Growth-Rings of Trees: Their Correlation with Climate

Patterns of ring widths in trees in semiarid sites depend on climate-controlled physiological factors.

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Early in the 20th century, A. E. Douglass was able to show that the widths of annual rings in trees in semiarid sites correlate with variations in climate (*1*). The sequence of wide and narrow rings was so predictable that he was able to recognize and cross-date the same pattern in tree stumps from nearby areas and to determine the actual year in which the trees were felled (*2*). These discoveries were followed by a vigorous program of tree-ring research that led to the development of a new discipline called dendrochronology. This discipline may be broadly defined as the study of yearly growth patterns in trees and their use in dating past events and in evaluating fluctuations in past climate.

In recent years dendrochronology has matured into a sophisticated science. Tree-ring relationships are readily measured and tested by quantitative means, and results are understandable in terms of modern physiological principles. In this article I describe the characteristics exhibited by a group of ring widths represented in the annual growth layers of the main stem from the center to the bark of the tree. I also attempt to account for some differences in these characteristics which are explainable in the light of modern concepts of tree physiology and recent results from studies at the Laboratory of Tree-Ring Research, University of Arizona.

Characteristics of Tree-Ring Series

A growth ring is formed inside the bark by division of cambial cells, which produce large, thin-walled wood or xylem cells (earlywood) at the beginning of the growing season and small, thick-walled wood cells (latewood) toward the end of the growing season. The abrupt change in cell size between the last-formed wood of one year and the first-formed wood of the next year usually delineates the boundary between annual growth increments (*3*). In the main stem of the tree these boundaries usually approximate a series of overlapping, superposed conical surfaces. However, in certain cases the surface may be better described as a cylinder or paraboloid (*4*).

Thus, each year's increment produces a continuous, or sometimes discontinuous, layer surrounding the previously formed wood, except in the newly formed twigs at the stem apex, where the year's increment becomes the first layer of wood. Each successive layer, when viewed in a transverse section, appears to be a ring, encircling many previously formed concentric rings, whose number increases toward the stem base.

The actual dimensions for this series of superposed conical surfaces are a function of the tree's heredity and environment acting throughout the life history of the developing and aging individual (*5, 6*). Therefore, measurements of any one dimension of this series of conical surfaces, such as the widths of rings along a transverse section at the stem base, represent the product of a variety of gradients acting through time within the existing structure of the tree (*7, 8*).

The foliage of the crown is the principal manufacturer of growth regulators and food, as well as the primary transpiring surface (*5*). As new layers of wood are added above and outside the existing layers, the tree crown is also growing and lower branches are dying; hence, the mean crown position is farther up the main stem. With the increased height of each year's terminal growth, materials must travel a greater distance down the stem to reach a given cambial area. Also, in a tree with a constant growth rate, the same ring width for any two rings represents a larger volume in the outer, more recently formed, ring.

It has been shown (*8*) that these changes with age and stem height cause changes in ring characteristics, especially in the lower stem portions of trees growing in semiarid sites. Near the center, as seen on a transverse basal section of the main stem, rings are generally wide. Toward the outside they become narrower and are likely to exhibit more relative variability in width from year to year. This change is attributed to increasing competition within the tree for materials manufactured in the crown. As the distance from the crown increases, materials, such as carbohydrates and hormones, moving from the crown to the lower portions of the stem may be largely consumed, or their concentrations may be reduced in transit.

This phenomenon is especially marked during dry-warm years, when the net production of food and growth-controlling substances by the crown may be low (*5*). In addition, the ratio of green to nongreen living tissue decreases with age (*5*). Also, cambial initiation occurs last in the basal cambium, while growth cessation may occur there first (*9*). As a result of these changes, both the relative growth rate and the length of the growing season may fluctuate more widely from one year to the next as the tree increases in size. This fluctuation produces more variable but narrower rings. These same phenomena may also explain the higher frequency of partial rings in the outer portions of the stem base, as well as the decrease in number of intra-annual bands of latewood sometimes referred to as false rings (*8*).

A transverse section through the upper crown portion of the same stem frequently reveals less pronounced changes in ring characteristics. Because of the proximity of the crown and the decrease in rates of terminal growth in the older tree, food and hormone supplies do not change as markedly, through time, in this portion of the stem as in the basal section. The rings in the

