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Title: THE EFFECT OF PLANT MOISTURE STRESS ON THE
PHYSIOLOGY AND ESTABLISHMENT OF PLANTED
DOUGLAS-FIR AND PONDEROSA PINE SEEDLINGS

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Dr. William K. Ferrell

The role of moisture stress in seedling physiology and establishment was studied in both the field environment and laboratory experiments. Plant moisture stress was measured using the pressure chamber technique. This technique was modified and tested using a fascicle of pine needles as a sample, an improvement which allows the technique to be used repeatedly in the same seedling and is equivalent to measurements on twigs.

Using the pressure chamber, ponderosa pine and Douglas-fir seedlings which were planted in early spring were monitored for both seasonal and diurnal changes in moisture stress throughout the first growing season until the fall rains recharged the soil. Differences in seedling growth and survival during the three years of measurement were related to moisture stress levels experienced by the seedlings. Needle length of ponderosa pine was a good indicator of seasonal

moisture stress levels.

The photosynthetic response of seedlings to different levels of moisture stress with light at saturation levels was evaluated in a series of laboratory experiments using an infra-red gas analyzer in a closed system. The relative net photosynthetic response of ponderosa pine and Douglas-fir to moisture stress showed distinct differences between the two species. Douglas-fir showed an almost linear decline in photosynthesis from a maximum when plant moisture stress (PMS) was less than 8 atm to 20% of maximum at 22 atm.

In contrast, ponderosa pine showed little decline in photosynthesis until about 15 atm PMS. There the decline, probably associated with stomatal closure, occurred abruptly with no measurable photosynthesis occurring after 20 atm PMS. Seedlings which had experienced 50 atm PMS showed reduced photosynthetic rates even two weeks after the moisture stress was relieved. PMS levels of 80 atm were lethal to the needle tissue of both species. There was more variability in response within the population of pine seedlings compared to the population of Douglas-fir.

The photosynthetic response of ponderosa pine seedlings to temperature and moisture stress varying independently was also evaluated. The resulting response surface showed the proportion of a given response attributable to temperature and the proportion attributable to moisture stress. A partial differential equation is

suggested for use in examining how the environmental factors contribute to a given plant response. An equation to describe how the plant occupies a predominant regulatory position in the soil-plant-atmosphere continuum is proposed.

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The Effect of Plant Moisture Stress on the
Physiology and Establishment of Planted
Douglas-fir and Ponderosa Pine Seedlings

by

Brian Dennis Cleary

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THE EFFECT OF PLANT MOISTURE STRESS ON THE PHYSIOLOGY AND ESTABLISHMENT OF PLANTED DOUGLAS-FIR AND PONDEROSA PINE SEEDLINGS

INTRODUCTION

One of the most difficult problems in forestry today is economical regeneration of cut-over lands. The necessity of obtaining rapid regeneration has led in recent years to a greater reliance on the planting of seedlings rather than artificial or natural regeneration from seed. In the shift to more planting, failures in plantation establishment have been numerous. One of the primary reasons for these failures is the radical change in environment associated with the use of clear-cutting. The environmental change often leaves a site which is so inhospitable that vegetation is sparse. Under these conditions failure is usually associated with inadequate levels of nutrition and water combined in many instances with extremes in temperature during the first several growing seasons particularly the first one. At other times seedlings are subjected to conditions such as improper handling of planting stock, inadequate light levels due to competition, or animal damage which contributes to poor survival. Success or failure is usually dependent on an interaction between these six factors rather than any one by itself. The water relations of the seedling are almost always affected by the severe conditions mentioned above.

The most critical period of high moisture stress for almost all plants occurs in the year of establishment, whether the establishment involves germination from seed or transplanting a seedling grown for a period under nursery conditions. Recent developments in the field of plant water relations, particularly the introduction and improvement of the pressure chamber technique, allow one to measure the moisture stress in a plant easily and directly. The advantage of direct measurement over inference based on other parameters cannot be over emphasized. The pressure chamber technique re-introduced by Scholander et al. (1965) was used to follow the seasonal and diurnal changes in seedling moisture stress during three growing seasons at several different sites and with a number of different treatments. It was obvious from early measurements that the very high levels of stress reached during the establishment phase greatly exceeded the stresses encountered once the plant was established. These data suggested that an examination of the physiological response of the seedling to moisture stress would be very helpful in evaluating the regeneration problem.

The two species most commonly planted in the Western United States are Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and ponderosa pine (Pinus ponderosa Dougl.). The study described here was conducted in an attempt to understand better the water relations of these two species during establishment. The study is divided into

two phases: (1) the collection of moisture stress data under field conditions, and (2) a laboratory study of the photosynthetic response of the seedling to different levels of moisture stress.

Seedlings grow in an environment which is constantly changing. The plant response studied should therefore be one which can also change continually and respond rapidly to the environment. For this reason the net assimilation of CO_2 or photosynthesis was chosen as the plant response to be examined in the laboratory rather than diameter growth, height growth, or dry weight accumulation.

LITERATURE REVIEW

The study of success and failure of seedling establishment has been conducted for many years. Most earlier workers and even some workers today examine establishment from a subjective or superficial point of view. The two factors most commonly studied quantitatively are water relations and heat. The heat problem has been analyzed quantitatively by many workers in recent years (Adams, 1960; Bates, 1924; Brawand and Kohnke, 1952; Cleary and Waring, 1969; Daubenmire, 1943, 1957; Hellmers, 1963; Hermann, 1963; Korstian and Fetherolf, 1921; Silen, 1960; and others).

Seedling water relations have also been evaluated quantitatively but primarily either in laboratory studies or by inference from soil and/or atmospheric moisture stress data collected in the field. Most of the laboratory work and some of the field work in water relations has been summarized in recent years with the publication of three excellent books (Slatyer, 1967; Kozlowski, 1968; Kramer, 1969). The reader is referred to these works for a detailed review of past studies in the general area of water relations. Publication of these works places proper emphasis on the importance of water for plant growth and survival so further review of the general area will not be attempted here.

The moisture status of plants has long been interpreted as being

very closely related to soil moisture. In the field the availability of moisture to a plant during the growing season has been expressed in different ways. Variables such as depth and stability of the water table, morphological features of the soil profile, and topographic position have been employed to classify sites in relation to a moisture gradient (Hill, 1959; Loucks, 1962; McMinn, 1960; Whittaker, 1960).

Waring and Major (1964) utilized minimum available soil moisture to derive a moisture gradient in a study of the California redwood region forest types. Hadley (1969), in a comprehensive study of ponderosa pine, measured growth and photosynthesis in relation to light, temperature and soil moisture, but other than field sampling of precipitation no attempt was made to assess moisture stress in the field. Whether the soil moisture is measured directly or indirectly, it must be recognized that soil moisture is only one factor influencing the plant water status. What is even more difficult than measuring soil moisture is prediction of what part or how much of the soil water the plant utilizes.

The water balance in a seedling depends on more than just the supply of water from the soil. The transpirational demand on the plant is equally important in influencing the plant water status at any time. The energy budget concept is probably the easiest approach to understanding how the plant fits into the above-ground environment. Geiger (1965) introduced this approach to biologists in his book on

microclimatology. Others have contributed to the expansion and elaboration of this approach (Gates, 1962; Monteith, 1965; Penman, 1956; Raschke, 1956, 1958; Tanner, 1960).

The use of either soil or atmospheric water stress alone however, is unsatisfactory for a detailed understanding of how the plant reacts to what has been described as the soil-plant-atmosphere continuum (Philip, 1966). Conceptually the model was formulated by Gradmann (1928), improved and simplified by van den Honert (1948), and further refined by Cowan (1965) and Cowan and Milthorpe (1968). This continuum approach to water movement through the environment is a great aid to understanding plant water relations.

As has been pointed out many times, the only reliable way to evaluate moisture stress within the plant is to measure it directly in the plant (Cleary, 1966; Kramer, 1969; Kramer and Brix, 1965; Slatyer, 1957, 1960, 1967; Weatherly, 1950; and others). The reason for a direct evaluation is the plant's ability to control water losses, and thus affect its water status, by changing its stomatal resistance to water flow. The rather simple phenomenon of stomatal closure greatly complicates the interpretation of this rather complex system. A second complicating factor is the inability to predict what water is available to the root in field conditions. Kramer and Brix (1965) summarized this point of view:

It is quite clear that we cannot make reliable assumptions concerning the degree of water stress existing in plants

from soil moisture data or estimates of evapotranspiration. The only safe procedure is to measure water stress of the plant by some direct method.

Direct measurement of plant moisture stress can be accomplished by a number of techniques which are summarized by Barrs (1968), Boyer (1969), and Kramer (1969). In this study the method utilized is the pressure chamber technique originally described by Dixon (1914) and reintroduced by Scholander et al. (1965). In Scholander's studies, a pressure chamber reading gave a good estimation of plant moisture stress and could be carried out under field conditions. No correction was made for the error due to the osmotic potential described by Boyer (1967). Kaufman (1968b) described large deviations in the pressure chamber technique compared to the thermocouple psychrometer, when measuring oak branches. At least when working with conifers, however, the pressure chamber gives a reproducible estimate of moisture (Kramer, 1969; Waring and Cleary, 1967). The term water potential, in units of negative bars, has been suggested by Slatyer and Taylor (1960) to replace other terminology in water relations. This term has received wide usage. In agreement with Philip (1966), who stated that convenience is the only pertinent criterion, I have chosen in this paper to use the term plant moisture stress (PMS) expressed in positive atmospheres to represent the values obtained using the pressure chamber technique.

To date few papers have been published which describe seasonal

changes in PMS and when they have, no attempt has been made to relate the changes to a plant response. Cleary (1966) measured the seasonal changes in relative water content of needles and soil moisture stress (SMS) in mature Douglas-fir trees. However, as has been discussed previously, SMS is only one of the factors affecting PMS. Two other factors making interpretation of these data difficult are (1) determination of available soil moisture, since root distribution was variable in the stands investigated, and (2) seasonal changes in relative water content not associated with changes in moisture stress. Zahner (1962) and Buckingham and Woods (1969) studied shoot elongation and wood formation in relation to soil moisture and soil moisture deficit. These two studies and one by Lotan and Zahner (1963) where shoot elongation and wood formation were related to an irrigation schedule, represent attempts to relate water relations to a plant response. These data have the shortcoming mentioned earlier in that moisture stress was not measured in the tree.

Over the past ten years since the introduction of the term water potential (Slatyer and Taylor, 1960) there has been a continuous dispute over the best or most accurate way to measure water potential (reviewed by Barrs, 1968, and Kramer, 1969). While this exchange has been valuable, much of the effort was undertaken as an "academic exercise" to prove one technique better than another. What is most important from a physiological viewpoint is (1) how does the plant

respond to the measure of water potential being used?, and (2) how reproducible is the method? The pressure chamber technique utilized in this study is easy to use, can be related to plant response, and is reproducible.

The photosynthetic response of trees to the field environment has been studied by Helms (1965), Hodges (1967), and Woodman (1968). In these studies, however, little was learned about the effect of any one component of the environment on photosynthesis since components were not separated. In laboratory studies the effect of light intensity and temperature on the rate of photosynthesis in Douglas-fir have been examined by Brix (1967), Krueger and Ferrell (1965), and Sorenson (1964).

Brix (1962) studied the photosynthetic response of tomato and loblolly pine seedlings to increasing moisture stress. He found little effect of moisture stress as measured with a thermocouple psychrometer on the seedlings until a moisture stress of -8 bars. In loblolly pine there was an almost linear decrease in photosynthesis from the maximum rate when the stress was less than -8 bars to no photosynthesis when the stress exceeded -14 bars.

Kaufman (1968a) studied the water relations of loblolly pine to dry matter production. Fry (1965) studied the effect of water stress on photosynthesis and transpiration rates of Douglas-fir seedlings. In all of these studies increasing water stress depressed the

photosynthetic rate and dry matter production. Zavitkovski and Ferrell (1970) examined the effect of soil water stress and relative turgidity on the photosynthesis of Douglas-fir seedlings and found a similar depression in photosynthetic rates.

MATERIALS AND METHODS

Instrumentation

The instrumentation used for this study consisted of standard components combined with fabricated equipment designed by the author and made by machinists on the Oregon State University campus.

Water Relations

The pressure chamber technique as used in this study was similar to that described by Waring and Cleary (1967) in which only twigs were sampled. The removal of a sample for measurement using the standard technique for twigs is destructive; only one sample per one year old pine seedling or up to ten samples per two year old Douglas-fir can be taken. This destructiveness led to the development of a special chamber to accommodate pine fascicles and other conifer needles. The pressure chamber instrument is shown in Figure 1, where the smaller fascicle chamber (A) is connected in parallel with the larger twig chamber (B).

A special tool was devised to insert a sample into the gasket and obtain an airtight seal without damaging the tissue. Measurement can be made to pressures as high as 60 atm without the sample extruding through the gasket. This insertion technique is depicted in Figure 2. It was found to facilitate the measurement of both needles

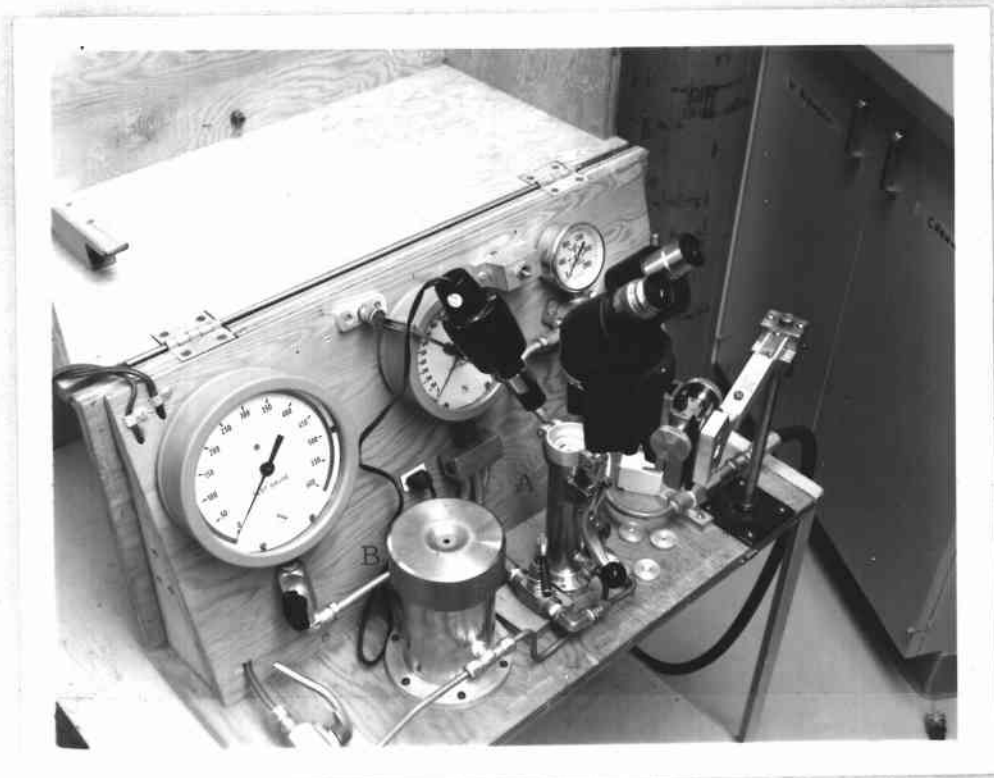


Figure 1. Pressure chamber instrument. The fascicle chamber is labelled A and the large chamber for twigs is labelled B.

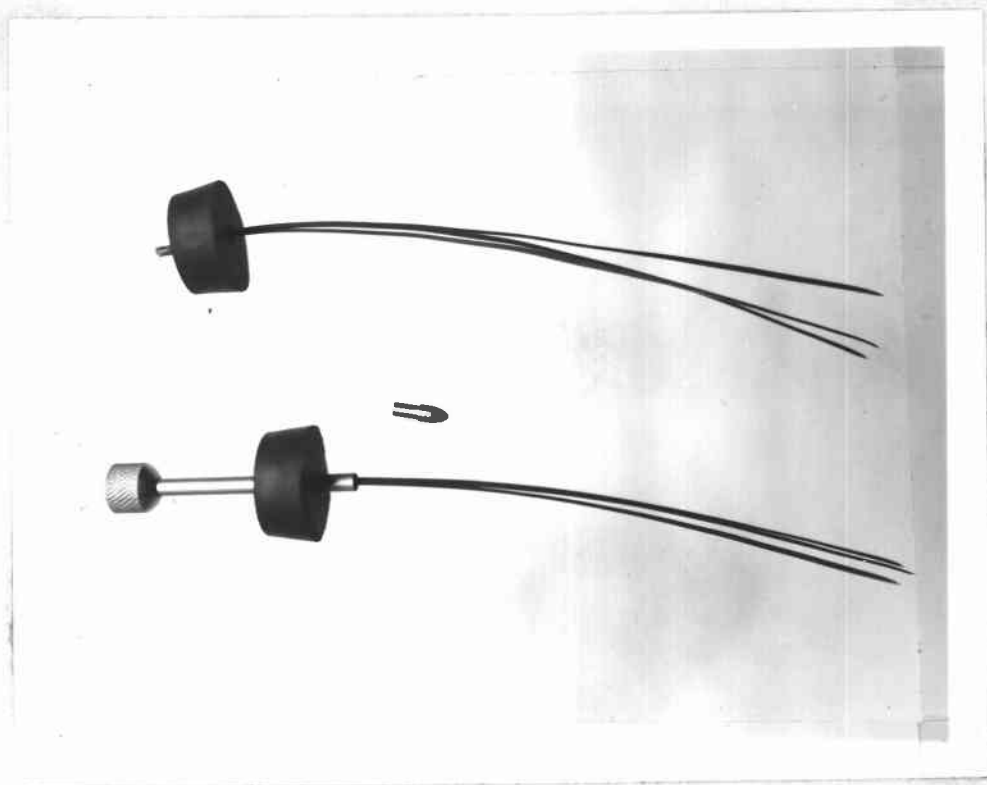


Figure 2. Tool used to insert a sample into the sealing gasket.

and fascicles and was also utilized on herbaceous plant material including sunflower and grass leaves.

The fascicle chamber design minimizes the gasket thickness and amount of sample external to the chamber while allowing easy sample insertion and extraction. The gasket thickness for this design is 0.5 cm plus 0.2 cm of sample protruding through the gasket for a total of 0.7 cm of fascicle external to the pressurized chamber. Tests conducted using the fascicle chamber indicated that errors are generated by having either a large proportion of the sample external to the chamber or a large proportion of the sample within the gasket or both. If a large portion of the sample (50%) is external to the pressurized chamber, the PMS measured is 1 to 2 atm greater than that observed for twigs or fascicles where less than one-tenth of the fascicle is outside the chamber.

Tests on paired samples of a fascicle and branch of ponderosa pine material indicated that there was no statistical difference between these two measurements of PMS using ten paired samples. However, this test was possible only when simultaneous measurements were made in the two chambers shown in Figure 1. The need for simultaneous measurement is caused by changes in PMS observed if a sample with open stomata is left exposed to the air for as little time as 1 min. The rate of change in PMS varies from 0.1 atm/min to 1.5 atm/min depending upon the exposure conditions. Samples

stored for 5 min in a plastic bag change as much as 2 atm PMS. The precision of the fascicle technique is better than that found when sampling twigs; the standard deviation is equal to 0.1 to 0.3 atm with five to ten samples. The advantage is that repeated sampling on the same seedling is possible. This technique was used exclusively in sampling pines in subsequent studies.

PMS measurements of single Douglas-fir needles were made in the small chamber used for measuring pine. These measurements appear to have a systematic error believed to be a function of gasket thickness. Using a gasket 1 cm thick rather than the usual 0.5 cm, and a 2.5 cm needle, one obtains PMS values as much as 2 atm lower than that observed using the thinner gasket. The magnitude of error is dependent on the level of stress in the sample material. Because of this error the measurement of PMS on single needles of Douglas-fir was discontinued and all subsequent data represent measurements taken using the small lateral branches of this species.

