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IN RELATION TO STRUCTURAL REQUIREMENT

DISSERTATION
Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

* * * * * * *

The Ohio State University
1967

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CHAPTER I

INTRODUCTION

PLANT ENVIRONMENT AND ENVIRONMENTAL FACTORS

Environment is of great interest to agriculturists and biologists. During the last 35 years or so, considerable attention has been given to plant environment. Efforts are being made to establish many new environmental concepts and principles. As a result, a radical departure in methods and philosophy and a marked shift in approach are being noticed. The introduction of the tower-glasshouse for commercial crop production is an example (Ruthner, 1963).

Types of Environment. According to Webster's New World dictionary (1964), the term "environment" refers to all external conditions. Hence, plant environment means all the conditions which are encircling it. Plant environment is basically of two types; (1) functionally related and (2) non-functionally related. The functional environment is that which is composed of a continually changing complex of all conditions and influences which are interacting with the plant. The non-functionally related environment, also known as potential environment, is not functionally necessary but sometimes may become part of the environment of any object. The sum total of the functional and potential environment constitutes "generalized" environment.

Mason and Langenheim (Griffith and Platt, 1964) have used language analysis for explaining an environment concept. They feel that environment deals with (a) the organism, (b) the physical phenomena that
enter into a significant relationship with the organism, and (c) the empirical relationship between the organism and the phenomena, either singly or in various combinations. Also, they consider that an environmental phenomenon must be (1) operationally significant to an organism, (2) directly effective at some time during the life cycle of the organism, and (3) effective in sequence as ordered by the life cycle of the organism. Thus, a functional environment is organism-directed, organism-timed, and organism-ordered and organism-spaced. We are primarily interested in the functional environment because it is directly related to plant growth.

**Environmental Factors.** Plant environmental factors may be grouped under different classifications. The most commonly used classification includes aerial factors and soil factors.

**Aerial environmental factors:**

(1) Air temperature - including the special effects of levels around the freezing point, and the effects of diurnal and seasonal fluctuations.

(2) Light - including the separate and different effects of intensity, duration (photoperiod) and frequency or quality.

(3) Moisture - includes the direct effects of frost, dew, rain, hail, snow, and fog.

(4) Composition of air - especially the percentage of carbon dioxide (CO₂) and air speed (wind).

**Soil environmental factors:**

(1) Soil temperature.
(2) Soil moisture - availability and tension due to osmotic pressure, etc.

(3) Soil aeration - composition of soil air with special reference to the balance between $\text{CO}_2$ and oxygen.

(4) Nature and extent of medium.

Another way of classifying the plant environment is to differentiate into intrinsic and incidental environmental factors. The intrinsic factors are ever present components of any typical plant environment and are all physical. Incidental factors are not always present and all are biotic ones. However, the incidental factors should not be considered as unimportant. As a matter of fact, in many instances these are vital.

(1) The intrinsic factors:

- Solar radiation
- Moisture
- Temperature
- Medium of the root - generally soil
- Atmosphere - humidity, composition and wind speed
- Pressure
- Gravity
- Magnetism
- Cosmic radiation

(2) The incidental factors:

- Floods
- Fires
- Man-made factors - air pollution, wastes
- Pests and pathogens
**Peculiarities of Environmental Factors.** Plant environmental inputs are in a broad sense well known to the plant scientists. However, precise quantitative information and interactions among the factors are yet to be understood. The response of plants to environment is complex because of the interaction of many variables which affect plant growth. Certain environmental factors may not only limit growth but may actively regulate it.

The levels of most of the factors enumerated above are constantly changing. The variations are random or cyclic.

The plant is known to react in specific ways to various levels of each environmental factor. It is also true that little is known about the way in which plants may be affected by different rates of change of the factors.

The amplitude of variation, duration at different levels, and rate of change may all be important in considering the effects of the plant environment factors. Results of the studies made in the past show that there is a range for each factor, within which the plant is capable of surviving. Further, there is a narrower range where it can grow. But the plant can only grow and yield to its capacity when all the factors are optimal at the same time.

Plant behavior responds to inductive factors or formative factors. In other words, plants exhibit memory. But the memory is not governed by energy storage phenomena as in an engineering system.

Plants in their course of development pass through a series of orderly and consecutive stages. The constant recurrence of environmental factors from season to season plays an important part in regulating the course of development of plants adapted to certain environments so that
they fit into such environments. The development is orderly, continuous, and definitely associated with the seasonal advance and progressive changes in the climatic factors; it has been appropriately designated as rhythmic.

All plant activities operate within certain, more or less, well-defined limits of the environmental factors. The requirements for life should be present at least in a minimum quantity, concentration, or form before the manifestations of life and growth can be either initiated or sustained. These manifestations proceed at the highest rate of activity at optimum conditions. Again they may sooner or later cease at the maximum points. Growth-depressing factors become greater and more active as the optimum point is approached, and beyond it accounts for the rapid downward trend of the growth. These points at which the relative rates of activity are more or less well-defined are called the cardinal points. The cardinal points are not definite but cover a considerable range, depending on the environmental factors under which the plant develops and the condition and age of the plant. Also, the cardinal points are valid only for a certain state of development or growth.

NEED FOR ENVIRONMENTAL CONTROL

The optimum yields of agricultural crops today are due to long-term experience in cultural practices and research findings. Under the natural climatic conditions, a stage of near maximum yield may soon be reached. The present world food production is far too low to support the rapidly increasing world population. It is estimated that by 1975 the world population will have reached 4 billion which is exactly 1 billion above 1961 (Patridge, 1963). Thus, the already existing food
shortage will become very serious and a chaotic one. Many suggestions have been made to increase the potentialities of the world food production. Adaptation of improved and modern agricultural techniques by the under-developed countries may increase production of grain crops and fisheries on a sufficiently large scale. It has often been suggested that new forms of food by novel or synthetic methods should be produced. Typical among these are food derived from algae, yeasts, marine plankton and crude petroleum. Man has subsisted on cereals, vegetables, fruits and animal and fish products for several thousand years and likely is unwilling to change habits in a short time. Social and economic adjustment would be essential. Thus, the production of food products likely will require a conventional agriculture for a long time to come. Indirectly, it may mean that man must continue his efforts to modify plant environment. Based on past experiences, and the encouraging results from research, the concept of environmental control may be extended without calling for severe changes in crop husbandry.

PURPOSE OF ENVIRONMENTAL CONTROL

The main purpose of environmental control is to provide plants with the conditions which would promote maximum possible growth response. There are other advantages of controlling plant environment. These are:

(1) Production of uniform plant material.
(2) Reproduction of seasonal conditions.
(3) Hastening of growth.
(4) Delaying maturity and development.
(5) Testing varietal responses.
TRENDS IN ENVIRONMENTAL CONTROL

Since the dawn of agricultural history, man has been aware of the effects of environment on crops. The cultural practices followed in crop production for centuries clearly indicate efforts to modify the environment near the plants. However, very little knowledge about the interactions among and the integration of individual factors of environment was known. About 70 years ago, interest in various aspects of plant growth was shown for the first time (Hudson, 1957). Glasshouses were erected with the purpose of conserving solar energy during the cold winter days. The plant scientists used glasshouses to control one or more factors permitting them to study the interactions. The controls were relatively inaccurate but the source of artificial light was then the main limitation for their success.

Gregory (1926) was probably the first to make a study of the growth of plants for long periods in a glasshouse. He defined the conditions inside the glasshouse but did not control them. The big break-through in the use of glasshouses for environmental control studies came when electric lamps with characteristics suitable for plant growth were introduced. This was the turning point in the history of environmental control.

Many glasshouses with improved arrangements for light and temperature control were available by the end of the thirties. The crane gantry arrangement at Boyce Thompson Institute, Yonkers, N. Y., may be cited for its mechanized arrangements (Arthur, et al., 1930).

Went (1943) was the first to visualize the importance of air conditioning glasshouses. He further modified the arrangements inside an air conditioned glasshouse to provide a variety of climatic conditions.
In 1948, the Earhart Research Laboratory was completed and unofficially called "The Phytotron". Natural sunlight and artificial light were used as source of illumination (Hudson, 1957). Such a facility was important to plant scientists all over the world. As a result of this, more phytotrons were constructed in the Netherlands, France, Russia and Australia (Morse and Evans, 1962). Another phytotron in the U.S.A. is now under construction at the University of Wisconsin.

Along with the development of glasshouses, came the development of other facilities for laboratory and field studies of environmental factors. (Refer to Appendix for detailed information.) Out of these, growth chambers, also called growth cabinets, are most popular. Growth chambers are of varying sizes, from small units, designed for taking single leaf to large cabinets accommodating several plants. The cabinets are generally glazed and have very fine control of temperature, light and humidity.

The success of the commercial glasshouses in the early days was due to the protection given to plants. Later when electric lamps were developed, the vegetable crop growers and floriculturists adapted glasshouses for higher yields and "off season" cash crops. Recently a firm in Austria introduced a vertical tower glasshouse. It is claimed that such a facility would be able to industrialize agricultural production. Basically, it has all the features of a phytotron plus a three-dimensional concept. Plants are moved on a vertical, endless conveyor belt. During their movement they are exposed to the desired environmental conditions.
ENVIRONMENTAL CONTROL AND GROWTH MODELING

Mathematical models may be used to predict and estimate growth rates. The engineers concerned with the design and operation of growth structures should obtain quantitative estimates of plant growth input needs. The increasing use of growth structures further accentuates the need for such models of plant growth. While developing such models it is necessary to translate the physiological aspects of each growth factor into suitable and simplified mathematical expressions. The individual functions may then be combined to express mathematical models that represent plant growth.

THE ROLE OF AERIAL PLANT ENVIRONMENTAL FACTORS

Plant development depends on the soil environment which provides the plant with water, plant nutrients and minerals, and heat and aeration for root development, and aerial environment which allows the fixation of CO$_2$ in the presence of light. The utilization of materials supplied by the soil environment, and the products formed depend entirely on conditions in the aerial environment. Thus, the aerial environmental factors are critically important to optimum plant growth and will be considered as the inputs to the growth model.
CHAPTER II
OBJECTIVES OF STUDY

The main objective of this study was to develop a better and more precise understanding of the aerial factors and their effects on plant growth conjointly. The specific objectives were as follows:

1. To analyze each individual aerial environmental factor, particularly light, CO$_2$, and temperature, with the view of understanding the design needs for environmental facilities.

2. To extend and integrate the known aerial environmental inputs to understand their combined effects on plant growth.

3. To propose a response model for potential growth response.

4. To test the proposed model.
CHAPTER III
REVIEW OF LITERATURE

RELATED CONCEPTS

In higher plants the aerial inputs furnish the energy required for growth and maintenance of the plant. This is achieved through photosynthesis, a process of synthesizing certain carbohydrates from CO$_2$ and water in chlorophyllous cells in the presence of light energy. In the presence of adequate quantities of edaphic factors, the best development and growth of the plant is possible only when the process of photosynthesis is at its best. A number of indices have been used to characterize the growth of plants, such as, increase in lengths, diameters, areas and volumes of plant organs, and the increase in fresh and dry weights of plant organs. But since the ultimate increase in dry matter is based on photosynthesis, photosynthetic rate has been considered synonymous with growth in this study.

Photosynthesis is influenced by light energy, CO$_2$, and temperature. In relation to the study of different factors acting simultaneously, important concepts have been generated in the past. A systematic study is necessary for understanding these factors and the related concepts.

Law of the Minimum. Liebig (Singh & Lal, 1935) postulated that the yields of field crops are determined by the quantity of the one nutrient element present in the lowest concentration.

