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THE QUANTIFICATION OF CLIMATIC CONSTRAINTS ON PLANT GROWTH

M. A. V. Devanathan

(*Tea Research Institute of Sri Lanka, Talawakele, Sri Lanka*)

Attempts to correlate yield of crops with climatic parameters have hitherto been unsuccessful. The evaluation of regression coefficients of yield with various climatic factors makes the assumption that the growth of a plant is a perfect differential with respect to the various climatic parameters. The yield itself is the culmination of a series of stages of growth and differentiation unless the yield is vegetative. The other approach based on the evapotranspiration assumes that there is a constant transpiration ratio, a concept devoid of theoretical and experimental support. Under conditions which preclude nutrient limitations, the growth of a plant must be necessarily proportional to the rate of photosynthesis since it is this process which provides all the carbohydrate matter, both structural carbohydrates and energy providing carbohydrates, for the plant. Using a simplified scheme for the overall photosynthesis, rate equations are obtained which relate the growth to the number of hours of sunshine above the saturation limit, the temperature coefficient as deduced from experimental data obtained with isolated chloroplasts, and a probability factor. For aquatic plants this probability factor is unity. For land plants this factor is the product of two factors, one of which relates to the maintenance of the desired level of leaf water potential for optimum photosynthesis, and the other an index of water availability defined as the ratio of the rainfall to transpiration. To avoid complications due to soil effects, and to get only climatic factors, plants are assumed to grow in an ideal soil defined as one which provides all nutrients and with an infinite capacity for water at zero water potential. By grouping terms characteristic of the plant, and climatic factors independent of the plants, it is shown that the photosynthetic yield is proportional to the product f_t RS where f_t is the temperature coefficient for photosynthesis, R is the rainfall on the ideal soil and S the number of hours of sunshine above the light saturation level. The commercial yield is given as a constant fraction of the photosynthetic yield and this crop coefficient depends on the type, variety and stand of plants. The product f_t RS is termed the phytoclimatic potential since it is an index of the suitability of the climate for plant growth. It is shown that the data for the yield distribution of tea, obtained in well planned experiments at Malawi where the soil is nearly ideal, provide proof that the monthly yield is directly proportional to the phytoclimatic index for the previous month, the predictive value being as high as 96% on the phytoclimatic potential. The application of the phytoclimatic potential to the yield of seasonal crops and perennial crops is discussed. The usefulness of the phytoclimatic index, representing the integrated value of the monthly values for the whole year, in assessing the potential for plant growth in various locations is illustrated. The use of the phytoclimatic index to assess the economic benefits of irrigation and conditions under which there could be apparent control of plant growth by temperature, sunshine or rainfall are discussed. It is shown that from the point of view of agriculture, it is necessary to invoke a soil correction factor, to account for run off and rooting depths of crops, in order that the agroclimatic potential can be assessed. The agroclimatic potential is defined as the product of the phytoclimatic and the soil correction factor. Some possible analytical expressions for the latter are indicated.

INTRODUCTION

A major objective of agrometeorological research is the quantification of the suitability of natural environments for the growth of various crops. The principal factors controlling the growth of plants may be grouped into climatic factors and edaphic factors (de Vries 1963). The latter group of factors pertain to the composition of the soil, its nutrient status, water retentivity, temperature and other physico chemical parameters. The importance of the soil as the supplier of inorganic nutrients to the plant so essential for its healthy growth has resulted in less attention being paid to the functional relationships of climatic factors which determine even the viability of various plant species in various locations and must therefore also control their growth rates.

1.1 Classification of Agroclimates

One classification of the climate is based on the ratio of annual precipitation to the mean annual temperature (Miller 1957). A more useful classification is due to Thornwaite (1948) in which the monthly balance between the potential evapotranspiration and precipitation, gives the duration and supply of water available for plant growth (Budyko 1956, Thornwaite & Mather 1962, Sellers 1967). Such classifications only confirm the existing natural vegetation pattern and are not useful for agricultural planning.

1.2 Relationships between climate and plant growth

From the point of view of commercial agriculture it would be desirable to correlate climatic factors with the yield of a crop. However, a preliminary step would be to establish the relationship between climatic factors and the growth of the plant since the commercial crop is the culmination of a series of stages of growth, differentiation and development. Unfortunately all previous attempts to correlate climate with crop have been centered on the commercial yield and not on the growth or vegetative yield.

1.3 Statistical correlations

Statistical evaluation of the regression coefficients of the yield with a number of climatic factors have been attempted (Fisher 1924, Watson 1963). The availability of modern computer facilities has given fresh impetus to this approach and as many as 21 different parameters have been screened (Monteith 1971, Carr 1972). The basic error in this approach is that the determination of linear regression coefficients presupposes that the yield is a perfect differential with respect to the several climatic parameters, *ie* it is a single valued function of the climatic parameters in the manner of thermodynamic functions. A complex process such as the growth and yield of a crop involves the interaction of several climatic and edaphic factors and cannot be analysed by a method which does not provide a functional basis for the interaction of these factors. It is therefore not surprising that the long series of such attempts made since the studies of Lawes & Gilbert in 1880 to correlate weather with the yield of crops have proved fruitless. Monteith (1971) cites a recent statistical study of orchard yields by Hurst & Cochrane in which the authors conclude that "there seems to be little hope of isolating any single meteorological parameter which significantly affects yield".

1.4 Correlation with Transpiration

A different but more useful approach is the correlation of yield with the empirically determined evapotranspiration of crops. Such a method would be satisfactory if there exists a constant ratio between the rate of photosynthesis and the transpiration. In a number of instances constant ratios have been observed but these are regarded by Monteith (1963) as purely fortuitous. Further it is well-established that this ratio itself for the same plant species is dependent on the climate and consequently it is not safe to use this method to predict the rate of growth (Iljin 1958). Laycock (1964) has however shown that annual yields of tea are strongly correlated with the integrated value of an empirically determined weather parameter E_{TW}

which is based on Penman's estimates of evapotranspiration. However, Penman (1956) has questioned the validity of the concept of the transpiration ratio on the grounds that there is no reason why a plant should transpire a certain quantum of water for the production of a specified amount of dry matter.

Thus there is no sound general approach of wide applicability suitable for determining the climatic limitations to plant growth.

GROWTH OF PLANTS

Except when as a seeding it draws on its food reserves a plant has to obtain its entire energy requirements from sunlight by photosynthesis. The growth differentiation flowering and fruiting depend on the utilization of the energy stored in the products of photosynthesis namely the carbohydrates. Consequently the ability to produce the maximum of photosynthesis in a particular climatic regime controls the viability of the plant community.

When we examine the chemical composition of plants we find approximately 80% is water. Of the residual dry matter of the plants less than 10% consists of the main mineral nutrients nitrogen, phosphorus, potassium and micronutrients. The 90% of the dry matter consists entirely of carbohydrates both as structural matter such as celluloses and as energy storage chemicals such as glucose sugar and starches. Thus the overall percentage of water, carbohydrate and mineral nutrients are approximately 80%, 18% and 2% respectively. Therefore, while the 2% minerals are essential for plant nutrition the overall growth rate must be limited by the availability of carbohydrates apart from that of water. Therefore, under conditions in which mineral nutrient limitations do not exist, the growth of any plant must be rate determined by the production of carbohydrates by photosynthesis.

From the above considerations it is evident that the study of the factors which control the rate of photosynthesis would enable the prediction of the rate of plant growth. It is therefore necessary to analyse the role of various climatic factors in controlling the rate of photsynthesis of plants in the absence of mineral nutrient limitations.

2.1 Factors controlling photosynthesis

The photosynthetic fixation of carbon dioxide takes place within the mesophyll cells of the leaves (Hill & Whittingham 1956, Rabinowitch 1956, Kamen 1963, Kok 1965). These are located in a manner so as to provide access to carbon dioxide and water and to permit the exit of oxygen and transpired water. The chloroplasts inside the mesophyll cells are the photocatalytic sites with a complex array of enzymes which catalyse the chemical reaction stages leading to the production of carbohydrates from the carbon dioxide. Thus the rate of production of carbohydrates will depend on the rates of the photochemical reaction and the subsequent chemical reactions promoted by specific enzymes. For maximum production of carbohydrates the factors which control the rates of all the individual reaction sequences must be optimal. Considering the overall reaction, the availability of suitable photochemical radiation, the transport to the mesophyll cells of carbon dioxide, the efficiency of the enzymic apparatus, the temperature and the availability of water are by far the more important factors which would control the rate of fixation of carbon dioxide.

2.2. Rate equations for photosynthesis

In order to obtain a functional relationship between the macro environmental factors which promote plant growth it is first necessary to have a simplified scheme of rate equations which govern photosynthesis.