Photosynthesis

The apparatus used for measuring photosynthesis in the laboratory portion of this study is shown in diagrammatic form in Figure 3. The closed system contains a primary environmental control loop where air is circulated at a rate of 40 l/min and a secondary loop where the rate of change of CO₂ is measured with a Beckman

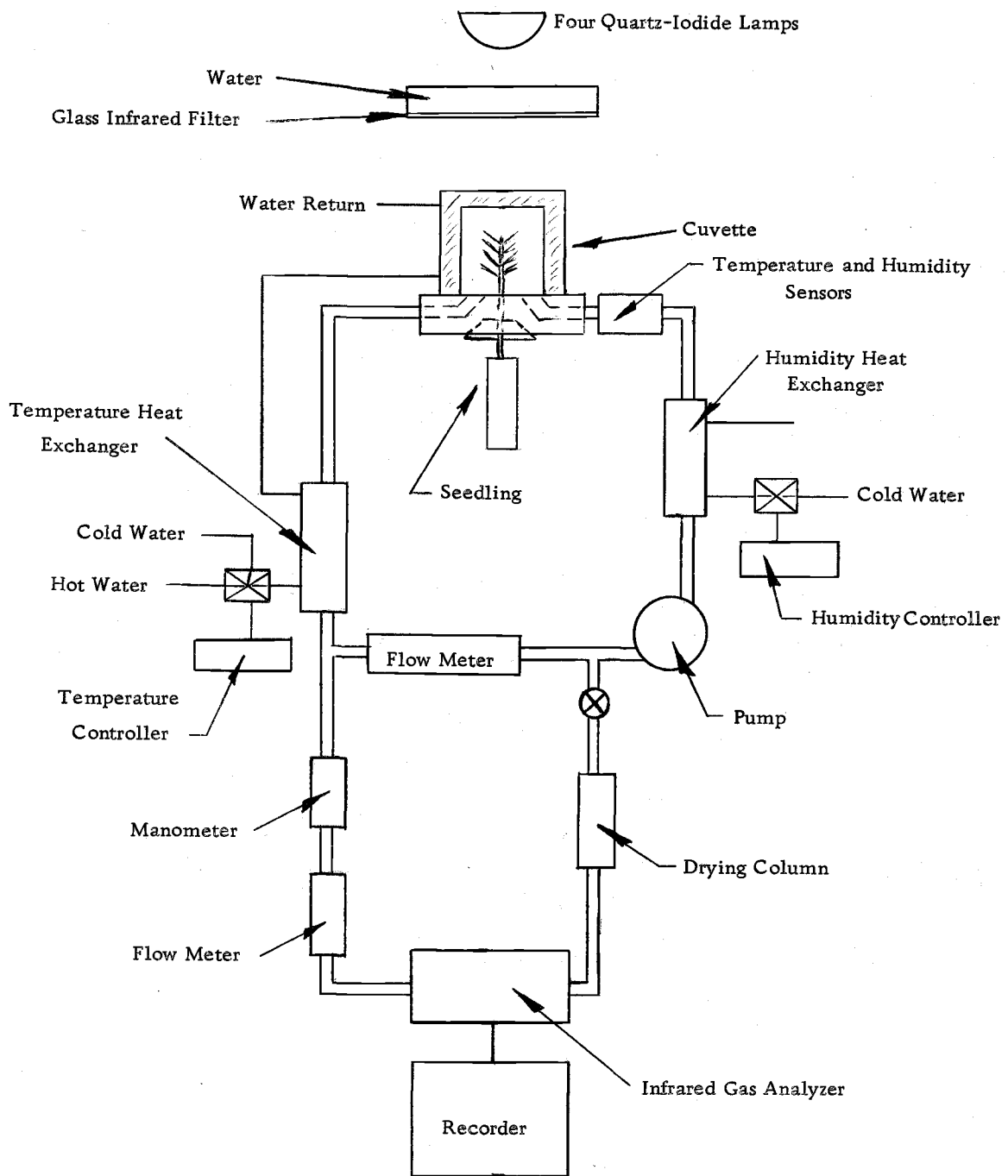


Figure 3. Diagram of photosynthesis measuring apparatus.

L/B-15A infrared gas analyzer. Control of the plant's environment in the cuvette was primarily through the use of the humidity and temperature heat exchangers. The humidity exchanger was used to condense water vapor within the system so that humidity could be maintained at the desired level. The air was then heated by the pump and brought to proper temperature by the temperature heat exchanger. Hot and cold water were passed alternately through the water jacket to maintain the temperature in the cuvette at the desired level. Temperature control in the cuvette was $\pm 0.2^{\circ}\text{C}$ and humidity control was $\pm 0.07 \times 10^{-6} \text{ g/cm}^3$. Addition of water to the system, when required, was achieved by passing air through a gas washing bottle containing a 10% phosphoric acid solution. In addition to precise temperature and humidity control, a 40 l/min flow rate through the primary loop gave good mixing of the air to break up the boundary layer resistance as well as a fast response time for the system. The total volume of this system was 3.8 liters.

The light source consisted of four General Electric Par-Quartzline 500 watt quartz iodide lamps. The light from these lamps passed through 8 cm of water and a glass interference filter (Berkey Colortran #122-7). This gave $.98 \text{ g cal/cm}^2/\text{min}$ (approximately 150% of full sunlight) between 400 and 700 nm at the plant level. The spectrum of these lamps after passing through the filter is shown in Figure A of the appendix.

The rate of photosynthesis was calculated from the rate of change of CO_2 concentration at 310 ppm CO_2 . The rate of change is easily calculated from the slope of a line drawn tangent to the recorder output at this concentration. Using this rate of change of CO_2 concentration expressed in ppm CO_2 /min and the dry weight of needle tissue present at the time of measurement, the net CO_2 exchange is calculated and expressed in $(\text{mg CO}_2) (\text{g dry weight})^{-1} (\text{hr})^{-1}$. Each plant moisture stress determination was made by the removal of a fascicle of needles or one twig from the seedling. In both species the removal of plant material required a continual dry weight correction in the determination of photosynthetic output. For estimating plant response the CO_2 assimilation rate was often converted to a percentage of the maximum rate observed during the experiment.

Growth Chamber

Plant material used in laboratory experiments was preconditioned in an Environmental Growth Chamber Inc. model M-13 growth chamber. This chamber has air temperature control of $\pm 0.25^\circ\text{C}$ and humidity control within $\pm 2\%$ relative humidity. A water jacket surrounding the plant containers controlled the root temperatures to within $\pm 0.5^\circ\text{C}$. The lighting in the chamber consisted of two 400 watt General Electric Multi-Vapor, two 400 watt General Electric

Lucalux, and six 50 watt standard incandescent lamps. This combination gave an intensity at the seedling top of $.25 \text{ g cal/cm}^2/\text{min}$ between 400 and 700 nm. This is approximately 50% of the full sunlight spectrum between 400 and 700 nm at Corvallis in July. The spectrum of this light system is shown in Figure A of the appendix.

Plant Material

The plant material used in this study consisted of either one- or two-year old seedlings grown in a nursery. One year old ponderosa pine seedlings were used in both the 1967 and 1968 field out-plantings. Two year old ponderosa pine were used in the 1969 out-planting as well as the laboratory study described later. Two year old fir were used exclusively in both field out-plantings and subsequent laboratory determinations. Seeds from both species originated in southern Oregon.

Field Procedures

Field data for seedlings planted during three growing seasons were obtained. The seasonal changes in PMS, survival and growth of seedlings were measured. The seedlings in the field were planted in a 30 cm x 30 cm spacing at a reasonably uniform site to reduce variability caused by differences in the environmental characteristics present in a larger area. These seedlings were planted in March each

year and sampled at irregular intervals throughout the growing season, the drought period, and until the fall rain relieved moisture stress. At that time survival and growth data were collected. Survival counts were repeated in the spring of the following year as a check on the fall mortality count. In the spring of 1967, 800 seedlings were out-planted at two locations where summer drought was expected to be very severe but probably not lethal. One area was located at the old state nursery site north of Corvallis (hereafter referred to as the Corvallis nursery) where herbaceous competition was severe. The other area was located in an open forest stand on Mt. Ashland, south of Medford, Oregon. In both areas seedlings were planted in 3 x 3 m plots with 100 seedlings per plot. One block of seedlings at the Corvallis location was irrigated at irregular intervals to maintain the moisture stress well below 45 atm.

Field out-plantings and measurements during the 1968 growing season were confined to two areas: the Corvallis nursery site used in 1967, and a recently logged area located approximately one mile from the nursery. These two areas were chosen to represent the two extremes in planting conditions encountered in McDonald Forest. The Corvallis nursery site with its vigorous herbaceous competition was representative of a planting site with strong competition. In contrast,, the recently cleared area adjacent to a forest stand with protection from afternoon radiation was representative of a planting

site with little competition and a high probability of successful establishment. The seedlings were planted in March and measurements made at irregular intervals throughout the growing season.

In 1969, the field plantings were confined to three plots in the Corvallis nursery. The treatment in this season consisted of a control plot and two irrigated plots which were irrigated so that the early morning PMS never exceeded a specified level. The heavily irrigated treatment was kept at a PMS of less than 5 atm early in the morning while the moderately irrigated plot was maintained at a minimum PMS of less than 10 atm and the control plot was not irrigated. The amount of water and frequency of watering was dependent on the moisture stress determinations.

Laboratory Procedures

In March 1969, at the time the seedlings were out-planted at the nursery, 200 additional seedlings were planted in one-quart milk cartons. These seedlings were grown for most of the growing season under natural conditions with watering frequent enough to prevent high moisture stress. Some seedlings were brought into the preconditioning growth chamber as soon as the bud was set, while others were not brought in until well into the winter. The plants brought into the growth chamber were preconditioned for at least ten days before any measurements were taken on them. The preconditioning

environment was 25°C day temperature, 10°C night temperature, 15°C root temperature, 14 hour photoperiod and constant absolute humidity (ρ_w) of $9.4 \times 10^{-6} \text{ g/cm}^3$. After the ten-day preconditioning period, the plants were measured in the photosynthesis apparatus at irregular intervals depending on the rates of change in PMS.

Measurements of photosynthesis were made under conditions identical to those in the growth room ($T = 25^\circ\text{C}$, $\rho_w = 9.4 \times 10^{-6} \text{ g/cm}^3$). The seedlings were removed from the growth chamber, placed in the photosynthetic apparatus and the CO_2 concentration monitored until the uptake rate stabilized. The time required to reach this stabilized rate varied from 15 to 40 min depending on the level of moisture stress. Once the stable rate was reached the plants were removed and sampled for PMS with the pressure chamber technique. After the initial maximum rate of photosynthesis at low moisture stress was determined, watering was stopped and the plant was allowed to utilize the water within the pot. The response of the plant to changes in both moisture stress and temperature was evaluated. Some measurements in addition to the more frequent measurements made at 25°C were made at 15, 20, 30, and 35°C. A limited amount of data on the stomatal aperture was also collected at that time using the Fry and Walker (1967) pressure infiltration technique.

RESULTS

Field Studies

Using the pressure chamber technique, field measurements of seedling PMS were made during the year of establishment. Changes in PMS, an important physiological parameter, involve two time scales; seasonal changes throughout the growing season, and diurnal changes during each day. These changes in PMS are important in metabolic processes such as photosynthesis, in integrative processes such as growth, and indeed in survival itself.

The seasonal changes in plant moisture stress were followed during three growing seasons. In 1967, plantings at Corvallis and Medford were monitored at irregular intervals. The fascicle technique for measuring PMS had not been developed and therefore the most detailed data were collected on Douglas-fir where small twigs were removed from the seedlings so that some repetitive sampling could be done on the same seedling. All measurements were made on what appeared to be live seedlings. If a seedling died during the season a new live seedling was selected to represent the population of survivors. Limited ponderosa pine data were collected because each sample required an entire seedling.

The seasonal change in moisture stress of Douglas-fir at the Corvallis nursery is shown in Figure 4. Each data point is the mean

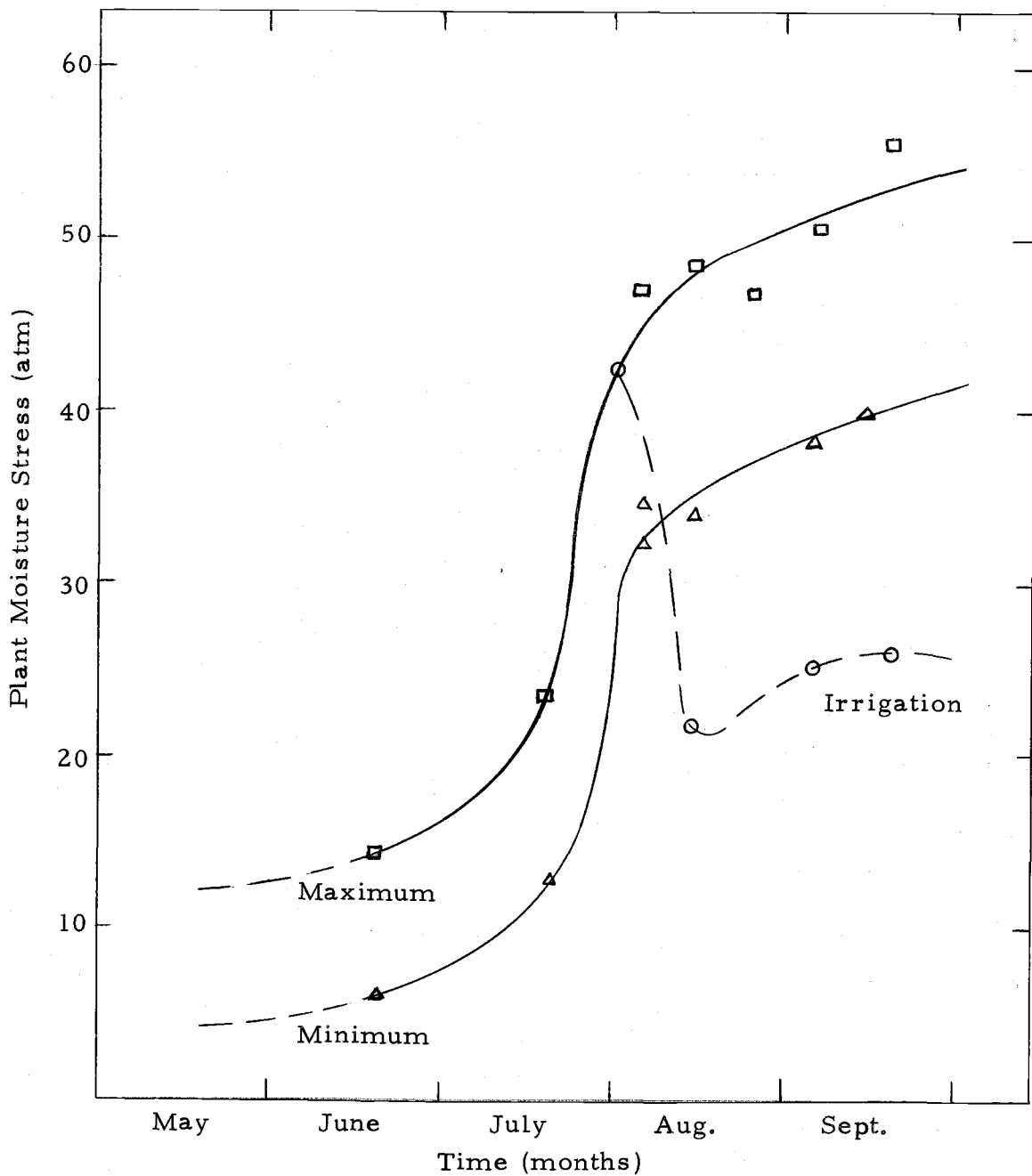


Figure 4. Seasonal changes in plant moisture stress of Douglas-fir; Corvallis, 1967. Each point is the mean of eight seedlings. The irrigated plot seedlings were kept below 45 atm PMS and suffered 10% mortality. The remaining seedlings suffered 90% mortality.

of eight seedlings. The minimum values were obtained during the one hour period before sunrise while maxima are those recorded on warm sunny afternoons between 2:00 PM and 4:00 PM. The choice of the times for minimum-maximum measurements was based on diurnal curves presented later. On days when the temperatures were lower or when cloud cover was present, the maximum PMS attained was as much as 10 atm lower than those values shown in Figure 4. One plot was irrigated periodically, when, based on laboratory data for the seed source used, the maximum stress values reached what appeared to be near-lethal levels. All of the other plots showed 90% mortality while the irrigated plot showed only 10% mortality at the end of the growing season.

Figure 5 shows the same type of data collected for the Medford location. The difference shown between plots is a result of differences in the amount of shade from the surrounding stand. Plot 8 had considerable shading during the day, while plot 1 was almost completely exposed. The diurnal changes in moisture stress are very small during July, probably because of the low water availability of the very coarse, granitic soil on this site. Large diurnal changes are present at Corvallis where the soil has a clay texture. Mortality in excess of 90% was recorded on all eight plots at Medford.

During the 1968 season, plantations were sampled at the Corvallis nursery and at a site approximately one mile away in the

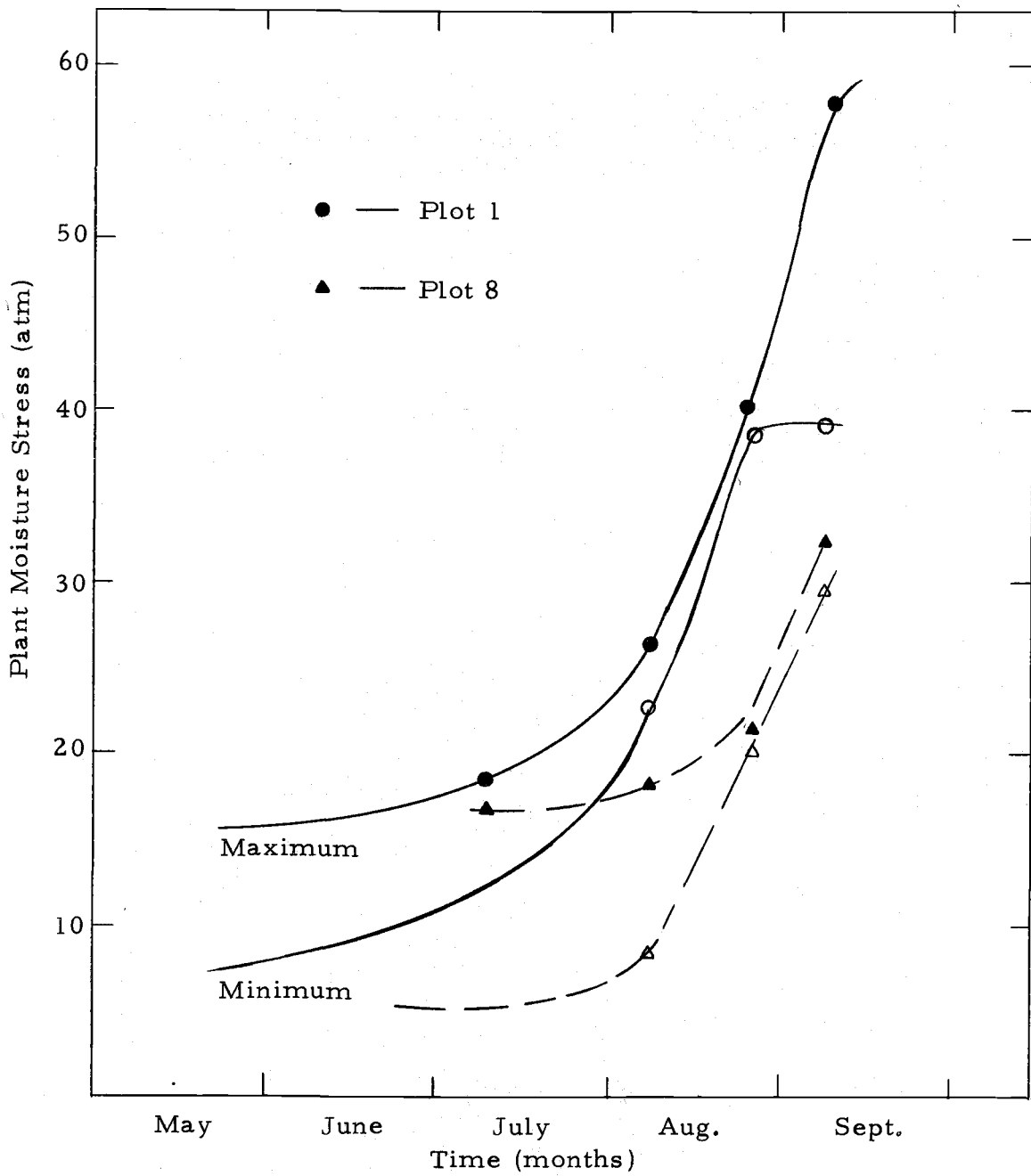


Figure 5. Seasonal changes in plant moisture stress of Douglas-fir; Medford, 1967. Each point is the mean of eight seedlings. The difference between plots was the amount of shade received from surrounding trees.

