranked only poor or fair in comparison to other sources. Although each population was planted with the others at its home site, seldom did it grow better there than most of the introduced populations.

I hypothesized that observed differences in growth among Douglas-fir populations were due to inherent differences in stomatal behavior and/or allocation of growth resources. I also hypothesized that definition of seasonal contrasts between field environments would

help identify periods of environmental stress which would, in turn, help determine the factors most important in limiting productivity on different sites.

I attempted to link studies of genetics, physiology and land classification together to provide a better biological foundation for improving forest productivity. I observed moisture stress, stomatal aperture, leaf resistance, cambial and leader growth for four populations of Douglas-fir at a Coast Range, Willamette Valley and Cascade Mountain plantation. Climatic factors including radiation, humidity, rainfall, soil and air temperature were recorded at each location for the 1971 growing season.

Stomatal behavior for the four populations at the three locations was similar. In the spring before soils had warmed, stomata were partly closed at night and nearly wide open during the day. In early summer, stomata were wide open day and night. Later, as drought stress increased, stomata were closed at night, and partly closed during the day. After fall rains, stomata were again open day and night.

Leaf conductance at the peak of drought was variable during the day, suggesting cyclic opening and closing of stomata. The southern source appeared to have higher conductance during the day although this trend could not be confirmed by statistical test.

Except for unusually high values in the spring, plant moisture

stress followed the expected daily and seasonal pattern. There were characteristic differences between locations but all populations were similar at a given area.

A simulation of photosynthesis was developed around a model which predicted daily CO₂ fixation per square decimeter of foliage. Functions were included to reduce potential photosynthesis under conditions of high moisture stress, cold soils, and frost. Predicted photosynthesis for three areas revealed major differences in seasonal activity and yearly potential.

The simulation was useful in defining seasonal contributions to total production, and the effect of drought and cold stress. It also provided an index to site productivity. At the dry interior Coast Range site, 31 percent of predicted CO₂ uptake occurred in the dormant season, while at the Cascade site, less than 10 percent accumulated in the same period. Almost 60 percent of growing season photosynthetic potential was not realized due to moisture stress in the interior Coast Range. At a Willamette Valley site on deep soils, less than 40 percent of growing season potential was lost because of moisture stress.

The photosynthesis index, along with indexes of moisture stress and temperature, helped define more clearly the environmental restrictions on forest productivity at different sites. These methods should be useful in matching the biological potential of seed sources to suitable forest environments.

Although there were accumulated differences in size of individuals from certain sources, cambial and leader growth of all populations were similar for the 1971 growing season. This was true for actual growth and when growth increment was normalized for initial tree size or needle mass. Partitioning of biomass into needles, branches and bole differed by area, but not by population. Trees at the Coast Range site had more needle mass per unit bole volume and grew more per unit leaf area than those in the mountain plantation.

The large differences in growth between areas were interpretable through the physiological indexes which were generated from environmental observations at each site. Analysis of growth indicated that size differences among populations were either diminishing or remaining constant. Variations in height which prompted this study were attributed to distinctive behavior effective during establishment. Allocation of carbohydrates, photosynthetic efficiency, hormone balance, or stomatal control may be involved in explaining contrasts in early growth.

Future efforts to explain genetic differences in growth of coastal Douglas-fir should concentrate on times when individual trees are under environmental or competitive stress.

Physiological Responses of Four Douglas-fir
Populations in Three Contrasting
Field Environments

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PHYSIOLOGICAL RESPONSES OF FOUR DOUGLAS-FIR POPULATIONS IN THREE CONTRASTING FIELD ENVIRONMENTS

I. INTRODUCTION

Research into the tree-soil-environment system continues with the practical goal of understanding how to increase wood production on a shrinking land base. This study is part of a larger effort to understand important plant processes affecting tree survival and growth.

The Douglas-fir provenance study started in 1959 under the direction of Dr. K.K. Ching (School of Forestry, Oregon State University, Corvallis) now provides an excellent opportunity to compare growth and physiological responses of 16 populations of Douglas-fir in a variety of field environments. Sources ranging from Vancouver Island, B. C. to southern Oregon are available.

The growth of all populations was compared 3 years after planting (Ching, 1965) and again after 7 years (Rowe and Ching, 1974). Height growth varied significantly by plantation suggesting marked climatic diversity. At each plantation, differences in growth of populations were also noted. This study is the first attempt to explain the growth differences through assessment of physiological behavior of populations growing in field environments.

I hypothesized that the observed variation in growth among

Douglas-fir populations was due to inherent differences in stomatal behavior and/or allocation of growth resources. Both of these possibilities were subject to direct measurement. I also hypothesized that definition of seasonal contrasts between field environments would help identify when populations were subject to stress, which would in turn determine the factors most important in limiting productivity. The latter possibility was evaluated by monitoring field environments and assessing photosynthesis by means of computer simulation.

Differences in growth and survival of various populations of Douglas-fir have previously been attributed to genetically fixed differences in stomatal control (Kral, 1965). Stomata control both water use and CO_2 fixation, so they are of primary importance in striking the balance between excessive water loss and reduced carbohydrate production. This is especially true in the Pacific Northwest where water supply is adequate during much of the year, but may be limited for part of the growing season.

To increase forest productivity, our ability to forecast long term implications of management decisions must be improved. This requires, in part, better knowledge of how plants respond to their environment, how populations differ in these responses, and how environment varies over a complex landscape (Haugberg, 1967). By combining knowledge of genetics, physiology, and environment we

may improve forest productivity by successful transfer of desirable seed sources to appropriate areas.

Experimental Design

From the ten plantations available in the provenance study I chose three, representing a diversity of environments in western Oregon. An interior Coast Range plantation near Corvallis, Oregon provided a warm, summer dry environment. A second plantation was located on a deep clay loam soil in the Willamette Valley 32 km north of Corvallis. This was a warm, relatively moist site. The third plantation was cool and moist, being located in the Cascade Mountains near Molalla, Oregon. These three locations provided a contrast in elevation, slope, aspect, soil, and winter snow pack which should be sufficient to promote genetic differences in growth and stomatal behavior. These plantations will be referred to as coast range, valley and mountain, respectively.

At each of the three plantations, 16 seed sources were planted in blocks of 121 trees each. For my study I chose four of the 16 sources to characterize stomatal behavior, plant moisture stress and growth. A Vancouver Island, B.C. source was selected because it grew best on 9 out of 10 sites (Rowe and Ching, 1974). A southwestern Oregon source was included because it grew slowly on all plantations. The other two sources were intermediate in growth and were from the

interior Coast Range and Cascade Mountain locations mentioned as study sites. These sources will be referred to as northern, southern, coast range, and mountain, respectively. A summary of source locations and their elevations is shown in Table 1-1.

Table 1-1. A summary of seed source names, locations, geographic positions and elevations.

Source	Location & cooperator	Latitude & longitude		Elevation (m)
northern	Vancouver Island, B. C.	49 ^o	10'	840
	MacMillan Bloedel Ltd.	126	50	
mountain	Molalla, Oregon	45	10	1,050
	Crown Zellerbach Corp.	122	0	
coast range	Corvallis, Oregon	44	30	570
	Oregon State University	123	40	
southern	Butte Falls, Oregon	42	20	915
	Medford Corporation	122	20	

Field studies were carried on in 1971-73, primarily during the growing season. Throughout the 1971 growing season, intense field sampling was conducted on the four populations at the three plantations. Three trees per population at each site were marked, and repeatedly sampled for stomatal aperture, plant moisture stress, cambial and leader growth. Stomatal opening and moisture stress were measured at selected times during the day, night, and growing season. In general, I made one night and one mid-day observation bi-weekly for each area. Growth was measured bi-weekly also.

Temperature, humidity and shortwave incoming radiation were recorded continuously at each location.

During 1972 and 1973 I observed plant moisture stress, stomatal aperture and leaf conductance at the peak of drought on the driest site.

Biomass distribution was determined by sampling three trees from each population at the mountain and coast range sites. Trees were cut off at ground level and set in concentrated cacodilac acid. After needles abscised, they were easily shaken off. Limbs were cut and total weight of needles, branches and bole determined. Later, wet weights were corrected to oven dry equivalents.

Detailed description of sampling and methods are included in other sections, where appropriate.

II. MODEL DEVELOPMENT

Photosynthesis is an important process through which light, water, and carbon dioxide are converted into carbohydrates needed to sustain life. All growth and maintenance of green plants depend upon this process. Therefore, a great deal of effort has gone into understanding photosynthesis as a process and how it is affected by the plant's environment. Models have been developed to summarize the relationship between CO_2 fixation and environmental variables such as light, temperature, stress or preconditioning.

Models for photosynthesis in Douglas-fir are being developed as part of Coniferous Forest Biome studies (Reed and Webb, 1972). Leaf, tree, and stand level models are being considered. At present, none of these models has been thoroughly tested.

Models of sufficient resolution and structure for prediction of primary production for entire plant communities are needed. In order to predict production following a variety of perturbations, we must treat the primary production system as a whole. We must understand how biotic and abiotic factors affect the many processes involved in carbon fixation, storage, and growth. The knowledge necessary for such models may take years to accumulate.

There are, however, advantages in simulating yearly photosynthesis, even with preliminary information (Innis, 1973). In this

chapter I will outline my approach to simulation of photosynthesis. A subsequent chapter will deal with studies of physiology necessary in adapting existing photosynthesis models to my purposes.

My objective was to simulate seasonal and yearly photosynthetic totals as a way of comparing forest environments. A basic hypothesis to be tested was that greater photosynthetic potential should be correlated with site productivity. Waring et al. (1972) have shown that plant response models can be useful in comparing environments, in terms meaningful for plant distribution and productivity. The approach is keyed on evaluating the "operational environment" of important members of a plant community (Mason and Langenheim, 1957) (see Chapter V). Plant response models were used to evaluate environment daily so that daily values could be summed to create a seasonal index.

Site productivity could be estimated by gross photosynthesis (Yoda et al., 1965); however, we can only measure net photosynthesis because of the difficulty in measuring photorespiration. The magnitude of this error is probably small, and for practical purposes net photosynthesis has the advantage of being what is available for plant growth and respiration.

Most models of photosynthesis have accounted for CO_2 fixation as a function of temperature, light and sometimes CO_2 concentration. Reed and Webb (1972) discussed the structural merits of several

models from the literature. They suggest it is helpful if the parameters of the models have biological meaning. Botkin (1969) used a laboratory based single leaf model to estimate photosynthesis of single leaves in an oak canopy. Most of his predictions (80 percent) were within plus or minus 30 percent of the observed. Wuenschel and Kozlowski (1971) used energy budget equations and laboratory derived single leaf models to estimate field photosynthesis of various species of hardwood in different environments. They interpreted their comparisons ecologically. Idso and Baker (1968) predicted photosynthesis of field crops from laboratory based models, but did not attempt to evaluate their predictions. Connor et al. (1971) simulated photosynthesis of an Acacia forest with laboratory based models. They included the effects of leaf area, leaf angle, non-optimum temperature, and water stress on photosynthesis and compared this with litter production for a two-year period. Their estimate of CO_2 fixation was 2.7 times the observed litter production, but they did not account for respiration. Sollins et al. (1973) incorporated estimates of annual CO_2 fixation into an organic matter budget and model for a Liriodendron forest. A rigorous validation is yet to be completed, but preliminary comparisons with literature were encouraging.

Typical photosynthesis models account for variation in CO_2 fixation due only to changes in light and temperature. They are formulated on plants in their active growth stage when conditions of

moisture, nutrition, and temperature are favorable. Of the papers reviewed, only Connor et al. (1971) had considered stress conditions. In addition the effect of temperature and light, photosynthesis of conifers may be affected by variations in humidity (Jarvis, 1974, personal communication), moisture stress (Cleary, 1970), and CO₂ concentration (Gordon and Gatherum, 1969). In addition to these effects, long term changes in photosynthetic ability may result from preconditioning by drought or cold, and related changes in phenology (Salsbury and Ross, 1969). Thorough investigations of all these factors for Douglas-fir are only now in progress. My strategy was to use an available photosynthesis model developed by Sollins (1974, personal communication) for Douglas-fir, and reduce fixation due to environmental stress.

Reed et al. (1974) used least squares techniques in a manner similar to Webb (1972) in developing a mechanistic leaf level photosynthesis model for Liriodendron. The model has recently been adjusted to represent Douglas-fir under field conditions. The time resolution of this model is seconds, which makes it impractical for yearly simulations (see Appendix I for equations). Total photosynthesis for a wide variety of day types was generated with this model.

Sollins (1974, personal communication) used the daily totals from Reed's model to develop a second model with a daily time resolution. Daily net CO₂ fixation was calculated from a photosynthesis model (Equation 1) and a respiration model (Equation 2). Daytime

fixation was computed from inputs of total shortwave solar radiation, average leaf resistance, day length, and average air temperature. Night respiration was calculated from average night temperature and night length. The results from both equations were added to give net daily CO₂ fixation.

$$PSN = [B_1(DL)(B_2 - T)^{B_4} (T - B_3)] \cdot \left[\frac{\frac{L}{60(DL)}}{B_5 + \frac{L}{60(DL)}} \right] \cdot \frac{1}{LR^2} \quad (1)$$

where:

- PSN = net daily photosynthesis (mg CO₂ dm⁻¹)
- DL = day length (hr)
- T = average day temperature (°C)
- LR = average leaf resistance (sec · cm⁻¹)
- L = total radiation (langleys day⁻¹)
- B₁ = 0.0097 (mg CO₂ hr⁻¹ dm⁻² (°C^{-(B₄+1)}) sec cm⁻¹)
- B₂ = 45 (°C)
- B₃ = -5 (°C)
- B₄ = 1.5 (dimensionless)
- B₅ = 0.1 (langleys min⁻¹)

$$R = -B_6 \cdot (1-DL) \cdot e^{B_7 TN} \quad (2)$$

where:

- TN = average night temperature (°C)
- B₆ = 0.1 (mg CO₂ dm⁻² hr⁻¹)

$$B_7 = 0.2 (^{\circ}\text{C}^{-1})$$

A thorough evaluation of this model has not been possible. The three days of data available were for cool, low light days (Table 2-1). Estimates were within 25 percent of the measured amounts when resistances from within the calculated range were used.

The model assumed no seasonal change in photosynthetic capability related to preconditioning or phenology. It did not account for short term changes due to extremes in environment. I adopted the strategy of modeling these independently as resistance changes as Brown (1969) suggested.

Light and temperature are most favorable during the growing season. In the northwest the summers are generally rainless, and plant moisture stress develops in many forest ecosystems (Waring, 1969). Cleary (1970) showed that photosynthesis in Douglas-fir drops rapidly as plant moisture stress increases from 8 to 20 atm. Drought may be the most important cause in reducing photosynthesis on a yearly basis. Cold or frozen soils, and frost may also reduce photosynthetic capability, but light and temperature are generally low under these conditions. My field efforts were thus concentrated on determining to what extent leaf conductance or stomatal behavior was affected by summer drought.

Table 2-1. Comparison of simulated and measured CO₂ fixation for three days in August and September 1973 (Salo, 1974, personal communication).

Date	Environmental conditions			Night PMS (atm)	Conductance		Photosynthesis		
	Day length (hrs)	Average temp. (°C)	Solar radiation (ly)		Calculated	Used in simulation	Measured (mg CO ₂ /dm ²)	Simulated	Simulated/ measured (%)
8-22	13.3	22.02	128.0	15.8	.055-.01	0.055	15.67	11.9	75
8-30	14.0	14.36	21.8	8.2	.25-.143	0.167	17.69	21.8	123
9-8	14.0	19.25	92.7	4.8	.33-.071	0.167	36.37	39.3	108

III. FIELD STUDIES OF PHYSIOLOGY

To determine the stomatal response of coastal Douglas-fir to climatic conditions I periodically sampled daily trends in stomatal aperture (SA) and plant moisture stress (PMS) of four populations at three genetics plantations during 1971. In 1972 new methods were adopted which allowed a direct measure of leaf conductance.

Stomatal Behavior Studies (1971)

Methods

Study of stomatal behavior is made difficult in conifers because stomata are located in depressions and cannot be observed directly. The most difficult problem in direct observation is occlusion of the stomatal pore by a waxy substance (Reed, 1973). Knowledge of stomatal behavior must be obtained by indirect methods.

A method of estimating relative aperture of stomata of Douglas-fir and other conifers was developed by Fry and Walker (1967). Their "infiltrometer" allows for determination of the pressure required to force a 50 percent alcohol solution through the stomatal pores. Detached needles are placed in a chamber so they may be observed via low power microscope as the pressure is increased. The end-point is the pressure at which 50 percent of the stomata are undergoing

infiltration. Major drawbacks of this method are the subjective end point and the non-linear, difficult-to-determine relationship between aperture and leaf conductance.

The pressure at which infiltration occurs has not been adequately correlated with definitive measures of leaf conductance. Fry (1965) showed only a theoretical relationship between stomatal aperture and leaf resistance. Reed (1972) developed a relationship between SA and leaf resistance by repeated weighing of cut twigs while observing SA. In addition to the question of whether stomata could respond normally during rapid drying, the relationship Reed derived conflicts with results of recent studies by myself and Running (1973). Reed's relationship predicts leaf conductances of 0.34 to 0.14 cm/sec at infiltration pressures of 0.27 to 0.68 atm. Numerous field observations with the diffusion porometer (Figure 3-8, p. 32) show leaf conductances to average 0.02 cm/sec or less when infiltration pressures were from 0.5 to 0.6 atm. In short, Reed's relationship predicts conductance values which are much too high at the low end of the infiltration scale. For purposes of presenting results of my infiltrometer studies, I established the convention shown in Table 3-1. This convention was established from field observations with the porometer and infiltrometer.

Table 3-1. A subjective relation between infiltration pressure and stomatal aperture for use in referring to field observations.

	Scale range (atm)				
	Less than 0.34	0.34- 0.61	0.61- 0.89	0.90- 1.36	Over 1.36
Stomatal aperture description	wide open	nearly wide open	partly closed	nearly closed	closed

A major controlling factor in stomatal movement is leaf water potential. Xylem water potential as estimated by the Scholander pressure bomb approximates leaf water potential (Scholander *et al.*, 1965; Waring and Cleary, 1967). We define plant moisture stress (PMS) as equal and opposite to xylem water potential (Waring and Cleary, 1967; Waring *et al.*, 1972). PMS is determined by sealing a freshly cut twig in a chamber. The severed end is exposed through a gas-tight seal. As pressure is gradually increased in the chamber, xylem sap is observed at the end of the twig. The pressure at which water is observed approximates the original tension on the water column. Errors involved with this procedure (Kaufmann, 1968; Richie and Hinckley, 1971) were not considered serious for this study since I made comparisons within a species.

Results

Daily Patterns. Three examples of daily SA and PMS

observations were selected as representative of early spring, late spring and late summer patterns.

May 11, 1971 was a warm, sunny, spring day at the Willamette Valley plantation. Before dawn, PMS had recovered to 6 atm and stomata were partly closed (Figure 3-1). The vapor pressure deficit (VPD) during the day was about 10 mb, but PMS did not rise above 11 atm, even though stomata were nearly wide open all day. The same spring pattern (stomata partly closed at night, but nearly wide open all day, and PMS slightly elevated at night while relatively low all day) was observed at the other locations, especially the coast range.

After spring rains, all sites showed a pattern similar to that recorded at the mountain location on June 28-29 (Figure 3-2). June 28 was a cloudy, cool, humid day. PMS did not rise above 9 atm even though the stomata were wide open. At midnight PMS was down to 6 atm and by 0400 hours it had dropped two more atm. The following day was clear, with air temperature up to 19°C and a 10 mb VPD. PMS reached a plateau at about 12 atm. Stomata were wide open day and night.

Later in the growing season (120 days after bud swell), daily fluctuations in PMS and SA were observed at the coast range plantation (Figure 3-3). August 22 and 23 were typical hot, dry summer days common to the Pacific Northwest. Temperatures peaked at about 20°C, and VPD was over 15 mb most of the day, while the

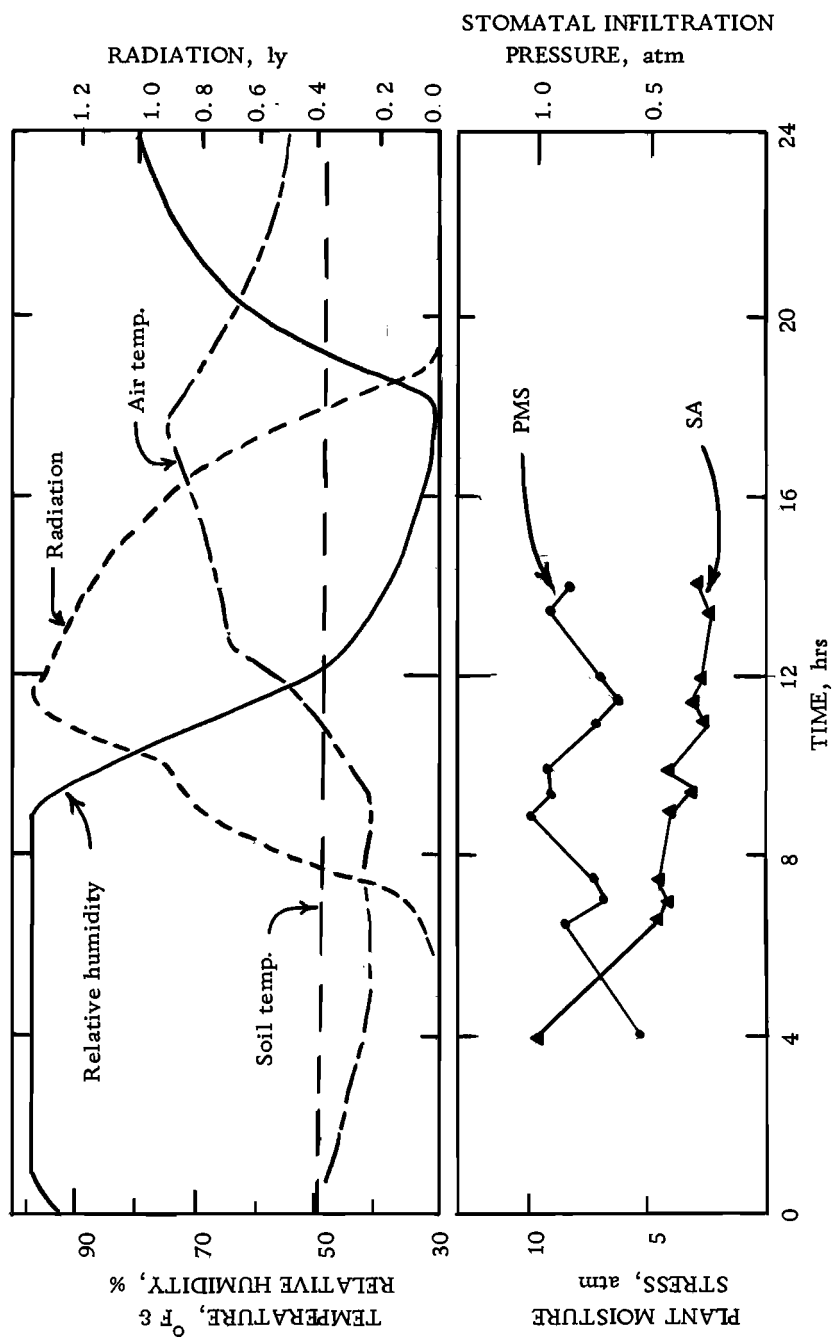


Figure 3-1. The daily pattern of plant moisture stress, stomatal aperture and climatic factors for a spring day in the Willamette Valley.

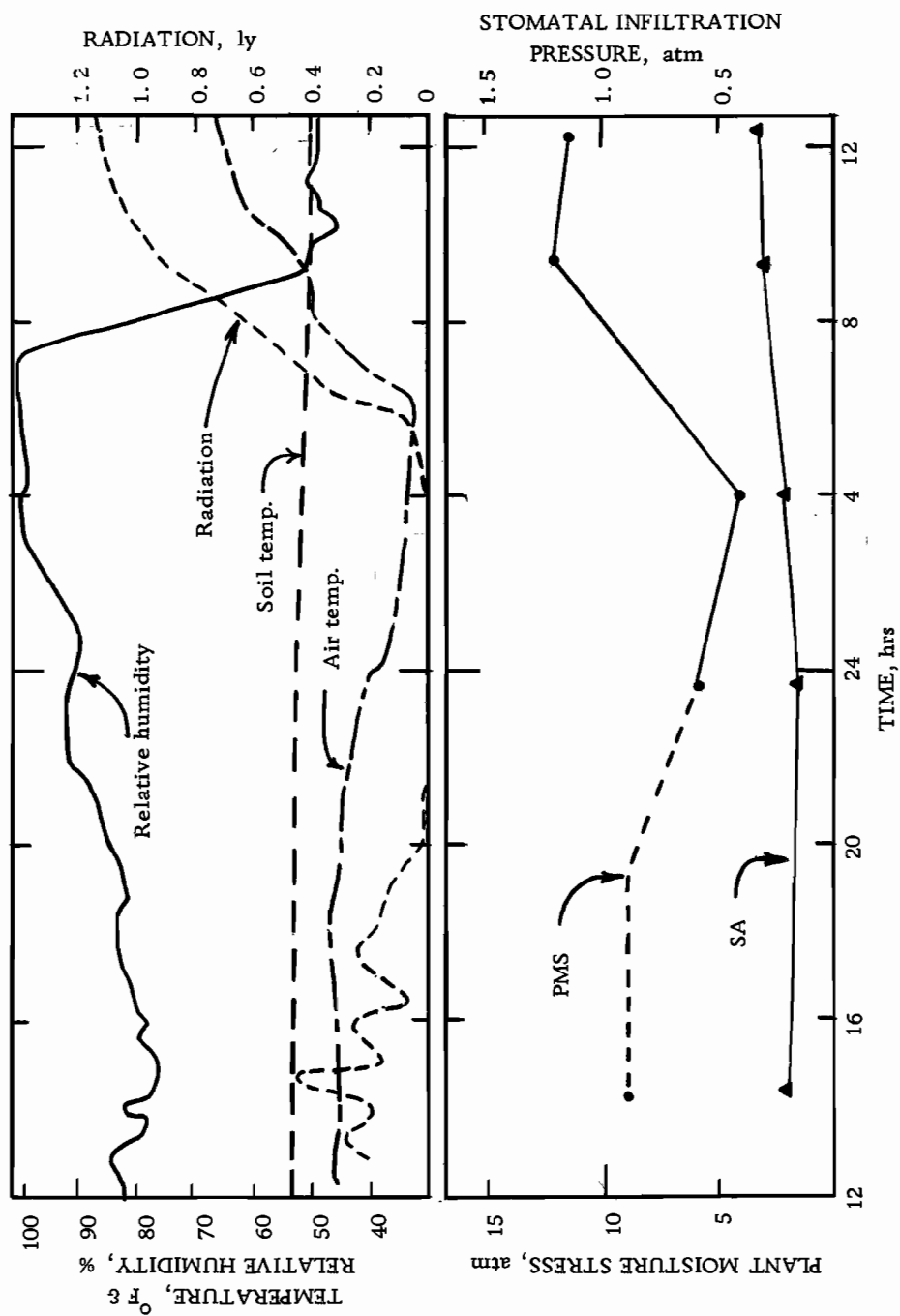


Figure 3-2. The daily pattern of plant moisture stress, stomatal aperture and climatic factors for a summer day in the Cascade Mountains.

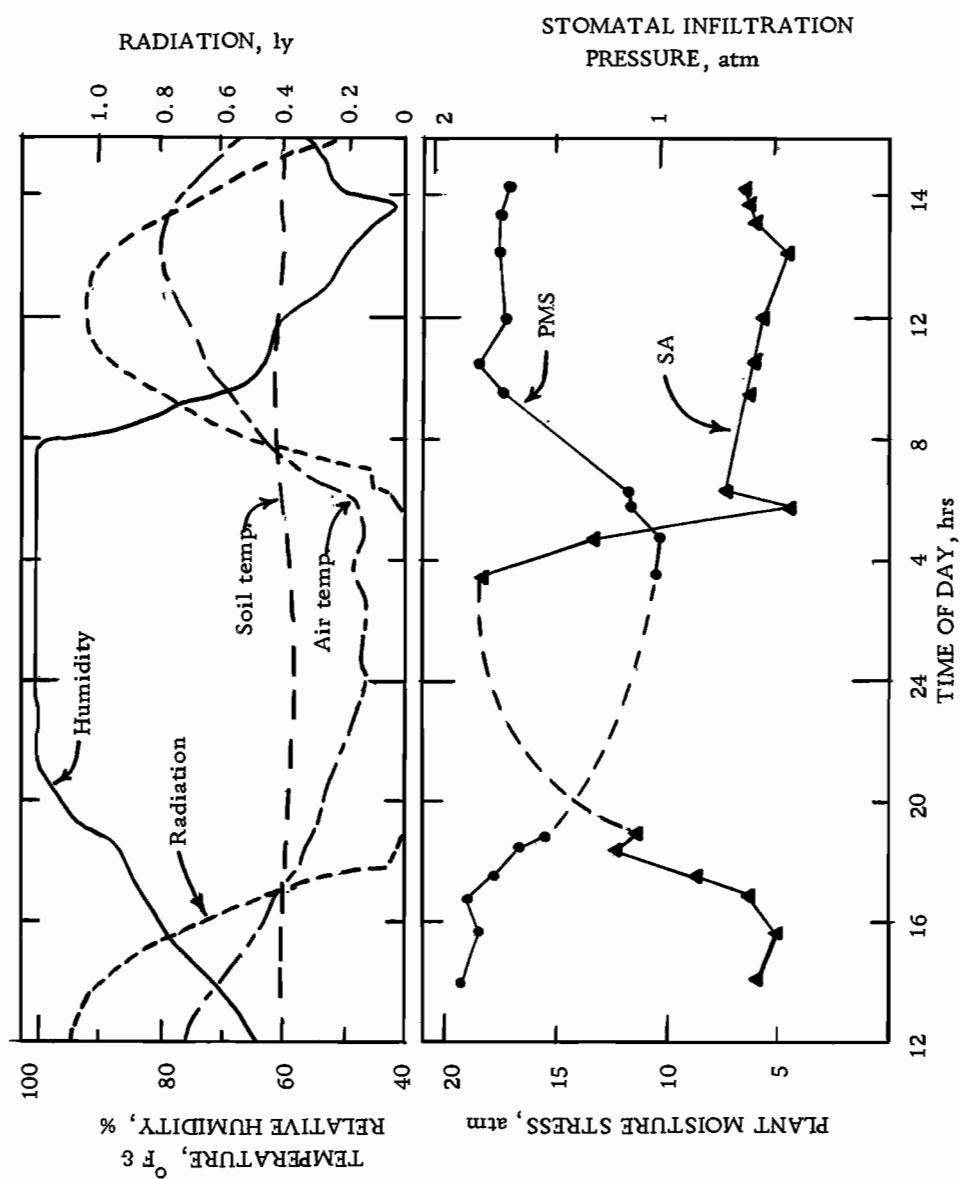


Figure 3-3. The daily pattern of plant moisture stress, stomatal aperture and climatic factors for a late summer day at a dry interior Coast Range site.

radiation load was over 1 langley per minute at mid-day. By mid-afternoon on the 22nd, PMS had risen to 19 atm and stomata were nearly wide open. At dusk stomata closed rapidly and PMS began to drop. By 1830 hours, PMS was down to 10 atm and stomata were still closed. At dawn stomata opened wide, but during a brief morning fog they seemed to close slightly. Later in the day the stomata re-opened although perhaps not to the extent they were at dawn. Three hours after sunrise PMS had increased by 8 atm and remained at that level until early afternoon. This was the driest part of the summer, since 10 cm of rain fell on this plantation a few days later.

