THESIS

THE EFFECT OF SOIL MOISTURE STRESS ON GROWTH AND FLOWERING OF CARNATIONS

Submitted by

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ABSTRACT OF THESIS

THE EFFECT OF SOIL MOISTURE STRESS ON GROWTH AND FLOWERING OF CARNATIONS

The effect of differences in soil moisture stress, provided by the use of different soils and depths of soil, on yield and quality of carnations was investigated. A technique that would offer a better indication of when to water carnations under greenhouse conditions was also evaluated.

The values of bulk density, moisture content at all suctions and total pore space of the best soils were an average of the extremes of all soils compared. Reduction of soil depth from 8 to 4 inches increased problems that result from too much or insufficient water. Yield and grade were best on plants grown in 8-inch soil. Raw field soil had a decreased yield due to an aeration problem when placed in a greenhouse bench.

The effect of stress was most noticeable in the flowering of the second crop which was delayed up to 5 weeks under high stress. Indications were that some stress may be essential for production of higher grade carnations.

The number of stomatal and epidermal cells per unit area increased as either solar radiation or soil moisture stress increased. Stomata on leaves from plants grown under high stress adapted to the unfavorable growing conditions by having a greater resistance to

transpiration. The use of stomatal index was not beneficial in understanding stomatal distribution. A higher correlation was found between transpiration rate and stomatal aperture than transpiration rate and solar radiation. Although the lithium chloride hygrometer was easy to use, it was not sensitive enough to be used in a greenhouse as an indication of when to water. The measurement of stomatal apertures by the use of silicon rubber impressions was too laborious to be used as a practical field technique.

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Chapter I

INTRODUCTION

There are several distinct differences between soils commonly found in the field and those in greenhouses. In the greenhouse, there is a restricted volume of soil available for root growth and water supply as compared to field conditions. Greenhouse soils may be characterized as shallow, intensively cultivated, restricted to pots and benches, and without restriction to drainage from the bottom of the bench (47). Depth of soil is important, since it is one of the factors determining soil water holding capacity.

According to Richards' "outflow law" (83), if the pressure of the soil water is equivalent to, or less than atmospheric pressure at the undersurface of soil layer, then water will not flow from the soil. This law may be applied to a greenhouse bench. After it has been watered and equilibrium reached, the suction at the undersurface is 0, while the suction affecting the water content in the upper surface of soil is equal to the soil's depth. A shallow soil of 10 cm would have a higher water content than a soil 20 cm deep, provided all other physical characteristics are the same.

Under conditions of low evapotranspiration (low light intensities and small plants), a 10 cm deep soil stays wetter longer than a 20 cm soil. This may result in aeration problems in the shallow soil. Overwatering problems may also occur in deep soils that do not

drain properly. However, given suitable characteristics, a deep soil will contain less water at its upper surface than a shallower soil.

When the total amount of water available to the plant per unit of ground area is compared, there is more water available for evapotranspiration in a soil 20 cm deep than one 10 cm deep. Thus, under conditions of high evapotranspiration (high light intensity), a shallow soil will usually dry out faster. When both a 10 cm and 20 cm soil are on the borderline of watering in the morning, the plants in the 10 cm soil may be subjected to higher stresses by midafternoon. To avoid problems of overwatering, growers tend to use a shallower soil, since shallow soils tend to dry more rapidly.

Watering of carnations has been an art based on experience, which, added to differences in cultural practices between growers, seriously complicates the proper application of water and diagnostic solutions. Because greenhouse growers use different cultural practices such as hand watering by hose versus various types of automatic systems, the effect on soil characteristics will vary. Consequently, no two greenhouse soils are alike and their problems must be dealt with individually. These problems include the determination of watering frequency.

There are indications that plants watered at low suction levels result in a higher yield and grade for both snapdragons and carnations (45, 49). However, Kramer (60) states that it is not known what constitutes an adequate water supply for optimum growth.

Since the stress to which a plant is subjected is controlled by many factors besides those of soil moisture content and suction, the determination of "when to water" should be a measure of the water

status inside the plant. It is the water status inside the plant that influences various physiological processes. Plant water status is indicated by a number of terms such as internal water stress, internal water potential, internal water balance, or diffusion pressure deficit (DPD). Previous research has usually involved the study of the effects of water without considering what is going on inside the plant. There is a definite need to determine the relationship between plant water stress and subsequent growth.

The Problem

There are two objectives of this study. First, what is the effect of soils and soil depth on yield and quality of carnations when so-called "problem" soils are treated identically; and second, can instruments used to measure transpiration rates of individual leaves be employed as a measure of indicating "when to water;" and are such measurements superior to present practices?

Specific Questions in this Study are:

1. Are transpiration rates capable of being used as an irrigation indicator?
2. What is the effect of cover, soil and depth on:
    a) transpiration rates as measured with a lithium chloride hygrometer
    b) stomatal density
    c) growth (yield and mean grade)
3. Does the variation of stomatal density affect transpiration measurements?

Significance of this Research

Few studies in the past concerning plant-soil-water relationships have dealt with the carnation. Considerable information on which to intelligently base future cultural practices should result. For practical purposes, the study should result in more reliable recommendations to commercial growers as to the effect of reducing soil depth and the behavior of common greenhouse soils when treated identically.

Chapter II

LITERATURE REVIEW

Introduction

It is well known that plant growth may be reduced when water supply to a plant is restricted (1, 6, 11, 22, 29, 57, 62, 63, 70, 74, 95, 96). The relationships between water and growth have been studied intensively for a number of years. Soil-water-plant relationships are complicated with the result that some contradictory information and subsequent controversy has occurred. Much of the controversy that results is probably due to variations in research techniques, or to an inadequate evaluation of the internal water balance of the plants under investigation.

Considerable research (31, 42, 74, 96) has been carried out on soil-water relationships as an indication of the internal water balance in plants. It is the consensus (3, 5, 11, 13, 62, 106) that determination of soil water stress alone is not always the best indication of plant response, nor does it indicate the internal water stress of the plant. Measurement of internal plant water deficits per se, is more likely to result in meaningful information, since the internal water stress is influenced by all those factors that determine water balance, of which soil water availability is only one. It appears from the literature (45, 48, 49) that there may be consistent relationships between yield and the internal water

balance of a plant. A valuable application would be correlating the internal water balance in plant tissue to plant growth responses.

It is the purpose of this study to examine some of the relationships between the plant and its environment as they are related to water. This review is divided into sections dealing with: 1) terminology used in soil-plant-water relations, 2) effect of water on growth, 3) factors affecting water supply, 4) methods of determining the water status of the plant and 5) summary.

Definitions and Terminology

Several authors (21, 25, 52, 64, 99, 101, 104, 123) have discussed the terminology currently being used to describe the state of water in both plants and soils. It is apparent from the literature that these terms often have the same meaning and are used interchangeably, the particular term employed depending on the author.

Some terms which have been used to describe the water status in plants include "water absorptive power," "suction force," "suction pressure," "suction tension," "net osmotic pressure," "diffusion pressure deficit" (DPD), "hydratur," "saturation deficit," "relative turgidity," "relative water content," "enter tendency," and "osmotic equivalent" (E) (60, 61, 62, 64, 71, 72, 87, 104, 123). Terms such as "total soil moisture stress" (TSMS), "total suction," "pF," "capillary potential," and "thermodynamic potential," have been used in soil water relationships (104). Meyer (71, 72) stated that DPD is a measure of the pressure at which water tends to move into plant tissue after it is placed in pure water and expressed it by the following equation:

$$DPD = OP - TP \quad (1)$$

where OP = osmotic pressure and

TP = turgor pressure

The terminology utilized most often to measure plant and soil water relations is DPD and TSMS respectively (101, 104).

The universal use of basic thermodynamic terms and units of expression would enable the factors affecting the thermodynamic state of water to be adequately evaluated and described. Slatyer and Taylor (104) expressed the following reasons for requiring a more unified terminology: 1) The terms which have been used to describe the water relations of soil and plants are thermodynamic in nature and are measured by thermodynamic methods, but have been expressed in terms of equivalent pressures which may be misleading in that actual pressures may not develop in the system. 2) The use of DPD refers to a cell which is completely vacuolated, which may not always occur in the plant, and the rigid use of the term can result in an erroneous interpretation and description of the phenomenon observed and 3) since the most appropriate thermodynamic function is one of free energy, the most acceptable term to use in expressing both DPD and TSMS is based on the Gibbs free energy function. Although the most common units of expression are in atmospheres of pressure, the conversion to energy units can be made if the specific volume of the water and the temperature and pressure are accurately known.

The basic thermodynamic term advocated for use in expressing soil-water-plant relations is "water potential." Kramer et al. (64) defined water potential as the difference in the partial specific

Gibbs free energy between water in plant tissue being observed and free pure water at the same temperature. They (64) point out that it is actually a measurement of the tendency of water to move into a system, such as plant tissue or soil, or from one part of the system to another. The term water potential is symbolized by the Greek letter Ψ and is made up of three main components expressed as:

$$\Psi = \pi + \tau + P \qquad (2)$$

The osmotic potential, π, is the potential due to solutes in the cell solution and is equivalent to a negative OP as used in equation #1 (64, 123). The potential due to the absorption of water by water-binding colloids and surfaces in the cell matrix is represented by τ (64). Kramer et al. (64) stated that, except in very dry tissue or in cells containing small vacuoles this potential is small and may be disregarded. However, Wilson (123) found that omission of τ from quantitative treatments of internal water relations might cause errors. He believed that τ is introduced to show that cell water is held partially by matric forces and is probably included in OP as used in equation #1. The potential represented by P is usually not evident in soils but in plants is represented by cell turgor pressure which is equivalent to TP in equation #1. Therefore, from equation #1

$$\Psi = -(OP-TP) \qquad (3)$$

and is negative except at maximum turgidity when it is 0. Water potential increases in magnitude but decreases in absolute value (becomes more negative) as stress increases (64). A rise in DPD

corresponds to a decreasing value for water potential. The water potential will be uniform throughout a tissue, provided it is in equilibrium, but the three components of water potential may vary among cell types and structural phases (cell wall, vacuole, and cytoplasm) (123). The use of water potential allows for the evaluation of the various components which make up the total water potential in different parts of the plant system.

Effect of Water Stress on Plant Growth

General effects -- The fact that a water deficit is detrimental to plant growth has been found by many investigators (22, 29, 45, 54, 62, 63, 70, 74, 95, 96). Although the correlation between turgor and growth is not fully understood, all of the processes involving the cell in growth are affected by water deficits and the dehydration of protoplasm. These cellular processes include cell division, enlargement, differentiation, and maturation. Growth of the plant itself is an expression of cell elongation brought about by turgor pressure (107). Kramer (61) believes that cell division is affected less by water stress than is cell elongation. It is believed that decreasing water potential reduces cell enlargement most of all since the expansion of cells is dependent upon turgor pressure (26). Reduced turgor results in shorter stems and smaller leaves and fruits (87). Wadleigh and Gauch (113) found that a stress of 1-3 atmospheres (A) had little observable effect on leaf elongation, but at higher stress values, leaf elongation was progressively reduced and ceased at 15 A.

Water deficits generally hasten maturation of cells and tissues, increase the thickness of cell walls, amount of cutinization and

lignification, and decreases succulence (60). Leaf area is usually reduced while leaf thickness is increased (62). The increase in supporting tissue may be beneficial since it increases stem strength.

Snapdragons watered at high soil moisture tensions had a reduced mean grade, stem length and fresh weight while the percentage of dry matter increased (45, 48). In work done on carnations, plants watered at high soil moisture tensions were visibly shorter and the foliage and stems harder (54). Drying the soil to a high moisture tension was also found to reduce the flower quality (49, 56). The keeping life of flowers grown under high stress conditions was slightly increased in comparison to those grown under low stress conditions (49). However, dye uptake was enhanced considerably on flowers grown at low soil moisture tensions. Hanan and Jasper (49) found a higher total yield and mean grade on carnations watered at low suction levels.

Stress and physiological processes -- There is a great deal of evidence that water deficits in plants influence various physiological processes such as photosynthesis, transpiration, translocation, and respiration (61, 62, 109, 116). Some of the effects on these processes may be observed at low stress values; and as stress increases, the effects become intensified. One of the first effects of stress is loss of turgidity (29, 35, 63, 95). Richards and Wadleigh (85) believed that permanent wilting was the end of a series of stages that occurred as stress increased.

The loss of turgor seems to affect stomatal opening as soon as it occurs. Some investigators (66, 68, 77) have observed stomatal closure with only small water deficits existing in the plant.