Law of the Limiting Factor. Blackman (1905) extended the law of the minimum in light of other environmental factors and called it the "law of the limiting factor". According to this law the rate of any
biological process would increase with an increase in the level of any factor acting slowly or which is limiting; but the dependence ceases when any other factor becomes limiting. Blackman applied this law to photosynthesis. He proposed that the functions must be characterized by a curve consisting of a linear ascending part, followed by a sharp breakoff point and terminated by a horizontal plateau. According to the law of the limiting factor, the rate of photosynthesis was assumed to be proportional to the limiting factor and independent of all other factors under particular conditions. The limitation of this law is that it does not take into consideration any other factor. Only one factor, the one which limits, governs the rate of the process. The rate can be increased only by increasing the intensity of this factor.

Law of the Relative Minimum. Harder (Singh & Lal, 1935) realized the limitation of the law of the limiting factor and considered any two factors, at a time, affecting the rate of a process. He postulated that of two factors, the one that is present at a minimum level governs the rate of the reaction to a greater extent. It is pointed out that relative magnitude in proportion to the amount actually required in the process is to be considered and not the absolute magnitude. The essence of this law is, then, the rate of any process may depend on several factors at the same time. When one factor gradually ceases to be limiting the influence of another factor increases.

Photosynthesis as a Catenary Process. Photosynthesis consists of several processes and its overall rate cannot exceed the rate of any of its individual process. Thus, saturation with respect to one factor is reached when the overall rate becomes equal to the maximum rate of a single process. Such an overall process is called a "catenary process".
With respect to the utilization of external aerial environmental factors, the processes can be categorized into the following three types:

1. a photochemical process which is responsible for the conversion of light energy into chemical energy,

2. a diffusion process for the transport of CO$_2$ from the environment to the chloroplast, and

3. biochemical processes which precede and succeed the reduction of CO$_2$ and finally result in the formation of certain carbohydrates.

The photochemical process is influenced by light, the diffusion process by CO$_2$ content of the environment and slightly by temperature, and the biochemical process by temperature.

THE LIGHT FACTOR

The energy to sustain plant life is received from the sun as solar radiation. It is in the form of electromagnetic waves varying in length from 290 to about 2,500 µm. Wavelengths extending from 290 to 390 µm are called ultraviolet radiation, while wavelengths in the 390-760 µm constitute the visible light. About 45 percent of the total energy of the solar radiation is contained in the visible spectrum which only is used by plant life.

Wavelengths longer than 760 µm characterize the infra-red radiation. Infra-red has insufficient energy to trigger chemical reactions but its heating quality may exert stimulating effects on the growth of plant organs, especially during germination and leaf growth (Calvert, 1963).

$1\mu = \text{millimicron} = 10^{-7}$ cm.
The ultraviolet band is invisible to the human eye but unlike infra-red, it actively stimulates chemical reactions. This band is not, however, of any particular importance to higher plants. A high portion of infra-red and longer wavelengths of visible light are absorbed by atmospheric gases and suspended particles. The shorter wavelengths and the ultraviolet band are scattered, which may form as much as 10-15 percent of total light falling on the earth (Calvert, 1963).

**Importance of Light to Plants.** A number of plant functions are affected by light. The cardinal values tend to vary with the particular process or function, the age and kind of plant, and variations in other environmental factors. Light energy influences a number of processes in the plants. They include (1) photosynthesis, (2) respiration, (3) transpiration in higher plants, (4) formation of pigments, especially chlorophyll in higher plants, (5) flower induction, (6) photoperiod, and (7) phototropism.

**The Light Compensation Point.** This is defined as the light intensity at which the rate of photosynthesis is balanced by the rate of respiration.

**Saturating Light Intensity.** It is the intensity of light at which the rate of photosynthesis attains a maximum.

**Effects of Light on Plant Growth.** There are three aspects of light which affect plant growth. They are intensity, quality, and duration.

(a) **Intensity of light.** Photosynthetic rate increases with an increase in light intensity until the saturation intensity is reached. Plants growing in the continued absence of light develop typical
characteristics known as etiolation. Such plants are characterized by elongated and weak stems, poor root development, poor or no development of leaves, relatively high water content, and practically no formation of chlorophyll. Under prolonged dark periods such plants ultimately die.

When exposed to low light intensity, the leaves of etiolated plants rapidly expand and develop a green color. Even a relatively low light intensity is enough to bring about this change.

Popp (1926a) suggested that, in general, stem elongation, length of internodes, and stem diameter and leaf thickness vary directly with light intensity.

Many workers have investigated the relationship between light intensity and growth. Shirley (1929) found that the light intensity needed for survival of the plants is very low, being less than 40 f.c.² in most plants. Further, at low intensities, up to about 20 percent of full summer daylight intensities, the dry weight produced is proportional to the light intensity received by the plant.

Bates and Roeser (1925) also reported a wide variation in the ability of different species to use low intensity light.

Saturation light intensity values have been investigated for different plants by several workers. Verduin and Loomis (1944) reported the saturation light intensity for corn to be 2500 f.c. Burnside and Bohning (1957) determined the saturation light intensities for leaves of a number of plant species. They found that for sun-type plants³ the

²f.c. = Foot-candle, a unit of measuring light intensity.
³Sun-type plants attain maximum photosynthetic rates between or above 2000-3000 f.c. light intensity.
value was between 2000-2500 f.c., whereas for shade-type plants it was between 500 and 1000 f.c.

Kramer and Decker (1944) reported that some plants attain a maximum photosynthetic rate receiving 90 percent of full sunlight, whereas others saturate around 10 to 20 percent of full sunlight.

Gaastra (1959) working with several plants of economic importance noticed that at 300 ppm carbon dioxide in the atmosphere, light saturation was reached at about $10 \times 10^4 \text{ ergs/cm}^2/\text{sec}$ light intensity. When the concentration of CO$_2$ was increased to 1310 ppm the light saturation values increased considerably. Similar results were reported by Singh and Lal (1935) for sugarcane, wheat and flax.

Saturation light intensities under field conditions have been reported to be much higher than observed for individual leaves and plants under an experimental (laboratory) setup. Went (1957) found saturation at 1000 f.c. for Beta Maritima with no self-shading, whereas for the same plant in the field, saturation was reached at 4400 f.c. For a single plant of wheat, Hoover et al. (1933) found a light saturation value of 2000 f.c., whereas Thomas and Hill (1949) found a value of more than 5000 f.c. in the field.

(b) Quality of light. From the point of observing the influence of different wavelengths, considerable work has been done on lower plants and isolated chloroplasts (Rabinowitch, 1946). In higher plants

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4Shade-type plants attain maximum photosynthetic rates at or below 1000 f.c. light intensity.

5ppm, parts per million.

6Ergs/cm$^2$/sec, a measure of light intensity. $43.2 \text{ ergs cm}^{-2} \text{ sec}^{-1} = 1.0 \text{ f.c.}$
the studies have been mostly limited to the effect of light quality on seed germination and flowering.

Popp (1926b) studied the effects of different wavelengths in the visible light spectrum on the growth of several plants. He observed that when wavelengths shorter than 529 μm were excluded, abnormal stem elongation occurred. When wavelengths shorter than 472 μm were eliminated, similar effects were produced but they were not so marked. Only the exclusion of ultraviolet radiation failed to produce this abnormality. In the absence of longer wavelengths of light, the blue end of the spectrum tends to produce a sturdy but stunted plant.

In green light the expansion of leaf blades of peas and beans was reported to be much retarded (Myers and Anderson, 1964).

Shirley (1928) used five light qualities and three light intensities on the sunflower, *Geum* and *Galinsoga*. He concluded that the plants studied produced more dry matter per increment of light under a complete solar spectrum. He further reported that without red light, plants grew more efficiently than without the blue light.

Dunn recorded higher dry matter production from blue plus red light compared to that from warm white light (Went, 1957).

Vince and Stoughton (Hudson, 1957) pointed out that the same saturation level was obtained for all wavelengths. However, the light energy required for saturation varied from band to band.

Johnston (1933) compared the role of infra-red to complete visible light. It was shown that light in the infra-red band was not effective for dry weight production.

Gaastra (1959) compared different sources of artificial light and sunlight in the 400-700 μm spectral region. See Table 1. From this
It can be concluded that light from an artificial source can readily be substituted for solar energy.

Table 1. Maximum Efficiency of Light Energy Conversion in the Spectral Region of 400-700 nm by Leaves with Average Absorption Characteristics for Quantum Requirements of 10 and 12 at all Wavelengths (after Gaastra).

<table>
<thead>
<tr>
<th>Source</th>
<th>Quantum Requirement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
</tr>
<tr>
<td>1. Solar Radiation (direct)</td>
<td>17.7</td>
</tr>
<tr>
<td>2. Incandescent Lamp - 500 watts</td>
<td>18.8</td>
</tr>
<tr>
<td>3. HPL 500</td>
<td>16.9</td>
</tr>
<tr>
<td>4. HO 450</td>
<td>15.0</td>
</tr>
<tr>
<td>5. Warm White Light TL 20</td>
<td>17.0</td>
</tr>
<tr>
<td>6. DeLuxe Warm White Light TL 32</td>
<td>18.2</td>
</tr>
<tr>
<td>7. White Light TL 33</td>
<td>16.8</td>
</tr>
<tr>
<td>8. DeLuxe Cool TL 34</td>
<td>18.9</td>
</tr>
<tr>
<td>9. Daylight TL 55</td>
<td>16.9</td>
</tr>
</tbody>
</table>

(c) Duration of light. To most plants the period of exposure to light, called photoperiod, is important. Unless specified, it means the daily light period in a natural diurnal cycle. In 1920, Garner and Allard (1920) for the first time demonstrated the effect of photoperiod in controlling the transition from vegetative growth to the reproductive stage. Later on they also found that photoperiod played an important role in vegetative growth (Allard and Garner, 1923).

Arthur, Guthrie and Newell (1930) worked with 30 different species of higher plants to study the effects of photoperiod on vegetative growth. They reported that plants vary considerably in their photoperiodic response. Arthur (1928) found that while many plants will successfully withstand continuous illumination, others are slightly
injured by it, and still others will not withstand continuous illumination and require some minimum dark period everyday. Went (1957) observed the amount of photosynthesis depends on the light-period duration as well as on its intensity. For tomato plants grown at 1000 f.c. light intensity, he found twice as much photosynthesis in a 16-hour day as in an 8-hour day.

Bohning (1949) studied the time effect of photosynthesis in apple leaves exposed to continuous illumination. He concluded that the previous history of plants also plays an important role in photoperiodic response. For instance, leaves already exposed to bright light could continue photosynthesizing under continuous light for about 18 days at 3200 f.c. and 25° C. On the other hand, a rapid decline in the rate of photosynthesis was observed for leaves which developed under low intensities.

(d) Interactions. Working with tomato plants, Went (1957) found that the increase in the dry weight depends on the intensity of light, which limits the rate of photosynthesis, and not on the total amount of energy received by the plants. He found that for an increase in dry weight at higher photoperiods, the intensity of light should be higher. Gregory (Hudson, 1957) suggested that the yield of a crop is a function of light intensity and photoperiod.

In contrast to the observations of Went and Gregory, Davis and Hoagland (1925) reported that for tissue production, plants function more efficiently when the radiation energy is well distributed over a longer period of time at relatively lower intensities. Arthur et al. (1930) concluded that low light intensities gave better growth response when the photoperiod is increased. Kramer and Decker (1944) reported
the rate of photosynthesis in four forest-tree plants declined rapidly after 56 hours of exposure to a higher light intensity.

Davis and Hoagland (1925) concluded that for each light intensity level there is a critical temperature where growth response is maximum. It is reported that Wassink observed a more noticeable effect of temperature at higher light intensities (Rabinowitch, 1951). Gaastra (1959) studied the relationship between the rate of photosynthesis and light intensity at different temperatures and concentrations of CO$_2$ in the leaves of several plants. He found that the photosynthetic rate increased with an increase in temperature.