It is well established that the mechanism of photosynthetic fixation of carbon dioxide consists of a temperature independent chloroplast catalysed photochemical reaction involving water, followed by a series of chemical reactions leading to the enzyme assisted reduction of carbon dioxide to carbohydrates (Hill & Whittingham 1956; Rabinowitch 1956). These chemical reactions are temperature dependent with characteristic energies of activations. While the details of this complex chain of reactions have yet to be elucidated, Van Niel's scheme of photosynthesis is believed to fit in reasonably well with known facts, and suits our purpose (Kluyver & Van Niel 1956). The simple representation given in Figure 1, shows the photochemical splitting or stretching of H-OH bonds in the photoactivated complex of the pigment chlorophyll Chl. The details of the cyclic enzymic reduction of carbon dioxide are not required for our analysis. However, the absence of oxygen evolution during illumination in the absence of carbon dioxide or a Hill oxidant would suggest that the controlling stage of the coupled reductive and oxidative reaction is hydrogen transfer from the activated complex. This means that we can ignore the kinetic details of the concomitant oxygen evolution reaction in photosynthesis. The photoactivated complex represented by (H-Chl*-OH) can undergo several reactions (Moelwyn-Hughes 1961).

1. It can deactivate itself by fluorescence.
2. It can also by collision with water molecules dissipate the extra energy into heat.
3. It could undergo chemical decomposition into products, but such decomposition is not observed in ordinary sunlight and this possibility may be ignored, except when bleaching occurs in very strong light.
4. Deactivation by collision of two photoactivated complexes is also extremely improbable because of the dimensions, structure and organisation of the chloroplasts.

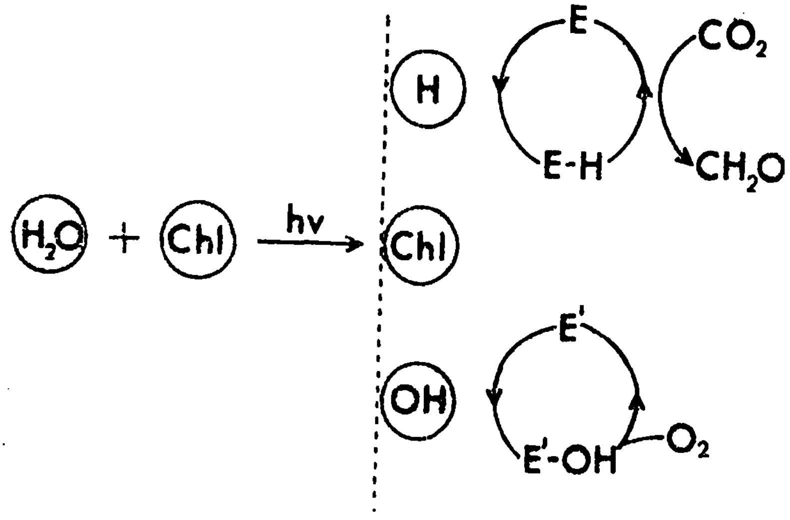

FIGURE 1—Photosynthesis mechanism after Van Niel

5. Finally the photoactivated complex could react with carbon dioxide molecules leading to the synthesis of carbohydrates and concomitant evolution of oxygen.

Ignoring for reasons adduced possibilities 3 and 4 we may write the simplified reaction schemes as follows :—

$$\mathrm{Chl + H_2O \xrightarrow{h\nu} (H\text{-}Chl^{*}\text{—}OH)}\ \text{photoactivation } k_a \qquad (1)$$

$$\mathrm{(H\text{—}\overset{*}{Chl}\text{—}OH \longrightarrow H_2O + Chl + h\nu}\ \text{Fluorescence } k_f \qquad (2)$$

$$\mathrm{(H\text{—}\overset{*}{Chl}\ \ OH) + H_2O \longrightarrow Chl + 2H_2O}\ \text{thermal dissipation } k_t \qquad (3)$$

$$\mathrm{(H\text{—}\overset{*}{Chl}\text{—}OH) + CO_2 \longrightarrow Chl + (CH_2O) + O_2}\text{reduction } k_r \qquad (4)$$

All rate constants will be deemed to apply to the standard temperature taken as 25°C in the ensuing treatment.

Assuming that in the steady state the concentration of the photoactivated complex is constant we get

$$\mathrm{(H\text{—}\overset{*}{Chl}\text{—}OH)} = \frac{k_a\,(H_2O)}{k_f + k_t + (H_2O) + k_r\,(CO_2)} \qquad (5)$$

The rate of carbon dioxide fixation is then

$$\frac{d\,(CH_2O)}{dt} = K_r\,(CO_2)\,\mathrm{(H\text{—}\overset{*}{Chl}\text{—}OH)} \qquad (6)$$

Hence

$$\frac{d(CH_2O)}{dt} \qquad \frac{k_r\,(CO_2)\,k_a\,(H_2O)}{k_f + k_t(H_2O) + k_r(CO_2)} = K\ (\text{say}) \qquad (7)$$

Again in the steady state the rate of carbon dioxide supply will be equal to the rate of photosynthesis and hence

$$K = \frac{D}{\delta}\Big[\,(CO_2)_{ex} - (CO_2)\,\Big] = k_d\Big[\,(CO_2)_{ex} - (CO_2)\,\Big] \qquad (8)$$

where (CO_2) is the external concentration of carbon dioxide away from the site of photosynthesis, D being the diffusion coefficient of the CO_2 in the cellular fluid and δ the diffusion layer thickness in the same medium. The maximum rate of mass transfer of carbon dioxide will be reached when (CO_2) at the photosynthetic site tends to zero. Denoting this maximum value $k_d\,(CO_2)_{ex}$ by K_m we may write

$$K_m - K = k_d\,(CO_2) \qquad (9)$$

which when substituted in (7) gives

$$K = \frac{k_a\,(H_2O)\,k_r\,(K_m - K)}{k_d\left[k_f + k_t\,(H_2O) + \dfrac{k_r}{k_d}\,(K_m - K)\right]} \qquad (10)$$

The expression for K from the above equation would be an unweildy quadratic. It is however possible to obtain a simpler expression by making use of the fact that maximum utilisation of absorbed radiation into photosynthates has a maximum efficiency of 30% and under natural conditions is even much less. Furthermore $(H_2O) >> (CO_2)$ in aqueous media (vide equations (3) & (4). Therefore $\frac{k_r}{k_d}$ $(K_m - K)$ *ie* $k_r (CO_2)$ must be much less than $k_f + k_t (H_2O)$, we may hence write

$$K = \frac{k_a (H_2O)\, k_r (K_m - K)}{k_d [\, k_f + k_t (H_2O)\,]} \qquad (11)$$

which gives on substituting $\frac{\alpha I}{h\nu}$ for k_a (Moelwyn-Hughes 1961)

$$K = \frac{K_m\, aI}{1 + aI} \qquad (12)$$

where $$a \equiv \frac{\alpha (H_2O)\, k_r}{h\nu\, k_d [\, k_f + k_t (H_2O)\,]}, \qquad (13)$$

Here α is a constant depending on the spectral parameters of the chlorophyll molecule and I is the intensity of illumination. When I reaches a value I_1 such that $aI >> 1$, then the photosynthesis rate reaches the light saturation value K_m determined by the mass transfer of carbon dioxide. In this condition K_m may also be expressed by

$$K_m = \frac{\alpha}{h\nu} (H_2O)\, I_1 = k_r (CO_2)(H{-}\overset{\circ}{\mathrm{C}}\mathrm{hl} - OH) = k_d (CO_2) \qquad (14)$$

since all steps in the chain of reactions proceed at the same rate.

2.3 Temperature effects

The great influence of the temperature in determining the rate of growth of plants is well recognised. However, there has been no theoretical basis for quantitatively assessing this influence of temperature. Rules of thumb such as the number of day degrees above a certain specified temperature have been used by agriculturists (Miller 1957a). Admittedly such empiricisms though useful will have to be evolved for each crop in the absence of guidelines of a fundamental nature.

If we accept the thesis that growth is in the final analysis governed by the rate of photosynthesis, then the effect of temperature on plant growth in simply the temperature coefficient of the photosynthetic processes. It is obvious that the temperature dependence of photosynthesis will be associated with the dark reactions which involve a very large number of enzyme catalysed steps leading to the production of carbohydrates. If these were only a simple chemical reaction then the temperature coefficient would be adequately accounted for by an Arrhenius energy of activation. In many studies of the temperature dependence of photosynthesis a Q_{10} of 2 corresponding to an energy of activation of about 12 kilocals have been reported to apply over the biokinetic temperature range of near zero to 35°C (Rabinowitch 1956). Other studies have indicated a Q_{10} varying from about 10 to 1.6 (Emerson & Green 1934). Much of this work has been based on the measurement of oxygen evolution by intact cells and the assumption that respiration continues unchanged in switching from darkness to light is implied. Studies with intact leaves of higher plants bring in the complications of stomatal aperture variations due to light.

Recently, Baldry, Bucke and Walker (1966) have carried out measurements of the rate of photosynthesis by isolated chloroplasts under saturating light and high carbon dioxide concentration by measuring the rate of fixation of C^{14} labelled carbon dioxide. These results indicate a variable Q_{10} ranging from 9 to 1.28. The results are in harmony with Warburg's suggestion that the rate of photosynthesis is a linear rather than an exponential function of temperature, in high CO_2 and high light (Emerson 1929, Warburg 1919). Their data converted into a velocity versus temperature graph are shown in Figure 2 where the velocity at the standard temperature of 25°C is taken as 100.