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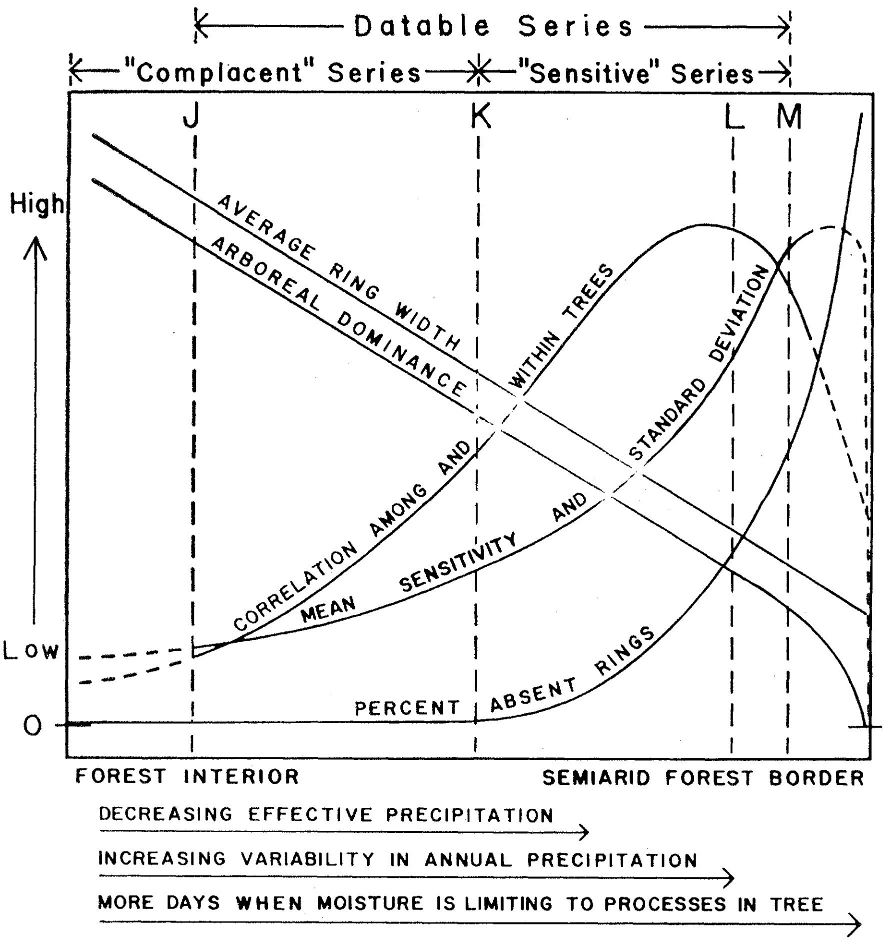

Fig. 1. Changes in tree-ring and vegetation characteristics that can be observed along a gradient from the forest interior to the semiarid lower forest border. Climatic differences are indicated below the graph and dendrochronological categories are indicated above it. (*J* to *M*) The area of datable tree-ring series; (*K*) the approximate boundary between trees with "complacent" and those with "sensitive" tree-ring series; (*L*) the area where tree-ring widths correlate best among trees and exhibit the closest relationship with climatic variation (*13*).

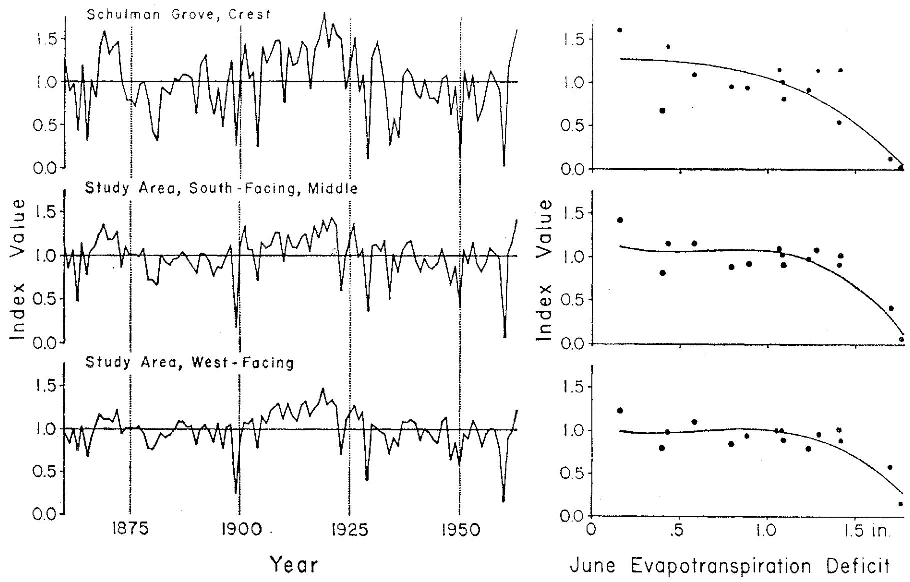

Fig. 2. Tree-ring-width chronologies (index values) for *Pinus aristata* from three contrasting sites, plotted (at left) against year of formation and (at right) against evapotranspiration deficits in June. The three curves at right represent a least-squares fit by a third-degree polynomial to the relationship between tree-ring width and evapotranspiration, and the major deviations of the points from this curve reflect the additional effects of winter temperature and autumn moisture on the subsequent season's ring growth (*18*).

crown portion resemble their counterparts in the outer stem base which were formed during the same growing seasons. However, the correlations of ring-width changes from year to year with ring-width changes in other trees, and with the associated variation in macroclimate, are frequently not as high for the upper portions of the stem as for the lower portions (*8*).

Thus, not only does the basal stem section provide the longest and oldest ring-width chronology in a tree but the patterns in ring widths provide the most reliable estimator of past variations in moisture and temperature which have limited the growth-controlling processes throughout the entire tree.

In order to properly relate ring patterns of the basal stem section to yearly climatic variation, it is necessary to remove, statistically, the gradually changing differences associated with the age, crown position, and mean growth of the tree (*8*, *10*). This is accomplished by fitting a regression line or curve to each ring-width series and dividing the actual ring width by each yearly value of this fitted curve (*10–12*). This transforms ring-width values from nonstationary time series to tree-ring indices which exhibit a mean of 1.00 and a variance that is independent of tree age, position within the stem, and mean growth of the tree (*12*). Since the mean index is the same for all radii, indices have an added advantage over ring-width measurements in that they all receive equal weight when averaged and manipulated, regardless of whether they come from fast-growing or slow-growing portions of a tree.

