**Temperature: collection of data and its analysis
for the interpretation of plant growth
and distribution**

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Suggestions for more meaningful collection, processing, and interpretation of temperature data are offered. Our suggestions are based upon characteristics of the organism under study. Research on plant–temperature interactions is reviewed and another approach is illustrated.

Temperature data, collected near shoots and roots of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings in different field situations, were assembled from computer-processed temperature traces. From laboratory studies in which day and night air and soil temperatures were controlled, potential seedling growth each day during a growing season was assessed. Then, by summation, a physiological index, expressed in equivalent units, was calculated to relate the possible effect of the field temperatures to plant distribution. This index was used to interpret the effect of temperature on the distribution of vegetation and patterns of leaf initiation in the field. The importance of interactions with the other environmental factors of moisture, chemicals, light, and mechanical forces is mentioned.

Introduction

Temperature is but one part of the physical environment capable of affecting plant growth and development; in a given environment, the effect of temperature depends upon interactions with other environmental forces. In a real sense, a plant's environment consists only of those forces that modify its moisture, temperature, light, chemical, and mechanical status (Walter 1960; Waring and Major 1964). Before interactions may be studied definitively, efforts must be concentrated upon quantitatively relating these particular forces to their effect upon plants.

A satisfactory procedure for the direct field assessment of plant moisture stress already has been developed (Scholander *et al.* 1965; Waring and Cleary 1967; Boyer 1967). In this paper, we review important stages in the evolution of ideas about meaningful ways to measure temperature as it is related to plant growth and distribution. We suggest ways of measuring temperature that are physiologically more significant. Data that relate plant distribution to temperature are presented. We did not consider the relation of temperature to growth in the field, but with precise growth data, this relation should be easy to evaluate.

Analysis of Temperature Records

Standard meteorological data can be used for interpreting plant responses (Lowry 1966; Lindsey and Newman 1956), but it is preferable that data be collected with the organism in mind. Usually, the geometry of an organism dictates where measurements should be taken. If data representative of shoot and root temperatures are desired, instruments should be placed so these objectives are satisfied; standard or arbitrary placement is often inappropriate.

Temperature data may be analyzed in many ways, but finding a biologically sound approach is difficult. For example, the procedure of calculating "heat sums" has proved helpful in scheduling cultural practices and in estimating harvest time for many crops, but has contributed little to our understanding of plant–temperature relations. Even when heat sum indices have been modified by summing only temperatures above certain minimum (threshold) values, calculating separate indices for day and for night (Brown 1953; Tukey 1952), or by subdividing the growing season into time periods related to stages in the plant's development, temperature is still considered an additive quantity. Because temperature and growth are not related linearly, the heat sum concept, in its conventional form, is biologically invalid (Went 1957).

Some investigators have recognized the non-additiveness of temperature and have attempted to assess the accumulative influence of temperature over segmented portions of the total temperature range (Brown 1953; Tukey 1952). This approach still ignores the contrasting effect of day and night temperature, and the interactions with root temperatures.

Response of plants exposed to artificially controlled temperatures has provided a method of studying plant–temperature relations. Went (1957) developed this approach and, from the performance of different varieties of tomato under controlled temperatures, he was able to predict field performance throughout much of the Central Valley of California. To make such predictions, Went assumed a relation between the sinusoidal pattern suggested from standard Weather Bureau data, and the stable day and night temperature patterns programmed in his controlled environments. Using meteorological records, he subtracted one-fourth the total range in daily temperature from the maximum, and added the same value to the minimum to calculate mean day and mean night temperatures, respectively. Kimball (1959) used similar calculations in the construction of plant climate zones for a number of agricultural crops in California. Went's success in part reflects the stability and predictability of climatic conditions in the agricultural areas of California. As we will show in later discussion, however, this procedure for calculating mean day and night temperatures gives incorrect values if applied to data collected in most ecological studies.