Seasonal Patterns. Repeated visits to the three plantations during the 1971 growing season made it possible to plot the seasonal patterns of PMS and SA for each area.

The valley plantation showed the least variation in SA and PMS (Figure 3-4). PMS during the day was about 12 atm early in the growing season, generally less than 10 atm early in the summer, and between 10 and 15 atm in late summer and fall. Night PMS remained below 5 atm for about 70 days before rising gradually to 6.5 atm at the end of August. After 6 cm of rain, night PMS recovered for a time, then rose to the highest point of the season in September. The rain in late August wetted the heavy clay soil only to about 50 cm. Except for two sample days in early summer, stomata were wide open during the day throughout the growing season. At night stomata were

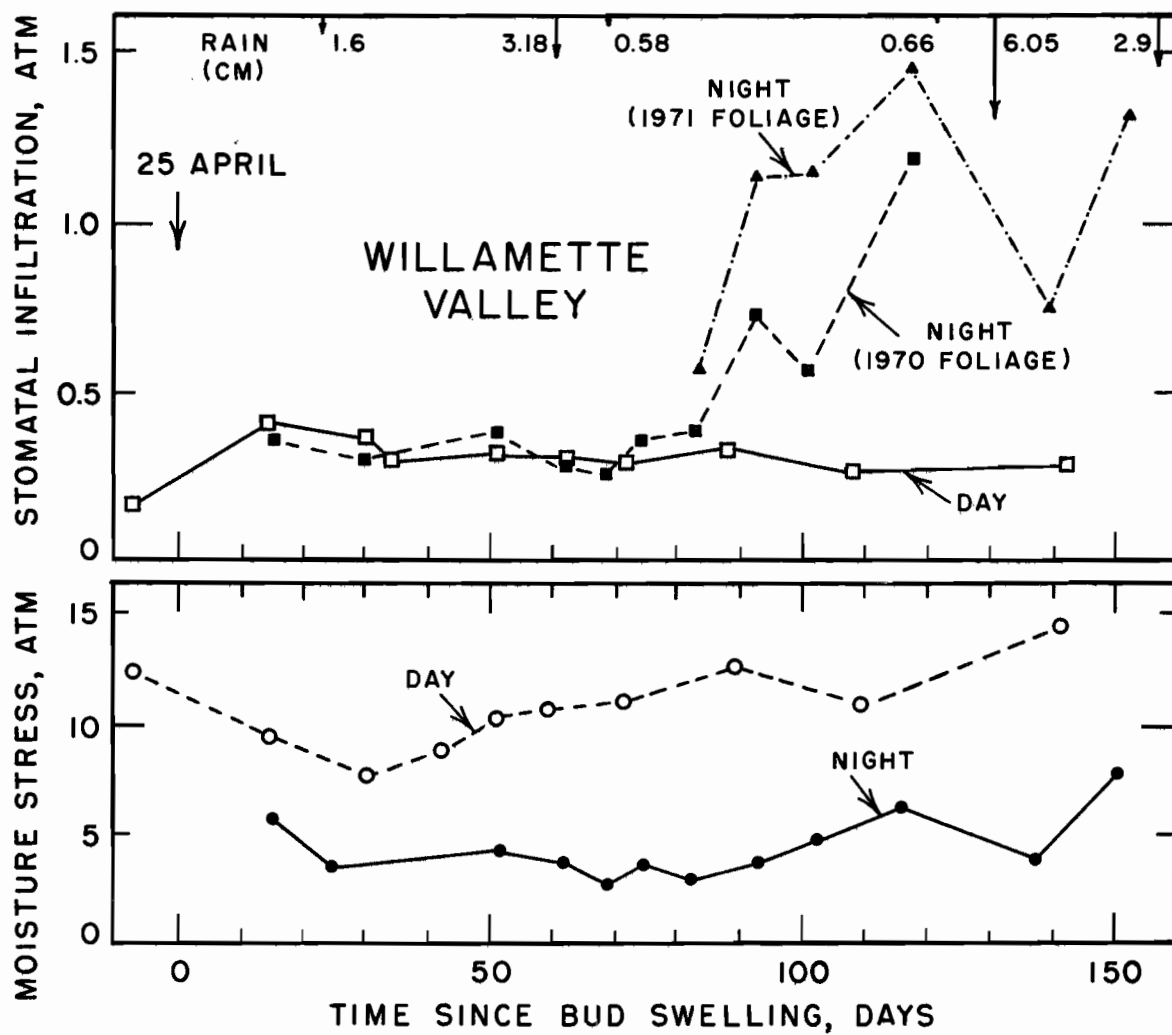


Figure 3-4. The seasonal pattern of plant moisture stress and stomatal aperture near mid-day and at night in the Willamette Valley.

open early in the summer, but closed later, just as at the other locations.

Both new (current year's growth) and one-year-old needles were sampled for stomatal behavior after the new needles were rigid enough to handle. No differences were discerned during the day between the new and old needle stomata. At night the new stomata were consistently more closed than the old (Figures 3-4 and 3-6).

At the Cascade mountain plantation spring PMS was very low (3 atm) when soils were saturated with snow melt and spring rain (Figure 3-5). In the two-month rainless period, night PMS rose to 6.2 atm. Only in August did the daily high PMS exceed 15 atm. Stomata were open during the day and closed at night in late summer, as at the other two locations. Only 3.8 cm of rain fell on this site at the end of August, and night PMS did not drop while stomata remained wide open through the day.

At the coast range plantation, variation in PMS and SA was more pronounced than at the other locations (Figure 3-6). For example, the spring physiological drought was more noticeable than at the valley plantation. Night PMS was over 8 atm and stomata were partly closed. After light spring rains, soils had warmed and night PMS was less than 5 atm for 50 days, while day PMS was 12 to 14 atm. About 80 days after bud swell, stomata began closing at night, and at 90 days PMS began to rise. Only at the peak of drought, when

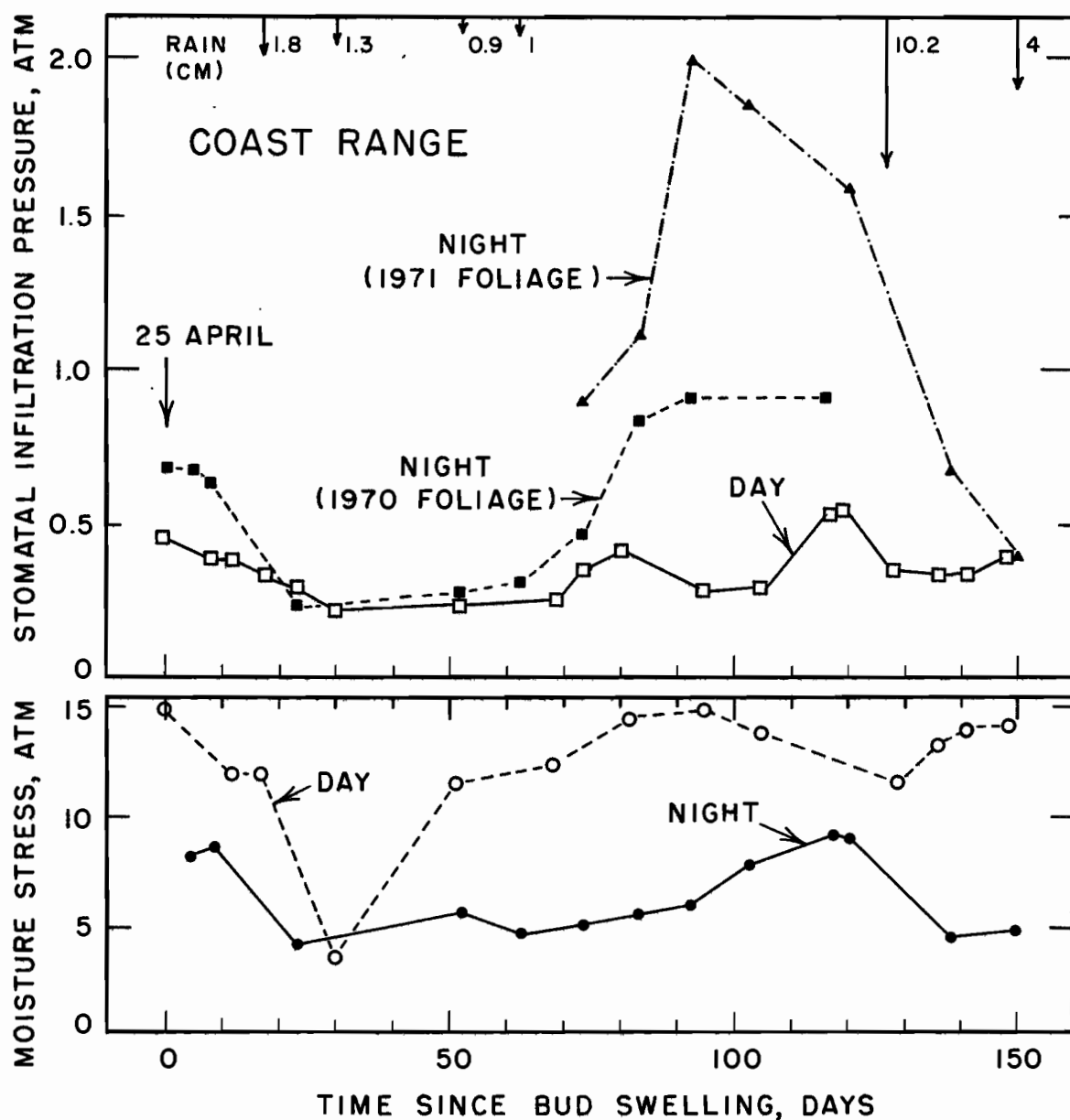


Figure 3-5. The seasonal pattern of plant moisture stress and stomatal aperture near mid-day and at night in the Cascade Mountains.

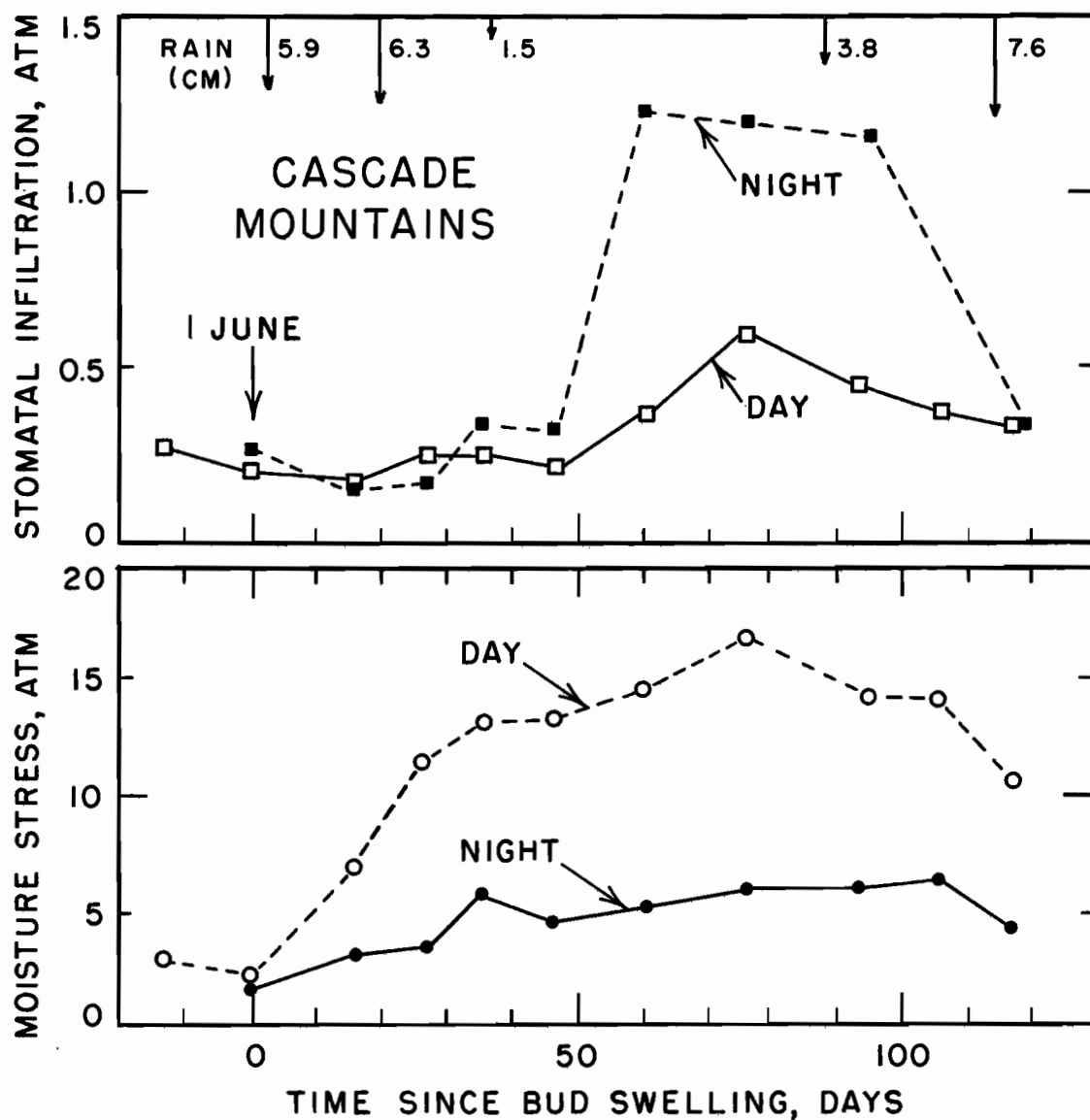


Figure 3-6. The seasonal pattern of plant moisture stress and stomatal aperture near mid-day and at night at a dry interior Coast Range site.

night PMS was over 9 atm, were stomata partly closed during the day. At that time, day PMS rose above 15 atm. After 10 cm of rain, night PMS dropped to less than 5 atm and stomata were wide open all day but partly closed at night. After additional rain, stomata were wide open day and night. During the winter, PMS was over 13 atm on sunny days when stomata were open. Stomata were closed when air temperatures were less than 2°C even on sunny days.

Discussion

The field observations revealed patterns that were valuable for developing models of stomatal behavior as functions of environmental factors.

During early summer, when 80-90 percent of growth took place, stomata were wide open day and night. Fry (1965) and Reed (1972) also observed stomata of Douglas-fir open at night under favorable moisture conditions. This may reflect: 1) blockage of the mechanism which normally causes stomata to close when CO_2 concentration is high inside the leaf (Slatyer, 1967), 2) the absence of such a mechanism in Douglas-fir, or 3) absence of high CO_2 concentrations inside the needle as in succulents exhibiting massive dark fixation of CO_2 (Nishida, 1963). Ludlow and Jarvis (1971) noted that stomatal resistance in Sitka spruce was unaffected by CO_2 concentration changes between 100 and 800 ppm.

Plant moisture stress was generally less than 6 atm at night when stomata were open day and night. During the day, PMS reached a plateau between 11 and 14 atm. Transpiration at night would not be great because of low VPD. Advantages of night opening may be additional nutrient uptake and relief of flooding under special conditions.

Douglas-fir apparently completes most of its growth when PMS varies between 4 and 15 atm. Presumably most growth occurs at night when PMS is from 4-6 atm. Boyer (1969) found that growth in sunflower stopped when leaf water potential was less than -3 atm. While PMS in needles of Douglas-fir was found to be nearly 2 atm less than that measured in the stem (Richie and Hinckley, 1971), it is obvious that some growth must take place when leaf water potential is greater than 6 atm; for example, the last 20 percent of both cambial and leader growth at the coast range. Considering the wide variety of conditions under which plants occur, there must be species differences in the minimum water potential at which growth can proceed.

During the drought period, stomata were not wide open all day, and were nearly closed at night. Stomatal closure at night began 10-30 days before noticeable closure occurred in light. Stomata of current year needles were more closed at night than one-year-old needles, but no differences were discernible in daylight hours. Readings taken throughout the day (Figure 3-3) indicated an initial wide opening at sunrise with slight closure in the afternoon. Stomatal closure at

night and partial closure during the day were loosely correlated with night PMS ($R^2 = 0.50$ for all areas). For the coast range plantation 75 percent of the variation in night SA was explained by night minimum and day maximum PMS, with night PMS explaining most of the variation. Temperature and VPD did not appear to be associated with changes in stomatal aperture. Reed (1972) found a similar pattern in the eastern Siskiyou Mountains of southwestern Oregon.

During spring, stomatal closure seemed to be associated with high PMS. PMS was elevated above what would be considered normal for the amount of water in the soil. The most likely explanation for this is that cool soil temperatures restricted water movement in the soil. Cox and Boersma (1967) and Babalola et al. (1968) found water transport inhibited "due to increased viscosity of water" in Trifolium repens and Pinus radiata at soil temperatures between 5 and 10°C. Havranek (1972) showed a reduction in both transpiration and photosynthesis of larch and fir when soil temperatures were 2 and 4°C. In my study, this condition was observed until plants were past the "bush" stage of leaf and twig growth while soil temperatures were below 10°C. This led to speculation that contributing factors were new leaf tissue which was unable to curb water loss, and inactive root systems.

Leaf Conductance Studies (1972 & 1973)

Methods

The intensive field studies during 1971 established a framework for less intense sampling during 1972 and 1973. Because 1971 was not a severe drought year, my objective during succeeding years was to sample at peak of drought on the driest site. Also, due to the difficulty of establishing the relationship between stomatal infiltration and leaf conductance, I sought new instrumentation.

The aspirated diffusion porometer (Turner et al. , 1969; Turner and Parlange, 1970) measures leaf conductance or leaf resistance. After a few needles are sealed in a chamber, the chamber is dried by introducing a desiccant. The desiccant is removed and increase in humidity caused by transpiration is timed. The leaf conductance for water vapor can be calculated given time required to increase humidity a fixed amount, chamber temperature, and surface area of leaves. This instrument has the advantage of estimating leaf conductance (C_l) for several attached needles. The estimates of leaf conductance are in cm/sec which are immediately useful in equations for transpiration or photosynthesis. Total leaf conductance (C_l) is the sum of the conductance through the stomatal pathway (C_s) and the cuticular pathway (C_c). Because conductance through the cuticular pathway is small in conifers, stomatal conductance is most important. Conductance

through the stomatal pathway depends on the resistances to vapor movement in intercellular spaces (r_i), mesophyll (r_w), boundary layer (r_a), and stomatal pore (r_p).

$$C_s = \frac{1}{r_i + r_w + r_a + r_p}$$

When intercellular, mesophyll and boundary layer resistances are large, as is generally true (Slatyer, 1967), stomatal pore resistance largely determines leaf conductance.

Operating procedures for the porometer are critical for accurate estimates of leaf conductance (Morrow and Slatyer, 1971). My procedures were the same as Running (1973). Additional information on operation and function has been published by Turner and Waggoner (1968).

Results and Discussion

On August 4, night minimum PMS and SA were taken on 12 trees at the coast range plantation in preparation for daytime measures of conductance (Figure 3-7). Night PMS averaged 11.8 atm indicating that 1972 was drier than 1971. Stomata were closed as expected from earlier work.

By mid-day, PMS had reached 15 atm and remained at that level until late afternoon. Stomatal infiltration values were 0.56 ± 0.02 atm, indicating stomata were "nearly wide open" (Table 3-1).

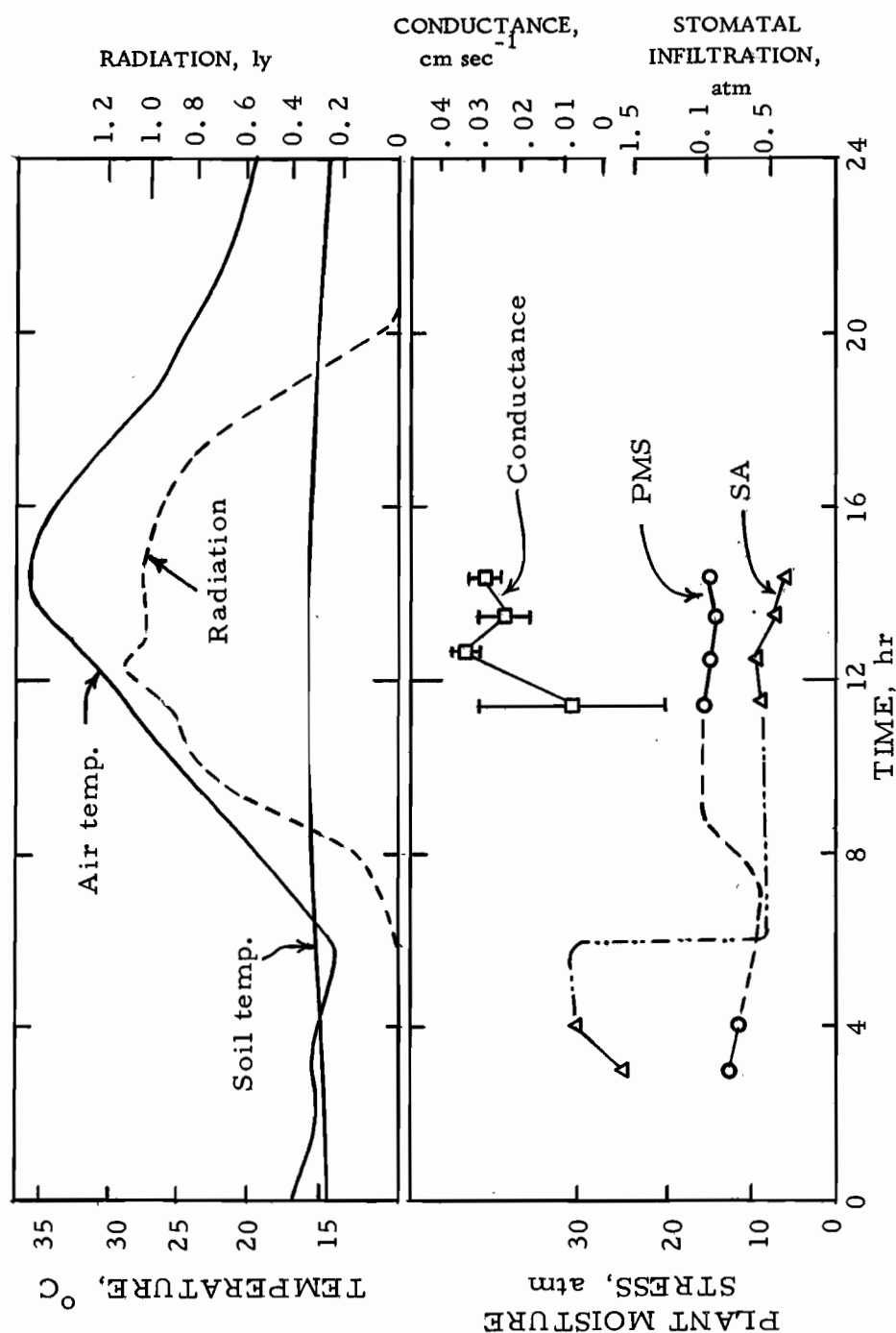


Figure 3-7. A comparison of leaf conductance, stomatal aperture and plant moisture stress observations with climatic factors at the interior coast range plantation on 4 Aug. 1972. Mean and one standard deviation of leaf conductance are shown. The standard deviation from the mean was less than 2 atm for plant moisture stress and less than 0.2 atm for stomatal infiltration pressure.

Leaf conductance observations ranged from 0.154 to 0.0013 and averaged 0.02 cm/sec. This spanned nearly the entire range of reported conductance of Douglas-fir (0.25 to 0.003 cm/sec). Our porometer was not designed or tested for extremely low leaf conductances, so the low observations should not be regarded as definitive. Low conductances similar to those here reported were observed in Sitka spruce by Beardsell et al. (1972) with a null-balance diffusion porometer.

Leaf conductance, SA and PMS observations were again taken during the 1973 drought (Figure 3-8). The stomata were closed at night when checked by infiltrometer. For the first time, diffusion porometer observations were possible at night due to absence of dew. Leaf conductances were less than 0.003 cm/sec on all trees measured well prior to first light. Night PMS was 12 atm.

Stomata generally begin opening at first light when incoming shortwave radiation is less than 0.01 langley per minute (Figure 3-3). By sunrise, infiltrometer readings indicated stomata were nearly wide open and leaf conductance was slightly more than 0.02 cm/sec. In the next 1-1/2 hours, PMS rose 5 atm, stomata were as open as at sunrise, but leaf conductance had decreased to 0.014 cm/sec. As VPD continued to rise, PMS rose to a plateau at 19-20 atm. Although individual trees varied widely from 0.02 to 0.005, average conductance dropped to 0.01 cm/sec. About half the trees had more than

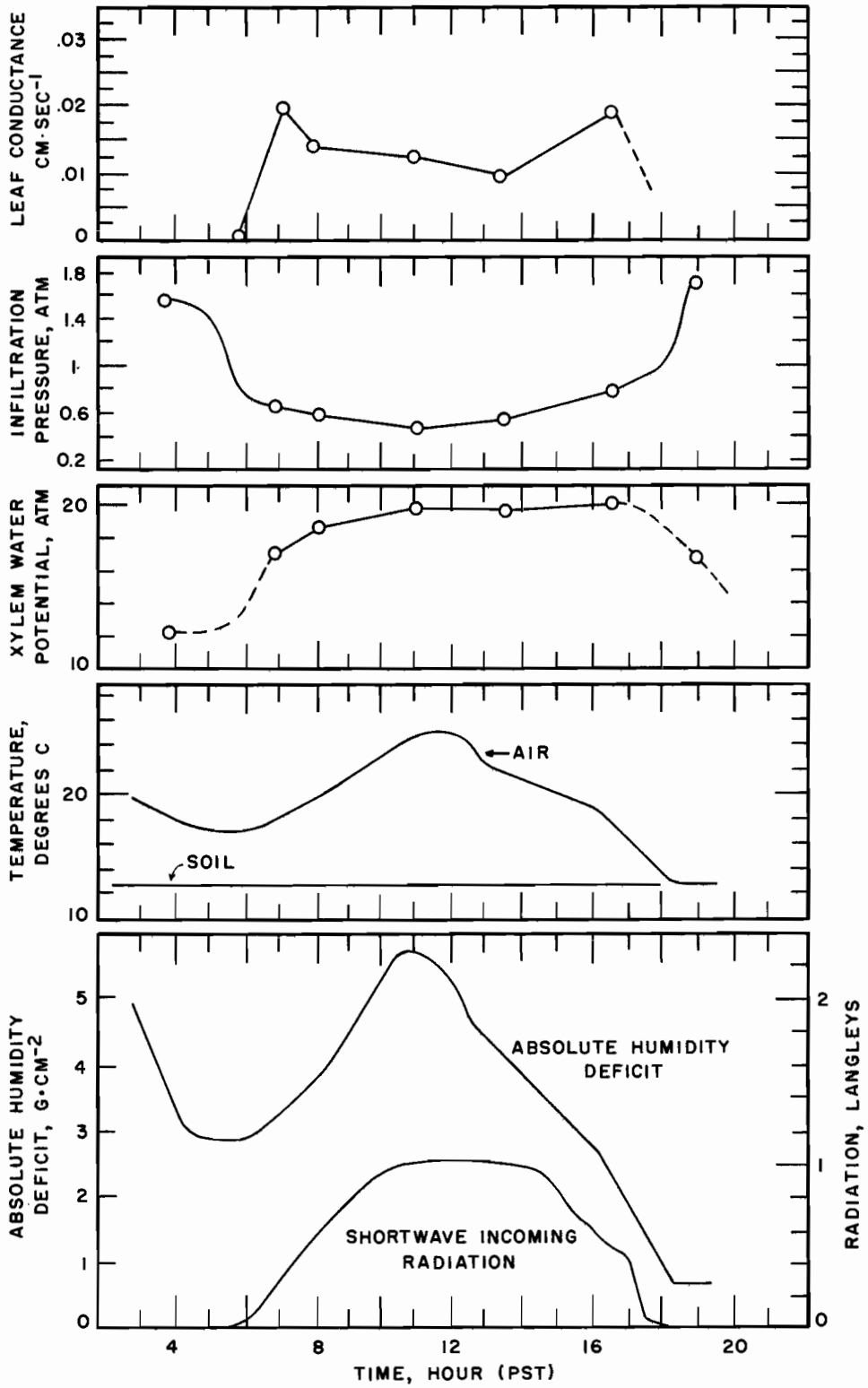


Figure 3-8. A comparison of leaf conductance, stomatal aperture and plant moisture stress observations with climatic factors at the interior Coast Range plantation.

one dip in conductance during the day, perhaps indicative of cyclic fluctuation in conductance.

A cold air mass moved over the area during the afternoon, reducing evaporative demand. PMS remained high, stomata were if anything slightly more closed, while leaf conductance was back up to nearly the sunrise level. After sundown, dew began forming on foliage, making the porometer inoperative. PMS had dropped to 17 atm, and stomata were closed.

Conductance varied widely on individual trees during daylight periods. On the other hand, SA was quite uniform for all trees and remained at nearly the same aperture all day. Stomata were open widest during mid-day when conductance was greatest. Running (1973) made repeated observations at this site under a wide variety of environmental conditions, and found only a $0.48 R^2$ between leaf resistance and stomatal infiltration. Some of the variation in leaf conductance while infiltration pressures remained constant may be due to insensitivity of the infiltration method and to difficulties in determining mid-range end points. The variation in leaf conductance could be explained on the basis of cyclic fluctuation of stomatal resistance, if infiltration observations could be ignored. Cyclic fluctuation is common in many plant species (Barrs, 1971), but has not to my knowledge been reported for conifers. The variation could also be explained on the basis of mesophyll resistance. This has been reported

to vary in Douglas-fir by Swank (1972) and Lopushinsky (1969); however, neither author suggested cyclic fluctuation.

A discussion of the relationship of leaf conductance to plant moisture stress is in Chapter IV.

Summary of Physiological Observations

Stomatal opening as measured by the Fry and Walker infiltrometer did not vary with plantation or population. During the spring, when night PMS was high, stomata were partly closed at night and wide open during the day. When night PMS was below 6 atm, stomata were open day and night. As night PMS rose above 6 atm, stomata were closed at night but nearly wide open during the day. When fall rains recharged soil water, stomata were open day and night. Stomata were closed during freezing weather.

Leaf resistance data as measured by the diffusion porometer were not easily interpreted. In late summer, leaf conductance was low at night (0.003 cm/sec), greatest at sunrise (0.025 cm/sec) and variable during the day (0.02 to 0.01 cm/sec).

Moisture stress patterns were as expected during the summer, but higher than expected in spring. PMS was high in winter and spring both at night (7 atm) and during the day (14 atm), probably due to cold soil temperatures. During early summer, night PMS recovered to less than 5 atm at all sites and gradually climbed until fall rains replenished soil moisture supplies.

There were marked differences between sites in seasonal and daily pattern of PMS. In the interior coast range, night PMS rose to nearly 10 atm at the end of the drought period. In the valley and Cascade Mountains, night PMS rose only to about 6 atm. In the valley, recovery after rains at the end of August was short-lived, and night PMS soon rose above previous levels. Daytime PMS depended on night PMS and atmospheric demand, but generally remained below 15 atm until night PMS was over 6 atm.

