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A MODEL OF THE PHYSIOLOGICAL SYSTEMS OF VEGETATION

by

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LIST OF SYMBOLS

r	Stomatal aperture
E	Active energy produced by respiration process
E_m	Active energy required for water transfer from guard cells to subsidiary cells
E_p	Active energy required for water transfer to the guard cells
ΔI	Net increment of rate of active water transfer to the guard cells
Ig	Rate of active water transfer to the guard cells
I_l	Rate of active water transfer from the guard cells
T	Turgor pressure defined by the comparator
ΔT	Turgor pressure difference between the guard cells and subsidiary cells
Tg	Turgor pressure in the guard cells
ΔTg	Increment of turgor pressure in the guard cells
T_l	Turgor pressure in the leaf cells
ΔT_l	Increment of turgor pressure in the leaf cells
A	Leaf area
C_l	Storage factor of the leaf system
C_r	Storage factor of the root system
R'_{st}	Resistance of stomata to Co$_2$ diffusion
R_{st}	Resistance of stomata to water vapor diffusion
R_l	Resistance of leaf system
R_m	Resistance of mesophyll
R_x	Carboxylation resistance in chloroplasts
R_e	Excitation resistance in chloroplasts
T	Rate of transpiration
Θ	Water content of the soil
τ_l	Water suction in leaf system

τ_r	Water suction in root system
τ_s	Water suction in soil system
V_w	Volume of water
V	Volume of soil
C_s	Storage factor of the soil system
D	Diffusion constant of water vapor in air
ϕ	Concentration of CO_2 at the atmosphere level in gm/cm^3
ϕ_o	Concentration of CO_2 at the stomatas
ϕ_1	Concentration of CO_2 in the Intercellular spaces and the guard cells
ϕ_2	Concentration of CO_2 above the chloroplasts
e_d	Water vapor pressure in external air
e_a	Water vapor pressure in intercellular spaces
h	Thickness of soil layer
n	Subscript denoting n^{th} soil layer
L	Length of roots per unit volume of soil
l_s	Length of throat of stomata
S	Number of stomata
q_l	Rate of water transfer through the leaf system
q_r	Rate of water transfer through the root system
q_s	Rate of water uptake per unit area of soil thickness h.
i	Subscript denoting i^{th} root layer
m	Number of root layers

A MODEL OF THE PHYSIOLOGICAL SYSTEMS OF VEGETATION

SUMMARY

Plants, though they appear commonplace and passive, prove to be complex and fascinating mechanisms and the functioning of a plant, and the various processes involved for plant growth and development can be well understood if represented in the form of a model. Several models have, so far, been put forth for explaining processes within the plant, all of them pertaining to a specific function within the plant and explaining a specific plant activity, like photosynthesis, transpiration, stomatal mechanism, etc. Here we correlate all the models to develop an overall model, which could prove useful in the explanation of working of a plant as a whole and in controlling the plant processes.

INTRODUCTION

Plant responses and plant activities are accurately controlled by some internal mechanism. Present work with control systems is beginning to give insight into how this might occur. The concept of feedback systems has been used to explain the stomatal mechanism [pp. 91, Ref. 9; pp. 251, Ref. 10], and such feedback control systems also exist in the various growth and metabolic processes of the plant [pp. 485, Ref. 9].

The block diagram shown in Figure 1, is self explanatory. It shows the various activities which result in the final growth of the plant. A flow chart for the life cycle of a plant is discussed in detail by Salisbury Frank [pp. 488, Ref. 9].

The active energy E, released during the respiration process is used up in the plant for its final growth, and various other reactions. Most of this energy is lost in the form of heat. However, the cells are able to trap significant amounts of this energy in chemical forms, that can be used later. Figure 3 shows the active energy as the inputs to the photosynthetic and respiration actuators which operate the stomatal mechanism, as will be seen in later discussion.

Each of the processes given in the block diagram are extremely involved, and details are obtained from standard books in Plant Physiology [6].

