A PROCEDURE FOR CALCULATING DAILY MOISTURE STRESS AND ITS UTILITY IN REGRESSIONS OF TREE GROWTH ON WEATHER

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Abstract. A method is described for computing daily values of moisture stress on forest vegetation, or water deficits, based on the differences between Thornthwaite's potential evapotranspiration and computed soil-moisture depletion. More realistic functions are used for soil-moisture depletion on specific soil types than have been customary. These functions relate daily rates of depletion to characteristics of soil-moisture tension. Separate functions account for surface soil wetting and drying processes following rain and during dry periods.

Two methods of summarizing the day-by-day distribution of moisture stress are illustrated. One utilizes directly accumulated stress values during such logical growth intervals as periods of leaf flushing or bud setting. In an example of a regression of red pine shoot growth on water deficits, 72% of the variation in annual growth was accounted for by moisture stress during certain periods of both previous and current growing seasons.

The second method computes moisture stress and weather variables as functions of time over two growing seasons and utilizes the coefficients of orthogonal polynomials as independent variables in regressions of growth. In an example of western white pine basal area growth utilizing this latter method, moisture stress accounted for a 28% reduction in the variance of growth remaining after the effects of temperature and precipitation *per se* had been removed. The complete model accounted for 78% of the total variation.

INTRODUCTION

Within-season growth responses of forest trees and most other woody vegetation are more sensitive to fluctuations in soil moisture than to any other environmental factors (Kramer and Kozlowski 1960, Kozlowski 1964). Through internal water deficits both shoot extension and cambial activity are known to be limited by low levels of soil moisture (e.g., Fraser 1962, Kramer 1962, Zahner 1962, Lotan and Zahner 1963). Day-by-day expressions of weather and water-balance factors are necessary to evaluate the within-season character of tree growth, and the investigator must be provided with a means of summarizing detailed measurements into a useful form.

Statistical methods for computing seasonal trends of environmental factors and their influence on growth have been available for some time (Fisher 1925, Lorenz 1931, cited by Schumacher and Meyer 1937). The necessary calculations are lengthy, however, and their use has been limited to relatively few applications (for example, Schumacher and Meyer 1937, Houseman 1942).

The objective of this paper is to describe and to justify procedures that utilize an electronic computer, facilitating daily evaluation of growth conditions, and providing a summarization technique that retains the day-by-day progression of growth conditions. Two detailed examples of the application of the method are given.

Ecological literature abounds with attempts to relate plant growth, trees in particular, to weather variables. Most are only partially successful, due to the treatment of weather measurements as absolute values. For examples, Fritts (1960) and Tryon, Cantrell, and Carvell (1957) report some significant correlations between tree growth and inches of precipitation and degrees of temperature *per se,* but none accounted for a large portion of the growth variance. Fritts (1960) went further and, by adding the effect of soil moisture and other factors, accounted for roughly 75% of the variation in radial growth of *Fagus grandifolia* Ehrh. in Ohio. McClurkin (1958) found that soil moisture alone accounted for very little of the variation in radial growth of *Pinus echinata* Mill. in Mississippi. Campbell and Rich (1961), on the other hand, related both rainfall and soil-moisture patterns to range-grass production and found soil moisture to be the more significant of the two. Thus, a more realistic method is required, one which can detect the logic in the following examples: Little effect on growth will result from an inch of rain during the growing season when the soil is already at field capacity from previous rains, or little positive effect on growth will result from warm temperatures when the soil is dry; however, the same inch of rain when the soil is dry, or the same warm temperatures when the soil is moist, will be positively correlated with growth. The water-balance approach does just this, by estimating water stress on the vegetation itself.

Water stress is difficult to evaluate in the field by leaf water potential or other direct methods. Several convenient indirect methods have been proposed, however, with the use of empirical computations from potential evapotranspiration and soil-moisture levels (Thornthwaite and Mather 1955, Zahner 1956, Havens et al. 1958, Arkley and Ulrich 1962, Bassett 1964, and others).

It is desirable to have a means of evaluating and summarizing within-season variations of all of these factors. Daily values of temperature and precipitation are generally available for most studies. At the same time, empirical methods are available for computation of the water balance, and consequently for estimation of soil-moisture levels, utilizing these two weather variables (e.g., Thornthwaite 1948, Penman 1949, van Bavel 1956, Nash 1963). Electronic computer programs have successfully used the Thornthwaite (1948) formula in computations of daily water balance (Englebrecht 1961).

As Penman (1956), Tanner (1960), and Pelton, King, and Tanner (1960) clearly point out, the use of temperature and rainfall data alone does not account for the complete water balance on a given site. An energy balance is more realistic (as Penman 1956), but requires atmospheric data of radiation, wind, and other variables which are not normally available in most ecological studies. Nash (1963) has improved the Thornthwaite and Mather (1955) method by taking into account radiation differences due to slope and aspect. It is hoped that the following discussion will justify the simplified approach taken in this paper to the computation of soil water deficits and internal moisture stress on vegetation.

Basic Considerations

In upland coniferous and hardwood forests of the United States and Canada, the total water available to tree roots is, for the most part, only that held in storage by the soil particles themselves. Additional sources, such as lateral underground seepage or shallow water tables, are often absent. The amount of stored water varies with soil texture and structure, with thickness of different soil horizons and with other soil characteristics, yet can be estimated or measured with a fair degree of accuracy.