These same characteristics of ring-width series may also vary with species and with differences in site. Some results from a study of replicated tree-ring samples from *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus ponderosa* Laws., and *Pinus edulis* Engelm., in northern Arizona, are summarized in Fig. 1 (*13*). A transect was studied along a gradient from the mesic forest interior on the shoulder of the San Francisco Mountains to the semiarid forest border approximately 29 kilometers northwest of the mountain mass, where trees are widely spaced and interspersed with grassland. At the sites in the forest interior (represented by *J* in Fig. 1), precipitation is high and less limiting to processes in the trees than it is in the other sampled sites. There is a dense forest cover. The average value for ring width is high. The average ring-width pattern for forest interior sites shows little variation from year to year, but there is a lot of variation in ring width from tree to tree in any given year. The ring-width chronologies from such trees are referred to as "complacent," for the chronologies do not correlate with each other and do not show a close relationship with macroclimatic variation. Since, at this site, there is almost always sufficient moisture for some growth, partial rings and local absence of rings are infrequent, except in suppressed trees.

Near the semiarid forest border (*L* in Fig. 1) there is less effective and more variable precipitation, and there are more days when moisture is limiting to processes within the tree. In such sites, rings are narrower and arboreal dominance is less, but there is more relative variation in ring width from year to year. Partial rings are more abundant, ring-width patterns are more highly correlated among and within trees, and the patterns relate more highly to climatic variation. Such trees produce "sensitive" ring-width chronologies.

These changes, which were measured along the environmental gradient extending northwestward from the San Francisco Mountains, document the fact that rings from trees of the semiarid forest border provide the best estimate of climatic variation, for it is in such sites that climate is most frequently limiting to the growth-controlling processes in the trees.

This relationship is illustrated further in Fig. 2, by the three tree-ring chronologies for *Pinus aristata* Engelm., in the White Mountains of California (*14*). Each of these chronologies was derived from ring-width measurements taken along 20 radii (two radii in each of ten trees). Each ring-width series was converted to index values, which were averaged for each group. At left in Fig. 2 the yearly averages are plotted against time; the bottom curve exhibits little variability from year to year. The trees came from a relatively dense and moist forest stand where there is abundant accumulation of snow. The standard deviation for this 104-year chronology is 0.199. The middle curve at left in Fig. 2 represents a more arid site on a south-facing slope and exhibits more variability, as shown by a standard deviation of 0.241. The top curve was obtained from gnarled and stunted trees growing on a dry, wind-swept, and rocky ridge. The ring-width indices from these trees are extremely variable, as shown by a standard deviation of 0.376.

The plotted points at right in Fig. 2 represent index values for the last 15 years of each chronology plotted against evapotranspiration deficit in June. This parameter was calculated from daily weather records (*15*) collected at the White Mountain Research Station, which is located approximately 11 kilometers north of the sampled stands and at about the same elevation. Extensive regression analysis (*14*, *16*, *17*) showed that the June evapotranspiration deficit was the climatic factor most highly related to tree-ring growth in all three of these sites. The regression line in Fig. 2 is a least-squares fit of a third-degree polynomial, and the major deviations from the line reflect the limiting effects of a cold winter and a dry-warm autumn on the subsequent year's growth (*18*).

The ring widths for trees from the more moist sites represented by the bottom and middle curves at right in Fig. 2 are small only in years in which the evapotranspiration deficit in June is extremely large. The rings of trees in the exposed site (top curve at right) exhibit decreasing widths for years of intermediate-to-extreme June drought, as measured by the evapotranspiration deficit. In fact, a straight line would provide almost as good a fit for these exposed-site trees as the polynomial function shown in Fig. 2. These three chronologies illustrate that a factor—topographic, edaphic, or altitudinal—which causes soil moisture to become more limiting to the growth of trees in the semiarid site may also increase ring-width variability and enhance the correlation between ring width and the macroclimatic variation.

In the remaining part of this article I consider only trees that are growing in semiarid sites, and that exhibit a close relationship between ring width and climate.