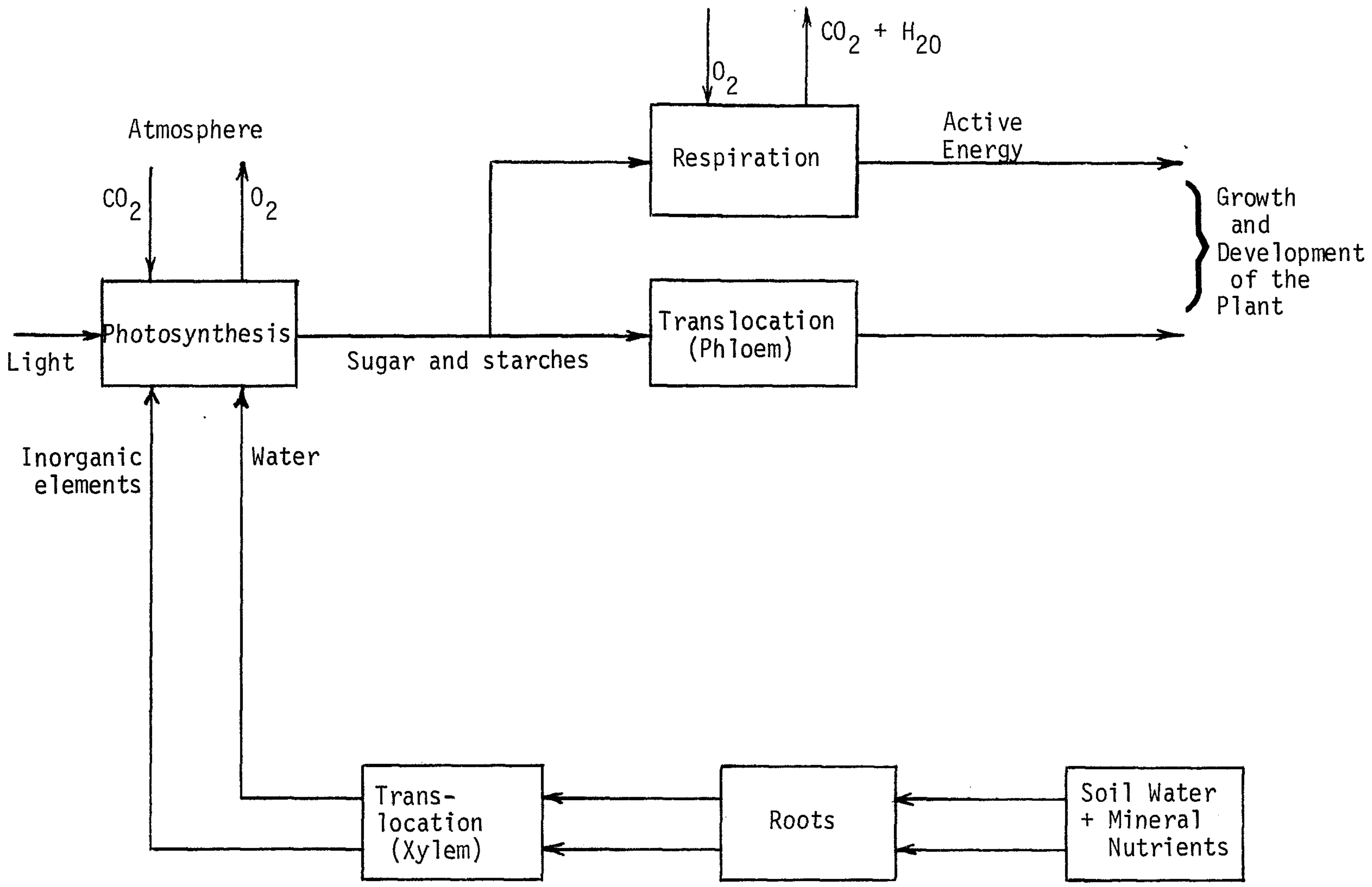

Figure 1 Simplified Block Diagram of a Plant

Diffusion of CO_2 from Atmosphere to Chloroplasts

The photosynthetic process involves a reaction between CO_2 and water in the presence of light and chlorophyll, resulting in the production of sugars and starch which are recirculated in the plant system by translocation. The process takes place in the chloroplasts and the carbon dioxide from atmosphere diffuses through various resistances in the leaf system before finally reaching the chloroplasts to react with water. This process has been explained by electric analogues [page 95, 5]. Figure 2 shows how the diffusion of CO_2 takes place and the various resistances in the pathway before finally reaching the chloroplasts. The reference level of CO_2 concentration in the atmosphere is taken to be ϕ gm/cm^3

Exchanges of matter and energy between plant communities and the air can be described by the fundamental equation

$$\text{Flux} = \frac{\text{Potential difference}}{\text{Resistance}}$$

Thus from Figure 2 it is seen that F_a, the flux of CO_2, may be written as:

$$F_a = \frac{\phi - \phi_0}{R_a} \qquad \text{etc.} \tag{1}$$

R_x and R_e represent the carboxylation and excitation resistances, all the resistances being expressed in units sec cm^{-1}.

The various resistances encountered for CO_2 diffusion, their measurement and estimation, is given in detail by J. L. Monteith [5].

Photosynthetic process

The carbon dioxide which has diffused to the chloroplasts from the atmosphere, now reacts with the water from the soil (the uptake of water from soil to the leaves is explained later) by the following reaction:

$$CO_2 + H_2O \longrightarrow (CH_2O) + O_2$$

The sugars are the main products of the above reaction which is translocated in the phloem tissues to take part in the respiration process.

Respiration is the conversion of sugars in the presence of O_2 to form CO_2 and H_2O. The carbon dioxide produced in this reaction is a very important factor, governing the opening and closing of the stomata.

Stomatal Mechanism

The resistance to the diffusion of CO_2 to the chloroplasts, and the uptake of water in the transpiration stream depends to a great extent on R_{st}, the stomatal resistance. Consequently the stomatal opening and closing, is a very important factor in determining the rate of transpiration, rate of photosynthesis, etc.

On observing the anatomy of stomates it is found that the inner wall of the two stomatal guard cells is somewhat thickened compared to the outer wall. The cells surrounding the guard cells are usually turgid, pushing against the guard cells. As the guard cells absorb water and expand, they tend (partially because of the thickened inner wall) to bow outward, separating at the middle and