Bendix and Went (1961) noticed that heat treatment in the presence of light resulted in greater plant heights as compared to the same treatment in the dark.

THE CARBON DIOXIDE FACTOR

Composition of Air and Variation in CO$_2$ Content. The main constituents of atmospheric air are nitrogen, oxygen and water vapor. In addition to these, small quantities of CO$_2$ and other gases, called rare gases, are present. Of these, only CO$_2$ plays a known and important role in plant life. Oxygen and nitrogen contents of air remain practically constant while the CO$_2$ content varies between 250-400 ppm (Chapman, 1954). CO$_2$ content increases during the night. Verduin and Loomis (1944) observed that the concentration of CO$_2$ at 100 cm above the ground, in a corn field, was 550-800 ppm during the night but rapidly declined to 450 ppm in the morning. Butterfield (1966) reported the diurnal CO$_2$ variation in a greenhouse follows a cycle similar to that reported by Loomis and Verduin. Since at lower temperatures CO$_2$
is more soluble in water, in colder regions the air may be comparatively lower in CO₂ content.

The CO₂ Compensation Point. It is defined as the CO₂ concentration at which photosynthesis first compensates for respiration and the net CO₂ exchange is zero. Below this level the respiration rate exceeds photosynthesis. The value of the CO₂ compensation point depends on two other important factors, light and temperature.

Effects of CO₂. Plant material contains about 40 percent carbon on dry-weight basis. The main source of this carbon is atmospheric CO₂ fixed through the process of photosynthesis. In the presence of light, most photosynthesizing organisms assimilate CO₂.

Bierhuizen and Slayter (1964) exposed a cotton leaf to different light intensities and observed the CO₂ saturation at about 800 ppm. They concluded that the apparent photosynthetic rate was nil at approximately 50 ppm CO₂.

Milner and Haisey (1964) reported the photosynthetic response of six races of Mimulus to be linear up to 350-500 ppm CO₂ concentration and to be progressive until the maximum photosynthetic rate is reached, at 1100-1500 ppm. The CO₂ compensation point was reported to be in the range of 55-94 ppm CO₂. They also observed that at 450 ppm CO₂ the photosynthetic rate was constant over a 12-hour period. However, when the CO₂ level was increased to 1500 ppm the photosynthetic rate increased gradually for the first 5.5 hours, maintained the same rate for about 30 minutes, and then it declined slowly until it reached the value of 450 ppm CO₂.

Under field conditions and up to 300-400 ppm CO₂, an increase in the rate of photosynthesis for several crops was reported by Thomas and
Hill (1949). Also this increase was found for only a short time. Moss and Musgrave (1961) found that under field conditions, added CO$_2$ increased the photosynthetic rate in corn. Further, the response of CO$_2$ was different at lower and higher light intensities.

Gaastra (1959) used a specially fabricated assimilation chamber to study the photosynthetic responses of fully developed leaves of several crops. He observed that CO$_2$ saturation for the crops studied was obtained at about 1000 ppm. Chang and Loomis (1945) concluded that different plant species respond in a similar way but the ranges of increase are different.

Many workers have reported the adverse effects brought about by very high concentrations of CO$_2$ (Chapman et al., 1954). However, the CO$_2$ concentrations so reported are different (Rabinowitch, 1951) and vary from a concentration of 3 percent to 12 percent.

Apparent equilibrium between photosynthesis and respiration in an unrenewed atmosphere was reported by Miller and Burr (1935). They found that leaves could deplete the normal air of its CO$_2$ content up to 100 ppm. Thomas et al. (1944) later supported this but reported that the depletion level varies between 40-90 ppm.

(a) Interactions. Hopen and Ries (1960) reported a differential utilization of CO$_2$ with an increase in light energy and time. They also observed that the CO$_2$ and light functions were mutually compensating factors in the growth of the crop.

Hoover et al. (1933) concluded that for wheat, CO$_2$ may limit the photosynthetic rate at high light intensities. Gaastra (1959), based on his observations on several plants, also concluded that under natural conditions CO$_2$ may limit photosynthesis. Further, he
found that below 300 ppm CO\(_2\) the rate of photosynthesis increases linearly with an increase in CO\(_2\).

Lundegardh (1934) reported that the addition of CO\(_2\) to the plant environment shifts the temperature for maximum photosynthesis from 20\(^\circ\) to 31\(^\circ\) C for potatoes, from 19\(^\circ\) to 36\(^\circ\) C for sugar beets, and from 30\(^\circ\) to 36\(^\circ\) C for beans.

THE TEMPERATURE FACTOR

Role of Temperature in Plants. All elementary processes in plants, other than the photochemical ones, depend on temperature. The enlargement and elongation of cells depend primarily on temperature. It provides a working condition for nearly all plant functions. Another important role of temperature is that it provides necessary energy for some processes. The effects of temperature may be direct or indirect. In some cases the effects of temperature are secondary, e.g., breaking the dormancy in seeds and buds, while in others the effects are direct. Then in some cases a combination of the two is evident. Went (1944) observed a marked temperature dependence of biological processes related to growth.

Cardinal Temperature Ranges. Each plant has well defined temperatures for the growth processes. These may differ for the same process in different parts of the same plant and also in different plant species. Hence, a cardinal temperature is a range rather than a fixed point. The cardinal temperatures are:

(1) minimal temperature below which a plant ceases to grow and in many cases may be injured or killed,

(2) maximal temperature above which the plant growth is checked
and plant may die if held here for a critical time, and

(3) optimal temperature which is most conducive to the harmonious
interactions of all physiological processes.

Optimum temperatures for growth for most species of temperate zones
are about 25° to 30° C. For most tropical and sub-tropical species
the optimum range is higher. Photosynthesis occurs, under favorable
field conditions, in the range between 15° to 30° C; but it was sug-
gested that this range may be low due to a limited supply of CO₂.

Thermoperiodicity. The phenomenon of thermoperiodicity refers to
responses of plants to cyclic temperature variations. Thermoperiodi-
city is of two types: (1) seasonal, and (2) diurnal. Because of its
more significant role on growth, only diurnal variation is described
below.

Diurnal thermoperiodicity refers to the response of plants to
higher day temperatures and lower night temperatures. Went (1944) was
the first to demonstrate the diurnal thermoperiodicity of tomatoes in
air-conditioned glasshouses. He suggested that thermoperiodicity is
a general phenomenon in higher plants. He also pointed out that plants
in different stages of development respond differently in the same
thermoperiods (1957). In tomatoes with advancing age, lower night
temperatures become favorable. In young plants a night temperature of
26.5° C, coupled with a day temperature of 26.5° C, gives consistently
greater growth, whereas in mature plants maximum growth occurred at
20° C night and 26.5° C day temperatures. Learner and Wittwer (1953)
made similar observations growing tomatoes outdoors.

Roberts (1943) observed some 240 plant species at different tem-
peratures and photoperiods. He came to the conclusion that night
temperature, rather than day temperature, influences plant growth more.

Although diurnal thermoperiodicity is known to occur more often, it is not a general phenomenon. Parker and Borthwick (1943) showed there was little evidence that thermoperiodicity influences soybeans. Hudson (1957) reported that Fortainer observed no thermoperiodicity in peanuts.

**Concept of the Temperature Coefficient (Q_{10}).** For expressing the effect of temperature on a chemical process, the most commonly used concept is Van't Hoff's coefficient, commonly known as the temperature coefficient (Q_{10}). Q_{10} is defined as the ratio by which the rate of a certain process changes due to a 10° C increase in temperature.

Blackman (1905) introduced the concept of Q_{10} in biology. He analyzed data on the photosynthetic rate of cherry laurel leaves at different temperatures and concluded that in a temperature range of 10° to 27° C, an increase in temperature increased the rate of photosynthesis.

Blackman obtained a perfect Van't Hoff curve by extrapolating the rate of photosynthesis at time zero before the rate reduction starts from the injurious effect of the high temperature, and by plotting the initial rates as a function of time.

The Q_{10} has been suggested to show the effect of temperature on plant growth. However, it has certain limitations which make it difficult to use to characterize the temperature effects in a multivariate plant growth system.

In the first place, as Blackman has suggested, in plants and animals the Q_{10} concept holds true only for a narrow range. The cardinal temperature range for most plants is wide, between 5° to 50° C.
The second limitation lies in the fact that $Q_{10}$ cannot be used satisfactorily near the maximal end of the temperature range because the time factor becomes very important. Above the optimum temperature, an increase in temperature increases the importance of time. Thus, at a particular temperature the $Q_{10}$ values for two different time intervals may differ significantly, especially if the plant has not been exposed to this temperature for long. Similarly, the same is true for the minimal end, but the magnitude of variation in the $Q_{10}$ is not so marked.

To use this concept, a number of $Q_{10}$ values would be required for every $10^\circ C$ interval. This means the $Q_{10}$ values should be available for all possible $10^\circ C$ intervals within the temperature range. This becomes unmanageable. Further, an interval may be covered by two different $Q_{10}$ values. It is possible to take the temperature interval less than $10^\circ C$; however, a great number of values are then required and the problem of overlapping intervals is not simplified.

Knowing $Q_{10}$ values for a section of the temperature range does not allow the approximation of rates in other sections close to the original one.

**Optimum Temperature.** Many workers studied the effect of temperature on the photosynthetic rate and reported that the optimum temperature varies from plant species to species (Went, 1957; Lundegardh, 1931). It is because of the time factor that it becomes difficult to clearly obtain an optimum temperature for any process. Thus, a modified definition of optimum temperature states that it is the highest temperature at which a growth process can be permanently maintained without a decrease in its photosynthetic rate.
Infractions. Arthur et al. (1930) found tuber production in the potato is favored by a low soil temperature (68°F), whereas the aerial portion grows best at 78°F. Oats grown at 68°F had stiff straw and small leaves but at 78°F the stem became flexible and leaves were larger and succulent.

Mooney and West (1964) acclimated five species of plants for not less than three weeks in desert and subalpine environments, and found both rate modifications and shifts in permeratures for maximum photosynthetic rates.

Decker (1944) studied the effect of temperature on the photosynthetic rate and respiration in two species of pine and reported that optimal temperatures for the two processes have different ranges.

OTHER AERIAL FACTORS

Humidity. Water vapor known as "humidity" influences plant growth. Usually the term "relative humidity" is used to refer to the invisible water vapor of atmospheric air, which expresses the amount of water vapor present as percentage of the maximum quantity the air can hold at the prevailing temperature.

In general, small variations in the humidity of the air have no appreciable effect on growth rates. This is especially true whenever the soil water supply is adequate. Went (1957) found that if the soil in which plants are growing was kept moist all the time, the humidity effect of the air on tomato plants was relatively slight. Similar results were also reported for strawberry, coffee, and grasses.

When the vapor pressure differences between the air and leaves are high, marked differences in the growth of plants are noticed. It
was reported that at 70°F tomato plants, when exposed to high humidity (17.17 mm Hg), were more succulent, grew faster and had thin-walled cells. On the other hand, at low humidity (6.64 mm Hg) the plants grew at a slower rate, had thick-walled cells, and lacked succulency (Hudson, 1957).

Humidity may also influence plant growth in indirect ways. Translocation of sugars occurs at a higher rate if the night time relative humidity is high (Hudson, 1957). It interferes with the solar radiation reaching the surface of the earth. Under dry conditions, adverse effects of strong solar radiation are prevented if the humidity of the air is high. Humidity also exerts an influence on the rates of evaporation and transpiration. If all the other factors are constant, with increasing humidity the rates of evaporation and transpiration are reduced.