Although closure reduces water loss, it also reduces the supply of carbon dioxide for photosynthesis. According to Kramer (61), photosynthesis may be decreased because protoplasm becomes dehydrated and is less efficient in carrying out the process. Brix (14) found that photosynthesis was decreased at a relatively low value of water stress in the leaves. This value may vary depending upon the type of plant investigated. In Loblolly Pine, photosynthesis decreased when leaf DPD increased above 4 A. For tomatoes, photosynthesis decreased at levels above 7 A. Brix (14) also found that changes in rates of transpiration and photosynthesis were similar as water stress increased. Virgin's (112) results showed that a small water deficit caused a strong inhibition of chlorophyll a formation. This was attributed to the effect water stress has on the formation of the precursor of chlorophyll a, protochlorophyll. As the water potential decreased in the plant system, there was a decreased production of protochlorophyll.

Schneider and Childers (91) noted that while photosynthesis had decreased by 80 per cent at the time of visible wilting, the respiration rate had increased. With an increased use of plant carbohydrates by respiration and a decrease in their synthesis, a depletion of reserve food material occurred. They (91) also noted that, at visible wilting, the transpiration rate had decreased by 87 per cent. After the plants were watered, recovery back to the maximum rate of transpiration took two days. Clark and Levitt (18) reported that plants grown under high water stress were found to transpire less than those grown under more optimum water conditions of low stress.

Morphological change in leaves and stomata -- Water deficits in a plant have an effect on its morphological as well as its physiological processes. According to Stocker (103), Zakenski was the first to report in detail the morphological effects of increasing water deficit on the structure of a leaf. These effects were: 1) the size of the stomata and epidermal cells were decreased and 2) the number of stomata per unit area of leaf surface and the formation of the waxy layers were increased. There are other factors that may affect stomatal distribution besides water stress. These include the kind of plant grown (24), and environmental factors such as light intensity (38, 82) and atmospheric humidity (38).

Relatively little evidence is available which clearly distinguishes the effects of different environmental conditions on stomatal distribution (24). Indications are that in some plants, when growing conditions are optimum and large leaves are produced, the number of stomata per unit area is small while they themselves are large. However, when leaf expansion is checked by water stress, the number of stomata per unit area is large and the stomata are usually small (24). In observations by Amer and Williams (2), leaves from plants grown under stress had small epidermal cells and large numbers of stomata and epidermal cells per unit area. But, they (2) found very little difference in the total number of cells per leaf on plants grown under both high and low water stress. Calculations of total stomatal area as a percentage of leaf area showed no consistent relationship (24). From this observation, it is doubtful that changes in cell size counterbalance changes in numbers.

In order to compare transpiration rates of various plants, it is necessary to have a constant number of stomata per unit area of leaf surface (15). Only then can the effect of different watering regimes on transpiration rates be accurately compared. According to Maximov (69), Heuser was unable to establish any correlation between the number of stomata per unit area and the needs of the plant for water. There does not appear to be any other report on the effect of stomatal density on the rate of transpiration per unit area of leaf surface.

Stomata develop in the early stages of leaf growth. Fully developed stomata were found in the small imbricated primordial leaves at the top of a growing shoot (82). At this point, water supply is very important to cell expansion as there may be considerable variation in cell size (73). Stomatal formation appears to cease when the young leaves are about one-quarter their final size (82). No further change in the stomatal density per unit area was observed after this time although the more rapid multiplication of intervening cells may result in a reduction of stomata per unit area (82).

The distribution of stomata may vary with the leaf position of the plant and on the leaf itself. Hirano (53) in working with citrus leaves found areas in the vicinity of large veins, glands and trichomes which had few stomata around them. Yocum (124) found that the base of the oak leaf and near the midrib always had fewer stomata. He (124) also found fewer stomata per unit area at the base of the leaf and near the midrib than in other areas of the leaf. Reed and Hirano (82) also found fewer stomata at the base of citrus leaves, most in the middle and an intermediate number at the tip. However,

they also found more in the apical rather than in the middle portion. Echerson (27) reported a greater stomatal area near the base of the leaf than at the tip and a greater area at the midrib than at the margin. According to Maximov (69), Salisbury found stomatal frequency to increase from the base to the apex of the leaf and from the midrib to the leaf margin. He (Salisbury) expressed the numerical relation between stomata and epidermal cells by means of a stomatal index:

$$I = S/E+S \times 100 \qquad (4)$$

where S = number of stomata per unit area

E = number of epidermal cells per unit area

He found that for a given species, the stomatal index (I) of leaves grown under different conditions are far more constant than stomatal frequency and believed that differences in stomatal frequency are due to differences in the size of the cells, rather than differences in the ratio of stomata to epidermal cells.

Factors Affecting Stress in the Plant

The internal water potential in a plant depends on the balance between rate of water loss by the shoots and the rate of uptake by the roots (10, 93, 101, 107). A decrease in water potential (more negative) can result from reduced absorption as soil moisture stress is increased and/or from excessive water loss through transpiration (62). On sunny days, wilting is often observed even though there may be an ample water supply in the soil. The factors affecting the internal water balance may be divided into two parts: 1) those

affecting the soil moisture availability and 2) those of the above ground environment influencing water loss.

Soil moisture availability -- There has been controversy in earlier literature concerning the availability of water to the plant over the range of field capacity to permanent wilting percentage (110, 111). Veihmeyer and Hendrickson (114) believed that reduced growth is not usually apparent until stress close to the wilting point has been reached. However, reduced growth has often been observed at what is usually considered insignificant soil moisture stresses (39, 89). In studying mild water deficits, Goode (39) found that both fruit and vegetative growth of apples were reduced at a maximum soil water tension of less than 1 atmosphere (A). Rutter and Sands (89) found that a maximum soil water tension of 1.5 A reduced dry weight and stem elongation. Thus, soil water becomes progressively less available to plants as total soil moisture stress increases (32, 39, 68, 74, 85, 89, 113). Clements (19) stated that to continue the argument is pointless.

Some factors affecting the rate of water absorption are the soil moisture stress at any given moment, soil temperature, soil aeration and the concentration of the soil solution (60, 62, 106). It is also known that the rate of water absorption depends on the rate of water loss and the extent and efficiency of the root system (60, 62). A plant may have an adequate amount of moisture available for its use, but the root system may lack sufficient surface area to absorb water in quantities equal to that lost by transpiration.

Atmospheric demand -- According to Gardner and Ehlig (36), when there is an ample supply of water available to the plant the rate

of water loss is controlled mainly by atmospheric factors. These factors include light intensity, CO_2 concentration, air and leaf temperature, relative humidity, and wind velocity. The water loss from the plant is generally influenced by several of these factors at any one time.

At a constant temperature the vapor pressure of water varies directly with relative humidity (R.H.) which is a ratio of the actual vapor pressure to the vapor pressure of the atmosphere when saturated at the same temperature (24). It is often assumed that the intercellular spaces of a leaf remain at 100 per cent R.H., while the external atmosphere is usually less than 100 (23, 33, 87). This results in a vapor pressure gradient between the leaf and the external atmosphere, and water vapor will diffuse through the stomata from the area of high vapor pressure to the area of low vapor pressure (24). The factor of major importance in determining the transpiration rate is the vapor pressure gradient from the leaf to the air (23, 100).

Vapor pressure is also influenced by temperature. The transpiration rate will generally increase as the temperature of the leaf or of both leaf and air is increased (25). A rise in temperature will increase the vapor pressure both inside and outside the leaf, but the increased difference is due entirely to the greater increase inside the leaf resulting in a greater vapor pressure gradient (24). According to Salisbury and Ross (87), every 10° C increase in temperature results in a doubling of the vapor pressure values. The most important effect of radiant energy is that it will generally increase leaf temperature 2-10° C above the air temperature (23),

resulting in a steeper vapor pressure gradient between the leaf and atmosphere. The high rate of transpiration can eventually lead to stomatal closure from loss of turgidity if the rate of water absorption does not keep pace with the rate of water loss. Light also has another important effect on water loss since stomata are usually found to be closed in the dark and open in the light (33, 51). A smaller percentage of stomata was found to be open under low than high light intensity (51, 78, 79). This would partly explain the low transpiration rates found at low light intensities.

The effect of air movement over a plant canopy may either increase or decrease transpiration. By decreasing the thickness of the boundary layer around the leaf, the path length for vapor movement is shortened increasing the transpiration rate (24, 87). The wind may also decrease the transpiration rate by cooling the leaf and lowering the vapor pressure gradient (87). Heath and Milthorpe (51) found that increasing the rate of dry air flow over a leaf caused stomatal closure. The amount of stomatal closure was lessened when the water content of the air was high. The effect is probably due to the greater vapor pressure gradient that existed when dry air was used and the plant guard cells were not able to maintain their turgidity while losing water at a rapid rate.

It has been found that increased concentrations of CO_2 depress the transpiration rate by closing the stomata on the leaf (34). It has also been found that a very low concentration of CO_2 will cause stomata to open both in the light (51) and dark (87). As can be seen from above, the effect of one environmental factor may either nullify or enhance the effect of another.

Measurement of Internal Water Stress

There has been some uncertainty concerning the best method for measuring plant water potential. Some of the methods used include: relative water content, gravimetric, cryoscopic, plasmolytic, osmotic pressure and DPD, beta-ray absorption, thermocouple psychrometer, stomatal aperture, electrical conductance and the pressure bomb.

Osmotic pressure and diffusion pressure deficit -- The concept of osmotic pressure is old and was once used extensively as an indicator of water balance in a plant. As the water stress in a plant increases, there is a subsequent increase in osmotic pressure and DPD. Osmotic pressure has its disadvantages in that large samples of materials are necessary to obtain the amount of sap required for measurements. According to Kramer (62), it is not sensitive enough to be used as an indicator of the internal water balance in a plant, because a plant with an osmotic pressure of 10 A may be in the same physiological condition as another with 20 A.

Interest has shifted from measuring osmotic pressure to DPD. DPD is a better indicator of the plant water balance partially because it is expressed in atmospheres which can be compared with soil moisture tension and the osmotic pressure of the soil solution. It also is an indication of the tendency for the plant to absorb water (58, 60, 62, 122).

Several investigators (14, 42, 96, 97) have used DPD in their investigations of plant water deficits and some (58, 122) believe that DPD is the most suitable measurement of the internal water potential in plant tissue. The determination of DPD in plant tissue

may be obtained by using any of the several techniques available. These techniques may give either a direct or indirect measurement of DPD.

Some of the classical techniques used include the cobalt chloride, gravimetric, cryoscopic, and plasmolytic methods. The cobalt chloride technique gives an indirect measurement of the rate of water loss from leaves. Since the paper is blue when dry and pink when wet, the rate of water loss is measured by the time required for a color change to occur (61). However, this method is unreliable as it measures the rate of water loss in a closed system and does not give an accurate indication of water loss in the open (61).

Both the cryoscopic and plasmolytic methods may be used to give a measurement of osmotic potential (87). The cryoscopic method uses the freezing point of the sap solution to determine its osmotic potential. The method has two problems in that a highly sensitive thermometer must be used and obtaining a pure sample of cell sap is difficult (87). The mixing of cytoplasmic contents with the cell sap may also result in variations of data. However, in spite of these problems, the method has been used for many years.

In the plasmolytic method, the osmotic potential of the cell sap is determined by placing strips of leaf tissue in solutions of different osmotic potential. When the tissue begins to show plasmolysis after a certain period of time, it is assumed that the osmotic potential of the solution, which started to produce plasmolysis, is equivalent to the osmotic potential of the cells within the tissue (7, 87).

The gravimetric technique is a classical method in which the weight of a whole plant is recorded over a period of time. The evaporation from the potted plant is prevented by wrapping it in plastic or metal foil. This method is often used in comparison with a new technique. Although it gives a good indication of water loss, it does not indicate the internal water status of the plant, and it is limited to small plants which can be easily handled. Problems may result from poor aeration and the soil media becomes much warmer than normal if the pot is exposed to the sun (61).

Relative water content -- According to Kramer (62), this is the oldest method to describe the amount of water in growing plant tissue relative to what it would be if the tissue were fully turgid (62). Water content has been expressed in many different terms which has resulted in confusion in studies of plant-water relations. The term "saturation deficit" was first suggested by Stocker in 1929 (60) and employs the following calculations:

$$\frac{\text{Saturated fresh weight - field fresh weight}}{\text{Saturated fresh weight - oven-dry weight}} \times 100 = \text{Saturation Deficit} \quad (5)$$

Halma (43) presented his measure of water deficits in citrus trees as the "relative saturation deficit" which was defined by Compton (20) as:

$$\frac{\text{Saturated weight - fresh weight}}{\text{Saturated weight}} \times 100 = \text{"Relative Saturation Deficit"} \quad (6)$$

These terms were disregarded after a variation was introduced by Weatherley (118) in 1950 called "relative turgidity," (RT). It is calculated from the relationship:

$$\frac{\text{Field fresh weight - oven-dry weight}}{\text{Saturated fresh weight - oven-dry weight}} \times 100 = \% \text{ Relative Turgidity} \quad (7)$$

This technique has been widely used in studying water stress in plants (16, 94, 96, 98, 106, 116, 121), with modifications by other investigators (3, 16, 17, 28, 41, 98). According to Slatyer (96) and Werner (121), its practical significance is that the degree of turgidity at any given stress value indicates the physiological activity of the plant. Others (60, 63, 120) suggested that the method may be used as an index of the DPD in leaf tissue. Weatherley (119) considered the method as a reliable indicator for the irrigation of cotton and could be applied to the irrigation of other crops. However, Unger and Danielson (106) found that RT values were not sufficiently sensitive to adequately evaluate differences in water potential. Slatyer (96) also found that the effect of a given turgidity value was not always the same in all species.