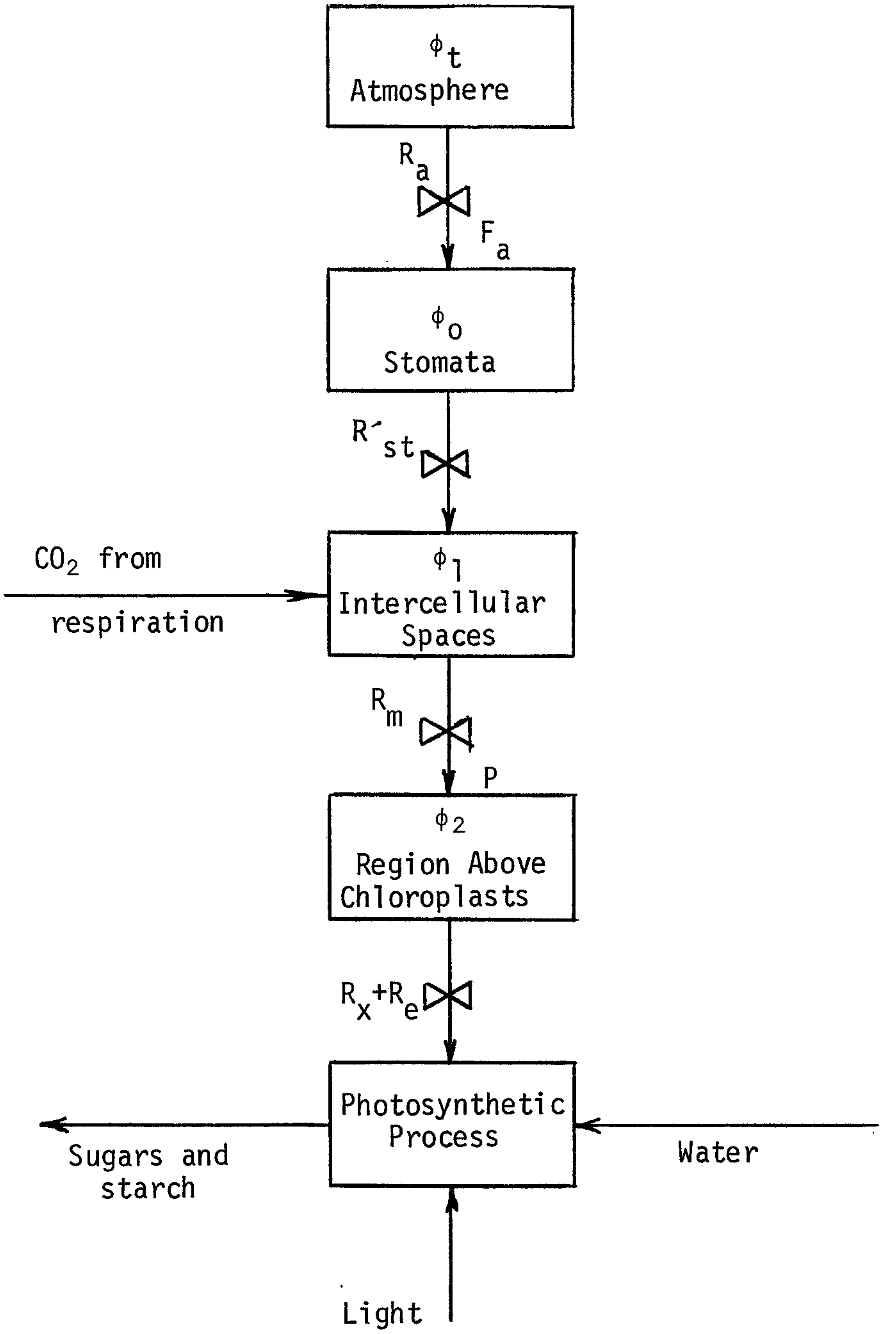

Figure 2.--The diffusion of carbon dioxide from the atmosphere to the chloroplasts.

causing the stomate to open. So opening is a turgor phenomenon in which stomates open as guard cells take up water.

The mechanism of stomatal regulation has been put forth by the so-called classical theory formulated by A.D. Sayre [p. 88, 9] and A.W. Scarth.

Sayre suggested that the carbon dioxide accumulating in the guard cells in the dark caused a reduction in PH (increase in acidity) of the cytoplasm. As the lights come on, this carbon dioxide was removed by photosynthesis raising the PH. In response to this PH change, the enzyme that catalyses the hydrolysis of starch to suger becomes more active. The increase in sugar concentration would make the water potential of the cell more negative. This increases PH, causing the stomates to open.

These phenomena are represented in the block diagram model by a bang-bang control which selects the inputs to the photosynthetic and respiration actuators.

In the absence of light, the process of respiration predominates the process of photosynthesis, thereby increasing the concentration of CO_2 in the intercellular spaces, and the CO_2 accumulating in the guard cells increases. The PH value is thus low, and the stomates are closed. This situation is represented by the condition when $\alpha > o$.

When the lights come on, CO_2 is removed from the intercellular spaces by photosynthesis. The concentration of CO_2 thus is lowered, and the PH value increases. This situation is represented by the condition when $\alpha < o$. This increase in PH value results in the opening of the stomata.

In between the two extreme positions discussed above the stomata oscillates between the open and closed positions and settles down to a certain value of the aperture opening r. Such oscillations have been observed by Raschke [p.92; 9].

Hence, by the facts considered above, we may assume that the CO_2 changes in the guard cells determine the energy available for active water transport to and from the guard cells. A model of the stomatal control mechanism based on these facts have been put forth by Woo K.B., et al [Ref. 11]. In light and normal air, the process of photosynthesis determines the CO_2 concentration in the guard cells.

The photosynthetic actuator operates under conditions when $\alpha < o$, and the actuator provides the energy which controls the gain constant of the photosynthetic control mechanism. This control mechanism does not operate in the absence of light, that is whenever $\alpha > o$.