IV. MODELING LEAF CONDUCTANCE

The photosynthesis model discussed earlier predicts net CO_2 uptake as a function of light, air temperature and leaf conductance. Light and temperature were measured continuously, but leaf conductance had to be estimated from other factors more easily measured, or known. My observations in the field and literature review led me to include light, drought, phenology, air and soil temperature as factors directly or indirectly related to changes in leaf conductance in some plants. I will consider each of these factors for inclusion in the simulation.

Stomatal movement is generally accepted to be brought about by a difference in turgor of guard cells relative to that in surrounding epidermal cells (Slatyer, 1967). How guard cells achieve a different turgor than surrounding cells is still a subject of intense research and some controversy (Levitt, 1967; Slatyer, 1967). Although knowledge of the mechanism may help in understanding stomatal behavior, for practical purposes I modeled leaf conductance as though it were directly controlled by environmental factors.

Environmental Factors Affecting Leaf Conductance

Moisture Stress

Plant moisture stress is one of the limiting factors on primary productivity in the Douglas-fir forests of western Oregon (Stand, 1964). As mentioned above, stomatal movements are controlled by relative turgor of guard and mesophyll cells, which is directly related to plant moisture stress (PMS). Laboratory studies of Douglas-fir have shown that as PMS increases, both transpiration (Unterschutze, 1970) and photosynthesis (Cleary, 1970) decreased. Cleary found that as stress increased above 20 atm, recovery of photosynthesis to pre-stress levels took longer.

Field studies with established saplings have been hampered by the difficulties associated with getting good instrumentation into the field. Reed (1972) found a loose correlation ($R^2 = 0.55$) between pre-dawn PMS and minimum daily stomatal infiltration pressure in the Siskiyou Mountains of southwestern Oregon. He found a daily minimum in stomatal infiltration pressure which generally occurred between 0800 and 1000 hours each day. Stomata then closed somewhat during the day, but this change was not explained by changes in temperature, vapor pressure deficit (VPD) or PMS. Running (1973) found weak correlations ($R^2 = 0.30$ and 0.65) between leaf resistance

during mid-day and night PMS of established Douglas-fir on various sites in the coastal and Cascade Mountains of Oregon. Temperature and VPD explained only 10 percent more variation in leaf resistance than night PMS. In my studies (Figures 3-4 to 3-6) 54 percent of the variation in daytime stomatal infiltration was explained by variation in night PMS. Further observations in 1973 (Figure 3-8) indicate that current evaporative demand and PMS account for less than 50 percent of the variation in conductance during the day in the coast range location.

Because of the high variability in field measured conductance, and possible cyclic fluctuations, a high degree of predictability may not be attainable. During the summer, the best predictor of average conductance still appears to be night PMS. Results from stomatal infiltration studies were not translatable into absolute measures of leaf conductance. Therefore, I utilized diffusion porometer data collected at the coast range site and at three other sites in western Oregon (Running, 1973) to model conductance as a function of PMS. These data are shown in Figure 4-1. Each point represents an average of several leaf conductance observations on current year's foliage of a single Douglas-fir sapling. The observations were taken over a 3-8 hour period centered around mid-day. PMS was measured on each tree before dawn. All four locations were visited in late August or early September, 1973, after new foliage had fully expanded.

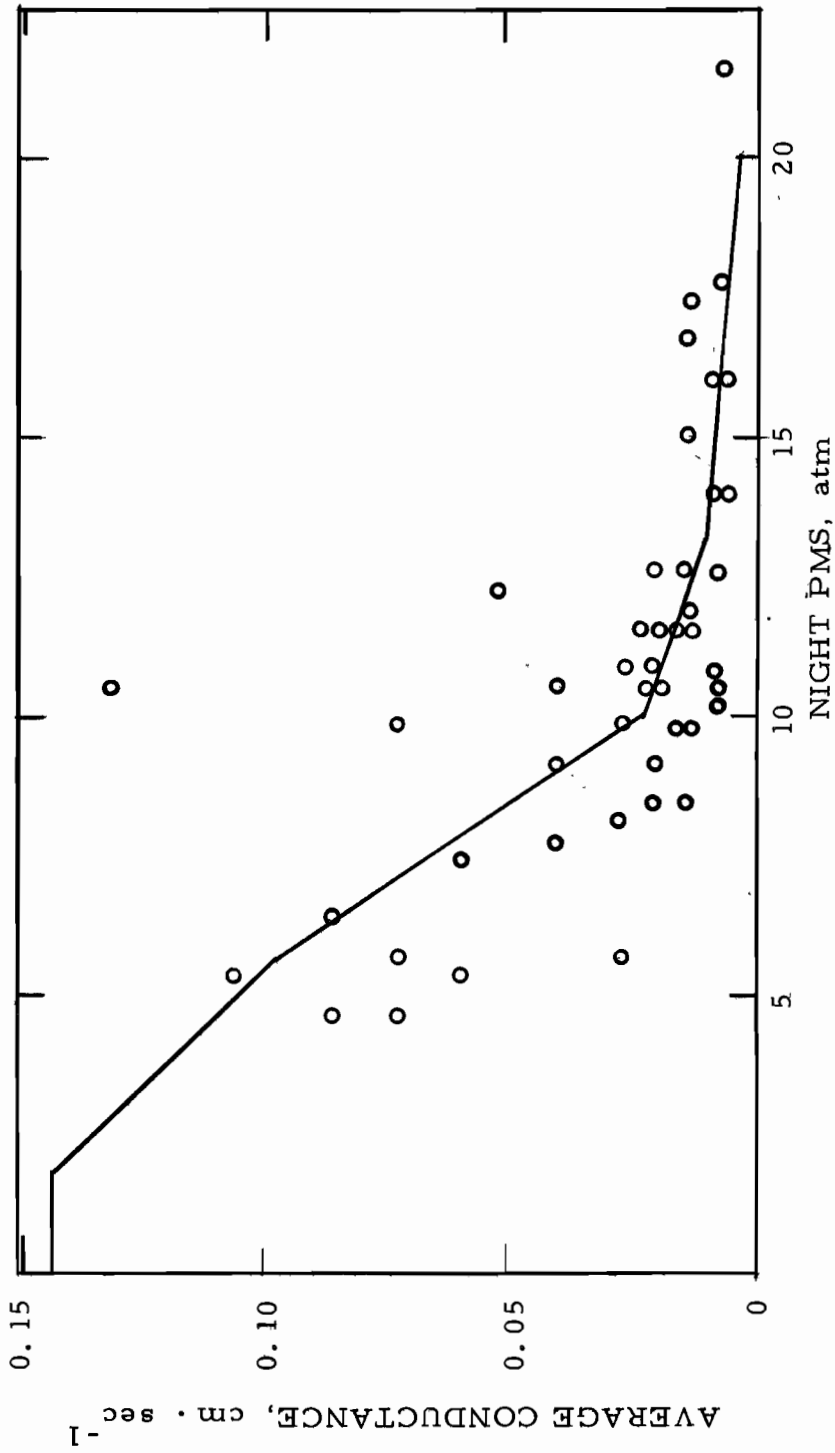


Figure 4-1. The decline of average day leaf conductance with increasing night plant moisture stress. Each leaf conductance value is the average of several observations taken throughout the day. The line was drawn to fit these data and assumed conditions at low stress.

Observations during low stress periods were not available, so average leaf conductance in that range was assumed to be slightly less than the maximum conductance of 0.25 cm/sec observed by Running (1973). The relationship between night PMS and average conductance during the day was highly non-linear. Therefore, a series of straight lines were drawn to fit the assumed values at low stresses and to fit the data points available. The coordinates of the line were 0, 0.1428; 2, 0.1428; 6, 0.1000; 10, 0.0250; 13, 0.0125; and 22, 0.0033.

Light

The stomata of Douglas-fir show a strong photoactive opening response, when they are closed at night. They responded long before our most sensitive solarimeter which records at about 0.01 langley. The effect of light on photosynthesis is included in the basic model (Equation 1) where PSN is given as a function of light and temperature. For modeling purposes, I assumed that stomata would be open when there was enough light to register on the instrument, unless other factors such as moisture stress or temperature of the soil interfered.

Freezing Air Temperatures

The effect of cold air temperature on leaf resistance can be immediate or delayed. The immediate effect of air temperatures less than -2°C on Douglas-fir was to induce stomatal closure (Reed, 1968).

In January, 1974, during sunny, winter days when air temperatures were -2 to -10°C , I observed stomata of Douglas-fir to be closed. Drew et al. (1972) found ponderosa pine to be similar. On the other hand, Walker et al. (1971) measured rates of $2 \text{ mg g}^{-1} \text{ hr}^{-1} \text{ CO}_2$ fixation at 0°C . Unfortunately, no observations of photosynthesis below 0°C have been made due to technical difficulties. The model was set to predict some photosynthesis down to -5°C , but the frost reduction function discussed next interacts to reduce the predicted amount.

The delayed effect of cold temperatures was modeled after relationships found in the literature. Larcher (1969) reported reduction in PSN for several days after "night frost" in Olea europaea, a Mediterranean evergreen. Unhardened Picea sitchensis shoots showed a gradual recovery in PSN for 6 days following exposure to 24 min at -1°C (Neilson et al., 1972). The reduction was due to increase in both stomatal and mesophyll resistance. Tranquillini and Machl-Ebner (1971) showed that in cut twigs of Pinus cembra, photosynthesis decreased in autumn until rates were negative between December and March. Preconditioning temperatures were below -15°C while test temperatures were 10 - 30°C . Photosynthetic capacity generally rose when branches were kept warm for up to 4 days. The amount of recovery depended upon the number of days and the initial physiological state. Drew (1973) found that transpiration in Douglas-fir

seedlings was reduced after a period of severe frost. Also, Zaerr (1973, personal communication) reported that photosynthesis in Douglas-fir seedlings was greatly reduced by heavy frost in December, 1972, and that they did not recover for many days.

The following frost reduction function was included in the simulation of photosynthesis, and it was patterned after the response of Olea europaea (Larcher, 1969) and Picea sitchensis (Neilson et al., 1972) to frost. Night temperatures below $-5/9^{\circ}\text{C}$ cause a frost reduction factor to be computed and multiplied by the succeeding days' PSN. The frost reduction function has two elements. Recovery days (Equation 3) is dependent on the severity of the frost, and ranges from 1 to 10 days for night minimum temperatures between $-5/9$ and -5.8°C .

$$\text{Recovery days} = \frac{9}{5} \left[-1 (\text{night minimum } ^{\circ}\text{C}) - \frac{5}{9} \right] \quad (3)$$

The frost reduction factor reduces PSN on the day following frost, and on succeeding days if the frost was severe enough.

$$\text{Frost reduction factor} = 1 - \left[\frac{(\text{Recovery days} - \text{Days since frost})}{\text{Recovery days}} \right] \quad (4)$$

Soil Temperature

Soil temperature has been recognized as an important factor in plant growth and distribution (Richards et al., 1952; Billings and Mooney, 1968). Plants of tropical origin, such as Zea mays, have

shown marked reduction in photosynthesis (PSN) and transpiration (TR) when soil temperatures were reduced from 10 to 3°C (Anderson and McNaughton, 1973). Some plants of temperate origin, however, did not show the same sensitivity to reduced soil temperature. These included species of Achillea, Geum, Solidago, and Salix. Ecotypes from higher elevations showed no difference in reduction of TR and PSN. Growth, however, was reduced for all plants at 3°C soil temperature. Growth reduction could be due to changed hormonal balance. Hormones such as abscissic acid affect stomatal function directly (Mittelheuser and Van Steveninck, 1969) and could affect growth indirectly in that manner. Cox and Boersma (1967) found reduction in TR in Trifolium repens at soil temperatures of 10°C, and attributed the reduction to decreased viscosity of water.

Conifers also respond to cold soils in several ways. Hinckley and Ritchie (1972) found that reducing soil temperature from 26 to 10°C reduced sap velocity, and caused PMS of two species of Abies to increase 1 atm. Babalola et al. (1968) showed a reduction in TR of Pinus radiata below 10°C. Havranek (1972) found a 40-60 percent reduction in PSN and TR when soil temperatures were reduced from 20 to 2°C over a sustained period in Larix decidua and Picea abies. For Picea abies and Pinus silvestris, Christersson (1972) reported increased cold hardiness coincided with decreased transpiration.

Although the effects of air and soil temperature have not been

separated in many experiments, it is certain that frozen soil stops water uptake by the plant. Either frozen soils or increase in viscosity could lead to high moisture stress if air temperatures were warm, stomata open, and atmospheric demand sufficient. At high PMS, stomata would close and PSN would be inhibited. Although no studies of increased PMS or reduction in PSN have been completed for Douglas-fir, it was apparent from field sampling of PMS and SA during winter and spring that some type of cold soil reduction was necessary. I included a soil temperature reduction function which changed night PMS, which in turn reduced photosynthesis. The reduction function increased PMS linearly from 2 atm at 5°C to 30 atm at -2°C soil temperature.

This completes the list of factors considered to be of major importance in controlling leaf conductance in Douglas-fir. The factors were plant moisture stress, night minimum air temperature below $-5/9^{\circ}\text{C}$, and soil temperature below 5°C . Other environmental factors considered but not included in the simulation (see Appendix II) were high air temperature, humidity, wind, needle age, and pre-conditioning.

The Photosynthesis Simulation

The photosynthesis simulator was coded for a general model processor called FLEX1 developed by Overton et al. (1973). The

"flexform" which outlines all aspects of the simulation in simplified flex notation is included with the Fortran program as Appendices III and IV. The simulation was thoroughly checked, and then used to evaluate the climatic data from three western Oregon forest sites.

V. ENVIRONMENTAL CLASSIFICATION

The ecologist, forester or geneticist must be able to predict plant responses to environmental change. Prediction is best achieved by an understanding of both the environment and the plant's response to it. Plant response models based on detailed knowledge of how plants "see" their environment should predict plant behavior outside the area of calibration (Overton, 1972).

Mason and Langenheim (1957) developed the concept of the "operational environment" which is simply stated: Operational environment is the set of stimuli which have a direct effect on the organism. Environment is therefore organism timed, spaced, and directed. These operational criteria were used to determine which climatic factors were measured, where they were measured, and when they were measured. Further, the same criteria were used in interpretation of measured factors.

A method of indexing forest sites based on the concept of operational environment has been developed by Waring et al. (1972). Important environmental gradients were indexed either by measurements taken on reference plants, or by plant response models based on detailed knowledge of plant physiology (Figure 5-1). Micro-climatic data from each site served as inputs to the physiological

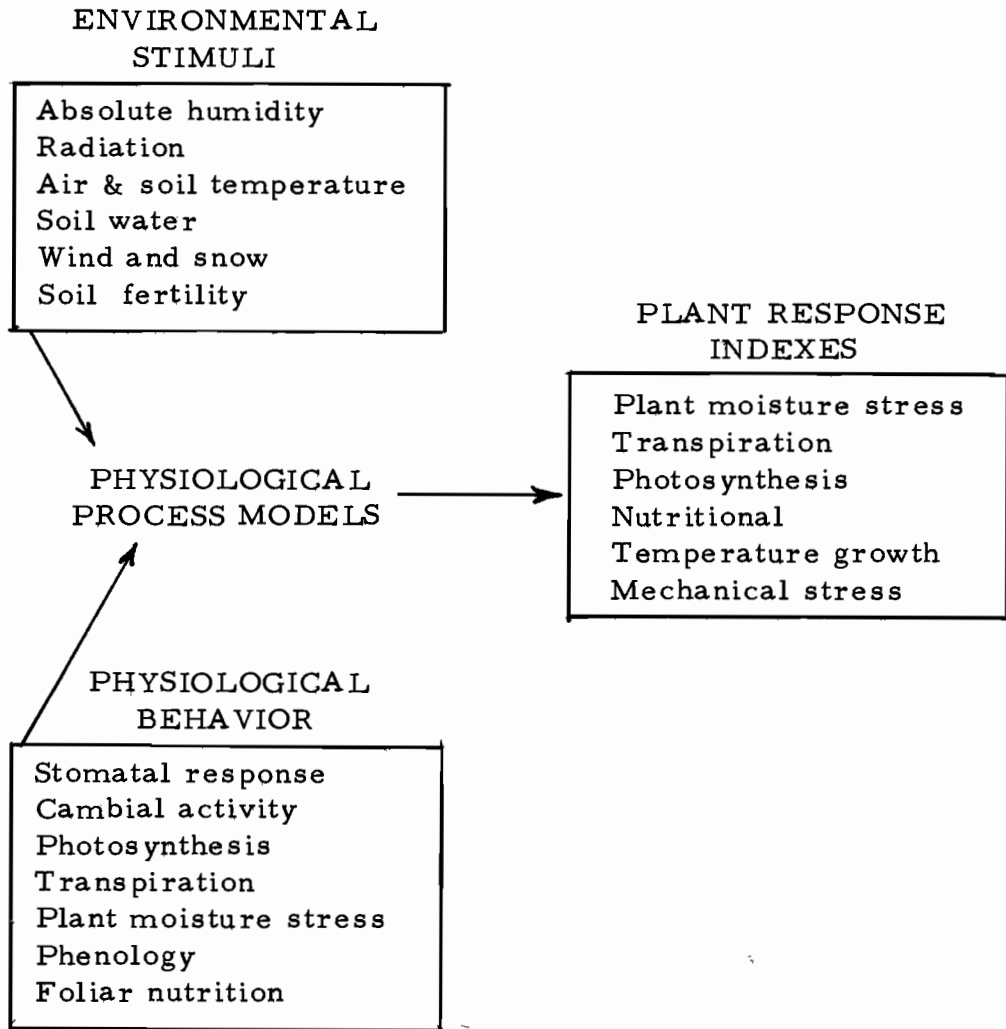


Figure 5-1. Schematic diagram of how environmental indexes are constructed from measures of the micro-climate and knowledge of plant responses. (modified from Waring et al., 1972)

process models. Outputs from these simulations were summed to produce an index value for each site of interest.

The indexes to the environment proved useful in predicting species composition, productivity of forest sites and interpreting why certain management practices fail. Once detailed information on how various populations of Douglas-fir respond to different environmental factors is available, the indexes should prove useful in predicting where particular populations will thrive. Therefore, I placed each plantation on environmental gradients defined by index values. Through these indexes, studies of genetics, land classification and plant physiology were linked.

Each important environmental factor can be evaluated as a separate gradient, or several factors may be combined into one index. Potential growth was evaluated by looking at air and soil temperature. Available moisture was evaluated by measuring plant moisture stress on reference trees at each site. Photosynthetic potential was estimated by models which evaluated several environmental factors. Together, these indexes constitute a multi-dimensional hyperspace useful in defining plant community, species, or population niches (Reed and Waring, 1974).

Each index is computed from records of climate taken at the site. A description of procedures used to collect the data follows.

Climatic Measurement

Climatic measures included temperature, humidity and short wave radiation. Temperature at 20 cm below ground and 1 m above ground was recorded continuously on Partlow thermographs. These were calibrated when placed in the field, and checked periodically.

Relative humidity was measured with hair hygrometers and corrected by correlation with sling psychrometer observations. The psychrometer values were regressed against concurrent hygrometer readings for each location. All regressions were highly significant, with R^2 values ranging from 0.71 to 0.97. Each reading taken from the hygrothermograph chart was corrected with the appropriate equation.

Short wave incoming solar radiation was recorded with American Instrument Co. solarimeters in conjunction with Thornthwaite-Rustrak recorders. Each instrument was calibrated in the field by passing a known voltage through the recorder. These instruments were powered by 12 volt car batteries, which had to be recharged every two weeks. Rainfall was measured at ten-day intervals with standard rain gauges.

Air temperature records were digitized for computer analysis. Average day and night temperatures were computed, and daily maximum and minimum extracted. Average daily soil temperature was read from the chart and later key punched. Maximum and minimum

relative humidity were visually taken from the chart, and after key punching, used to compute an average vapor concentration for each day. Radiation charts were analyzed by summing visually estimated, 15-minute averages to obtain total radiation in langleys per day.

Temperature Growth Index

Growth potential for Douglas-fir was computed for each day using average day air and soil temperature. Each day's values were determined using the methods of Cleary and Waring (1969). Their evaluation was based on growth room studies by Lavender and Overton (1972). Daily values were summed for the growing season which is defined as that period between bud swell and last cambial cell division. I arbitrarily set the end of growing season to the last of September, when over 95 percent of cambial growth was complete. Although some cambial growth continued until the end of October, soil and air temperatures were so low in all areas that this early cut off had little effect on the index value.

As expected, the mountain plantation had the lowest temperature growth index with 62 temperature growing days. The coast range was warmer, with a total of 87, while the valley site was warmest. At the valley plantation the temperature recorder was fully shaded because the trees were three times the size of those at the other plantations. Therefore, an additional thermograph was placed in a

nearby opening. Temperatures in the open were consistently 2-5°C higher than in the stand. The estimated temperature growth index for the stand was 81, while in the open it was 103. As a compromise I chose 95 as representative of the site for comparison with the other plantations.

Moisture Index

Night plant moisture stress (PMS) was measured bi-weekly throughout the 1971 growing season at each plantation (Figure 5-2). Four types of index were derived from this information. A "fall PMS index" was taken as the highest night PMS reached before fall rain, as suggested by Waring and Cleary (1967). Where summers are rainless, this method gives good comparisons between sites. In areas where summer rains occur, or trees respond unequally to fall rains, a "cumulative PMS index" based on daily evaluation of stress, yields additional information about relative drought at each area. In addition, however, length of growing season varies with site. The cumulative PMS index for an area with high PMS and a short growing season could equal the cumulative index for an area with low stress and a long growing season. The "average PMS index" is derived by dividing the cumulative index by the number of days in the growing season.

A fourth way of evaluating moisture stress was to accumulate

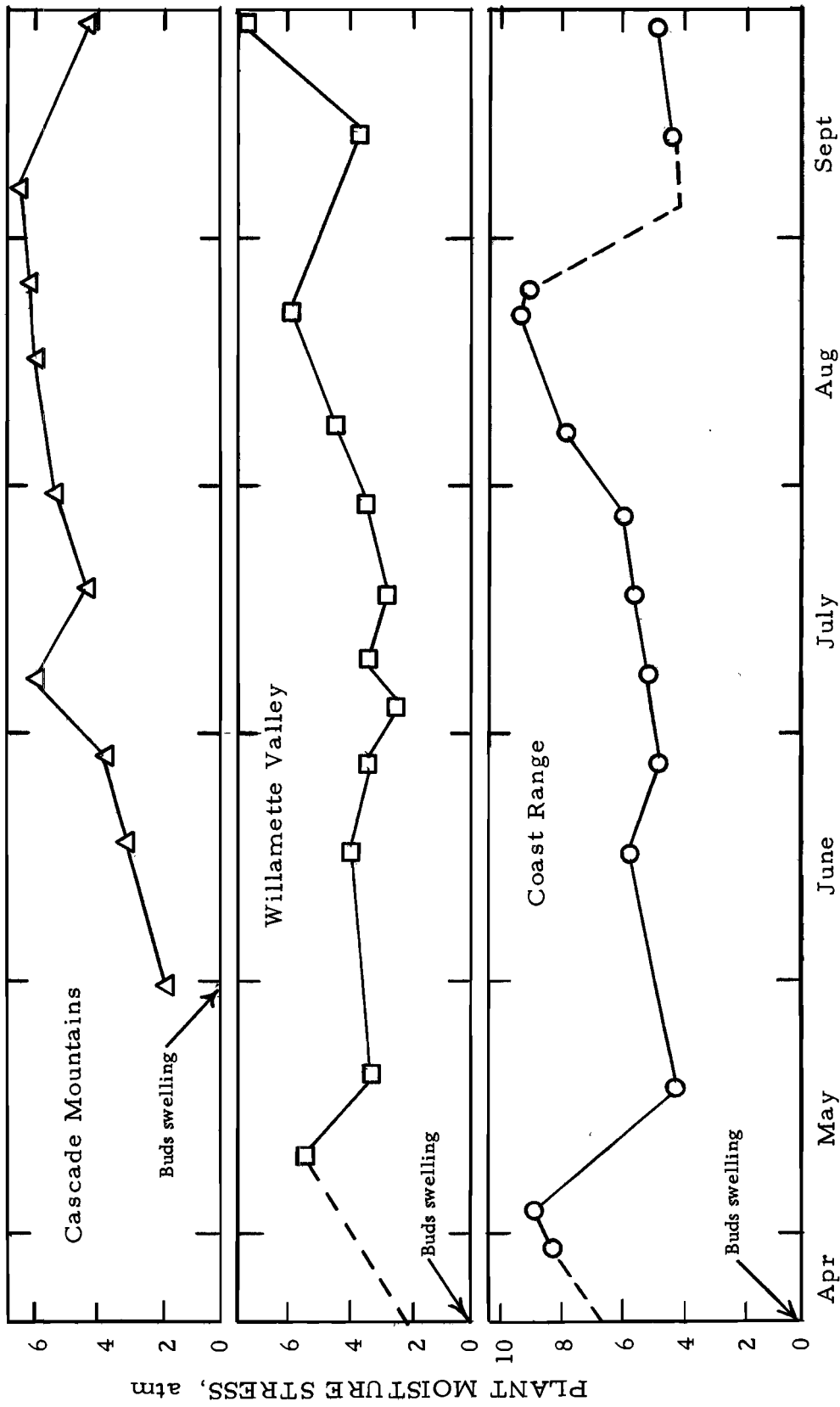


Figure 5-2. Comparison of night minimum plant moisture stress for three plantations during the 1971 growing season.

the reduction in photosynthesis caused by moisture stress on a daily basis. This was accomplished with the simulation of photosynthesis.

The fall moisture stress index measured in late August just before rains was about the same in the valley (6.5 atm) and mountains (6.2 atm). The coast range had a significantly higher index (9.4 atm) as expected. These values helped locate each plantation with respect to the other plantations, and with respect to other forest sites in western Oregon (Figure 5-3).

Drought stress did not reach high levels in 1971, because of late spring and early fall rains. In 1972 the fall moisture stress index was 15 atm for the coast range site. Zobel (thesis in progress) found that the relative positions of forest sites remained the same in years of different drought intensity. Thus, the 1971 index values indicated the relative severity of drought on these three sites during a mild year. The position of these sites on the environmental axes in Figure 5-3 may be shifted toward drier sites in other years.

The fall moisture stress index did not tell the whole story of drought for the three areas. Each site received different amounts of spring and fall rain, and there were differences in soil moisture holding capacity between sites. All locations had anomalous high night PMS readings early in the growing season. More important were striking contrasts in pattern of recovery in the fall. At the mountain plantation 3.8 cm of rain fell at the end of August, and

PMS may have recovered briefly; however, it rose to its highest level by September 7. In the valley 6 cm of rain caused night PMS to drop to 3.5 atm on September 10. By late September, night PMS had risen to the highest level of the growing season (7.8 atm). In the coast range 10.2 cm of rain caused a drop to 4.3 atm and stress rose only slightly in the next two weeks. In short, spring and fall patterns of PMS differed by area, and these differences could be important to the plant.

Because of the above differences, and because summer rain is common in some parts of the west, I defined a new "cumulative PMS index." It was derived by summing the atmospheres of night PMS for the growing season. Thus, a period of 5 days when night PMS equaled 5 atm would have accumulated 25 atm of stress. This represents the area under the PMS curves in Figure 5-2. The cumulative PMS indexes for the valley, mountain and coast range sites were 667, 577 and 874 atm, respectively. Note that the ranking of areas by both methods is identical (Table 5-1).

Table 5-1. A comparison of the various indexes to moisture stress on three plantations.

Plantation	Plant moisture stress index							
	Fall		Cumulative		Average		Photosynthetic	
Mountains	6.2	(1)*	577	(1)	4.93	(2)	43%	(2)
Coast range	9.4	(3)	874	(3)	5.71	(3)	58%	(3)
Valley	6.5	(2)	667	(2)	4.35	(1)	38%	(1)

* Ranking in relation to other locations.

Careful examination of Figure 5-2 revealed a long period when PMS was favorable in the valley, but a relatively short time when PMS was favorable at the mountain plantation. This suggests a third index to correct for length of growing season. The "average PMS index" was computed by dividing cumulative PMS index by the number of days in the growing season. This index showed that although the mountain location did not reach as high a night stress as the valley did, the average for the growing season was greater. The coast range site still showed the greatest stress by this index.

The fourth index was derived by keeping track of the percentage reduction of potential photosynthesis caused by PMS induced decrease in leaf conductance (Figure 4-1 and Equation 1). The total reduction due to moisture stress is shown in Table 5-1 as "photosynthetic PMS index." The ranking of the three areas was the same with this method as with the average PMS index. Since the photosynthetic PMS index incorporates more plant-environment interaction and integrates more environmental factors, it has the advantage for comparisons of widely separated areas. If there is not sufficient information to derive this index, then the average PMS index would be preferred.

With temperature and moisture index values for each plantation it was possible to compare these sites with other forest ecosystems (Figure 5-3). The coast range and valley sites are warm and moist, comparable to some hemlock types on the H. J. Andrews Experimental

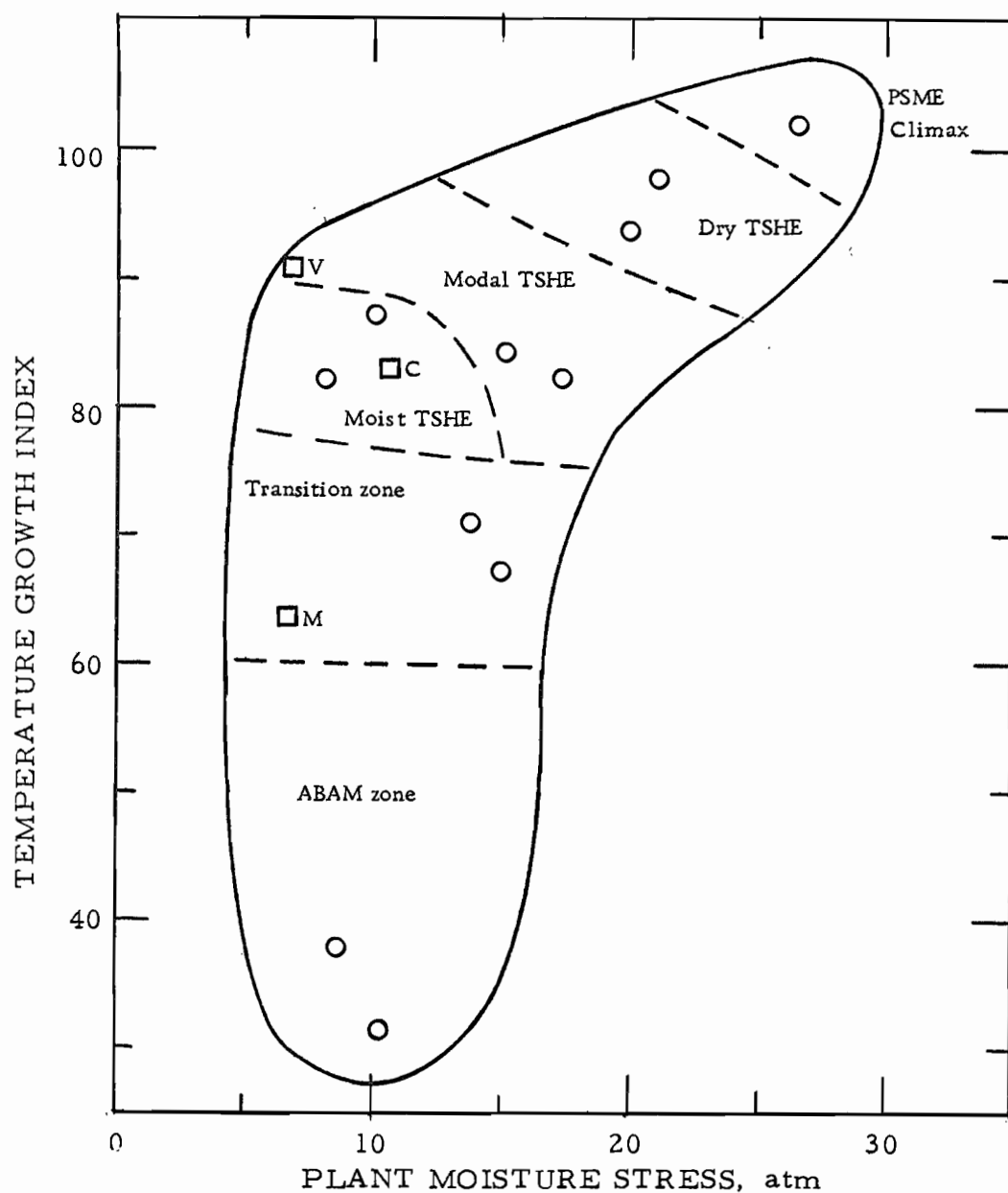


Figure 5-3. Comparison of the Willamette Valley (V), Cascade Mountain (M) and Coast Range (C) plantations with other forest locations in western Oregon on the basis of moisture and temperature indexes (from Zobel, 1974).