The use of the term relative turgidity is critized because turgor is a physiological state where pressure is exerted by the vacuole and protoplast against the cell wall. It is not properly expressed as a percentage of water content (52). Although not completely acceptable, relative turgidity is a classical method and is often used as a basis upon which new techniques are evaluated.

Stomatal aperture -- The relative opening of stomata is controlled by the turgor present in the guard cells. Since the turgor is affected by the water balance in plants, the measurement of stomatal apertures has been used as an indicator of the water stress in plants. Muturi (74) found that the degree of stomatal opening

was directly related to relative turgidity values of bean leaf tissue. However, this type of measurement is qualitative and does not provide a good quantitative basis for the comparison of internal water conditions between plants.

The measurement of stomatal openings may be obtained in several ways. The infiltration technique utilizes a graded series of liquids which vary in viscosity (42). The infiltration of the liquid into the leaf is indicated by a water soaked appearance of the tissue. The most viscous grade of liquid that the leaf will absorb in a given length of time is used to determine the relative degree of stomatal opening. Infiltration is a good field technique (50); but because the leaf cannot be used again, it is poor for laboratory use (8). Several investigators have used this technique (1, 31, 41, 42).

Stomatal aperture may also be measured by direct microscopic examination (15). The method is not practical since it is: 1) laborious to use and 2) time consuming due to the variation in width among stomata and requiring several experimental plots to be examined to obtain an average width (8).

Direct microscopic observation has been replaced with a new technique utilizing silicone rubber impressions. This technique was reported by Sampson (88) and subsequently used by Zelitch (125, 126) in stomatal studies. The method enables the measure of stomata in large numbers of samples without alteration of the leaf environment (125). The impressions can be stored and stomatal measurements can be made microscopically at a later date. Another technique used to

determine relative stomatal opening is the porometer. Although this technique is good laboratory method, it has the following disadvantages (8): 1) it is not practical as a field technique, 2) attachment to the leaf is difficult, and 3) attachment to the leaf changes the environmental conditions.

Methods utilizing electrical conductance -- Much research concerns water deficits affecting electrical resistance. One such method includes measuring the effect water stress has on the electrical conductance between electrodes implanted in a plant stem. Namken and Lemon (76) utilized this technique, but found that the method lacked sensitivity and did not appear to be correlated with relative turgidity values. In work done by Box and Lemon (10), the results indicated that the method showed promise as an indication of the water potential in the plant, but additional research was needed to evaluate the method more completely.

Another method is the electric hygrometer in which electrical resistance of a lithium chloride cell varies inversely with humidity. This method is based upon measuring the rate of water vapor diffusion through the stomata. Wallihan (115) employed the instrument to estimate the relative opening of stomata. Van Baval et al. (108), modified Wallihan's method and designed a special porometer cup which measures the resistance to water-vapor in the leaf structure itself. The effect of number, relative aperture and morphology of the stomata is directly evaluated in terms of the resistance (109). Correlating the data obtained with the environmental factors present, the actual rate of transpiration may be obtained. Since the internal

water balance affects the turgor of the guard cells which is reflected in the rate of transpiration, this method may become very useful in determining plant water potential. Unger and Danielson (106) state that this type of technique should provide a well correlated indication of the leaf water potential and plant growth.

Pressure-bomb technique -- Kramer (59) stated that most of the large, rapid changes in water content of plant tissue can be accounted for in terms of movement along osmotic or free energy gradients. The pressure-bomb technique permits the quantitative measure in atmospheres of the turgor or hydrostatic pressure of sap in the xylem of vascular plants. However, from the literature there is a variation in the accuracy reported for the technique. Scholander et al. (92) stated, that when carefully done, reproducibility of repeated readings were obtained within 1 per cent. Waring and Cleary (117) compared pressure bomb readings in twigs with Slatyer's (97) vapor equilibrium technique and found agreement between the two methods within $\pm$1 A. In tests with sunflower and yew plants (12), pressure bomb readings were within $\pm$2 A of psychrometer measurements while there was a greater discrepancy when rhododendron plants were used.

Possible errors were reported to be of two types (117): 1) those related to the rate of pressure increase (too high readings when pressure is increased too rapidly) and 2) those related to the sample preparation (length of xylem extending from the bomb is critical). Boyer (12) concluded that the pressure bomb readings were sufficiently close enough to the psychrometer measurements that they could be used for the relative measure of leaf water

potential. For accurate values of leaf water potential, the pressure bomb measurements must be calibrated with a thermocouple psychrometer (12).

Thermocouple psychrometer -- Up to now, the most accurate method, giving an absolute value of DPD in detached leaves, is Spanner's (102) or Richards and Ogata's (86) thermocouple psychrometer. A comparison has been made of the measurements between the two methods and although they were found to be comparable, Spanner's technique has advantages (4, 5). Several investigators (6, 9, 14, 28, 36, 80, 104) have used the technique to measure DPD in leaves of different plants including sunflower, pepper, cotton, and tobacco. Manohar (67) and Lang and Barrs (65) both modified the method to make it possible to measure water potential using plant leaves still attached to the plant. However, there were certain inaccuracies in the determinations that had to be accounted for. These included heat produced by respiration (4), the presence of water on the walls of the psychrometer chamber (37), and the resistance of leaf tissue to vapor transfer (4, 81). The psychrometer also needs frequent calibration to maintain its accuracy (28). An improved method which attempts to take these errors into consideration is called the isopiestic technique. Its degree of accuracy is increased over that of Spanner's (13). Boyer (11) states that if the corrections applied in the isopiestic technique are valid, it would be a good quantitative measure of water conditions in the plant.

Beta-ray absorption -- Other investigators (30, 70, 75, 122) have used a beta-radiation gauge to measure the changes in water

content of a leaf. Mederski (70) showed that beta-radiation absorption was highly correlated with relative turgidity and was sensitive to small changes in turgidity values. He advocated that this technique could provide a continuous non-destructive record of changes in the internal water balance of a plant. Nakayama and Erhler (75) showed reliable responses to rapid changes in the internal water condition of cotton plants. However, Whiteman and Wilson (122) contend that while beta-radiation absorption follows the trend of water content, it is inadequate for useful estimation of DPD because of the wide variation between measurements on the same plant.

Summary

It appears from the literature that there are consistent relationships between plant water stress and growth response. Since water stress is the result of many environmental factors, its measurement would simplify controlling growth by environmental and cultural practices. However, until very recently the lack of a practical and accurate technique for measuring plant water potential has hindered research on the relationship of growth to water potential.

Most of the techniques used give an indirect or qualitative value of plant water potential. These include relative water content, relative turgidity, electric hygrometer and stomatal aperture. A quantitative measure of water potential would make it possible to compare definite values of stress to various growth processes. A measurement of this type would be a more direct and exact representation of the water potential in the plant tissue.

Up to now, only the pressure bomb and thermocouple psychrometer provide a direct quantitative measure of plant water potential. Little work has been done utilizing the pressure bomb and more research is required to ascertain its advantages and disadvantages for practical use. The thermocouple psychrometer is the most accurate technique available. However, it is not a good field technique since it is expensive, time consuming, and requires precise temperature control.

The most desirable method would be one that is simple to use, cheap to obtain, and expresses accurate and quantitative values. When such a technique is found, a commercial greenhouse grower will be able to have more control over growing his crops. By being able to measure the water potential in the plant, he can get the maximum growth possible by growing the plants at low stress values. If additional stress is required for better handling or production, he can easily control the amount with the technique. It is possible that if a dependable method to measure water potential is found, there will be a major change in the method of growing carnations.

Chapter III

METHODS AND MATERIALS

This section is divided into three parts: 1) experimental design, 2) soil and plant measurements, and 3) transpiration, stomatal aperture, and stomatal frequency determinations.

Part 1. Experimental Design

General -- The research was conducted in the Colorado State University temperature greenhouse originally constructed for temperature research on carnations (44, 90). The greenhouse was oriented east-west, divided into four compartments, each 15 X 17 feet, and lettered from A to D beginning with the west unit. The coverings on each compartment were:

A. frosted fiberglass installed June, 1964,

B. clear fiberglass installed November, 1965,

C. rigid polyvinylchloride installed June, 1964, and

D. original glass, house constructed the summer of 1955.

A more complete description of the structure was given by Hanan and Holley (46).

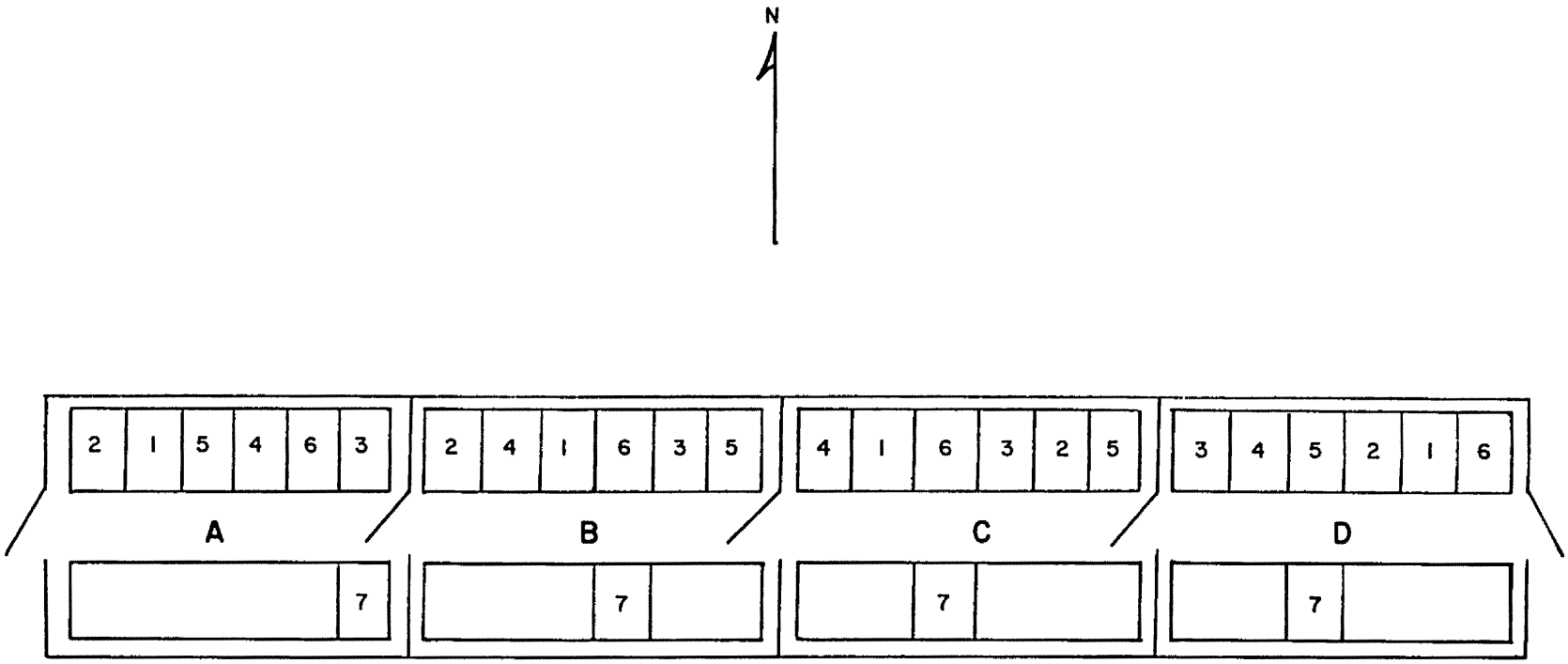
Day temperatures in all compartments were set to heat to 62° and cool at 65°. Night temperatures were maintained at 53° F $\pm 1^{\circ}$. CO_2 was added to maintain approximately 600 ppm concentration when cooling fans were off.