Photosynthetic Control Mechanism

The increase in PH value in the guard cells (under conditions when $\alpha > o$) appears as active energy which controls the photosynthetic control mechanism. The control mechanism is also controlled by the water content in the leaf cells (the mesophyll cells and the subsidiary cells in the leaf), and hence the above two quantities -- the active energy, E_p, supplied by the actuator and, T_1, the Turgor pressure in the leaf cells -- are inputs to the photosynthetic control mechanism. This control mechanism is analogus to a valve controlling the flow of water in a pipe, and in the presence of inputs T_1 and E_p allows water to flow into the guard cells, represented by I_g. This represents the rate of water flow into the guard cells and the increment in turgor pressure due to this water flow into the guard cells is given by:

$$\Delta T_g = \frac{1}{C_1} \int Ig\ dt \qquad (2)$$

The mathematical relationship describing the control mechanism may be written as:

$$I_g \propto F_1 \ (T_1, E_p) \quad \text{for } \alpha < 0 \qquad (3)$$

$$I_g = 0 \qquad \text{for } \alpha > 0 \qquad (4)$$

Respiration Actuator:

The respiration actuator functions under conditions when $\alpha > o$ (an increment in CO2 concentration in the intercellular spaces when respiration predominates photosynthesis). In this case the PH value in the guard cells is low and thus there is a reduction in the available active energy. Thus in effect, there is an energy loss in the guard cells. The respiration actuator controls the functioning of the respiration control mechanism, which has for its input the negative energy E_m from the actuator and T_g the guard cell turgor pressure. The loss in active energy in the guard cells results in a loss of water in the guard cells and there is a flow of water from the guard cells to the leaf cells denoted by I_1. The decrease in turgor pressure in the guard cells as a result of the flow of water out of the guard cells is given by

$$\Delta T_1 = \frac{1}{C_1} \int I_1 \ dt \qquad (5)$$

The mathematical relationship governing the respiration control mechanism may be written as

$$I_1 \propto F_2 \ (T_g, E_m) \quad \text{for } \alpha > 0 \qquad (6)$$

$$I_1 = 0 \qquad \text{for } \alpha < 0 \qquad (7)$$

T_g (0) and T_1 (0) being the initial values of turgor pressures in the guard cells and leaf cells we have the following mathematical relationships:

$$T_g = \Delta T_g + T_g \ (o) \ - \ \Delta T_1 \qquad (8)$$

$$T_1 = \Delta T_1 + T_1 \ (o) \ - \ \Delta T_g \qquad (9)$$

The difference in turgor pressure between the guard cells and the leaf cells is thus:

$$\Delta T = T_g - T_l \tag{10}$$

This change in the turgor pressure in the leaf system is the input to the comparator which selects the input function to the turgor pressure mechanism. The turgor pressure mechanism brings about the changes in the stomatol aperture "r," a steady state being reached for a particular value of ΔT the difference in the turgor pressures. It could be concluded that under strong illumination ($\alpha < o$) the stomatal aperture "r" is a minimum. In between these two extremes the stomata oscillates between the open andclosed positions, and settles down to a particular value of its aperture "r." Such oscillations of the stomata have been recorded [p. 93; 9].

The stomatal resistance R'_{st} to CO_2 diffusion is given by

$$R'_{st} = 1.7 \frac{1 + \Pi r/2}{S \Pi r^2} \quad \left[\text{From } \begin{matrix}\text{Page } 209 \\ \text{Ref. } 8\end{matrix}\right] \tag{11}$$

and that to water vapor diffusion by

$$R_{st} = \frac{1 + \frac{\Pi r}{2}}{S \Pi r^2} \tag{12}$$

the additional multiplication factor of 1.7 in equation 11 is due to the ratio of molecular diffusion coefficients of CO_2 and water vapor [p. 97; 5].

Since R'_{st} controls the diffusion of CO_2 and R_{st} controls the transpiration process, and since both these quantities are functions of the stomatal aperture "r," we may conclude that the stomatal mechanism plays a vital role in determining the rates of transpiration and photosynthesis.

Transpiration: Introduction

Transpiration is the process of water flow in the soil plant atmosphere system. Various electrical analoges have been put forth [p. 202; 8] for explaining the transpiration process. The absorption of water from the soil is not an independent process but is related to and controlled by the rate of water loss in transpiration. The water movement through plants from soil to air is a series of linked processes in which the overall rate is controlled by the slowest process; that, is the stage at which the greatest resistance to water movement occurs. A complete model of the transpiration process was first proposed by Van den Honert [13]. This model is based on the analogy of water flow, to the flow of electric current in an electric conductor viz.,

$$\text{Current} = \frac{\text{Potential}}{\text{Resistance}} \tag{13}$$

The steady-state water flow may thus be written as:

$$\text{Rate of water movement} = \frac{\psi_{soil} - \psi_{root\ surface}}{r_{soil}} \quad \text{etc.} \tag{14}$$

The overall transpiration process may be summarised as the flow of water from the soil to the atmosphere through the soil, the roots, the xylem and the leaf system. The process of transpiration results in a loss of water in the plant and creates a suctional force in the soil and plant system. This suction, is the cause of water uptake by the roots from the soil.