Thus if the limiting rate of K_m is saturating light at 25°C is taken as unity, then rather than having an Arrhenius like expression $K_m \exp - \frac{\Delta G}{RT}$, it is more convenient to use in the biokinetic range a temperature coefficient f_t taken from the data of Baldry Bucke and Walker defined as

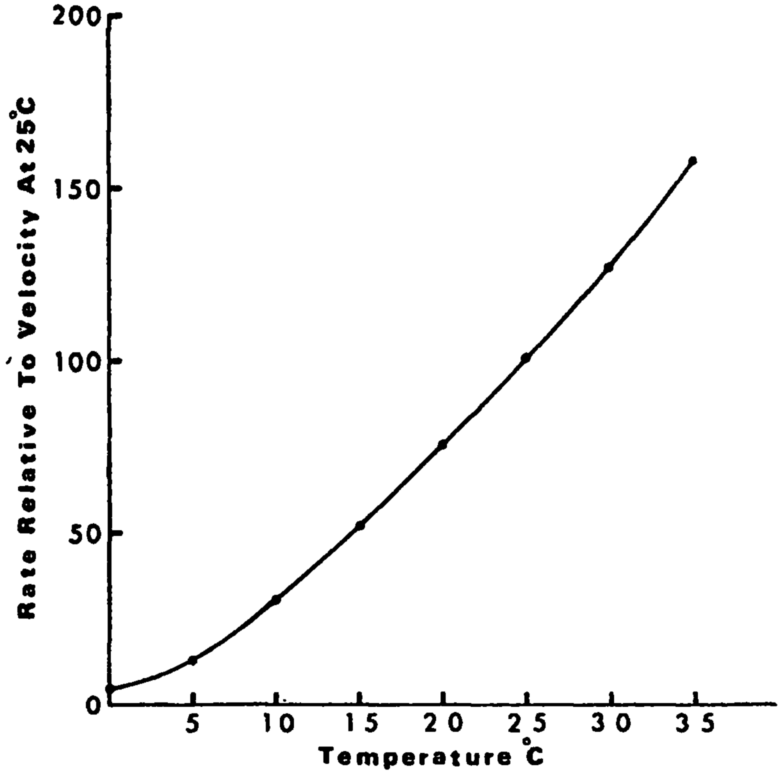

FIGURE 2—*Velocity temperature graph computed from the data of Baldry* et al 1966

TABLE 1 — *Rates of Photosynthesis at various temperature relative to 25°C*

(Baldry et al. 1966)

0°	1°	2°	3°	4°	5°	6°	7°	8°	9°
3.4	4.5	5.9	7.6	9.9	12.3	15.2	18.9	22.6	26.7
10°	11°	12°	13°	14°	15°	16°	17°	18°	19°
31.1	35.2	39.8	44.3	48.4	53.0	57.5	62.2	66.7	71.2
20°	21°	22°	23°	24°	25°	26°	27°	28°	29°
75.6	80.4	85.1	90.1	94.9	100.0	105.0	110.1	115.5	120.9
30°	31°	32°	33°	34°	35°				
126.8	132.9	138.9	145.0	151.2	157.0				

TABLE 2 — *Meteorological Data for Malawi*

(Laycock 1964)

Month	Rainfall (inch)	Sunshine (hrs)	Mean Temp. (°C)	f_t	f_t RS	% Yield Distribution
Jan	11.62	6.3	23.3	91.5	66.9	16.5
Feb	12.11	5.7	23.6	93.0	64.2	17.1
Mar	12.06	5.5	23.1	90.6	60.1	18.4
Apr	5.86	6.7	22.2	86.1	33.8	13.1
May	2.04	7.1	20.1	76.1	11.0	7.3
Jun	2.00	5.9	18.2	67.6	7.9	2.6
Jul	1.51	6.1	17.3	63.5	5.8	0.9
Aug	1.50	7.3	19.1	71.6	7.8	0.9
Sep	1.58	7.3	21.8	84.2	9.7	2.7
Oct	2.06	8.7	24.2	95.9	17.2	3.3
Nov	6.91	7.6	24.8	99.0	51.9	3.9
Dec	9.79	5.8	24.2	95.5	54.4	13.3

$$ft = \frac{V_T\ °C}{V_{25}\ °C} \tag{15}$$

Hence to describe the rate of photosynthesis at any temperature in the biokinetic range under light saturating condition we write equation (12) as

$$K_T = K_m\, ft \tag{16}$$

Values of ft derived from the data of Baldry *et al* are given in Table 1 at one degree intervals. This coefficient, ft would then describe the effect of temperature on plant growth to the extent to which photosynthesis determines it. It would also be independent of the structural details by any plant so that the same coefficient would apply to the photosynthetic rates of any plant. In this way a major environmental factor, the temperature may be made independent of the nature of the crop. Any difference from this standard temperature coefficient may be attributed to rate limitations imposed by the structural orgnisation of the plant under consideration and characteristc of that type of plant structure.

2.4 Photosynthetic yield

Since the rate of photosynthesis under natural conditions is given by equation (16), the photosynthetic yield Q over a specified period will be given by

$$Q = N\, K_m\, ft\, t \tag{17}$$

where t is the time period of light saturation, and N is the number of photosynthetic sites per unit area. This will be largely valid under natural conditions since sunlight is usually much in excess of the limiting intensity I_1. If the average yield per day per unit area over a specified period of say a month is required then

$$Q = N\, K_m\, ft\, S \tag{18}$$

where S is the average hours of sunshine per day for the month above the limit I_1. Equation (18) would apply to the rate of photosynthesis by cultures of unicellular organisms, to algae in water bodies or to plankton in the sea. Since the factors N and K_m need not be determined we may write for the monthly yield of photosynthesis for such systems

$$Y = K_o\, ft\, S \tag{19}$$

where the constant K_o would include all constants and conversion factors and the stipulated time period of 30 days, S being as before the daily average number of hours of sunshine above the limiting value in that month.

3—APPLICATION TO LAND PLANTS

The environment of land plants is very different from that of hydrophytes. The latter draw their requirements of carbon dioxide from the aqueous medium surrounding them. For the same reason water stress in the photosynthesing cells cannot exist. Hence the main limitation is sunlight since the carbon dioxide concentration in the aqueous environment is substantially constant. In the evolution from aquatic forms to land forms, the plants have adapted themselves by providing the photosynthesing mesophyll cells with an elaborate structure designed to maximise their photosynthetic functions. The structure of the leaf permits the entry of carbon dioxide gas, and an elaborate system conveys water and nutrients from the soil to supply the mesophyll cells with carbon dioxide and nutrient containing solution. With this apparatus functioning efficiently the mesophyll cells would photosynthesize with the same efficiency as they would, were they immersed in water bodies. In other words the plant structure is designed to provide the mesophyll cells with a microenvironment in which they would function best, namely the equivalent of immersion in a suitable water medium.

Another basic difference with land plants is that the solar radiation not used up in photosynthesis, and this is almost 99 percent, would be converted to heat which will evaporate the water in the leaf or heat the surrounding atmosphere the partition being determined by Bowen's ratio. Since the water available to the plants is limited to the available moisture of the soil, the physiological behaviour of the plant is oriented towards the conservation of water. An extreme case of adaptation to conserve water are the group of xerophytes which have to survive in deserts.

3.1 Photosynthesis and water stress

Although the equation for photoactivation (1) involves the concentration or activity of water the actual amount of water required for the photolytic reaction is negligibly small, less than 0.2% of the water requirements of the plant (Sutcliffe 1967). Within the mesophyll cell the activity or concentration of water is substantially constant since we are dealing with very dilute aqueous solutions which form the cell contents. We would therefore expect the rate of photosynthesis to be constant. If the sole reaction were photolysis this would be so, but the photolysis of water is followed by the chain of enzymic reactions leading to the conversion of carbon dioxide to carbohydrates. The enzymes which are hydrated proteins are very sensitive to dehydration. If these are even marginally dehydrated fixation rates of carbon dioxide drop rapidly. If the dehydration is severe the enzymes may not recover their activity even if later the hydration levels are restored. Experimental data (Troughton 1969) show that in terms of leaf water content, the photosynthetic activity is constant until a critical level around 88% is reached, thereafter the activity drops rapidly. This occurs far ahead of any visible symptoms of water stress such as wilting. That this decrease of activity in carbon dioxide fixation is due to dehydration and not due to stomatal closure which also accompanies water stress is shown by studies with aquatic plants such as algae which when subjected to dehydration by immersion in high osmotic pressure aqueous solution showed loss of photosynthetic activity (Rabinowitch 1956).