McDonald Forest. This site was located on the edge of a recent clear-cut adjacent to standing timber. The seasonal changes in ponderosa pine for the Corvallis nursery site are shown in Figure 6. During this year several weeks of intermittent rain in the latter half of August reduced the moisture stress to a very low level. As a result, there was no ponderosa pine mortality during 1968, even on this site which had greater than 90% mortality the previous year.

The seasonal changes in PMS during 1968, for ponderosa pine in McDonald Forest, are given in Figure 7. Here moisture stress never became very high and again the rain in August reduced the stress to a very low level for the rest of the growing season. The mortality at both Corvallis locations was less than 1%. The needle elongation on these two sites appeared to be a sensitive measure of the stress in each location. At the nursery, the average needle length for more than 100 seedlings was 5.2 cm, while at the McDonald Forest site the average needle length was 8.4 cm.

During the 1969 growing season, three plots were established at the nursery: a control plot, and two irrigated plots. Averages of ten seedlings in each of these three plots are shown in Figure 8. Data for three individual trees representative of the range of variation found within each treatment are shown in Figures B, C, and D.

The seasonal change of PMS in ponderosa pine for the years 1967, 1968, and 1969 are presented in Figure 9. Data shown in Figure

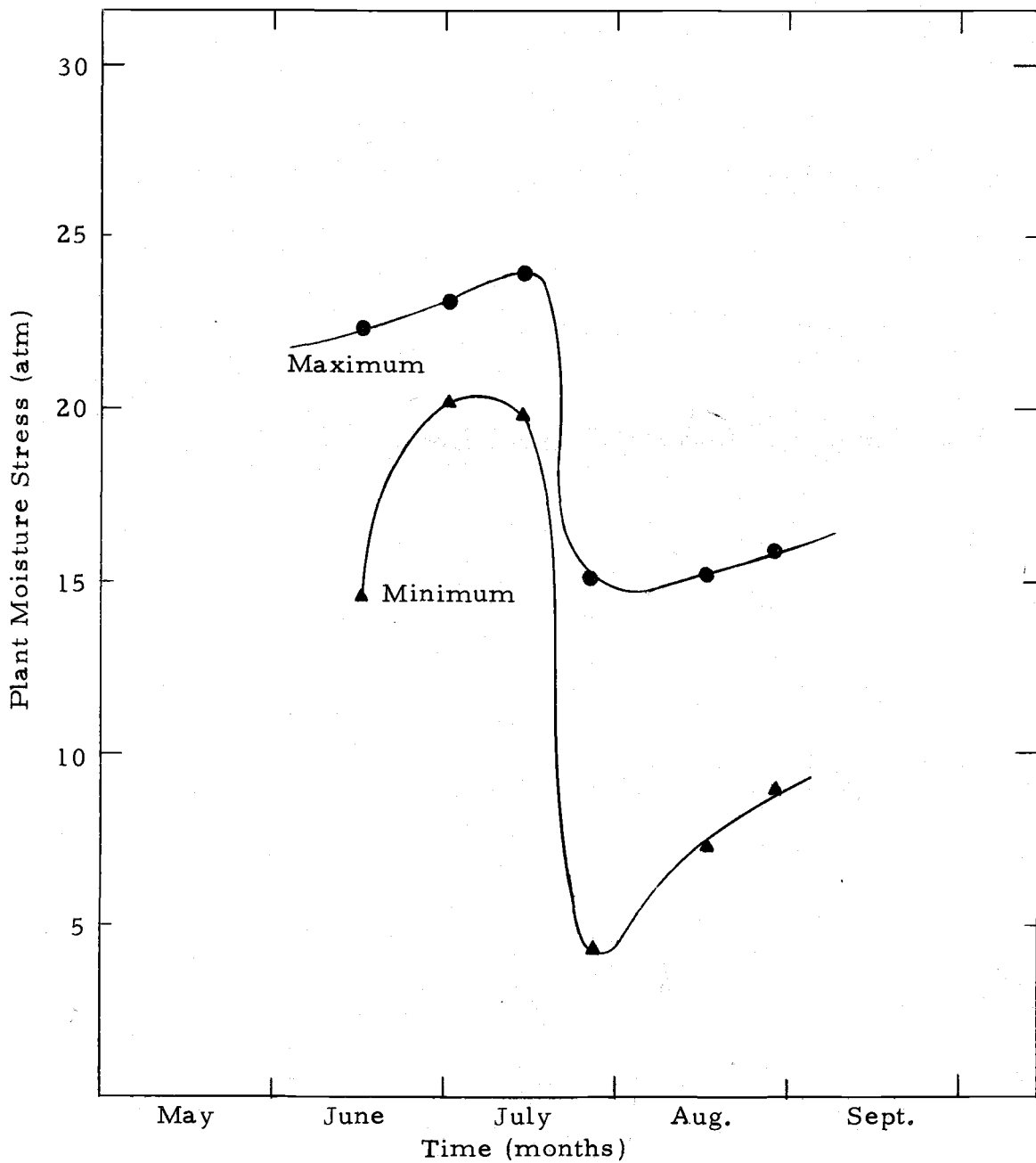


Figure 6. Seasonal changes in plant moisture stress of ponderosa pine; Corvallis, 1968. Each point is the mean of ten seedlings. Average needle length for upper whorl of needles was 5.2 cm.

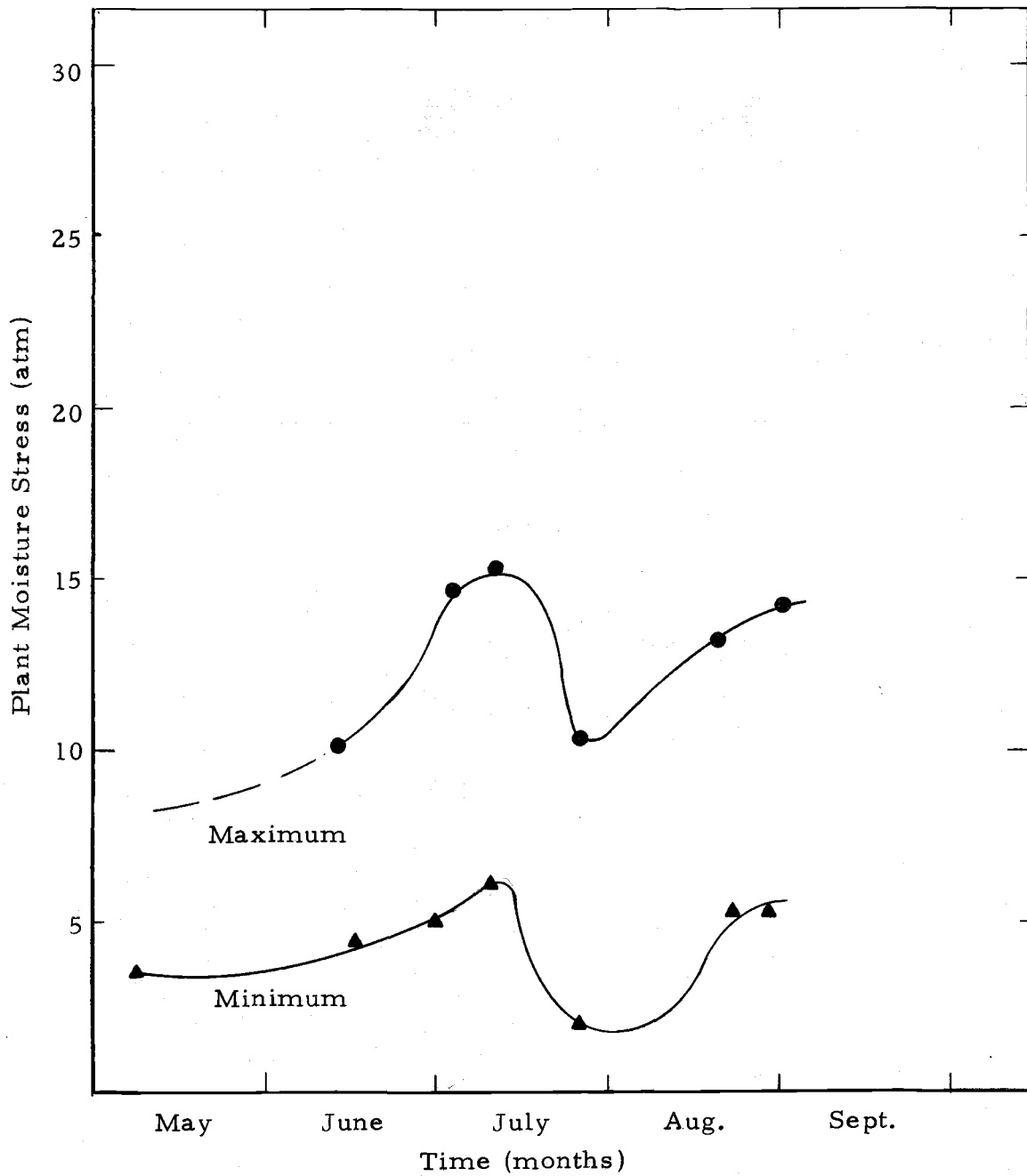


Figure 7. Seasonal changes in plant moisture stress of ponderosa pine; McDonald Forest, 1968. Each point is the mean of ten seedlings. Average needle elongation for the upper whorl of needles was 8.4 cm.

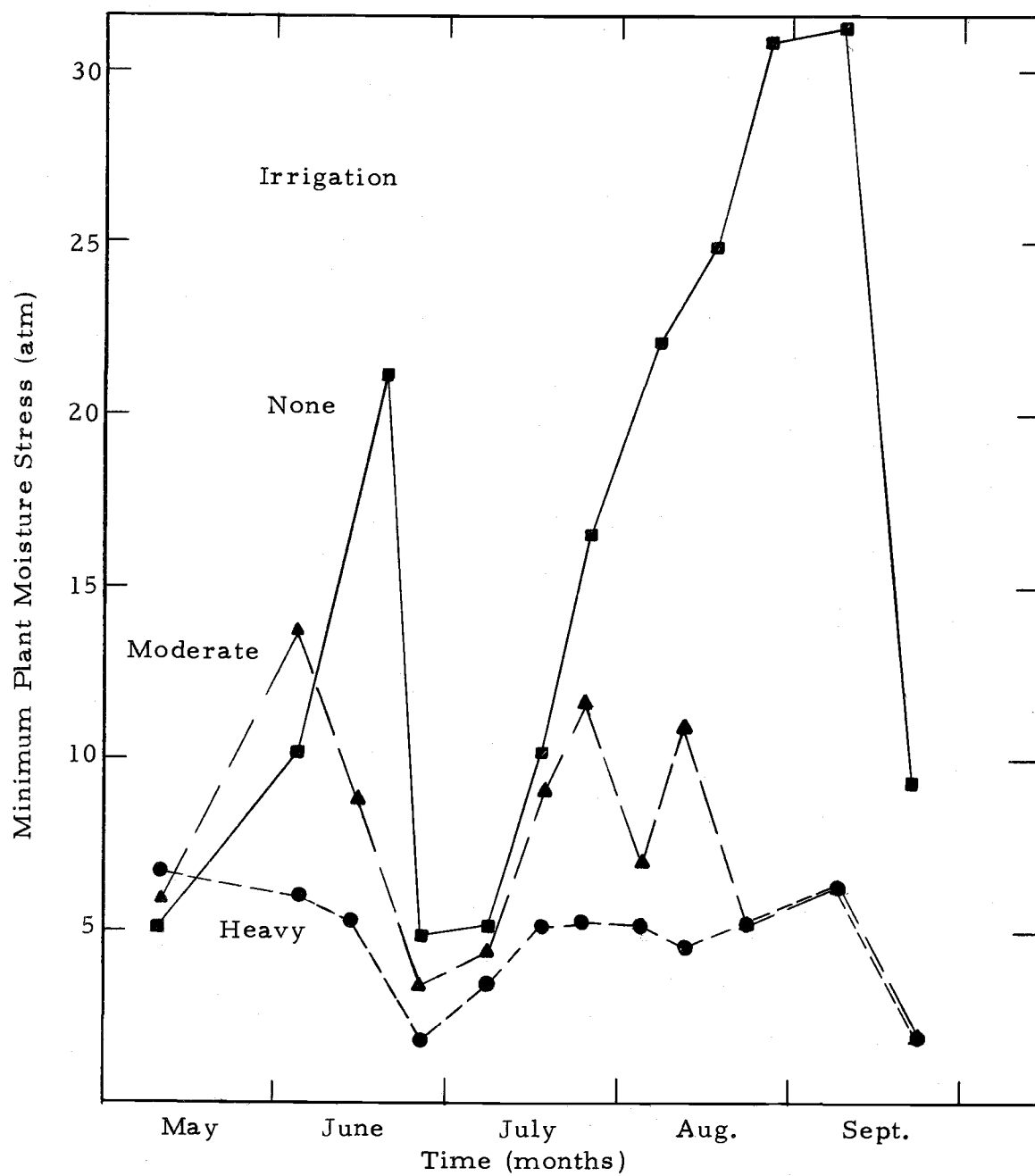


Figure 8. Seasonal changes in minimum plant moisture stress of ponderosa pine under three irrigation regimes; Corvallis, 1969. Each point is the mean of ten seedlings.

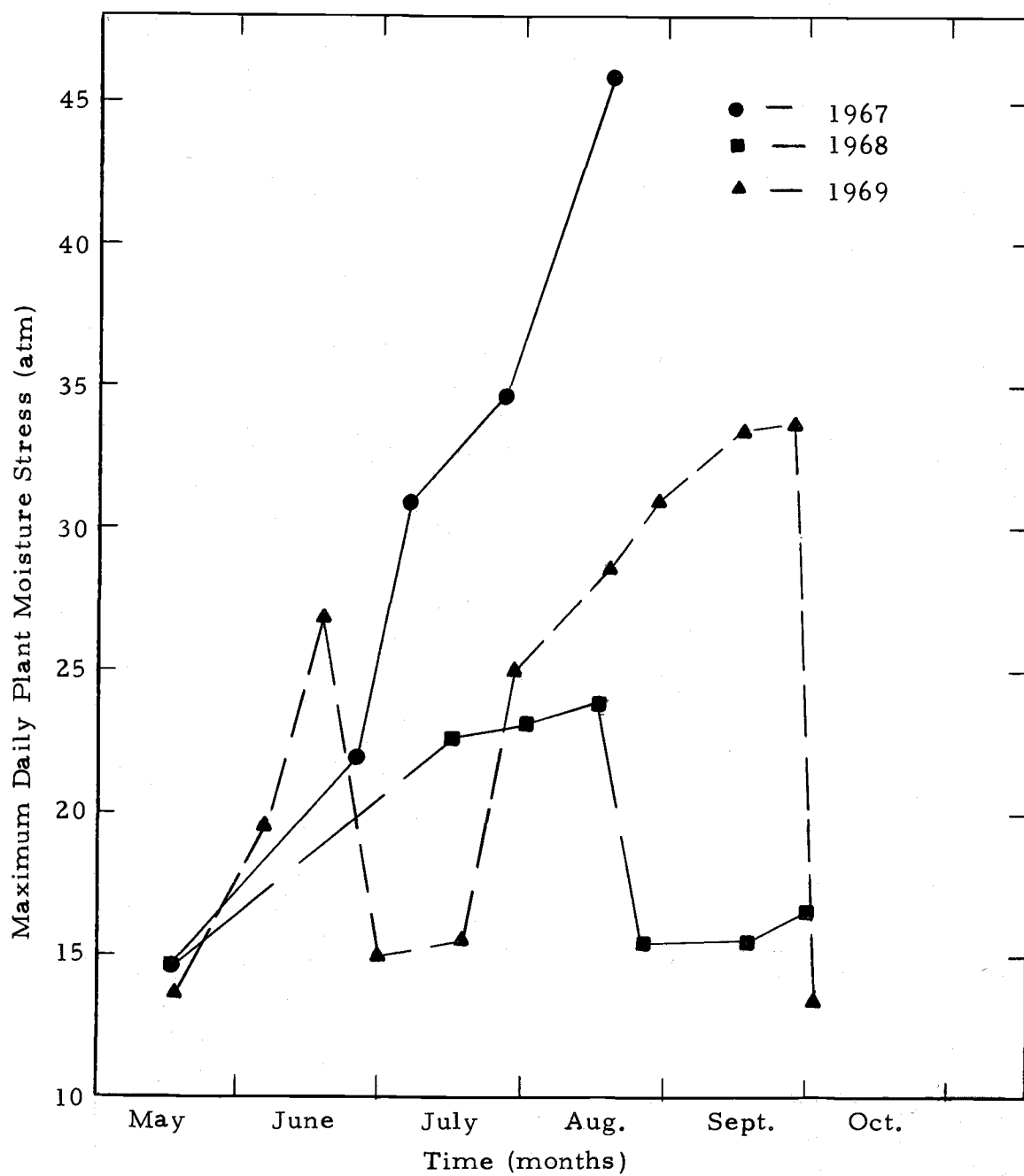


Figure 9. Seasonal changes in the maximum plant moisture stress of ponderosa pine; Corvallis, 1967, 1968, 1969. Mortality was 90% in 1967, less than 1% in 1968, and 27% in 1969. Needle elongation was 5.2 cm in 1968 and 4.4 cm in 1969.

8 for the control plot and replotted in Figure 9 indicate that the drought experienced by unirrigated seedlings was intermediate in severity compared to that of the two previous years. The highest minimum seasonal moisture stress was 31 atm and mortality was 27% on this plot. There was no mortality on the two irrigated plots. The average needle elongation for the two irrigation treatments and control plot was 9.1, 6.5, and 4.4 cm respectively, again showing the sensitivity of the seedling's needle elongation to differences in moisture stress. Another measure of the difference between plots is cross sectional increment of wood laid down during the growing season. This area was measured at 1 cm above the node in the terminal of five randomly selected seedlings from each plot. The increments for the heavily, moderately, and unirrigated seedlings were 1.07, 0.64, and 0.54 cm² respectively.

The diurnal changes within the maximum-minimum seasonal changes are probably most important for explaining the plant's photosynthetic response, while the seasonal changes are more important in relation to gross changes such as total elongation or survival of the seedling in question. In 1968, after the measurement of PMS using plant fascicles was developed, three trees having different early morning radiation loads were chosen for sampling diurnal variation. The trees were sampled at one-half or one hour intervals throughout the day. Data for these three trees are plotted

in Figure 10, where each point represents the average of three fascicles. The reproducibility of PMS readings in this figure was ± 0.2 atm. The seedling showing the fastest increase in PMS early in the morning received full sunlight first, while the one receiving sunlight last showed the slowest increase, and the other seedling increased at an intermediate rate. In each case the seedling reached a plateau at 15 atm and then began to decline about 1400 hrs. Fifteen atm is thought to represent the point of stomatal closure for these plants since temperatures continued to increase and vapor pressure decreased as the day progressed until 1500 to 1600 hrs in the afternoon. These examples show the effect of partial shade and radiation load on the increase in moisture stress during the early part of the day.