Treatment -- Every compartment contained two benches, 42 inches X 12 feet, oriented east-west. The benches were divided into six plots, each 24 inches long. The plots in the north bench were randomly assigned (Fig. 1) to different soils and soil depths. The soil mixtures were selected to give the range of soil types commonly incurred in commercial greenhouses. Two, obtained from growers, were known to apparently give trouble. The treatments were:

1. CSU Old Soil: A well aggregated greenhouse mixture used for about six years with consistent records of high yield and grade.
2. CSU New Soil: A Fort Collins loam brought directly from the field with no additions.
3. Grower's Soil A obtained from a commercial range in the Denver area, well aggregated; but under the grower's conditions, apparently causing reduced production either from deficient aeration or disease.
4. Grower's Soil B obtained from a commercial range in Colorado Springs, well aggregated, but apparently causing plant loss from root rots generally associated with high water contents.

In an attempt to reduce, or overcome, difficulties with Soils A and B, both growers had reduced the soil depth in the greenhouse bench from about 6 inches to 4 inches. To test the effect of soil depth, Grower's Soils A and B were replicated once in the north bench in each compartment, and one of the two plots reduced to a depth of 4 inches, while the other was left at a depth of 8 inches (Fig. 1). CSU Old and New soils were 8 inches deep.

Figure 1: Plot locations in the CSU temperature house.



1. SOIL A-4"
2. SOIL A-8"
3. CSU OLD
4. CSU NEW
5. SOIL B-4"
6. SOIL B-8"
7. SCORIA-IDEALITE

Various inert media were being tested in the south beds of each compartment during this investigation. To act as a check, one plot from each compartment, consisting of a volcanic ash (Scoria) and a synthetic clay aggregate (Idealite) mixed in a 1:1 ratio, were selected.

Cultural practice -- Plant material was Dianthus caryophyllus, cv "CSU Red" in the soil plots and "Pink Coquette" in the Scoria-Idealite treatments. Disease-free cuttings, selected for uniformity, were obtained from the CSU clean stock program. All plots were steamed, and the cuttings planted direct from the propagating bed on June 26, 1966, at a 6- X 8-inch spacing, 18 plants per plot.

All soil plots were watered simultaneously by a peripheral sprinkler system when any plants in the 4-inch soil depths showed signs of wilting in the morning. Records were kept of the irrigation frequency. Tensiometers were placed in the 4-inch soil A plots in each compartment to indicate approximate soil suction. Nutrients were automatically injected into the water line during each irrigation at the following approximate concentrations (55): N-125, P-15, K-97, and B-1 ppm. Periodic soil tests were made and dry fertilizers were added to ensure adequate nutrient levels as indicated below:

1. 1 lb. K_2SO_4 per 100 sq. ft. on all soil plots February 1, 1967, and March 8, 1967
2. 5 lbs. lime per 100 sq. ft. on plots A6, B6, C6, and D6 February 12, 1967, and March 8, 1967
3. 1 lb. treble superphosphate per 100 sq. ft. on plots A1, B1, C1, and D1 February 12, 1967, and March 8, 1967

The Scoria-Idealite plots were irrigated automatically with a peripheral sprinkler system and the same nutrient solution. Beginning on June 26, 1966, the irrigation intervals were at 8:00 a.m., 12:00 noon, and 3:00 p.m., each cycle for 2½ minutes. This was dropped to two cycles on July 14 at 8:00 a.m. and 2:00 p.m., and finally to one 8:00 a.m. irrigation August 1 to completion of the experiment.

The terminal shoots of all plants were removed in the period June 14 to 21 to hasten the development of side shoots. A sterilized leaf mulch was added to the soil plots on August 8, 1966.

Part 2. Plant and Soil Measurements

General yield was recorded for each treatment as the total weekly number of flowers cut from the start of flowering October 10, 1966, to April 29, 1967.

Mean grade was determined on a weekly basis from all flowers cut. Grading was based on the Colorado State University grading system which comprises four grades:

1. Fancy - all flowers 24 inches long and a minimum weight of 25 g.
2. Standard - all flowers 20 inches long and a minimum weight of 20 g.
3. Short - flowers less than 20 inches long or a weight less than 15 g.
4. Design - all malformed flowers and those not meeting the above specifications (44).

The mean grade was calculated by assigning each grade, beginning with fancy, the numerical values of 5, 4, 3, and 2.

Cut flower life was measured on 4- and 8-inch plots. Samples of eight flowers from both depths were placed in warm water after cutting, and preconditioned at 33° for 24 hours. The flowers were removed, placed in a Cornell solution[1], and into a keeping chamber held at 70° F ±1°. The keeping of each flower was considered finished when the petal edges and flower color darkened. One day was subtracted from the actual number of days the flower was in the keeping room to arrive at total keeping life.

Height of plants was measured in all plots 12 weeks (September 19) after being benched. The top carnation leaves on 20 shoots on each plot were extended vertically, and shoot length measured from the tip of the highest leaf to the junction of the branch and main stem.

Solar radiation was measured at periodic intervals with calibrated silicon solar cells, expressed as gm-cal cm^{-2}.

Soil moisture release curves were determined for the four soils by the pressure plate membrane technique (84). Undisturbed core samples from soil plots in D compartment were used for suction levels from 10 cm water to 1 A.

Part 3. Transpiration and Stomatal Measurements

Preliminary experimentation with several methods used to measure transpiration, and indicate plant water stress, included the electric hygrometer with a lithium chloride sensor, pressure porometer, relative turgidity, and stomatal apertures. The electric hygrometer

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[1]Cornell solution consisting of 100 ppm oxyquinoline, 50 ppm silver acetate, and 5% sugar.

was selected as the method most feasible for use in the greenhouse. The study also indicated that the best place to obtain reasonably consistent readings was at the top of the plant, top of the leaf. The third leaf pair from the top was used for all measurements, since the leaves at this position were the first of sufficient size.

Transpiration -- The electric hygrometer was constructed (Fig. 2) according to Van Bavel, et al. (108). The narrow range humidity sensor was a Hygrodynamic Hygrosensor[2] #4-4832 type TH with an effective range of 18 to 33% relative humidity at 80° F. Because of the narrow, linear dimensions of the carnation leaf, the leaf cup was modified by reducing the aperture to 1.0 X 1.7 cm.

The following procedure was used in taking measurements for all experiments. Before clamping the cup onto the leaf, the cup chamber was purged with dry air, until a reading of less than 3 ua was obtained. The cup was always placed across the middle of the leaf, the time required for current to increase from 3 ua to 6 ua was measured and this designated as transit time ($\triangle t$). All measurements are expressed as $\triangle t$ which was the time required for a definite relative humidity change in the leaf cup, and was a direct measurement of transpiration (105). Six readings were taken per plot, with measurements limited to plants on the inside rows.

Determinations -- Hygrometer measurements on soil plots started one day after watering. They were taken on all soil plots and the

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[2]The manufacturer's name is included for the benefit of the reader and does not infer any endorsement of the product.

Figure 2: Leaf resistance meter and associated equipment.


AC RESISTANCE METER
RESISTANCE METER LEAF CUP
VOLTAGE SUPPLY
LEAF CUP PURGING APPARATUS

Scoria-Idealite plot in a particular compartment during the following periods:

1. Ten a.m. MST, September 27 to October 5, 1966, in compartment D.
2. At 9:00 a.m. and 1:00 p.m. MST in compartment D from March 21 to March 26, 1967.
3. At 10:00 a.m. MST, June 17 to June 23, 1967, with soil B at both 4- and 8-inch depths, Scoria-Idealite and CSU Old in compartments A, B, C, and D.
4. At hourly intervals between 7:00 a.m. and 4:00 p.m. in compartment D on April 3, 1967.

Stomatal apertures were measured as described by Sampson (88). A fluid silicon rubber, mixed with a curing agent was spread over 5 to 6 cm^2 of upper leaf surface. After setting 3 to 5 minutes, it was peeled off to provide an imprint of the leaf surface. Clear fingernail polish was applied to the rubber strip and allowed to dry. The dried colloid strip was peeled off and examined under the microscope. Stomatal apertures were measured perpendicular to the length of the opening at the widest dimension.

Measurements of stomatal apertures were made on all soil plots in compartment D. Plants were watered September 26 and rubber impressions taken September 27 to October 5, 1966, at 10:00 a.m. MST.

Stomatal frequency on the upper surface of carnation leaves was studied under low solar radiation, comparing all soil plots and Scoria-Idealite in D compartment on February 8, 1967. The same study was conducted under high solar radiation utilizing the previously

mentioned plots in all compartments on June 12. The same leaf position and area of leaf, as used in hygrometer measurements, were utilized. The upper epidermal layer of 14 leaves from each plot was peeled off and placed on a slide. Water and a cover slip were added. The number of stomata and epidermal cells were counted in a 0.5 mm^2 area.

Chapter IV

RESULTS

The results are presented in four parts: 1) soil moisture relationships, 2) plant response, 3) distribution of stomatal and epidermal cells, and 4) transpiration measurements. Complete statistical analyses are given in the Appendix.

Part 1. Soil Moisture Relationships

The four soils employed in this study were found to differ in the amount of moisture retained at nearly all suctions (Table 1).

Table 1. Bulk density and comparison of soil moisture content at various suction levels expressed as the number of grams water per gram dry weight soil.

Soil type	Bulk density		Suction - bars							
			15	10	5	1	.67	.33	.10	.02
Soil B	.68	g/g	.15	.16	.18	.25	.27	.31	.38	.43
Soil A	.70	g/g	.13	.13	.15	.21	.24	.26	.36	.46
CSU Old	.80	g/g	.13	.13	.15	.20	.21	.26	.30	.35
CSU New	1.06	g/g	.10	.11	.12	.16	.17	.19	.25	.28

Soil moisture retention curves as a percent of dry weight are shown in Fig. 3. Fig. 4 presents the same curves plotted logarithmically and extrapolated to 0.01 bar, the theoretical moisture content in the upper soil surface when the soil depth is 4 inches deep and at

Figure 3: Soil moisture retention curves expressed as percent dry weight.