Wind. Wind may influence plant growth indirectly by affecting certain phenomena associated with the process of growth. In perennial plants, in addition to the effect on growth, wind may also influence the shape of the plants.

Within limits, the rate of transpiration increases with increasing wind velocity. But a very high wind velocity retards the rate of transpiration because the stomates close.

In nature, wind tends to produce a relative turgidity (also called saturation deficit) which in turn may result in a decrease of the dry matter increment, a desiccation of aerial parts, and perhaps death. Plants provided with an abundance of water may show a saturation deficit in leaves when the wind velocity is very high. In an experiment, Whitehead (1957) observed no assimilation at and after a 16 percent
saturation deficit in leaves when they were exposed continually to 40 mph wind for three hours.

Winter (Luti and Whitehead, 1957) found the growth of potato shoots higher when nights were windy and days were calm. Luti and Whitehead (1957) studied the effect of wind velocity in a wind tunnel in which the velocity was maintained at 30 mph continually for 40 days. It was observed that at higher wind velocities the height of the plants was reduced noticeably and the stems were modified anatomically.
CHAPTER IV
EXTENSION OF KNOWN AERIAL ENVIRONMENTAL INPUTS

THE LIGHT FACTOR

The plant is dependent on light for photosynthesis and growth; with an increase in light intensity, the rate of photosynthesis increases until it reaches asymptotically a maximum level corresponding to light saturation (Fig. 1). Beyond a certain intensity, much higher than initial saturation intensities, the plants may be injured.

![Figure 1. Relationship Between Photosynthesis and Intensity of Light](image)

The rate-intensity relationship curves for photosynthesis show a smooth transition between no response and a maximum rate at light saturation. The initial response has been considered to be linear. Since plants do not show sharp changes in response at any particular light intensity it seems that the linear relationship is not valid. Further, some
workers have presented photosynthetic responses to light intensity by showing a coincidence of slope. The experimental results, however, do not justify this approach. It seems that these workers have considered the law of the limiting factor and overlooked the law of relative minimum. The rate of photosynthesis depends on light and other factors at the same time. While light ceases to be limiting there is a possibility that others may become increasingly limited. Thus, the response under such a situation is better represented as in Fig. 1.

Some minimum light intensity is required for a net photosynthetic rate and as such the curve does not start from the origin but is shifted toward the right by an amount corresponding to the light compensation point. The value of the compensation point varies from species to species and plant to plant. For most higher plants its value is between 100-250 f.c. The compensation point of shade-type plants is lower than for sun-type plants.

The saturation light intensity level depends on the CO₂ concentration and the temperature of the air. An increase in CO₂ content and/or temperature increases the saturation intensity level. Each light intensity level has a critical temperature value where growth is maximum. Within the minimal to optimal range of temperature, the rate of photosynthesis at a particular light intensity is increased with an increase in temperature. In general, for most of the sun-type plants the saturation light intensity is between 2000-2500 f.c. and for shade-type plants, between 500-1000 f.c. These values are for individual leaves receiving direct light under an experimental setup. Under field conditions the light reaching the plant is modified considerably because of natural
shading, orientation and shape of the leaf, and the location of the plant. Under such a situation, the average saturation intensity is much higher than that reported for individual leaves.

The range between the compensation point and the saturation point is of importance because an increase in the rate of photosynthesis is more or less restricted within it.

Leaf growth is affected by the intensity of light. In general, leaf area, stem elongation and length of internodes vary inversely with the intensity. Dry weight of plants, stem diameters and leaf thicknesses vary directly with the intensity of light. Hence, for dry matter production the intensity of light is more important than the total amount of light energy absorbed.

THE CARBON DIOXIDE FACTOR

The photosynthetic rate increases with an increasing concentration of CO$_2$ in the environment (Fig. 2). At first it increases very rapidly (A to B), then slowly (B to C), and finally reaches saturation level (C to D). This trend applies to a maximum of 3000-5000 ppm CO$_2$ in the air and this also may be regarded as the maximal response range for CO$_2$. The saturation level is attained near or in the range of 1000-1500 ppm CO$_2$. Beyond the indicated maximal response range for CO$_2$ harmful effects of CO$_2$ may be observed. Some workers have claimed the CO$_2$ maximal response range is as high as 6 to 12 per cent. This seems to be too high and would result in the death of the plant if the plant were exposed to this level for some time.

There is a minimum level of CO$_2$ below which no true photosynthesis is observed. This has been called the CO$_2$ compensation point. The value
of the compensation point varies with the type of plant, light intensity and temperature. Keeping light intensity constant and increasing the temperature of the air, the compensation point shifts toward higher CO₂ concentrations. On the other hand, keeping the temperature constant but increasing the light intensity, the compensation point moves toward lower levels of carbon dioxide.

An increase in the concentration of CO₂ in the presence of a higher light intensity has a tendency to shift the optimum temperature toward a higher temperature range. Thus, the influence of temperature and light must be considered at higher levels of CO₂. At low light intensities and high temperatures or at low CO₂ levels, high light intensities and high temperatures, the response is not significantly changed.

It has been noticed that most of the workers have tried to present the photosynthetic response due to CO₂ concentration on the basis of
the law of the limiting factor. As discussed elsewhere, the presentation on the basis of the law of relative minimum would be a better approach.

THE TEMPERATURE FACTOR

Plant growth starts at a certain minimum temperature, rises very rapidly at first, then slowly and finally at the optimum temperature there is no further growth increase. Above the optimum, the growth-rate reduces rapidly until the maximum temperature is reached, beyond which growth stops. Thus, the optimum and maximum temperatures are closer together than are the optimum and minimum temperatures. The higher the temperature, above the optimum temperature, the more rapid is the growth-rate reduction. The temperature-growth relationship may be expressed mathematically by a suitable expression developed after due consideration of empirical results.

In general, the lower the light intensity to which a plant is exposed, the lower is the optimum temperature for growth. At higher temperatures the process of photosynthesis is not influenced as much as the process of respiration. Photosynthesis, in most of the cereals and other crops, attains a maximum value between 20° to 35° C, whereas respiration reaches a maximum rate above 40° to 45° C.

Under natural conditions, temperature has a slight effect only in the range between 15° and 30° C.
CHAPTER V

MATHEMATICAL MODELS FOR INDIVIDUAL AERIAL ENVIRONMENTAL FACTORS AND THE PROPOSED MODEL FOR POTENTIAL PHOTOSYNTHESIS

The concept of growth in physiological studies of the effects of environmental factors on plants is very important. Growth has been defined by plant scientists in a number of ways. Because of the relative importance of photosynthesis, the effect of aerial factors requires more attention for an expression of growth mathematically. Earlier effects of plant nutrients on growth were studied in detail by Mitscherlich (1913). Baule (1918) further extended the work of Mitscherlich. Blackman (1919) studied plant growth on the basis of an increase in dry matter. Recently Visser (1963) revived the interest in formulae for plant growth. However, these attempts were based on plant nutrients and soil factors. Monteith (1966) is probably the first to try to express photosynthesis in terms of light intensity.

Like most physical and chemical systems, biological systems may be described either by statistical models or by deterministic models. Statistical models are non-deterministic and therefore probabilistic in nature. These models can predict only the probabilities of certain future occurrences. In the absence of large number of data they are very valuable. Biological processes are not easily described by deterministic models but the role of models is important. Deterministic models are quite reasonable in many situations and they can be utilized to approximate complicated situations which are difficult and likely are non-deterministic to deal with otherwise.
MODEL OF THE LIGHT FACTOR

The light requirements of plant growth lie in the range from the light compensation point, , to the saturation light intensity, \( i_{\text{sat}} \). At the saturation light intensity the rate of photosynthesis reaches a maximum. In general, for most higher plants the light compensation point is around \( 0.5 \times 10^4 \) to \( 10^4 \) ergs/cm\(^2\)/sec (125 -250 f.c.) and the saturation intensity varies in the range of 10 to 30 \( \times 10^4 \) ergs/cm\(^2\)/sec. Beyond the saturation light intensity, \( i_{\text{sat}} \), a further increase in the intensity does not increase the rate of photosynthesis, but at some high level may injure plants. Let the growth response due to light be \( P_1 \), mm\(^3\) CO\(_2\)/cm\(^2\)/hr. At the saturation light intensity, \( i = i_{\text{sat}} \), the light, \( P_1 \), attains its maximum value, \( P_1_{\text{max}} \); and that at the light compensation intensity, \( i = \alpha \), the response is zero.

It is assumed that the change in photosynthetic rate with regard to light intensity is proportional to the photosynthetic level. This dependence for the sake of simplicity, is assumed to be linear. It is also assumed that other factors influencing the photosynthesis of plants remain constant. That is,

\[
\frac{dP_1}{di} = -a_1 P_1 + B_1
\]

where \( a_1 \) and \( B_1 \) are constants.

Equation (1) is the well-known linear differential equation. Consider the boundary conditions that

\[ P_1 = 0, \text{ at } i = \alpha \]

and \( P_1 = P_1_{\text{max}}, \text{ when } i = i_{\text{sat}} = \infty \)

the solution of Equation (1) is

\[
P_1 = P_1_{\text{max}} \left[ 1 - e^{-a_1 (i - \alpha)} \right]
\]
where \( i \) = intensity of light, ergs/cm\(^2\)/sec

\[ a = \text{light compensation point, ergs/cm}^2/\text{sec} \]

\[ I = \text{light constant, ergs/cm}^2/\text{sec} \]

\( P_1 \) = photosynthetic rate due to light intensity, mm\(^3\) CO\(_2\)/cm\(^2\)/hr

\( P_1 \text{ max} \) = maximum attainable rate of photosynthesis when light is variable but at any fixed level of carbon dioxide and temperature, mm\(^3\) CO\(_2\)/cm\(^2\)/hr

Equation (2) may be rewritten as

\[ P_1 = P_{1 \text{ max}} \left[ 1 - e^{-\left( \frac{i - a}{I} \right)} \right] \quad (3) \]

The light constant, \( I \), is defined as the intensity of light at which the total photosynthetic rate is 63.2 percent of the maximum photosynthetic rate. It may be compared with the rate constant in any chemical reaction. The value of the light constant is different for plant species and types. As a rule the value of \( I \) is higher for sun-type plants.

Equation (3) has been developed assuming that light falls on a single leaf and is measured under laboratory conditions. It was assumed that the light intensity was uniform all around the leaf. This expression is not immediately applicable to field conditions because the sunlight reaching the plant canopy is shared by many leaves. Some are directly exposed while others are mutually shaded. The orientation of the leaf and the direction of light rays are also equally important.

As a result of this, light saturation under field conditions is attained at a much higher light intensity. The total photosynthetic response by all leaves of a crop can be estimated by modifying Equation (3). It is proposed that the field light-intensity values be made comparable to laboratory values by introducing a constant which would account for the shading effect. This constant, \( S \), will be referred to as the "shade constant".
Then the light factor equation may be rewritten as,

\[ P_1 = P_{1\ max} \left[ 1 - e^{-\left(\frac{S_i - \alpha}{I}\right)} \right] \]  

(4)

where \( S_i \) is the actual light intensity to which the leaf is subjected. Further, it has been assumed that the soil moisture and nutrients are in abundance.