Another example of the effect of soil moisture on PMS and the diurnal variation occurring under different conditions is found in Figure 11. Here seedlings in the irrigation treatment at the nursery site were sampled throughout the day. Each data point represents the mean of three trees in one of the three blocks. The heavily irrigated plot had the largest diurnal change, the moderately irrigated, intermediate, while the control plot had the least amount of diurnal change, approximately 5 atm. To show the effect of irrigation, the same trees were sampled several days later, the day after the moderately irrigated treatment had been irrigated (Figure 12). The moderately irrigated seedlings had a lower moisture stress than the

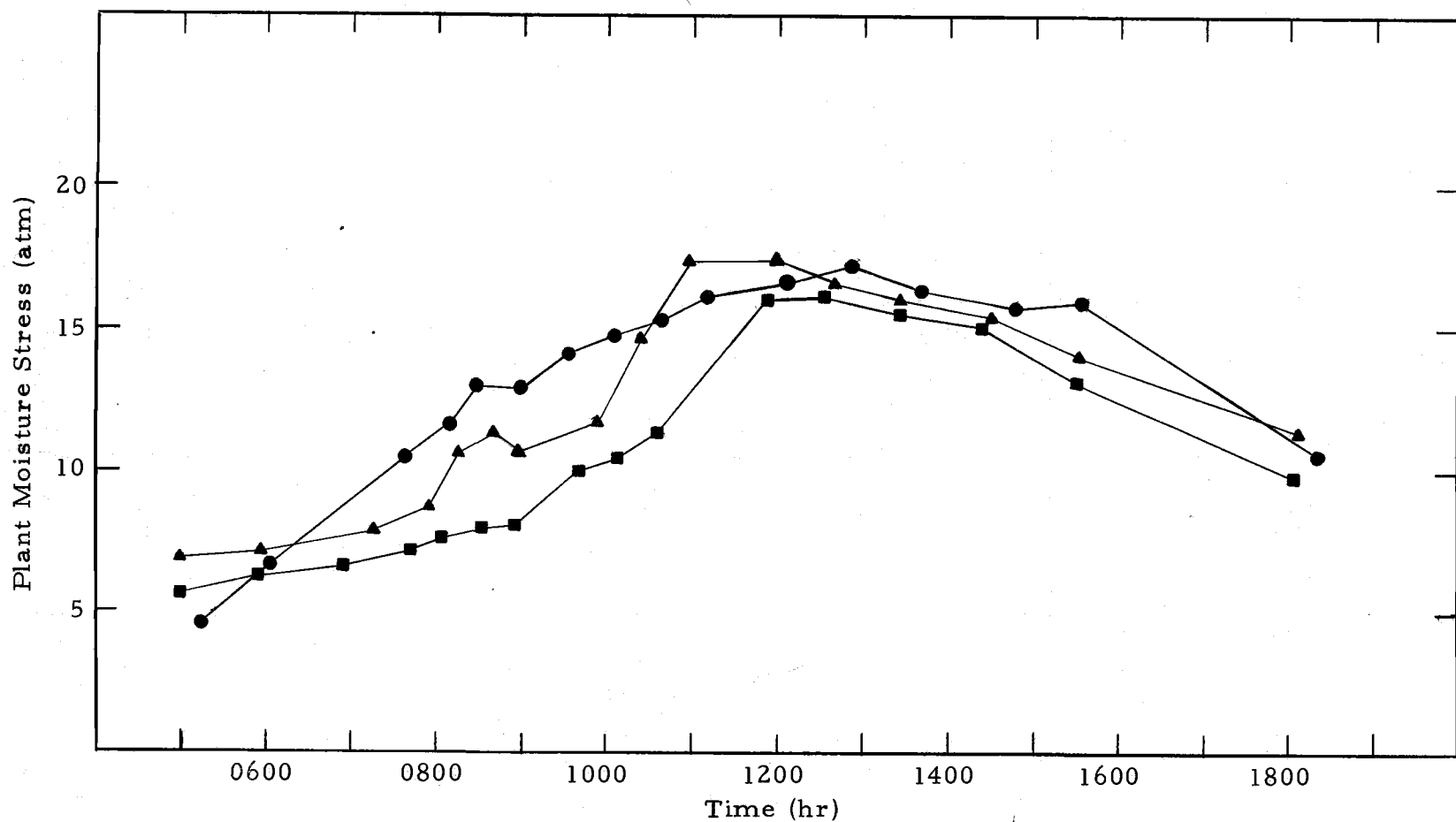


Figure 10. Diurnal changes in plant moisture stress for three ponderosa pine seedlings on July 31, 1968. Points shown are the means of three measurements where the reproducibility was ± 0.2 atm.

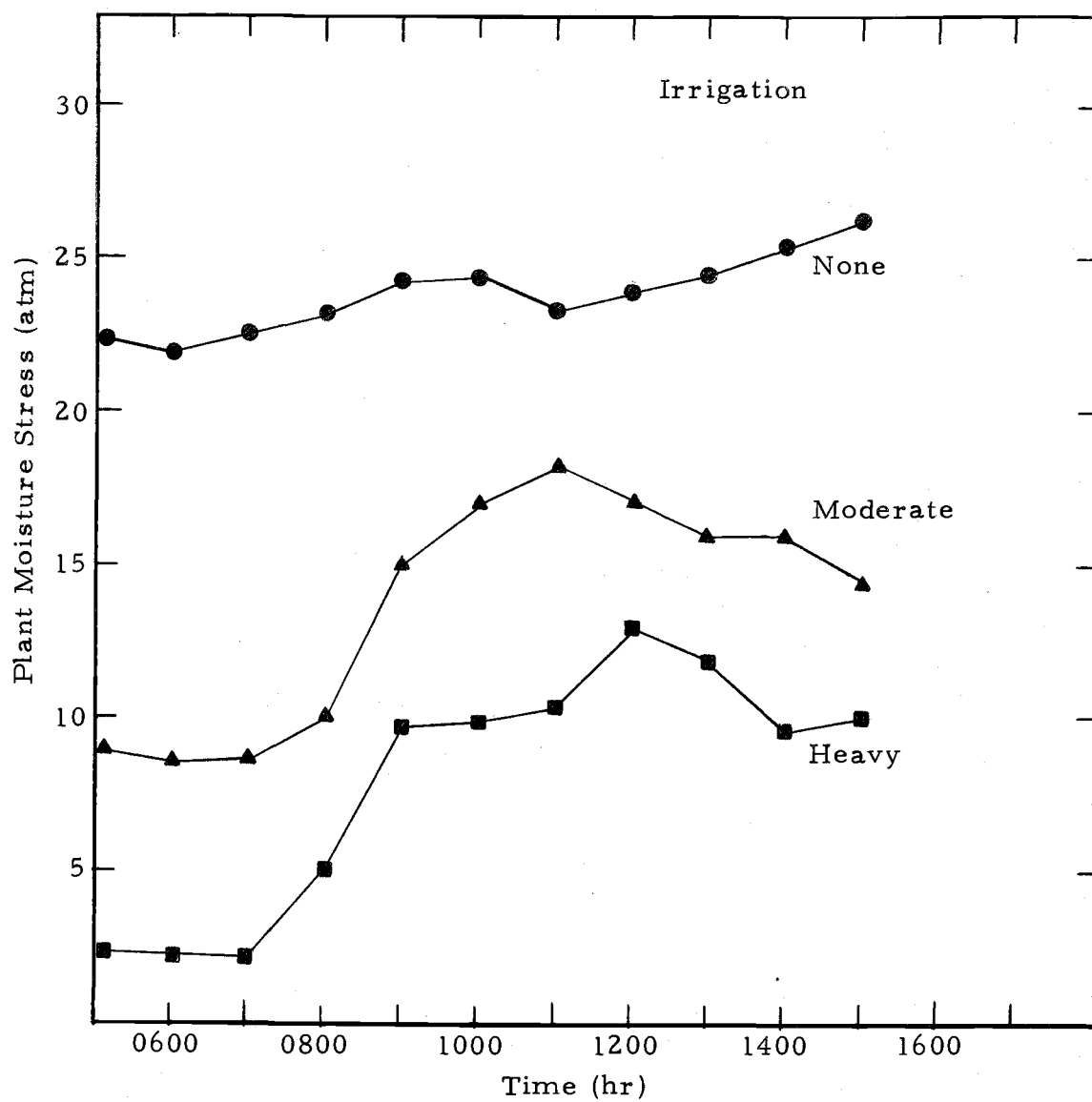


Figure 11. Average diurnal changes in plant moisture stress for three ponderosa pine seedlings under three irrigation regimes. Each treatment taken on August 26, 1969.

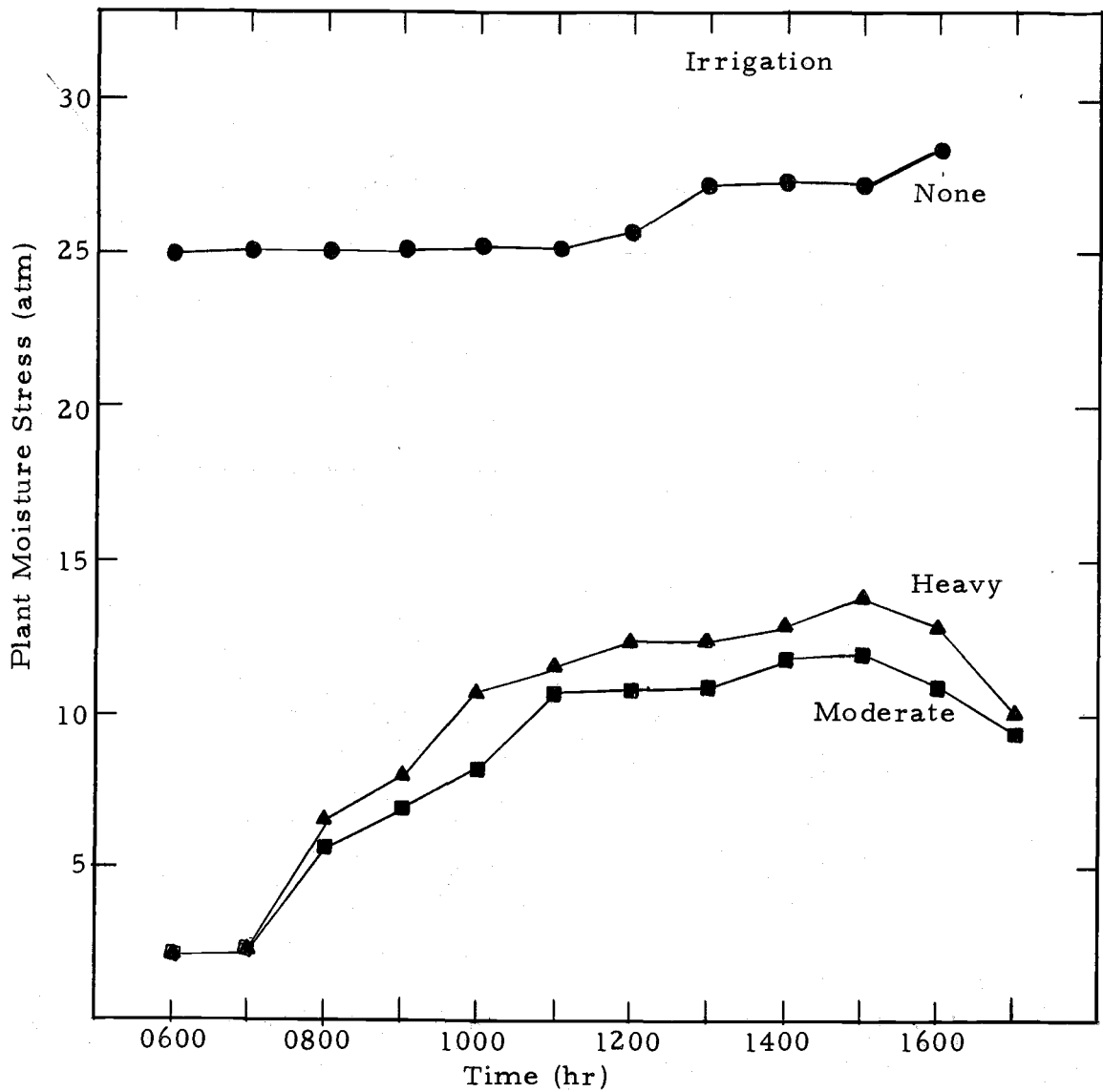


Figure 12. Diurnal changes in plant moisture stress of three ponderosa pine seedlings in each treatment taken on August 29, 1969. Moderate irrigation treatment received water on the previous day.

heavily irrigated treatment, showing an overlap in these two treatments, particularly immediately following irrigation. These diurnal measurements were made on representative warm clear days.

Laboratory Studies

Once a quantity of field data has been collected to determine the range of the physiological parameter of interest, verification and understanding of the plants' responses can be obtained much faster with experiments carried out under laboratory conditions. Under these conditions many factors can be held constant while those of particular interest are varied. The following experiments represent an attempt to understand better the quantitative difference within and between the two groups of planting stock from southwest Oregon. Ideally, the relationships found in such laboratory experiments are further tested in field conditions, but this has not been done to date.

The maximum rates of photosynthesis for eight ponderosa pine and seven Douglas-fir seedlings selected from these groups are presented in Table 1. These data, as well as all other data presented in this section, are for a 25°C air temperature and $9.4 \times 10^{-6} \text{ g/cm}^3$ water vapor concentration preconditioning and measurement environment unless otherwise specified. The range in net photosynthesis is to be expected and represents one of the differences between individual seedlings as well as between the two species.

Table 1. Maximum photosynthetic rate for ponderosa pine and Douglas-fir seedlings sampled intensively.

Ponderosa Pine		Douglas-Fir	
Seedling Number	Net Photosynthesis (mg CO ₂ /g/hr)	Seedling Number	Net Photosynthesis (mg CO ₂ /g/hr)
69	6.30	87	4.10
70	5.66	88	3.31
71	5.94	89	4.10
72	5.25	90	3.76
73	5.40	91	3.84
74	5.71	92	3.58
75	5.74	93	4.09
76	4.86	94	4.46
77	5.63	95	2.74
78	6.54	96	4.27
79	4.69	97	4.48
80	5.23	98	3.88
81	5.14	99	4.53
82	4.88	100	3.69
83	5.25	101	3.84
84	5.27	102	5.25

$\bar{x} = 5.47$

Range = 4.69 to 6.54

Standard Deviation = .51

$\bar{x} = 3.99$

Range = 2.74 to 5.25

Standard Deviation = .625

The photosynthetic response of ponderosa pine to changing plant moisture stress is shown in Figure 13. Here the net photosynthesis is presented as a percent of the maximum rate of photosynthesis as tabulated in Table 1. Individual data points have been plotted for two seedlings representing the range of response to increasing PMS. For clarity the remaining six seedlings have been plotted together in the same symbol. An additional plot of the computer fit of the pooled data is also shown.

A similar response curve for a sample of seven Douglas-fir seedlings is found in Figure 14. In this figure the data from all of the individual seedlings has been pooled and plotted together. Figures 13 and 14 show one of the differences between ponderosa pine and Douglas-fir seedlings which is best characterized by an analysis of the curve shape. Since both of these curves have a characteristic logistic shape they were analyzed using both computer and graphic solution of the important parameters.

The computed least squares non-linear curvfit of the pooled data from Figures 13 and 14 are shown in Figure 15. A visual comparison of the data and computer fitted curve showed that the fit of the Douglas-fir data was excellent, but the fit with the pine data was poor, particularly between 13 and 18 atm PMS. Data for an individual pine seedling fit better in this region, but the data still showed steeper decline than the computer fit to the logistic curve shape. This

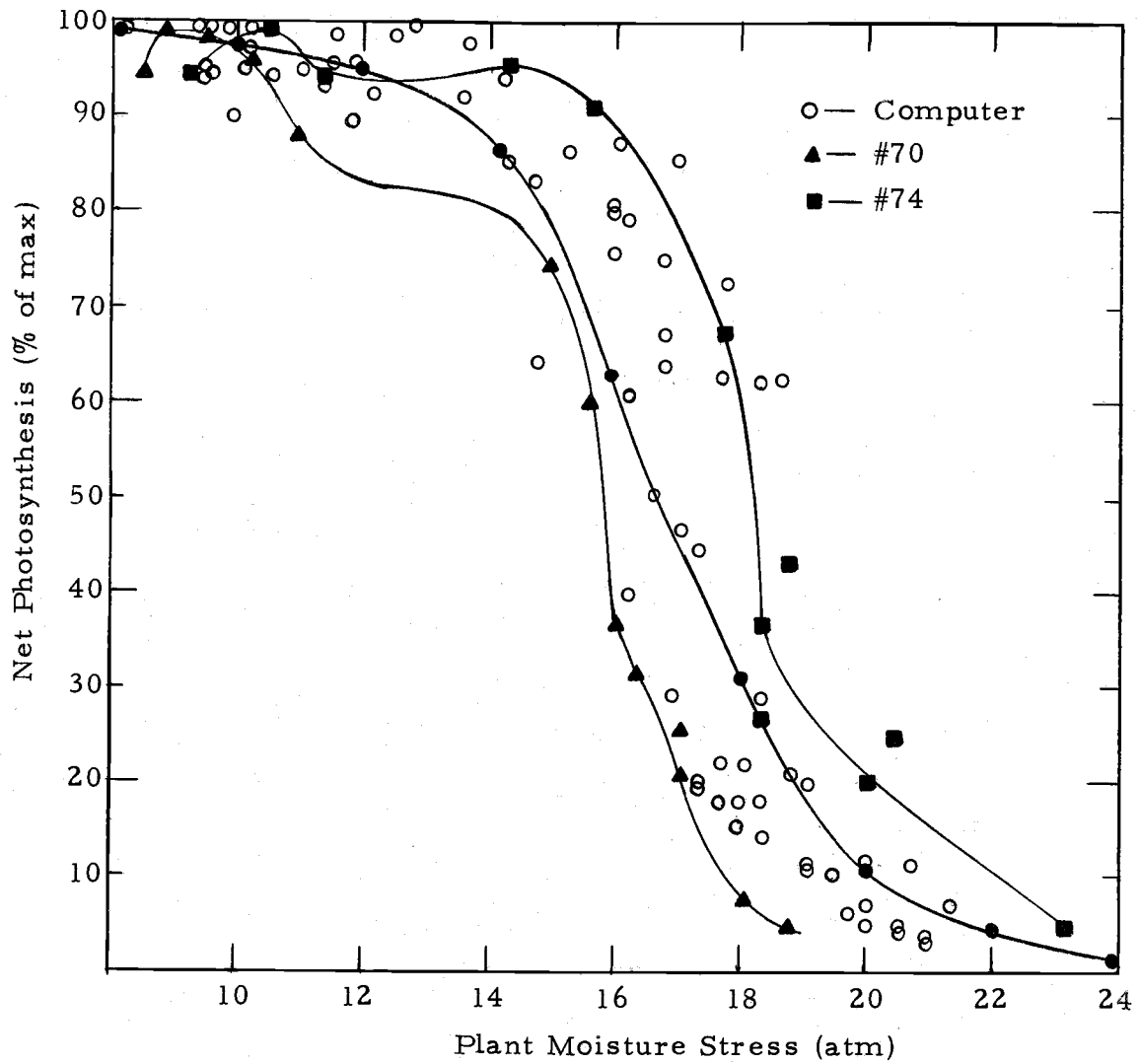


Figure 13. Net photosynthesis in ponderosa pine as affected by plant moisture stress. Data points for individual trees #70 and #74 and the computer fit curve are shown separately while the remaining points are for six other plants.

