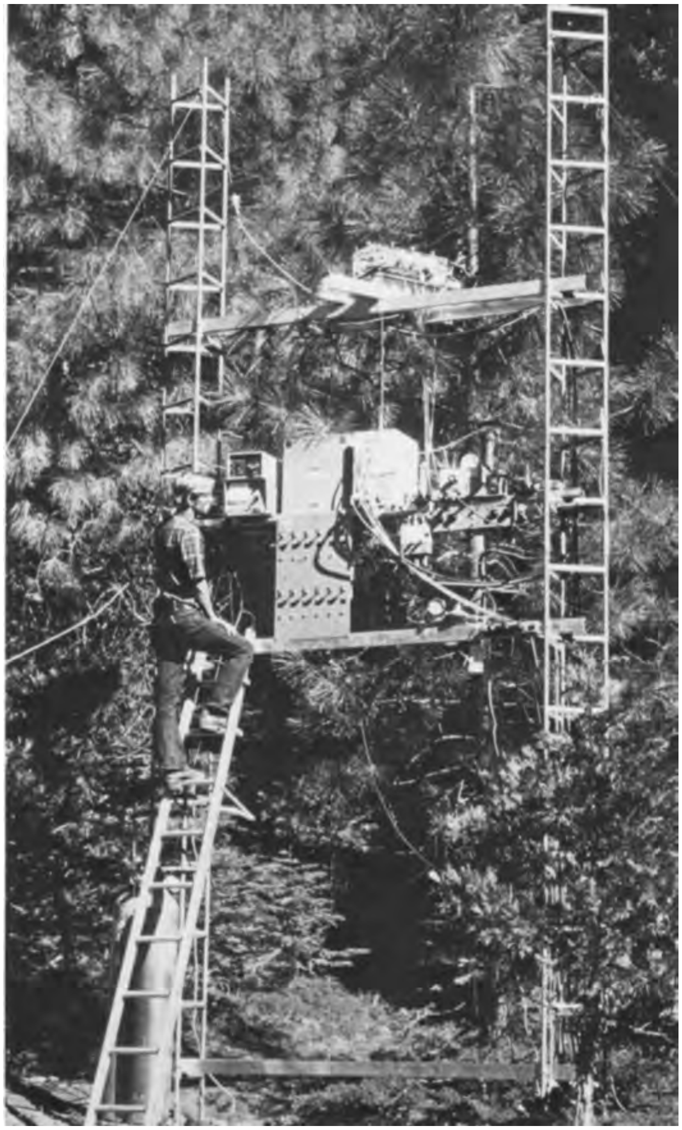

To measure photosynthesis, respiration, and transpiration in the field, a curvette for measuring gas exchange is attached to a series of branches. Underneath the cuvette is a rack bearing analytical equipment for monitoring physiological processes.

Tree physiology as a basis for better silviculture

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Differences in growth among forest trees depend partly on their inherent (genetically defined) growth characteristics and partly on how this potential is expressed in a particular environment. This concept is basic to forest manipulation because the silviculturist influences both genotype and environment in choosing trees for regeneration, the kind of site and its preparation, and the method of thinning or harvest.

Inasmuch as any silvicultural treatment directly influences the dynamics of stand structure and composition, it follows that we must be able to predict the relative growth of vegetation. Once this is known, silvicultural treatments can, ideally, create an environment favorable to desired plants and, if possible, unfavorable to undesired plants.

Study of tree growth in California's Sierra Nevada is based on two physiological factors: (1) the capacity to control water loss through transpiration so that undue stress does not develop and (2) the capacity of the tree to produce more carbohydrate through photosynthesis than is concurrently consumed in respiration. Control of transpirational water loss is particularly important in the hot, dry Sierra. Without this control high levels of plant water stress develop that detrimentally affect physiological functioning, tree growth, and vigor. This article describes the application of this physiological approach to understanding relative tree performance in a mixed conifer forest.

Physiological studies of plants, similar to equivalent studies in animals and people, are aimed at evaluating health and overall functioning. Most commonly, such studies have been made in controlled environment chambers where one or two environmental parameters are allowed to vary and the remainder are held constant. Precise measures of process rates are obtained, but the studies are commonly confined to small, usually juvenile plants.

The same process rates can be measured in the field employing larger, naturally growing plants. The disadvantages of this approach are: The researcher has to deal with the complexities of a continually changing field environment and the sampling problems associated with evaluating the physiological performance of large plants. The advantages are: The analyses retain a high degree of ecological and applied relevance, and one can evaluate the relative performance of large trees in terms of their naturally fluctuating field environment which, after all, is the situation of interest to forest managers.

In actual practice, the laboratory and field approaches are mutually interdependent; hypotheses can be tested and relationships developed in the field, validated in the laboratory, and vice versa.

This study's approach is to recognize the tree as an integral part of a soil/plant/environment continuum. Physiological performance is evaluated by monitoring net carbohydrate production and rates of transpiration. Both photosynthesis and transpiration are controlled by the degree of stomatal opening. Stomata, pores in leaves controlled by the plant, allow for a free exchange of water and carbon dioxide when open and restrict water loss and carbon dioxide flux when closed. Ecological adaptability may depend partly on the species' capacity for stomatal closure with increasing environmental stress. The degree of stomatal opening was monitored by measuring "leaf conductance." Concurrent with physiological functioning, we monitored the levels of particularly important environmental driving variables: solar radiation, air and leaf temperature, and vapor pressure deficit (VPD). VPD is the difference between the amount of water vapor currently in the air and the amount needed to saturate the air at that temperature, and is a measure of atmosphere evaporative stress.