MODEL OF THE \( \text{CO}_2 \) FACTOR

It was established earlier that the \( \text{CO}_2 \) concentration-photosynthetic relationship, like light intensity, behaves similarly. Assuming that the same law is valid for \( \text{CO}_2 \), the \( \text{CO}_2 \) response may also be considered as a first order system and the model for it may similarly be derived. Then,

\[ \frac{dP_2}{dc} = -a_2 P_2 + B_2 \]  

(5)

where \( a_2 \) and \( B_2 \) are constants. Considering the boundary conditions that

\[ P_2 = 0, \ \text{at} \ c = \beta \]

\[ P_2 = P_{2\ max}, \ \text{at} \ c = c_{\text{saturated}} = \infty \]

The solution of Equation (5) is given by

\[ P_2 = P_{2\ max} \left[ 1 - e^{-\left(\frac{c - \beta}{C}\right)} \right] \]  

(6)

where \( c = \text{CO}_2 \) concentration, ppm

\( \beta = \text{CO}_2 \) compensation point, ppm

\( C = \text{CO}_2 \) constant, ppm
\[ P_2 = \text{photosynthetic rate due to } CO_2, \text{ mm}^3 CO_2/cm^2/hr \]

\[ P_2\text{ max} = \text{maximum rate of photosynthesis when } CO_2 \text{ is variable but at any fixed intensity of light and temperature, } mm^3 CO_2/cm^2/hr. \]

The development of this model was based on the assumption that the CO\(_2\) concentration is uniform around the leaf. In order to use this model for field conditions, it must be further assumed that the CO\(_2\) concentration in the crop canopy is uniform. No measurements of CO\(_2\) gradients adjacent to, and within leaves are yet available; therefore, the assumption is justified for simplification. Since the CO\(_2\) gradient between the crop canopy and atmosphere above it does exist, it is important that the CO\(_2\) concentration for the crop canopy be used for the model.

This model may be used for a CO\(_2\) concentration as high as the CO\(_2\) saturation level, which for most of the plants is between 1000 - 1500 ppm. The gradient of the CO\(_2\) response curve is determined by the CO\(_2\) constant, C, which may be in the range of 150 - 250 ppm.

MODEL OF THE TEMPERATURE FACTOR

It was mentioned earlier that for each plant system three cardinal temperature ranges exist. However, all plants behave, more or less, in a similar fashion in the interval between the minimal and maximal ranges. This interval, minimal-maximal, varies considerably from plant species to species. The interval between the minimal and optimal temperature ranges is larger than that between the optimal-maximal ranges. The growth rate increases in the minimal-optimal interval and falls rapidly in the optimal-maximal interval. The growth rate is maximum in the optimal range. For most higher plants, maximum growth occurs in the range of 20 - 35\(^\circ\) C. Unlike the light and CO\(_2\) factors, a declining
response must be considered in the temperature interval of optimal-maximal. This behavior of plants to temperature looks similar to a pure enzymatic system. To take into account the effect of temperature on plant growth, temperature coefficient, $Q_{10}$, has been used frequently. Because of the limitation of $Q_{10}$, it may lead to erroneous results.

Considering the above facts, it appears that the temperature function can be represented by a parabola. Since the intervals between minimal-optimal and optimal-maximal ranges are not equal, for simplicity, two parabolas were used - one for the increasing growth effect and another for decreasing effect. Further it is assumed that the maximum growth rate attained at the optimal temperature is unity. Then relative rates of growth are considered at other temperatures. Thus the function will be simply a constant which incorporates the effect of temperature in the overall growth process. The parabolic function may be represented as follows:

$$T = k + 10 + me^2$$

where $k$, $l$ and $m$ are constants

$\theta = \text{leaf temperature, } ^\circ\text{C}$

$T = \text{temperature constant}$.

DEVELOPMENT OF THE PROPOSED MODEL OF POTENTIAL PHOTOSYNTHESIS

Potential photosynthesis refers to the maximum rate of photosynthesis when all the aerial factors, within growth-favoring limits, are simultaneously in abundance. The individual models for photosynthesis have been considered separately in terms of light, CO$_2$, and temperature factors. It seems reasonable and important from the application point of view that photosynthesis be regarded as a function of the three
variables simultaneously. In developing a model of this type, simplicity and practicability are important. The model will be devised in various steps and is justified somewhat on intuitive grounds. The fit of empirical data to the model, points to the appropriateness of the assumptions made.

The first assumption made for the proposed model is that the saturation photosynthetic rate attained due to one factor is maximum when considering the other factors in abundance.

The second assumption made is that the model was developed by taking the three factors in a sequence. Since photosynthesis is a catenary process this assumption seems justified. The essential characteristic of a catenary process is that the overall rate of the process cannot exceed the rate of any of its individual processes. The three processes of photosynthesis, in sequential order, are the photochemical reaction, carbon dioxide diffusion, and the biochemical reactions. Hence, the factors will be considered in the order of light, CO₂, and temperature.

Most of the physical and biological systems are non-linear in nature. But as the analysis of a non-linear system is complicated, useful information can still be obtained from simple linear models. The proposed model assumes linearity.

The sequential development of the proposed model, using linear differential equations, may be obtained as follows:

Let light be the first variable. The differential equation relating it to photosynthesis was expressed in Equation (1) as,

\[
\frac{dP_1}{dt} = -a_1 P_1 + B_1
\]
The light response for different levels of CO₂ and temperature, \( T \), is observed to be a family of curves (Fig. 3). For the purpose of the light model development, the curve for the highest CO₂ concentration was used. The values of \( P_1 \text{max} \) and \( I \) for the deterministic model was obtained.

The solution of Equation (3) is once again given as

\[
P_1 = P_1 \text{max} \left(1 - e^{-\frac{i - a}{I}}\right)
\]

Identical with Equation (4) the above Equation may be rewritten as,

\[
P_1 = P_1 \text{max} \left(1 - e^{-\frac{S_i - a}{I}}\right)
\]

At any level of CO₂ concentration and at saturation light intensity,

\[
P_1 = P_1 \text{max} \left(1 - e^{-\frac{c - g}{C}}\right) \quad (8)
\]

and

\[
P_1 \text{max} = P_2 \text{max} \left(1 - e^{-\frac{c - g}{C}}\right) \quad (9)
\]

The second factor to be considered is carbon dioxide. The differential equation for the CO₂ factor is the same, as for the light factor. However, for any rate of photosynthesis it is assumed that light effect is already included and the growth is \( P_2 \). Hence,

\[
\frac{dP_2}{dc} = a_2 P_2 + B_2.
\]

The solution of the above equation given earlier in Equation (6) becomes

\[
P_2 = P_2 \text{max} \left(1 - e^{-\frac{c - g}{C}}\right) \quad (10)
\]
Figure 3. Photosynthesis in Relation to Light Intensity at Different CO₂ Concentrations. Leaves of Tomato; Leaf Temperature 21° - 24°C. After Gaastra (1959).
where $P_2\text{ max}$ is the maximum rate of photosynthesis due to the CO$_2$ factor and it depends on temperature only.

Substituting the value of $P_1\text{ max}$ from Equation (9) into Equation (4) the combined effect of CO$_2$ and light can be expressed as

$$P_1 = P_2\text{ max} \left[ \frac{-\left(\frac{iS - a}{I}\right)}{1 - e} \right] \left[ \frac{-\left(\frac{c - b}{G}\right)}{1 - e} \right]. \quad (11)$$

When both the light intensity and CO$_2$ concentration are at saturation levels (Fig. 3)

$$P_1 = P_1\text{ max} = P_2 = P_2\text{ max}.$$  

Hence, the rate of photosynthesis can be expressed as potential maximum rate, $P$, instead of being denoted by $P_1$ or $P_2$.

The third factor is temperature. As mentioned earlier, its main effect is on the biochemical reactions. It accelerates or decelerates the rate of photosynthesis and as such its influence is incorporated by treating it as a constant of multiplication. Thus, the final growth response including all these factors may be written as

$$P = P_{\text{max}} \left[ \frac{-\left(\frac{iS - a}{I}\right)}{1 - e} \right] \left[ \frac{-\left(\frac{c - b}{G}\right)}{1 - e} \right] (k + \theta + m\theta^2) \quad (12)$$

**SOLUTION OF INDIVIDUAL FUNCTIONS**

The curve-fitting procedure described in Appendix II was used to obtain coefficients for the individual functions for a particular environmental factor (Gaastra, 1959). This made possible the finalizing of the potential photosynthesis function. The functions are given below:
(a) Light Factor:  \[ P_L = P_{L_{\text{max}}} \left[ 1 - e^{-\left( \frac{18 - 0.55}{2.77} \right)} \right] \]  (13)

The value of \( S \) was taken as one because the leaf was exposed directly to the source of light intensity.

(b) \( \text{CO}_2 \) Factor:  \[ P_2 = P_{2_{\text{max}}} \left[ 1 - e^{-\left( \frac{c - 150}{250} \right)} \right] \]  (14)

(c) Temperature Factor:

\[ T = -0.296 + 0.063(\theta) - 0.00075(\theta)^2 \]  \hspace{1cm} (15a)

for minimal-optimal interval

\[ T = -1.6845 + 0.157(\theta) - 0.0023(\theta)^2 \]  \hspace{1cm} (15b)

for optimal-maximal interval

(d) Potential Photosynthesis Function:

\[ P = 185 \left[ 1 - e^{-\left( \frac{18 - 0.55}{2.77} \right)} \right] \left[ 1 - e^{-\left( \frac{c - 150}{250} \right)} \right] \left[ -0.296 + 0.063(\theta) - 0.00075(\theta)^2 \right] \]  \hspace{1cm} (16)

where \( P \) is the growth response considering all the three factors simultaneously, and maximum growth, \( P_{\text{max}} \), has a value of 185 mm\(^3\) \( \text{CO}_2/\text{cm}^2/\text{hr} \).
CHAPTER VI
APPLICATION OF THE PROPOSED MODEL

APPLICATION OF THE MODEL

Testing of the Model. The objective in proposing a model has not been attained unless the model has been applied and tested. There are two possible ways in which a model can be tested:

1. By designing and conducting an experiment based on the conditions assumed in the development of the model.
2. By judiciously selecting data from already existing experiments.

The first approach is more satisfactory than the second, but it has limitations. In many cases, it is not possible to procure proper equipment and facilities. The time requirement is also an important limitation. The major drawback of the alternate method lies in the fact that it is necessary to depend on data obtained from an experiment designed for a different purpose and conducted in a particular manner. At times, it may be difficult to find the desired set of data which furnish the necessary details. Furthermore, the reliability of the equipment used and procedure followed must be unquestionably accepted. In spite of all these drawbacks, this method has been used because of obvious advantages in the saving of time and resources. In the present study, this method was followed.

Selection of Data. Gaastra (1959) carried out an extensive study on the effect of light intensity and CO₂ concentration upon photosynthesis. The experiment was run under well-defined conditions on plants.
of agricultural importance. He used equipment which was especially de-
signed and fabricated. Gaastra's data for tomatoes were used for this
study (Tables II and III). The data were obtained from graphical pre-
sentations.

Table II. Photosynthesis at Different Light Intensities and CO₂ Con-
centrations at Leaf Temperature 21° - 24° C Observed Data
after Gaastra (1959)

<table>
<thead>
<tr>
<th>CO₂ Concentration ppm</th>
<th>Light Intensity 10⁴ ergs/cm²/sec</th>
<th>Photosynthesis Rate mm³ CO₂/cm²/hr</th>
</tr>
</thead>
<tbody>
<tr>
<td>320</td>
<td>1.6</td>
<td>30</td>
</tr>
<tr>
<td>320</td>
<td>6.6</td>
<td>60</td>
</tr>
<tr>
<td>320</td>
<td>14.8</td>
<td>60</td>
</tr>
<tr>
<td>850</td>
<td>1.6</td>
<td>37.50</td>
</tr>
<tr>
<td>850</td>
<td>6.6</td>
<td>105.00</td>
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<td>850</td>
<td>14.8</td>
<td>117.00</td>
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<td>1.6</td>
<td>42.0</td>
</tr>
<tr>
<td>1310</td>
<td>6.6</td>
<td>111.0</td>
</tr>
<tr>
<td>1310</td>
<td>14.8</td>
<td>121.0</td>
</tr>
</tbody>
</table>

Appraisal of the Proposed Model. At a higher CO₂ concentration
(1310 ppm) and a low temperature, 12.5° C, the calculated value is
lower than the observed one at a low light intensity (1.6 x 10⁴ ergs/cm²/
hr). It seems that light predominate the temperature influence and the
proposed model does not account for the high response from light. How-
ever, in practice such a set of conditions would not be desirable for
any controlled facility.