The water content of the soil has been expressed on a volume basis

$$\theta = \frac{V_w}{V} \qquad \text{[Ref. 8]} \tag{15}$$

and the water capacity C in terms of the water content and suction force as

$$C = \frac{\partial\theta}{\partial\tau} \qquad \text{[Ref. 8]} \tag{16}$$

Thus for the soil medium the above equation is represented as

$$C_s = \frac{\partial\theta_s}{\partial\tau_s} \tag{17}$$

The rate of water uptake per unit cross sectional area of soil layer of thickness 'h' is given by

$$q_s = h\,\frac{d\theta_s}{dt} \tag{18}$$

If the soil is assumed to consist of 'n' layers each of thickness h, then the rate of water uptake in the nth layer is

$$\begin{aligned} q_{sn} &= h\,\frac{d\theta_{sn}}{dt} \\ &= h\,\frac{d\theta_{sn}}{d\tau'_{sn}} \quad \frac{d\tau'_{sn}}{dt} \\ &= h\,C_{sn}\,\frac{d\tau'_{sn}}{dt} \end{aligned} \tag{19}$$

Thus

$$\tau'_{sn} = \frac{1}{hC_{sn}} \int_0^t q_{sn}\,dt + \tau'_{sn}(o) \tag{20}$$

This represents the water suction in the n^{th} layer of the soil system. The total suction force in the first soil layer is given as:

$$\tau_{s1} = \tau'_{s1} + \tau_{s1(o)} \tag{21}$$

The water transfer through the root system as proposed by Gardner [1] is given as

$$q_r = \frac{\tau_r - \tau_s}{R_s + R_r} \tag{22}$$

Again considering the root to be divided into `m´ discrete layers of thickness `h´ we have the flow rate in the i^{th} layer as

$$q_{ri} = \frac{h\left(\tau_{ri} - \tau_{si}\right)}{R_{si} + R_{ri}} \tag{23}$$

The total rate of water uptake may be obtained by summing q_{ri} from 1 to m.

$$\begin{aligned} q_r &= \sum_1^m q_{ri} \\ &= h \sum_1^m \frac{\left(\tau_{ri} - \tau_{si}\right)}{R_{si} + R_{ri}} \\ &= h \frac{\left(\bar{\tau}_r - \bar{\tau}_s\right)}{R} \end{aligned} \tag{24}$$

where $\bar{\tau}_r = \sum_1^m \tau_{ri} = \tau_{r1} + \sum_{i=1}^{m-1} \tau_{ri}$ (25)

$$\bar{\tau}_s = \sum_1^m \tau_{si} \tag{26}$$

$$R = \sum_1^m (R_{si} + R_{ri}) \tag{27}$$

From equation 24 we have

$$\bar{\tau}_r = \frac{q_r R}{h} + \bar{\tau}_s \tag{28}$$

This gives the integrated suction of the root system and can be used to determine the suction of the plant root at each different layer. A detailed analysis of the differential equations involved, and a simulation model for the transpiration process is given by Woo, et al., [12].

The model for the transpiration process is included in the complete plant model, the water and mineral nutrients uptake taking place from the soil which is the reservoir of storage place for water and the mineral nutrients. The rise of water takes place by capillary action in the roots, due to the suction created by the loss of water in the transpiration process.

The water enters the plant xylem with a total suction $\bar{\tau}_r$ given by equation 25. The water enters the leaf system with a suction τ'_1 where the water is used for the photosynthetic process. There is a change in phase of water from liquid to vapour, and the water vapour leaves the leaf system with a vapour pressure e_a. The vapour pressure in the external air is e_d and `T' the rate of transpiration is given by

$$T = \frac{e_a - e_d}{R_{st} + R_a} \tag{29}$$

Whereas, R_{st}, the stomatal resistance has been shown to depend on `r' the stomatal aperture, the atmospheric resistance R_a is seen to vary considerably with wind speed [p. 304; 4].

If u is the velocity of wind, then the resistance R_a of the atmospheric layer is given as

$$R_a = \frac{3.26}{0.14} \, u^{-0.70} \tag{30}$$

The variation of R_a with wind speed for different leaf widths is illustrated in Figure 4.

Effect of the Environment

The variation of R_a with the wind velocity is just one example of the effect of environment on the resistances and various plant activities. In the development of the model, we have all along assumed a closed environment, wherein, the temperature, intensity of light, etc., are all constants. This is far from true, and a collection of data, of variations of different quantities with environmental changes is given below which gives an insight as to how complex the model would become if these changes are to be incorporated, in the model.

Variation of R_{st} with Light Intensity

In earlier discussions the variation of R_{st} was seen to be affected only by `r' the stomatal aperture, and the changes in the illumination level was assumed to be instantaneous. However the change from dark to lighted conditions is gradual, and the variation of R_{st} with light intensity is as shown in Figure 5.

R_t the rate of respiration depends on the percentage of the oxygen content available for the metabolic process. Above a certain percentage of the oxygen