Forest in the Oregon Cascades (Zobel et al., 1974). The mountain site is similar to transition zone forest types (Franklin and Dyrness, 1973). Zobel's indexes were derived for 1972, a considerably drier year. The procedures for adjusting for yearly variation are now being worked out, and it will be possible to more accurately compare these plantations with his forest types. Thus, the three plantations can be effectively placed on quantitative environmental gradients for comparison with other sites. These methods not only quantify source environment, but provide a basis for predicting to which areas particular seed sources could be transferred.

Photosynthesis Index

A third environmental gradient was derived by evaluating photosynthetic potential at each plantation. I chose to simulate photosynthesis on a daily basis because of the tremendous expense involved in measuring photosynthesis in the field for even short times. By building on the gas exchange work done at the University of Washington, and the modeling of photosynthesis by Reed et al. (1974) and Sollins (1974, personal communication), I constructed a computer simulation which estimated net CO₂ uptake for 1 dm² of unshaded leaf area. Inputs were daily total shortwave incoming radiation, average day air temperature, average night air temperature, minimum night air temperature, and average daily soil temperature. Output was daily net CO₂ fixation (daytime photosynthesis minus night respiration).

The climatic data to run the simulation were collected at each plantation. During the winter it was not possible to measure radiation at each site, so five-year average radiation from near Corvallis was substituted (Bates and Calhoun, 1969).

The simulation was executed for two sets of assumptions. First, I evaluated "potential" photosynthesis by running the simulation on only average air temperature and radiation. For this I assumed abundant soil water and that frost or cold soils did not affect photosynthesis. Leaf conductance was held constant at 0.143 cm/sec. This represents an over-optimistic view of the photosynthetic capability of Douglas-fir, but one that sets an upper limit. Second, "predicted" photosynthesis was estimated with functions that reduced photosynthesis due to drought, frost and cold soils. Predicted photosynthesis reflected what were believed to be realistic restrictions on CO₂ fixation.

The simulation was designed to evaluate each site for annual fixation of a fully exposed square decimeter of leaf area. In addition, it helped separate the effect of various stresses. Further, it was a way to contrast seasonal contribution to primary productivity.

This information may be helpful in evaluating the potential influence of management practices. Where neither temperature nor moisture restricts photosynthesis, only improved nutritional status or genetic efficiency could increase yields. For example, irrigation

should not be attempted where drought causes little reduction of CO_2 fixation.

The results of the photosynthesis simulation for the three plantations are summarized in Figure 5-4. Since daily photosynthesis (PSN) varied widely from day to day, 5-day averages were used to show the general pattern. In each graph, the upper line represents "potential" and the lower line "predicted" photosynthesis per day. The area under the potential curve represents the amount of CO_2 that could have been fixed if only air temperature and light were considered. The vertically hatched area represents potential not realized because of plant moisture stress. The horizontally hatched area is potential unrealized because of either cold soil or frost. The area under the lower curve represents the total net CO_2 fixation for the entire year. Tables 5-2 and 5-3 summarize the above information.

Photosynthetic potential was greatest in the coast range, and least in the mountains. However, predicted PSN was greatest in the valley, since the valley had less moisture stress than the dry coast range site. Growth of cambium and leader, as well as bole weight, increase; all rank in the same order as predicted PSN (Table 5-2). Growth per unit basal area, which on these small trees is analogous to growth per unit leaf area (Grier and Waring, 1974), was also most closely correlated with predicted PSN. These correlations add credibility to the functions used in the model.

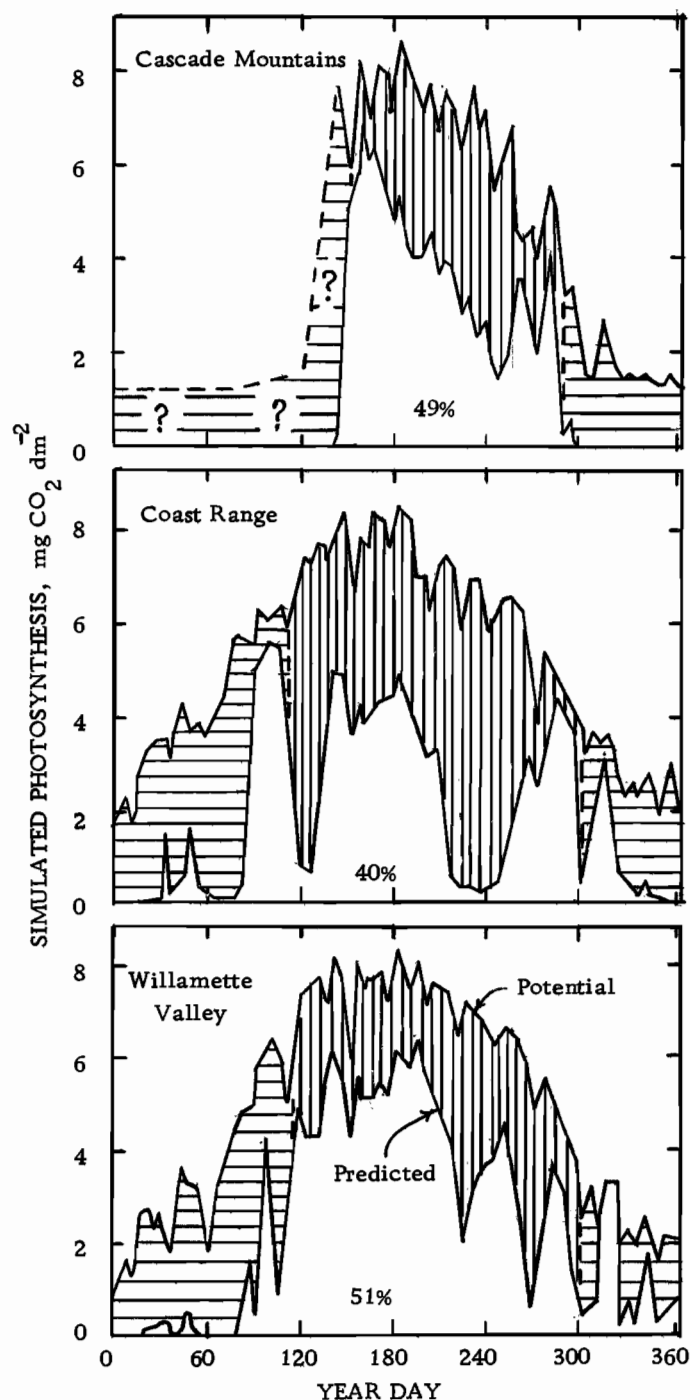


Figure 5-4. Comparison of three genetics plantations for simulated predicted and potential photosynthesis. The vertically hatched area represents potential lost because drought, while the horizontally hatched area represents potential lost because of frost and cold soil. The percentage of potential realized is noted for each area.

Table 5-2. A comparison of predicted and potential photosynthesis with growth for three genetics plantations.

Location	Photosynthesis (mg CO ₂ dm ⁻¹)		Growth			
	annual "potential"	annual "predicted"	average cambial (mm)	average leader (cm)	estimated bole mass (g)	corrected bole mass/ leaf area
Mountain	1, 157	565	2.8	36	558	15
Coast Range	1, 893	762	6.4	66	1, 040	41
Valley	1, 821	930	9.0	122	9, 896	63

Table 5.3. Comparison of predicted versus potential photosynthesis on a seasonal basis, and the importance of the dormant season for three sites in western Oregon.

Location	"Predicted"/"potential" (%)			Dormant predicted/ annual predicted (%)	% Growing season potential lost to drought
	annual	growing season	dormant season		
Mountain	49	57	17*	7	43
Coast Range	40	42	36	31	58
Valley	51	62	25	15	38

* The entire dormant season was not included.

Winter comparisons reflect differences in temperature between the sites, since the same radiation data were used for all areas. In the valley, cool air accumulation restricted PSN. Sixty percent of the nights between 11 November and 1 May were frosty in the valley plantation, versus 30 percent in the coast range. Consequently, in the coast range 31 percent of the yearly predicted PSN accumulated in the non-growing season (1 November to 25 April) (Table 5-3). For the same time period only 15 percent of yearly predicted PSN occurred in the valley. The mountain location was not accessible during the winter so the climatic record needed to run the simulation from January to May was not available. However, the area was covered with snow from November until late May, with the soil temperature at or below 1°C . This has the effect of reducing leaf conductance so that less than 10 percent of potential could be realized. Night frosts, common at that elevation, would further reduce predicted PSN. Even in the coast range most of the predicted PSN occurred in early spring rather than in mid-winter.

Seasonal comparison of photosynthate production prompted several observations. First, in the Pacific Northwest there is considerable dormant season potential for photosynthesis. Even under the rather rigorous assumptions in this model, over 30 percent of the annual potential in the coast range accumulated during the dormant season. Second, photosynthesis at near freezing temperatures must

play an important role in the ecology of the region. Third, there would appear to be considerable advantage in adapting to cold soils and frost in this region. For example, when restrictions on fixation due to cold soil and frost were removed, over 50 percent of the annual photosynthate accumulation in the coast range was during the dormant season.

Future studies of photosynthesis in Douglas-fir should include observations at low temperatures. Comparison of seed sources with respect to dormant season photosynthesis could reveal important genetic differences.

Another important reduction in photosynthesis at all areas was due to plant moisture stress. The mountain and valley locations lost about 40 percent of the summer potential, while the coast range site lost 58 percent. During the last few weeks of drought, nearly all photosynthesis at the coast range site had stopped. Obviously there would be great adaptive advantage to photosynthesis under drought conditions.

The percent loss to drought was another way to index moisture stress for a site, and this index paralleled the average PMS index (Table 5-1).

Comparison of the seasonal pattern of photosynthate production reveals some interesting differences between sites (Figure 5-5). A negligible amount of PSN took place during the mid winter months

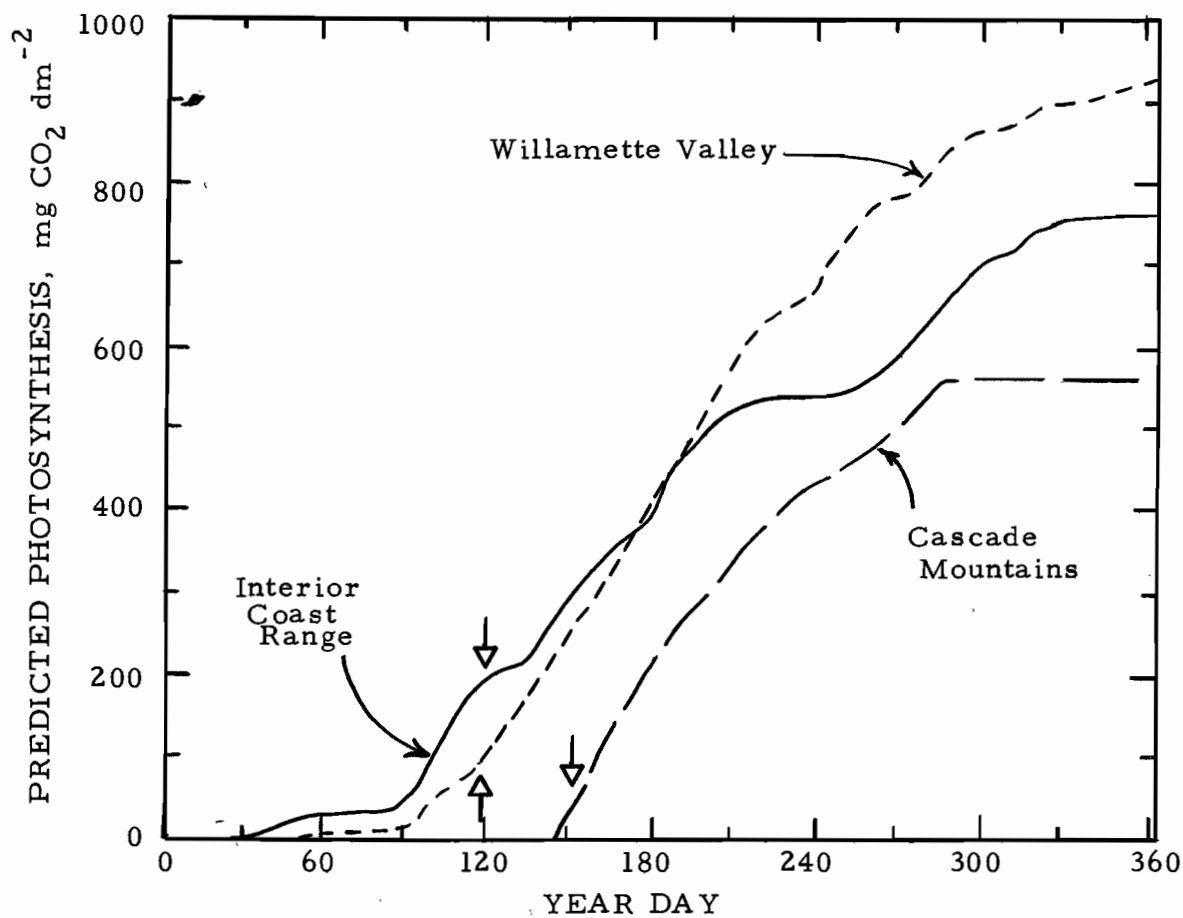


Figure 5-5. Comparison of three genetics plantations for accumulated predicted (simulated) photosynthesis.

→ = Time when buds were swelling

even at the warmest location. In the coast range there was considerable accumulation early in the growing season, but as moisture stress increased the rate of accumulation slowed down. In the valley, accumulation began later, and steadily increased throughout the summer. The effect of fall rains was apparent in the coast range with a rapid rise, after a period of almost no accumulation. In the mountains there was little accumulation until June, but the rate of accumulation thereafter was similar to the other areas. Thus, the major factor accounting for reduced productivity in the mountain location was the shortness of the growing season.

With development of the PSN index, it was possible to compare the three plantations in three dimensions (Figure 5-6). The general pattern of high PSN where moisture stress was low and temperatures warm was expected. Once other areas have been located on this surface, fine resolution separation of sites should be possible. For example, the coast range and valley plantations had appeared similar in Figure 5-3, but were well separated by the addition of the PSN index.

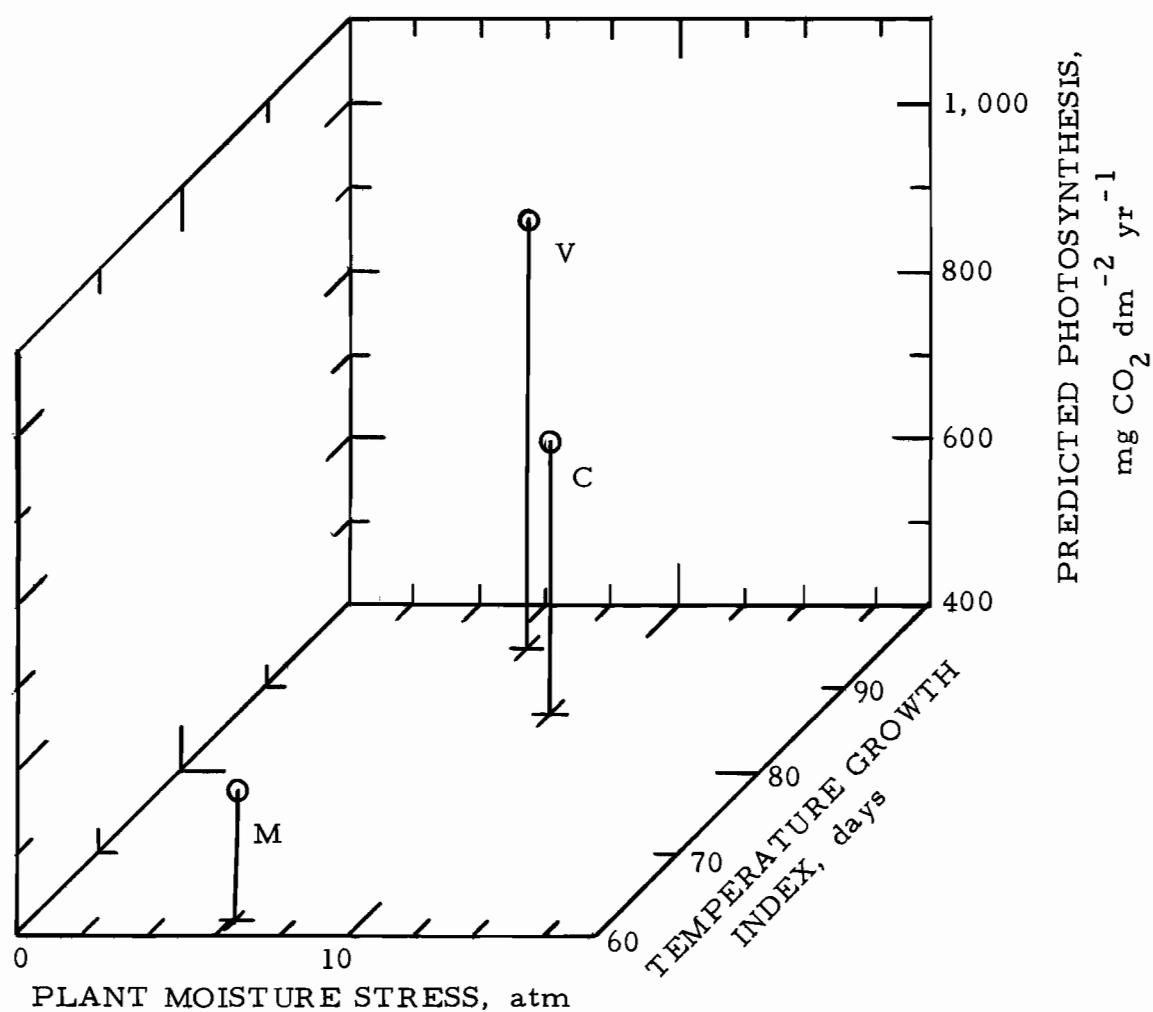


Figure 5-6. Location of mountain (M), coast range (C) and valley (V) Douglas-fir plantations with respect to moisture, temperature, and photosynthesis gradients.

VI. GROWTH COMPARISONS IN CONTRASTING ENVIRONMENTS

Following quantification of environment, comparisons of growth at the three plantations were possible. In this chapter, amount, pattern, and environmental control of growth are discussed. Genetic comparisons of amount and pattern of growth are in Chapter VIII.

Methods

Growth was measured at about 10-day intervals from prior to bud swell until the end of September when cambial cell divisions had nearly ceased. Terminal growth was measured by reading leader length from a meter stick held adjacent to the leader. This method worked well with trees less than 5 m tall, but was difficult for taller trees or for trees with "droopy" leaders.

Cambial growth was marked by inserting a pin into the cambium about 40 cm above ground level (Wolter, 1968). Each pin injured the cambium, causing cell deformation for the remainder of the growing season. After growth had ceased, that portion of the xylem was removed and carefully sectioned for microscopic examination. The distance from the end of the previous year's growth ring to the start of the wound tissue was measured along with total width of the growth ring at that point. Determination of the number of cells laid down to within ten cells, or distance to the nearest 0.05 mm, was achieved with confidence.

Initiation and Cessation of Growth

Comparisons of phenology showed that the timing of growth was in many cases related to environment. Growth phases are summarized in Figure 6-1 and Table 6-1.

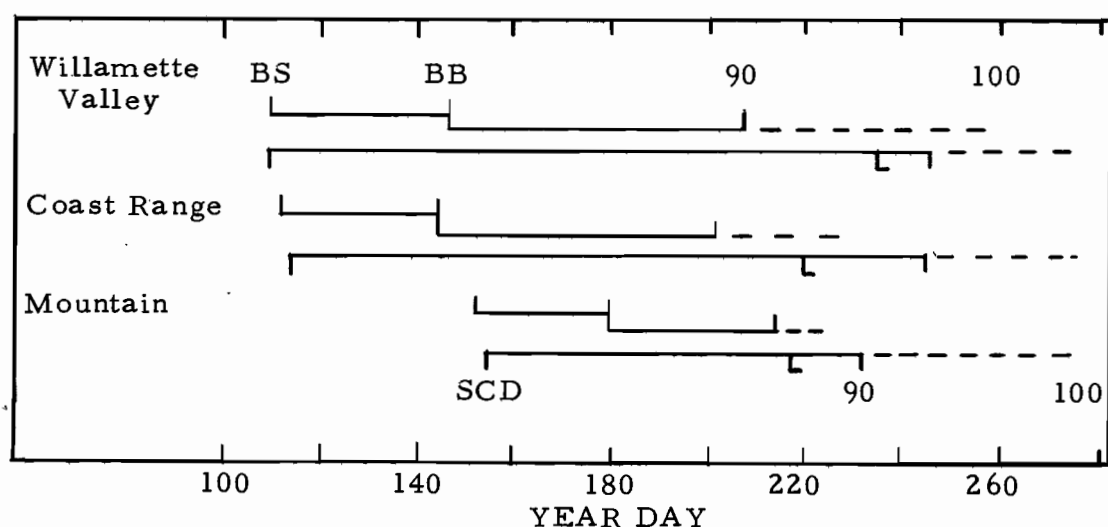


Figure 6-1. Phenologic comparisons of leader growth (upper lines) including: BS = bud swell; BB = bud burst; 90% and 100% completion of leader yearly growth. Comparisons of cambial growth (lower lines) phases include: SCD = start cambial cell division; L = start latewood formation; 90% and 100% completion of cambial growth.

Initiation of growth nearly coincided in the coast range and valley plantations. In the mountains, growth initiation was delayed until the first week of June because the snow did not melt until the last week of May. Bud swell occurred at all three plantations when

Table 6-1. A summary of timing for phenology and growth at three genetics plantations.

Area	Initiation of cambial growth		Leader growth (days)		Cambial growth (days)		Active cambial growth after leader growth slows (days)
	date (1971)	day	90% complete	days to 90% completion	90% complete	days to 90% completion	
Willamette Valley	20 / 4	110 *	208 *	98	245 *	135	37
Coast Range	25 / 4	115	202	87	245	130	43
Cascades	1 / 6	156	215	59	232	76	17

* Day = Julian year day

soil temperatures reached about 5°C (Figure 6-2). This was consistent with field observations in a wide variety of plant communities (Waring, 1974, personal communication). In another plantation where both coastal and Rocky Mountain sources of Douglas-fir were planted, this pattern did not hold. Recently, the hypothesis that initiation of growth in Douglas-fir was controlled by hormones produced in the roots was confirmed by Lavender et al. (1973). They found that the inhibiting effect of cold soil could be relieved by applying gibberellic acid to shoots.

Cessation or slowing of growth was affected by moisture stress, cool temperatures, and day length. Cessation, in contrast to initiation, occurred within a short time span. Ninety percent completion of leader growth was within a 15-day span for all sites, probably reflecting photoperiodic control. Cambial cell divisions continued until cool weather set in, indicating a temperature rather than photoperiod control.

Cessation of shoot growth may be affected by moisture stress, but it seems to be more strongly controlled by day length. In all areas, 90 percent of leader growth was completed by the first week in August. Where PMS was greatest in the coast range, growth slowed first. There was no second flushing at any of the areas despite a complete recharge of the soil profile and lowering of moisture stress. Thus, even if leader growth stopped early due to moisture stress, it

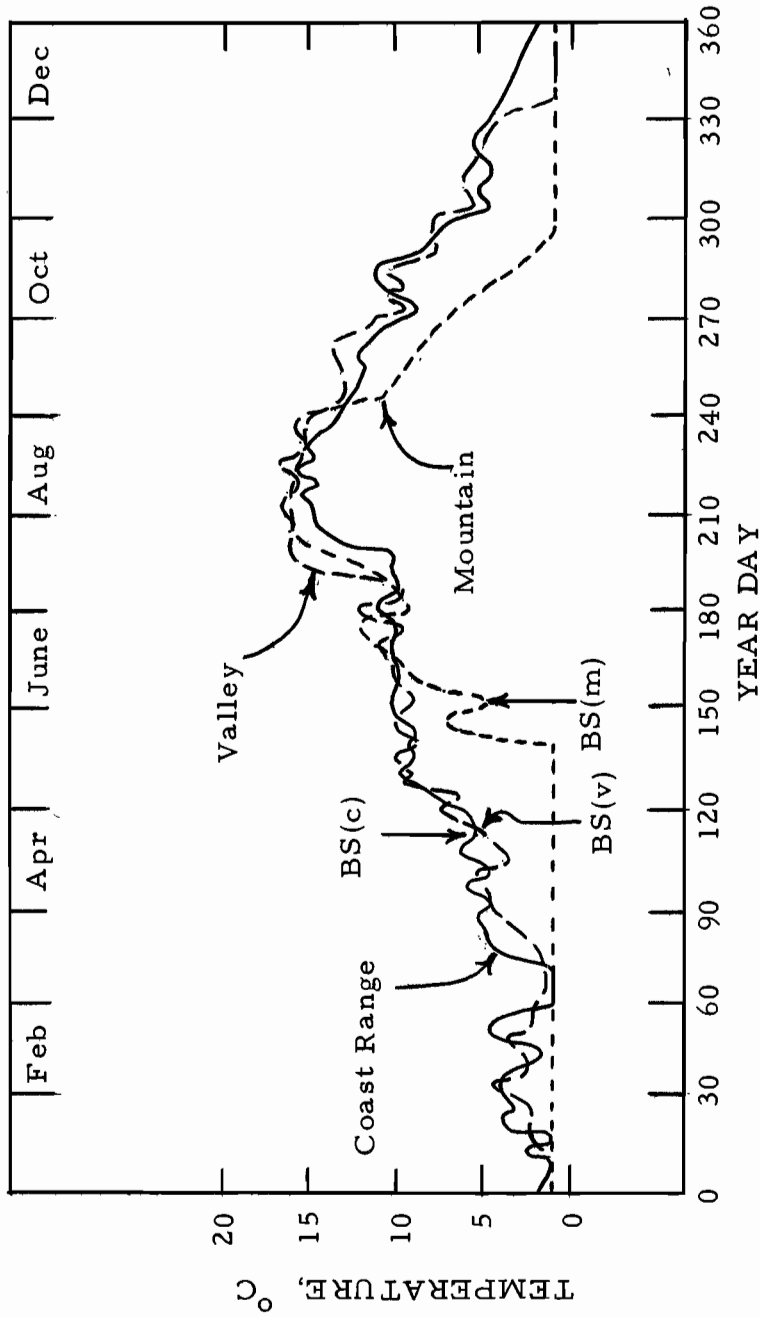


Figure 6-2. Comparison of annual soil temperature (-20 cm) traces for the three plantations, and timing of bud swell. BS = Buds swelling at (c) coast range, (v) valley, and (m) mountain plantations.

was prevented from starting again by photoperiod. Obviously there has been strong selective pressure to complete leader growth and harden off before early fall frosts.

Cambial growth cessation seemed to be controlled more by moisture stress and temperature than by day length. The cambium of trees sampled in late September in the mountains was still active. At the valley and coast range plantations, growth continued until the end of October. By that time cell divisions had nearly ceased. Soil temperatures were down to 7°C and there had been several killing frosts. Predicted PSN was low due to frost and cool daily temperatures. In the coast range cambial growth showed a definite increase after late August rains relieved moisture stress. My conclusion was that cambial growth was restricted by a lack of photosynthate brought about by restrictions on the photosynthetic process from moisture stress and cool temperatures (see Figure 5-4). The cambium is apparently well enough insulated to be impervious to early frost, and therefore can take advantage of late fall photosynthesis.

Latewood formation may be initiated by increase in moisture stress which reduces photosynthate accumulation. In all cases, latewood formation began after 90 percent of leader growth was complete. This generally corresponded to the point where 80-88 percent of cambial growth was complete. Cell walls became much thinner after

fall rains at the coast range, and cell wall thickness may be related to the rate at which carbohydrate becomes available for growth.

Total cambial and leader growth varied significantly with location, but not with seed source. Both leader and cambial growth in the valley were three times greater than at the mountain plantation (Figure 6-2). At the coast range site, leader and cambial growth were 70 and 50 percent of that in the valley. Trees in the mountains and coast range were smaller and had less leaf area than those in the valley, so growth differences would be expected.

Total growth was normalized in two ways. Growth was divided by total size and by basal area at the beginning of the growing season. The basal area correction is equivalent to normalizing by leaf area since basal area of small trees is proportional to leaf area (Grier and Waring, 1974). In terms of growth per unit of size, or per unit of leaf area, the coast range location is greatest. Trees in the coast range plantation were 1.7 times more efficient than those in the valley, and 2.8 times as efficient as those in the mountains. There was considerable mutual shading between trees in the valley, which could explain the lower efficiency there; however, the trees in the mountains were as open as those in the coast range. Although the coast range trees grew more per unit leaf area than those in the valley, they were not growing more at a given size than those in the valley. When trees in the valley were 3 m high, they grew 1 m per year. At

comparable heights, trees in the coast range grew 50-60 cm per year. Presumably, when trees in the valley were smaller, they were more efficient than those in the coast range.

Pattern of Growth

Typically, growth started slowly, reached and maintained a fairly high rate, and gradually slowed (Figure 6-3). The rate during the active linear phase of growth was nearly constant from week to week. That is, growth was relatively unaffected by periods of cool or hot weather. Rate of accumulation of simulated photosynthate and temperature sums were not affected by short term weather fluctuations either (see Figure 6-4).

Total growth at the end of growing season is a function of growth rate and duration of growth. The difference in total leader growth at the coast range and valley plantations was due largely to unequal growth rates; that is, 1.1 versus 2 cm/day during the linear growth phase (Table 6-2). On the other hand, elongation occurred at the same rate in the coast range and mountain sites, but the duration of active growth was about 20 days less in the mountains. Trees in the mountains had both slower rates and shorter duration of growth than in the valley. Leader elongation was completed in a shorter time in the more stressful environments.