Rates of photosynthesis and transpiration were obtained by monitoring the net uptake of carbon dioxide and net discharge of water vapor by an attached branchlet enclosed in a small gas exchange chamber. Electronic sensing units match the chamber's environment with fluctuating external field conditions or control chamber conditions independent of external ambient conditions. The chamber is placed around a branchlet within the tree's crown; equipment needed to monitor gas exchange is mounted nearby to minimize time-lag errors. Electronic control systems and computer-driven data acquisition equipment are housed in a mobile trailer.

The site of this study was the University of California's Blodgett Forest Research Station. The study site selected included vigorous ponderosa pine, white fir, incense-cedar, and Douglas-fir, 20 to 30 feet tall, growing side by side.

Results

The results reported here are restricted to tree performance during August and September when the Sierra is hot and dry. No appreciable precipitation falls after May; thus, soil water availability becomes low. Typical diurnal patterns of light intensity, leaf temperature, CO_2 concentration, and vapor pressure deficit have a close relationship. The levels of these parameters indicate that trees in late summer are exposed to high stress. Mean leaf temperatures are above 25°C and vapor pressure deficits are greater than 20 millibars much of the day. Relative humidities at mid-day are approximately 30 percent. Pre-dawn xylem pressure potentials (a measure of plant water stress) average approximately -5 to -10 bars for all species, indicating that the trees commonly become adequately recharged with water overnight and thus begin the day nonstressed.

The impact of light intensity, leaf temperature, and VPD on net photosynthesis, transpiration, and leaf conductance was evaluated for various species. Conventional two-dimensional analyses were used to describe basic interactions between a process and changes in one environmental parameter. A reduction in variability and better comparison between species were obtained by using three-dimensional analyses, which segregate a family of curves on the basis of a second driving environmental variable and produce a response surface for a particular physiological function. This approach shows the response surface for net photosynthesis as a function of increasing leaf conductance and light energy.

A statistical evaluation of results permitted a comparison of the relative capacity of tree species to function in a field environment. Net photosynthesis was characterized in terms of light compensation, light saturation, and relative efficiencies of carbohydrate production. The most interesting finding was that incense-cedar has a significantly higher capacity for net photosynthesis (the production of carbohydrate) than do other species. In particular, it should be noticed that incense-cedar maintains considerably higher rates of photosynthesis as stomata close (i.e., as leaf conductance decreases). The productive capacities of white fir and Douglas-fir were found to be between those of incense-cedar and pine.

A study of transpiration showed that water loss increased rapidly for all three species with increasing light energy to about one-fourth of the maximum intensities recorded. Beyond this level, the average transpiration rate becomes relatively constant with increasing light energy for ponderosa pine; for white fir and incense-cedar it continues to rise slowly to levels of approximately 1.0 gm $H_2O/dm^2/hr$.

Interestingly, there is a difference in transpiration rates among the three species with increasing leaf temperature. Transpiration of ponderosa pine and white fir has a similar pattern, increasing almost linearly with temperature reaching, at 35°C, a maximum of 0.6 gm $H_2O/dm^2/hr$ for ponderosa pine, and a significantly higher rate of 1.0 gm $H_2O/dm^2/hr$ for white fir. Average transpiration of incense-cedar, however, rises to a maximum of 0.7 and then, remarkably, declines to 0.3 gm $H_2O/dm^2/hr$ at 35°C.

Differences in transpiration among species are even more dramatic when evaluated over increasing levels of VPD. At high levels of VPD, white fir continues to transpire at very high rates of 1.2 mg $H_2O/dm^2/hr$, ponderosa pine controls water loss to 0.4 mg $H_2O/dm^2/hr$, and incense-cedar has the greatest control by limiting rates of water loss to 0.2 mg $H_2O/dm^2/hr$. This very interesting difference in transpirational behavior of incense-cedar is no doubt associated with this species' capacity to close its stomata with increasing stress. This behavior is further verified in analyses of leaf conductance which show that, of the three species, incense-cedar has the greatest capacity to close stomata with increasing stress while white fir has the least.

Discussion

The study has demonstrated that it is indeed possible to characterize the relative physiological capacity of trees in terms of response surfaces for net photosynthesis, leaf conductance, and transpiration. Light intensity was found to be the most important single variable governing the carbohydrate production of trees in the mixed conifer forest. However, differences in stomatal closure and control of transpiration were best defined by changes in VPD or evaporative stress.

The summertime performance of incense-cedar in the Sierra was found superior to that of associated conifers. Whether this holds true for other seasons and for other sites and age classes remains to be shown. It is well known that incense-cedar is capable of growing on a variety of sites and that it has variable shade tolerance. The study has indicated that this is probably because of its great capacity to control water loss by closing stomata. On the other hand, white fir fails to compete on drier sites because of its apparent incapacity to close stomata as VPD increases, thus resulting in excessive water loss and high plant stress.

This kind of understanding of how trees react to different environments is helpful in justifying the development of silvicultural prescriptions that recommend choice of species and practices on particular exposures. The more we know about the relative physiological capacity of trees to function in particular environments the better silviculturists can make rational decisions regarding stand treatments.

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