Recent studies have brought to attention the importance of root temperature. Hellmers (1963) showed root temperature can significantly affect the growth of redwood seedlings for a range of controlled shoot temperatures. An ecological interpretation of his data suggests that low root temperatures may restrict the northward distribution of redwood. Wierenga and Hagan (1966) showed that irrigation water at 10 °C reduced the yield of kidney beans by 20% as compared to the yield with water at 25 °C. In Colorado's alpine zone, low soil temperatures contribute to the absence of many non-woody plants (Holway and Ward 1965). Unless root temperatures are considered, ecological interpretations of both field and laboratory studies are difficult to make.

Proper timing of data collection seems obvious, but it is often overlooked. Temperature data must be collected with reference to stages in a plant's development (Azzi 1955). Only by linking temperature with development can the effect of altitudinal and year-to-year climatic variations be analyzed rationally. This implies a shift from a calendar year to one based on phenology.

The most critical requirement for understanding plant–temperature relations is a knowledge of the plant's response to temperature, for the best field data cannot be interpreted without this information. Went's assumption that constant day temperatures are equivalent to averages derived from fluctuating temperatures needs further testing. On this general question, Evans (1963) pointed out that 1-minute cycles of 2 °C produced a significant increase in growth when compared to a more constant temperature regime. Until we can distinguish between "background noise" and significant effects of changes in temperature, appropriate temperature sensors cannot be selected, and temperature data cannot be studied in a fundamental way.

Growth and Development of Douglas Fir in Relation to Temperature

The following examples provide illustrations of how field temperature records may be collected, processed, and interpreted to further understanding of temperature–plant interactions. In the Siskiyou Mountains of southwestern Oregon, we are studying the distribution of vegetation along a number of environmental gradients, one of which is temperature. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) can be used as a reference species because of its wide distribution. Seedlings rather than trees were selected for study, because they represent a more critical stage in plant development.

Temperatures were measured near the growing tips of seedlings (20 cm above ground with an A-frame shielded probe) and near the center of the functioning root masses (20 cm below ground). Continuous records were obtained throughout the growing season. We defined the growing season as that period during the year when new cells are being laid down in samples collected from the secondary cambium of Douglas fir. This period includes the stage when new foliage is developing, as well as the later phase when only secondary cambial activity occurs. In this paper, we will assume moisture stress does not limit the growing season. This permits

comparison between trees with different root systems and represents a potential growing season if irrigation were possible. Only on the driest sites does moisture stress actually stop seedling growth, and rarely does this occur before the middle of August.

Temperature traces from 30-day, circular thermograph charts were directly transcribed to magnetic tape using a CALCOMP digitizer. Integrated averages of day and night temperatures were obtained by computer analysis. Repeat runs on the same trace agreed within 0.5 °C, the same precision as our original data. Day length was defined for each month as the period between sunrise and sunset at a latitude of $42\frac{1}{2}°$ N.

We encountered several problems in the analysis of the field data. These data do not support assumptions of sinusoidal daily temperature patterns, nor do they indicate that minimum temperatures occur only at night (Fig. 1). If a sinusoidal pattern existed, the

*Lavender, D. P. Some effects of air and soil temperatures upon the growth of Douglas-fir. Manuscript in preparation.

mean would be 64% of the range rather than 50%. On September 20 and 21 (Fig. 1), the average night temperatures were equal to or above the average for the day period, which would be an impossibility with the procedures followed by Went. The short record shown in Fig. 1 also illustrates the disadvantage of averaging one day's temperature with another's. If days representing the passage of storm fronts, such as September 19, in Fig. 1, were averaged with more typical days, a misrepresentative, intermediate average would result.