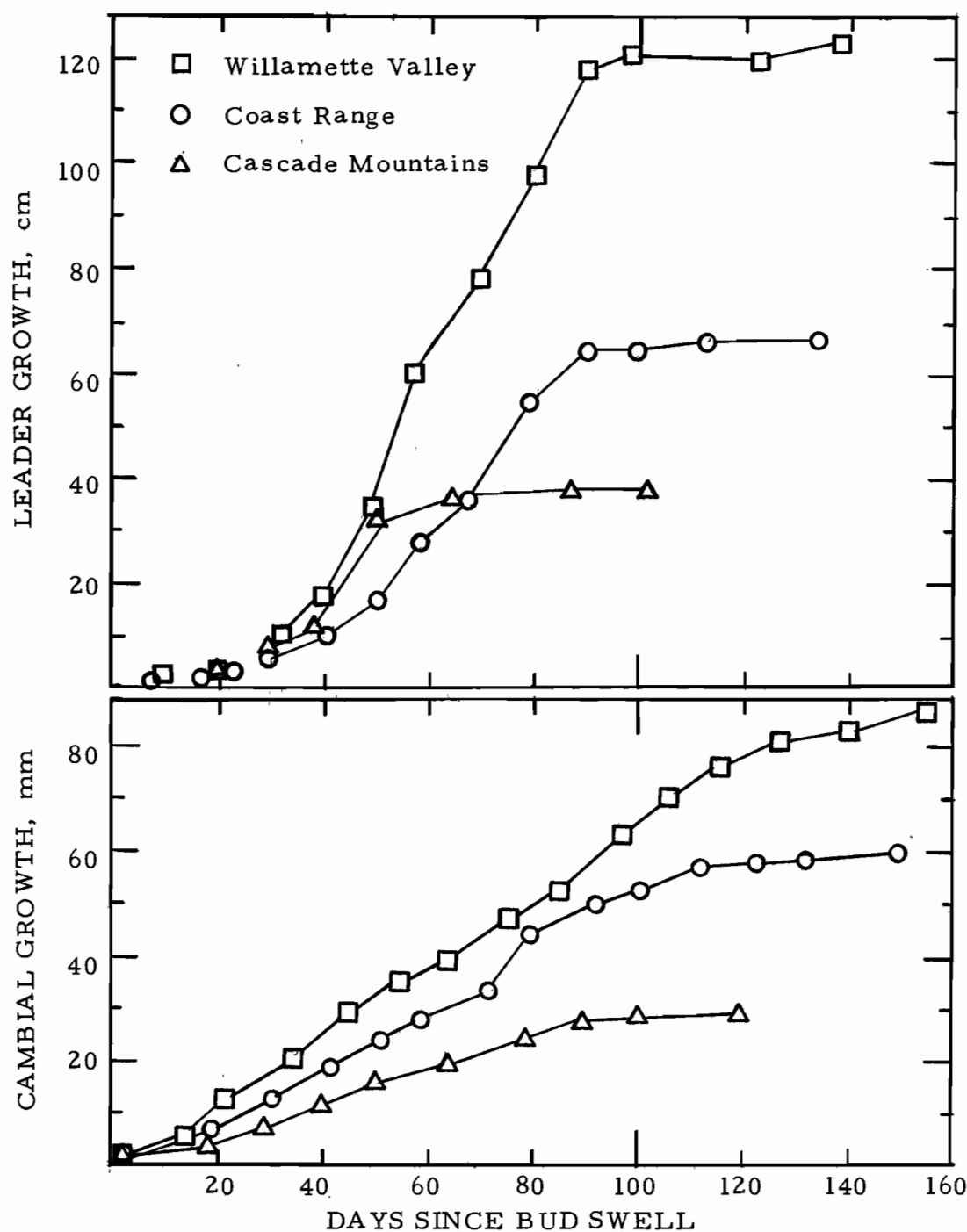


Figure 6-3. Average leader and cambial growth at Willamette Valley (bud swell = 20 April 1971), interior Coast Range (bud swell = 20 April 1971), and Cascade Mountain (bud swell = 1 June 1971) plantations.

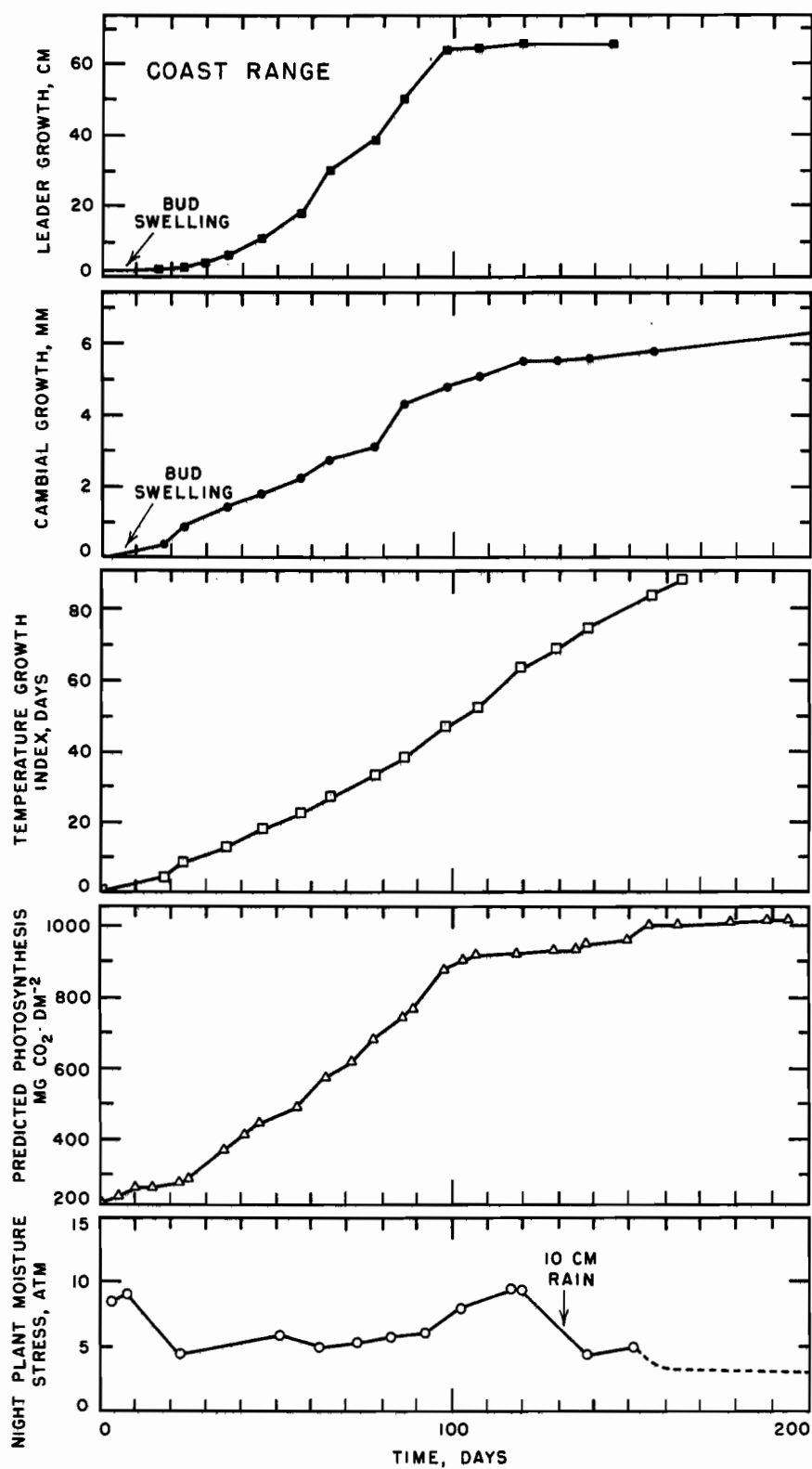


Figure 6-4. A graphic comparison of cumulative growth with cumulative indexes to environment.

Table 6.2. Comparison of actual and normalized cambial and leader growth at the three plantations. Each observation is the mean of 12 trees.

Area	Cambial growth (mm)			Leader growth (cm)		
	actual	normalized for diameter	normalized for leaf area	actual	normalized for height	normalized for leaf area
Mountains	2.89	0.425	0.079	36	0.125	0.99
Coast range	6.47	1.139	0.255	66	0.229	2.61
Valley	8.95	0.635	0.057	122	0.149	0.78

The general pattern of cambial growth was similar to that of leader growth, but there was more variation in rate during the linear phase. Also, as mentioned earlier there was a renewal of growth in the fall (Figure 6-3).

Each location had a distinct rate and duration of cambial growth which accounted for different totals. The cambial growth rate in the valley was three times that in the mountains and 1.4 times that in the coast range (Table 6-3). Active cambial growth lasted 135 days in the valley and only 50 in the mountains. The major difference in growth of cambium between areas was in length of time during which active growth could continue.

Growth rates were normalized for leaf area just as total growth was. Again, there was a reversal in ranking. The coast range trees had the highest growth rates for both cambium and leader (Table 6-2). This reflects a greater efficiency per unit foliage in the coast range plantation probably due to the open grown nature of the trees.

Environment and Growth

Short Term Correlations

Environment affects growth through a complex series of operations including photosynthesis, translocation, and cell construction. The indexes developed for referencing environments were derived by

Table 6-3. A summary of growth statistics for 1971 at a Willamette Valley, Cascade and interior Coast Range genetics plantations. Each entry is an average of 12 trees, with three trees from each of four populations.

Area	Cambial growth			Leader growth		
	total (mm)	rate (mm/day)	n-rate (mm/day/ LA $\times 10^{-6}$)	active growth (days)	total (cm)	rate (cm/day) n-rate (cm/day/LA) active growth (days)
Willamette Valley	8.95	0.066	4.2	135	122	2.00 1.3 60
Coast Range	6.47	0.057	22.5	93	66	1.10 4.3 55
Cascade Mountains	2.89	0.032	8.9	50	36	1.15 3.2 36

* Rates were determined for the linear or rapid growth portion of the curve.

** Normalized rates were derived by dividing the rate by the basal area, which is proportional to leaf area.

summing a measured or modeled effect of physical factors on plant operations. If these indexes truly evaluate operation environment, then there should be correlations between the index values and plant growth. Temperature, moisture and photosynthetic index values were plotted with cambial and leader growth for the coast range site (Figure 6-4). Some correlations were obvious.

Initiation of growth, and growth rate early in the spring were highly dependent on air and soil temperature; however, 2 weeks after bud swell, the temperature growth index accumulated at a nearly constant rate until long after leader and cambial growth slowed. Thus, while temperature of the air or soil appeared limiting for growth initiation, it did not appear to limit growth during the active phase. Leader growth stopped and cambial growth slowed at about the same time as night PMS began to climb. Day length is generally conceded to be important in cessation of leader growth (Irgens-Moller, 1962). Leader growth in the coast range stopped 20 days earlier than in the nearby valley plantation. The only apparent difference between the two areas was higher PMS in the coast range. The slowing of cambial growth was also correlated with increased PMS, whereas the renewal of cambial growth followed reduction of PMS. The reason PMS was so important in growth is suggested by results of photosynthesis simulation.

The growth curves closely parallel the curve of predicted photosynthesis (Figure 6-4). Cambial growth slowed and nearly stopped as simulated photosynthesis was cut by increasing PMS. Renewal of cambial growth after fall rain paralleled an increase in predicted PSN. Leader growth followed the same pattern during spring and summer. The lack of a leader growth response to fall rains was interpreted as photoperiodic control of leader growth. Growth is highly dependent on the products of photosynthesis, so a correlation between growth and PSN was expected. In fact, the correlation was, in a loose way, validation of the functions limiting photosynthesis in the simulation. Early studies by Hiley and Cunliffe (1922) showed positive correlations between daily height growth of Corsican pine and maximum shade temperature. Total seasonal growth was inversely related to soil temperature (at 15 cm) during May and June. These studies were in England where temperature may well be a limiting factor for photosynthesis and growth; however, such a limitation was not apparent in this study.

Long Term Correlations

Methods of dendrochronology (Fritts et al., 1971) were helpful in analyzing climatic variation. These methods correlate monthly precipitation and temperature for a year prior to the end of growing season with current year's growth. Sixty cores from the forest

adjacent to the coast range plantation were analyzed at the Dendro-chronology Laboratory in Tucson, Arizona through the courtesy of Dr. Harold Fritts, and Donna Marcynyszyn. There was a positive correlation between temperature and ring width for the months of January, February and March. This suggests the importance of winter photosynthesis. There was a negative correlation between growth and winter precipitation, but a strong positive correlation with precipitation in April, May and June. This indicated the importance of spring rains. High temperatures and no precipitation in August (i. e., high moisture stress) led to reduced growth the following year. An ideal growth year would be a rainy spring and summer with a sunny mid-winter. Growth in the present year was positively correlated with the previous year's growth, but negatively correlated with growth of the third year previous. This suggests a cyclic climatic pattern or within tree cycles of carbohydrate reserve.

Growth and Environment

Initiation of growth in both cambium and terminal was temperature controlled, with a small component of genetic variation. All sources started within ten days at a given site. Cessation of leader growth nearly coincided for all sources at all areas, indicating control by photoperiod. Conditions which restricted photosynthesis restricted both cambial and leader growth. At the driest location, leader growth

slowed slightly earlier than at the other locations, perhaps because increased moisture stress reduced photosynthesis. Cessation of cambial growth was related to both moisture stress and cool temperatures. In contrast to leader growth, cambial growth continued into early fall when night frost was common.

The growth rate of cambium and leader during the two-month active growing season was uniform. Likewise, the rate of accumulation of photosynthate and temperature sums were relatively uniform.

VII. GENETIC COMPARISONS

Background for Comparisons

Rowe and Ching (1974) demonstrated that differences in growth and survival of the Douglas-fir populations in this study were related to the origin of seeds. Explanations for observed variation in growth are yet to be found. Without such knowledge, we cannot be confident that a source which did consistently better than others can be freely transplanted to new areas.

Several problems associated with moving sources to new areas are responsible for this uncertainty. First, early growth advantages may reflect only differences in becoming established, and superior growth rates may not persist up to rotation age. Second, severe climatic stress may occur infrequently, but must be recognized as a major selection force. Third, we do not yet know which physiological processes are responsible for superior performance, or which climatic factors are most critical.

The different growth rates observed in populations of Douglas-fir may result from differences in photosynthetic capability, allocation of carbohydrates, or in conversion of photosynthate to plant use. Unequal total production of photosynthate could result from more efficient chemical processes, light adsorption, or stomatal control.

Stomatal control could be a major factor where droughty conditions are common.

Dry summers are typical of the Douglas-fir region, and drought is regarded as a major factor restricting growth (Strand, 1964). Sources with superior strategies of drought resistance could benefit by being able to photosynthesize longer into a drought period. During drought periods, plant moisture stress (PMS) gradually increases as soil water is depleted. Moisture stress has both direct and indirect effects on growth. Boyer (1969) showed that cell divisions in sunflower leaf cease at 3.5 atm leaf water potential. Waring (1969) found that all cambial cell divisions in Douglas-fir ceased when night minimum PMS reached 18 atm. In addition to the direct effect, stomata generally close in response to increased PMS (Slatyer, 1967), causing a reduction in photosynthesis, leading indirectly to loss of growth. Drought induced reduction of leaf conductance is of great importance because drought occurs in the growing season when all other factors are favorable for photosynthesis and growth.

In this study I attempted to develop methods for better assessment of site and seed source growth potential. This ability is critical, for genetics studies have shown that significant genetic variation may occur within a few 100 m from a south to north slope (Ferrell and Woodard, 1966). Only when we can predict performance from knowledge of environment can we advise that seed of a given origin be established elsewhere.

The objective of this portion of my study was to determine whether populations of Douglas-fir have evolved special mechanisms or tolerances which could account for observed differences in early growth. Specifically, I address the following questions:

1. Have certain populations of Douglas-fir evolved stomatal control which enables them to make better use of water?
2. Have certain populations evolved other mechanisms which allow them to escape summer drought as measured by plant moisture stress?
3. Have certain populations evolved different seasonal growth patterns of either the cambium or leader? Should such differences be found, they could be used in the simulation of photosynthesis to determine yearly net effect.

Some sources of Douglas-fir have already been shown to have different photosynthetic efficiencies in laboratory tests (Irgens-Moller, 1967; Pope, 1973). In other work, Krueger and Ferrell (1965) found inland sources had a better ability to maintain photosynthesis under prolonged high light intensities. Laboratory studies, however, only point to adaptations which may be important in nature. Field studies are needed to confirm the plant response patterns found in the laboratory.

I measured plant moisture stress (PMS), stomatal aperture (SA) and leaf conductance along with climatic factors at three plantations to

compare the four sources. Fortunately, field methods needed to look at SA (Fry and Walker, 1967) and leaf conductance (Turner and Waggoner, 1968; Byrne et al., 1970; Beardsell et al., 1972) have become available (see Chapter III for operational procedures). By using porometry, the pressure bomb and the infiltrometer, I gained a better understanding of how environment affects plant processes.

Intense sampling of plant responses and climatic factors was conducted during the 1971 growing season. In 1972 and 1973, comparisons were made at the driest plantation at the peak of drought.

As mentioned in Chapter I, four seed sources of Douglas-fir were sampled at each of three plantations. The northern source (Vancouver Island) was fast growing, while the southern source (southwestern Oregon) was slow growing. The mountain and coast range sources were intermediate in growth and native to the mountain and coast range sites respectively.

Comparisons of Physiological Responses

Plant Moisture Stress

Night minimum PMS has proven important as a way to assess soil water status, and was correlated with stomatal opening (Reed, 1972) and leaf conductance (Running, 1973) during the day. I measured night minimum and day moisture stress at the peak of drought (Figure 3-2) on trees of comparable size. The averages of three night

PMS readings for each of four populations were within 2 atm in the mountain and coast range sites, and within 3 atm in the valley (Figure 7-1). Analysis of variance showed no significant differences among populations. The variation shown at the valley plantation did not persist, and was not observed at the other areas.

Moisture stress during the day is also important for it has been linked to stomatal closure (Slatyer, 1967; Reed, 1972) and to decreased photosynthesis (Cleary, 1970). Day PMS is extremely variable being a function of atmospheric demand (Haas and Dodd, 1972; Sucoff, 1972). Day PMS observations did not differ systematically with population (Figure 7-1) when tested by analysis of variance.

Having confirmed that day and night PMS of various populations was similar in late summer, we can now turn to seasonal comparisons. These comparisons are based on the premise that small but persistent differences in stress could have great effect over the entire growing season. Figure 7-2 shows mean and standard deviation for 12 nights on the driest site. Although all populations are remarkably close throughout the season, the southern source is near the top in night PMS. At the mountain plantation (Figure 7-3), however, the northern source was consistently higher, and in the valley the mountain source was higher in night PMS. In the coast range and mountain sites the slight difference in night PMS throughout the season is easily explained as a microsite effect. In both cases the soil is

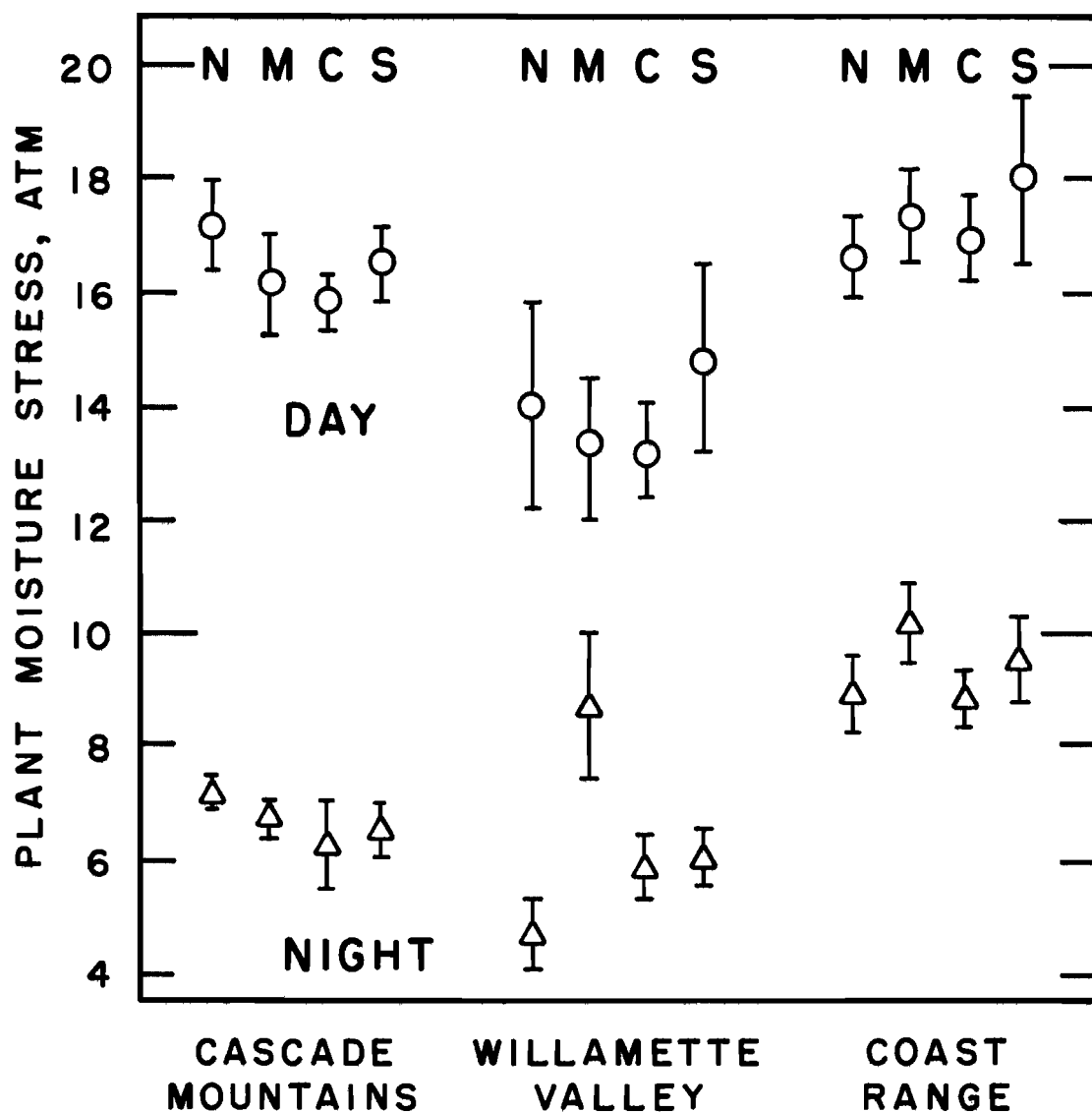


Figure 7-1. A comparison of day and night plant moisture stress at the peak of drought for three locations and four populations: N - Vancouver Island; M = Cascade Mountains; C = Coast Range Mountains; S = southern Oregon.

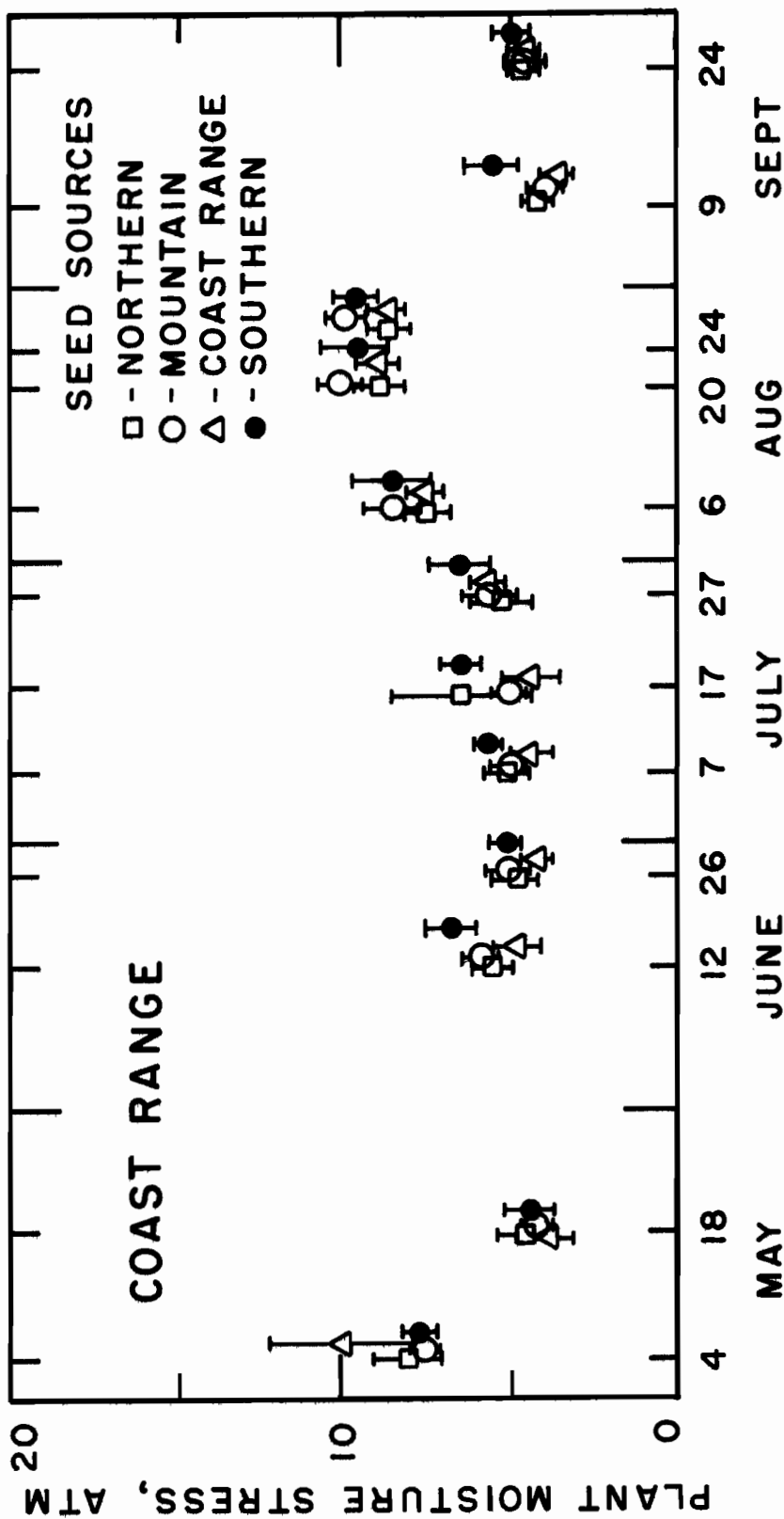


Figure 7-2. A comparison of night minimum plant moisture stress for four populations at the coast range site for the 1971 growing season. The standard deviation is generally less than 1 atm.

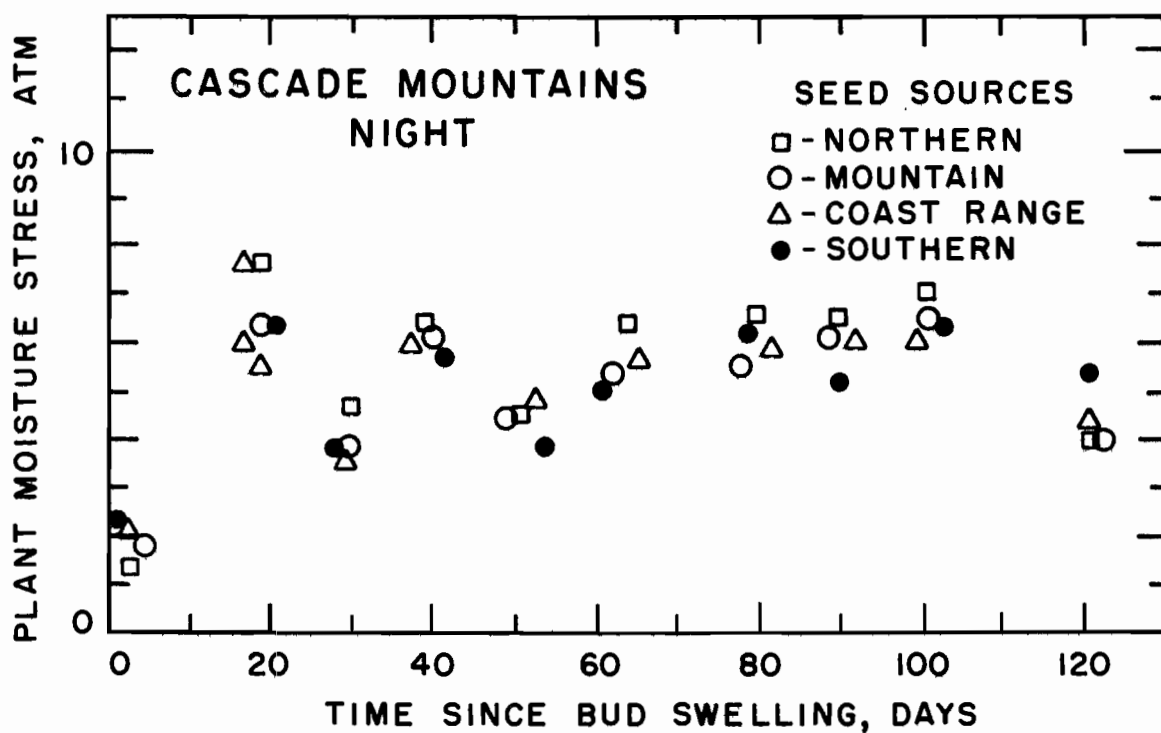


Figure 7-3. A comparison of night minimum plant moisture stress for four populations at the Cascade Mountain site for the 1971 growing season. The standard deviation is generally less than 1 atm.

thinner where the PMS was greatest. At the valley location the difference among populations in night PMS was small and inconsistent. Considering measurement error, microsite and tree size differences, it was remarkable that there were not contrasts among populations. I concluded there were no biologically significant differences among sources.

The seasonal pattern of PMS during the day is more variable because daily PMS depends on varying atmospheric demand. Figure 7-4 shows mean and standard deviation for 13 days at the mountain plantation. As with night PMS, the northern source is often slightly higher. In the coast range the southern source was often slightly higher during the day as was true at night. Again, microsite rather than physiological differences were probably responsible. When all areas were considered, day or night patterns in PMS did not vary persistently with seed source.