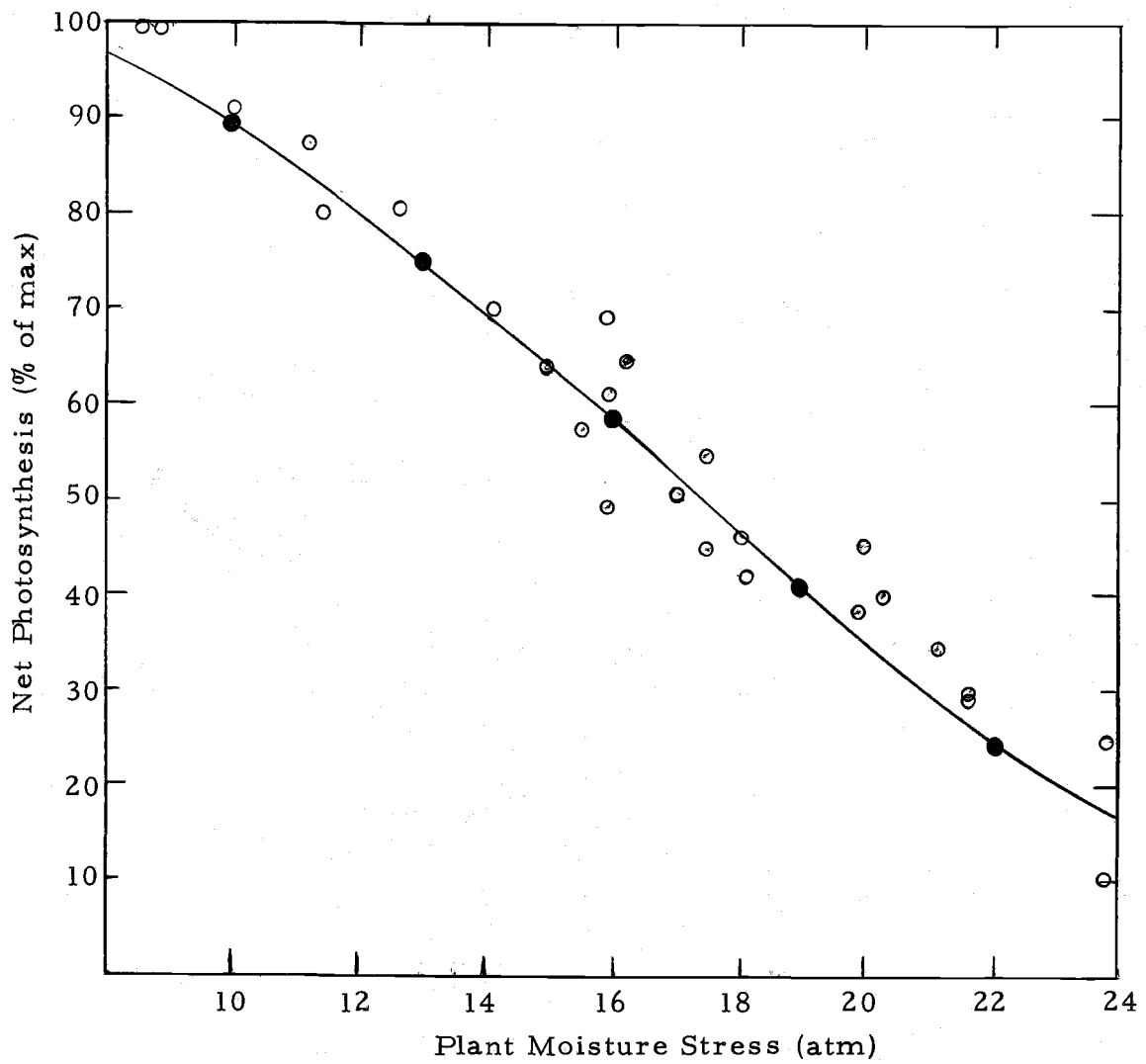


Figure 14. Net photosynthesis in Douglas-fir as affected by plant moisture stress. Data points are for seven different seedlings.

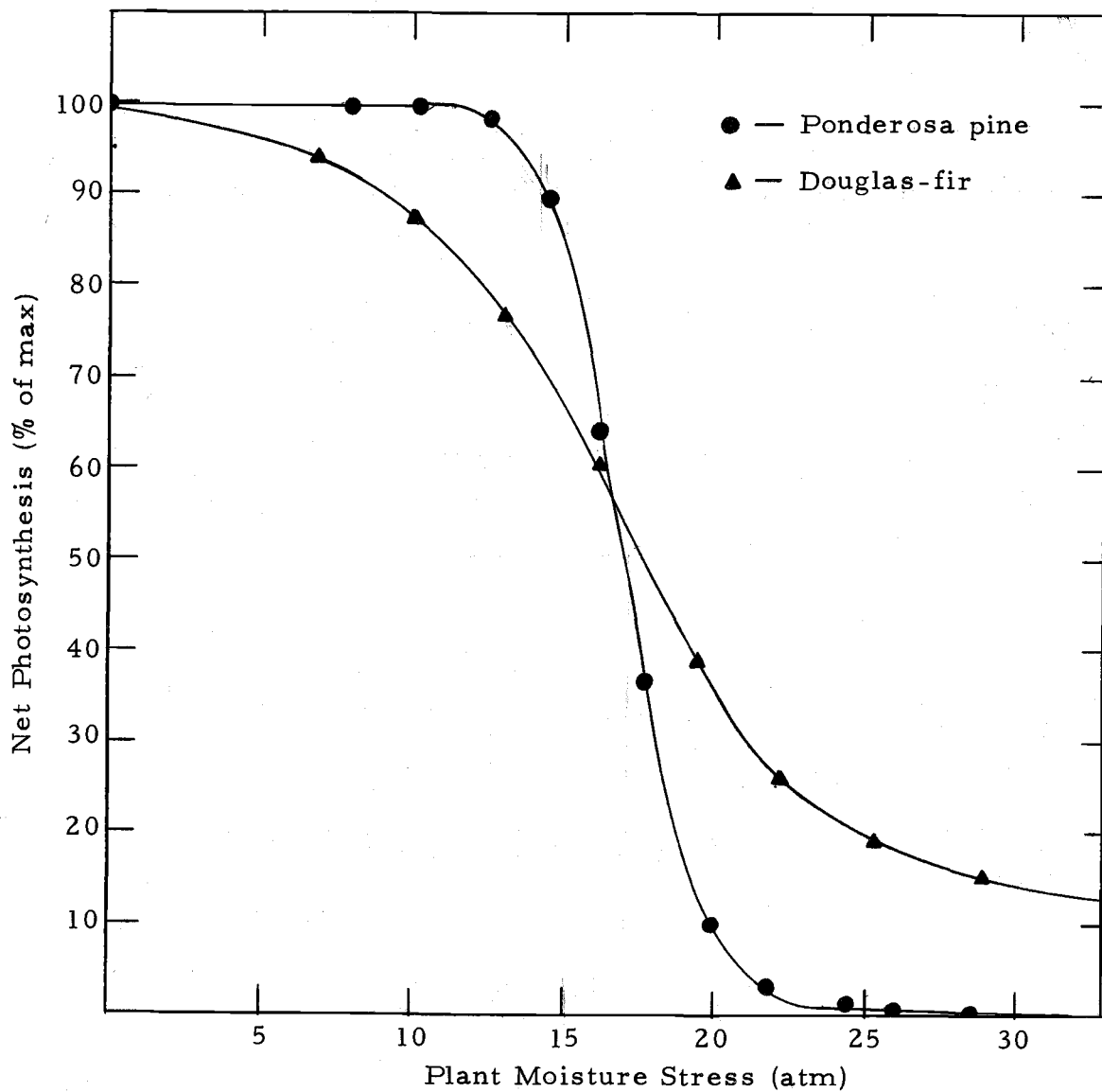


Figure 15. Computer fit of the data from Figures 13 and 14 to the logistic form using non-linear least squares curvfit program.

difference probably indicates that the response of ponderosa pine is not strictly logistic and the slope at the inflection point is better interpreted from a graphic solution based on the recorded data points. Since the computer was unable to give a good fit to the data in the 13 to 18 atm region, the graphic solution rate of change was used as the best estimate of true plant response. A comparison of rate of change of photosynthesis with respect to PMS at 50% photosynthesis, the inflection point, shows that the two species are quite different. While the mean PMS values at 50% photosynthesis are almost identical, 17.5 atm in the case of Douglas-fir and 17.3 atm for ponderosa pine, the slope at this point is 5.8%/atm for Douglas-fir and 60.8%/atm for ponderosa pine.

Figures 13 and 14 show the effect of moisture stress at constant temperature. Another experiment was conducted to evaluate the interaction between moisture stress and temperature using plants preconditioned as before ($T = 25^{\circ}\text{C}$, $\rho_w = 9.4 \times 10^{-6} \text{ g/cm}^3$). Using ponderosa pine seedlings a series of photosynthetic measurements were made where the temperature was varied while holding moisture stress relatively constant. At intervals during a drying cycle (different PMS values) photosynthesis was measured beginning at 15°C and increasing at 5°C increments to 35°C . PMS was maintained relatively constant by changing the humidity at each temperature. The results of this experiment are given in Table 2. Data from seedlings 104 and

Table 2. The interaction of temperature and PMS and their effect on the photosynthetic response of ponderosa pine seedlings.

Seedling Number	Air temp (°C)	PMS (atm)	% Max (Psn)	Seedling Number	Air temp (°C)	PMS (atm)	% Max (Psn)
103	15	6.8	83.4	106	15	6.5	85.0
		19.7	80.3			12.2	84.8
		19.7	41.8			13.2	60.0
	20	8.5	95.3		16.0	33.2	
		20.3	72.5		20.3	23.2	
					20.3	25.5	
	25	10.5	87.6		23.1	13.5	
		11.2	100.0		20	8.1	96.5
		20.3	46.2			13.9	93.9
		20.3	24.3			14.6	71.7
		22.0	2.4			17.7	27.9
	30	11.8	88.8		25	10.2	99.0
		19.7	24.8			14.6	100.0
	35	12.9	82.8		16.0	72.8	
		19.4	25.5		18.3	22.6	
		19.4	4.5		18.0	11.4	
	104	15	6.8		96.6	20.3	7.8
17.6			65.6	20.3	9.4		
20.3			40.5	23.4	3.0		
21.7			26.3	30	10.5	95.9	
22.0			23.8		17.0	91.6	
20		7.8	103.2		16.3	41.3	
		16.9	33.3		17.3	2.9	
					35	12.2	83.2
25		9.2	100.0	17.0		65.8	
		10.5	92.7	16.0		24.0	
		12.9	90.4	16.3	1.3		
		15.3	65.1	19.7	1.3		
		16.6	21.7	20.7	0.4		
19.7		11.3					
21.3		2.8					
22.4		2.9					
30		9.5	95.4				
35		10.5	87.2				
	17.0	7.0					
	19.0	0.0					

106 were used as the best estimate of the photosynthesis-temperature-moisture stress response surface as shown in Figure 16.

A factor held constant during the previously described experiments was light intensity. New tests were conducted beginning at the lowest light intensity and progressively increasing the level by removing layers of cheesecloth interference filters which were used to reduce the light intensity. The effect of light intensity on seedling photosynthesis with different PMS's was tested by measuring CO_2 uptake of a ponderosa pine seedling for three conditions: 10 and 15 atm, and two hours after water had been added to a seedling at 23.1 atm PMS. The photosynthesis at seven different light intensities for these three PMS conditions is shown in Figure 17. These response curves show that ponderosa pine is not light saturated until very high light intensities. It also is apparent from this figure that both the light and dark reactions were affected since both the initial slope and final level of CO_2 uptake were reduced by increased moisture stress. For ponderosa pine seedlings of the size and age tested, light intensities are probably often limiting in field situations.

In both ponderosa pine and Douglas-fir, little CO_2 assimilation occurs when moisture stress is greater than 25 atm. The effects of higher levels of moisture stress were assessed by two methods: (1) the reduction of moisture stress by the addition of water to the seedlings, and (2) recovery of the seedling's ability to assimilate CO_2

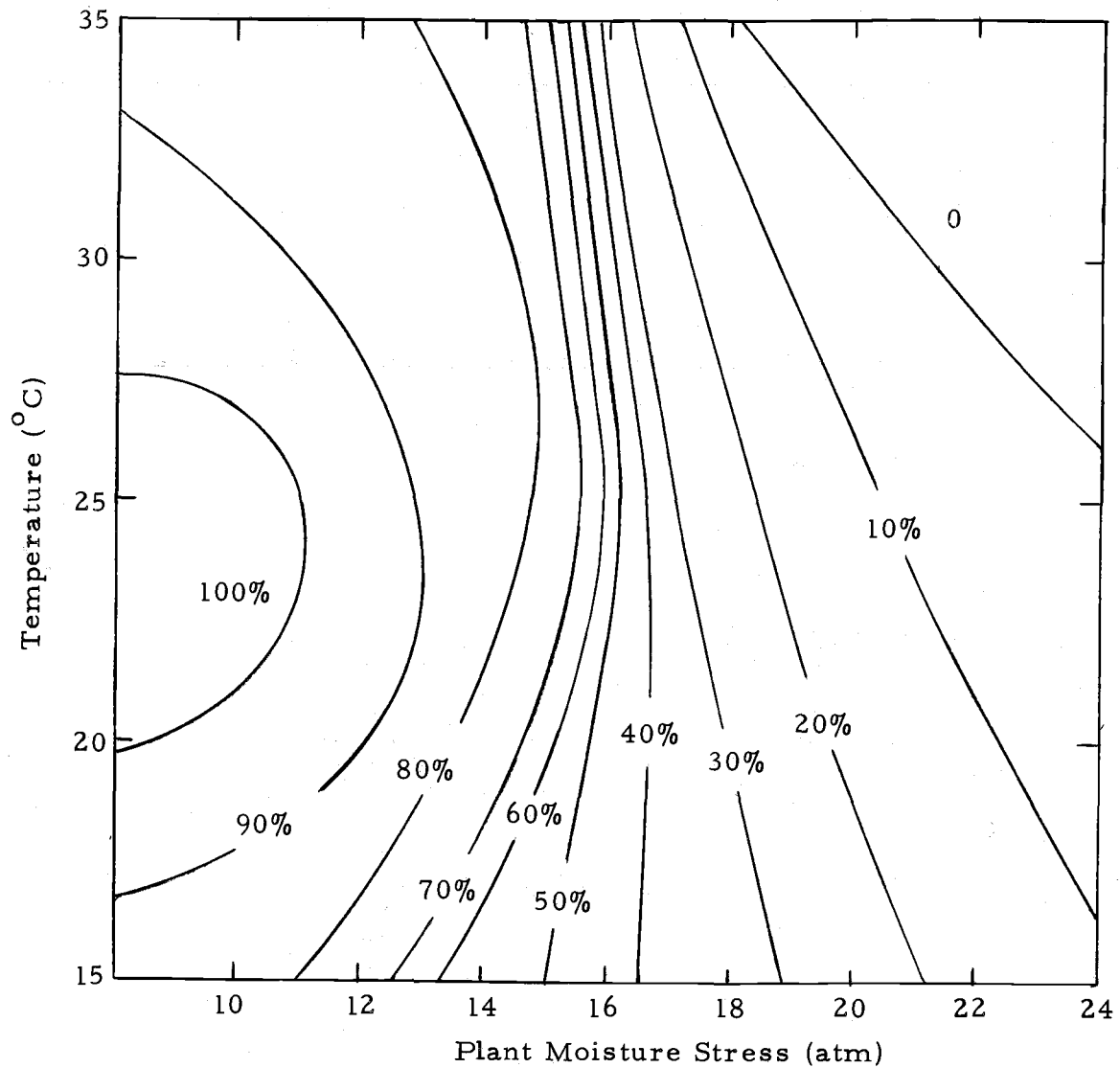


Figure 16. The response of net photosynthesis to plant moisture stress and temperature in ponderosa pine seedlings. Isolines are percentages of maximum net photosynthesis based on data from seedlings #104 and #106 in Table 2.

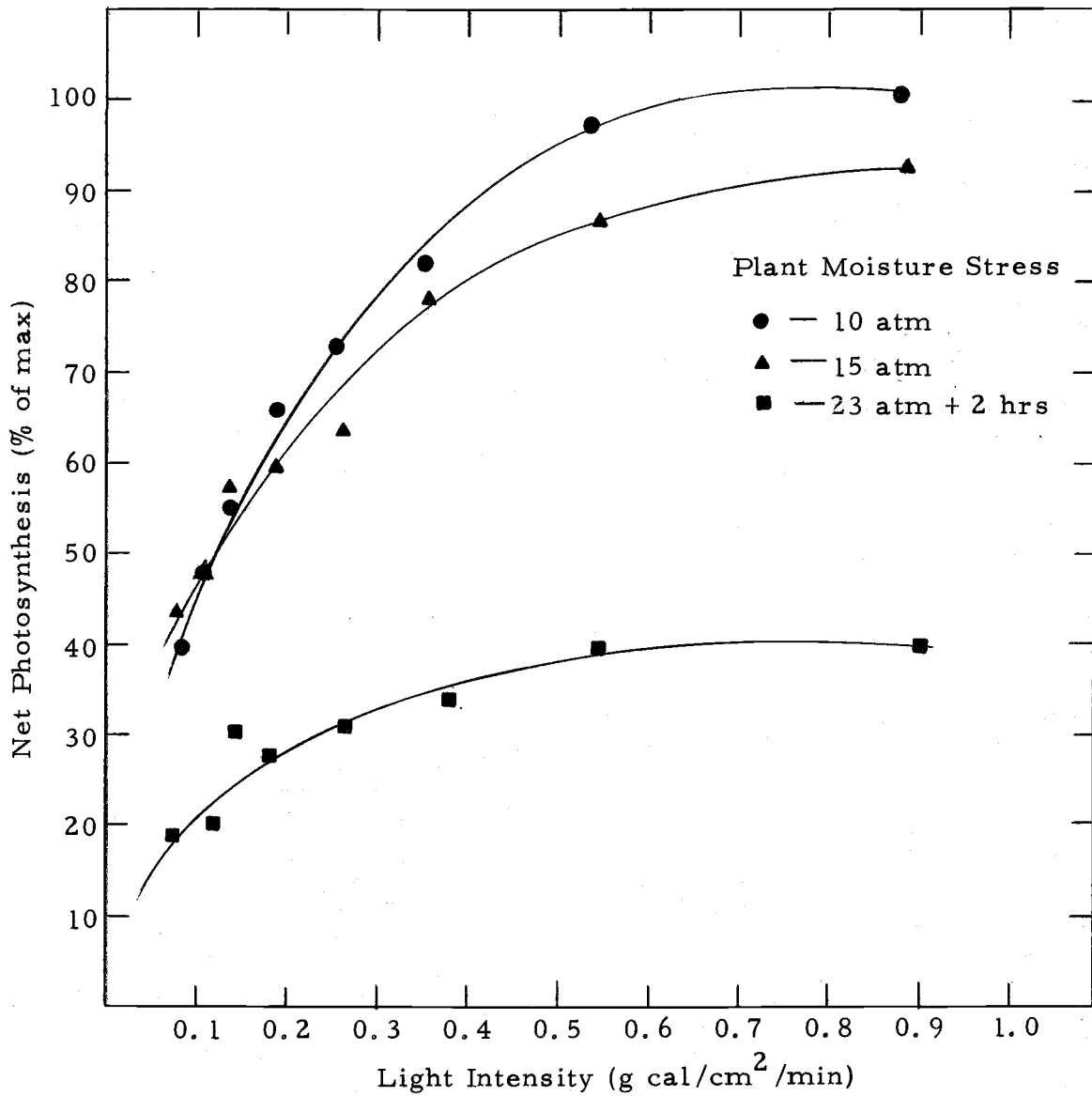


Figure 17. Response of net photosynthesis of ponderosa pine seedling to different light intensities and plant moisture stresses.

after watering. Provided the water conducting system has not been irreparably damaged, recovery from high levels of moisture stress will begin immediately after water reaches the root surfaces. If the PMS was below 50 atm in either Douglas-fir or ponderosa pine, seedlings began recovery which was usually complete by the next morning. Lack of recovery from high water stresses within one day indicates that the plant is probably dead. At PMS levels as high as 80 to 90 atm, recovery occasionally occurred within two to three days but all of the needle tissue eventually died.