When rain or snowmelt has wet the soil for the entire depth of the root zone, and after excess water has drained away, the quantity of available water under a forest stand may vary on different soils from the equivalent of only 2 inches of rainfall to as much as 15 inches. Additional water may, in some areas, come from seasonal, perched, or temporary water tables which are common in parts of the country. Water depletion on such sites behaves much as in well-drained soils, once the capillary fringe falls below the major root zone. Shallow permanent water tables are common in parts of the Coastal Plains, the Great Lakes region, and eastern Canada. Such forest sites present moisture problems quite different from those which are characteristic of well-drained sites considered in the remainder of this paper.

Soil-moisture depletion

On upland sites, water absorption by roots occurs at its maximum rate under given weather conditions when the soil is at maximum storage capacity (Penman 1949, Slatyer 1956, 1957*b*, 1960). As the soil is depleted of moisture, the rate of absorption usually decreases as water-film adjustment and transport to root surfaces becomes slower. As the soil approaches wilting point, during long periods without rain, actual water utilization may become negligible. With each rainfall rates of absorption and evapotranspiration pick up immediately (e.g., Slatyer 1956; Bloodworth, Page, and Cowley 1956). It is when the soil is moist and in the process of drying that it becomes important to know how rapidly and how much moisture is being made available day-by-day from storage. The amount of water moving from the soil to the plant each day obviously regulates the physiological functioning of the plant on that day.

Several methods are available for predicting soil-moisture depletion and accretion trends, based on weather and soil data (Penman 1949, 1956, Blaney and Criddle 1950, Mather 1954, Carlson, Reinhart and Horton 1956, van Bavel 1956, Havens et al. 1958, Stearns and Carlson 1960). Most of these techniques do not permit curvilinear depletion of water as a result of increasing soil-moisture tension, or they do not provide for realistic surface soil wetting following rains. Therefore, it is felt that further refinement in computational technique is necessary, based on concepts reviewed by Zahner (1966) and summarized in the following discussion.

The soil-moisture tension–soil-moisture content relationship (also known as the soil-moisture characteristic curve and the moisture-release curve) holds the key to the shape of the soil-mois-

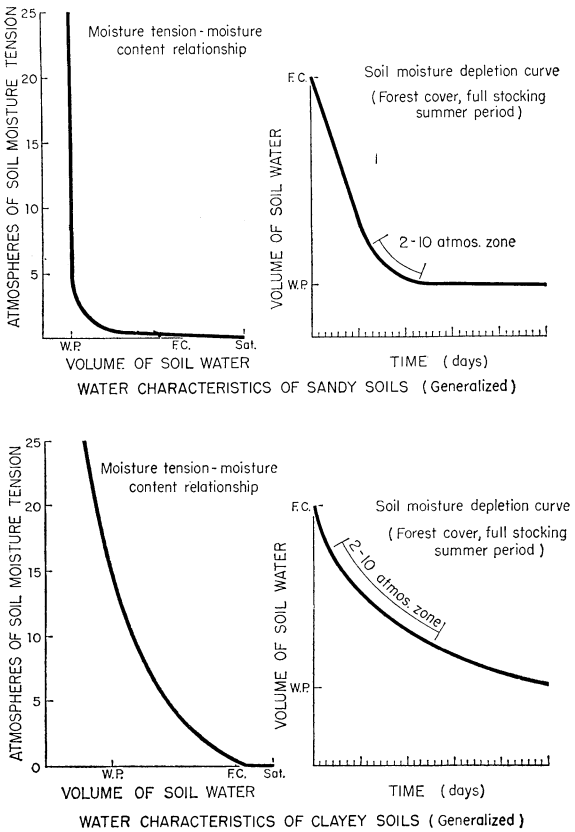

FIG. 1. Generalized soil-moisture depletion curves and corresponding moisture tension-moisture content curves for sandy soils (top) and clayey soils (bottom) (for root zone of complete vegetative cover under constant high potential evapotranspiration). Note linear depletion of soil moisture until water remaining in soil is held at tensions greater than approximately 2 atm.

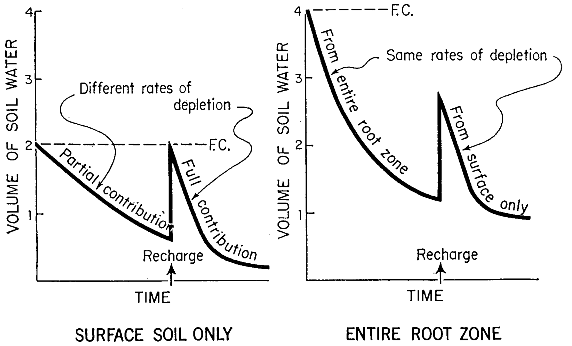

Fig. 2. Generalized example of moisture depletion from the surface soil, when entire root zone is depleting from field capacity (at left on time scale of both graphs), and following a surface soil recharge (near middle on time scale of both graphs). Both graphs represent the same soil profile uniformly occupied by roots during a period of constant high potential evapotranspiration.

ture depletion curve (Kramer 1949, Richards and Wadleigh 1952, Ashcroft and Taylor 1953, Slatyer 1957a, 1960, Gardner and Ehlig 1963). In sandy soils, for example (Fig. 1, top) where up to 70% of the total available water is held at tensions of less than 2 atm, depletion is approximately linear between 0 and 2 atm of soil-moisture tension. As the soil dries to greater tensions, the depletion curve strongly suggests an exponential function with time (Veihmeyer 1956), and depletion virtually stops when the soil is between 5 and 30 atm of moisture tension. In clay loam or heavier soils (Fig. 1, bottom), the moisture-release curve is more concave throughout its range, and the depletion curve is correspondingly asymptotic from the beginning. Most soils exhibit water-release curves that result in combinations of these types of depletion trends. Empirical depletion functions for various soil textures used in this paper are discussed in detail by Zahner (1966).