Stomatal Aperture

What strategy of stomatal control have populations of Douglas-fir evolved in adjusting to a summer dry climate? Maximum drought stress in the Pacific Northwest comes in late summer when trees have experienced 2-3 months of drought. In many coniferous forest communities PMS of trees did not fully recover at night (Waring, 1969; Zobel, 1974). Stomatal closure during mid-day when vapor pressure

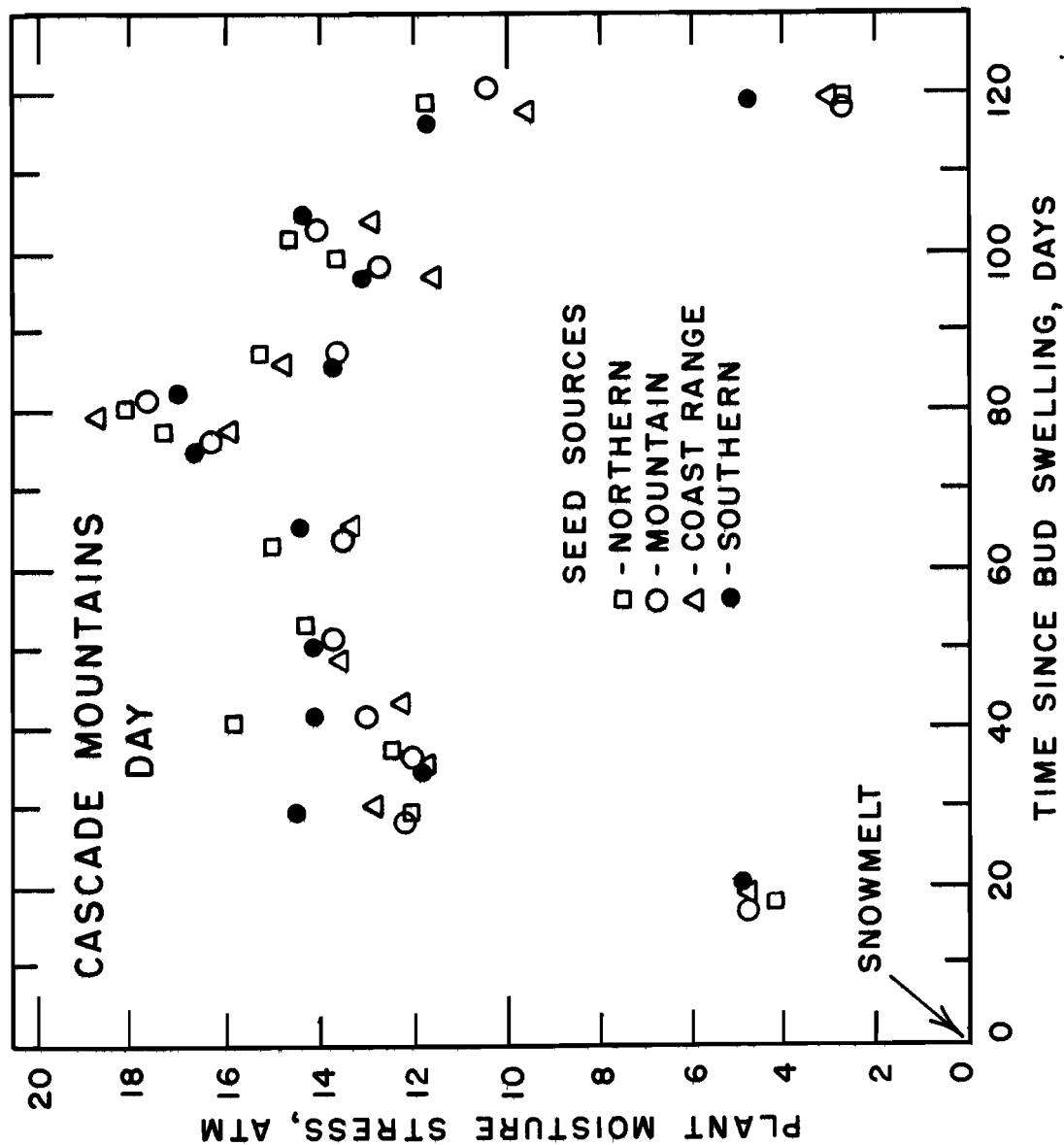


Figure 7-4. A comparison of day plant moisture stress for four populations at the Cascade Mountain site for the 1971 growing season.

deficit (VPD) is high, and opening in the morning and evening when VPD is low would conserve water and still allow for considerable photosynthesis. The often observed mid-day depression in photosynthesis (Hodges, 1967) fits in with this strategy. Therefore, I compared the degree of stomatal opening of the four populations at mid-day in late summer.

During warm summer days at the peak of drought, stomata of all populations were relatively wide open (Figure 7-5), although not as wide open as during early summer (Figure 7-6). Analysis of variance indicated that stomatal opening at the peak of drought did not vary significantly with population or plantation.

The seasonal pattern of stomatal opening for the four populations did not differ at the mountain location (Figure 7-6). For the first 50 days of the growing season stomata were wide open all day. During the last half of the growing season, all populations showed a slight closure at mid-day. After fall rains, stomata were again nearly wide open all day. Similar comparisons at the other plantations showed the same pattern.

The stomata of all populations were nearly closed or completely closed during the night at all three locations at the peak of drought (Figure 7-5). The observed infiltration pressure of 1 atm or more corresponds to a conductance of less than 0.01 cm/sec which means a negligible amount of transpiration could occur. My conclusion was

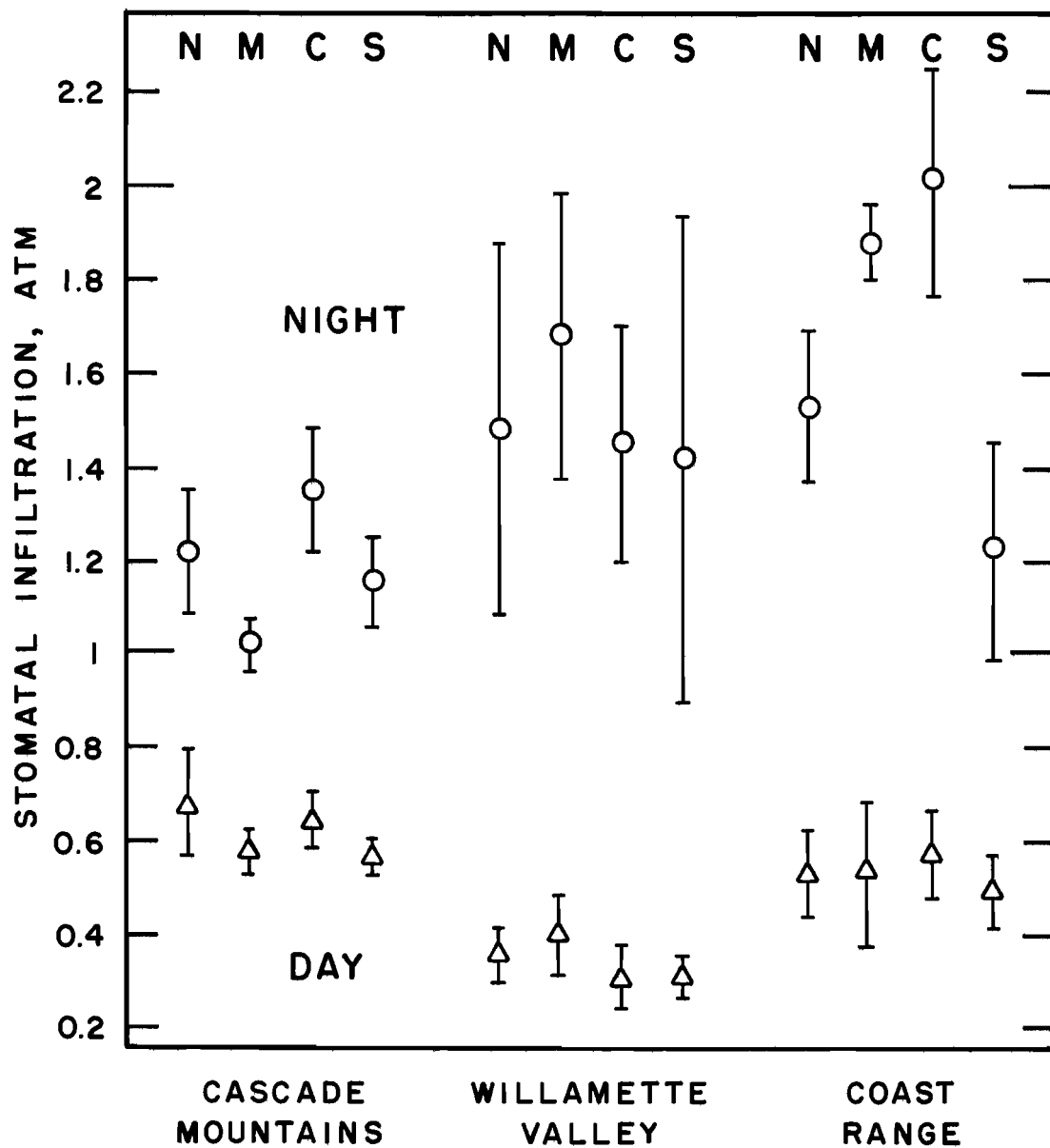


Figure 7-5. A comparison of day and night stomatal aperture for four populations of Douglas-fir at three locations in western Oregon during a drought period.

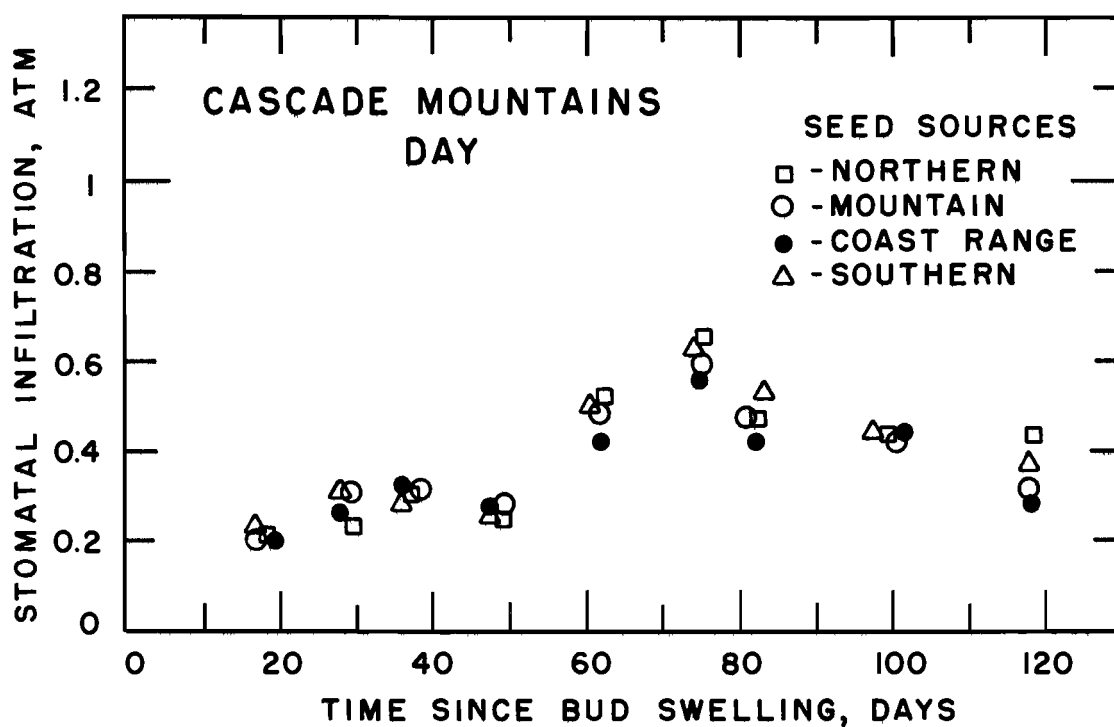


Figure 7-6. A seasonal comparison of day stomatal aperture for four populations at the Cascade Mountain plantation. Standard deviations were generally less than 0.05 atm, the largest being 0.15 atm.

that there were no biologically significant differences in night aperture at the peak of drought.

In the spring and early summer, stomata remained open at night at all locations as in Figure 7-7. Others, including Fry (1965) and Reed (1972), have observed stomata open at night during periods when moisture is abundant.

Although it is generally assumed that water use at night is negligible, a transpiration simulation based on responses of Douglas-fir showed a potential for significant night water loss. The amount of water transpired from a unit leaf area was computed daily for an entire growing season from averages of temperature and dew point for day and night periods. Average stomatal resistance for each day was predicted from night minimum moisture stress (Running, 1973). At night, however, stomata were assigned a constant minimum conductance of $0.1 \text{ cm}^2/\text{sec}$. Thus, potential night transpiration could be compared to a predicted day transpiration. When data for one growing season at a typical Douglas-fir-hemlock site were used to drive this simulator, night potential water use was about 10 percent the predicted day use.

Unlike daytime opening, night stomatal opening serves little apparent purpose. The leaves do not require evaporative cooling, nor can photosynthesis take place. Water is translocated, however, so there would be mineral uptake, and the water could be used for growth processes.

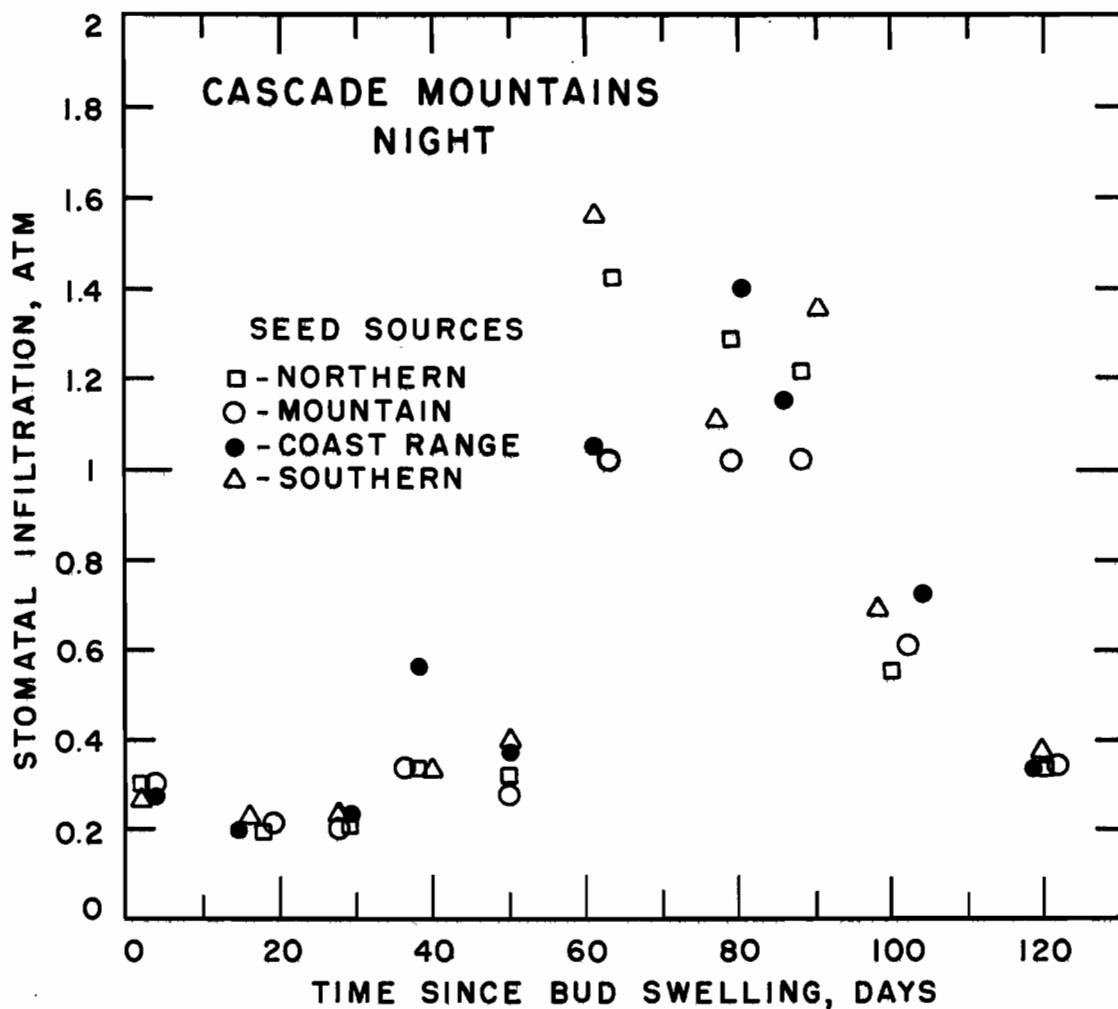


Figure 7-7. A seasonal comparison of night stomatal aperture for four populations at the Cascade Mountain plantation.

Are there differences in night stomatal behavior which could benefit particular sources? In the spring, all populations were uniformly open at night (Figure 7-7). About the time stomata began to close slightly during the day, stomata began to close relatively tightly at night (Figures 7-6 and 7-7). There was considerable variation among populations in the transition period. More intense sampling would be necessary to determine the biological importance of this variation.

Comparisons of Leaf Conductance, 1972-1973

Further tests were made during summer drought at the driest site in 1972 and 1973. In addition to previously used instruments, I measured leaf conductance with the diffusion porometer (see Chapter III). Table 7-1 is a summary of night PMS, day and night SA, and day leaf conductance for three years. Night PMS was higher the latter two years due to longer, more severe drought conditions. Stomatal aperture varied at night, but all populations were closed or nearly closed each year. During the day, stomata were uniformly nearly wide open all three years for all populations.

Observations of leaf conductance were extremely variable, making interpretation of the data difficult. In 1972 there were significant differences among populations, with the coast range source having lower conductance. This may have been due to a small sample

Table 7-1. Summary of day and night PMS and SA, and day leaf conductance for four populations of Douglas-fir for three years at the coast range plantation during summer drought (mean and standard deviation).

Sources	Year					
	1971		1972		1973	
	mean	s. d.	mean	s. d.	mean	s. d.
Plant moisture stress at night (atm)						
Northern	8.8	0.6	10.0	0.3	10.0	0.1
Mountain	10.2	0.5	12.7	1.7	12.5	0.3
Coast Range	8.6	0.5	12.9	1.0	11.8	0.2
Valley	9.6	0.5	11.7	0.4	11.7	0.2
Stomatal aperture at night (atm)						
Northern	1.5	0.2	2.0	0.02	1.8	0.03
Mountain	1.9	0.1	2.0	0.10	1.2	0.14
Coast range	2.0	0.3	2.0	0.05	1.5	0.14
Valley	1.2	0.2	2.0	0.10	1.8	0.10
Stomatal aperture during the day (atm)						
Northern	0.60	0.05	0.55	0.04	0.54	0.01
Mountain	0.50	0.03	0.48	0.03	0.57	0.03
Coast Range	0.51	0.03	0.51	0.03	0.51	0.03
Valley	0.61	0.07	0.61	0.03	0.51	0.03
Leaf conductance during the day (cm/sec)						
Northern	-	-	0.0312	0.0625	0.0085	0.0222
Mountain	-	-	-	-	0.0083	0.0385
Coast Range	-	-	0.0161	0.0125	0.0066	0.0114
Valley	-	-	0.0217	0.0250	0.0128	0.0345

size. Such a difference could be interpreted as an adjustment to the warm, dry slopes where the source originated.

In 1973, a much more thorough test was conducted (Figure 7-8). The lower portion of the figure shows how PMS and SA for all populations remained quite close throughout the day. At night, all trees had very low leaf conductances associated with closed stomata. At dawn the stomata opened and conductance rose. The southern Oregon source had higher conductance at that time than any of the other populations. After dawn, variation in conductance was large. The southern source generally had higher conductance, while the coast range source was lowest, as in 1972. There was no statistical difference, however, when averages between 0800-1600 hours were compared. Because three of the eight trees measured had more than one dip in conductance, cyclic variation in stomatal control was suggested (see Chapter III). If such were the case, definitive genetic comparisons would require intense sampling at short time intervals.

Discussion: The Strategies of Drought Resistance

In the Pacific Northwest, where long, dry summers are the rule rather than the exception, plant adaptations to drought conditions are of major importance. Coniferous species have evolved various adaptations which allow them to tolerate drought. They develop an

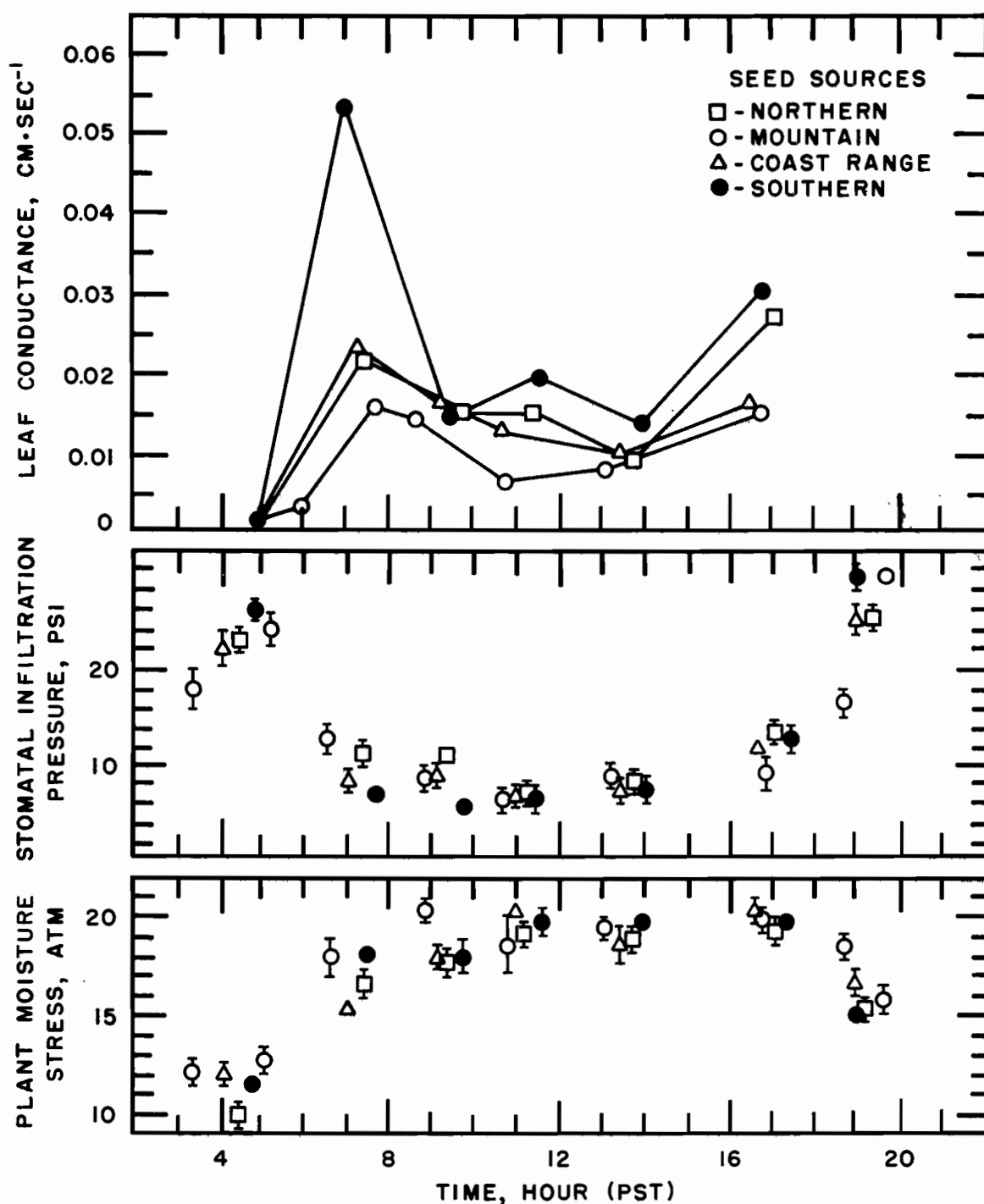


Figure 7-8. A one-day comparison of leaf conductance, stomatal aperture and plant moisture stress for four populations during late summer drought at the Coast Range plantation.

extensive, fast growing root system which makes the most of available soil water. Long, narrow leaves are well adapted to dissipating heat through convection so that evaporative cooling is unnecessary. Evergreen needles allow for photosynthesis during favorable dormant season periods as discussed in Chapter V. The ability to close stomata coupled with a high cuticular resistance help conserve water.

Stomata are of primary importance because they are located in the restrictive vapor segment of the water pathway through the plant (Slatyer, 1967). In addition, they act as controllers of CO_2 diffusion into the plant, thereby restricting photosynthesis.

A plant population which has sole claim on the water supply would benefit by maximizing the ratio between photosynthesis and transpiration (Cohen, 1970). Under such a strategy, plants would open stomata only when conditions were favorable for photosynthesis and poor for transpiration. On the other hand, when two or more well adapted populations are in competition for the same water, it becomes advantageous to keep stomata open under any conditions up to some critical desiccation point. It is advantageous to have a high threshold for damage, and to strictly control water loss near the threshold.

This type of strategy appears to apply to coniferous species. Ponderosa pine photosynthesized at near maximum rates up to 16 atm PMS, and was completely closed at 20 atm (Cleary, 1970). Douglas-fir showed a nearly linear decrease in photosynthesis from 10 to

22 atm PMS, but was not completely closed at 28 atm. Larcher (1969) found a similar pattern in two Mediterranean oaks. Lopushinsky (1969) found that transpiration was reduced and stomata apparently closed on cut twigs of Englemann spruce, ponderosa pine and lodgepole pine when moisture stress was 14-17 atm. Douglas-fir and grand fir stomata were not closed until PMS reached 19-25 atm. The closure of stomata of pine and spruce was more complete than that of Douglas-fir and grand fir. In many of the above cases the least drought resistant species began to close prior to the other, but was unable to restrict water loss as effectively as stress increased.

Similar adaptations exist within a species. Unterschuetz (1970) found that Douglas-fir seedlings of xeric origin transpired more at intermediate moisture stress than did seedlings of mesic origin. In marginal conditions the more drought resistant population would restrict water use and photosynthesis when other sources continue to "waste" water, but continue to photosynthesize. Thus, a population with "poor" stomatal control should grow best in all but the critical areas where its extravagant use of water causes it to desiccate to the point of injury.

Natural populations must be conservative if they are to survive the critical and harsh establishment period. The ecological role of Douglas-fir over much of its range is that of establishment in the open. Evaporative demand is great during warm, summer days, and

stomatal control of water loss, especially prior to root proliferation, is critical. During establishment, a conservative closure point and tight closure would be advantageous. Later, however, when root systems are extensive and micro-climate has modified, conservative behavior may curtail photosynthesis excessively. When plantations are established artificially, critical stresses may be avoided, giving less conservative populations a chance to compete. This may help explain why local sources have not always been most productive in provenance trials (Rowe and Ching, 1974).

Once plantations are established, the trees may be buffered against stress so that the critical closure point is never reached. In that case, all populations would show the same stomatal behavior, as observed in this study. Perhaps this is true for mild years, and during stressful years different behaviors could be detected.

Another strategy is for a drought resistant population to put more energy into root growth during establishment. Hermann and Lavender (1968) found this true for south slope sources grown in nurseries for two years. A population which has this adaptation will be penalized in areas where sufficient water is available, because root growth can only be increased at the expense of top or leaf growth. In the present study, the southern Oregon source was the shortest in most of the plantations after seven years.

The above strategies are easily compared where leaf resistance is relatively constant over time. Where cyclic fluctuations of various magnitudes and periods occur, comparisons are difficult. Although no mention of cyclic fluctuation in conifers was found in the literature, observations by Helms (1972, Figure 3) and Lassoie et al. (1972, Figure 3) could be interpreted as showing cyclic fluctuations for ponderosa pine and Douglas-fir, respectively. Both were on days with high radiation intensities, high temperatures and low humidities, although the pine seemed to fluctuate even on low stress days. The variable leaf conductance observed in our 1973 studies could also be explained on this basis. If cyclic fluctuations do occur in Douglas-fir, induction points, amplitude, and period could be different for various populations.

In addition to the above explanations for lack of genetic differences in stomatal behavior there are the following. Sampling intensity in time or space was insufficient to reveal existing differences. Since my study was designed to investigate both environmental and genetic differences, much of the sampling effort was directed toward critical times for plant-environment interaction. Thus only a few trees from each population were sampled. Substantial or persistent differences were not found under these conditions. Fine time resolution sampling might reveal more subtle variation. Such

studies require sophisticated instrumentation including data acquisition systems capable of handling large quantities of data.

My conclusion was that stomatal behavior of these four populations was similar during the 1971 growing season, and during drought for 1971, 1972, and 1973. Differences in stomatal behavior may appear only in times of severe stress such as during establishment. On the other hand, many other factors such as hormonal balance (Lavender et al., 1973) or distribution of carbohydrates (Ledig, 1969) could account for growth differences without involvement of stomatal behavior.

Summary of Stomatal Behavior Comparisons

Comparisons of the stomatal behavior of four populations of Douglas-fir at three locations revealed no significant differences in plant moisture stress or stomatal opening. I made comparisons of several kinds:

1. I compared PMS and SA at the peak of the drought period during mid-day and at night. All populations were similar.
2. Seasonal comparisons of PMS and SA showed distinct patterns at three locations, but not among populations.
3. Diurnal patterns of PMS and SA at the driest site at the peak of drought exposed no characteristic behavior for any particular population; however, measurements of leaf conductance

suggested there may be some differences. Two trends were apparent, but not confirmed by statistical test. The southern source had the highest average leaf conductance for the day. A coast range population had the lowest afternoon conductance for the two years measured. Leaf conductance observations should be confirmed by further tests during drought in subsequent years.

Differences in size which led to this study are now interpreted as being caused by factors which operate primarily during periods of extreme stress such as establishment. These factors could be one or more of many which affect plant growth (e. g. , photosynthetic efficiency, hormone balance, or stomatal control).

VIII. COMPARISONS OF PHENOLOGY AND GROWTH

Background

Traditional provenance studies of Douglas-fir have concentrated on field or nursery comparisons of bud activity and height growth (Wright, 1962; Sweet, 1965). Ching and Bever (1960) reported on nursery performance of sources in the present study. They found a distinct correlation between height growth in the second year after sowing and geographic location of origin. Both bud burst and bud set of certain sources were distinct in timing. Northern sources grew best while southern sources grew least. In contrast, Sweet (1965) found a negative correlation between two-year height growth and both latitude and altitude with more southerly populations. His study showed that time lag between lateral and terminal bud burst was correlated with a number of climatic factors at the origin of the source.

Other genetics studies of Douglas-fir have shown that coastal and low elevation sources were not as responsive to photoperiod, and consequently grew more than high elevation or inland sources when planted in a mild climate (Irgens-Moller, 1962, 1967). Other investigations have shown a strong interaction between temperature and photoperiod, that is, when night temperature was low, long photoperiod was required for initiation of growth (Irgens-Moller, 1962).

Methods

For this study, I measured cambial activity in addition to phenology and height growth on a bi-weekly basis. This provided an opportunity to compare both height and cambial growth on a genetic as well as environmental basis. Growth was measured at 10 to 15-day intervals on three trees from each of four populations at three plantations.

Genetic differences in accumulated height growth (Ching, 1965; Rowe and Ching, 1974) were the impetus for this study. Figure 8-1 is a summary of survival and growth performance at the three study sites. Note that although survival was best at the mountain plantation, growth was less there than at either of the other plantations.

My measurements and analysis were directed toward answering the following questions:

1. How do patterns of seasonal height growth vary from one location to another?
2. Do growth rates correlate with short term weather conditions?

(Questions 1 and 2 were addressed in Chapter VI. This chapter deals with the third question.)