The response of the plant's photosynthetic system to rewatering is depicted in Figures 18 and 19. For ponderosa pine, PMS levels of up to 35 atm did not appear to do permanent damage, with complete recovery in about one week. Higher levels of PMS apparently did more permanent damage, probably at the biochemical level. After using the infiltrometer technique to assess stomatal aperture on a number of seedlings, it was concluded that this technique as used was useful only in determining if the stomata were wide open or completely closed. Infiltration pressures in the intermediate range showed a very poor correlation with CO_2 assimilation rates of plants which had not experienced high moisture stress levels. The technique was used, however, to assess response of stomata after recovery from higher levels of PMS. Measurements on seedlings which were under a PMS of 37 and 43 atm and then watered, showed that the stomata were wide

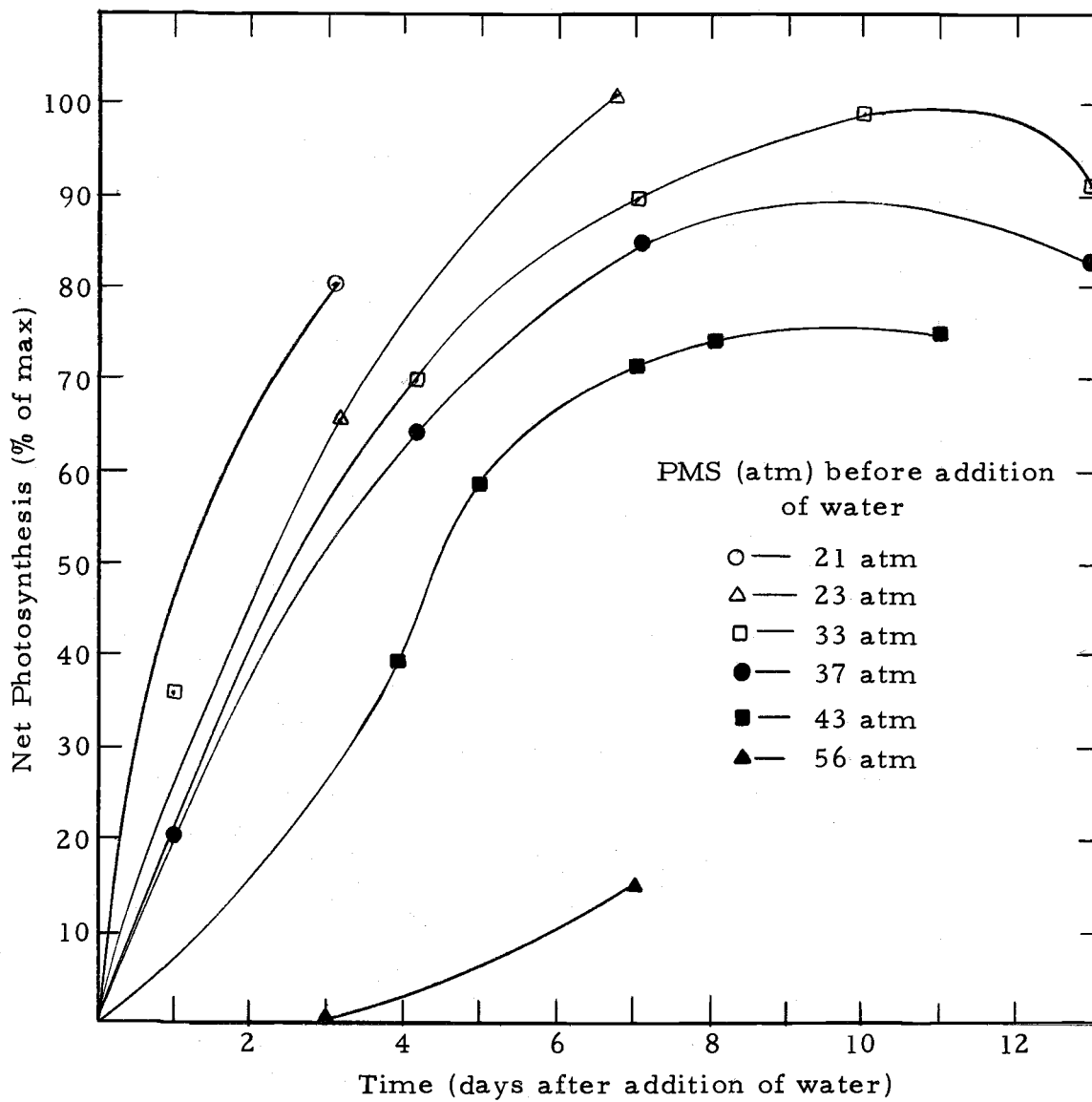


Figure 18. Photosynthesis of ponderosa pine seedlings as a function of time after watering and the level of plant moisture stress before the addition of water.

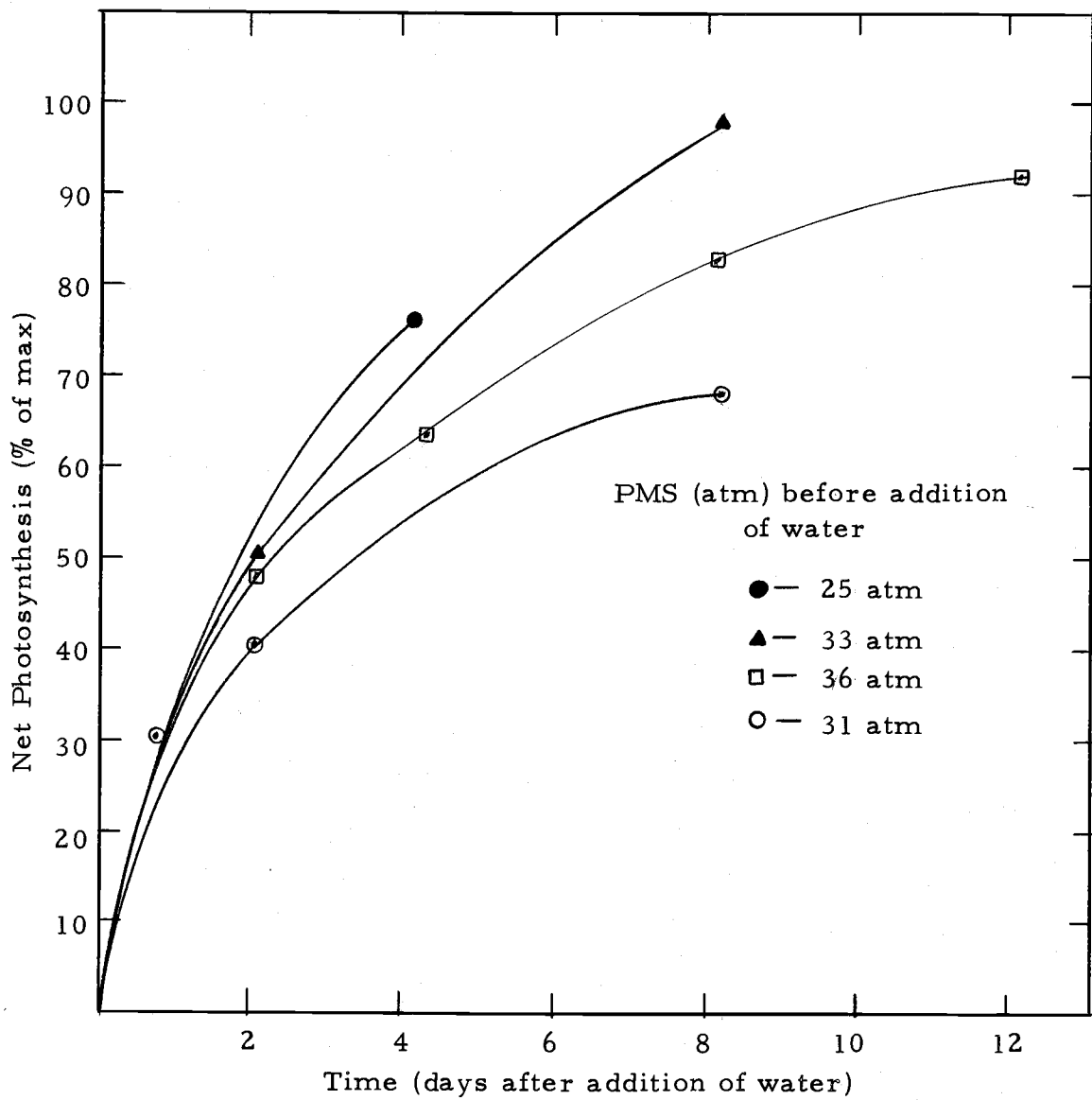


Figure 19. Photosynthesis of Douglas-fir seedlings as a function of time after watering and the level of plant moisture stress before the addition of water.

open while photosynthesis was still depressed. These data would indicate damage to some part of the system other than the stomata. However, a seedling under 56 atm PMS showed a high infiltration pressure after rewatering indicating a combined damage to both the stomatal and biochemical portions of the assimilation system at this higher level of PMS. Figure 19 shows the recovery curve of PMS for Douglas-fir seedlings. Based on these data there was no large difference in the tolerance of high levels of PMS in the two species. It should be remembered that only one seed source for each species was tested.

At very high levels of stress, the damage to needles occurs in a predictable pattern. With increasing PMS, the top, most recently formed needles die first; next the lower, oldest needles on the plant dry and turn brown; and finally, the first formed of the current year's needles shrivel and die. The bud is the last portion of the plant to desiccate and not respond to rewatering. Several plants experiencing up to 80 to 90 atm PMS as measured with the pressure chamber did have all of their needles killed, but after watering the bud broke and subsequent growth took place. However, damage of this sort is very severe for a seedling growing in a field environment and establishment of a seedling after such a setback is unlikely.

The effect of air water vapor concentration or soil moisture stress (SMS) on PMS was not studied in detail since both of these factors

are only indirectly operative on the seedling through PMS. They do, however, combine with other factors such as wind speed or soil temperature to operate on either the atmospheric demand on the plant or the moisture supply from the soil, thus ultimately influencing the PMS as well as photosynthesis. For this reason the SMS in the container of each seedling was determined gravimetrically by assessing the moisture content and then comparing this value with a moisture content:tension curve. The relationship between PMS measurements ($T = 25^{\circ}\text{C}$, $\rho_w = 9.4 \times 10^{-6} \text{ g/cm}^3$) and SMS is shown in Figure 20. The role of ρ_w and SMS in determining a given level of PMS will be discussed later.

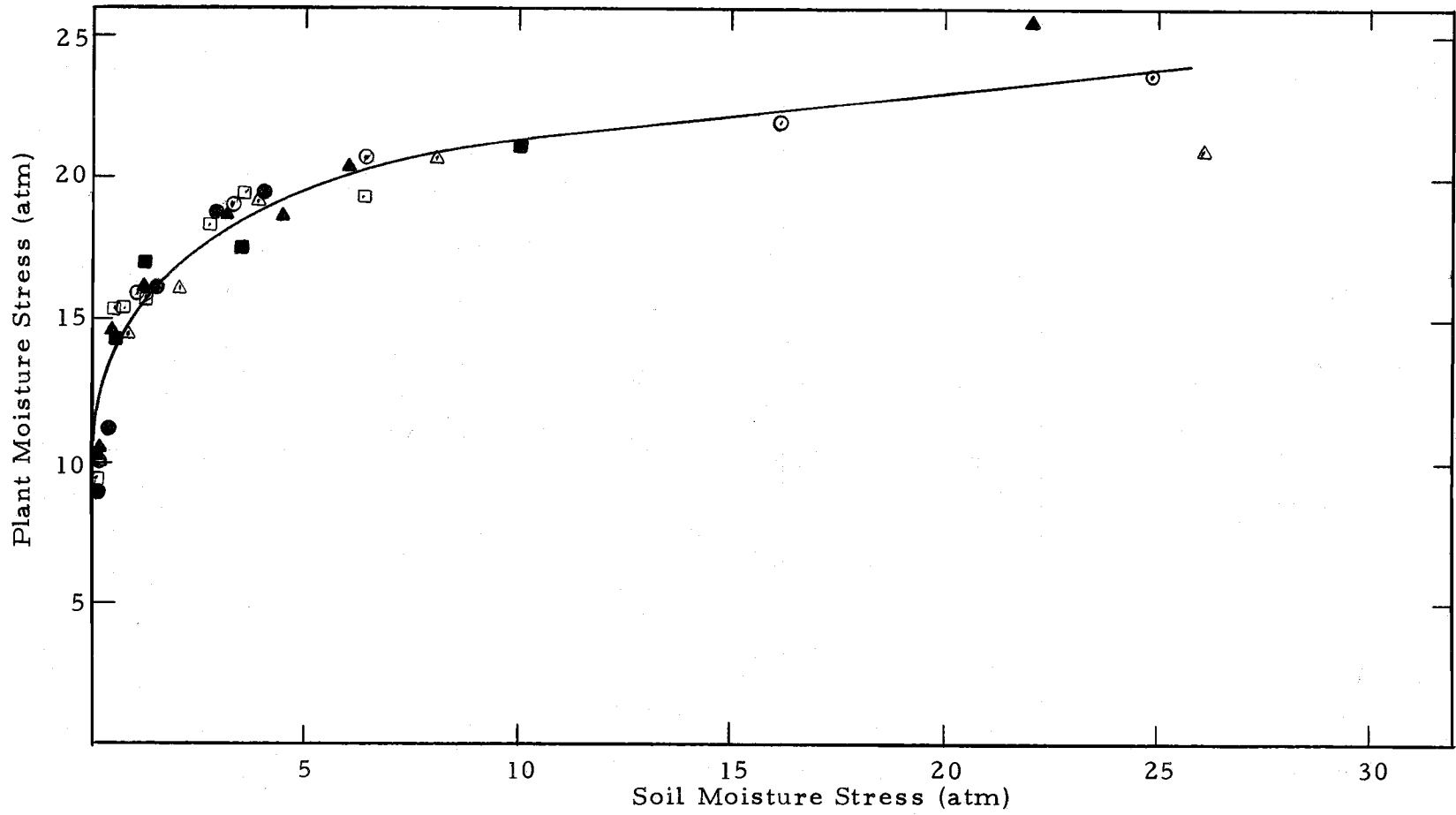


Figure 20. Plant moisture stress for a ponderosa pine seedling at 25°C and $\rho_w = 9.4 \times 10^{-6} \text{ g/cm}^3$ compared with soil moisture stress.

DISCUSSION

The moisture stress experienced by plants has been estimated in the past by examining seasonal changes in soil moisture (Newton, 1964; Waring, 1964), topography (Whittaker, 1960), and evaporative potential (Penman, 1948). These single factor indirect approaches to estimation of plant reaction to its environment are not precise and likely to give erroneous results. Due to the complex interaction of the plant into what Philip (1966) calls the soil-plant-atmosphere continuum (SPAC), all of the above approaches to explaining plant responses are inadequate except where differences in the environment are very large. More intensive management of forest lands demands a more refined approach to environmental classification, one based on a physiological parameter such as PMS, rather than inference from one or more of the factors influencing PMS.

A more direct quantitative approach to evaluation of plant moisture relationships was taken by Waring and Cleary (1967) where they measured the minimum plant moisture stress at the peak of the drought in 1 to 2 m established trees. This new approach was a real improvement over the earlier indirect methods, but it also had several shortcomings. First, in working with established trees little knowledge was gained concerning the water stress levels during the critical establishment stage in the tree's life cycle. In contrast, the moisture stress levels recorded in the seedlings in the present study

(Figures 5 and 9) are almost double those reported by Waring and Cleary. Second, a more detailed examination of seasonal rates of change in PMS is necessary to distinguish between areas where changes in vegetation and environment are subtle. Only by examining the dynamics of changes in PMS can we fully understand seedling water relations.

A hypothetical case where seedlings in two different areas reach moisture stress levels of greater than 20 atm by the end of the season is depicted in Figure 21. In both areas photosynthesis and growth would be stopped because of high PMS. Provided neither area reached a permanently damaging PMS level, it is much more important to know how the moisture stress changed earlier in the season than what the maximum level was at the peak of the drought. As shown in Figure 21, the effect of PMS on growth would be the same in both areas even though the PMS at the end of the growing season is considerably different. As shown in this figure, the moisture stress during the period of growth is identical for both areas. Differences in PMS occurring later are not important because the plant has stopped growth due to high PMS. Another example with the opposite result would occur in areas where the seedlings have the same PMS at the end of the growing season but reach that maximum PMS at different rates.

Seasonal changes in PMS are important in understanding gross

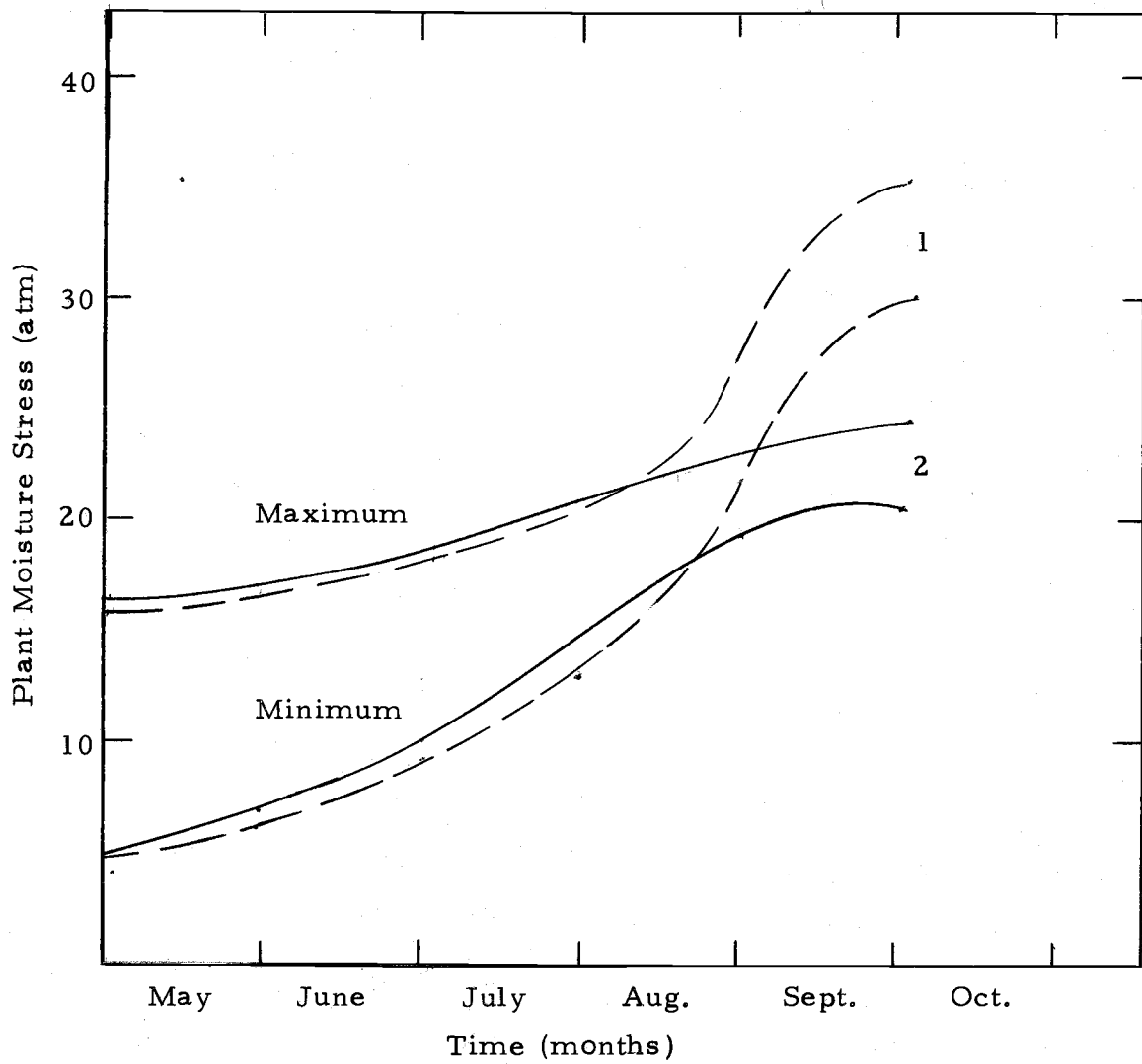


Figure 21. Seasonal changes in plant moisture stress in two different areas (hypothetical case).

phenomena such as yearly increment or seedling survival, but much can also be learned from examination of the diurnal changes that occur within this seasonal time scale. Response of seedlings to changes in temperature, radiation, and irrigation can be evaluated (Figures 10, 11, and 12). In Figure 10, the differences in the rate of change of PMS are due to differences in temperature caused by differential radiation loads. The gradual decline in PMS between 1100 and 1500 hours is probably due to recovery of the plant after stomatal closure, since the air temperature increased until reaching a maximum at 1600 hours. Figures 11 and 12 show how seedlings with different soil moisture stresses respond to the same atmospheric conditions. Based on response data (Figures 13 and 14) collected in the laboratory, each group of seedlings in Figure 11 would be expected to have different photosynthetic output for the day. In Figure 12, however, neither of the irrigated groups would be expected to be limited by PMS.