At higher temperatures, 21° C and 31° C, the observed values are
either very close or slightly lower than the calculated values (Figs. 4
and 5). It may be possible that the law of the relative minimum is
Figure 4. Photosynthetic Rates Observed and Predicted at 31°C Temperature and High CO₂ Concentration, 1310 ppm. Observed data after Gaastra (1959).
Figure 5. Observed and Predicted Photosynthetic Rate at 21°C Temperature and High CO₂ Concentration, 1310 ppm. Observed data after Gaastra (1959)
Table III. Observed and Calculated Values of Photosynthesis of Tomato Leaves in Relation to Light Intensity at Different CO₂ Concentrations and Wall Temperatures. Observed Data after Gaastra (1959)

<table>
<thead>
<tr>
<th>CO₂ Concentration ppm</th>
<th>Light Intensity $10^4$ ergs/cm²/sec</th>
<th>Leaf Temperature °C</th>
<th>Photosynthesis Rate, mm³ CO₂/cm²/hr</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Observed</td>
<td>Calculated</td>
</tr>
<tr>
<td>300</td>
<td>1.6</td>
<td>12.5</td>
<td>30.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>5.5</td>
<td>&quot;</td>
<td>60.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>12.0</td>
<td>&quot;</td>
<td>63.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>14.8</td>
<td>&quot;</td>
<td>64.0</td>
</tr>
<tr>
<td>300</td>
<td>1.6</td>
<td>20.5</td>
<td>33.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>5.5</td>
<td>&quot;</td>
<td>65.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>12.0</td>
<td>&quot;</td>
<td>70.0</td>
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<tr>
<td>&quot;</td>
<td>14.8</td>
<td>&quot;</td>
<td>75.0</td>
</tr>
<tr>
<td>1310</td>
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<td>12.5</td>
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<tr>
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<td>&quot;</td>
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<td>21.0</td>
<td>41.0</td>
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<tr>
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<td>5.5</td>
<td>&quot;</td>
<td>108.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>12.0</td>
<td>&quot;</td>
<td>119.0</td>
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<tr>
<td>&quot;</td>
<td>14.8</td>
<td>&quot;</td>
<td>130.0</td>
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<tr>
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<td>5.5</td>
<td>&quot;</td>
<td>112.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>12.0</td>
<td>&quot;</td>
<td>167.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>14.8</td>
<td>&quot;</td>
<td>174.0</td>
</tr>
</tbody>
</table>

effective. As the light intensity is increased from low to near saturation, the calculated values are invariably higher. The difference between the two sets of values increases at higher temperatures (Figs. 4 and 5). This further supports the above explanation. It is further observed that the difference is a maximum at some intermediate range of light intensity and tapers down on either side. Thus, the model is inadequate in this sense.

In the range of the saturation light intensity, the calculated values
are lower than the observed values at 21° C and 31° C. It is likely that light saturation was not attained. The values are practically the same at 12.5° C (Fig. 7).

The above discrepancies lead to the speculation of the possibility of some sort of interaction between light and temperature and also interaction between light and CO₂.

At low temperatures and low and high concentrations of CO₂ the observed photosynthetic-rate values are more or less the same (Figs. 6 and 7). This may point to the fact that the CO₂ concentration is not important at this temperature. However, the influence of CO₂ becomes apparent at higher temperatures (Fig. 4). The proposed model works satisfactorily at high concentrations and low temperatures. However, it needs improvement to account for the differences at lower CO₂ concentrations. A relationship between temperature and CO₂ for different temperatures and different levels of CO₂ would be desirable to account for the interaction between the two factors.

The two sets of photosynthetic-rate values for low CO₂ and low and medium temperatures, 12.5° and 20.5° C, are presented in Figs. 7 and 8. It is observed that the calculated values in both cases are considerably lower and especially so at lower temperature. The difference narrows at a low to medium temperature, and it is likely that a similar trend will be maintained at higher temperatures. Under such a condition the model may work satisfactorily.

The proposed model works satisfactorily when light, CO₂ and temperature are in abundance. However, at sub-optimal conditions, particularly low temperatures and low CO₂ concentrations, the model needs
Figure 6. Observed and Predicted Photosynthesis at Low Temperature, 12.5°C and High CO₂ Concentration, 1310 ppm. Observed data after Gaastra (1959).
improvement. Many of the deviations between the observed and predicted values likely are due to interactions among the factors.
Figure 7. Observed and Predicted Photosynthetic Rate at 12.5° C Temperature and Low CO$_2$ Concentration, 300 ppm. Observed data after Gaastra (1959).
Figure 8. Observed and Predicted Photosynthetic Rate at 20.5°C and 300 ppm CO₂ Concentration. Observed data after Gaastra (1959).
CHAPTER VII

THE DIURNAL COURSE OF PHOTOSYNTHESIS OF PLANTS,
FIELD CONDITIONS SIMULATED

The potential yield of plants is largely determined during vegetative growth. High yields can only be obtained if the plants' daily needs are met in an optimum manner throughout the growing period. If environmental conditions do not fully satisfy the needs of plants at any stage, growth is lower. The daily total carbon dioxide assimilation is determined by the diurnal course of photosynthesis. From the instantaneous daily photosynthetic rates, the potential photosynthetic yield over the growing season may be estimated. Hence, an understanding of the diurnal variations in growth factors may make possible the calculation of photosynthetic potentials under a given set of conditions. Also, under field conditions the actual measurement of photosynthesis is not possible, but the potential photosynthetic yield per day may be easily estimated by simulating the environmental inputs. In this Chapter the diurnal photosynthetic yield is estimated with the help of the proposed growth model.

DIURNAL CYCLES OF AERIAL FACTORS FOR PLANT GROWTH

A typical summer day was selected to study the diurnal response. The diurnal cycles for the individual factors are discussed as below. It was assumed that plants were growing under adequate water and nutritive supply.

Diurnal Light Intensity Cycle. The main source of light to plants is the solar radiation, which varies from place to place depending on
Figure 9. Diurnal Light Intensity Cycle, $S_i$, for Average Leaf Cover for a Clear Day in the Month of July at Columbus. Modification after Myers and Anderson (1961).
its altitude, latitude and time of the year. However, the diurnal radiation cycle follows a more or less definite pattern. During the early morning and evening hours, light intensity is low. During mid-day hours, the intensity is high with its peak coming after noon. In the Northern Hemisphere, during the summer months, the daylight period is 14-15 hours, whereas during the winter it is 10-11 hours.

All the solar radiation energy available does not reach plants because of a random leaf orientation, mutual shading effect, and diffusion and reflection of the incoming radiation. On a day when the sky is clear, maximum light intensity is available to the plants. On the other hand, dust storms, clouds, smog, etc. reduce the light intensity considerably.

The diurnal light intensity cycle was selected for a typical clear summer day (Myers and Anderson, 1961). It was assumed that the average leaf cover receives about 25 percent of the solar radiation; that is, the value of shade constant, $S$, is 0.25 (Nichiporovich, 1956). The diurnal light intensity cycle for the average leaf cover is presented in Fig. 9.

**Diurnal Carbon Dioxide Cycle.** Plants combine CO$_2$ and water in the presence of optimized light intensities to form sugars by the process of photosynthesis. During the daytime, atmospheric CO$_2$ reserves are consumed by the plants and CO$_2$ level in the atmosphere is lowered. During the night the light energy, essential for photosynthesis, is not available; therefore, CO$_2$ is not required. On the other hand, the CO$_2$ level increases because respiration continues, sugars are oxidized and CO$_2$ is released. Also, some CO$_2$ is released by organic decay. Based on the above argument a hypothetical diurnal CO$_2$ cycle, as presented in
Figure 10. Diurnal Carbon-dioxide Cycle
Figure 11. Diurnal Temperature Cycle for a Clear Day in the Month of July at Columbus (Myers and Anderson, 1961)
Figure 12. Diurnal Potential Photosynthetic Response
Fig. 10, was selected (Butterworth, 1966).

**Diurnal Temperature Cycle.** Like the light intensity cycle, the daily temperature cycle may vary considerably in pattern from day to day and season to season. However, a definite diurnal cycle of temperature was selected for a typical summer day to characterize the leaf temperature response. Further, the cycle was considered to be sinusoidal in nature such that the minimum temperature of $12^\circ \text{C}$ occurred at 5 a.m. and a maximum of $32^\circ \text{C}$ at 3 p.m. This diurnal temperature cycle is represented in Fig. 11 (Myers and Anderson, 1961).

**GENERATION OF DIURNAL CYCLES ON THE ANALOG COMPUTER**

The diurnal cycles for light, CO$_2$, and temperature were programmed on the Face TR-48 analog computer (Appendix III) for convenience in calculating the expected photosynthetic rate.

**DIURNAL POTENTIAL PHOTOSYNTHETIC YIELD**

The proposed mathematical model was simulated on the analog computer (Appendix III). The expected relative photosynthetic response was then computed for a typical summer day from the diurnal cycles programmed on the computer (Fig. 12). Also, the response-time relationships for temperature, light and CO$_2$ were individually computed and are presented in Figures 13, 14, and 15.

From the diurnal temperature response curve (Fig. 13) it may be observed that maximum growth response is attained at 5 p.m. But the response is high between 1:00 - 9:00 p.m. Response due to light is higher between 9 a.m. to 5 p.m. Higher growth response due to the combined effects of light and temperature would be expected between 1:00 - 5:00 p.m. when both the factors, individually, are favorable for
Figure 13. Diurnal Temperature Response
Figure 14. Diurnal Light Factor
Figure 15. Diurnal Carbon-dioxide Factor
growth. The CO₂ response is maximized in the early morning hours and then again in the late evening. Since light is not sufficient during these hours the advantages of higher CO₂ concentration cannot be exploited. Further, the growth during the rest of the photoperiod is reduced because of a lower CO₂ concentration.

The diurnal response curve for the photosynthetic rate follows, at least qualitatively, the diurnal course of solar radiation. Further, each of the factors influences the shape of the curve. One single peak at the mid-day is observed. Under field conditions such a response is expected only when the plants do not experience water stress. This is based on the observations of Moss et al. (1961) and Thomas and Hill (1949).

There are only few data available with which the computed photosynthetic rates may be compared with the rates observed under field conditions. Furthermore, the data available are not for the specific crop, tomatoes. In general, photosynthetic rates under field conditions vary between 25 to 120 mm³ CO₂/cm²/hour (Verduin and Loomis, 1949; Singh and Lal, 1935; Moss et al., 1961), and are much lower than the simulated potential photosynthetic rates. The difference between the two sets of values points out the fact that most favorable environmental conditions are necessary for maximum photosynthetic rates.

It may also be concluded that best response from a crop is possible only when it gets an optimal diurnal environmental input. Meteorological data may be used to program accordingly.

The variation in response during the dark period, between 18.5 - 5 hours of the day, suggests the need of a modification in the computer program. In the absence of light, CO₂ normally does not influence the
process. Hence, the CO$_2$ circuit needs to be cut off during the dark period. Also, the temperature response for the respiration process differs from that for photosynthesis; therefore, a different temperature response function, for night hours, should be used. The limitation of components available on the computer did not permit these modifications in the circuits.

For industrial plant production and research, where precise control of each factor becomes more critical, the analog computer may prove to be a convenient tool to analyze the response under different sets of conditions.
CHAPTER VIII
SUMMARY AND CONCLUSIONS

1. This study has suggested an approach for the analysis of aerial environmental inputs of plant growth. Under natural conditions, the growth of plants varies enormously because of the variations in the intensity of environmental factors.