3. Are there differences in total growth or pattern of growth for either cambium or leader?

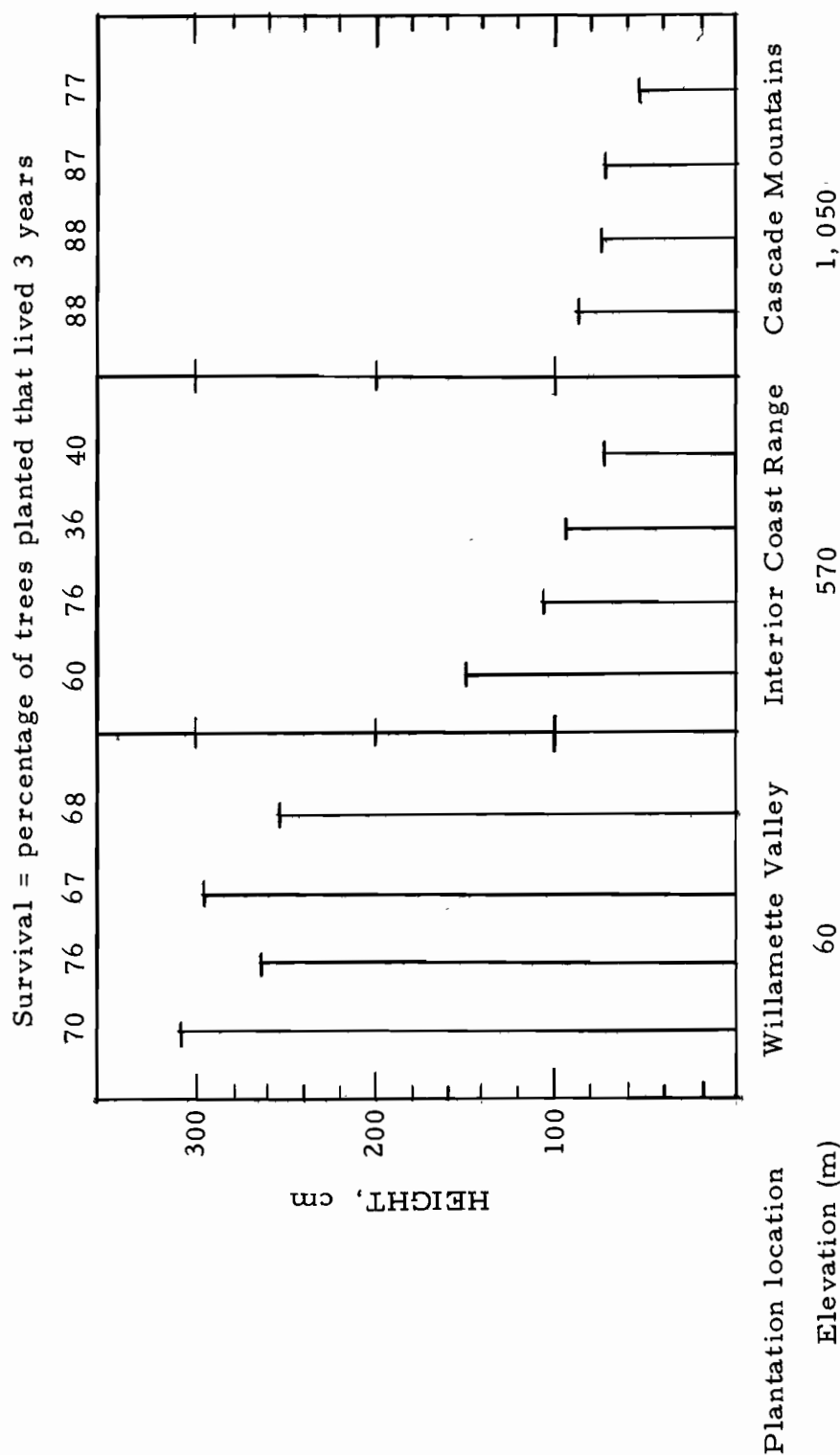


Figure 8-1. Comparison of survival and height of four populations of Douglas-fir at three locations in western Oregon at age 9 (from Ching and Rowe, 1974).
 N = Vancouver Island source; M = Cascade Mountains source; C = Coast Range source;
 S = Southern Oregon source.

Comparisons of Growth

Initiation and Cessation

Many genetics studies have concentrated on initiation and termination of shoot growth (i. e. , bud swell, bud burst and bud set). Bud activity is related to both frost hardness and total height growth. Cambial activity is important for volume growth, but the cambium is not as susceptible to frost injury as the terminal meristem. I observed bud swell, bud burst, initiation of cambial cell divisions, cambial growth, and onset of latewood formation (Figure 8-2).

Within the limitations of a 5-14 day sampling interval there were no persistent trends among populations at all areas. In general, a phenologic event at a given plantation was confined within a 10-day period. At the mountain location there was a sharp rise in soil and air temperature after snow melt. Growth of all trees began within a few days. Cessation was equally uniform. In the valley and coast range locations the mountain source appeared to begin cambial growth slightly later (4 and 10 days) than the other sources. The southern source initiated cambial growth last in the coast range, some 10-15 days after other sources. All sources reached 90 percent completion of cambial and leader growth within 10 days at a given site, except for the mountain population in the valley. It had nearly stopped cambial growth in August, but apparently responded to improved soil

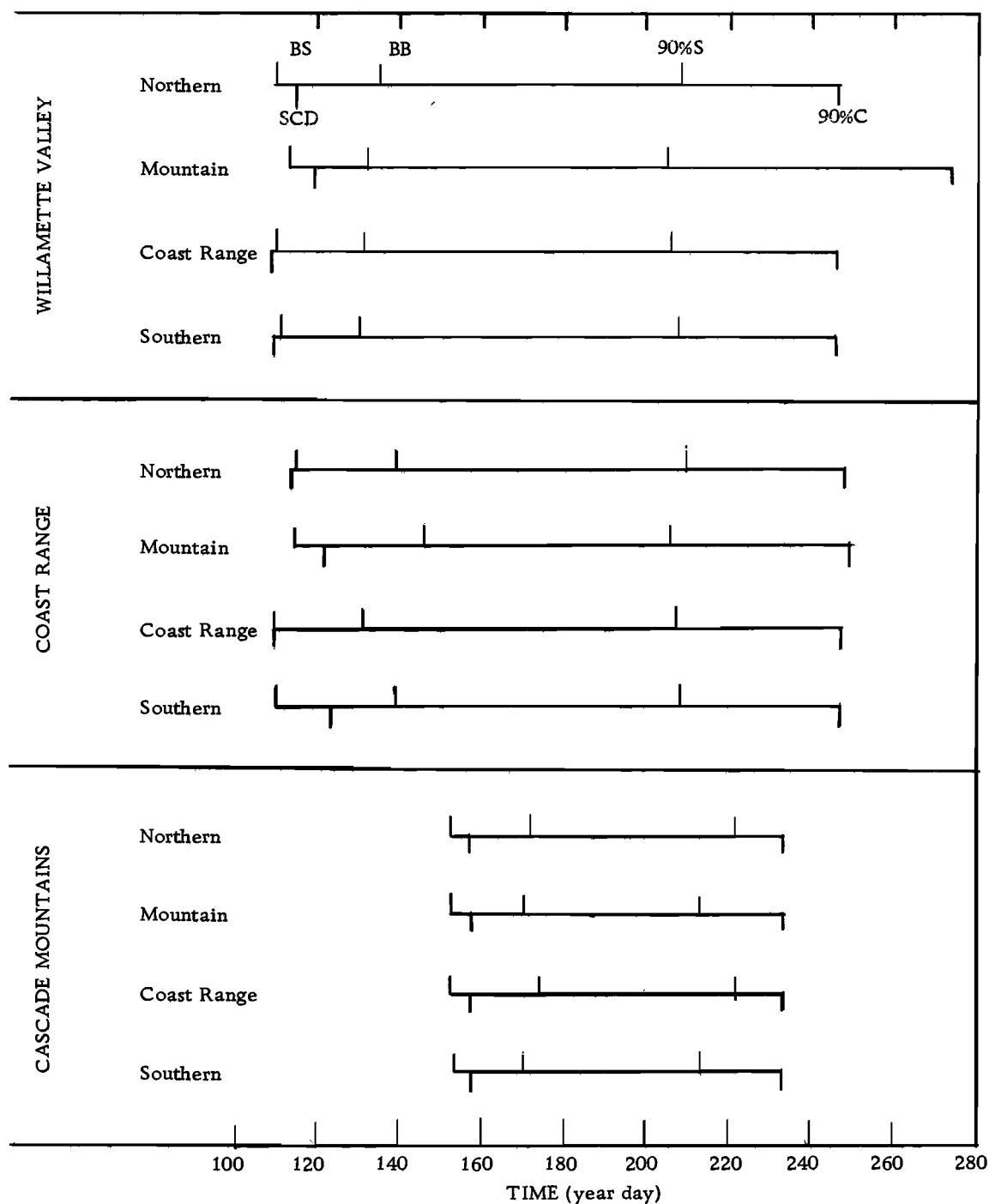


Figure 8-2. A comparison of phenology for four populations at three plantations. Shoot growth phenophases include bud swell (BS), bud burst (BB) and 90 percent completion of extension (90%S). Cambial growth phenophases include initiation of cell division (SCD) and 90 percent completion of expansion (90%C).

moisture conditions after fall rains. It grew 13 percent of the season's total in September and October. In a normally dry fall it probably would have completed growth in unison with other sources. This ability would seem to have the least adaptive significance for a high elevation source since cool temperature in early fall would generally limit fall growth. On the other hand, the ability to resume (or continue) cambial growth whenever soil moisture was adequate could be a useful characteristic for sources used in irrigated plantations.

Considering the nearly 8° latitude between southern and northern seed sources, it is remarkable that more genetic differences in phenology have not evolved. This is probably due to similarity in climate or "operational environment" at the origin of the sources. It also indicates the importance of environmental control over growth and development of coastal Douglas-fir.

Latewood

Latewood formation for all sources began within an 8-day period at each site. The average date was 5, 8 and 23 August at the mountain, coast range and valley locations respectively.

Total Cambial Growth

After actual cambial growth was measured from cross sections,

the seasonal pattern of growth for each population at each plantation could be plotted (Figure 8-3). Comparison of total cambial growth showed no consistent differences between populations as demonstrated by analysis of variance (Table 8-1). There were obviously significant differences between plantations.

Table 8-1. Results of analysis of variance tests on actual and corrected total growth of cambium and leader for four populations at three locations.

Factor	d. f.	F level				Growth efficiency
		Cambial growth		Leader growth		
		actual	corrected	actual	corrected	
Location						
	2 /24	69.8	43.5	16.5	24.8	46.9
Population						
	3 /24	2.88	1.97	1.28	1.40	0.39
Location x Population						
	6 /24	3.00	0.64	1.93	0.60	0.39

When population averages were compared at the coast range and mountain locations there were no differences in total growth. However, at the valley plantation, northern and valley sources grew significantly more than mountain and southern sources. These sources had larger trees to begin with, so corrections for size were made (Table 8-3). Diameter growth was normalized by diameter and basal area at the end of the growing season. These will be termed "corrected growth." All populations were similar in corrected growth (Table 8-1).

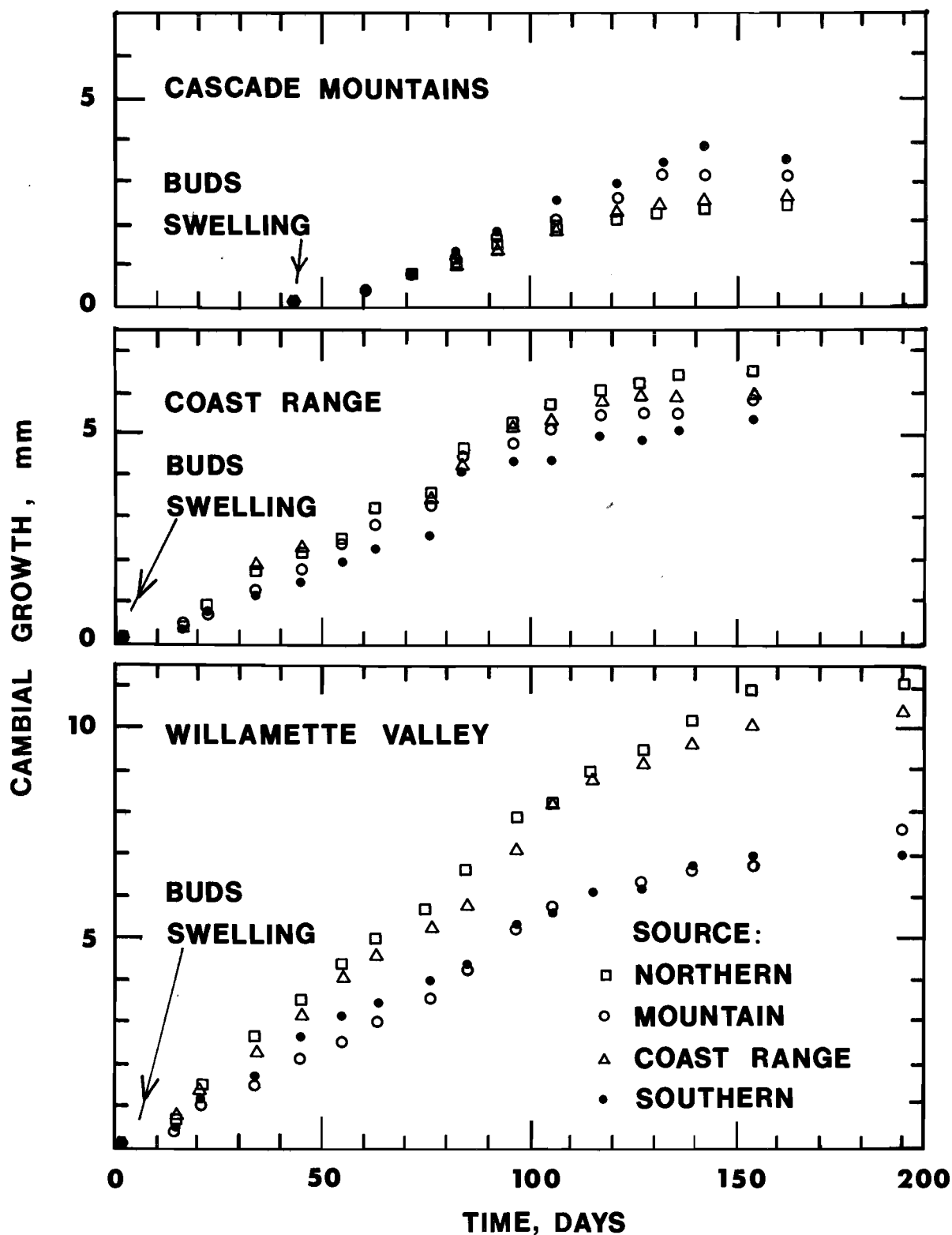


Figure 8-3. A comparison of actual cambial growth of four populations at three areas.

Table 8-2. Comparative ranking of Douglas-fir populations by various measures of diameter and leader growth.

	Site		
	Northern	Cascade Mountain	Coast Range Southern
Diameter growth (average actual, cm) Ranking	0.68 1	0.57 3	0.66 2 0.53 4
Corrected growth ($\frac{\text{growth}}{\text{diameter at seasons end}}$, in cm) Ranking	0.062 3	0.061 4	0.065 2 0.067 1
Growth/basal area ($\frac{\text{growth (cm)} \times 10^2}{\text{basal area at seasons end, cm}^2}$) Ranking	0.862 4	0.885 3	0.987 2 1.240 1
Growth efficiency ($\frac{\text{basal area growth}}{\text{basal area at seasons end}}$, in cm ²) Ranking	0.319 3	0.305 4	0.339 2 0.346 1
Average actual leader growth (cm) Ranking	80 1	78 2	75 3 70 4
Corrected leader growth (height) ($\frac{\text{growth}}{\text{tree height at start of growing season}}$, in cm) Ranking	0.148 4	0.166 1	0.154 3 0.159 2
Corrected leader growth (basal area) ($\frac{\text{growth, cm}}{\text{basal area at end of growing season, cm}^2}$) Ranking	0.96 4	1.11 2	1.06 3 1.39 1

Since leaves capture the energy for growth, a measure of "growth efficiency" was obtained by comparing growth per unit of leaf area. At the end of the growing season trees from the coast range and mountain plantations were harvested, defoliated and weighed. Thus, exact weights of bole, branches and leaves were determined for each tree. When diameter growth was normalized by leaf weight, and submitted to analysis of variance there were no significant differences due to population. However, this test did not include the valley plantation where actual cambial growth of populations was dissimilar.

Recently, Grier and Waring (1974) have noted that leaf weight is directly related to sapwood basal area. Others have established a direct relationship between leaf weight and leaf surface area. Since the young trees included in this study were entirely sapwood, growth efficiency could be obtained by dividing basal area growth by total basal area at the beginning of the growing season. In this way all plantations were included in comparisons of growth efficiency. Again, analysis of variance showed no significant difference in growth per unit leaf area (Table 8-1).

Interestingly, the positions of the populations are reversed when actual growth was compared to corrected growth or growth efficiency on a population basis. The ranking of each category is shown in Table 8-2 under the actual measurements. Whereas the northern population grew best and the southern source least in diameter, the

southern source grew best per unit leaf area or per unit diameter. This lends credence to the notion that size differences between sources are not increasing.

Total Leader Growth

Actual leader growth of the four populations at each plantation is shown in Figure 8-4. As with cambial growth there were no persistent differences between populations, but large variation between plantations. Total actual leader growth of the northern source was greatest in the valley, second in the coast range and third in the Cascades. The mountain source grew least in the valley, most at its home location and third in the coast range. Obviously, there was no one population that was best suited to all three locations. Analysis of variance confirmed the casual observation that both actual and corrected leader growth were significantly different between areas, but nonsignificant for source or interaction (Table 8-1).

As with cambial growth there was a reversal in ranking when height growth was corrected by size (Table 8-2). A plot of annual growth (Figure 8-5) indicated that all populations were growing at about the same rate at the valley plantation. That is, the cumulative height growth curves are now parallel. Growth rates for the last few years were similar, averaging 125, 116, 117 and 117 cm per year for the northern, mountain, southern and coast range sources

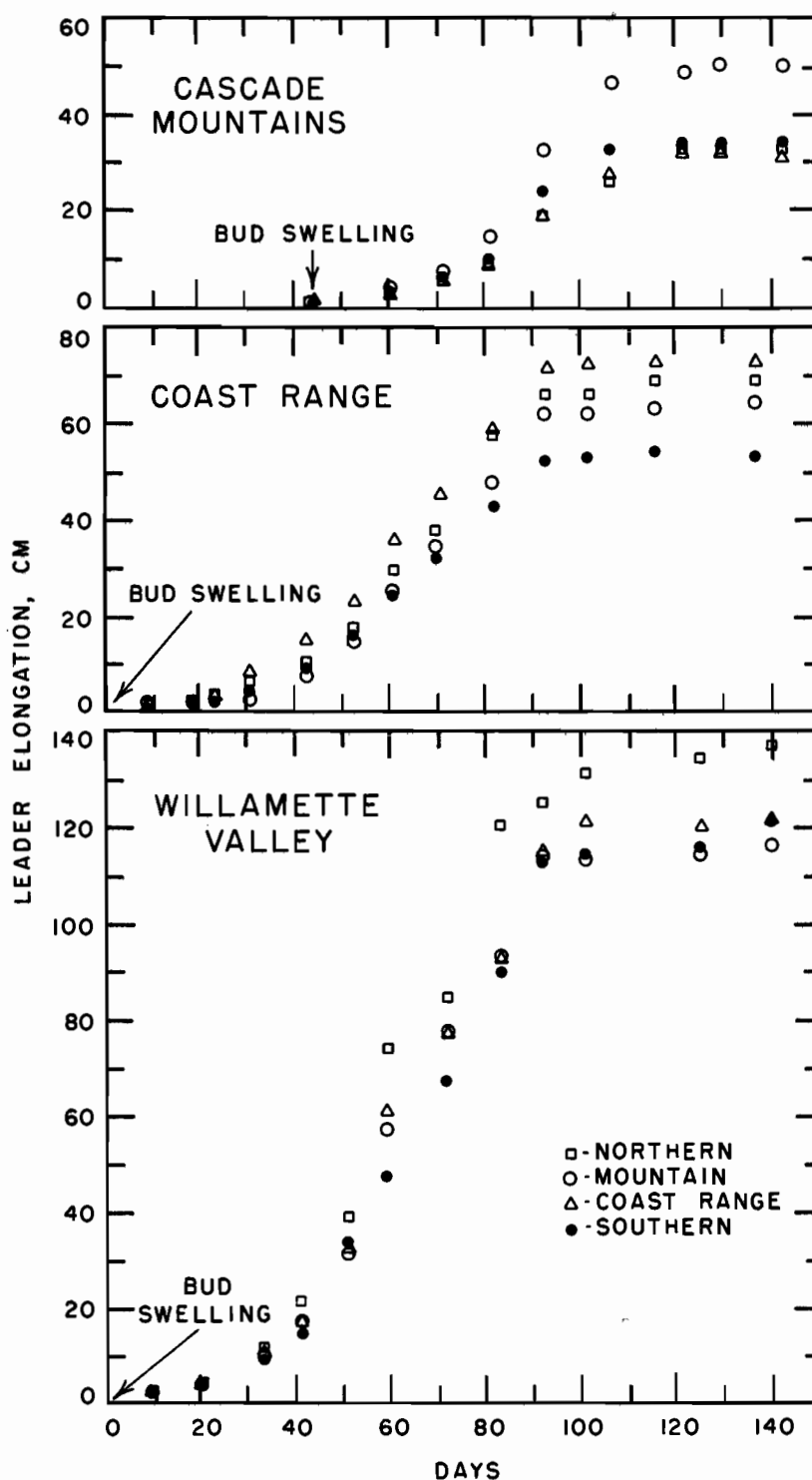


Figure 8-4. A comparison of actual leader growth of four populations at three areas.

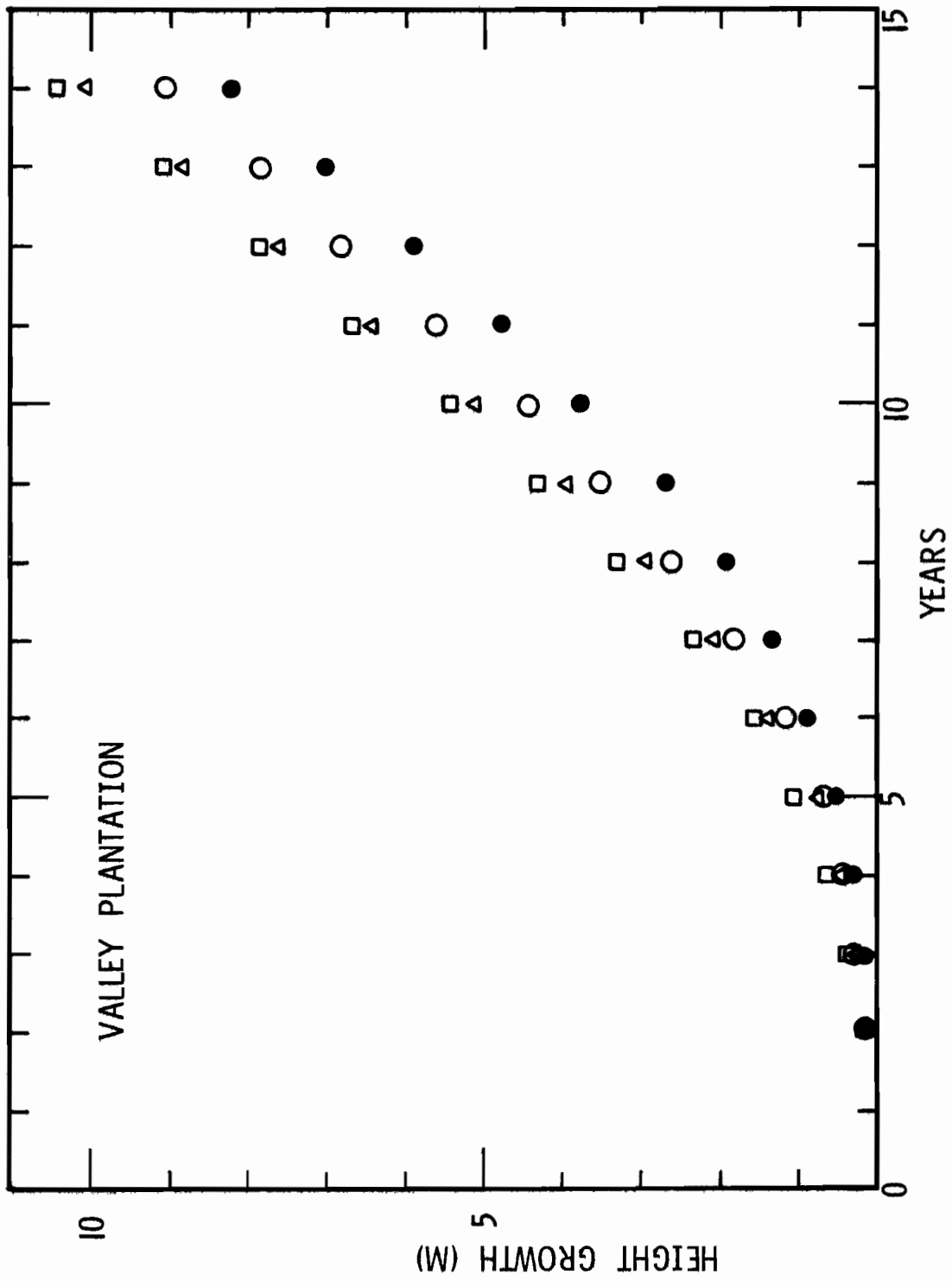


Figure 8-5. A comparison of yearly leader growth for four populations at the Willamette Valley plantation.

respectively. Further, when the trees were in the same height range they grew at much the same rate.

This analysis supports the interpretation that annual growth on a given plantation was not greatly different for these populations.

Discussion of Growth Comparisons

After adjusting for size, the cambial and height growth for the 1971 growing season was similar for all populations. How can this be explained when past studies of accumulated growth have shown significant variation among populations? One possible explanation is that it takes several years for small annual growth differences to accumulate before they are detectable. A second is that the sample size was not sufficient to show any contrasts. A third is that growth of all populations is similar in low stress years such as 1971, but different for high stress years. The fourth explanation is suggested by the data. That is, the trees from all populations are now growing in proportion to their size, and that accumulated differences have resulted from better establishment by superior sources. Now that all trees are well established, they are able to buffer out environmental stress, and grow in proportion to their size.

Comparison of Biomass Distribution

We have examined one year's growth for four populations at

three areas and found little genetic variation. Growth differences between areas were significant. In contrast, accumulated growth varied significantly among both sources and locations (Rowe and Ching, 1974).

A critical factor in determining whether size diversity persists is how each population distributes its energy. Ledig (1969) suggested that since growth is a compounding process, energy put into photosynthetically active tissue will lead to greater production.

Therefore, I checked distribution of biomass for the four populations at two plantations by harvesting, dissecting and weighing the above ground biomass. Differences in tree size made normalizing for size important. Two methods were used. First, the bole, branch and needle weights were divided by diameter squared, which has the same effect as normalizing for basal area (basal area differs from diameter squared by a constant factor). Second, I normalized by stem volume. Analysis of variance showed all populations similar in distribution of biomass to needles, branches or bole (Table 8-3). There were significant differences in distribution between the mountain and coast range plantations.

Comparisons of Growth Pattern

The pattern or rhythm of growth is an important genetic variable because of interaction between growth periods and environmental

Table 8-3. Results of a two-way analysis of variance on corrected biomass distribution at Coast Range and Cascade Mountains plantations for four populations.

Factor	<u>Bole wt.</u>	<u>Branch wt.</u>	<u>Needle wt.</u>	<u>Bole wt.</u>	<u>Needle wt.</u>
d. f.	(dia) ²	(dia) ²	(dia) ²	(D ² H)	(D ² H)
Location					
1/16	15.4	1.89	6.29	25.7	9.26
Population					
3/16	2.1	0.88	3.10	2.67	3.05
Location x Population					
3/16	1.0	0.45	0.99	2.09	1.28

extremes such as frost (Dietrichson, 1968). Plants must time growth to coincide with generally favorable conditions. Thus, trees in the mountain plantation began growth immediately after snow melted and completed growth in about 60 days. In the coast range trees began a month earlier and completed most growth before moisture stress became severe. Timing may become genetically fixed (Irgens-Moller, 1967) as has been demonstrated for Douglas-fir by Irgens-Moller (1958). Genetic differences in bud burst and bud set were shown during the nursery phase of this provenance study (Ching and Bever, 1960) and after outplanting (Ching, unpublished data). Growth totals obviously depend heavily on what happens between initiation and cessation. Therefore, I examined the pattern of both cambial and leader growth for an entire growing season.

Seasonal plots of actual cambial and leader growth (Figures 8-3 and 8-4) gave some indication of the similarity in pattern for different populations. They showed that the growth rate and duration of growth was similar for all sources measured at a given plantation. Another way to compare that pattern is to compute and plot the cumulative growth as a percentage of the year's total, i. e., "percent growth." This standardizes the end point at 100 percent, so that timing of growth is emphasized.

Cambial Growth Pattern

The pattern of cambial growth was similar for all populations at each location (Figure 8-6). The mountain source lagged in completing its growth at the coast range and valley sites. This trend was apparent when populations were ranked for completion of 50 and 90 percent of cambial growth (Table 8-4).

After 10 cm of rain fell at the coast range site in early September, all populations responded and about 10 percent of the 1971 cambial growth was in September and October. The northern source responded to early fall rains slightly more than the other sources. These trends were not very obvious, and the similarity among the populations is striking.

Leader Growth Pattern

Leader growth is much more compressed in time than cambial growth. Patterns of leader growth at each location for all populations were similar (Figure 8-7). Ranking of percent completion in the same manner as for cambial growth revealed no regular pattern for all areas (Table 8-4). The mountain source completed leader growth late at the coast range as with cambial growth; however, the pattern was reversed in the valley, where it completed leader growth first. Ninety percent completion of growth for all populations for all locations

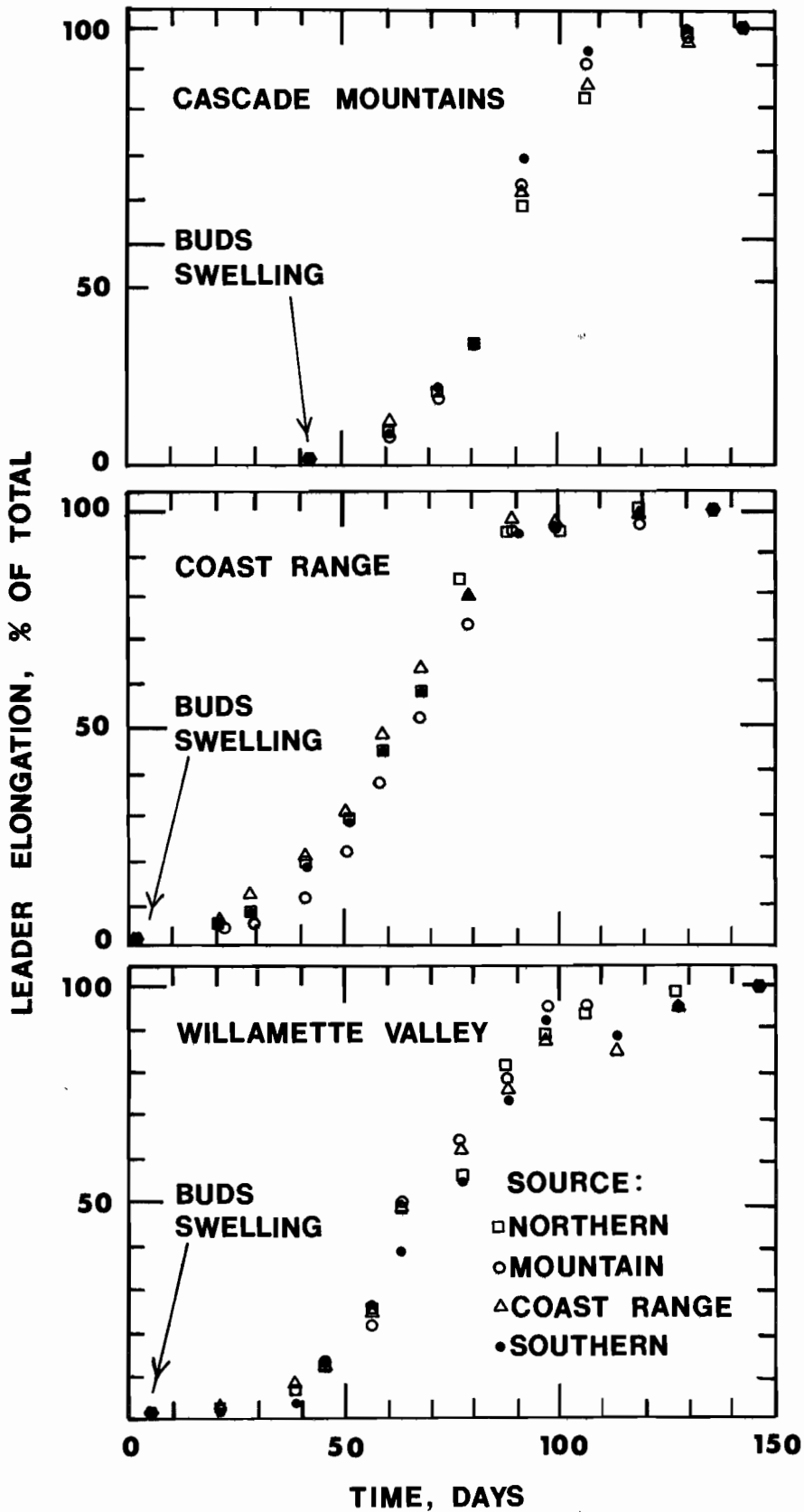


Figure 8-6. A comparison of cambial growth pattern of four populations at three plantations.