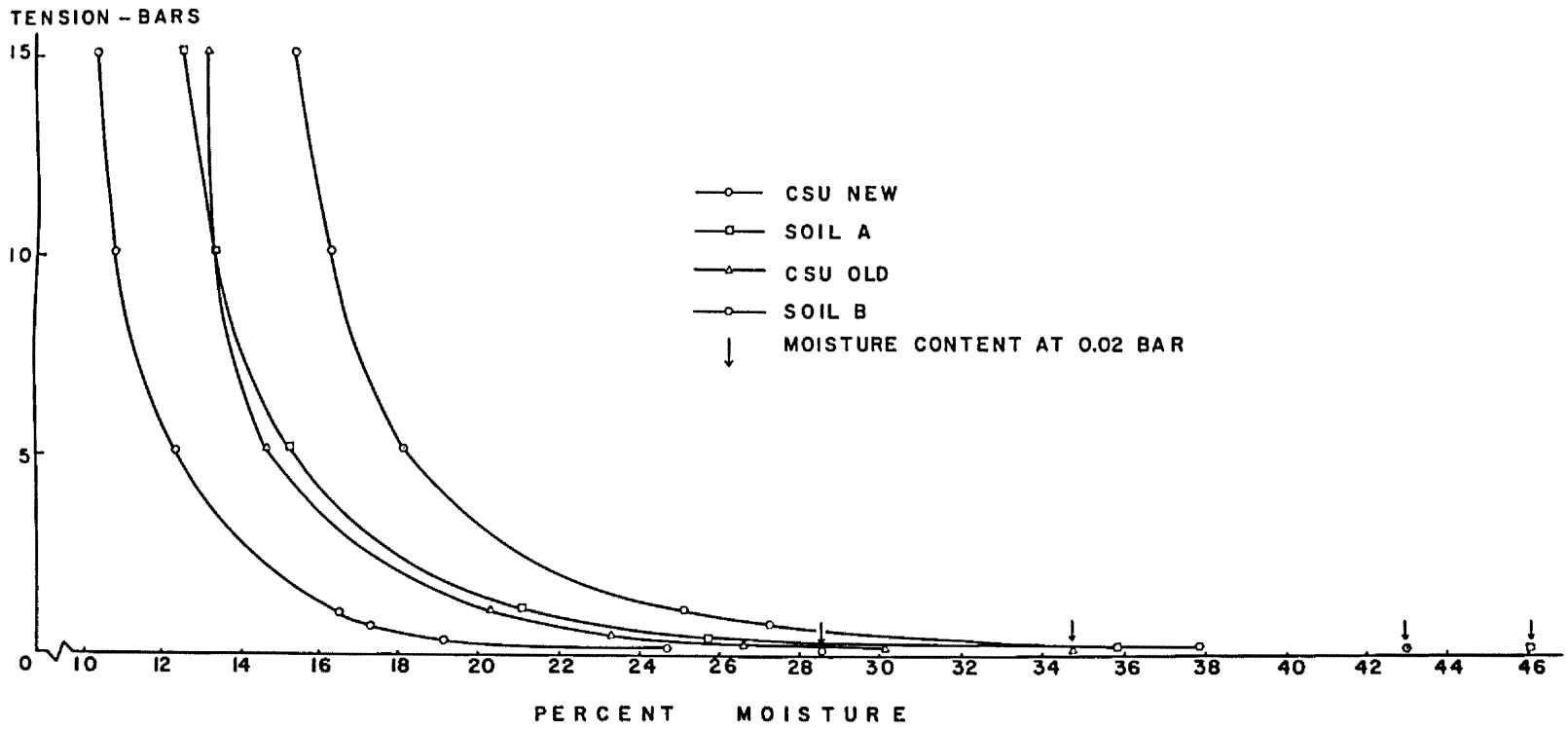
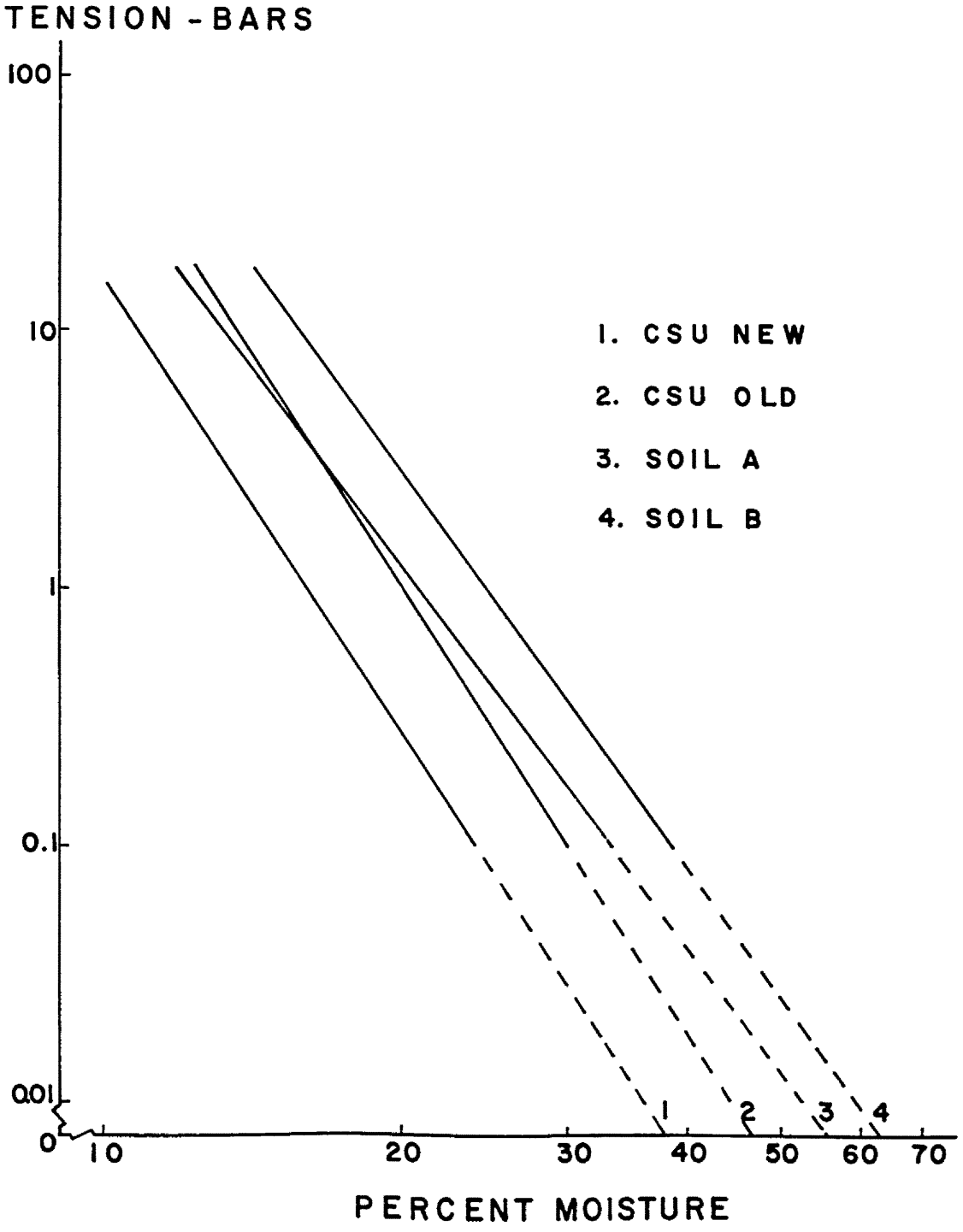

TENSION - BARS
15
10
5
0
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
46
PERCENT MOISTURE
CSU NEW
SOIL A
CSU OLD
SOIL B
MOISTURE CONTENT AT 0.02 BAR

Figure 4: Logarithmic expression of soil moisture retention as percent dry weight.


TENSION - BARS
100
10
1
0.1
0.01
0
10
20
30
40
50
60
70
PERCENT MOISTURE
1. CSU NEW
2. CSU OLD
3. SOIL A
4. SOIL B
1
2
3
4

equilibrium. Undisturbed soil cores taken at equilibrium after irrigation showed moisture contents less than the theoretical (Table 2). However, the extrapolated values indicate the maximum

Table 2. Suction levels and water content on a percent dry weight basis in all soil plots before and after watering.

Plot	Before watering		After watering		Percent moisture difference
	Suction bars	Percent moisture	Suction bars	Percent moisture	
Soil B-4"	15+	12.5	0.01	45.8	33.3
CSU New	9.8	10.8	0.02	28.5	17.7
Soil A-4"	9.3	13.7	0.01	49.3	35.6
CSU Old	5.4	14.4	0.02	34.7	20.3
Soil B-8"	2.6	21.0	0.02	42.9	21.9
Soil A-8"	2.0	18.0	0.02	46.0	28.0

moisture holding capacity of the various soils if entrapped air had not influenced the results. Table 1 shows the bulk density of the different soils with soil B having the lowest and CSU New soil the highest values.

The determination of moisture retention-suction values showed distinct differences between all soil plots. At all suctions, CSU New soil contained less moisture than any of the other three soils. It was also observed to have a low organic matter content compared to the other soils. Grower's soil B had the highest moisture content between 0.1 and 15 bars suction. However, soil A had the highest and CSU New soil the lowest moisture content of all soils when the bench was watered after a drying cycle. Soils A-4", B-4", and CSU New had

the highest soil suction and the lowest moisture content before watering. In contrast, soils A-8", B-8", and CSU Old had lower values of soil suction and a higher water content. In comparing 8- and 4-inch soil depths, the total water content in a given plot was less in the 4-inch than 8-inch depths, even though the 4-inch plots were initially wetter after watering.

Part 2. Plant Response

Carnations exhibited statistically significant differences in response as the result of substrate treatment (Table 3). CSU Old, soil A-8", and soil B-8" had the highest yield and mean grade, as defined in Chapter III, of all plots (Figs. 5-8, Table 4). In comparing soils A-8", A-4", and B-8", B-4", total yield and mean grade were highest for plants grown in 8-inch deep media. As seen in Figs. 5 and 6, plants grown in inert media, and watered daily, produced flowers one week earlier during the first crop than plants grown in soil. On the second crop, production in the inert media was less than the three highest producing soil treatments. However, total yield differences between Scoria-Idealite, B-8", A-8", and CSU Old were not statistically significant. The flowers grown on Scoria-Idealite plots were observed to be brittle after the first crop was cut with a relatively high proportion of design grade resulting from numerous "splits" (flowers with split calyxes). Solar radiation was the lowest of the year at this time and total vegetative surface area was decreased due to flower removal. Flowering of the second crop in 4-inch plots was delayed 5 weeks and had a lower total yield than the plants in corresponding soils at 8-inch depths (Fig. 5). Carnations

Table 3. Summary of production by compartment of "CSU Red" on all soil plots and "Pink Coquette" on Scoria-Idealite October 10, 1966, to April 29, 1967.

	Total yield	Flowers/ sq. ft.	Mean grade	Percent distribution of grade			
				Fancy	Standard	Short	Design
Compartment A							
Soil A-4"	180	25.7	3.96	45.0	13.9	33.3	7.8
Soil B-4"	201	28.7	4.02	47.8	14.9	28.8	8.5
CSU New	217	31.0	4.20	49.8	28.1	14.7	7.4
Soil B-8"	237	33.9	4.51	61.2	30.0	8.0	0.8
CSU Old	248	35.4	4.43	57.7	30.6	8.5	3.2
Scoria-Idealite	260	37.1	4.15	40.8	42.3	8.1	8.8
Soil A-8"	264	37.7	4.29	58.0	16.3	22.3	3.3
Compartment B							
CSU New	202	28.9	4.24	53.5	21.3	20.8	4.4
Soil A-4"	214	37.0	4.00	50.0	10.8	28.0	11.2
Soil B-4"	214	30.6	4.03	41.1	26.7	27.1	5.1
Scoria-Idealite	231	33.0	4.05	36.4	45.4	5.2	13.0
CSU Old	243	34.7	4.47	60.9	29.6	5.4	4.1
Soil B-8"	259	37.0	4.39	57.1	28.2	10.8	3.9
Soil A-8"	291	41.6	4.44	61.5	23.4	13.0	2.1
Compartment C							
Soil A-4"	203	29.0	4.33	53.2	27.6	18.7	0.5
Scoria-Idealite	215	30.7	4.18	40.5	44.7	7.4	7.4
CSU New	216	30.9	4.19	48.2	26.4	22.2	3.2
Soil B-4"	218	31.1	4.13	47.2	23.4	24.8	4.6
Soil A-8"	220	31.4	4.35	51.8	33.6	12.3	2.3
CSU Old	244	34.9	4.45	59.9	29.5	6.1	4.5
Soil B-8"	253	36.1	4.38	57.3	26.1	13.4	3.2
Compartment D							
Soil A-4"	216	30.9	3.95	36.6	31.5	22.7	9.2
Scoria-Idealite	223	31.9	4.25	43.9	44.8	3.6	7.7
CSU New	232	33.1	4.15	45.3	30.6	17.7	6.4
Soil B-4"	238	34.0	4.09	42.9	27.3	26.0	3.8
Soil A-8"	271	38.7	4.38	57.6	26.9	11.8	3.7
Soil B-8"	283	40.4	4.39	55.5	30.7	11.0	2.8
CSU Old	317	45.3	4.59	64.7	30.6	3.5	1.2

Figure 5: Effect of soil type and depth on the total number of carnation flowers produced weekly. Start of flowering October 3, 1966.

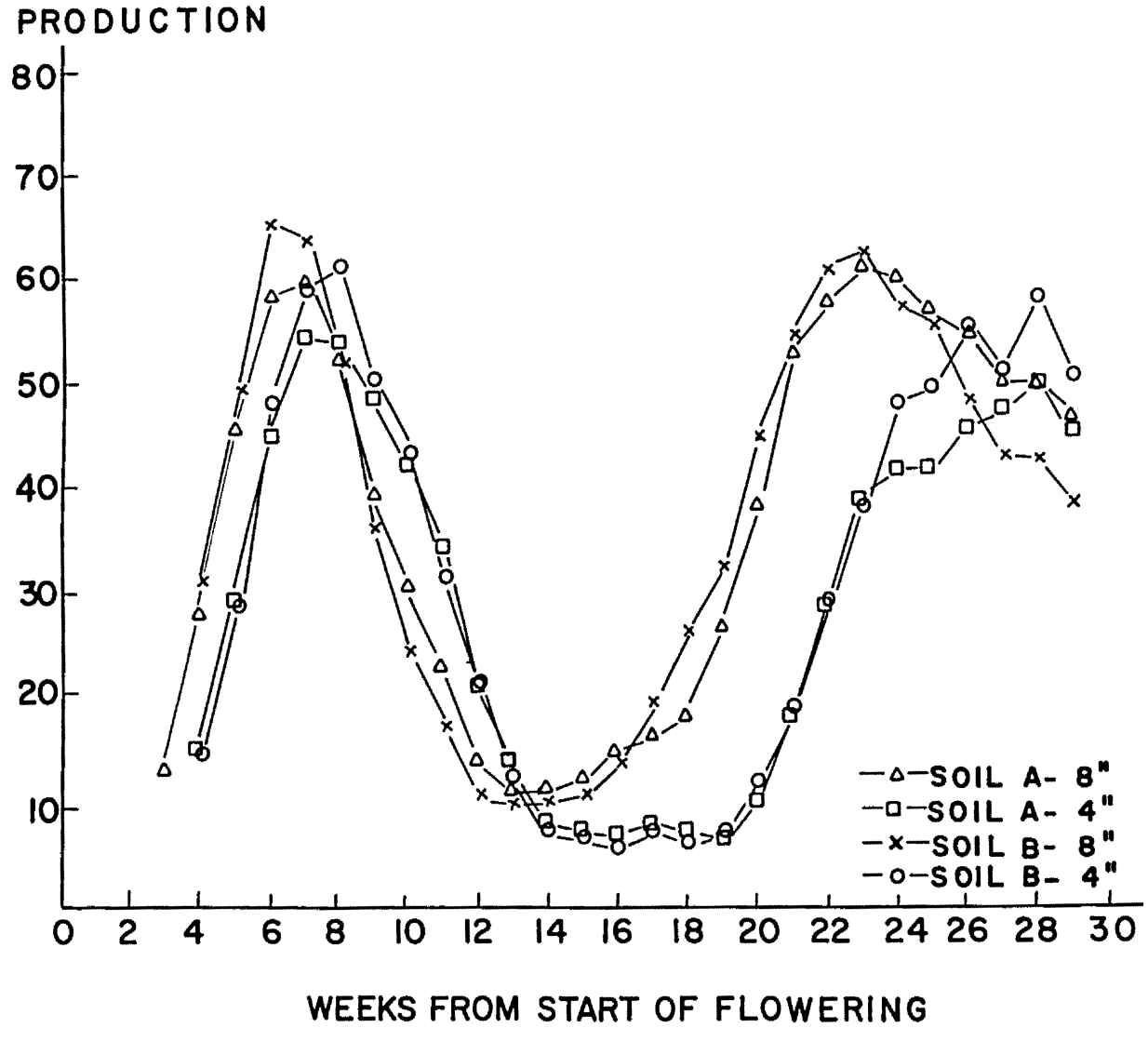

PRODUCTION
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
WEEKS FROM START OF FLOWERING
—△—SOIL A- 8"
—□—SOIL A- 4"
—×—SOIL B- 8"
—○—SOIL B- 4"