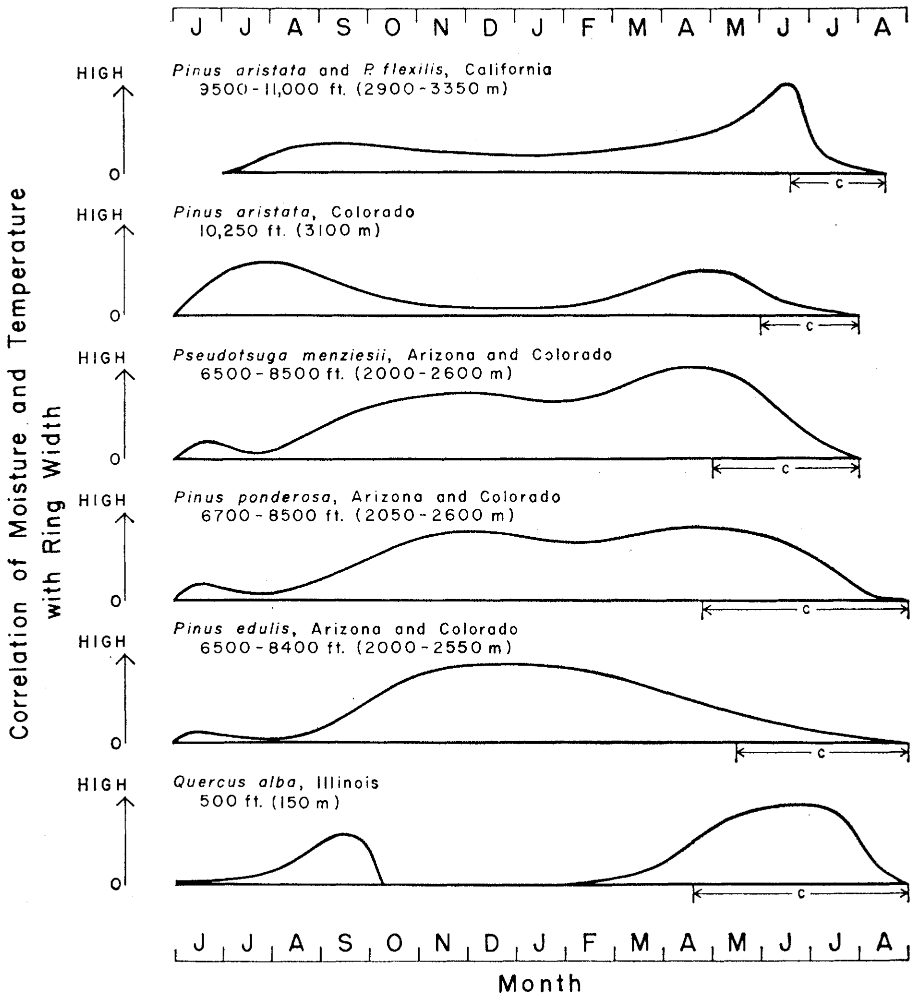

Fig. 3. Diagrammatic representation of the correlation of ring widths from trees in semiarid sites with moisture and temperature for a 15-month interval that includes the growing season and the period that precedes it. The area under the curve for each monthly interval represents the degree of correlation with the two climatic factors and is proportional to the apparent influence of the climate during that period on ring growth. (c) Period of cambial activity.

Climatic Relationships

Through several different studies my associates and I have accumulated more than 40 replicated samples of tree rings from a variety of species and sites near weather stations having relatively long and continuous records, in Arizona, Colorado, California, and Illinois (*13, 14, 17, 19, 20*). The climatic factors and intervals that correlate with ring-width variation were ascertained by means of a series of stepwise multiple regression analyses (*16*). The curves of Fig. 3 are a diagrammatic representation of the correlation results for five species and are ordered according to the approximate elevational range of each species. The abscissa represents the 15 months prior to and including the period of growth which is indicated by *c* on the diagram. The ordinate represents the average correlation of precipitation and temperature during each month with the ring width of that year. Therefore, the distribution of the area under the curve provides an estimate of the relative influence of the primary climatic factors, precipitation and temperature, during different portions of the year, on the amount of growth occurring in late spring and summer (*17, 19, 21*). Frequently a combination of temperature and precipitation data in a parameter representing evapotranspiration deficit produces the highest correlation.

A comparison of the areas under the curve prior to the growing season and during the growing season shows that, at least for conifers in semiarid sites, the variation in ring width is more highly correlated with the climate prior to the initiation of growth than with the climate during the growing season. Fig. 3 also shows that growth of conifers at low elevations relates most closely to the winter component of climate and least closely to the summer component, while growth of conifers at high elevations relates more closely to the climate of late spring and early summer and to that of the previous summer and early autumn. The rings of deciduous species, such as *Quercus alba* L., relate to conditions during the current growing season and during the latter part of the previous growing season up to the time of leaf fall.

Of primary importance in control of the relative ring width from year to year is precipitation as it affects soil moisture and the water balance of the tree; but high temperature, probably through its effect on evapotranspiration and on processes such as respiration and photosynthesis, may also be a controlling factor (*17, 20, 21*). Studies on the soil-moisture regimes show that the lag in the effect of climate on growth cannot be explained adequately in terms of soil-moisture storage (*14, 17*). Therefore, it was proposed (*17*) that the climate during the summer, autumn, winter, and spring that precede growth must in some way precondition the tree and indirectly influence the rate of cell production during the growing season.