Interpretation of field data requires that we define the influence of temperature on Douglas-fir seedlings. Data supplied by Lavender* (unpublished) provided the basis for our interpretation. Seedlings from eight geographic sources of Douglas-fir seed were grown for 6 months under various combinations of controlled day and night air and soil temperatures. Results showed that the influence of day temperature and soil temperature greatly outweighed that of night temperature during the growth period (Fig. 2). We have averaged out the small effect of night temperature and present a pre-
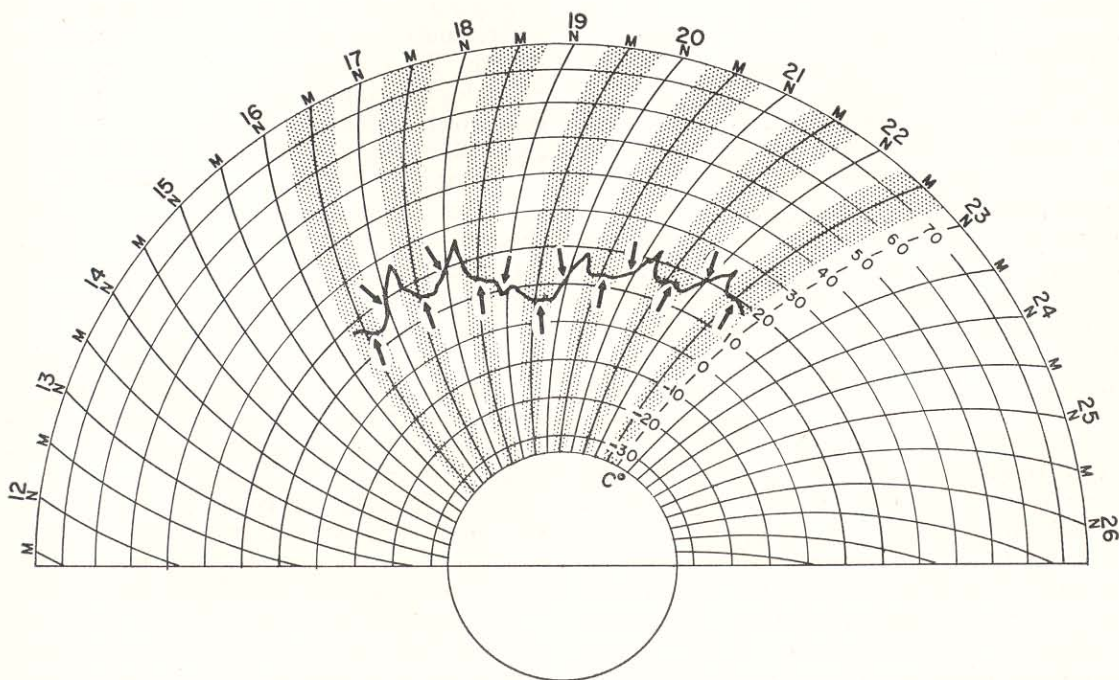

FIG. 1. Illustration of a temperature trace recorded under a forest canopy during September. Shaded area represents the night; clear area represents the day. Arrows indicate the integrated average temperature during day and night.
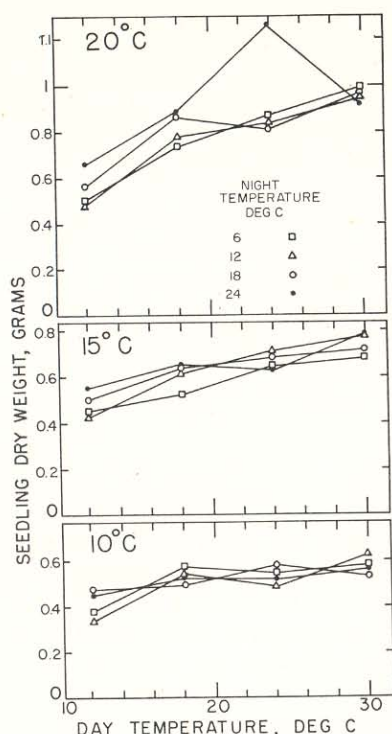
FIG. 2. Growth of Douglas-fir seedlings in relation to constant day and night air temperatures. The three graphs illustrate the growth response at constant soil temperatures of 20°, 15°, and 10 °C. Experimental conditions at each point were replicated and represent the average growth of 80 seedlings from eight seed sources after 6 months (Lavender 1968).
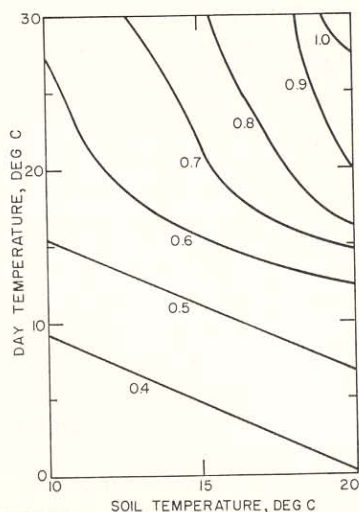