The decrease of photosynthesis with dehydration of the protoplasmic contents of the mesophyll cells is a fundamental phenomenon associated with the enzymic activity within the cell and is not due to external restrains such as closure of stomata (Slatyer 1967). Thus for maximum photosynthetic activity of the mesophyll cells the cell turgor must be kept at a maximum level. The loss of photosynthetic activity with decreasing turgor is best related to the leaf water potential ψ_{leaf} a parameter which is preferable to an analytical parameter such as leaf water content. Thus data

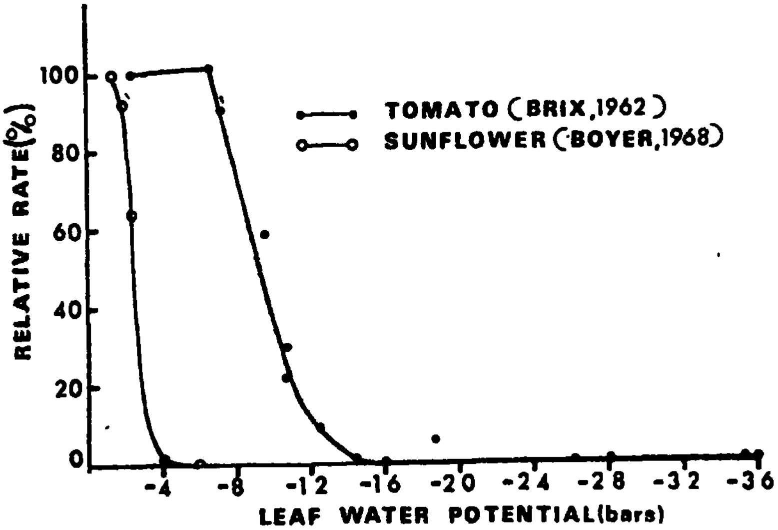

FIGURE 3—*Photosynthetic rate* vs *leaf water potential for the tomato plant* (Brix 1962) *and Sunflower* (Boyer 1968)

obtained by Brix (1962) (Figure 3) with tomato plants show that the photosynthesis rate is constant at 100% efficiency from ψ_{leaf} 0 to -8 bars beyond which it drops rapidly and becomes negligible at about -14 bars. The wilting point is usually around -14 to -16 bars. For sunflower plants the critical potential is -2 bars (Boyer 1968). Thus long ahead of the observation of wilting, photosynthesis has practically ceased. In order to ensure maximum rate of photosynthesis the leaf water potential should not fall below a critical value denoted $\psi_{p\ leaf}$. We may therefore say that the yield of photosynthesis of mesophytes will also be proportional to a probability factor P defined as proportional to the time the water supply system maintains the leaf water potential above $\psi_{p\ leaf}$ during illumination. The equation for the yield (19) will then become

$$Y = K\,f t\,S\,P \qquad (20)$$

3.2 Components of the probability factor

In the absence of transpiration the leaf water potential is equal to that of the soil water potential since the water transport system would tend to equalise these water potentials (Slatyer 1967a). A transpirational load would tend to lower the leaf water potential below that of the soil, since the transport capacity of the plant is finite. As the soil moisture levels are depleted the soil water potential drops effecting corresponding decreases in ψ_{leaf}. Since it is our object to determine the effect of climatic factors on plant growth without the complication brought in by soil factors we would have to assume that the plant has its roots in an ideal soil.

This would be defined for purposes of this study as a medium which provides all the nutrients required by the plant and has an unlimited water capacity at zero water potential. A plant growing in this hypothetical soil would have its supply of water available at zero soil water potential along with the necessary nutrients. Thus it should be able to sustain the leaf water potential, also at zero, as long as the water supply lasts provided its water transport system has zero resistance. As a matter of fact every plant has a maximum rate of water supply that it can sustain and this is determined by the structure of its various parts. Let this rate be given by a water conductance factor $\frac{1}{Z}$. The water flux to the mesophyll cells lost by transpiration will be given by an expression called the water supply function (Cowan 1965)

$$E_W = \frac{(\psi_{leaf} - \psi_{soil})}{Z} \qquad (21)$$

For a plant growing in our ideal soil for which ψ_{soil} is zero we get

$$\Delta \psi = E_W Z \qquad (22)$$

where $\Delta \psi$ is the change fro zero ψ level.

The maximum water flux that can be sustained without letting ψ_{leaf} drop below the critical lower limit for 100% efficiency in photosynthesis is

$$E_{max} = \frac{\Delta \psi_P}{Z} \qquad (23)$$

Thus if due to the transpirational load the evaporation exceeds E_{max} then ψ_{leaf} will drop below the lower critical limit and photosynthesis will become rapidly negligible. This is illustrated in the schematic diagram given in figure 4. Here the diurnal solar radiation which causes the evaporation from the leaf is shown as a sinusiodal curve. The critical ψ_{leaf} for photosynthesis and the leaf water potential at the wilting point are shown as lines parallel to the time axis at the appropriate ψ_{leaf} level in bars. The diurnal variations of the leaf water potential for various values of Z are shown. It will be seen that when Z is very small ψ_{leaf} changes are negligible and well above the ψ_{leaf} line. As Z increases the deviations from zero are more marked when at Zc, ψ_{leaf} just grazes the ψ_p leaf line around mid-day. Thereafter over increasing periods around mid-day ψ_{leaf} falls well below ψ_p leaf during which time photosynthesis almost ceases. With further increase of Z, ψ_{leaf} can fall even below the ψ_{wilt} line around mid-day. Since the evaporative load is also variable it is evident that it will be necessary to obtain expressions connecting all these factors with the water requirements and water availability.

We therefore proceed as follows. To a first approximation the solar radiation can be assumed to be sinusoidal function with an angular frequency w given by $\frac{\pi}{N}$ where N is the maximum possible number of sunshine hours in the locality. Let the maximum amplitude expressed in terms of water evaporated in inches or millimeters be E_A. If the absorption coefficient of the crop cover is ϵ and if we assume that the supply of latent heat from solar radiation is the main controlling factor in evapotranspiration i.e. Bowen's ratio ——> O, we may write for the diurnal variation of evapotranspiration E. $E = E_m \sin wt$ (24)

where E_m represents the product ϵE_A. This transpirational load will be dissipated by the water flux to the leaves.

Combining (24) with equation (21) we get for the leaf water potential

$$\psi = ZEm \sin wt + \psi_{soil} \qquad (25)$$

Since for our ideal soil ψ_{soil} is zero we may write

$$\psi_{leaf} = ZEm \sin wt \qquad (26)$$

In order that photosynthesis can proceed at maximum rate ψ_{leaf} should not exceed ψ_p. Therefore times for which sin wt exceeds $\frac{\Delta\psi p}{ZEm}$ will not be suitable for photosynthesis. Therefore, the fraction of the time N during which photosynthesis is possible Pp will be given by

$$Pp = \frac{2}{\pi} \sin^{-1} \frac{\Delta\psi p}{ZEm}. \qquad (27)$$

The above estimate of the probability for photosynthesis assumes that water is freely available. If this were not the case then the probability of the availability of water for the plants needs must be evaluated. The water needs of a plant are primarily to dissipate the heat load by evapotranspiration. The quantity required per day if ψ_{wilt} is not exceeded will then be

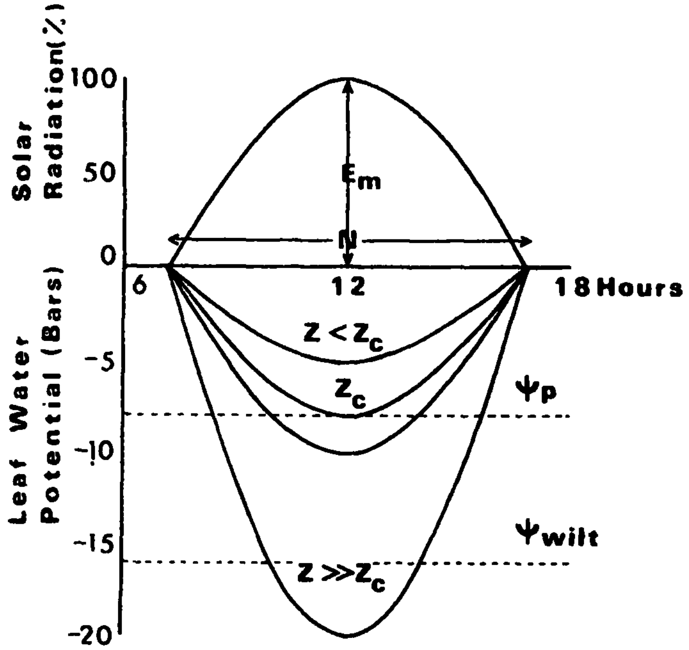

FIGURE 4—*Diurnal variation of solar radiation and corresponding variation of leaf water potential*

$$\int_{0}^{N} E_m \sin wt \, dt = \frac{2 N E_m}{\pi} \qquad (28)$$

The probability factor for water availability P_W will be the ratio of water available to water required namely

$$P_W = \frac{\pi R}{n^{*} 2 N E_m} = \frac{R}{E_T} \qquad (29)$$

where $\overset{*}{n}$ is the number of days in the month for which the rainfall is R on our ideal soil. E_T then is the monthly evapotranspiration for that stand of plants. This ratio is an index of the wetness and is similar to the moisture index used by Thornwaite (1948) for the classification of climates and its reciprocal, the radiational index of dryness used by Budyko (1956). These however do not take the plants need into account but are concerned with the total evaporative capacity of the solar radiation.

The probability factor P may then be expressed as the product of the photosynthesis and water availability probabilities thus

$$P = P_p P_W \qquad (30)$$

It may be noted that cloud coverage will not affect P since this factor will multiply the numerator in P_p. and the denominator in P_W. Expanding (30) using (27) and (29) we obtain

$$P = \frac{2}{\pi} \sin^{-1} \frac{\Delta \psi p}{Z E_m} . \frac{R}{E_T} \qquad (31)$$

Equation (31) brings out the plants interactions with the environment with respect to water supply. The wetness index $\frac{R}{E_T}$ has already been used as the basis of climate classification. The P_p factor has not been hitherto explicitly discussed. This factor brings out the classifications of plants in a quantitative way.