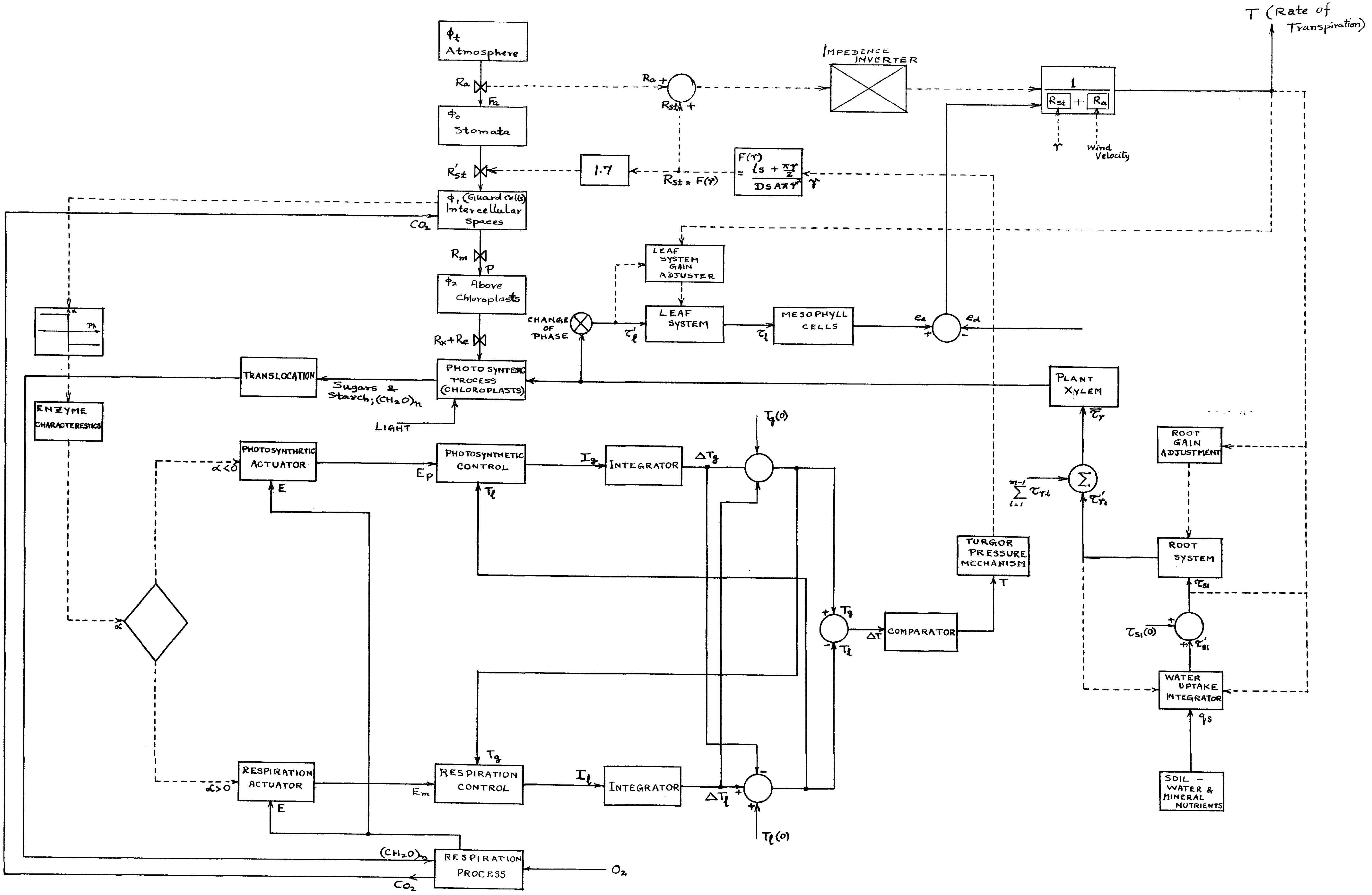

Figure 3.--Block diagram model of a plant

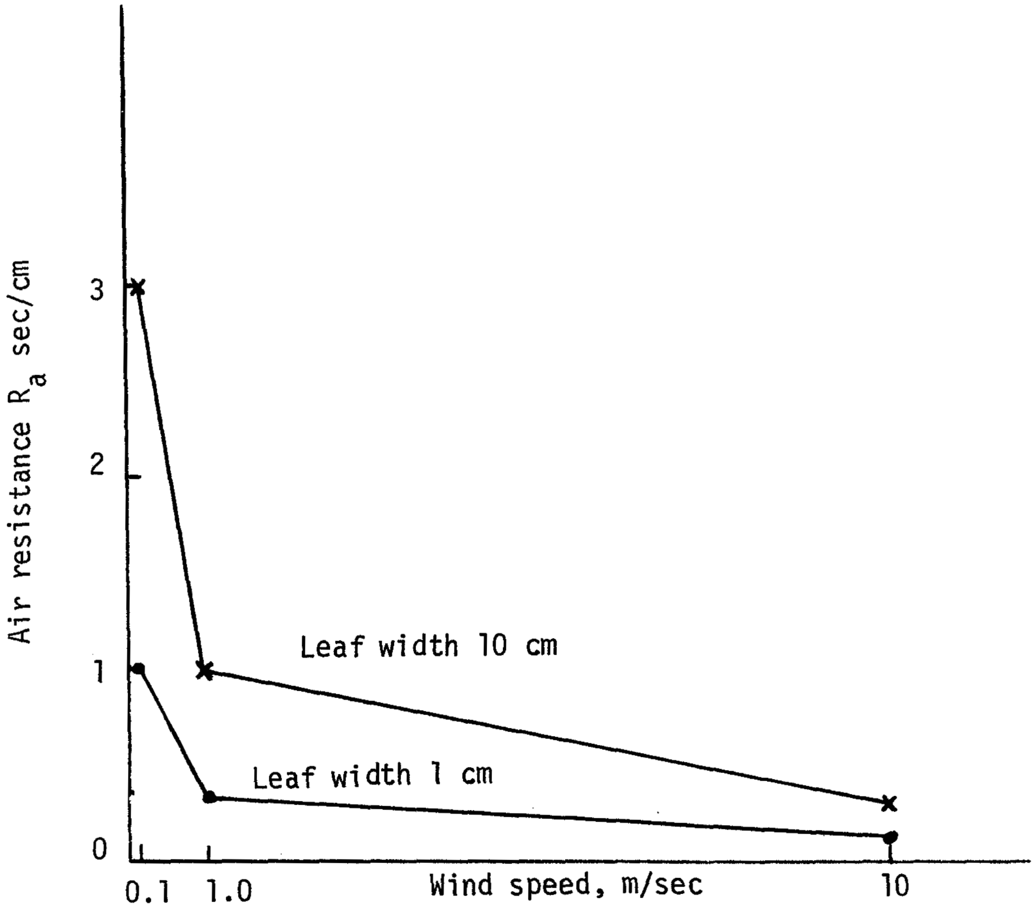

Figure 4.--Graph showing the variation of R_a, the air resistance, with wind speed, for two different leaf widths of two different plant species (from Ref: 4; Page 304)