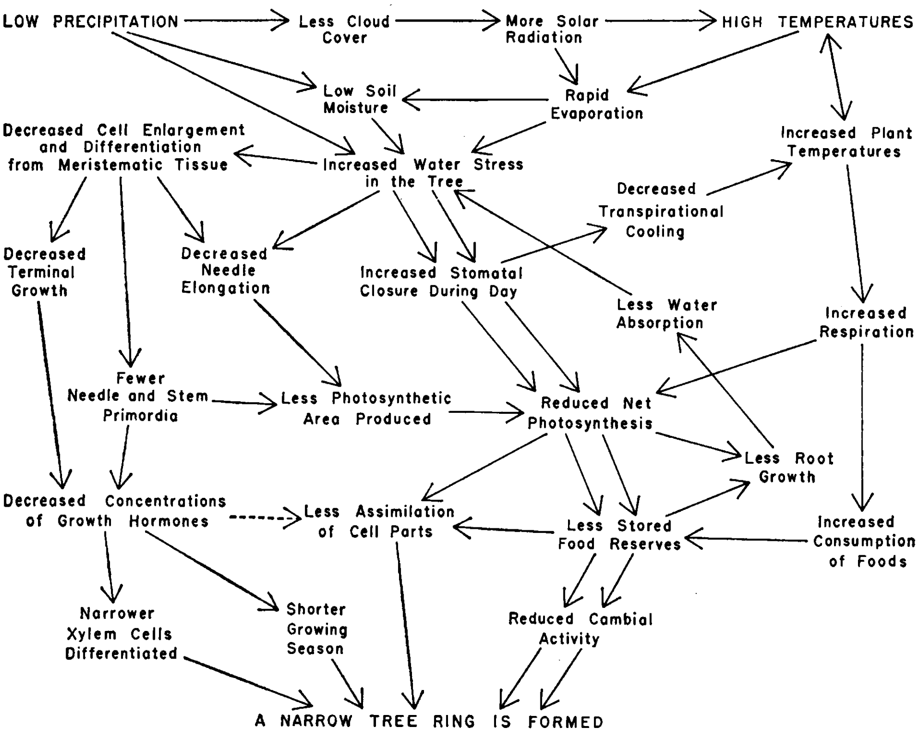

Fig. 4. Schematic diagram of the model hypothesized for the relationship between low precipitation and high temperature and the production of a narrow tree ring (*17*).

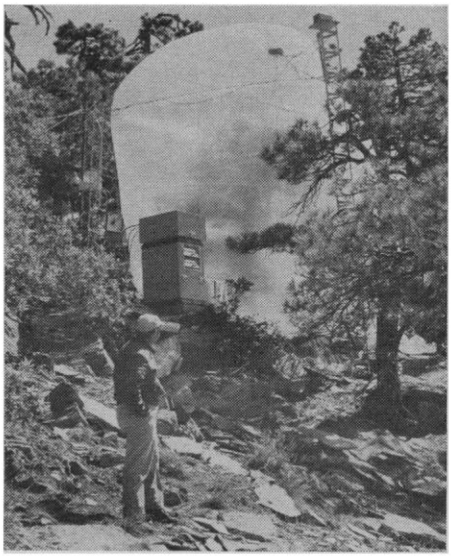

Fig. 5. Measurement of net photosynthesis, respiration, and transpiration through enclosing a tree in an inflated polyethylene tent and measuring the carbon dioxide and atmospheric moisture entering and leaving the tent. The two stacked rectangular units in front of the tent are (bottom) the blower and (top) the air-cooling systems. Louvers on these units control the amounts of ambient and cooled air entering the tent. The towers and cables are for erecting and anchoring the equipment and tent (*23*).

The chain of events which, according to this hypothesis, occur and produce these relationships is illustrated in Fig. 4. The primary climatic factors—low precipitation and high temperatures—are shown at the top of Fig. 4, and the resultant formation of a narrow tree ring is indicated at the bottom. The path of double arrows indicates what I and my associates believe to be the primary sequence: increased water stress, reduced net photosynthesis (photosynthesis minus respiration), and low accumulation of food as a reserve, resulting in reduced rates of cambial activity and the formation of a narrow ring (*22*). Some interacting factors affecting this food storage are shown at right in Fig. 4, and some direct effects of growing-season climate upon growth are shown at left.

Physiological Evidence

What evidence beyond correlation of analytical results is there for such an interacting series of relationships? Since most of the published physiological work has dealt with trees on relatively cool and mesic sites, we were forced to initiate investigations of our own. Several *Pinus ponderosa* trees on an exposed south-facing slope at 2600 meters (8500 feet) in the Santa Catalina Mountains north of Tucson, Arizona, are being studied intensively (*23*). In these studies branches are enclosed in polyethylene bags ("branch bags") for several months at a time, and a whole tree is enclosed in a polyethylene tent for shorter periods (*24*). The tent (Fig. 5) is inflated with a continuous air stream, and the carbon dioxide and water content of the air entering and leaving the tent are monitored. An air-conditioning or heat-exchange system is used to help maintain the temperature of the enclosure as close to the ambient temperatures as possible. We also measure a number of environmental factors, diurnal changes in stem size [by means of dendrographs (*25*)], and cambial activity [by examining anatomical samples (*17*)].

Some measurements obtained by means of a branch bag during four selected, clear, 24-hour periods are shown in Fig. 6. Since the radiation load in such mountain environments is high during clear days even in winter, branch temperatures may rise markedly above air temperatures and photosynthetic rates can be high, especially during calm days (*26*). During early spring, after the winter snow has melted (Fig. 6, top left), there is sufficient moisture in the soil to permit high rates of photosynthesis. A slight midday depression suggests that, under peak radiation loads, water deficits or excess heating of the plant tissue occur, at least in the branch bag. As seasonal temperatures rise and soil moisture is depleted throughout the spring period, the midday depressions in photosynthesis become more and more pronounced and transpiration rates decline. By June (Fig. 6, top right), water has become so limiting and daytime temperatures have become so high that positive net photosynthesis is measurable in the branch bag only during the cool early morning hours. During the balance of the daytime period more carbon dioxide is produced than is used, indicating higher rates of respiration than of photosynthesis (*27*). During such a period the green tissue of the tree is possibly consuming more food than it produces, and cambial growth can occur only at the expense of stored food reserves. Similar but less dramatic summertime observations on *Pseudotsuga menziesii* growing in Washington were recently published (*28*).