How a plant interacts with its environment and comes into equilibrium with it at some PMS is best understood and evaluated using the SPAC concept (Philip, 1966). The factors directly acting on the plant in the three areas of the SPAC are shown diagrammatically in Figure 22. According to van den Honert (1948) this can be described by the equation:

$$Q = \frac{\psi_a - \psi_s}{R} \quad (1)$$

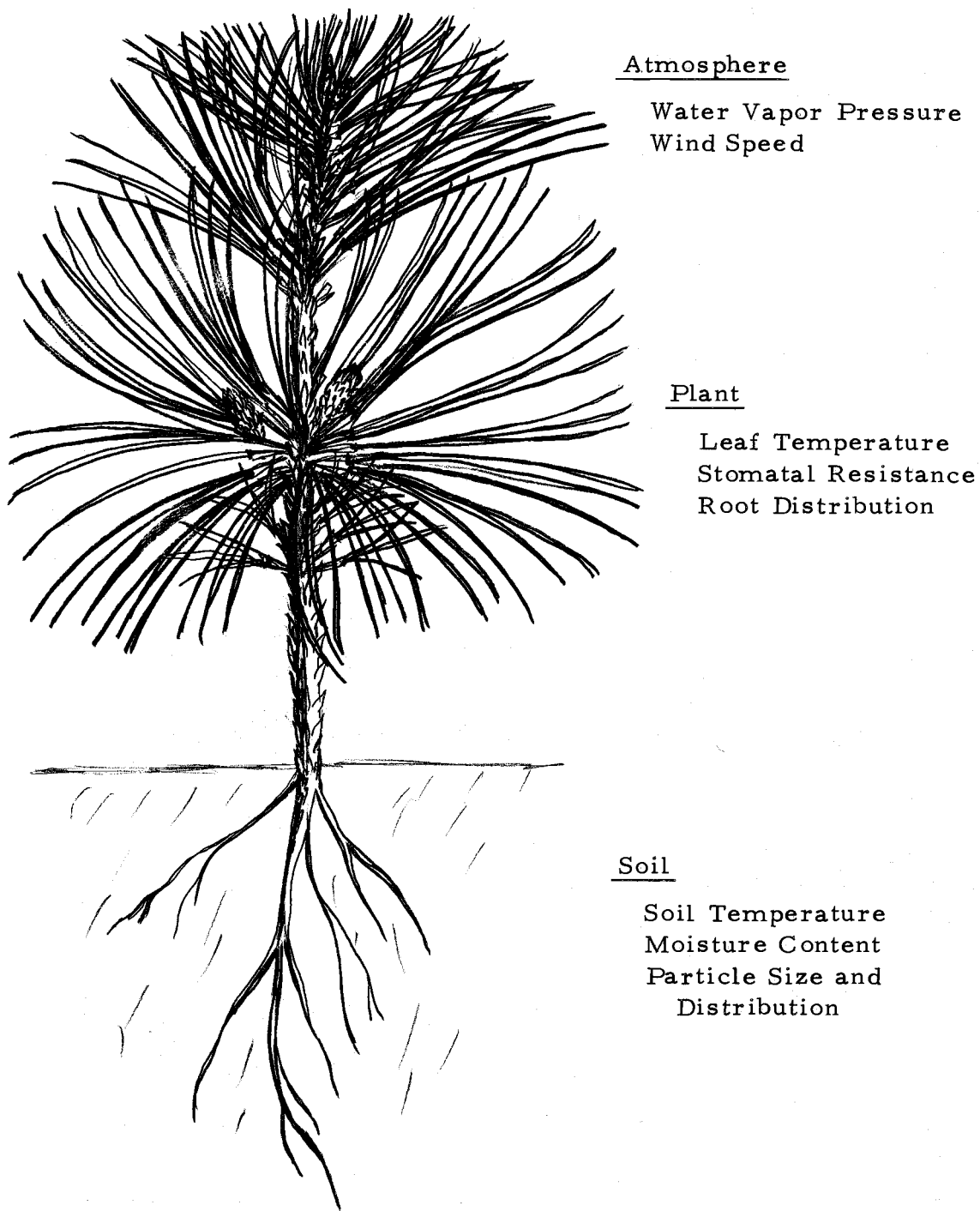


Figure 22. Factors affecting plant moisture stress.

where:

Q = flow rate of water

ψ_s = water potential of the soil (units of positive bars)

ψ_a = water potential of the air

R = total resistance to flow

As Philip points out, this approach is grossly oversimplified. It can, however, be useful in understanding the process of water movement and water stress in plants and will therefore be developed further here. Equation (1) can be divided into separate phases: supply in the liquid phase from the soil to the leaf (2), and water transpired in the vapor phase from the leaf to the air (3):

$$Q = \frac{\psi_1 - \psi_s}{R_1} \quad (2)$$

$$Q = \frac{\psi_a - \psi_1}{R_2} \quad (3)$$

where:

ψ_1 = leaf water potential (estimated by PMS in this paper)

R_1 = absorptional resistance
 $r_{\text{soil}} + r_{\text{root}} + r_{\text{xylem}}$

R_2 = transpiration resistance
 $r_{\text{stomata}} + r_{\text{boundary layer}} + r_{\text{mesophyll}}^*$

Q = flow rate

* Note that the parallel cuticular pathway has been deleted here for simplicity since it is commonly assumed to be very resistant to water flow in conifers.

Combining equations (2) and (3) solving for ψ_e gives:

$$\text{PMS} \approx \psi_1 = \frac{\psi_a + \psi_s}{2} - \frac{Q}{2} (R_2 - R_1) \quad (4)$$

Despite the shortcomings of not being quantitatively correct for reasons discussed later, several interesting points are emphasized by equation (4). This equation points out that under normal conditions a plant has a PMS equal to the average of the soil and atmosphere potentials as modified by the flow rate times the difference in resistances (transpirational-absorptional). All conditions which modify and change the plant moisture stress really work indirectly to modify one or more of the terms in equation (4). Table 3 tabulates the changes in various environmental factors as they affect changes in the resistances to flow and therefore PMS. The two left-hand columns show the environmental factors affected by changes in radiation load or precipitation which ultimately affect the resistances and therefore PMS. Note that from a theoretical point of view any of the factors can cause a change in stomatal resistance and therefore change PMS. Thus stomatal control is potentially the most important factor in limiting the PMS level of the plant. It would appear from Figures 13 and 14 that Douglas-fir and ponderosa pine are different in this respect since in Douglas-fir there is a gradual decrease in photosynthesis over approximately 20 atm PMS, while in pine this decrease occurs over about 5 atm PMS. Thus, looking at this rather complex

Table 3. Effect of environmental variables on resistance components in the soil-plant-atmosphere continuum.

Indirect Factors		Direct environmental factor affecting PMS	Resistance				
Precipitation	Radiation Load		Soil	Root	Xylem	Stomatal	Boundary Layer
c		Water vapor concentration	a			a	
c	d	Soil temperature	b			a	
d		Soil moisture stress	b	b		b	
		Photoperiod				b	
		Wind speed				a	b
c	d	Leaf temperature				b	

^a Secondary change in resistance significant at extremes in flow rate or in the environmental factor.

^b Primary change in resistance directly attributable to the environment factor.

^c Secondary effect of change in radiation load or precipitation on the factors affecting resistances.

^d Primary effect of change in radiation load or precipitation on the factors affecting resistances.

relationship using equation (4) helps one to understand and focus on the intermediate position the plant occupies in the soil-plant-atmosphere system.

The lack of low PMS values in Figures 13 and 14 can be explained by examining SPAC. The maximum photosynthesis occurs at 10 atm plant moisture stress, considerably higher than one would anticipate with the soil moisture near saturation. In ponderosa pine the atmospheric demand is responsible for 7 atm of PMS when the seedling is under a saturated soil moisture condition, and the stomata are open. The 7 atm stress is a computed value obtained by taking the PMS of 10 atm and subtracting the minimum PMS of 3 atm under a closed stomata high humidity condition.

The experimental measurements were made at 25°C and $9.4 \times 10^{-6} \text{ g/cm}^3$ water vapor concentration which results in a 5 to 10 atm PMS regardless of the soil moisture conditions. By increasing the temperature and windspeed while decreasing the water vapor pressure a PMS of 16 atm can be obtained with soil at near field capacity. By increasing the atmospheric demand on the plant in this manner it is possible to close the stomata and even cause wilting in herbaceous plants.

The result of examining the soil-plant-atmosphere system for a given species shows that the two factors most important in determining the moisture stress level in the plant are the resistance to flow in the

soil phase and the resistances to movement in the vapor phase, particularly the stomatal resistance. For a given environmental condition the plant reaches an equilibrium where the resistance to flow in the soil phase and the losses through the stomatal area are in equilibrium and any changes in condition are reflected primarily through changes in these resistances. In examining Figures 13 and 14 where the photosynthetic response of pine and Douglas-fir to moisture stress are presented, one notices a distinct species difference in response to increases in plant moisture stress.

It is important to keep in mind that the atmospheric demand or stress was held constant in this laboratory experiment. The relationship between soil moisture stress and PMS is presented in Figure 20. The correlation between these two parameters looks very impressive. However, since the atmospheric demand portion of SPAC was held constant, this is to be expected. If the same correlation were attempted with varying wind speeds and water vapor pressures, the relationship would disappear.

As a tool for rigorous quantitative evaluation however, the model just derived is unacceptable. Van den Honert's original derivation assumed isothermal conditions and reversible thermodynamics for the transfer process (van den Honert, 1948). Philip (1966) criticized quantitative use of the SPAC concept, as did Ray (1960) and Rawlins (1963), because the vapor phase and liquid phase must be treated

separately if resistances such as those in equation (4) are used. Therefore, the concept of resistance to water flow using the resistances calculated from the continuum equation presented earlier is only valid as an aid in understanding the general level of water stress. Any quantitative estimation requires the use of coefficients of conductivity in the liquid phase and diffusivity in the vapor phase. In the liquid phase the driving force is the difference in water potential whereas in the vapor phase the difference in water vapor concentration between the leaf and air is the driving force.

Transformation of equation (4) is necessary to make it quantitatively and dimensionally correct in both the liquid and vapor phase. One way in which this might be accomplished is using limiting values and assigning a modified driving potential unit to the vapor phase. Let the units in the liquid phase equation (2) remain the same except that limits of from zero to 100 bars are assumed, and potentials greater than 100 bars will not be evaluated. Next, assign the same range of values, 100 bars, to the driving force in the vapor phase. Let ψ'_a equal this driving force in the vapor phase and be defined by the equation:

$$\psi'_a = \psi_l + \psi_{pw} \quad (5)$$

where:

$$\psi_l = \text{leaf water potential (estimated by PMS in this paper)}$$

$$\psi_{\rho w} = \frac{\rho_w(lm) - \rho_w(a)}{\rho_{ws}(lm)} \times 100 \quad (6)$$

and:

$\rho_w(lm)$ = water vapor concentration in the leaf mesophyll

$\rho_w(a)$ = water vapor concentration in the atmosphere

$\rho_{ws}(lm)$ = $40 \times 10^{-6} \text{ g/cm}^3$
the absolute humidity for a saturated mesophyll
at 35°C

These equations set limits for the atmospheric driving force at 100 bars in excess of the leaf potential. The driving force is the difference between water vapor concentration in the leaf which is assumed not to exceed that of saturated air at 35°C and the concentration in the atmosphere which could be zero. The redefinition of ψ_a to ψ'_a also allows for simplification of equation (4). Substitution of equation (5) into (4) gives:

$$\psi_1 = \psi_s + \psi_{\rho w} - Q(R_2 - R_1) \quad (7)$$

The choice of limits for this type of reparameterization are arbitrary but have been chosen to represent the possible range of conditions of most plants. Other limits could be chosen should these prove inadequate once the model is tested.

One way in which laboratory data such as those presented in Figures 13, 14, and 16 can be used to explain field behavior will be developed here. The single factor approach to the study of seedling physiology or ecology has limited application to the dynamic multi-

variant field environment unless this environment is evaluated from an approach such as Mason and Langenheim's "operational environment" which will be expanded upon here (Mason and Langenheim, 1957). They state that a plant's operational environment consists of only those factors which influence a plant during its life cycle.

Waring and Major (1964) related the vegetation of the California redwood region to gradients of moisture, temperature, light and nutrients. These two approaches can be combined to give a mathematical description of how a plant will respond to a given change in its environment.

The following generalized equation describes a given plant response, R:

$$R = f(M, T, L, N, P, \dots) \quad (8)$$

where:

R = plant response

M = moisture effect

T = temperature effect

L = light effect

N = nutrition effect

P = pre-conditioning effect

Taking the partial derivative with respect to R

$$dR = \left(\frac{\partial R}{\partial M}\right)_{TLNP} dM + \left(\frac{\partial R}{\partial T}\right)_{MNL P} dT + \left(\frac{\partial R}{\partial L}\right)_{MTNP} dL + \left(\frac{\partial R}{\partial N}\right)_{MTLP} dN +$$

$$\left(\frac{\partial R}{\partial P}\right)_{MTLN} dP + \epsilon_1 \Delta M + \epsilon_2 \Delta T + \epsilon_3 \Delta L + \epsilon_4 \Delta N + \epsilon_5 \Delta P \quad (9)$$

where:

$$\frac{\partial R}{\partial M} = f_1 (M, T, L, N, P) \quad (10)$$

$$\frac{\partial R}{\partial T} = f_2 (M, T, L, N, P) \quad (11)$$

$$\frac{\partial R}{\partial L} = f_3 (M, T, L, N, P) \quad (12)$$

$$\frac{\partial R}{\partial N} = f_4 (M, T, L, N, P) \quad (13)$$

$$\frac{\partial R}{\partial P} = f_5 (M, T, L, N, P) \quad (14)$$

and $f_1, f_2, f_3, f_4,$ and f_5 are continuous functions in the region studied,

and $\epsilon_1, \epsilon_2, \epsilon_3, \epsilon_4, \epsilon_5$ are error terms which approach zero as $\Delta M, \Delta T, \Delta L, \Delta N,$ and ΔP approach zero (Thomas, 1953).

Equation (9) says that a given change in response can be evaluated by examining separately or independently the changes in moisture, temperature, light, nutrition, and preconditioning while holding all other factors constant and then summing those changes to get the total response. Note that in equation (9) if there is no change in a given factor it is reduced to zero and omitted from the equation

(i. e., if $dm = 0$, then

$$\left(\frac{\partial R}{\partial M}\right) dm = 0).$$

If one has this generalized equation in mind he can eliminate many of its terms by verification that they are constant in the study. The terms used in equation (8) will depend upon the objectives of the study and the amount of sophistication necessary to obtain the precision required by those objectives. The five variables suggested here, moisture, temperature, light, nutrition, and preconditioning, should serve as the minimum required in any physiological or ecological study of plant response. It should also be kept in mind that equation (9) is for the general case, and that each non-linear variable such as moisture stress used in that equation will have to be stored in matrix form or transformed to a linear function before mathematical solution is possible. An alternative is a graphic or numerical solution which has been used in this study. In the use of such solutions it is important to recall that equation (9) is precise only where ΔM , ΔT , ΔL , ΔN , and ΔP approach zero. This is not the case in the following examples particularly for the data in Figure 16, where $\Delta T = 5^{\circ}\text{C}$ and ΔM (PMS) > 1 atm. Elimination of these errors was impossible and therefore the solution should be considered an approximation which is useful in demonstrating a plant response but not for very accurate interpretation. Once the response surface is more precisely defined an exact solution will be possible.

At this point, let us return to an examination of how laboratory photosynthesis data such as is shown in Figures 13, 14, and 16 can be used to explain field behavior. For these data, N, L, and P were all held as constant as possible. Temperature (T) was maintained at a constant except for the collection of data for Figure 16, where PMS (M) was held as constant as possible while changing the values of T. Figures 13 and 14 show the relative net photosynthesis for ponderosa pine and Douglas-fir seedlings at different levels of PMS. These data are tabulated in Table 4 where each percentage of photosynthesis now represents the percentage of activity attributable to PMS. These percentages can be used to analyze the diurnal variation curve shown in Figure 11. Taking the percentage photosynthesis at each hour from Table 4, and using them to integrate the curve for the entire day, the heavily irrigated plants were never limited by water stress. The moderately irrigated seedlings would fix only 75% as much CO_2 as the heavy irrigation treatment, while the control seedlings would have no CO_2 fixation. From these calculations one can easily see that moisture was the factor limiting photosynthesis in the control plot and reducing photosynthetic rate in the moderately irrigated trees. If the data in Figure 11 had been for Douglas-fir rather than ponderosa pine, the differences between the two treatments and the control would have been substantial. The control trees would have fixed approximately 20% as much CO_2 as the heavily irrigated trees.

Table 4. Average relative photosynthetic output of ponderosa pine and Douglas-fir (in percent).

Plant Moisture Stress	Ponderosa Pine	Douglas-Fir
8	99	99
10	98	92
12	96	81
14	93	70
16	78	58
18	30	47
20	10	36
22	5	26
24	1	21
26	--	17
28	--	14

The response of seedlings to the combined effect of moisture stress and temperature can be interpreted from the first two terms of equation (9). The graphical interpretation of data for photosynthetic response is given in Figure 16. Using this response surface one can predict the seedling response to changes in the environment. For example, consider two different changes in the environment. First, a change from $T = 15^{\circ}\text{C}$ and $\text{PMS} = 11 \text{ atm}$ to $T = 30^{\circ}\text{C}$ and $\text{PMS} = 17 \text{ atm}$ will cause the seedling to change from 80% of maximum net photosynthesis (Psn) to 25% Psn or a 55% change in Psn . The response can be divided into two parts: one for moisture stress and one for temperature, where the approximate solution is given by:

$$\Delta\text{Psn}_{\text{PMS}} = \frac{\text{PMS}_2}{\text{PMS}_1} \left(\frac{\partial \text{Psn}}{\partial \text{PMS}} \right) d \text{PMS}$$

and

$$\Delta\text{Psn}_{\text{T}} = \frac{\text{T}_2}{\text{T}_1} \left(\frac{\partial \text{Psn}}{\partial \text{T}} \right) d \text{T}$$

In this example, $\Delta\text{Psn}_{\text{PMS}} = 52\%$ and $\Delta\text{Psn}_{\text{T}} = 13\%$ and the linear partial coefficients over this range are $\left(\frac{\partial \text{Psn}}{\partial \text{PMS}} \right)_{\text{T}} = 6.8\%/\text{atm}$ and

$\left(\frac{\partial \text{Psn}}{\partial \text{T}} \right)_{\text{PMS}} = 0.8\%/^{\circ}\text{C}$. Second, consider a change from 10 to 16 atm

PMS and 25°C to 35°C temperature for a response of maximum Psn to 28% Psn or a 72% change in Psn . For this example the moisture stress contribution to change in Psn is 40% and the temperature effect contribution 32%. The linear partial coefficients in this example are

$\left(\frac{\partial P_{sn}}{\partial PMS}\right) = 6.7\%/atm$ and $\left(\frac{\partial P_{sn}}{\partial T}\right) = 3.2\%/^{\circ}C$. These two examples show that the relative importance of temperature and PMS in photosynthetic response of the seedling depends upon where these conditions occur on the response surface in Figure 16. In the first example most of the response was the result of changing moisture stress while in the second example the plant response was just about equally divided between temperature and PMS.