Thus for herbaceous plants which show a mid-day wilt even in the presence of water in the soil $\frac{\Delta \psi p}{Z E_m}$ must be small compared to unity, since $\Delta \psi$ p is approximately $\frac{\Delta \psi}{2}$ wilt, and for wilting $\frac{\Delta \psi}{Z E_m}$ wilt < 1. Since the expansion of $\sin^{-1} X$ is is $X + \frac{X^3}{6} + \frac{3 X^5}{40} \ldots\ldots$ for $X^2 < 1$, $\sin^{-1} X = X$ is a good approximation.

Hence for herbaceous plants we get

$$P = \frac{2\,\Delta\psi_p}{\pi\, Z\, E_m}\;\frac{R}{E_T} = \frac{\Delta\psi_p\; R}{n\; {*}NZ\, \epsilon^2 E_A{}^2} \tag{32}$$

Thus herbaceous plants are characterised by low ψ_p (vide figure 3), large Z or poor water transport systems, and high susceptibility to radiation damage since the probability of photosynthetic activity is inversely proportional to the square of the maximum intensity of solar radiation E_A. Herbaceous plants will therefore thrive in the temperate zones where solar radiation is less intense.

Woody plants do not wilt easily in the presence of soil moisture and it is likely that $\frac{\Delta\psi_p}{Z\,E_m}$ is close to unity if not larger. For $\frac{\Delta\psi_p}{Z\,E_m}$ close to unity $\frac{2}{\pi}\sin^{-1}\frac{\Delta\psi_p}{Z\,E_m} = 1$ and if this ratio is larger than unity then at all times during the day the leaf water potential is above the critical value ψ_p and so P_p is unity.

Hence for woody plants

$$P = \frac{R}{E_T} \tag{33}$$

With xerophytes the prime need is to conserve water by minimisation of evapotranspiration and to absorb rapidly whatever precipitation falling in the desert. For such plants then Z will be very small to permit rapid absorption of rainfall and ψ_p will also be large to permit maximum time for photosynthesis. Such plants reduce transpiration by reducing the density of stomata, and by decreasing the area to volume ratio. This results in a decrease in the accessibility of carbon dioxide and so such plants operate on the crassulacean acid mechanism for photosynthesis. We can therefore conclude that since P_p will also be unity, the same equation as for woody plants (33) will apply for xerophytes.

3.3 Equations for the yield

We may therefore write the general expression for plant yield from (31) and (20) as

$$Y = \left[K\;\frac{2}{\pi}\;\frac{1}{E_T}\;\sin^{-1}\frac{\Delta\psi_p}{Z\,E_m} \right] f_t\ \text{S.R.} \tag{34}$$

where terms characteristic of the plant have been grouped within the brackets. The evapotranspiration term has also been included within this group since E_T although it depends on the geographical location is determined in magnitude by the absorption coefficient ϵ which is characteristic of the plant community. We may emphasize that K apart from including conversion factors will also include plant factors such as density of photosynthetic sites per unit area, the leaf area index, and management factors such as density of plants per unit area. We shall therefore write (34) in the simple form

$$Y = B\, ft\, R.\, S. \qquad (35)$$

since we have already discussed the conditions which determine the magnitude of the group of terms now denoted by B. The group of terms ft R S cover the major environmental factors. Y therefore represents the monthly increase in dry matter content of a monoculture of a plant species. If the commercial yield is a vegetative harvest preferably reported as weight of dry matter, and if the vegetative harvest is a constant fraction of the total increase in dry weight then by multiplying (35) by the appropriate fraction q we would get the commercial yield

$$Y_{com} = q\, B\, ft\, R\, S \qquad (36)$$

With non-vegetative commercial harvest such as the fruit of perennial plants or say the grain yield of short term crops, it is likely that the commercial crop would be a constant fraction of the total growth of the species within the period concerned. This fraction would of course depend not only on the type of crop but also on the varieties of the same crop. If this fraction is also denoted by q then the commercial yield would be given by

$$Y_{com} = q\, B \sum_{0}^{n} ft\, R\, S \qquad (37)$$

where for the annual harvest of perennials the summation would cover all twelve months. The same expression would also give the total yield for the year for a perennial crop such as tea which is harvested at approximately weekly intervals right throughout the year.

For short term crops n would be the number of months after which the crop would be ready for harvest. In these cases the plant factors contained within B are likely to vary with the age of the crop so that in application the term qB would have to be ascertained in well planned field trials. For practical purposes it would be adequate to replace qB by a single crop factor ϵ_{crop} so that the commercial yield would be expressed as

$$Y_{com} = \epsilon_{crop} \sum_{0}^{n} ft\, R\, S \qquad (38)$$

where ϵ_{crop} would be characteristic of the variety and under standard planting densities. This equation then provides a method for the quantitative assessment of the main climatic factors which determine the yield of plants, namely temperature, rainfall and sunshine hours.

4-APPLICABILITY OF THE FORMULA FOR CLIMATIC FACTORS

The expression derived in the previous section for the yield relates is a very simple product function of the major climatic factors, sunshine, rainfall and temperature. Although on a global scale solar radiation is the main factor since it controls the rainfall and hence the humidity and the temperature, in any location rainfall can be considered to be an independent climatic factor. Similarly the temperature can also be considered an independent factor since the ambient temperature also depends on the temperature of air masses moving from adjacent regions with different terrain and vegetation. The elevation, the cloud cover, rainfall, transpiration etc. affect the temperature to large extent although solar radiation is in the final analysis the determining factor. Our expressions therefore combine the effects of main climatic factors which control photosynthesis, the elevation a purely geographical factor being involved indirectly through the temperature.

4.1 Some limitations of the Formula

Before we attempt to look for data in support of this formula, it is advisable to bear in mind some of the limitations imposed on the derivation.

Although the expression for the yield under limiting light conditions has been obtained, no allowance for photosynthesis below the limiting light intensity value has been made. This error will be least when the limiting light intensity is a small fraction of the solar illumination intensity. In general about 10% of maximum solar illumination is adequate to light saturate the photosynthetic activity of most plants, so that this error is not likely to be substantial.

Another factor which has been ignored is the respiration of the plants. In this process a part of the photosynthates are used up in sustaining the metabolic activity of the plants. The effect of including this factor would be to produce an apparent reduction in the photosynthetic efficiency. However, this effect is in the opposite direction to that involved in the light saturation assumption. It is possible that these effects may compensate each other. Even if these do not, no absolute estimate of the yield is involved so that so long as these two errors are constant fractions of the absolute photosynthetic yield the formula obtained can be used.

The other important limitation is that the derivation assumes the soil is ideal as far as nutritional requirements and capacity to hold all the precipitation at zero water potential. Since it is our object to eliminate soil factors in the derivation and focus attention on only the climatic factors this assumption is essential. However, in applying the formulae we have to seek soils which approach the ideal soil as closely as possible. This means in effect that only those locations which have been expressly selected to study the effect of climate and which have ideal soil conditions will provide data suitable to verify the formulae. A further geophysical limitation is that the gradient of the location should be close to zero as far as possible so that run off of precipitation is minimal.

4.2 Tea as a climate indicator crop

It will be evident that a suitable climate indicator crop will have to be a perennial which is harvested throughout the year as often as possible. The harvest should be vegetative and obtainable as weight of dry matter. The vegetative harvest itself should be a constant fraction of the total growth of the plant. Perhaps the only commercial crop which meets all these criteria is tea. It is a unique crop in that it is harvested some 45 to 60 times a year. The yield is vegetative and the yields of made tea represent the day weight of the tender shoots. Further Eden (1949) has shown that the harvest represents a constant fraction of about 25 percent of the total growth of the plant. Tea is therefore an excellent climate indicator plant. It also has the added advantage in that clones can be propagated vegetatively in very large numbers so that performance can be studied in different climatic zones.

4.3 Malawi experiments on tea yields

Although field experimentation on the effects of fertilizer on tea yields have been carried out in some of the classical statistically designed experiments set out at St Coombs by Eden and replicated in several countries, experiments to test the effects of climate on tea yields are of recent origin. The impetus to these studies was provided by the availability of formulae for the computation of evapotranspiration from meteorological data evolved by Penman (1948) and Thornwaite (1948). Experiments to correlate annual yield with the evapotranspiration as computed from meteorological data were laid out at Malawi in 1956. The findings have been reported by Laycock (1964). These relate to the annual yields and not to the monthly variations. However, data for the average monthly yield as a percentage of the annual total along with average monthly data have been published in the same paper.

These data are suitable for testing our formulae for several reasons.