Figure 6: Effect of CSU Old, CSU New, and Scoria-Idealite on the total number of carnation flowers produced weekly. Start of flowering October 3, 1966.

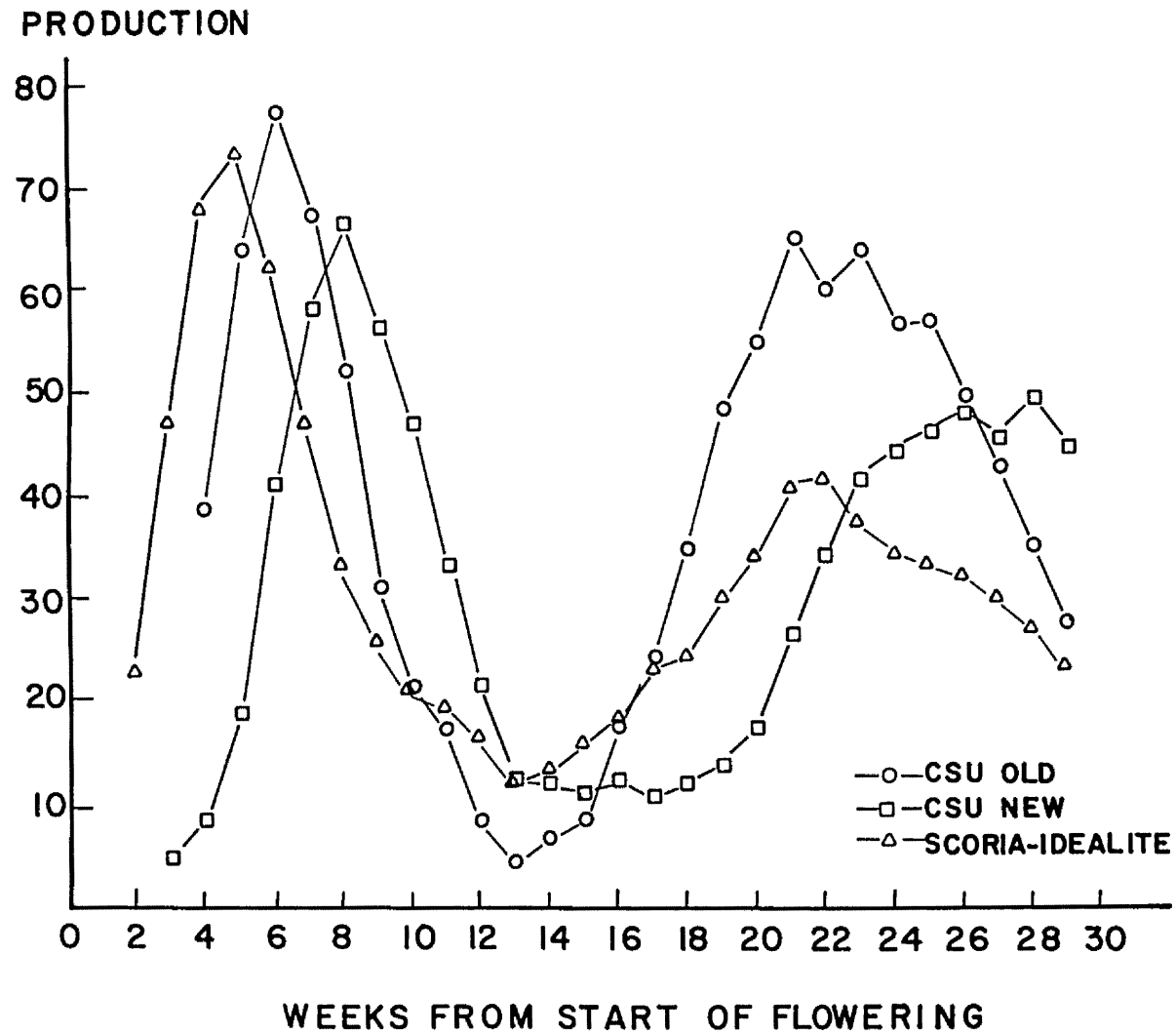

PRODUCTION
80
70
60
50
40
30
20
10
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
WEEKS FROM START OF FLOWERING
—o—CSU OLD
—□—CSU NEW
—△—SCORIA-IDEALITE

Figure 7: Effect of soil type and depth on weekly mean grade of carnations. Start of flowering October 3, 1966.

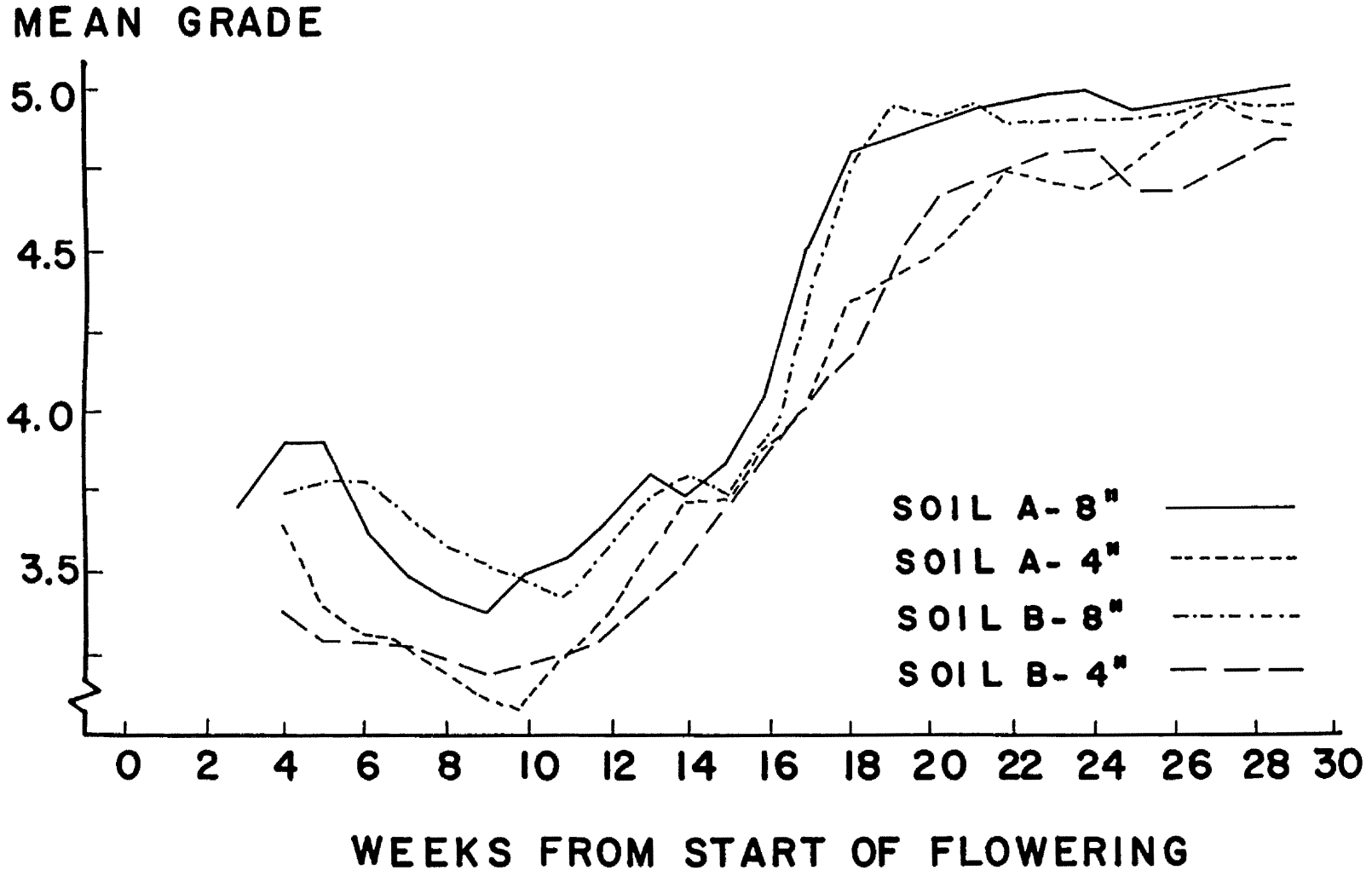

MEAN GRADE
5.0
4.5
4.0
3.5
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30
WEEKS FROM START OF FLOWERING
SOIL A- 8"
SOIL A- 4"
SOIL B- 8"
SOIL B- 4"

Figure 8: Effect of CSU Old, CSU New, and Scoria-Idealite on weekly mean grade of carnations. Start of flowering October 3, 1966.

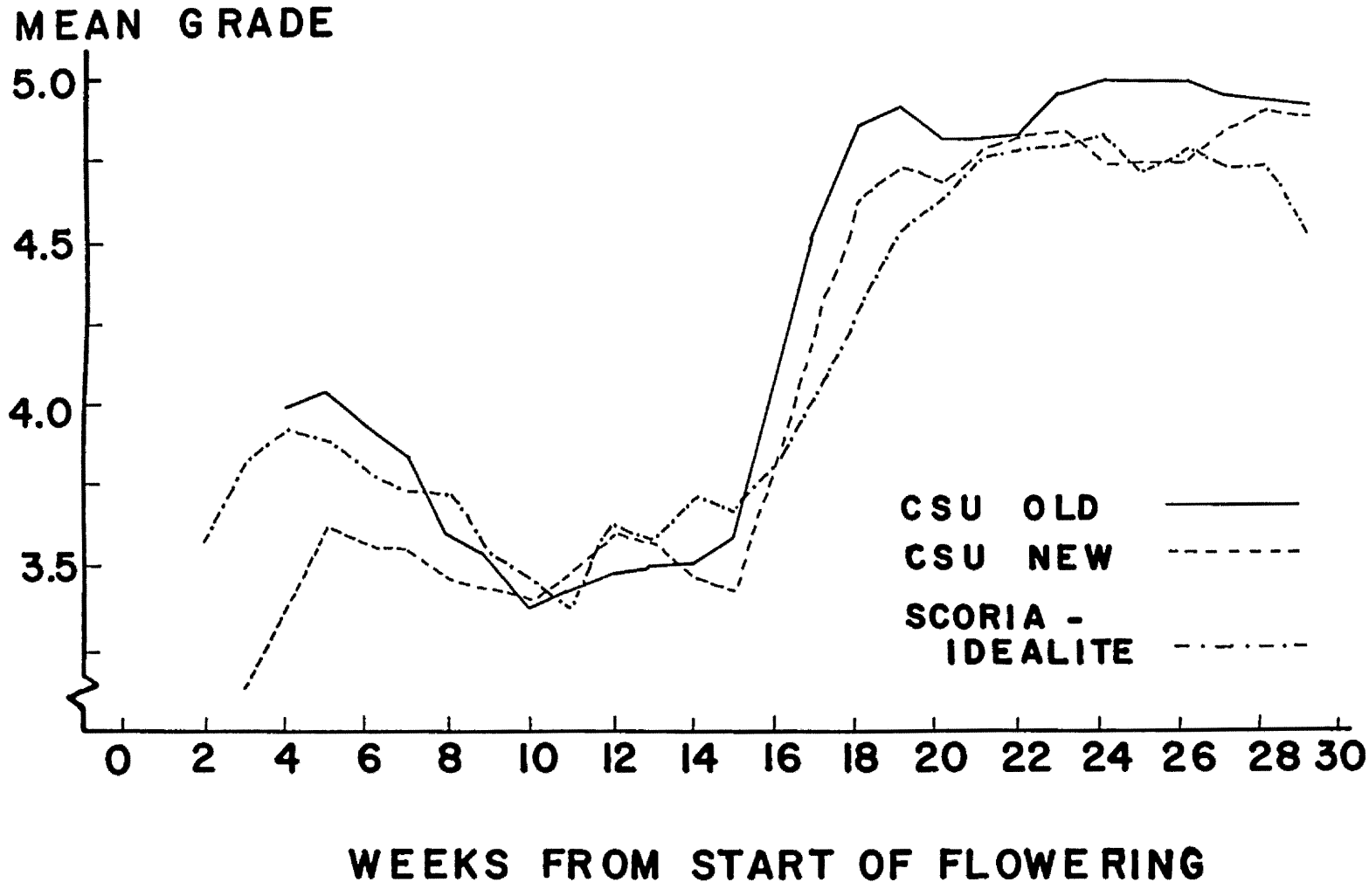

MEAN GRADE
5.0
4.5
4.0
3.5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
CSU OLD
CSU NEW
SCORIA - IDEALITE
WEEKS FROM START OF FLOWERING

Table 4. Summary of production of "CSU Red" on all soil plots and "Pink Coquette" on Scoria-Idealite, October 10, 1966 to April 29, 1967. Horizontal lines indicate non-significance.