2. A mathematical model of potential photosynthesis was developed and tested. The model supposes that edaphic factors are adequate. Furthermore, the model is based on the findings of short-time studies and as such does not consider the time factor.

In general, the model proved to be satisfactory. Discrepancies in the predicted and observed values were observed. These probably are due to interactions. Deviations suggest further studies to investigate the effect of interactions.

3. The proposed model was simulated on an analog computer for calculating the expected photosynthetic rate for a typical summer day. The model may prove to be useful in estimating the photosynthetic rates under field conditions and for controlled environmental facilities. It also points out the importance of a better understanding of the optimum course of photosynthesis and the need for proper planning for an optimal course during vegetative growth.

The use of the analog computer in this study suggests a convenience with which similar problems can be simulated and analyzed for research as well as industrialized plant production.
4. The growth model developed may prove to be very useful in estimating and predicting growth and in programming crop production, especially under controlled growth structures.

5. It is very apparent that the understanding of environmental influences is insufficient to construct a growth model acceptable for all the conditions. More information is needed for refining the growth model.
CHAPTER IX
SUGGESTIONS FOR FUTURE WORK

The problem of accounting for variation in crop growth response, expressed in terms of the photosynthetic rate, is obviously very complex. It involves interactions between aerial factors - the light intensity, CO$_2$ concentration, and leaf temperature. Experiments should be designed to obtain information on the interactions. For this, simultaneous and continuous measurement and control of each factor would be essential.

Growth response variations between and within plant species suggest the need of selecting different types of plant materials. Further, the interactions should be studied in terms of the time factor so that the exact course of photosynthesis, responsible for highest growth rates, may be possible.
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APPENDIX I

ENVIRONMENTAL CONTROL FACILITIES

The increasing interest in the relation between plants and their environment has resulted in the introduction of different types of plant growth structures. A brief account of these structures is presented in this section for better understanding of these.

TYPES OF FACILITIES

Many facilities have been built for the production of plants under conditions of controlled environment. These facilities may differ in size, arrangement and type of equipment used, degree of mechanization and the purpose. Some facilities have been developed and designed exclusively as research facilities while the others have been used basically for commercial crop production structures. These facilities may be grouped in two types:

1. Research Facilities.
   (a) Growth boxes
   (b) Growth chambers or growth cabinets
   (c) Growth rooms
   (d) Glass and plastic houses
   (e) Phytotrons and climatron

2. Commercial Facilities
   (a) Glass and plastic houses
   (b) Phytotrons
   (c) Tower glasshouses
Research Facilities.

(a) Growth cabinets. These are also called growth chambers. The plants are grown inside and the operator can gain access to the plants from the outside. Such cabinets are provided with temperature and humidity control but not always with CO₂ control. Cabinets may have opaque walls and provided with internal artificial light. In that case, they are referred to as artificial light cabinets. When natural daylight is used as the source of illumination, the cabinet walls are transparent and are called natural-light cabinets or miniature glasshouses. Some have arrangements for supplementary artificial light. Fresh air is drawn in from outside by a blower which provides several changes of air per hour.

(b) Growth boxes. Growth boxes may be considered as modified growth cabinets. Since they have better and more precise control of a number of factors concurrently, all these factors are controlled automatically. A CO₂ gas analyzing unit is connected to the main box where plant is kept. By addition of some additional equipment the variable factors can be cycled for a time-cycle programming.

Some boxes are designed so that a continuous recording of different factors is possible over the entire experimental period.

(c) Growth rooms.

Temperature-controlled rooms. The rooms are large enough to admit the operator inside. The temperature of such rooms is normally kept constant but may be cycled for diurnal cycles. Artificial low intensity light arrangements are provided. No control of CO₂ is available but the forced ventilation system provides relatively high circulation of air. Humidity control in such rooms is now available.
Light-controlled growth rooms. They are large growth cabinets into which the operator can go and higher plants can be grown for longer periods. Since artificial light is the source of illumination in these rooms, higher light intensities are available. In some rooms the lights are part of the room while in others a transparent screen separates the lights from the main growing space.

(d) Phytotrons. These are buildings in which a large number of rooms having different controlled environments are possible for the study of the plant responses to climatic conditions. The term "phytotron" was used first for the Earhart Research Laboratory, but later when similar facilities were planned elsewhere it was an accepted term for such a class of structure.

Since at Earhart Laboratory a systematized scheme is followed for moving the plants mounted on trucks, some plant scientists regarded phytotrons as a system of management using a collection of growth rooms. Flexibility of the phototron is achieved in large measure by management (Morse and Evans, 1962). Recently a phytotron was built in Canberra, Australia, in which flexibility was attained chiefly through the development of basic units rather than through management. Each basic unit is capable of operating over a wide range of conditions, but they vary in size, in the climatic factors controlled, and in the precision of control. The basic units can be modified to provide independent control of additional climatic factors as needed (Morse and Evans, 1962). Thus, the management emphasis in phytotrons is no longer justified, and phytotrons may be considered as large glasshouses provided with some basis for obtaining a great number of climatic conditions.

(e) Climatron. Went (1963) developed an entirely new type of
facility in the Missouri Botanical Gardens. He used an air conditioning system that creates two cross gradients of temperature and humidity inside a dome-shaped structure of aluminum and plexiglass. This structure is provided with a series of graded climates.

**Commercial Facilities.**

(a) Glasshouses. Romans were known to grow plants in pits which supplied fruits and vegetables for special occasions. During cold weather decomposing manure, hot air flues and hot bronze pipes were used to keep the temperature of the pit high enough for plant growth. They covered the pit with translucent stone slabs. This may have been the origin of the greenhouse concept.

In modern times structures have undergone a gradual development, from houses containing no glass to the house employing as much as 95 percent glass.

It is reported that the first greenhouse, of which records are available, was built by Solomon de Caus (Taft, 1928) about 1619. Originally, glasshouses were used for storing the heat energy during winter months. Glasshouses now have a provision for heating, usually steam or hot water system, and ventilation. During the summer months, when heating system is not required, temperature is controlled by opening all the ventilators and doors and/or operating a forced ventilation system. Sunlight entering through a glazed roof and walls is the source of illumination. In general, no provision is made for controlling CO₂. Humidity and temperature controls are not very accurate.

(b) Tower glasshouses. In 1963, the first tower glasshouse, also known as a "Growth Tower", was erected in Austria. Instead of using horizontal land area as in conventional glasshouses, the tower glasshouse
uses more effectively the third dimension. The floor area is small and fixed but the plant growth volume depends on the height of the tower. In order to utilize natural daylight to a maximum, the tower is usually made cylindrical. The surface-to-volume ratio of the tower glasshouse is much smaller compared with the conventional glasshouses. The glass surface per unit of growing volume is reduced between 25-30 percent for small towers and 50 percent or even more for large towers.

The plants are kept in motion with an endless conveyor system. The conveyor system consists mainly of two endless chains or steel cables, running over a number of sprockets or pulleys. Horizontal supports are pivoted loops. The conveyor forms a closed circuit of vertical segments in series and the plants move upward and downward. The speed of the conveyor is adjustable but usually it does not exceed two meters per minute.

The spacing of the supports can be varied depending upon the height of the plants. The plants are handled at floor level while they are in motion. Plants are grown in pots or containers perforated at the bottom. At regular intervals of time the plants are submerged in a nutrient solution.

The tower glasshouse is fully air-conditioned. The conditioned air is introduced at the base of the tower and it ascends to the top from where it is drawn off by a fan and recirculated.

Since the tower is air-conditioned, fresh air cannot be admitted. To supply CO₂ to the inside air, CO₂ generators are used. This allows higher CO₂ concentration inside the tower.
APPENDIX II
PROCEDURE FOR OBTAINING MODELS FOR LIGHT,
CO₂ AND TEMPERATURE FACTORS

THE LIGHT FACTOR

For a maximum CO₂ concentration and a given temperature, a non-linear curve was drawn representing the observed data (Table II). The highest value on the plateau of this curve was regarded as the maximum photosynthetic rate and was assigned unity. The light compensation point, a, was approximated to be in the range of 0.5 - 1.0 \times 10^4 \text{ ergs/cm}^2/\text{sec} (which corresponds to 100 - 200 f.c.). The difference between the saturation light intensity and the light compensation point gives the light intensities used for plant growth. Dividing the effective light intensity level (\(i - a\)) by the light constant, I, the power of exponent (e) was obtained. Then the estimated or predicted values of the light factor at different light intensities were obtained. From these values a curve was drawn.

As the observed points did not lie on this curve, further adjustments were made in the value of I, and maximum rates of photosynthesis were made singly or conjointly until a good curve-fit was obtained. The values of the light constant and the light compensation point were found to be 2.7 \times 10^4 \text{ ergs/cm}^2/\text{sec} and 5.5 \times 10^3 \text{ ergs/cm}^2/\text{sec}, respectively. The estimated values of light factor at different light intensities are presented in Table IV. Fig. 16 presents the estimated curve.

The light factor function may be expressed as,

\[
P = P_{\text{max}} \left[1 - e^{-\left(\frac{Si - 0.55}{2.7}\right)}\right] \tag{20}
\]
Figure 16. Relative Rate of Photosynthesis and Light Intensity, $S_i$, at Saturated Level of CO$_2$ Concentration of Tomato Leaves (after Gaastra, 1959).
THE CO$_2$ FACTOR.

Since the CO$_2$ factor is also an exponential function, the values of the CO$_2$ constant, the CO$_2$ concentration point, and the estimated values of CO$_2$ factor at different CO$_2$ concentrations were obtained in a similar way, as discussed above. A maximum light intensity of $14.8 \times 10^4$ ergs/cm$^2$/sec was used as the parameter.

The values so obtained were 150 ppm for the compensation point and 250 ppm for the light constant. The estimated values are given in Table V and the curve is presented in Fig. 17.