1. The experiments have been under constant agricultural management, and constant and non-limiting fertilizer application.
2. In the constant treatment plots care has been taken to ensure that all stages of the pruning cycle are represented at any one time in the plots.
3. The soil is deep volcanic in origin permitting a deep rooting system for the tea extending to about 15 feet. The terrain is generally flat with the available water capacity of the soil for the stand of tea as large as 32 inches

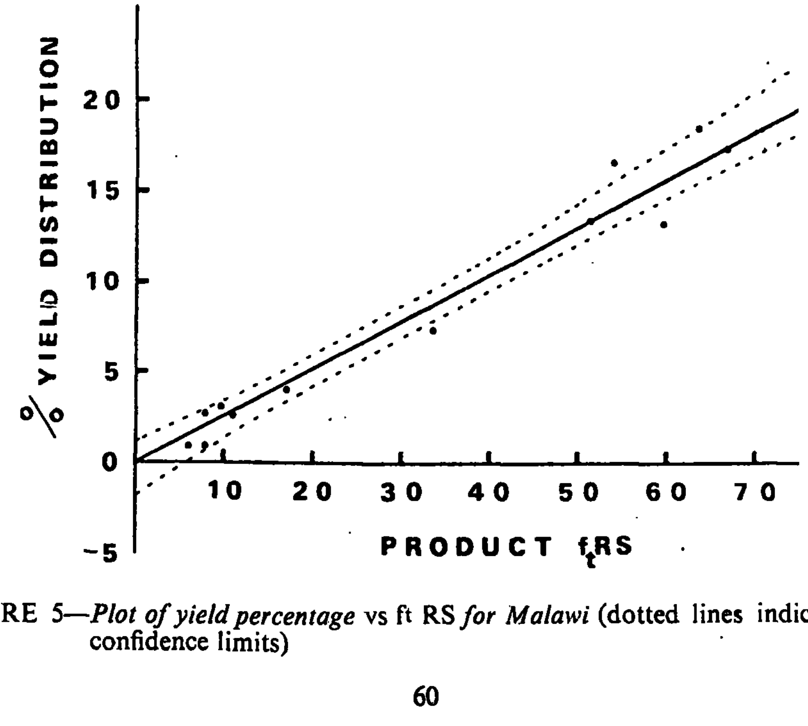

FIGURE 5—*Plot of yield percentage* vs ft RS *for Malawi* (dotted lines indicate 5% confidence limits)

as opposed to a maximum monthly rainfall average of only about 12 inches. The soil therefore closely approximates to the ideal soil we have postulated in our derivation.

4.4 Time lag in response of tea

The response in the form of a vegetative harvest by tea will be apparent only after a certain period of time determined by the physiological function of the tea bush. It is widely believed by tea planters that it takes about a month for tea to respond to the weather it has experienced. Confirmation of this view has been obtained by Devanathan and Thevadasan (1973) who plotted the weekly product of R and S for certain experimental data on a time scale and the weekly pluck on the same time scale. It was found that peaks in RS were matched by corresponding peaks in the pluck four weeks later in the case of second, third and fourth year pruned fields,while for the first year pruned field the lag was five weeks. The increase in the lag in the first year fields is understandable since the bush will be diverting a larger portion of its photosynthates for frame formation in the first year.

4.5 Application to Malawi data

Since it is also the practice to report meteorological data averaged over a calendar month, it appeared likely that the average yield for the month would be well correlated with the monthly average of the climatic parameter RS for the previous month. We have computed the Malawi data using the temperature functions given in Table I, and the results are given in Table 2. On calculating the correlation coefficient we get $r = 0.980$ corresponding to a predictive value of 96% on climatic factors. In a previous communication (Devananthan 1974) without the temperature correction the correlation coefficient was $r = 0.972$ corresponding to a predictive value of 94% on climate alone. The increase in predictive value by 2% on including the temperature coefficient shows that it is correctly accounted for. Larger increases in predictive value due to temperature corrections are not likely since the temperature variation over the year is small. The improvement shows that the formulae will be most useful when the climate displays extremes of temperature.

Figure 5 shows a graph of the same data. It will be seen that the points can be taken to fall on a straight line passing through the origin corresponding to the equation.

$$Y = 0.257\,[(f_t\,RS)] \tag{39}$$

The regression line conforms to

$$Y = 0.266\,[(f_t\,RS)] - 0.33 \tag{40}$$

Equation (39) falls well within the 5% confidence limit lines of equation (40). It will be noted that the linear graph covers a yield variation of a factor of about 20 with a corresponding variation of ft RS. Since the range is large and not restricted to points falling within a narrow range, the range of extrapolation to zero is very small. Unlike other claims that the regression lines based on a narrow range of points far remote from the origin pass through the origin, the wide distribution of points makes the uncertainty in extrapolation negligible. This is an important consideration since data from tea areas which do not show a wide disparity in monthly yield will not be reliable from the point of view of the extrapolation of the regression. We may therefore conclude that our climatic parameter represented by ft RS does reflect the rate of growth of the tea plant as revealed by the vegetative yield month by month.

TABLE 3 — *Phytoclimatic indicates for some Tea Stations*

Month	Malawi	Tocklai	Cachar	Darjeeling	Dooars	St Coombs	Hantane	St Joaçhim	Passara
Jan	66.9	2.7	4.6	1.6	2.3	10.1	16.4	36.0	19.3
Feb	64.2	5.2	12.7	1.7	4.3	14.2	27.9	38.0	25.4
Mar	60.1	17.2	30.4	9.4	12.2	20.9	27.2	58.4	29.0
Apr	33.8	40.8	71.5	15.8	40.4	34.3	38.8	85.1	37.9
May	11.0	57.4	106.8	32.8	76.5	29.3	24.3	101.1	16.4
Jun	7.9	66.0	108.7	41.6	144.3	22.5	36.7	101.5	112.2
Jul	5.8	83.5	109.0	52.8	165.5	20.9	28.5	60.4	9.6
Aug	7.9	78.5	95.9	48.2	132.9	22.1	28.6	54.3	33.8
Sep	9.7	56.0	91.0	39.1	121.3	27.6	39.2	86.6	20.2
Oct	17.2	25.9	61.0	26.3	60.4	31.6	76.6	100.1	29.5
Nov	51.9	5.2	6.4	1.8	3.9	31.7	58.2	66.4	28.3
Dec	54.4	1.5	1.7	0.3	0.9	18.4	48.1	45.5	31.2
Total	390.8	439.9	699.7	271.4	764.9	283.6	450.5	833.4	291.8

This result has a far reaching significance in that for the first time a functional combination of climatic parameters derived theoretically has been shown to be quantitatively a good measure of the growth rate and therefore of the photosynthetic activity of a plant. Considering the difficulty of finding a suitable climate indicator plant and the paucity of data from field experiments expressly designed to test the climatological effects on near ideal soil, the Malawi experiments must be considered to be unique in that all conditions necessary for the elucidation of climatic effects have been satisfied. Similar experiments will have to be laid out elsewhere meeting these stringent requirements if it is necessary to repeat such experiments in different climatic zones. For the present we may consider the analyses of the Malawi data as providing strong experimental evidence for the validity of the equations for the yield of crops with the new climatic parameter ft RS.

5—THE PHYTOCLIMATIC POTENTIAL

The agroclimatic potential of any location would depend on the climatic factor and soil factors. Our objective has been to obtain a functional relationship between the major climatic factors which would describe quantitatively the suitability of any locality for plant growth under ideal soil conditions. The climatic parameter ft RS computed monthly has been shown to account for at least 96% of the variation in the vegetative yield of a climate indicator crop, tea, in well planned experiments at Malawi, where the soil appears ideal because of its volcanic origin, depth and water holding capacity. The factor ft RS appears therefore to describe almost quantitatively the suitability of the climate for the growth of any plant since it is a measure of the environmental factors which control the fundamental requirement for plant growth, namely photosynthesis. It appears therefore reasonable to term this combination of climatic factors the phytoclimatic potential. That is, this function is adequate to quantify the environmental constraints for the growth of any plant. The actual growth of any plant apart from edaphic factors will of course be determined by its ability to adapt itself to a particular climatic environment described by ft RS and this will be reflected in the magnitude of the constant B and the commercial crop in the coefficient ϵ_{crop} defined as qB.

5.1 Availability of data for phytoclimatic potential

It would appear that ample meteorological data would be available readily for the computation of the phytoclimatic potential. However, on examination it is evident that the significance of sunshine hours has not been appreciated and hardly ten stations out of eighty in Sri Lanka are equipped with sunshine resorders and this appears to be the pattern in the equipment of meteorological stations all over the world. Recent trends are to substitute solar radiation recorders for the sunshine recorders. Solar radiation monitoring would certainly be useful in studies of evapotranspiration but not particularly suitable for evaluation of the extent of photosynthesis. Meteorological data required by various technical departments are varied and it would appear that at least for agrometeorological stations, sunshine recorders and solar radiation recorders are essential. Because of the lack of any theoretical indications as to the type of meteorological data required for crop productivity studies, the data available for the calculation of phytoclimatic potential is unsatisfactory. Wherever the meteorological data are satisfactory no crop data from adjacent crop research stations is available. Despite these limitations in the suitability of data we can nevertheless collect sufficient evidence for the usefulness of the phytoclimatic potential as a guide to crop productivity.