Rains in the summer may replenish the soil-moisture supply, allowing higher rates of transpiration and reducing the water stress and heat load on the leaves (Fig. 6, bottom left). Rates of photosynthesis comparable to those for the early spring may be noted. The summer rains were markedly above average during 1964, hence soil moisture was plentiful well into the autumn. As a result of the lower temperatures of autumn, the abundant moisture, and the reduced heat load, some of the highest rates of daily net photosynthesis ever observed by us were recorded (Fig. 6, bottom right).

The net 24-hour carbon dioxide exchange and some environmental conditions throughout a 15-month period for the same branch bag are shown in Fig. 7. During the dry periods in May through July the monitored branch contributed little photosynthate to the total tree food reserve, and during many days it appeared to consume more food than it made. However, the summer rains

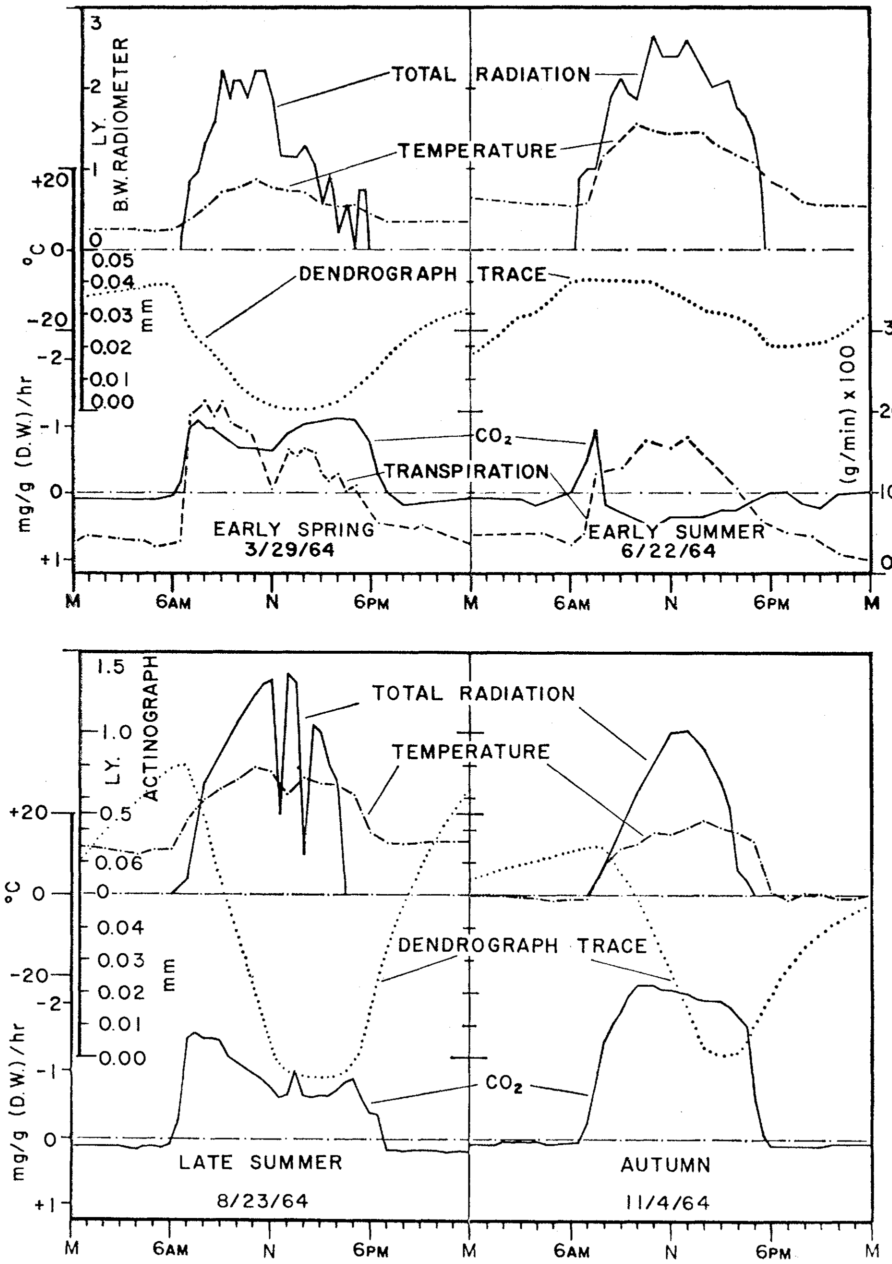

Fig. 6. The daily regime, during 4 selected days, of several measured environmental parameters and plant processes for a branch of *Pinus ponderosa* enclosed within a polyethylene bag. Solar radiation was measured with a Beckman and Whitley radiometer and later with a black-and-silvered-plate actinograph. Air temperature was measured in the airstream of the outlet from the bag. Transpiration and carbon dioxide exchange are measured as a difference between values at the inlet and outlet of the bag [expressed in milligrams per gram dry weight (*D.W.*)]. The dendrograph trace is from an instrument on the upper main stem of the tree (*23*).

raised the rates of net photosynthesis. With high summer temperatures, the rates of respiration throughout the entire tree were also high; hence, the total net gain in foods was probably not as great during the summer as it was in the cooler, early spring. During the summer growing season a large portion of the current photosynthate and accumulated food reserves is probably consumed in the metabolism of the active meristematic tissues.