Soil water is withdrawn from zones where it is most readily available and is removed most rapidly where root density is highest (Taylor and Haddock 1956, Vasquez and Taylor 1958). Forest root distribution is inversely proportional to soil depth, even in deeper, well-aerated soil horizons, and water is thus withdrawn in inverse proportion to depth. Where effective root depth is severely restricted by poor aeration, most water is supplied from surface layers (e.g., Zahner 1955). Where roots do not permeate the soil completely, water moves to roots by capillary adjustment so slowly that, in effect, it is not available for absorption except over long periods of time (Kramer 1949, Richards and Wadleigh 1952). When partially wet by a summer thunderstorm a dry soil is depleted rapidly from the moist zone at the soil surface (Fig. 2), while practically no water is removed from dryer layers below the wetted front (reviewed by Slatyer 1957*a*). Since surface horizons are recharged frequently by rain, the most prolific root penetration occurs in this zone. This concentration of roots, in turn, results in a very rapid water depletion from surface layers. On the other hand, when the entire soil profile is depleting from field capacity, the surface soil contributes water to transpiration only in proportion to the root occupancy.

Stand disturbances, such as partial cuttings, which reduce root occupancy, also modify patterns of soil-moisture depletion (reviewed by Zahner 1959). Although depletion functions can be written to account for such disturbances this paper considers methods well suited to land areas of uniformly stocked forest stands, perennial crop and pasture lands, and other types of vegetation which occupy fully a definable volume of soil.

Moisture stress

Vegetation experiences internal moisture stress whenever the rate of transpiration exceeds the rate of soil-water absorption (reviewed by Kramer and Kozlowski 1960, Kramer 1962). Even when the soil is at field capacity, stress doubtless occurs to some degree on warm days. For the sake of simplicity, however, it seems reasonable to assume that deficits are minimum when the soil is at field capacity or is losing readily available water held at tensions of less than 2 atm. As the soil dries to greater moisture tensions, stress becomes ever greater within vegetative tissue, depending on the magnitude of the potential evapotranspiration.

A logical estimate of the magnitude of internal moisture stress is some measure of the lag of absorption behind transpiration. A quantitative evaluation of moisture stress can be computed from the day-to-day differences between the amount of water that is actually transpired (supplied from soil) and that which potentially could be transpired if soil moisture were at tensions less than 2 atm. Summations of daily values of these differences yield estimates of periods of relatively high and low moisture stress that are useful in studies of growth-response correlations (Zahner 1956, Campbell and Rich 1961, Smith and Wilsie 1961, Arkley and Ulrich 1962, Bassett 1964).

Employed in this sense, "moisture stress" on vegetation is numerically equal to the "water deficit" as defined by Thornthwaite and Mather (1955). The two terms will be used synonymously through the remainder of this paper. Thornthwaite's (1948) potential evapotranspiration is probably satisfactory for most calculations of moisture stress in temperate and cool climates which support forest cover or tall grass prairie. The scope of this paper does not permit an evaluation of Thornthwaite's method applied to other cover types, especially to sparsely vegetated arid or tundra lands or to heavily vegetated tropical types, in which soil-moisture utilization is related to unusual root occupancies.

Inventory of Soil Moisture and Moisture Stress

Upland forested areas of deep, light- and medium-textured soils offer the simplest models for developing mathematical relationships between soil-moisture content and time. The complete vegetative cover insures full root occupancy of the soil, and the litter mulch gives protection against soil puddling and crusting. Relatively level topography eliminates the need of correcting for slope and aspect as proposed by Nash (1963). Overland run-off is negligible on such sites, for all growing season rainfall either contributes to soil-moisture recharge or, if soil storage is filled, percolates to ground water. Soil-moisture characteristic curves for loam soils indicate that approximately 50% of total available water is held at tensions of less than 2 atm. Thus much of the stored water on such sites is quickly extracted through evapotranspiration during periods of high potential evapotranspiration.

As an example, a silt-loam terrace soil in southern Arkansas stores a total of 12 inches of water available in the root zone of a typical well-stocked pine or hardwood forest (Moyle and Zahner 1954). Therefore, it is assumed that approximately 6 inches of water are readily extractable at a rate essentially equal to the potential evapotranspiration, and the remaining 6 inches are extractable at a fraction of the potential rate, equal roughly to the proportion of available water remaining in the soil. When the entire profile is being depleted, mathematical computations for daily water use might be as follows:

1. When the current soil-moisture level is greater than, or equal to, 50% of total storage, depletion equals potential evapotranspiration for the day.
2. When the current soil-moisture level is less than 50% of total storage, daily depletion equals potential evapotranspiration times the factor current soil-moisture level/total storage.