5.2 Seasonal variations

The variation of the suitability of a particular location for crop growth throughout the year can therefore be described in terms of the monthly value of the phytoclimatic potential. The sum total of the phytoclimatic potential for the year would give a number which would be a measure of the productivity of perennial crops such as tea. We give in Table III calculations of the phytoclimatic potentials for various stations devoted to tea. These data are also displayed as histograms to depict the seasons for tea. It will be noted that Malawi, Tocklai, Dooars, Cachar and Darjeeling have one peak corresponding to one plucking season. The low phytoclimatic potentials in the rest of the months indicate poor or negligible growth which makes plucking uneconomic. On the other hand histograms for locations in Sri Lanka show two peaks or seasons corresponding to the two monsoonal periods but there are no periods of negligible phytoclimatic potential. Thus plucking of tea in Sri Lanka can be carried out throughout the year simply because the phytoclimate is favourable for year round cropping and not due to any characteristic of the tea stands in Sri Lanka. It will also be noted that the data for St Coombs which is in the Dimbula district show a minimum in the month of January indicating that the crop around February-March would be minimal. This also coincides with the flavour season for the Dimbula district and it would appear that flavour is possible only if the vegetative growth of the tea bush is stunted or constrained by weather factors. The histogram for the Uva district also shows a minimum in the month of July which precedes the flavour months August-September. The annual indices for tea stations in Sri Lanka show a gradation which broadly confirms the gradation in productivity viz. Low-country (St Joachim) > Mid-country (Hantane) > Up-country (St Coombs), Uva (Passara) having its characteristic drought season of low productivity but high quality. The yield data from clonal trials in these stations do not permit quantitative comparison with the phytoclimatic index since the experiments laid down do not satisfy the criteria in Section 4.3.

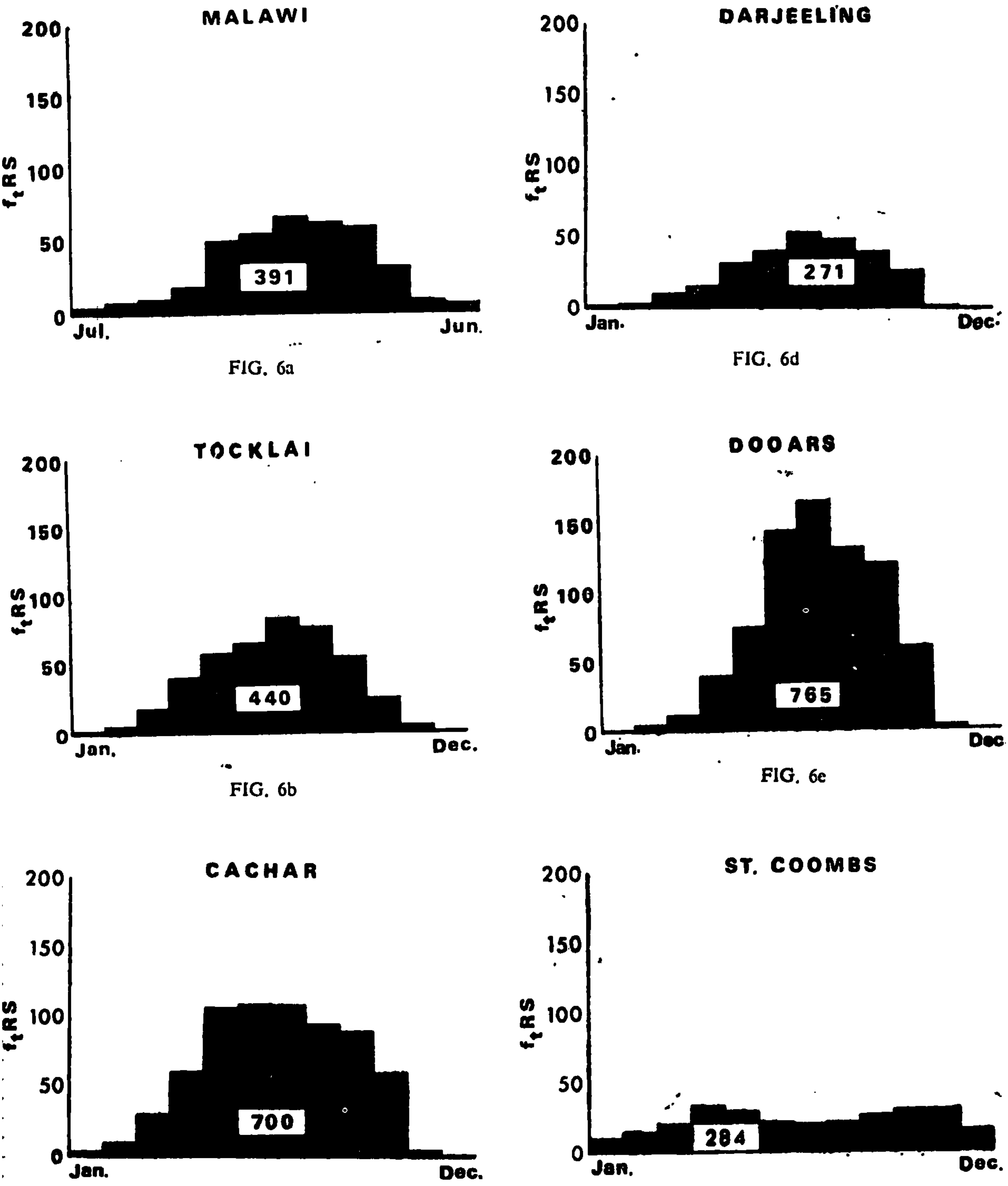

FIG. 6a

FIG. 6d

FIG. 6b

FIG. 6e

FIG. 6c

FIG. 6f

FIGURE 6—Phytoclimatic histograms for various tea research stations

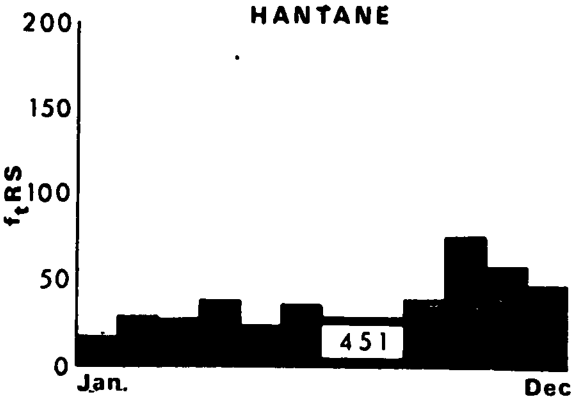

FIG. 6g

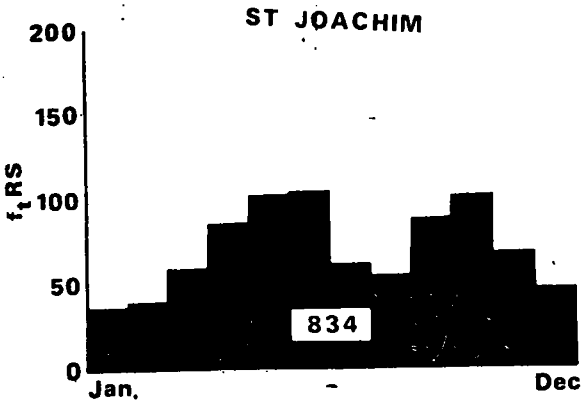

FIG. 6h

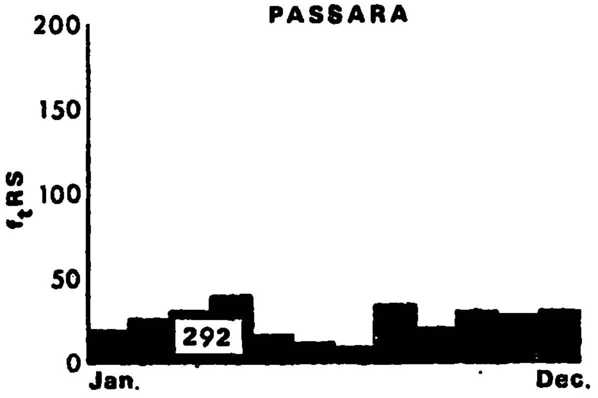

FIG. 6i

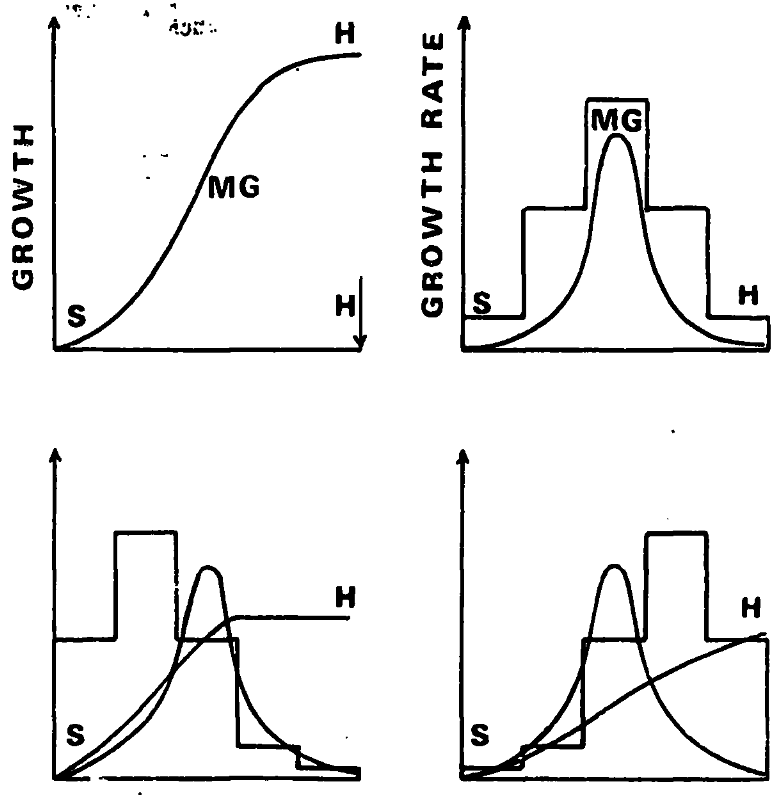

FIGURE 7—*Schematic diagram of plant growth for patterns of monthly phytoclimatic index*