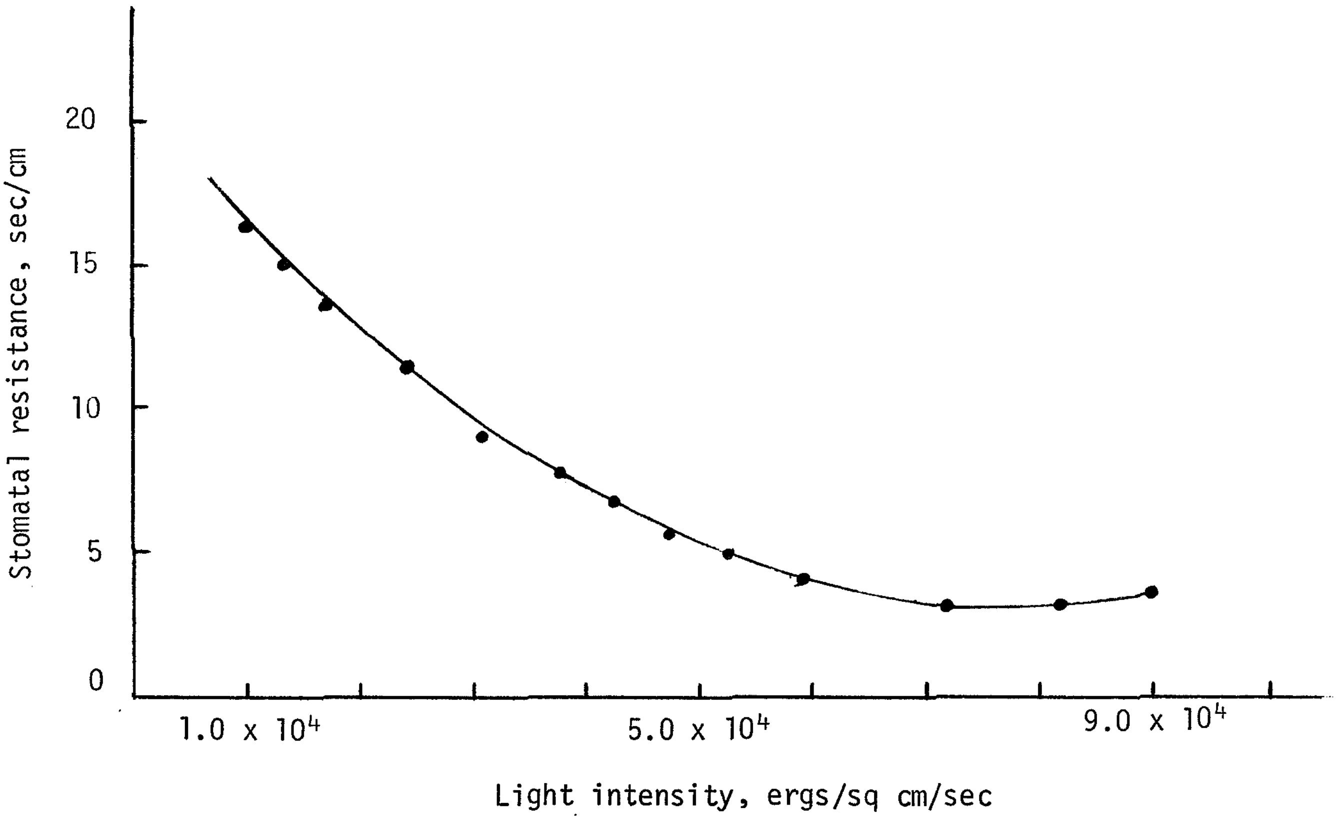

Figure 5.--Graph showing the variation of R_{st}, the stomatal resistance, with light intensity (from Ref: 4; Page 305)

concentration, the rate of respiration is essentially a constant. *T*, the rate of transpiration has been shown to depend on soil water potential [p. 291; 4]; the temperature of the soil [p. 196, 4], the wind velocity [p. 401; 6]; the stomatal aperture [p. 403, 6; p. 319, 4].

The rate of water uptake from the soil depends on the soil water content and the weather conditions [p. 272, 4]. *P*, the rate of photosynthesis depends on the water potential of the leaves and the intensity of the incident light [p. 22, 6].

Conclusions and Feasibility of the Model

The block diagram model for the plant functions and plant activities as shown in Figure 3, has been derived from mathematical equations, and existing mathematical models which has so far been used to explain the various interactions within the plant. Reference has been made to various theories which are yet in the conceptual stage. The problem of regulation of stomatal mechanism, for example, still remains to be solved. However, Levitt's Modified Classical Theory [p. 90, 9], on the basis of which the present model has been formulated, is the most recent, presented by Jacob Levitt in 1967, who has shown that stomatal regulation is essentially a turgor mechanism. Other theories for the stomatal regulation are given in Salisbury and Ross [9].