As the cooler but moist autumn season approaches, respiration decreases but photosynthesis remains high. Only during the cold winter days is net photosynthesis markedly reduced. This reduction in net photosynthesis is associated with freezing of the soil or freezing of the trunk at night. This freezing appears to prohibit water transport to the crown and creates a water deficit during the day. The reduction is also associated with subfreezing cloudy days when leaf temperatures are low and directly limiting to photosynthesis. Although some workers report complete suppression of net photosynthesis at high elevations during relatively warm winter days (*29*), on our semiarid low-elevation sites we observe rapid recovery of photosynthetic capacity within 24 hours after prolonged cold treatment.

During the drier autumn of 1965, soil-moisture supplies for the trees were significantly lower than in 1964. We obtained regimes of low photosynthesis and high daytime respiration very comparable to, but not as extreme as, the June pattern shown at upper right in Fig. 6.

Recently I measured ring widths and made analyses of variance on nine well-watered seedlings of *Pinus ponderosa* from an experiment by Hellmers (*30*). The seedlings had been subjected to controlled temperatures at two different levels for three growing cycles. A 15°C day and an 11°C night throughout the growing period produced a significantly wider ring at the base of the stem than a 23°C day and a 19°C night. In this case, high temperatures, without any apparent water stress, appear to have reduced ring-width growth at the stem base.

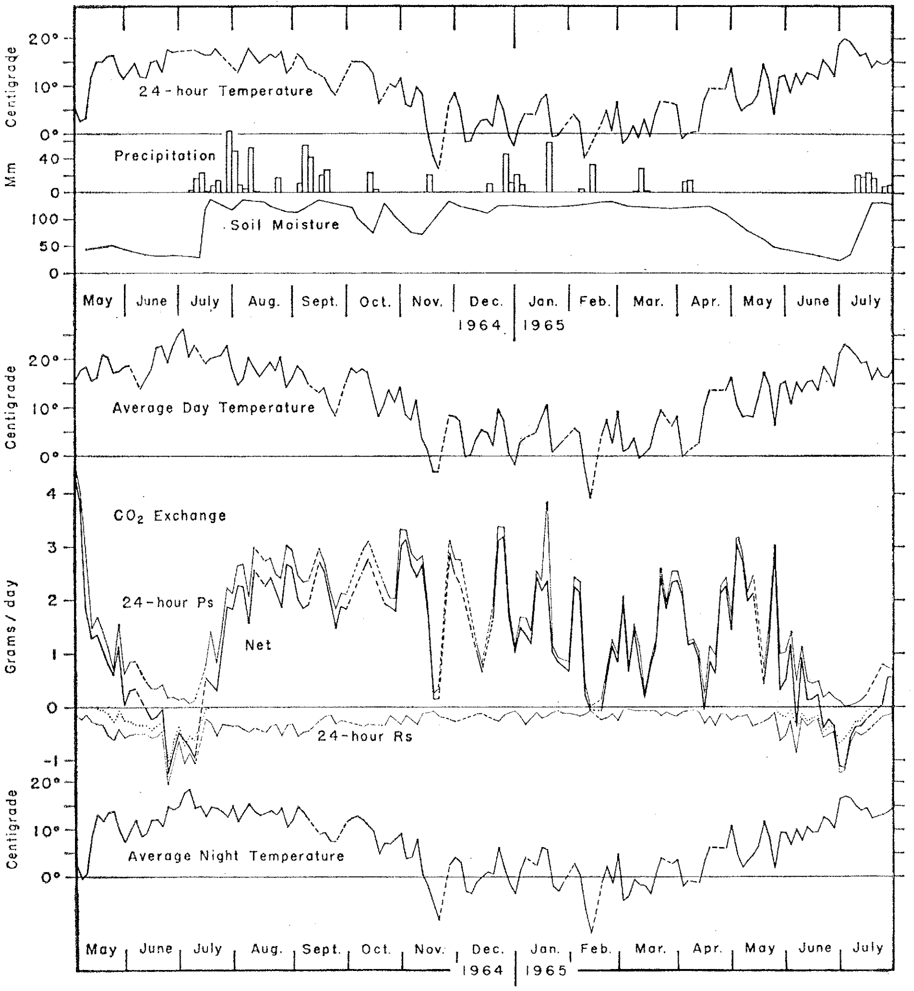

Fig. 7. Climatic regime and carbon dioxide exchange for an enclosed branch of *Pinus ponderosa*, from May 1964 through July 1965. The data are plotted as 3-day averages. Dashed lines connect points through time periods for which no data were obtained. (Light lines above and below zero) The net amount of photosynthesis and respiration measured during the 24-hour period; (heavy line) the daily net carbon dioxide balance, or the difference between the amount consumed and the amount released during the 24-hour period; (dotted line below zero) the net release of carbon dioxide during the daylight hours, from 7 a.m. to 7 p.m. (*23*).

It has also been observed that, during drier seasons, some semiarid-site conifers produce shorter needles than they produce during more moist seasons. Variations in needle length have been observed in the field for *Pinus ponderosa, P. aristata,* and *P. edulis.* In the last-named species we were able to significantly increase the amount of needle elongation by supplementing the soil moisture around a tree for one growing season (*17*). Preliminary regression analysis of these needle-length measurements indicates that needle elongation is directly related to the moisture, and inversely related to the temperature, occurring during and just prior to the growing season. Since climate does influence needle growth, it can control the photosynthetic area produced in any one season and thus influence the food-making capacity and ring growth of the tree for several years following (Fig. 4) (*31*). This lag in the effect of the climate on tree growth is commonly observed and can be measured by the serial correlation exhibited in a series of ring-width indices (*32*).