Such a function allows for essentially linear depletion until soil-moisture tension becomes so high that depletion is reduced gradually to a curvilinear function. A depletion trend using the above function is illustrated in Fig. 3. The data are taken from the same soil, forest cover, and period (1953) as measured and reported by Moyle and Zahner (1954) in their Fig. 6. Following each rain, depletion is linear at the potential rate until the amount of recharge is removed; depletion then returns to the original rate, either linear, as following the small recharge on June 11 in Fig. 3, or curvilinear, as following the recharges subsequent to June 20.

Moisture stress on the vegetation, measured as the difference between potential evapotranspiration and daily soil-moisture depletion, in the above example (Fig. 3) begins on June 18 when computed soil moisture drops to 50% of total storage. Stress increases daily from June 18 to June 21, when the recharged surface soil drops stress back to zero. The recharge of June 21 is quickly depleted, and daily stress values again are high. It is not realistic to assume that large recharges, as on July 21-23 in this example, are entirely available at the potential rate. Based on trial and error, large recharges are dealt with in two portions. That portion in excess of 2 inches goes into the main soil-moisture account, so that a maximum of 2 inches may be accumulated in the recharge account for linear depletion when the main account is below 50% full storage. Thus from July 22 to August 2 there is no deficit because depletion occurs at the potential rate until the recharge maximum of 2 inches is used. On August 3 deficits are again recorded as the moisture is drawn uniformly from the entire root zone at less than full potential rate. That this function satisfactorily represents soil-moisture depletion for a silt-loam soil, when compared with the measured depletion trend, is evident in Fig. 3.

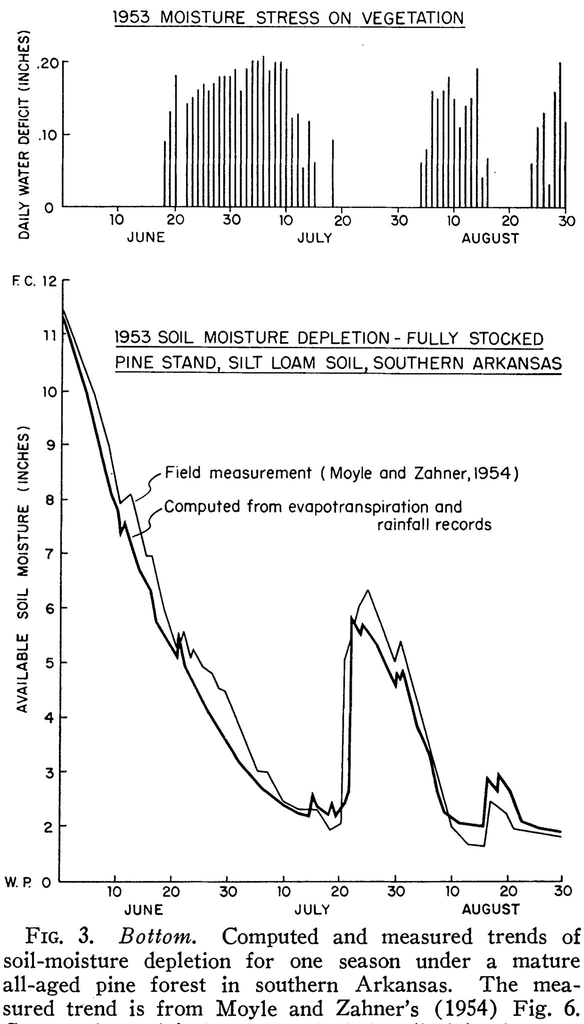

FIG. 3. *Bottom.* Computed and measured trends of soil-moisture depletion for one season under a mature all-aged pine forest in southern Arkansas. The measured trend is from Moyle and Zahner's (1954) Fig. 6. Computed trend is by the method described in the text, using the 1953 records of the weather station at the Crossett Experimental Forest, USDA Forest Service, located 200 yards from the forest stand.

Top. Diagram of daily water deficits computed as the difference between calculated potential evapotranspiration and the quantity of water depleted from the soil each day.

Meaningful moisture-stress trends can still be computed from imprecise estimates of soil water-storage capacity or of the amount of water held at low tensions. Where the estimate may be in error by as much as 1 or 2 inches of available water, year-to-year variations of stress on the same site are similarly biased and therefore permit valid comparisons of relative stress. Site-to-site comparisons, however, are more subject to error if estimates of storage capacities are poor, and particularly if estimates of soil texture are too generalized. For example, a forest site in eastern United States on a sandy loam soil which stores 8 inches of available water, most of which is held at low tensions, may accumulate a water deficit of 10 inches during a moderately dry year; an adjacent forest site on a shallow clay soil which stores 6 inches of available water, only half of which is held at low tension, will accumulate a water deficit of 15 inches during the same period.

SUMMARIZING WEATHER AND WATER-DEFICIT VARIABLES

Summaries of day-by-day calculations of weather conditions and their effect on moisture stress are useful not only by individual days, but also when accumulated for logical periods within the growing season and by seasonal trends. The electronic computer program described later summarizes output data in two ways: first for direct utilization, as sums of daily values of moisture stress during an interval (illustrated in Fig. 3, top); and second for indirect use, as parameters of the seasonal march of daily values of moisture stress, precipitation, or temperature, expressed as a polynomial function of time throughout the season.