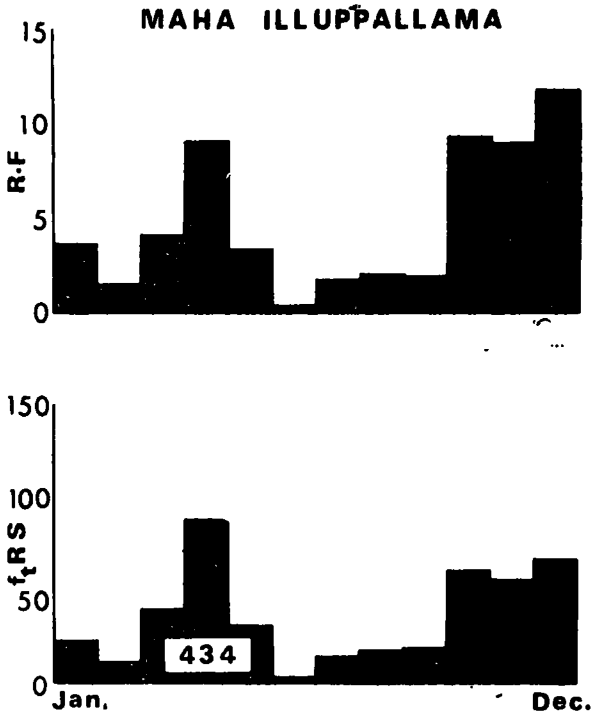

FIG. 8a

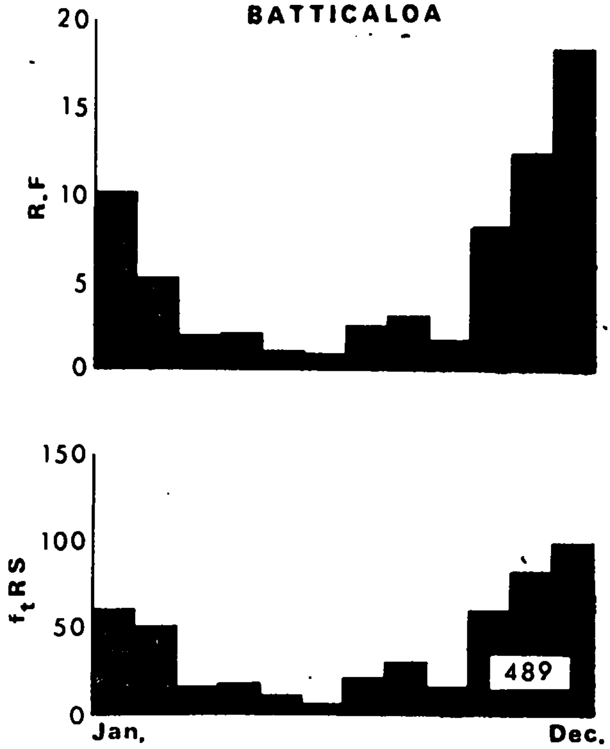

FIG. 8b

FIGURE 8—*Histograms of rainfall and phytoclimatic index for Maha Illuppallama and Batticaloa*

5.3 Phytoclimatic potential for seasonal crops

While the long-term average of the phytoclimatic index would generally describe the productivity of any location for plants, it is likely that the index calculated for a particular year will be a guide to the productivity of that year. Thus it should be possible to assess quantitatively the bumper years and the lean years. Such indices would be particularly important for seasonal crops such as wheat or rice, where a seasonal index characterising summer or winter yields for wheat or southwest monsoonal or northeast monsoonal seasons for rice in the tropics can be calculated.

For such crops the growth can be represented schematically as in figure 7 by an S shaped curve corresponding to a bell shaped rate of growth curve representing the differential of the former. It is obvious that the phytoclimatic potential must closely match the differential curve because with such crops sustained growth throughout the season is not desirable. A period of reduced or retarded growth is required for maturing, fruiting or grain filling. Thus when the farmer sows at a particular time of the year determined by the experience of several years, he hopes that the season would be normal meaning that the peak of phytoclimatic potential would match the peak of the growth curve. If the weather pattern is slightly changed in that year by either the advancing or the retarding of the onset of rains from the long-term mean, then the missmatch in the phytoclimatic and growth rate curves would dramatically affect the growth of the crop, leading to a very poor season (vide figure 7). In assessing the yield potential of pure strains of annuals it appears desirable to relate the yield to the integrated value of the phytoclimatic index for the season and also allow mathematically for retarded growth due to missmatch of growth and phytoclimatic peaks. From this discussion it is evident that the computation of the phytoclimatic potential provides a useful technique for the evaluation of yield potentials of crops without resorting to extensive co-ordinated trials in various agroclimatic zones. It appears likely that a re-examination of the accumulated data of agricultural experimental stations in terms of the phytoclimatic potential would lead to very useful conclusions.

5.4 Assessment of irrigation

In many crops rainfall has to be supplemented by irrigation. The formula for the phytoclimatic potential enables the calculation of the expected increase in yield. It would thus enable the calculation of the cost benefit ratio for supplementary irrigation. Irrigation experiments on tea have been reported but the data have not been given month by month but only by seasons or by arbitrary divisions of the year (Dale 1971, van Eck 1971, van der Laan 1971, Dutta 1971). Further the sunshine hours are not available instead only the solar radiation data have been recorded. Consequently the calculations of the increase of yield vis a vis the cost of irrigation are not decisive. For crops such as sugar cane which are irrigated according to strict schedules the calculation of the increase in productivity from the phytoclimatic potential would be useful not merely from the cost angle but also from the point of view of water conservation, in order to maximise crop within the limited water storage in reservoirs.

5.5 Limiting conditions in the phytoclimatic potential

The main climatic factors in the formula for phytoclimatic potential can reach certain limiting conditions. Thus it is possible to have in the tropics a constant average of sunshine hours resulting in a nearly constant high temperature with rainfall confined largely to heavy over night showers. This would lead to maximum phytoclimatic potential and the pattern of the histogram would follow that of the rainfall see figure 8. This pattern of climate would result in lush tropical rain forests.

Such a situation would also exist in deserts where again rainfall-would be limiting but at a low level. In the more temperate zones the rainfall may be uniform and adequate at a constant ambient temperature, but sunshine hours may be inadequate. In such cases the phytoclimatic histograms would follow the sunshine hours histogram and it would appear that only sunshine hours determine the yield. In the very cold latitudes the temperature is probably the dominant factor virtually suppressing all growth in winter and permitting a limited growth in the summer. It will thus be evident that such limiting conditions have obscured the recognition of the importance of the product function of temperature, rainfall and sunshine hours, with protagonists favouring for good reasons one climatic factor or the other, thereby inducing the statisticians into calculating regression coefficients regarding all the climatic factors as independent variables.

6—EXPRESSION FOR THE AGROCLIMATIC POTENTIAL

From the deduction of the formula for the phytoclimatic potential and the experimental data indicating its validity discussed in the foregoing sections, it would appear that the main climatic factors controlling plant growth have been functionally linked in a demonstratably successful way. This treatment would provide a superior basis for classification of the climatic factors than what has hitherto been available. But from the point of view of crop production this is inadequate since soil conditions may not be ideal. We should therefore devise a suitable formula to take into account the shortcomings of real soils as compared to the ideal soils. Let us call this the soil correction factor. We are then in a position to define the agroclimatic potential as the product of the phytoclimatic potential and the soil correction factor *i.e.*

Agroclimatic potential = phytoclimatic potential x soil correction factor.

Although a full discussion of the soil correction factor has to be reserved for a further communication, it is useful to give in outline here the type of soil correction factor necessary. The main factor to be taken into account is the finite available water capacity of the soil F. While this is estimated at 32 inches for Malawi the corresponding value in tea soils for Sri Lanka are as small as 4 to 6 inches. Thus rainfall above this value would disappear as surface run off. Further the ability to accept precipitation would depend also on whether the soil is partially or fully at field capacity. A functional relationship of the form $F\left[1-\exp\left(-\frac{R}{F}\right)\right]$ for the available water capacity has been derived and found to be satisfactory for both St Coombs and Malawi data. St Coombs terrain is hilly and calculations by Devanathan and Thevadasan show that up to 85% of the yield can be accounted by climate and soil factors if the soil correction factor is defined as equal to $\frac{F}{R}\left[1-\exp\left(-\frac{R}{F}\right)\right]$ so that the agroclimatic potential expression would be $f_t\,S.F\left[1-\exp\left(-\frac{R}{F}\right)\right]$. Further internal drainage factors and of course fertilizer limitations will also have to be allowed for. It must also be emphasized that the agroclimatic potential thus obtained will relate to a plant species where roots extend to the entire depth of the soil of available water capacity F. If, however, the plant s shallow rooted, then the corresponding F will be less and it would be necessary to specify the agroclimatic potential not as a maximum for the location and soil depth but as specific for the particular species.

These matters are under study and the findings will be reported in due course.

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