FIG. 3. Relative growth of Douglas-fir seedlings (from Fig. 2) in relation to constant day and soil temperatures where the contours represent equal fractions of optimum growth. The effect of different night temperatures is slight as shown in Fig. 2, and has been averaged out.

diction of potential growth (Fig. 3) as a fraction of the maximum observed under experimental conditions indicated in Fig. 2. We refer to the temperature regime favoring maximum dry weight (and height) growth as the optimum. Brix (1967) has shown that at temperatures above 30 °C growth of Douglas fir is greatly reduced.

From field-temperature traces, integrated averages were obtained for the entire day and for the night period. The relative growth of Douglas-fir seedlings under controlled temperatures (Fig. 3) served to estimate the potential growth of seedlings in the field. For example, an average day temperature of 30 °C and an average soil (root) temperature of 20 °C would represent optimum temperature conditions. We refer to such a day as an optimum temperature day (OTD). With an average temperature of 15 °C and a soil temperature of 10 °C, only 0.5 of the optimum growth would be possible (0.5 OTD). The temperature effect during a given growth period may be calculated by accumulating the daily fractions of estimated growth. The conversion of temperatures to a physiological unit produces a modified heat sum which eliminates the shortcomings of the conventional heat sum concept. This procedure is admittedly still crude, but further refinements await more physiological data concerning changes in a plant's temperature requirements with changes in its development and studies of interactions with the other variables. With more precise plant response data than is now available, we could carry out this integration at periods much shorter than one day (i.e. hourly or even 5-minute intervals). With such information programmed into a computer, an estimate of growth for a plant in a known stage of development could be made under any given environment (expressed in terms of moisture stress, temperature regime, light quality and intensity, nutritional stress, etc.).

The question whether plants growing on different sites require equivalent temperature regimes to reach the same stage of development can be answered by comparing daily temperature regimes in terms of their effect upon growth. In Table I, the temperature effect upon growth

TABLE I

Comparison of temperatures and their effect on growth of Douglas-fir seedlings during the period from bud swell to full leaf at eight plots in the Siskiyou Mountains

Plot	Date of bud swell	Days to full leaf	Av. day temp., °C	Av. night temp., °C	Av. soil temp., °C	Optimum temp. days for period
1	6/18	20	15.6	10.2	8.8	9.2
2	6/2	29	13.4	10.0	9.1	11.5
3	5/24	29	12.9	8.3	9.9	12.3
4	6/6	23	15.3	9.2	11.6	11.9
5	5/10	28	14.6	9.3	9.6	12.6
6	5/16	31	14.2	9.5	11.7	9.9
7	5/10	21	15.0	10.6	10.6	10.0
8	5/3	23	12.2	12.4	8.3	8.7
			14.3±1.2*	10.0±1.2*	10.0±1.2*	10.8±1.5*

*One standard deviation.

TABLE II

Comparison of accumulated temperature effect throughout the entire growing season (water not limiting) for eight plots characterized by differences in physiography and vegetation

Plot	Elevation, m	Slope, %	Aspect	Potential growing season, days	Temperature effect†	Vegetation type*
1	1530	10	N	95	47.3	PIe, PSm, ABc
2	1800	60	WNW	111	61.8	ABc, PSm
3	1650	25	W	120	74.0	ABc, Pp, PSm
4	1730	70	WSW	107	77.2	Pp, PSm
5	840	70	NNW	134	83.3	PSm, TAb
6	1400	40	SW	128	95.5	Pp, PSm, Qk
7	870	45	N	134	98.1	PSm, Qk, Pp
8	600	75	N	141	94.0	PSm, Qk, Qg

*Abbreviations follow Day (1967): ABc = *Abies concolor*, PIe = *Picea engelmannii*, Pp = *Pinus ponderosa*, PSm = *Pseudotsuga menziesii*, Qk = *Quercus kelloggii*, Qg = *Quercus garryana*, TAb = *Taxus brevifolia*.
†Temperature effect is expressed as optimum temperature days in potential growing season.

during the period from bud swell to full leaf is compared on eight different sites, without regard to the time of initiation on the site in question. At this stage in growth, moisture stress is comparatively low on all sites. We calculated that the equivalent of about 11 OTD would be required to progress from bud swell to full leaf. Although phenological observations may be in error by 3 or 4 days, the inference that rate of development reflects a non-linear response to temperature, similar to that shown in Fig. 3, is supported.