The method of computing a regression of growth on weather variables using the second type of summarization was originally conceived by R. A. Fisher in 1925. Later his method was applied to growth of trees, range grasses, and crops with good results (Schumacher and Meyer 1937, Lister and Schumacher 1937, Schumacher and Day 1939, Houseman 1942). Seasonal trends of weather factors are computed by fitting a polynomial to their daily values. Coefficients of this polynomial are then used as independent variables in a growth regression. This analysis differs from the daily growth–daily weather regressions proposed by Fritts (1960), in that annual growth is related to the annual progression of environmental factors. The dependent variable, growth, is usually some quantity of annual increment, such as centimeters of height, square meters of basal area, or grams of dry weight, or some annual deviation of average annual increment, such as percentage of normal growth. The seasonal trends of weather, soil moisture, or water deficits set the polynomial coefficients which are in turn tested through regression for their effects on growth.

Relation between models using the two types of variables

To illustrate the connection between the two ways of generating weather variables for use in growth regressions, consider growth as a phenomenon that starts and is completed in four natural intervals (as shoot flushing, needle elongation, bud setting, and food storage, for example). Then it would be natural to explain the growth variation (y) as a regression on the four variables representing the causative factor, s_i, in the i^{th} interval.

The model is then:

$$y = \sum_{i=1}^{4} a_i s_i \tag{1}$$

and the constants would be estimated by a least-square method. This method is illustrated by the red pine example later in this paper (Fig. 4).

However, if consideration of the process makes it reasonable to assume that these constants change from interval to interval in a smooth fashion, as in the case of basal area increase, then they might be represented by a low order polynomial in time. For example:

$$a_i = c_o + c_1 i + c_2 i^2 \tag{2}$$

Substituting this estimate of the constants in the original model (1):

$$y = \sum_{i=1}^{4} (c_o + c_1 i + c_2 i^2)\, s_i \tag{3}$$

or

$$y = c_o \Sigma s_i + c_i \Sigma i s_i + c_2 \Sigma i^2 s_i \tag{4}$$

This last model (4) is mathematically identical to an orthogonal polynomial model (Houseman 1942, for example), but in a less convenient form for solution if the highest power of i in equation (2) is not predetermined.

It is possible, by computing a weighted average of values of equation (2) over several adjacent intervals, to arrive at the regression coefficient that would result if the model (1) were applied to the wider intervals. In the western white pine example, later in this paper, relation (2) alone is extended to the fourth power of i (Fig. 6).

Interpretation of the polynomial model for perennial plants

For annual plants the interpretation of the effects of weather implicit in the model has been well described by the several authors previously cited. For perennial species and especially trees, however, there is a pronounced ante-dependence in the growth response. That is, the growth of the individual in the year previous is, *per se,* predictive of the growth in the current year. For example, if growth is poor one year because of adverse weather during that year, then growth will tend to be poor also the following year, independent of both growth and weather of the following year. Current growth is governed not only by environment but also by preconditioned physiological and anatomical characteristics which may be manifested in previous growth.

Thus, the model appropriate for perennial plants is somewhat more complex than that described by previous authors. Consider the problem of evaluating current growth (y_i) using only one weather factor, say moisture stress (S_i). Then the model would be:

$$y_i = b_1 y_{i-1} + B_2 S_i + B_3 S_{i-1} \tag{5}$$

where upper case symbols are used to represent vector-valued variables. B and b are regression coefficients.

The derivative of y_i with respect to the moisture stress on the j^{th} day of the i^{th} season (S_{ij}) is the partial regression coefficient of growth on the j^{th} day's moisture stress. It represents the effect on the total year's growth that can be attributed to moisture stress on that day.

To demonstrate the differentiation, the model in equation (5) is rewritten in full for stress of the preceding year:

$$y_i = b_1^2 y_{i-2} + (B_2 b_1 + B_3)\, S_{i-1} + B_2 S_i + B_3 S_{i-2} \tag{6}$$

The k^{th} term of the vector

$$S_{i-1} = \sum_{j-1}^{n} C_{kj}\, s_{i-1,j}$$

for a season of n days where the c_{kj} are the values of the orthogonal polynomial for the k^{th} power term on the j^{th} day of the season. Hence, the derivative of equation (6) with respect to $s_{i-1,j}$ is:

$$\frac{d\, y_i}{d\, s_{i-1,j}} = \sum_{k=1}^{n} (b_{2k}\, b_1 + b_{3k})\, C_{kj} \tag{7}$$

Interpretations of several weather effects using this approach are illustrated by the example of western white pine presented later in this paper. The trends of their effects through the season, obtained by solving equation (7), are shown in Fig. 6.

The computer program[1]

Input data.—The principal input variables to this program are daily weather data, relative day length, and periodic estimates of the available moisture stored in the soil. In addition, a separate function is provided to describe the moisture-depletion curve corresponding to physical characteristics of particular soils. Suiting the function to the soil permits more refined estimates of daily withdrawals of moisture from storage than would be possible if a single function were applied universally.