The CO$_2$ factor is expressed as,

$$P_2 = P_2 \max \left[ 1 - e^{-\frac{(c - 150)}{250}} \right]$$

(21)

THE TEMPERATURE FACTOR

As proposed earlier, the temperature response factor is expressed as,

$$T = K + l \theta + m \theta^2$$

Using the observed values of Gaastra for tomato plants (Table III), a parabolic curve for the photosynthetic rate-temperature relationship was drawn for a maximum CO$_2$ concentration (1310 ppm) and a maximum light intensity ($14.8 \times 10^4$ ergs/cm$^2$/sec). From this curve (Fig. 18) it was approximated that the maximum rate attained was $185 \text{ mm}^3 \text{ CO}_2/\text{cm}^3/\text{hr}$ at 35° C. Hence, 35° C was taken as optimum temperature. It was assumed that the photosynthetic rate is zero at 5° C (41° F). The maximum rate was assigned unity and the observed rates at other temperatures were given relative values. Using the relative values for 35° C, 21° C and 5° C, a parabolic function as given below was developed.

$$T = -0.296 + 0.0630(\theta) - 0.00075(\theta^2)$$

(22)
Figure 17. Relative Rate of Photosynthesis and CO$_2$ at Saturation Level. Light Intensity, $14.8 \times 10^4$ Ergs/cm$^2$/Sec (After Gamstra, 1959).
Figure 18. Photosynthesis in Relation To Temperature, CO₂ Concentration, 1310 p.p.m. and Light Intensity, $1.48 \times 10^6$ Ergs/cm²/Sec
The above equation represents increasing growth rates. When plants are exposed to temperatures higher than the optimum temperature, the growth response declines. Another temperature response factor was required for the declining rates. Assuming that the growth rate at 55°C (121°F) is zero and the value of the temperature factor at 39°C was the same as at 31°C, the following expression was obtained.

\[ T = -1.6845 + 0.1572 (\theta) - 0.0023 (\theta^2) \]  

(23)

The maximum rate of photosynthesis was found to be 185 mm³ CO₂/cm²/hr.
TABLE IV

Predicted Values of the Light Factor, $P'_1$, at Various Light Intensities
Shade Factor, $S = 1.0$

\[ P'_1 = \frac{P_1}{P_{1 \text{ max}}} \]

<table>
<thead>
<tr>
<th>Light Intensity (I)</th>
<th>Light Compensation Point, $\alpha$, $10^4$ ergs/cm$^2$/sec</th>
<th>Light Constant, $I$, $10^4$ ergs/cm$^2$/sec</th>
<th>Light Factor, $P'_1 = \frac{(S_1 - \alpha)}{I}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>0.55</td>
<td>-0.55</td>
<td>2.7</td>
</tr>
<tr>
<td>1.0</td>
<td>&quot;</td>
<td>0.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>1.6</td>
<td>&quot;</td>
<td>1.05</td>
<td>&quot;</td>
</tr>
<tr>
<td>3.0</td>
<td>&quot;</td>
<td>2.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>5.5</td>
<td>&quot;</td>
<td>4.95</td>
<td>&quot;</td>
</tr>
<tr>
<td>6.6</td>
<td>&quot;</td>
<td>6.05</td>
<td>&quot;</td>
</tr>
<tr>
<td>8.0</td>
<td>&quot;</td>
<td>7.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>10.0</td>
<td>&quot;</td>
<td>9.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>12.0</td>
<td>&quot;</td>
<td>11.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>13.0</td>
<td>&quot;</td>
<td>12.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>14.8</td>
<td>&quot;</td>
<td>14.25</td>
<td>&quot;</td>
</tr>
<tr>
<td>16.0</td>
<td>&quot;</td>
<td>15.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>18.0</td>
<td>&quot;</td>
<td>17.45</td>
<td>&quot;</td>
</tr>
<tr>
<td>20.0</td>
<td>&quot;</td>
<td>19.45</td>
<td>&quot;</td>
</tr>
</tbody>
</table>
TABLE V

Predicted Values of the CO\textsubscript{2} Factor, \(P'_2\) at Various CO\textsubscript{2} Concentrations

\[ P'_2 = \frac{P_2}{P_2^{\text{max}}} \]

<table>
<thead>
<tr>
<th>CO\textsubscript{2} Concentration ppm</th>
<th>CO\textsubscript{2} Compensation Point ppm</th>
<th>(c-(\beta)) CO\textsubscript{2} Concentration ppm</th>
<th>CO\textsubscript{2} Constant ppm</th>
<th>(\frac{P'_2}{P_2^{\text{max}}} = 1-e^{-\frac{(c-\beta)}{C}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>200</td>
<td>150</td>
<td>50</td>
<td>250</td>
<td>0.1813</td>
</tr>
<tr>
<td>320</td>
<td>&quot;</td>
<td>170</td>
<td>&quot;</td>
<td>0.4980</td>
</tr>
<tr>
<td>500</td>
<td>&quot;</td>
<td>350</td>
<td>&quot;</td>
<td>0.7534</td>
</tr>
<tr>
<td>700</td>
<td>&quot;</td>
<td>550</td>
<td>&quot;</td>
<td>0.8892</td>
</tr>
<tr>
<td>850</td>
<td>&quot;</td>
<td>700</td>
<td>&quot;</td>
<td>0.9392</td>
</tr>
<tr>
<td>1000</td>
<td>&quot;</td>
<td>850</td>
<td>&quot;</td>
<td>0.9667</td>
</tr>
<tr>
<td>1200</td>
<td>&quot;</td>
<td>1050</td>
<td>&quot;</td>
<td>0.9850</td>
</tr>
<tr>
<td>1310</td>
<td>&quot;</td>
<td>1160</td>
<td>&quot;</td>
<td>0.9903</td>
</tr>
<tr>
<td>1500</td>
<td>&quot;</td>
<td>1350</td>
<td>&quot;</td>
<td>0.9955</td>
</tr>
<tr>
<td>1800</td>
<td>&quot;</td>
<td>1650</td>
<td>&quot;</td>
<td>0.9986</td>
</tr>
</tbody>
</table>
APPENDIX III

ANALOG SIMULATION

GENERATION OF STANDARD DAY CONDITIONS ON THE ANALOG COMPUTER

Temperature Cycle. The daily temperature cycle follows a more or less definite pattern. The following was assumed for the purpose of simulation on the computer:

\[ \theta = 22 - 10 \cos \frac{\pi}{2} t \]  
\[ \theta = \left( \frac{\pi}{12} \right) (22 - \theta) \]  

where \( t \) is the time in hours measured from 5:00 a.m.

The above equation (17) is the solution to the differential equation

\[ \ddot{\theta} = \left( \frac{\pi}{12} \right)^2 (22 - \theta) \]

with \( \theta_0 = 12^\circ \) and \( \dot{\theta}_0 = 0 \). And, since \( \theta \) is less than 40\(^\circ\) C the equation can be scaled as follows:

\[ - \frac{12}{\pi} \frac{\ddot{\theta}}{4} = \frac{\pi}{12} (\theta/4 - 5.5) \]

The computer circuit solving this equation is given in Fig. 19. The time scale is taken such that the simulation is 3600 times faster than the actual (1 second machine time = 1 hour actual time), since the time \( t \) of Equation (18) is in hours. The diurnal temperature cycle generated on the computer is given in Fig. 11.

Light Intensity Cycle. To simulate the light intensity cycle on the analog computer, the following assumptions were made:

1. That the sky was clear and bright.
Figure 19. Computer Circuit for Diurnal Temperature Cycle

2. That the diurnal light intensity cycle represents a day in the month of July.

3. That a maximum intensity of $8 \times 10^5$ ergs/cm$^2$/sec is reached at about 12 noon.

4. That the actual light intensity, $S_i$, received by the leaf cover in the crop canopy was 25 percent of the intensity reaching the surface of the earth. That is, the value of $S$ was 0.25 and the value of $S_i$ is $2 \times 10^5$ ergs/cm$^2$/sec.

The diurnal light intensity cycle was generated on the analog computer using the temperature circuit (Fig. 19). The function $\frac{12}{\pi} \sin \frac{\pi}{12} t$ was rectified and passed through a first order filter to generate $U_i$ (Fig. 20). The filter controlled the lag of the peak intensity. Minor on-the-spot corrections were made in the potentiometer setting to make up for diode imperfections. The diurnal light intensity cycle is presented in Fig. 9.
Carbon Dioxide Cycle. The diurnal CO₂ cycle selected is presented in Fig. 10. The cycle has two phases for CO₂ changes which can be described by,

\[
\text{Phase I: } c = 300 + 0.211 (1 - e^{-(t-3)}) \\
\text{Phase II: } c = 500 - 200 e^{-2t}
\]

These equations are expressed in the differential scaled form,

\[
\text{Phase I: } \frac{dc}{50} = \frac{c}{50} - 10.21; \quad \frac{c_0}{50} = 10 \\
\text{Phase II: } \frac{dc}{50} = 2(10 - \frac{c}{50}); \quad \frac{c_0}{50} = 6.
\]

A logic-controlled circuit was used to generate the diurnal CO₂ cycle by solving Eqs. (19, 20) during the first three seconds of the computer cycle, holding the solution for 9 seconds, and then solving (22) during the remaining 12 seconds. The signals \(-2.5 \sin \frac{\pi}{12} t\) and \(3.53 \sin (\frac{\pi}{12} t - \frac{\pi}{4})\) were used to energize relay comparators 1 and 2, respectively. They were obtained from the circuit simulating the diurnal temperature (Fig. 19). It may be observed that
3.53 \sin\left(\frac{\pi t}{12} - \frac{\pi}{4}\right) = 2.5 \sin\frac{\pi t}{12} - 2.56 \frac{\pi}{12} t

Fig. 21 shows the performance of the comparators. The computer circuit for the diurnal CO\textsubscript{2} cycle is presented in Fig. 22.

GENERATION OF RESPONSE FACTORS ON THE ANALOG COMPUTER

The Temperature Factor. The growth response to temperature as described by the temperature factor T is given below:

\[ T = -0.296 + 0.063(\theta) - 0.00075(\theta^2) \]  

(23)

Amplitude Scaling.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimated Maximal Value</th>
<th>Scaling Factor</th>
<th>Computer Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \theta )</td>
<td>35</td>
<td>1/4</td>
<td>( \theta/4 )</td>
</tr>
<tr>
<td>T</td>
<td>1</td>
<td>10</td>
<td>10T</td>
</tr>
</tbody>
</table>

The amplitude-scaled equation for the temperature factor may be written as:

\[ 10T = -2.96 + 2.52 \left[ \frac{\theta}{4} \right] - 1.20 \left[ \frac{\theta^2}{160} \right] \]  

(24)

Response to temperature (\( \theta \)) is presented in Figure 13.

The Light Factor. The plant growth response to light is expressed mathematically by the light factor (L) as follows:

\[ L = \left[ \frac{1 - e^{-\frac{(S_i - a_i)}{I}}} {1 - e} \right] \]  

(25)

where \( L \) = plant growth response due to light = \( \frac{P_l}{P_{l max}} \)

\( i \) = intensity of light available to the plant (leaves) for photosynthesis, ergs/cm\textsuperscript{2}/sec
FIGURE 21. OPERATION OF COMPARATORS FOR CO₂ CYCLE.
Figure 22. Computer Circuit for the Diurnal CO₂ Cycle
Figure 23. Computer Circuit for Temperature Response Factor (T)

\[ S = \text{shade factor, varies between 0 to 1.0. On a \ bright and clear day, } S = 1.0 \]

\[ = \text{light compensation point, ergs/cm}^2/\text{sec} \]
\[ \text{For tomato plants } 5.5 \times 10^3 \text{ ergs/cm}^2/\text{sec selected.} \]

\[ I = \text{light constant, ergs/cm}^2/\text{sec} \]
\[ \text{For tomato plants a value of } 2.7 \times 10^4 \text{ ergs/cm}^2/\text{sec \ was selected.} \]

The function \( 10 \left[ 1 - e^{0.2703 - 0.74X} \right] \) was set on a Variable Function Generator driven by \( X = 5 \times 10^{-5} \text{ Si} \) (Fig. 24), thereby generating \([10L]\).

The computer circuit generating the light factor is given in Fig. 24.

Figure 24. Computer Circuit for Light Factor
The Carbon Dioxide Factor. Let $D$ represent the plant growth response due to CO$_2$. The expression used for this factor is,

$$D = \left[ \frac{c - \beta}{C} \right]$$

where $D =$ plant growth response due to CO$_2$ — \[
\frac{P_2}{P_2_{\text{max}}}\]
$c =$ concentration of CO$_2$ in ppm
$\beta =$ CO$_2$ compensation point, ppm
150 ppm for tomato plants
$C =$ CO$_2$ constant, ppm
250 ppm for tomato plants

The function $10 \left[ 1 - e^{0.667 - 0.2X} \right]$ was set on a Variable Function Generator driven by $X = \frac{C}{50}$ (Fig. 25), thereby generating $[10D]$.

The computer circuit generating the CO$_2$ factor is given in Fig. 25.

![Figure 25. Computer Diagram for CO$_2$ Factor](image)

**Figure 25. Computer Diagram for CO$_2$ Factor**

**GENERATION OF THE DIURNAL PHOTOSYNTHETIC RESPONSE**

The computer circuit for the diurnal photosynthetic rate is presented in Figure 26. The response is discussed elsewhere.
Figure 26. Computer Circuit for Growth Response