The response of the seedling to watering after high levels of PMS is depicted in Figures 18 and 19. From these data it is obvious that plants subjected to stresses in the vicinity of 30 atm recovered completely within three to four days, which is in agreement with similar data presented by Brix (1962) and Kaufmann (1968a). Higher levels of stress were increasingly damaging to the plant. This is in agreement with data presented by Slatyer (1957) and Macklon and Weatherly (1962). No attempt was made here to assess the effect of a given plant moisture stress at an equilibrium since moisture stress was continually increasing until the addition of water. Tests of plant response to varying durations of specified PMS levels would be very informative.

In terms of survival of planting stock, there appears to be a large variation from one year to the next at the Corvallis nursery. Figure 9 shows that the moisture stress of seedlings planted at the Corvallis nursery was quite different in the three years under

consideration. The major environmental differences which affected PMS during these three years was the spring-summer precipitation pattern and amount. From the measurements made in this study one can conclude that the summer precipitation may be very important in the survival of seedlings planted in severe grass competition. Growth was also affected by these water stress patterns as is shown in Figures 6, 7, and 8. It should be reemphasized at this point that the effects of preconditioning were eliminated from the laboratory experiments and extrapolation to field conditions under these circumstances is hazardous. For this reason more studies on preconditioning effects in terms of temperature and other environmental factors along with actual field testing of the relationships found in laboratory studies would be desirable.

SUMMARY AND CONCLUSIONS

The level of moisture stress in ponderosa pine and Douglas-fir seedlings planted in a natural environment has been measured with the pressure chamber technique during the first growing season after planting. These seedlings experienced moisture stresses up to two times greater than trees which were already established in the area. Seedling growth and survival were both affected by levels of moisture stress. Spring and summer rains appeared to greatly enhance survival in two of the years when data were collected. Irrigation of seedlings increased both the growth and survival.

The photosynthetic response of the seedlings to moisture stress was evaluated in laboratory experiments. These experiments indicated that in the range where plant moisture stress (PMS) affected net photosynthetic rate (P_{sn}), ponderosa pine and Douglas-fir reacted differently. Douglas-fir had an almost linear decline from maximum P_{sn} at 8 atm PMS to 20% P_{sn} at 23 atm PMS. Ponderosa pine in contrast showed little decline in P_{sn} until 15 atm and declined rapidly to zero photosynthesis at 22 atm PMS. The action of temperature and moisture stress on photosynthesis was assessed. PMS was found to be the more important factor in determining the P_{sn} for most of the range of conditions tested.

A mathematical approach to evaluation of PMS as it fits into the soil-plant-atmosphere continuum is proposed. This approach

emphasizes a predominant regulatory position the plant occupies within the continuum and should be useful in the design of future experiments in plant water relations.

It is suggested that the quantitative evaluation of plant interaction with its environment can be accomplished by application of a standard partial differential equation to the environmental variables operating on a plant. The separation of plant response into the portion contributed by each of these variables is done using this equation.

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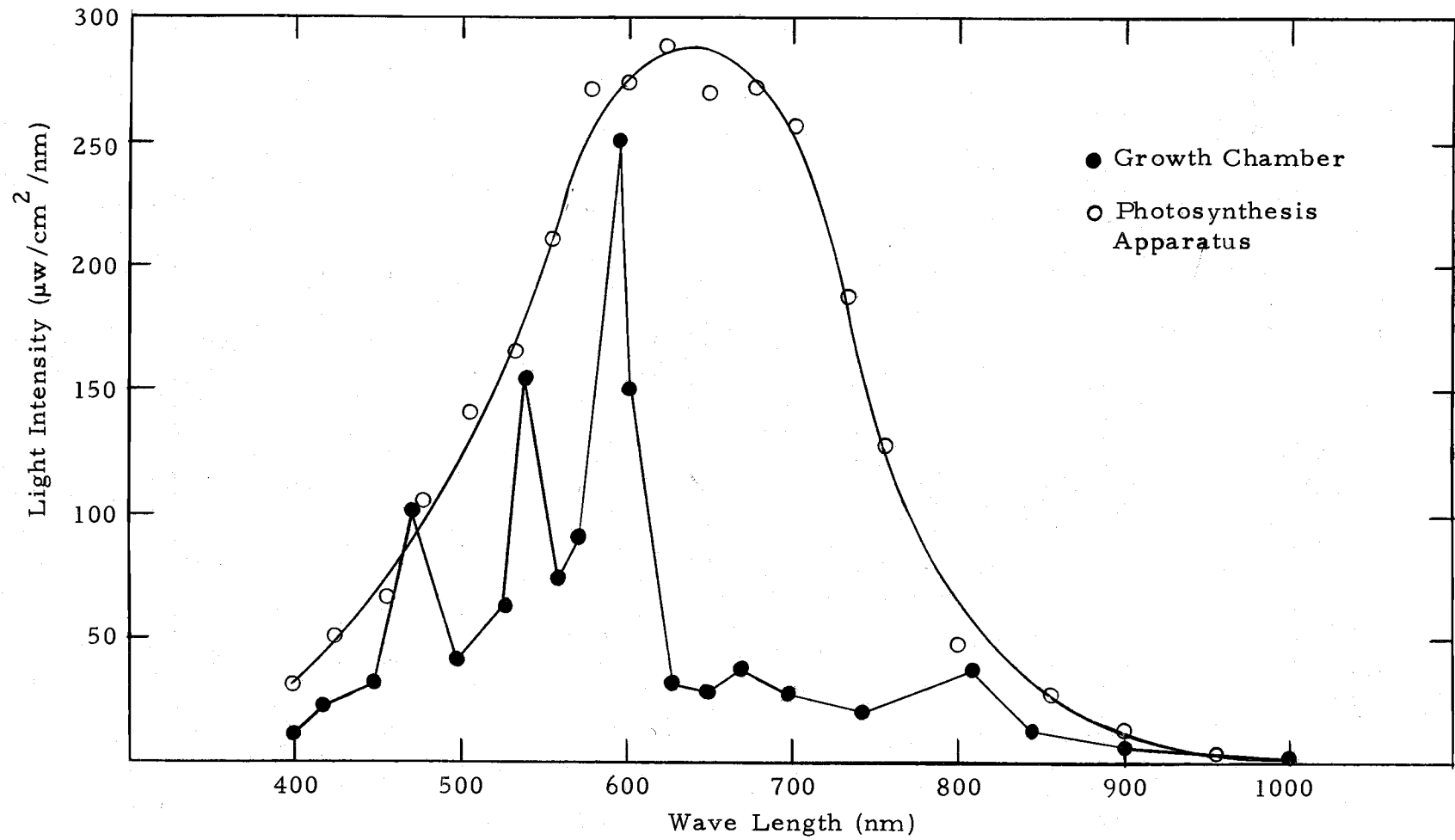
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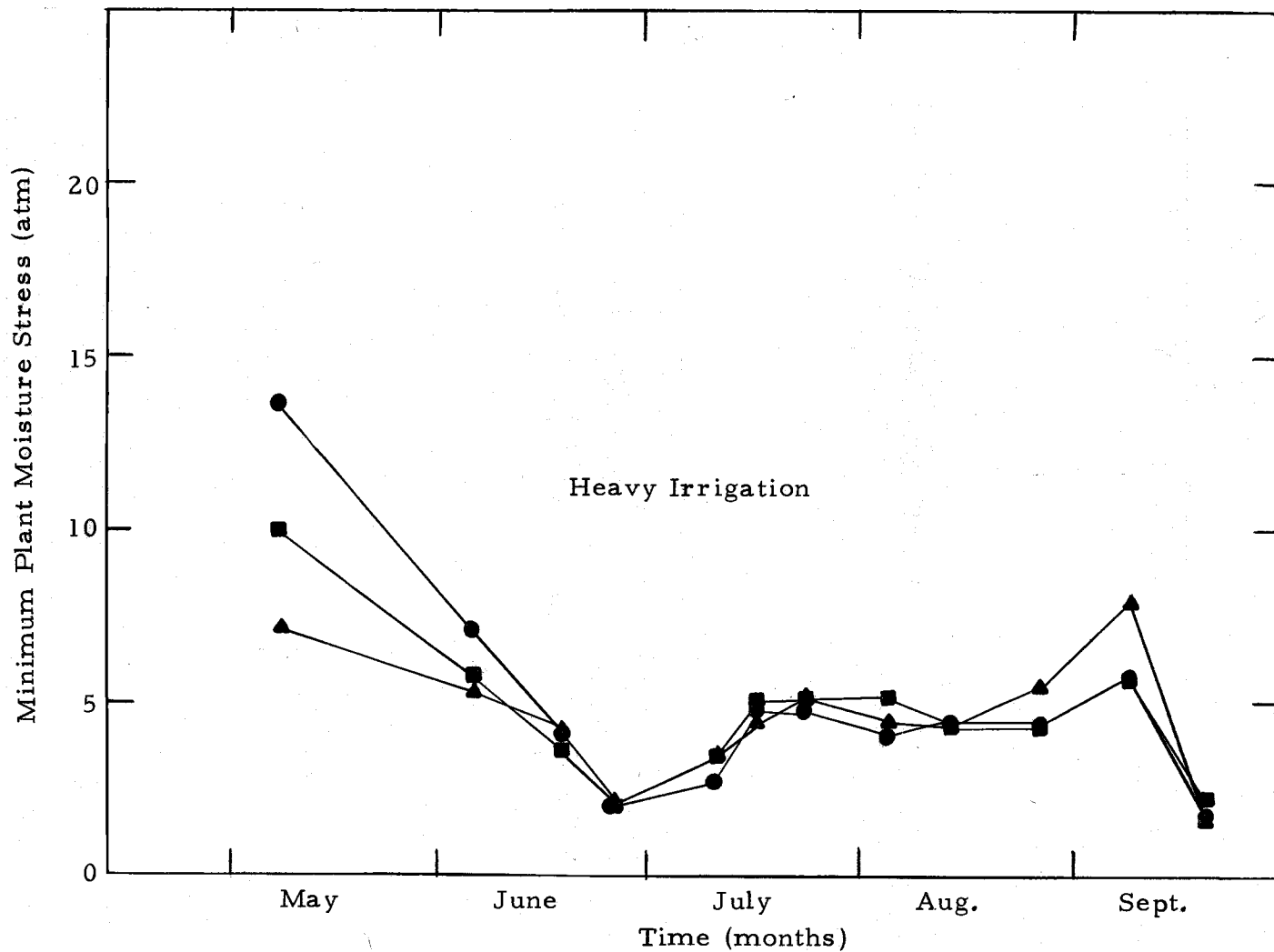
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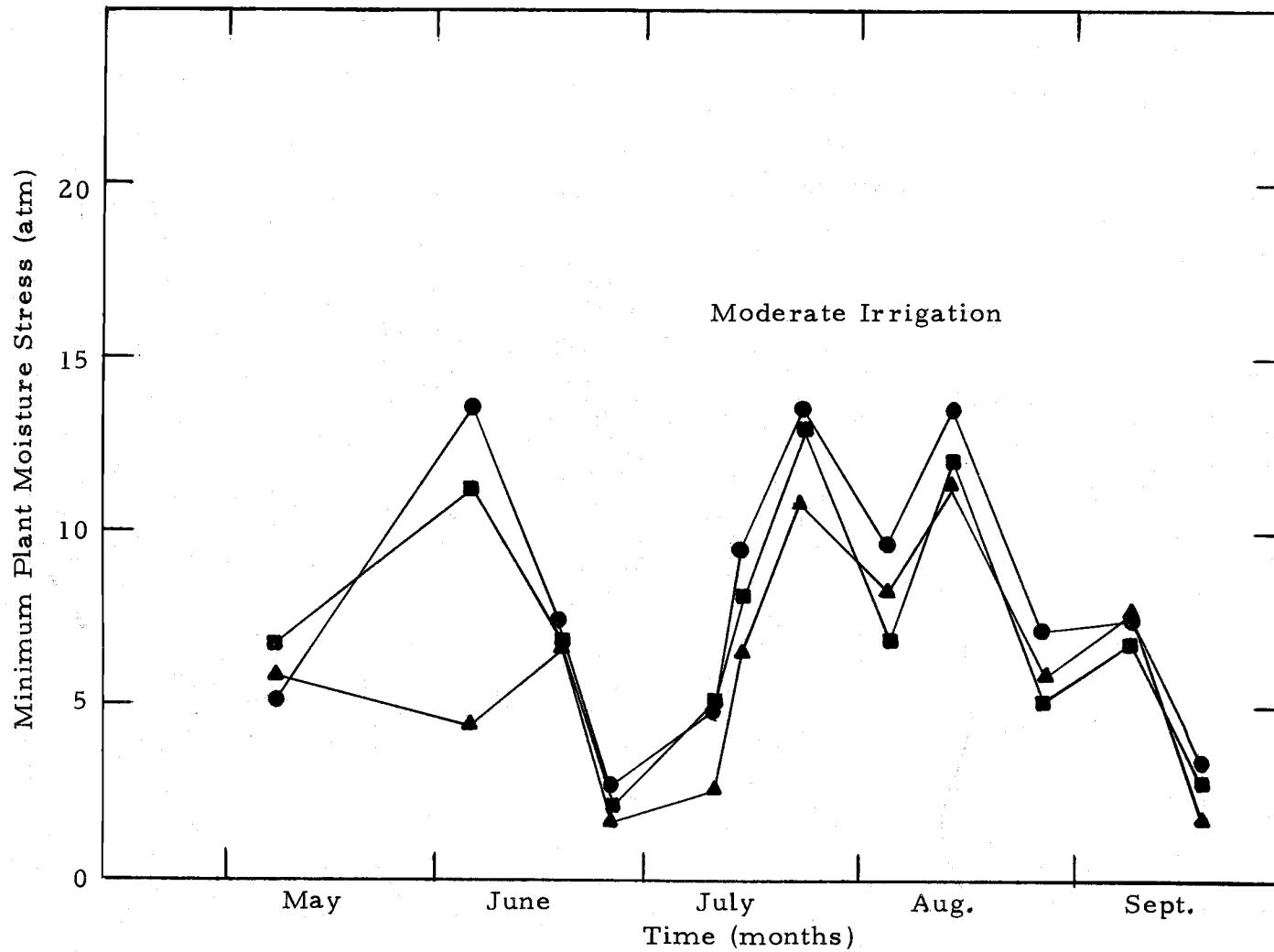
APPENDIX



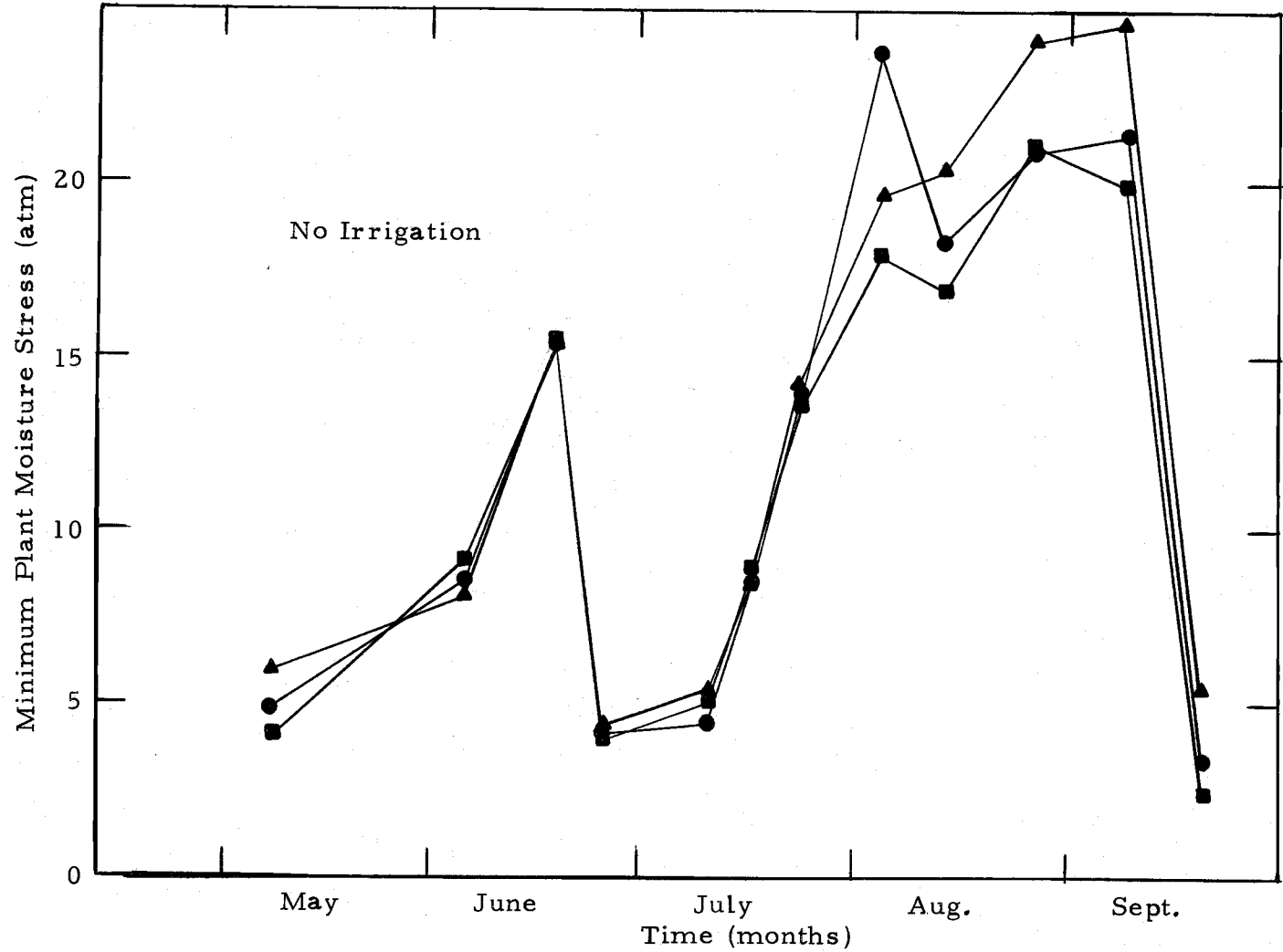
Appendix Figure A. Spectral intensity at the plant level for the growth chamber and photosynthesis apparatus light sources.



Appendix Figure B. Seasonal changes in minimum plant moisture stress of three randomly selected heavily irrigated ponderosa pine seedlings. Plot was irrigated whenever the minimum PMS measurements exceeded 5 atm.



Appendix Figure C. Seasonal changes in minimum plant moisture stress of three randomly selected moderately irrigated ponderosa pine seedlings. Plot was irrigated whenever the minimum PMS measurements exceeded 10 atm.



Appendix Figure D. Seasonal changes in minimum plant moisture stress of three randomly selected ponderosa pine seedlings. Plot received no irrigation treatment.