Daily observations of maximum and minimum temperature and amount of precipitation punched according to the standard U. S. Weather Bureau format for cooperative climatological stations are the weather data input. If less than a full year's daily data are entered, an estimate of Thornthwaite's (1948) heat index for the omitted months must be supplied.

Measurements or estimates of available moisture in storage must be supplied at the start of the period of water-balance calculation. If available, subsequent observations of soil moisture can be entered into the calculations on appropriate dates to correct water-balance bookkeeping. Water-balance data can be computed concurrently for as many as 10 different capacities of soil-moisture storage to which the same climatological data and depletion curves apply.

Computations.—As noted above, moisture stress is computed as the difference between potential evapotranspiration and moisture withdrawn from the soil. The withdrawal, in turn, depends on the potential evapotranspiration and the amount of water currently in storage. Potential evapotranspiration is calculated according to equations developed by Thornthwaite (1948).

Soil moisture is recorded in two accounts—the main storage account and the recharge storage account. The main storage account is used to represent moisture in the entire root zone, in which depletion starts with the soil at field capacity. By keeping these two accounts separate, it is possible to recognize in the logic of the program the fact that moisture in the recharge storage is available at lower tensions than it would be if the same amount of moisture were distributed uniformly throughout the mantle (i.e., simply added to the main storage account). The depletion function has a separate entry for each storage account.

The daily water-balance computations begin with the precipitation deficit, that is, potential evapotranspiration minus precipitation. Whenever the deficit is positive, moisture is drawn first from recharge storage at the depletion rate calculated for this storage category and its present level. If recharge storage is inadequate to meet the calculated withdrawal, the main storage category is drawn upon according to the remaining deficit and the amount of moisture in the main storage account. Moisture stress for the day is then the difference between the precipitation deficit and the water supplied from the two soil-moisture accounts.

Precipitation exceeding potential evapotranspiration is added to the recharge account. If the sum of the two storage accounts exceeds the field capacity of the soil, the excess is added to a record of moisture surplus, the main storage account is set to field capacity, and the recharge account is set to zero.

Output variables.—Execution of this program yields two types of output. The first type is a printed record of daily calculations of the water balance: (a) precipitation, (b) difference between potential evapotranspiration and precipitation, (c) soil moisture stored in the entire root zone, (d) soil moisture in storage from surface recharge by current rainfall, (e) moisture stress, and (f) accumulated moisture stress.

The second type of output is composed of two sets of punched cards that are utilized in further analyses. One set of cards characterizes, by means of coefficients of orthogonal polynomials to the fifth degree (Anderson and Houseman 1942), the day-by-day progression of (a) daily mean temperature, (b) daily precipitation, and (c) daily moisture stress. The other set of cards contains the daily values of moisture stress for the growing season. The latter are used in a related program that summarizes moisture stress for any combination of periods, either arbitrary (as months) or logical (as growth periods), at the user's discretion.

Examples

To illustrate how the method described in this paper may be applied to ecological studies, two examples are presented on widely different subjects.

Red pine shoot growth in Michigan: An analysis utilizing water deficits by periods

It is generally recognized that shoot growth in red pine (*Pinus resinosa* Ait.), which makes one flush of height growth each year, is influenced by the growing conditions of 2 years. The previous year's weather affects bud development and food

[1] This program was written originally for the IBM 650 computer, and later modified for the IBM 7090; printouts are available in FORTRAN and MAD languages; binary decks may be obtained in specific cases upon correspondence with either author.

storage, while weather in the current year influences elongation of the shoot directly. Compilation of daily values of moisture stress provides a technique for evaluating the 2-year effect of weather on shoot growth in red pine.

For this example, the data from five 30- to 40-year-old red pine plantations growing on glacial outwash sand in northern Lower Michigan are used. Stem analysis of dominant trees provided accurate shoot growth measurements of each of the plantations for each year over the 10-year period 1951 through 1960.

Data on precipitation and maximum and minimum temperatures were taken from standard U. S. Weather Bureau 1009 IBM cards for five weather stations located within 3 miles of the respective plantations. The soil-moisture tension–soil-moisture content relation of sandy soils indicated an average storage capacity of 3.75 inches of available water in the root zones of these five sites (all on nearly identical soils), of which 70% by volume is held at tensions of less than 2 atm. Employing the appropriate soil-moisture depletion function, daily values of moisture stress were computed and summarized for the growing seasons of the years 1950 through 1960 for each of the five sites.

Previous observations had shown that elongation of red pine shoots ceases each year, regardless of soil-moisture conditions, in early July in this part of Michigan (Lotan and Zahner 1963). Thus the influence of weather on shoot elongation during the current growing season should not extend beyond the middle of July in any year. Buds for current year shoot growth are set by early July of the previous year; thus weather prior to mid-June of any year probably has little influence on bud formation and development of tissue within the bud. Needle elongation in red pine and production of new photosynthetic area occurs from mid-June to early September. Finally, during the late season predormancy period from September until the end of October, little or no new growth normally occurs in red pine; but conditions often favor continuation of photosynthesis and probable food storage for the subsequent year's spring growth.