It is apparent, from these results, that the correlations between ring width and climate in a semiarid region, as shown in Fig. 3, have a meaningful biological explanation: climate basically controls the initial food-making process of the tree. Low amounts of food reserves are accumulated during years of dry, warm climates, and growth in the late spring and the summer is slow (*14, 17*); hence, the ring is narrow. If moisture is abundant for long periods when the roots and trunk are not frozen and if daytime leaf temperatures are above freezing, there will be high rates of photosynthesis and accumulation of abundant food reserves, which can maintain high rates of growth during the summer, so that a wide ring is produced.

At low elevations in southwestern North America, summer temperatures and drought are extreme but the winter climate is mild (*33*), so that the greatest rates of food accumulation probably occur during the cool autumn, winter, and spring. Thus, ring-width growth is most dependent upon, and therefore most highly correlated with, the climate during the cooler portions of the year. At high elevations, or in more northern continental areas, trees are frozen during most of the winter, and summer temperatures are mild (*14, 29*). Trees in these environments probably make and accumulate more of their food during the late spring, the summer, and the early autumn, so that the ring widths correlate more strongly with this interval of climate. Soil moisture in spring is partially dependent upon winter snows, so that growth in these summer-responding trees may also correlate, but to a lesser extent, with winter precipitation. In the high-elevation *Pinus aristata,* winter temperature is positively correlated with the next summer's growth—an observation which suggests an inhibiting effect of cold winter temperatures on net photosynthesis (*18, 21*).

Conclusions

Many differences in the ring-width growth within a tree may be attributed to changing supplies of food and hormones. In moist sites or during periods of favorable climate, there may be sufficient food for the production of wide rings throughout the tree. But in dry sites or during years of low moisture and high temperatures, food competition within the tree is likely to be greater and the cambium at the base of the stem is likely to receive a limited food supply and may produce narrow rings. The cambium at the stem base depends upon the entire crown for food, hence ring growth reflects the tree's ambient climate. But, the cambium in the top of the tree or in the upper branches depends upon a more restricted portion of the crown for its food and hormone supplies. The rings produced by the cambium vary greatly from branch to branch and are less reliable indicators of the climate surrounding the entire tree than rings at the tree base. Therefore, ring series at the base of trees in semiarid sites provide the most reliable, as well as the longest, record of macroclimatic variation.

Tree-ring widths in certain coniferous species growing in semiarid sites appear to represent the integrated effect of climate on food-making and food accumulation in the crown throughout the 14 to 15 months previous to and including the period of growth. Trees in warm, low-elevation sites may utilize winter moisture most efficiently; trees in cool, high-elevation or more northern sites may utilize early summer and early autumn moisture most efficiently. But even with these differences, a significant amount of variance is found to be common among tree-ring series from a wide range of sites, species, and geographical areas in western North America (*14, 19, 34*), emphasizing a common dependence of ring widths on the gross regional patterns of precipitation and temperature. The remaining variance, which is not correlated among sites, may be attributed to local environmental and climatic differences, to variability among and within trees, and to compounding effects of occasional fires, insect or other infestations, and recurring years of high seed production.

It is evident that a large portion of the variability in ring-width patterns from semiarid sites in western North America does reflect differences in climate from year to year. If ring chronologies are derived from a number of trees in semiarid sites and if adequate corrections for age and trend are made, these chronologies may be used to reconstruct a first approximation of annual, or somewhat longer period, climatic fluctuations in the past (*19*).

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22. We now believe that reduced transpiration and the resulting reduction in heat dissipated by evaporation during periods of low soil moisture may be as important in reducing net photosynthesis as the direct effects of high water stress on stomatal closure.
23. These investigations are being conducted by C. A. Budelsky, J. M. Brown, and A. P. Drew under the supervision of H. C. Fritts, and are supported by NSF grant GB-1025.
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27. Under conditions of low soil moisture and high solar radiation, significant heating of plant tissue can be measured in needles inside the enclosure. This heating obviously can produce some upward temperature bias inside the enclosure. On the other hand, reduced rates of net photosynthesis persist even during partly cloudy and cooler days, when the measured heat load is markedly less. Reduction in net photosynthesis also occurs in the air-conditioned tent. Because of these observations, we believe our results indicate a real phenomenon, even though natural conditions may be less extreme in undisturbed trees on semiarid sites.
28. J. A. Helms, *Ecology* **46**, 698 (1965).
29. W. Tranquillini, in *The Formation of Wood in Forest Trees*, M. H. Zimmermann, Ed. (Academic Press, New York, 1964), pp. 505–18.
30. H. Hellmers, in preparation.
31. The decreasing efficiency of aging needles may progressively reduce rates of net photosynthesis, so that the youngest needles probably remain the primary food producers [R. O. Freeland, *Plant Physiol.* **27**, 685 (1952)].
32. Other lagging effects may be attributed to phenomena, such as root growth, flower initiation, and fruit growth, which may influence the water balance or compete for food in the tree.
33. See H. C. Fritts, *Monthly Weather Rev.* **93**, 421 and Table 1 (1965).
34. See H. C. Fritts, *Tree-Ring Bull.* **25**, No. 3–4, 5 and Fig. 2 (1963).
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