Table 8-4. A ranking to show the order in which sources completed 50 and 90 percent of cambial and leader growth.

Location	Percent completion	Source			
		northern	mountain	coast range	southern
<u>Cambial growth</u>					
Valley	50	2	4	3	1
	90	3	4	2	1
Coast Range	50	1	4	2	3
	90	3	4	1	2
Mountain	50	1	2	4	3
	90	All populations similar			
<u>Leader growth</u>					
Valley	50	*	*	*	4
	90	3	1	4	2
Coast Range	50	2	4	1	3
	90	1	4	3	2
Mountain	50	4	2	3	1
	90	4	2	3	1

* Too similar to rank

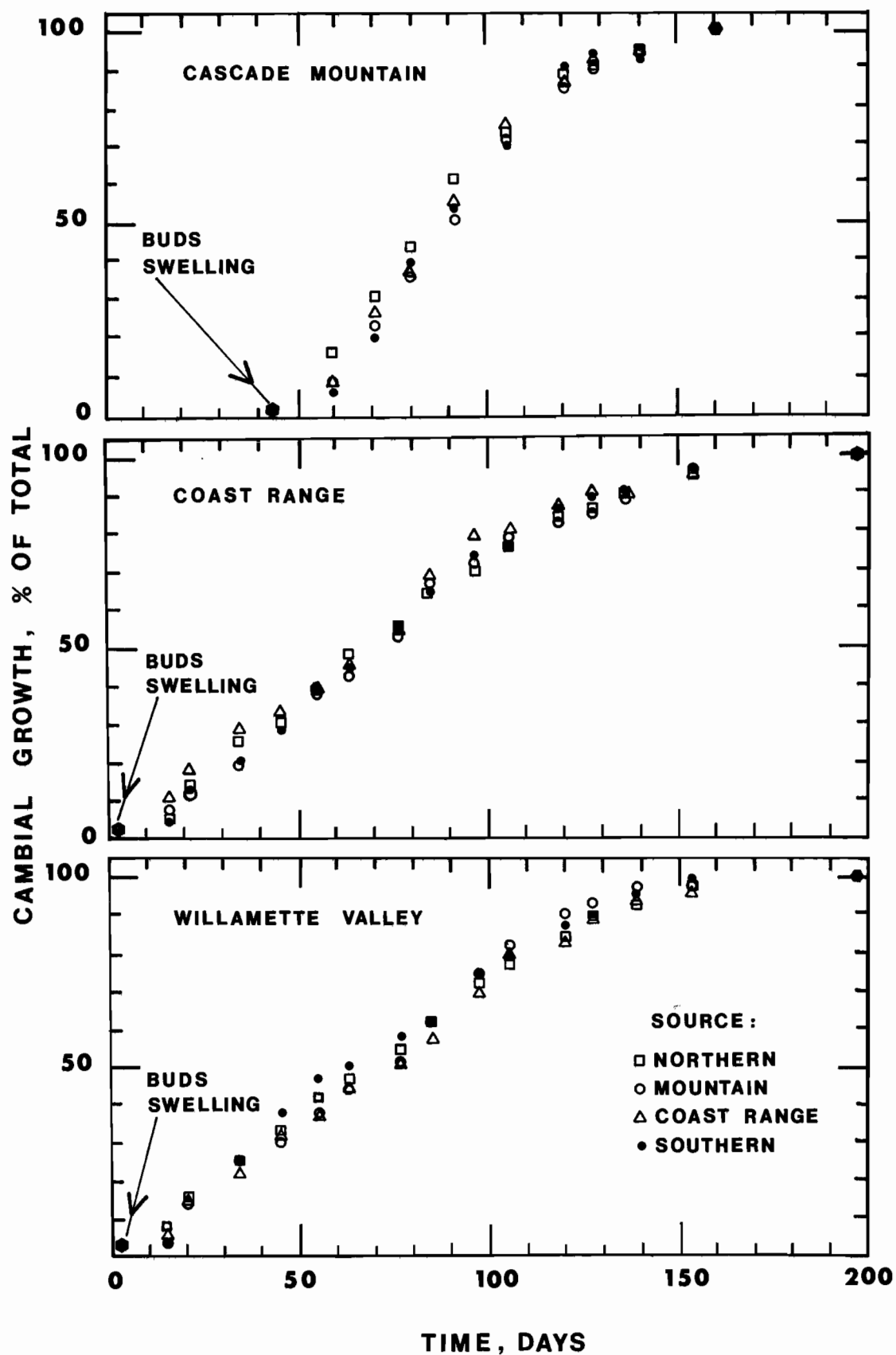


Figure 8-7. A comparison of leader growth pattern of four populations at three plantations.

was within 16 days (Figure 8-2). This suggests that cessation of leader growth may be cued by photoperiod.

Summary of Growth Comparisons

When northern, mountain, coast range, and southern sources of Douglas-fir were compared for yearly phenology, growth, growth pattern and biomass distribution on a mountain, valley and coast range site, there were no persistent or striking genetic differences. Phenologic events were within 10 days for all sources at each location with few exceptions. In the valley and coast range, initiation and cessation of cambial growth of the mountain source tended to lag behind other sources. The southern source averaged least for both cambial and leader actual growth. However, it grew best per unit of leaf area, diameter, or basal area. Pattern of growth was similar for all populations at each plantation, and biomass distribution did not differ with source.

IX. SUMMARY AND CONCLUSIONS

1. The stomatal behavior and plant water relations of the Douglas-fir populations tested were similar, at least under the present stand conditions. Likewise, both actual and corrected growth of leader and cambium were not significantly different. Future efforts to identify population differences in stomatal behavior or plant water status should be concentrated at times of extreme stress.
2. No differences in allocation of resources to needles, branches or bole were found in this study. Hermann and Lavender (1968), however, demonstrated that southern sources allot more resources to roots during establishment. I found the southern source, once established, most efficient in utilizing energy as evidenced by a larger growth to leaf area ratio.
3. An assessment of plantation environment by means of a photosynthesis model suggested that plants growing in the coast range would have adaptive advantage were they capable of adjusting to cold soil and frost.
4. Analysis of simulation results confirms the belief that adaptation to drought would also be advantageous. Drought stress had a major impact on photosynthesis at even the most mesic site tested during a relatively mild drought year. During the critical

period of establishment or when stand maintenance increases, the effect of drought on photosynthesis and productivity may be accentuated.

5. A seasonal assessment of environments through physiological process models is helpful in explaining how different environments may reach similar productive capacities. Also, seasonal assessment provides more insight into how selection pressures may operate, and what adaptive strategies might prove valuable to plant populations.
6. Physiological assessment of field environments provides a useful means of matching seed source locations, or capabilities, with prospective plantation sites.

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APPENDICES

APPENDIX I

EQUATIONS FOR CO₂ FIXATION OF A SINGLE LEAF(Reed et al. , 1974)

$$F = \frac{1}{r_{\ell}} (C_a - C_i)$$

$$C_i = -b + \frac{\sqrt{b^2 - 4ac}}{2a}$$

$$F = \text{CO}_2 \text{ fixed (in mg dm}^{-2} \text{ sec}^{-1}\text{)}$$

$$a = k, \text{ internal conductance of CO}_2 = \frac{1}{r_2}$$

$$b = P_i(E, T) + k[r_l P_i(E, T) - C_a - r_l W_d]$$

$$c = P_i(E, T) (-C_a - r_l W_d)$$

$$P_i(E, T) = \text{internal net } P_s \text{ as fn}(ET)$$

$$E = \text{light}$$

$$T = \text{temperature}$$

$$r_{\ell} = \text{stomatal and boundary layer resistance}$$

$$k = \frac{1}{r_2} = \text{internal conductance of CO}_2$$

$$C_a = \text{ambient CO}_2 \text{ concentration}$$

$$C_i = \text{sub stomatal CO}_2 \text{ concentration}$$

$$W_d = \text{dark respiration}$$

APPENDIX II

DISCUSSION OF FACTORS AFFECTING LEAF
RESISTANCE IN SOME PLANTS

(with explanation for exclusion from the simulation
of photosynthesis for Douglas-fir)

Humidity

Atmospheric humidity may affect leaf conductance directly or indirectly. Plant moisture stress will develop when vapor pressure deficit is high, indirectly leading to decrease in leaf conductance caused by stomatal closure. Lange et al. (1971) reported that stomata of Polypodium vulgare and Valerianella locustra seem to be controlled directly by peristomatal transpiration. Stomata closed in dry air within a couple of minutes, and opened in moist air in about an hour. Similar sensitivity to humidity has been reported for Zea mays by Raschke (1970). Field observations of stomata of Douglas-fir with the infiltrometer at a 21 mb VPD showed the stomata to be nearly wide open. Concurrent measurements with the diffusion porometer show total leaf conductance to be variable. It ranged from 0.25 to 0.003 cm sec^{-1} and averaged 0.011 cm sec^{-1} . The VPD remained at the same level for several hours, while conductance varied widely.

For modeling purposes, the variation in leaf conductance was subsumed into the daily average conductance. Average conductance

was modeled as a function of night plant moisture stress. The vapor pressure deficit during the day and resulting daytime moisture stress would thereby indirectly affect night PMS and predicted leaf conductance.

Wind

Tranquillini (1970) found that transpiration was reduced 6 percent for Pinus cembra and 30 percent for Rhododendron at wind speeds as low as 1.5 m sec^{-1} (3.36 miles/hr). Photosynthesis (PSN) of Rhododendron was reduced by 10 percent at the same wind speed, but increased slightly for pine. At ten times that wind speed, pine PSN was reduced 15 percent, while Rhododendron PSN was reduced to zero. On the other hand, larch was affected little by any but very high wind speed.

The differences between species have obvious ecologic implications in an alpine environment. Although no observations of wind speed effect on Douglas-fir have been made, I have assumed it reacts like pine and larch, and that days with high wind speeds ($3,540 \text{ m sec}^{-1}$, or 22 miles hr^{-1}) are uncommon enough to be ignored.

Needle Age

The age of needles also has an effect on photosynthesis. Krueger (1963) found that PSN rates of Douglas-fir seedlings declined

significantly as they aged from 13-35 days. On the other hand, Geppert (1968) found that transpiration of seedlings age 2-16 weeks was independent of age. Electron micrographs (Reed, 1972) showed that stomatal "pits" of Douglas-fir became increasingly occluded with waxy deposits with age. The effect of the wax is unknown, but it presumably increases resistance. Waggoner and Turner (1971), using a diffusion porometer in Pinus resinosa stands, found leaf resistance of 1-year-old needles to average about 10 sec/cm greater than new needles. This held from the time of emergence until the end of the growing season. Neilson et al. (1972) found a seasonal change in minimum stomatal resistance of Sitka spruce measured at 20°C. Resistance was lowest in young shoots from June to October, then rose steadily in the winter.

Our studies of newly emergent Douglas-fir needles were hampered by extreme fragility of new needles until about one month after bud break. Once needles were rigid enough to sample, the new needles' stomata were statistically more closed at night than stomata of 1-year-old needles. During the day, however, there was no difference between stomatal openings of old and new needles. The same pattern was evident at three locations for approximately one month after which comparative measures were stopped. The lack of difference during the day may be due to insensitivity of the infiltrometer method.

Woodman (1971) found that current year needles had PSN rates

significantly higher than older needles at the end of the growing season. Older needles showed a 20-30 percent reduction with each additional year. Kunstle (1972) showed a seasonal trend in relative photosynthetic and transpirational efficiency of three age classes of Douglas-fir needles. Early in the growing season new needles had large net losses in PSN and no transpiration. Later, new needles showed the highest rates of PSN and transpiration.

For accurate estimates of seasonal photosynthesis for an entire stand, leaf resistance, needle weight, and position for each age class may be necessary. For comparison of photosynthetic potential between sites, estimated average leaf resistance for new needles was used.

Preconditioning

Many kinds of stress may damage the photosynthetic apparatus and reduce CO₂ fixation. Such effects have been recorded for high and low air temperature, water and nutritional stresses (Larcher, 1969). Larcher states, "In normal soils without specific nutrient deficiency, mineral nutrition is of little importance as a limiting factor in CO₂ uptake compared with climatic variables." Reduction of PSN due to low air temperature was included in the simulation. Air temperatures high enough to damage Douglas-fir (about 50°C) are rare within the natural range of the species.

Cleary (1970) found that it took Douglas-fir seedlings 8 days to

return to maximum PSN rates after day moisture stress reached 33 atm. Seedlings stressed to higher levels did not recover after 12 days. Models for prediction of day moisture stress have been constructed for Abies spp. (Hinckley and Ritchie, 1973) and for Picea engelmannii (Evens, 1973) but such models are probably site specific because they did not include all factors affecting day PMS. Day PMS depends on soil water transfer characteristics, daily evaporative demand, size of trees, and daily leaf resistance.

I did not include a function for high stress preconditioning because the well-established saplings in this study did not go above 20 atm. Such functions would be important for models dealing with establishment.

Plants may also adjust to different conditions of temperature and light (Larcher, 1969; Lange et al., 1969; Bjorkman and Holmgren, 1963). Mooney and Harrison (1969) found that plants of Encelia californica responded to warm treatment after cool preconditioning by changes in leaf resistance to CO₂ transfer and in the chemical process of photosynthesis. A systematic study of Douglas-fir with respect to temperature preconditioning is needed. Walker et al. (1971) showed that moderately high rates of carbon uptake by Douglas-fir were possible near 0°C in early April. In contrast, Drew (1973) found leaf resistance high during the dormant season. There is probably some interaction between adaptive preconditioning and the frost or low soil

temperature functions discussed earlier. Until better response functions for Douglas-fir become available I will allow soil temperature and frost reduction functions to reduce summer fixation rates instead of modeling possible pre-conditioning for more efficient CO₂ fixation at lower temperatures.

APPENDIX III

FLEXFORM

FLEX Model of: Photosynthesis of Douglas-fir

Investigator : W.H. Emmingham

Programmer: Al Brown

Date: 7 March 1974

Time Resolution: one day

Quantity: milligrams CO_2 fixed decimeter⁻² of leaf area

Variables and Functions

- | | | |
|----|---------------------|--|
| 1. | X list: | Description |
| | X(1) | Predicted day photosynthesis |
| | X(2) | Predicted night respiration |
| | X(3) | Predicted daily net [X(1) + X(2)] |
| | X(4) | Potential day photosynthesis |
| | X(5) | Potential daily net [X(4) + X(2)] |
| | X(6) | Predicted (total every 5 days) |
| | X(7) | Potential (total every 5 days) |
| 2. | Z Functions: Inputs | |
| | Z(1) | Average day temperature (°C) |
| | Z(2) | Average night temperature (°C) |
| | Z(3) | Total radiation (langley's day ⁻¹) |
| | Z(4) | Plant moisture stress, night (atm) |
| | Z(5) | Minimum night temperature (°C) |
| | Z(6) | Length of day (hr) |
| | Z(7) | Average daily soil temperature (°C) |

$$Z(6) = [3.5 \cdot \sin(xk \cdot .0172) + 12]$$

where: $xk = k - 79$, and $k = \text{Julian year day}$

if ($xk \cdot LT \cdot 0$), $xk = xk + 365$

3. M list not used

4. G Functions (intermediate functions) Description

G(1) First term of daytime photosynthesis equation

$$G(1) = B(1) Z(6) [B(2) - Z(1)]^{B(4)} [Z(1) - B(3)]$$

G(2) Second term of daytime photosynthesis equation

$$G(2) = Z(3) / 60 Z(6) / [B(5) + Z(3) / 60 Z(6)]$$

G(3) One day's net photosynthesis

$$G(3) = G(1) \cdot G(2) / S(1)^2$$

G(4) Night respiration

$$G(4) = -B(6) \cdot [1 - Z(6)] \cdot e^{B(7) Z(2)}$$

G(5) = G(3) + G(4) Predicted daily net photosynthesis

G(6) = G(1) / B(8)^2 \cdot G(2) Potential day's net photosynthesis (with minimum leaf resistance)

G(7) = G(6) + G(4) Potential daily net photosynthesis

G(8) = G(5) / G(7) One day's ratio of predicted to potential photosynthesis

G(9) = X(3) / X(5) Accumulative ratio of predicted to potential PSN

G(10) = Z(1) Average day temperature

G(11) = Z(2) Average night temperature

G(12) = Z(3) Total radiation

G(13) = Z(4) Plant moisture stress (night)

G(14) = Z(5) Minimum night temperature

G(15) = Z(6) Length of day

G(16) = Z(7) Average daily soil temperature

G(17) = S(1) Diffusion resistance (computed in special function one)

G(18) = S(2) Frost reduction factor (computed in special function two)

5. **F Functions (flux functions)** **Description**
- F(0101) = G(3) Predicted day photosynthesis (PSN)
- F(0202) = G(4) Predicted night respiration
- F(0303) = G(5) Predicted daily net PSN
- F(0404) = G(6) Potential day PSN
- F(0505) = G(7) Potential daily net PSN
- F(0606) = G(5) 5-day summation of predicted daily net PSN
- F(0707) = G(7) 5-day summation of potential daily net PSN
6. **S Functions (special functions)**
- S(1) Diffusion resistance. Linear interpolation between points (night PMS, diffusion resistance) (0, 7), (2, 7), (6, 10), (10, 40), (13, 80), (22, 300).
- S(2) Frost reduction factor
- $$S(2) = 1 - \frac{(\text{Recovery days} - \text{Days since frost})}{\text{Recovery days}}$$
- defined between 20 and 31 °F
- $$\text{Recovery days} = -1 (\text{night min } ^\circ\text{F}) + 31$$
- S(3) Soil temperature effect on plant moisture stress
- $$\text{PMS} = -2.952 (\text{soil temp } ^\circ\text{C}) + 16.286$$
- defined between -2 to 5 °C
7. **Y Functions: Output**
- Y(1) = X(1) Predicted day photosynthesis (PSN)
- Y(2) = X(2) Predicted night respiration
- Y(3) = X(3) Predicted daily net PSN
- Y(4) = X(4) Potential day PSN
- Y(5) = X(5) Potential daily PSN
- Y(6) = X(6) Predicted (total every 5 days)
- Y(7) = X(7) Potential (total every 5 days)
- Y(8) = X(6)/X(7) Ratio of predicted to potential (5-day)

8. B Parameters

	Description
B(1) = .0097	(mg CO ₂ hr ⁻¹ dm ⁻² (°C ^{-[B(4)+1]}) sec cm ⁻¹)
B(2) = 45	(°C)
B(3) = -5	(°C)
B(4) = 1.5	dimensionless
B(5) = 0.1	(langley's min ⁻¹)
B(6) = 0.1	(mg CO ₂ dm ⁻² hr ⁻¹)
B(7) = 0.2	(°C ⁻¹)
B(8) = 7	(sec cm ⁻¹)

The computer program written to execute the simulation of photosynthesis.

```
SUBROUTINE ZCOMP (K,X,B,R,Z)
  DIMENSION X(1),B(1),R(1),Z(1)
```

```

C
C      LUN      FILE NAME
C      5        *MPSNDA-, M FOR MAC FOR; S FOR STUMP; L FOR
C      MOLALLA  ALL TEMPS ON ABOVE FILE IN DEG. C
C
C      Z(1)      DESCRIPTION
C      1        AVE. DAY AIR TEMP (C)
C      2        AVE. NIGHT AIR TEMP (C)
C      3        INSOLATION (LYS/DAY)
C      4        PLANT MOISTURE STRESS (ATM)
C      5        NIGHT MIN. AIR TEMP (C)
C      6        DAYLENGTH (HRS)
C      7        SOIL TEMP (C)
C
C
10  IF (IFLAG.NE.1) GO TO 20
    READ (5,1000) Z(1),Z(2),Z(5),Z(3),Z(7),Z(4)
1000 FORMAT (11X,F3.1,F4.1,5X,F3.1,19X,F3.0,6X,F3.1,1X,F3.1)
    IF (EOF(5)) CALL EXIT
C
C      COMPUTE DAYLENGTH (HOURS)
C
C      .01721=360/365*PI/180
C
    KK=MOD(K,365)
    XK=KK-79.
    IF (XK.LT.0.) XK=XK+365.
    Z(6)=3.5*SIN(XK*.01721)+12.
    RETURN
20  IFLAG=S5(K)
    GO TO 10
    END
```

C
C
C

PARTIAL RESULT FOR DAY PHOTOSYNTHESIS (PSN)

FUNCTION G01 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G01=B(1)*Z(6)*Z(1)*(B(2)-Z(1))*B(3)
RETURN
END

C
C
C

PARTIAL RESULT FOR DAY PSN

FUNCTION G02 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G02=(Z(3)/(Z(6)*60.))/(B(4)+(Z(3)/(Z(6)*60.)))
RETURN
END

C
C
C

ACTUAL DAY PSN

FUNCTION G03 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G03=(G(1)/G(17)**2)*G(2)*G(18)
RETURN
END

C
C
C

ACTUAL NIGHT RESPIRATION

FUNCTION G04 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G04=(B(5)*(24.-Z(6))*EXP(B(6)*Z(2)))/G(17)**2
RETURN
END

C
C
C

ACTUAL DAILY NET PSN

FUNCTION G05 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G05=G(3)-G(4)
RETURN
END

C
C
C

POTENTIAL DAY PSN

FUNCTION G06 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G06=(G(1)/B(7)**2)*G(2)
RETURN
END

C
C
C

POTENTIAL DAILY NET PSN

```

FUNCTION G07 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G07=G(6)-G(4)
RETURN
END

```

C
C
C

RATIO ACT/POT DAILY NET PSN

```

FUNCTION G08 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G08=G(5)/G(7)
RETURN
END

```

C
C
C

RATIO ACCUMULATED ACT/POT NET PSN

```

FUNCTION G09 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (X(5).EQ.0) RETURN
G09=X(3)/X(5)
RETURN
END

```

C
C
C

AVE. DAY AIR TEMP (C)

```

FUNCTION G10 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(1).NE.0.) GO TO 10
G10=0.
10 G10=Z(1)
RETURN
END

```

C
C
C

AVE. NIGHT AIR TEMP (C)

```

FUNCTION G11 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(2).NE.0.) GO TO 10
G11=0.
RETURN
10 G11=Z(2)
RETURN
END

```

C
C
C

INSOLATION (LANGLEYS/DAY)

```

FUNCTION G12 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(3).NE.0.) GO TO 10
G12=0.
RETURN
10 G12=Z(3)
RETURN
END

```

C
C
C

PLANT MOISTURE STRESS (ATMOSPHERES)

```

FUNCTION G13 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(4).NE.0.) GO TO 10
G13=0.

RETURN.
10 G13=Z(4)
RETURN
END

```

C
C
C

NIGHT MIN. AIR TEMP (F)

```

FUNCTION G14 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(5).NE.0.) GO TO 10
G14=0.
RETURN
10 G14=Z(5)
RETURN
END

```

C
C
C

DAYLENGTH (HOURS).

```

FUNCTION G15 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(6).NE.0.) GO TO 10
G15=0.
RETURN
10 G15=Z(6)
RETURN
END

```

C
C
C

SOIL TEMP (C)

```

FUNCTION G16 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
IF (Z(7).NE.0.) GO TO 10
G16=0.
RETURN
10 G16=Z(7)
RETURN
END

```

C
C
C

DIFFUSION RESISTANCE (SEC/CM)

```

FUNCTION G17 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G17=S1(Z(4),Z(7),K)
RETURN
END

```

C
C
C

FROST REDUCTION FUNCTION

```

FUNCTION G18 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
G18=S2(Z(5),B(8))
RETURN
END

```

C
C

ACTUAL DAY PHOTOSYNTHESIS (PSN)

```

FUNCTION F0101 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0101=G(3)
RETURN
END

```

C
C
C

ACTUAL NIGHT RESPIRATION

```

FUNCTION F0202 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0202=G(4)
RETURN
END

```

C
C
C
ACTUAL NET DAY PHOTOSYNTHESIS TO DATE

FUNCTION F0303 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0303=G(5)
RETURN
END

C
C
C
POTENTIAL DAY PSN TO DATE

FUNCTION F0404 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0404=G(6)
RETURN
END

C
C
C
POTENTIAL DAY NET PSN TO DATE

FUNCTION F0505 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0505=G(7)
RETURN
END

C
C
C
5-DAY SUM ACTUAL NET DAY PSN

FUNCTION F0606 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0606=G(5)
IF (MOD(K,5).EQ.0) F0606=-X(6)+G(5)
RETURN
END

C
C
C
5-DAY SUM POTENTIAL NET DAY PSN

FUNCTION F0707 (K,X,B,R,Z)
DIMENSION X(1),B(1),R(1),Z(1)
F0707=G(7)
IF (MOD(K,5).EQ.0) F0707=-X(7)+G(7)
RETURN

C
C
C
S1 IS DIFFUSION RESISTANCE FOR STOMATAL -
APERTURES (SEC/CM)

FUNCTION S1 (Z,S,K)
DIMENSION DR(10),FMS(10)

GRAPH READ-IN (INPUT/CUTPUT GRAPH)

DATA ((DR(I),I=1,6)=7.,7.,10.,40.,80.,300.)
 DATA ((PMS(I),I=1,6)=0.,2.,6.,10.,13.,22.)

S IS SOIL TEMP (C)

Y,Z IS Z(4), PLANT MOISTURE STRESS (ATM)

Y=Z

IF (S.LE.5.) GO TO 40

FIND WHICH (I) THE PMS VALUE FITS INTO (LOOK UP
 X-VARIABLE AND FIND Y-VARIABLE, WITH LINEAR INTERP.)

10 DO 20 I=1,8

IF (PMS(I).GE.Y.OR.PMS(I+1).LT.Y) GO TO 20

GO TO 30

20 CONTINUE

WRITE (61,1000) Y

1000 FORMAT ('#1ERROR IN INTERP.-S1-PMS=#,F3.1)

CALL EXIT

30 S1=DR(I)+((DR(I+1)-DR(I))/(PMS(I+1)-PMS(I)))*(Y-PMS(I))

RETURN

S3 CORRECTS PMS FOR COLD SOIL CONDITIONS

40 X=S3(S,Z,K)

IF (X.GT.Z) Y=X

GO TO 10

END

S2 IS FROST REDUCTION FUNCTION

FUNCTION S2(Z,B)

Z IS Z(5), NIGHT MIN. AIR TEMP (F)

B IS B(8)=1.1

N CONVERT NIGHT MIN TEMP TO INTEGER (ROUND UP)

N=S4(Z)+.5

I=0

S2=1.

IF (N.LE.31) GO TO 12

IF (J.EQ.0) RETURN

GO TO 10

I STORES COMPUTED NUMBER OF RECOVERY STEPS (IN DAYS)
RESTRICTED TO LESS OR EQUAL 10 STEPS

J STORES MAX. OF J AND A NEWLY COMPUTED (I) NUMBER
OF RECOVERY DAYS

KK IS THE DAILY COUNTDOWN VARIABLE - DAYS SINCE LAST
FREEZING DAY

```

12 I=32-N
   IF (I.EQ.1) I=2
   IF (I.GT.10) I=10
   IF (I.GT.J) GO TO 20
   IF (J.NE.0) J=J-KK+1
   KK=0
   IF (I.GT.J) GO TO 20

```

STEP FUNCTION FROM .091 TO 1.0 WITH FROM 2 TO 10 STEPS

```

10 S2=1-(J-KK)/(B*J)
   IF (KK.EQ.J) GO TO 30
   KK=KK+1
   RETURN
20 J=I
   KK=0
   GO TO 10
30 I=J=KK=0
   RETURN
END

```

S3 IS SOIL TEMP CORRECTION FOR PMS IN S1

Z IS SOIL TEMP (C)

FUNCTION S3(Z,X,K)

```

WHEN SOIL TEMP LESS THAN -2 (C), PMS=22 ATM
  THUS DIFF. RES.=300 SEC/CM (BY S1)
WHEN SOIL TEMP GREATER THAN 5 (C), PMS READ FROM FILE
  AS THIS FUNCTION IS NOT CALLED FROM S1
WHEN SOIL TEMP LESS OR EQUAL 5 (C), PMS=2 THRU 30,
  THUS D.R.=7 TO 300 SEC/CM (BY S1)
  (OR, IF FILE HAS A LARGER PMS, THEN IT IS USED)
THIS ROUTINE IS A LINEAR INTERPOLATION FROM
2 TO 22 ATM (FOR PMS CORR TO S1) WHEN SOIL TEMP
LESS OR EQUAL 5 (C)

```

IF (Z.GT.-2.) GO TO 10

S3=22.

RETURN

10 S3=-2.857*Z+16.286

RETURN

END

S4 CHANGES TEMP (C) TO TEMP (F)

FUNCTION S4(Z)

S4=Z*9./5.+32.

RETURN

END

S5 GETS THE INPUT FILE IN THE RIGHT PLACE

FUNCTION S5(K)

10 READ (5,1000) IDAY

1000 FCRMAT (7X,I3)

IF (EOF(5)) CALL EXIT

IF (K.NE.IDAY) GO TO 10

BACKSPACE 5

S5=1.

RETURN

END

SUBROUTINE YCCMF (K,X,B,R,Y)

DIMENSION X(1),B(1),R(1),Y(1)

X()	DESCRIPTION
1	ACCUM ACTUAL DAY PSN (PHOTOSYNTHESIS)
2	ACCUM ACTUAL NIGHT RESPIRATION
3	ACCUM ACTUAL DAY NET PSN
4	ACCUM POTENTIAL DAY PSN
5	ACCUM POTENTIAL DAY NET PSN
Y(6)	5-DAY RATIO ACT/POT NET DAILY PSN

Y(1)=X(1)

Y(2)=X(2)

Y(3)=X(3)

Y(4)=X(4)

Y(5)=X(5)

Y(6)=0.

IF (X(7).EQ.0.) RETURN

IF (MOD(K,5).EQ.0) Y(6)=X(6)/X(7)

RETURN

END