The model of the transpiration process, also included in the figure, serves to explain the balance between the water demand of the atmosphere and the availability of water to the plant roots. Van den Honert's suggestion of the use of Ohm's law for describing water flow into, through and out of plants has been incorporated in the model, the water flow and the energy status having been represented in terms of the suction of water at various positions in the plant. The relationship between the transpiration process and the availability of water at the plant roots from soil, could be determined by the simulation of the model on an analog computer. Such simulation models have already been formulated (Ref. Woo, et al). The stomatal mechanism greatly affects the transpiration rate. As has been shown in the discussion, the water suction change in the leaf system affects the movement of stomata, this being the main factor controlling transpiration.

Although the present model has been derived from mathematical models and other hypothesis, the results which follow, can only be thought of as conceptual, due to lack of information available from field measurements for the dynamic nature of the soil-plant atmosphere system. However, the model does suggest the need for more compact models, which could in mathematical terms confirm the theories put forward by biologists.

Research Needs

1. The gains of each of the blocks in the block diagram model may be written in terms of transfer functions. This is the next stage of the model formulation. Once such a model has been constructed, it is not difficult to simulate the model on an analog computer. Such simulations could prove very helpful in understanding the cause and effect and the input and output relationships of the plant.

2. The process of translocation has been represented as a single block in the model. However, this process is not as simple as to be written only in one

block. It seems, from the various theories put forward for the translocation process a separate model could possibly be formulated for this process alone.

3. In the flow of water through the soil-plant atmosphere system we have not considered the effect of mineral nutrients on the water suction. This could also be combined with the present model for completeness.

4. The problem of growth and development, of the plant involves an interaction of all the processes discussed so far. A quantitative analysis for growth is given in detail in "Plant Physiology" by Steward [14]. No complete block diagram model for this process has so far been formulated.

5. The various differential equations used in deriving the model, could be put in the state-variable form, thus giving a set of state-variable equations. These equations could lead to the more sophisticated method of equation solving by matrix methods and also could prove helpful in programming the whole model on a computer.

BIBLIOGRAPHY

References Cited

1. Gardner, W. R. "Relation of Root Distribution to Water Uptake and Availability." Agronomy Journal 56(1):41-45, 1964.

2. Gardner and Ehlig. "The Influence of Soil Water on Transpiration by Plants." Journal of Geophysical Research, 68(20):5719-5724, 1963.

3. Gaastra, P. "Climatic Control of Photosynthesis and Respiration." Environmental Control of Plant Growth, (L. T. Evans ed.) :113-140.

4. Kramer, P. J. "Plant and Soil Water Relationships -- A Modern Synthesis." McGraw-Hill Book Company, 1969.

5. Monteith, J. L. "Gas Exchange in Plant Communities." Environmental Control of Plant Growth, (L. T. Evans ed.) :95-112, 1963.

6. Leopold, C. A. Plant Growth and Development. McGraw-Hill Book Company, 1964.

7. International Society of Soil Science. Soil Physics Terminology Bulletin 23:7 1963.

8. Rose, C. W. Agricultural Physics. Pergamon Press :121-159, 1966.

9. Salisbury, F. B. and C. Ross. Plant Physiology. Wadsworth Publishing Company, Inc., Belmont, California, 1969.

10. Slatyer, R. O. Plant Water Relationships. London, New York, Academic Press, 1967.

11. Woo, K. B., L. N. Stone, and L. Boersma. "Conceptual Model of the Stomatal Control Mechanism." Water Resources Research, 2:72-84, 1966.

12. Woo, K. B., L. N. Stone and L. Boersma. "Dynamic Simulation Model of the Transpiration Process." Water Resources Research, 2:85-97, 1966.

13. Van den Honert, T. H. "Water Transport in Plants as a Catenary Process." Discussion, Faraday Society, 3:146-153, 1948.

14. Steward, F. C. "Analysis of Growth: Behavior of Plants and Their Organs." Plant Physiology, VA, Academic Press, Inc., 1969.

Other References

1. Crafts, A. S. "Movement of Organic Materials in Plants." Plant Physiology. 6:1-41, 1931.

2. Ducet, G. and A. J. Rosenberg. "Leaf Respiration." Annual Review of Plant Physiology. 13: 171-200.

3. Gaastra, P. "Photosynthesis of Leaves and Field Crops." Netherland Journal of Agriculture Science, 10:311, 1962.

4. Hackett, D. P. "Respiratory Mechanism in Higher Plants." Annual Review of Plant Physiology, 10:113-146.

5. Hoch, G. and B. Kok. "Photosynthesis." Annual Review of Plant Physiology, 12:155-194.

6. Horwitz. "Mathematical Treatment of Translocation in Plants." Plant Physiology, 33(2): 81-93, 1959.

7. Levitt, J. "Mechanism of Stomatal Action." Planta, 74: 101-118, 1967.

8. Moss, D. N. "Respiration of Leaves in Light and Darkness." (Electrical Analogue) Crop Science, 6:351.

9. Nichiporovich, A. A. and Che'n. "Photosynthesis and Absorption of Mineral Nutrients by Plant Roots." Soviet Plant Physiology, 6:531, 1969.

10. Slatyer, R. V. and S. A. Taylor. "Terminology in Plant and Soil-Water Relations." Nature (London) 187:922, 1960.

11. Voznesenskii, V. L. "Absorption of CO_2 by Plant Roots." Soviet Plant Physiology, 5:325, 1958

12. Cowan, I. R. "Transport of Water in the Soil-Plant Atmosphere System." Journal of Applied Ecology, 2:221-239, 1965.

13. Meyer, B. S. and D. B. Anderson. Plant Physiology, Second Edition. D. van Nostrand Company, Inc., Princeton, N.J., 1952.