This information provided a basis for accumulating daily values of moisture stress (water deficits) for four periods that logically influence current shoot growth in red pine: (1) previous year June 15–July 15, the bud-set period; (2) previous year June 15–August 31, the needle-elongation period; (3) previous year September 1–October 25, the predormancy food-storage period; and (4) current year May 1–July 15, the

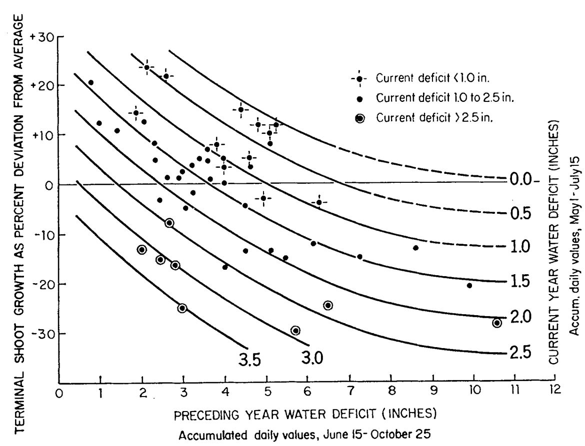

FIG. 4. Computed relation ($R = .85$) between deviations from average shoot growth in red pine and previous and current season's water deficits. Plotted points are individual observations.

shoot-elongation period. Accumulated total water deficits for these periods, their squared values, and various combinations and interactions were used as independent variables in a multiple regression analysis. Percentage deviation from average shoot growth was the dependent variable for each of the 10 years and five pine plantations. Annual growth deviations from a second degree equation of height increment over age were calculated separately for each plantation, in order to minimize effects of site variation and tree size.

A stepwise regression analysis resulted in the following highly significant relationship, accounting for 72% of the variation in annual shoot growth ($R = 0.85$):

Deviation from average growth $= a_0 + a_1$ (water deficit of current year shoot-elongation period) $+ a_2$ (sum of deficits of preceding year needle-elongation plus food-storage periods) $+ a_3$ (square of sum of deficits for preceding year).

This relationship, illustrated graphically in Fig. 4, shows that the weather in each of the current and preceding years explains approximately equal portions of the variation in shoot growth of red pine in the plantations studied in Michigan.

A similar stepwise multiple regression analysis of pine shoot growth on total precipitation and average temperatures of the same four growth periods accounted for about 52% of the variation. This example indicates clearly that better correlations can be obtained when weather factors are expressed indirectly through water deficits rather than directly as observed values of rainfall or temperature. Twenty per cent additional variation in shoot growth was accounted for by the conversion to water-deficit values.

Basal area increment of western white pine in northern Idaho: An analysis utilizing the polynomial model

Sites on which western white pine (*Pinus monticola* Dougl.) grows in northern Idaho receive most of their precipitation in the winter as snow. Hence, moisture in the soil mantle is at or very near field capacity at the start of the growing season. Available moisture-storage capacities range from 3 to 8 inches for western white pine sites. Average precipitation during the growing season ranges from 5 to 7 inches. Thus, growth is about equally dependent on moisture initially stored in the soil and moisture added to the soil by precipitation during the growing season. Since western white pine depends so much on moisture stored from winter precipitation, it might be considered less sensitive to the timing of water deficits during the growing season. Nevertheless, as will be shown, the additional information provided by daily computation of moisture stress does explain a substantial proportion of the variance in growth that is independent of direct effects of temperature and precipitation.

For a study of the pole blight disease of western white pine, it was necessary to establish a connection between climate and basal area increment. Effects of tree age and size were minimized by analyzing deviations from a second degree regression of the logarithm of relative basal area increment on age. These deviations were collated by date, and the yearly averages were calculated for each of six plots in the vicinity of the Priest River Experimental Forest in northern Idaho for the years 1912 through 1958. In the regression analysis which follows, the dependent variable is the deviation from average growth of annual increment in basal area for this 47-year period.

Six sets of weather and water-deficit variables were used in the growth model. Each set included the six coefficients of a fifth degree orthogonal polynomial representing the trend of water deficit and weather factors during the period from April 1 to October 24. The polynomial for the daily trend of water deficit, using 1958 as an example, is shown in Fig. 5. Two weather factors and one water-deficit variable were included for the current year and for the year preceding. These factors represented as a six-element column vector were designated as follows:

S_{i-1} = the six coefficients describing moisture stress in the preceding year (calculated for the appropriate storage capacity)

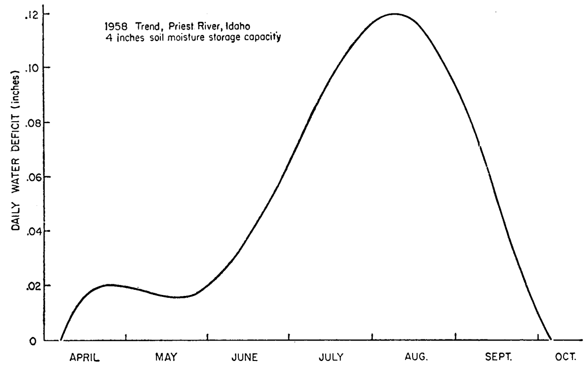

FIG. 5. The daily trend of water deficits for the 1958 growing season at the Priest River Experimental Forest, northern Idaho, represented by polynomials to the 5th degree. The site stores 4 inches of available water at field capacity.