	CSU Old	Soil A-8"	Soil B-8"	Scoria-Idealite	Soil B-4"	CSU New	Soil A-4"	LSD 5% level
Total number flowers produced	1,054	1,046	1,032	929	871	867	813	178.0
Flowers per sq. ft.	37.6	37.4	36.9	33.2	31.0	31.0	29.0	
Mean grade	4.49	4.37	4.32	4.15	4.07	4.19	4.06	0.18
Percent distribution of grade								
Fancy	60.9	57.6	57.7	40.3	44.7	49.0	46.1	
Standard	29.7	24.7	28.8	44.2	23.3	26.8	21.2	
Short	5.9	14.8	10.8	6.1	26.6	18.8	25.4	
Design	3.5	2.9	2.7	9.4	5.4	5.4	7.3	

grown in soil A-4" had the lowest total yield and mean grade of all media, while CSU New soil had the lowest total yield and mean grade of all 8-inch plots (Table 4). During the initial stages of growth, chlorosis occurred on plants grown in CSU New soil, but this later disappeared after the plants had grown and the irrigation interval had been increased. Daily solar radiation also decreased during this period.

There were slight differences in mean grade and yield due to the type of greenhouse cover (Figs. 9 and 10), which were not statistically significant. The first crop peaked at the same time in all compartments. However, compartment D had the highest and earliest peak for the second crop, followed closely by compartment B. It also had the highest total production of all compartments to the end of April (Table 5). Second crops in compartments A and C were

Table 5. Summary of production of "CSU Red" October 10, 1966, to April 29, 1967, between compartments.

	Compartment			
	A	B	C	D
Total number flowers produced	1,347	1,423	1,354	1,557
Flowers per sq. ft.	32.1	33.9	32.2	37.1
Mean grade	4.26	4.28	4.31	4.29
Percent distribution of grade				
Fancy	53.9	54.7	53.2	51.7
Standard	22.7	23.6	27.8	29.6
Short	18.5	16.8	16.0	14.5
Design	4.9	4.9	3.0	4.2

Figure 9: Effect of cover on total number of carnation flowers produced weekly. Start of flowering October 3, 1966.

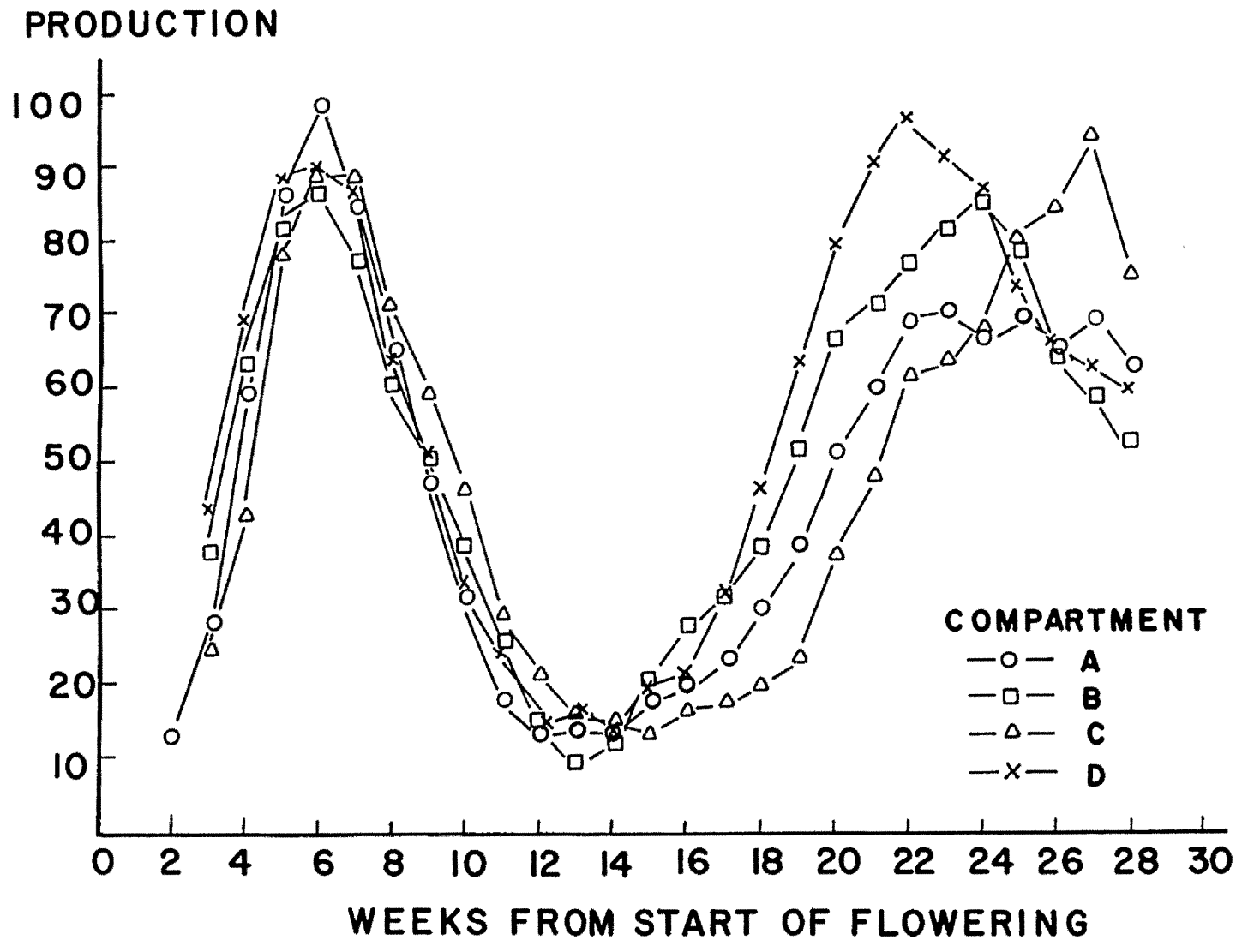
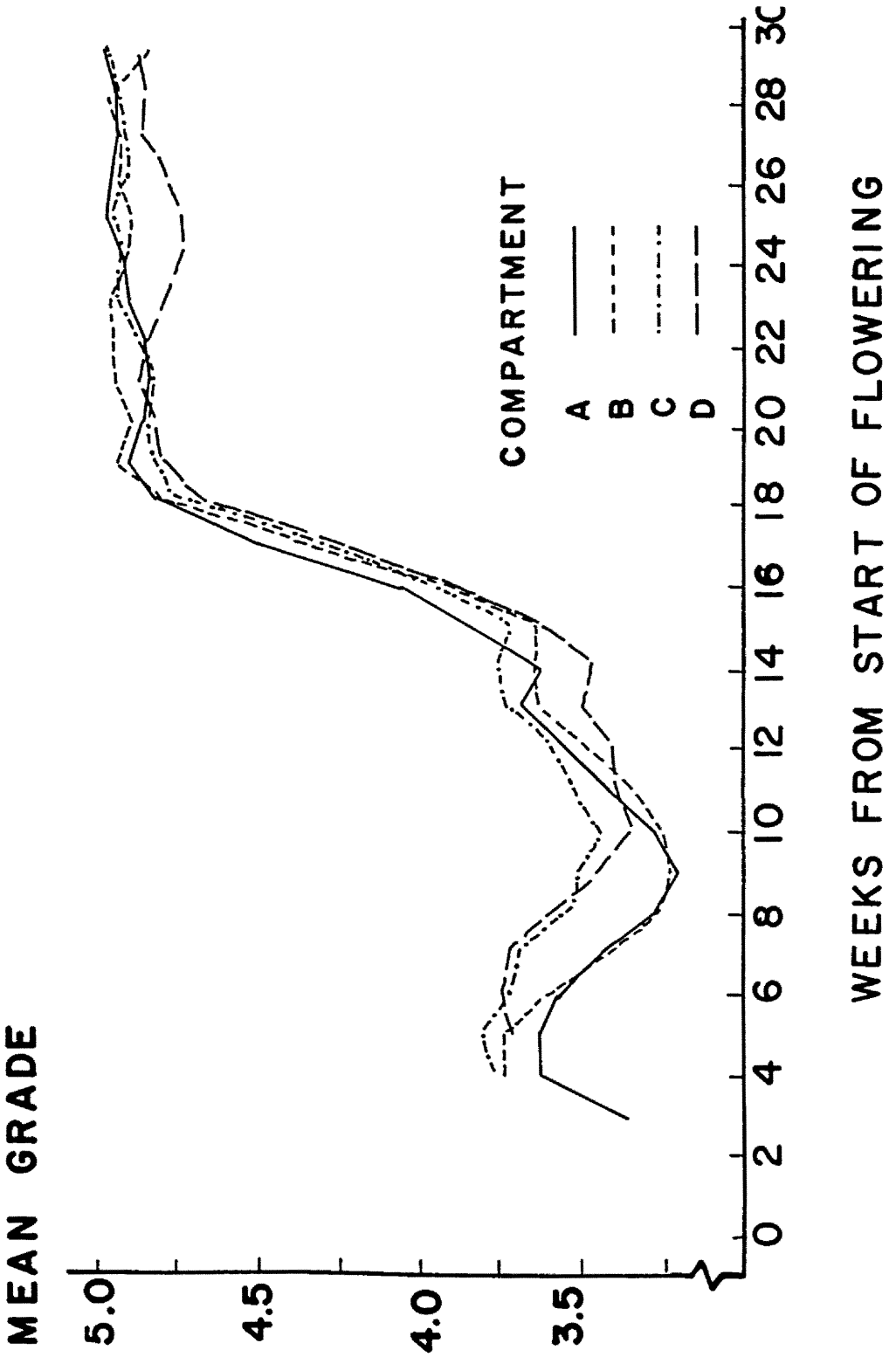

PRODUCTION
100
90
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
WEEKS FROM START OF FLOWERING
COMPARTMENT
A
B
C
D

Figure 10: Effect of cover on weekly mean grade of carnations.
Start of flowering October 3, 1966.


MEAN GRADE
5.0
4.5
4.0
3.5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
WEEKS FROM START OF FLOWERING
COMPARTMENT
A
B
C
D

extended and delayed. By the end of April, yield from these two compartments was below that from B and D.

Plant heights measured September 19, 12 weeks after planting, varied according to treatment (Fig. 11). These differences were readily observable, but due to the variation were not mathematically significant. However, there was a statistically significant cover effect. Compartment A was found to have the highest average plant growth followed by compartments B, D, and C in descending order. Variation in keeping life was not significant although the keeping life of flowers produced in the 8-inch treatments averaged 0.5 day longer than those grown in the 4-inch plots.

Part 3. Stomatal and Epidermal Cell Distribution

Stomata were found to vary in their distribution on the leaf surface from relatively few near the midvein (Fig. 12) to more numerous near the margins (Figs. 15 and 17). They were present on both surfaces of the leaf and sunken below the cuticle (Figs. 13 and 14). While cross-sections of leaves from various treatments were not examined, surface photographs (Figs. 15-18) indicated considerable differences. Stomata from plants in the 4-inch treatments appeared to have a greater amount of cutin deposited about the stomata, and the stomata also appeared to be set deeper within the leaf itself. Epidermal cells were smaller, with stomata more frequent on leaves of plants subjected to greater soil moisture stress (4-inch depths).