Average day, night, and soil temperatures during the period from bud swell to full leaf do appear similar. This agreement, however, may be more apparent than real. The problem of averaging one day with another has already been mentioned. Although the few days representing storm fronts (with less than 5°C

variation between extremes) have been excluded in arriving at the averages presented in Table I, the values are still misleading. The average temperatures given for each of the eight plots is a combination not observed on any one day during the 20- to 31-day period. Days representing storm fronts were included when calculating OTD.

In Table II, we have extended the comparison of the eight plots to an entire growing season to note any relation between estimated temperature effect and plant distribution. Although the growing season may be quite similar, as it is for plot 1 and plot 4, the effect of temperature upon growth can be strikingly different (47.3 compared with 77.2 OTD). Too, physiographic conditions may differ substantially, as they do at plot 6 and plot 8, yet a similar temperature effect results.

Where the number of optimum temperature days during the growing season totalled less than 40, Douglas fir was absent in our Siskiyou study area. Such sites are inhabited exclusively by forests of *Abies magnifica* var. *shastensis* Lem. and *Tsuga mertensiana* (Bong.) Sarg. Although temperature only in part controls plant distribution (Waring and Cleary 1967), a definite influence is apparent. On the cooler sites (OTD below 50) *Picea engelmannii* Parry grows; on intermediate sites (OTD 62–83), some with moisture regimes similar to those where *Picea* is found, *Abies concolor* Lindl. and *Pseudotsuga menziesii* dominate. Oaks such as *Quercus garryana* Dougl. and *Quercus kelloggii* Newb. are on the warmest sites; they do not occur until the OTD total for Douglas fir exceeds 90.

Partly for explanatory purposes, partly for the assessment of potential growth, and partly for lack of data, we have discussed temperature mainly as an independent variable. Temperature, of course, is not an independent variable, but interacts with the other environmental forces. The independent action of the other forces, such as moisture stress, can be studied in a way similar to our treatment of temperature. Combined experiments, in which more than one variable is studied, are necessary. Growth of Douglas fir in relation to light and temperature has been studied recently by Brix (1967). The relations between moisture, temperature, and the distribution of Douglas fir in the Siskiyou mountains of southern Oregon are shown in Fig. 4. The highest productivity of Douglas fir occurs at 80 OTD with a maximum moisture stress of 6 atmospheres in early morning, and low productivity is found where both temperature and moisture stress are extreme, either high or low. A system analysis of the plant's responses to the combined effect of all the environmental forces is a logical next step in the integration of factors affecting plant growth and distribution.
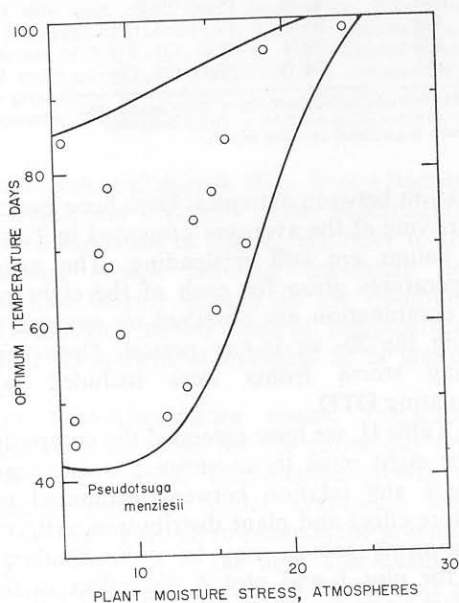
FIG. 4. Distribution of Douglas fir along gradients of temperature and plant moisture stress. The plant moisture stress gradient is defined as the minimum stress measured at the peak of the drought in early September. Points shown are for individual sites in the Siskiyou study where Douglas fir is present.

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