T_{i-1} = as above, for mean daily temperature
P_{i-1} = as above, for daily precipitation
S_i = the six coefficients describing moisture stress during the current year (calculated for the appropriate storage capacity)
T_i = as above, for mean daily temperature
P_i = as above, for daily precipitation

To remove the effects of a pronounced serial correlation in the dependent variable, the value of the dependent variable in the preceding year was included as an independent variable for predicting the current year's growth.

Linear and quadratic trends with time were also included for each plot. These trend variables were designated collectively as D, for date.

The final regression model was thus:

$$Y_i = b_1 y_{i-1} + B_2 S_i + B_3 T_i + B_4 P_i + B_5 S_{i-1} + B_6 T_{i-1} + B_7 P_{i-1} + B_8 D$$

where the B's are regression coefficients in row vector format. That is, for example:

$B_4 P_i$ represents the sum of the six terms:

$$b_{4,1}\, p_{i,1} + b_{4,2}\, p_{i,2} + \ldots\ldots + b_{4,6}\, p_{i,6}$$

In all, there were 49 independent variables in the regression.

The complete model, using all six sets of water-deficit and weather variables, accounted for 78% of the variance of the deviations from normal basal area growth ($R = 0.88$). Water deficit, temperature, and precipitation factors together explain 56% of the variance remaining after the effect of the lagged dependent variables was removed.

The order of the polynomial selected for each factor was determined by the highest order variable that was significant at the 95-% level when

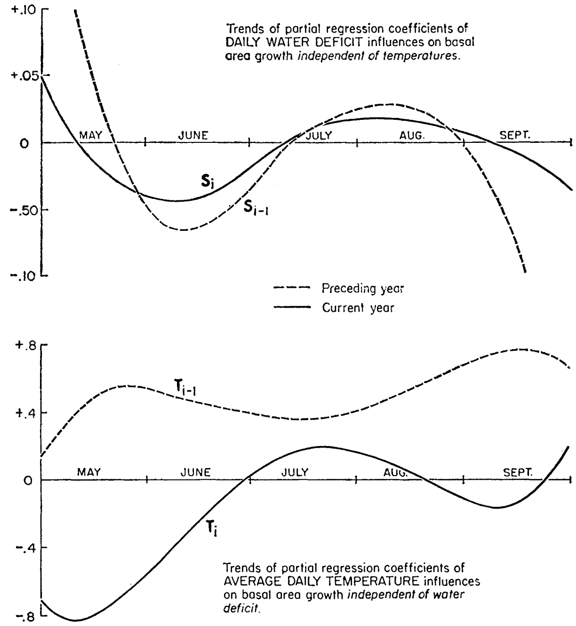

FIG. 6. Trends of partial regression coefficients of water deficit (above) and average temperature (below), illustrating the importance of these independent variables in the basal area growth of western white pine at various times during the growing season.

all orders to the fifth were included in the regression. All significant water deficit and weather relations were at least fourth order. The significance of fifth order terms depended on which other factors were included to the fifth power; however, features of the curve representing the effect of water deficit (Fig. 6) were securely established by the first four powers, and the fifth power term added little to its effect.

Curves showing the trend of the partial regression coefficients for predicting relative basal area increment from water deficit and temperature are shown in Fig. 6. The upper pair of curves shows effects of water deficit independent of temperature. As one would expect, deficit during June is detrimental to growth. The position of zero on the vertical axis is quite arbitrary in that it depends on the average values of all the other variables in the model. Hence, the small positive effects during August should be interpreted only as indicating a period during which growth is insensitive to moisture stress.

Temperature (lower pair of curves in Fig. 6) reverses its effects from the preceding to the current year. Whereas higher than average temperatures in the year previous appear generally favorable to growth in the subsequent year, higher than normal concomitant temperature is detrimental to growth early in the season and has relatively little effect later in the season.

TABLE I. Western white pine basal area increment example. Value of combinations of moisture stress (S), mean daily temperature (T), and daily precipitation (P) for predicting deviations from normal growth in the i^{th} year

Variables already in regression in addition to y_{i-1}, D	Variables added[1]	Proportion of remaining variance explained by added variables
None	S_i	.17
S_i	S_{i-1}	.11
None	S	.26
"	T	.22
"	P	.21
"	T, P	.39
"	T, S	.42
"	P, S	.37
T, P	S	.28

[1]Subscripts on the variables indicate the year of observation. Thus S_i is moisture stress in current year, S_{i-1} is moisture stress in year preceding the year when growth took place. S (likewise T or P) without a subscript indicates S_i and S_{i-1} taken together.

Results of solutions of sub-sets of the complete model are shown in Table I. Moisture stress when considered as a single factor explains the greatest proportion (26%) of variance remaining after serial correlation of the dependent variable and trend has been removed. For comparison, temperature and precipitation, which together determine the calculated moisture stress, account for 39%. Thus, the calculated moisture stress is a good index to conditions favoring growth, but not quite as good an index as its basic components when taken in combination. The real information added in the moisture-stress computation is derived from the effect of timing and intensity of precipitation interacting with the available storage capacity of the soil. That this added information is worthwhile is shown in the last line of Table I. Adding moisture stress to a model already including temperature and precipitation results in a 28% reduction in the remaining variance.

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