A relationship was found to exist between the number of stomata, epidermal cells and their size. Plants grown in inert media had

Figure 11: Effect of root substrate on average plant height.

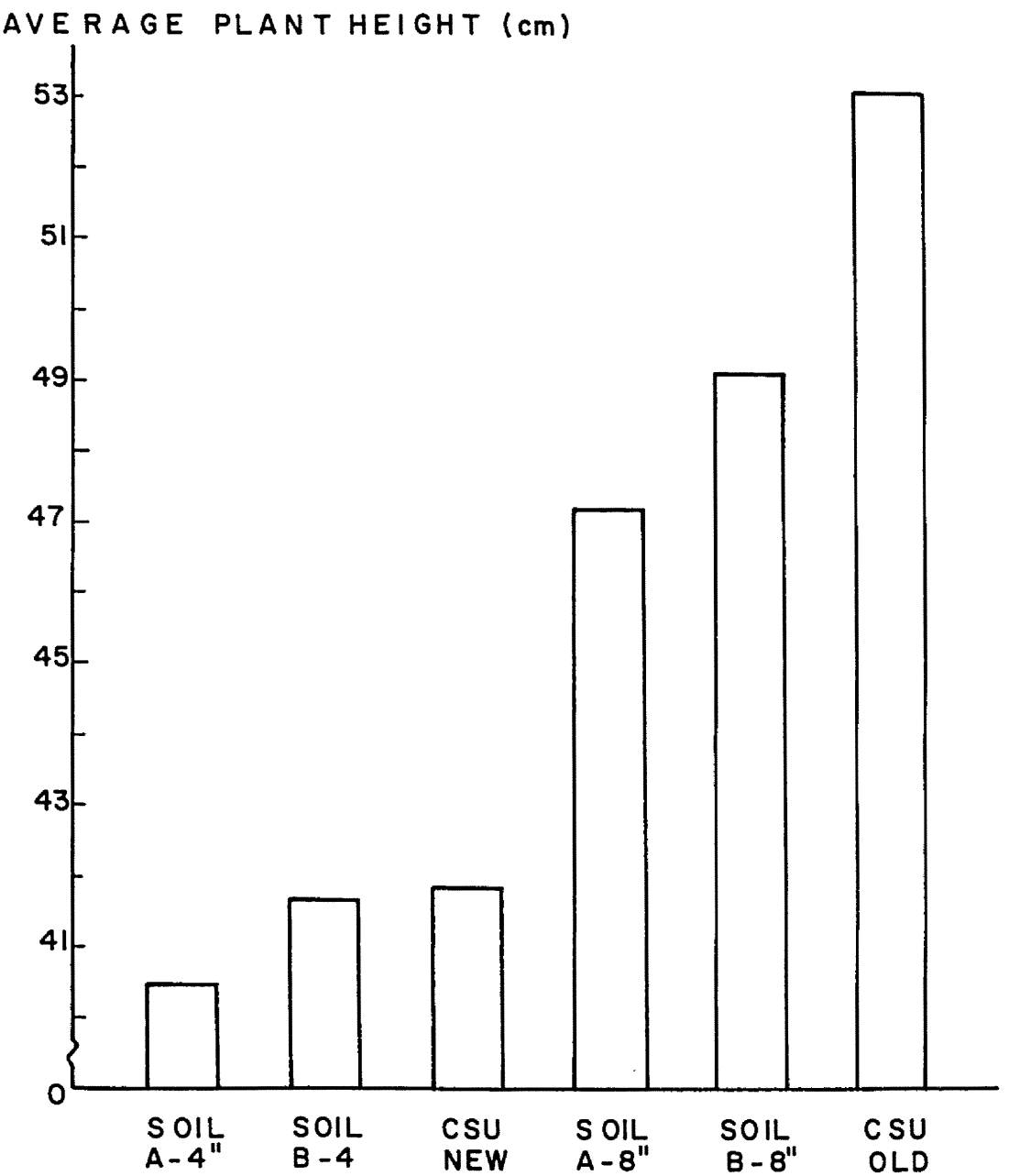
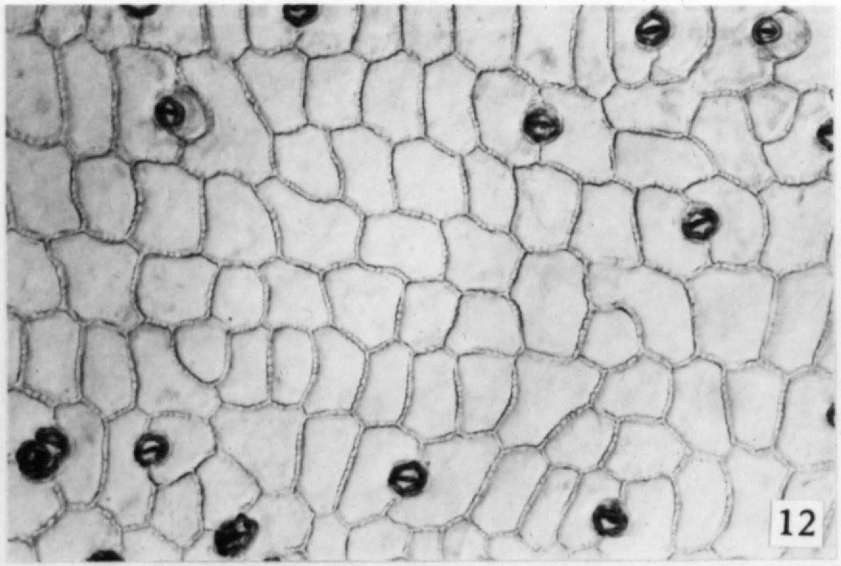
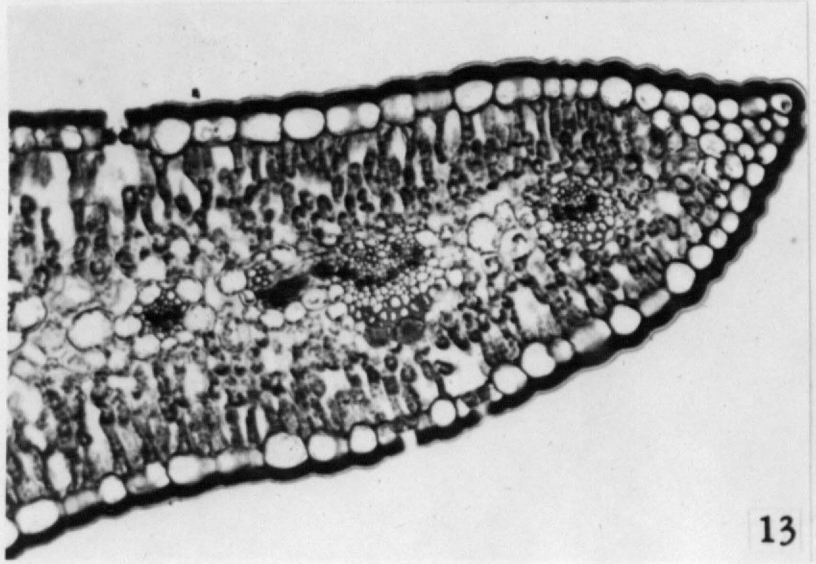

AVERAGE PLANT HEIGHT (cm)
53
51
49
47
45
43
41
0
SOIL A-4"
SOIL B-4
CSU NEW
SOIL A-8"
SOIL B-8"
CSU OLD

Figure 12: Upper epidermis of carnation leaf showing stomata distribution in the region of the midvein. X145.

Figure 13: Carnation leaf in transverse section showing stomata on both upper and lower surfaces. X145.

Figure 14: Enlargement of upper epidermis. Note sunken stomata and thick cuticle layer. X636.


12


13

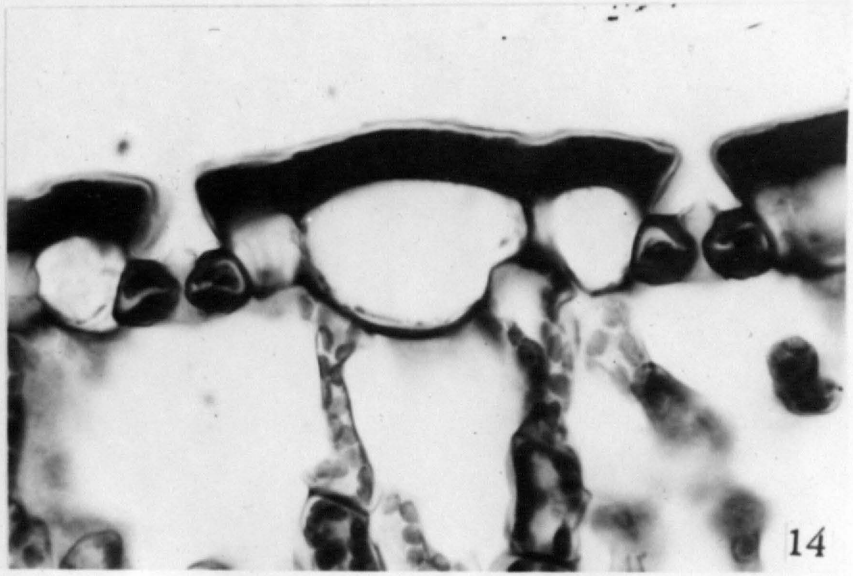
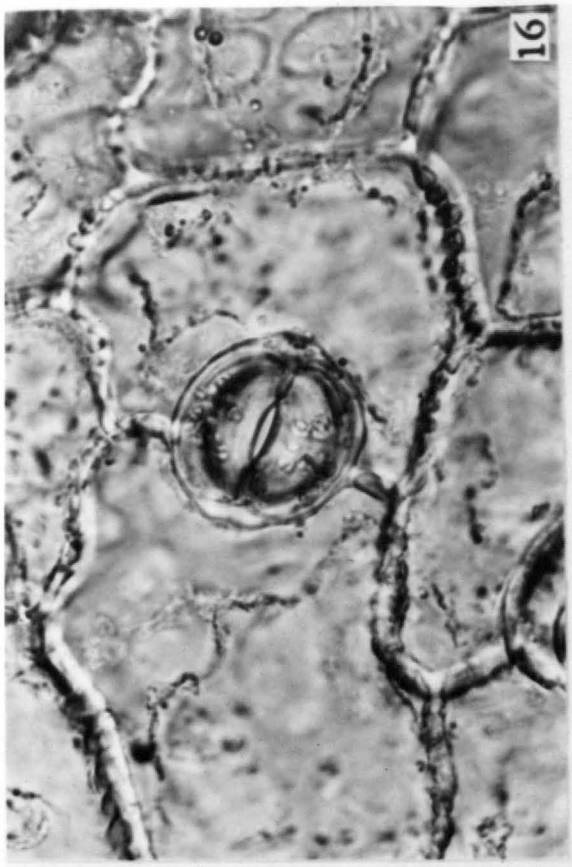

14

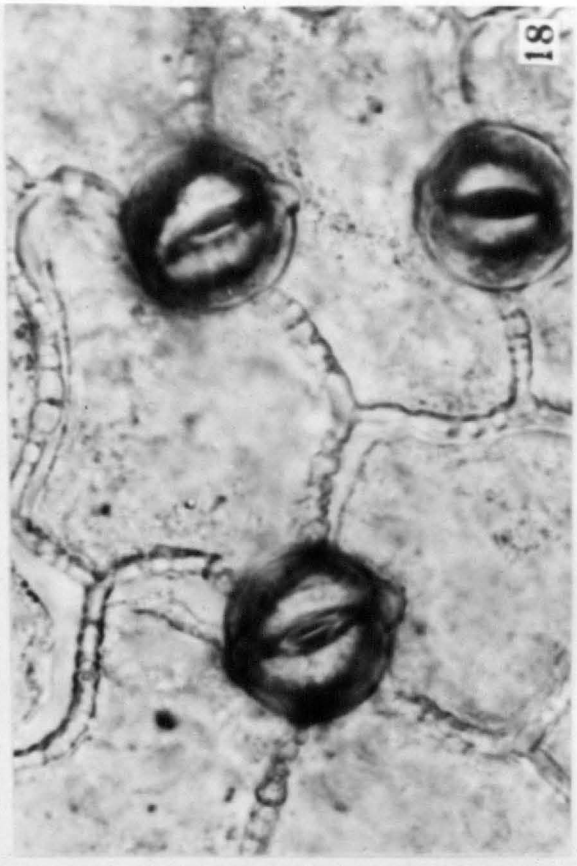
Figure 15: Upper epidermis of carnation leaf from a plant grown in Scoria-Idealite. X145.

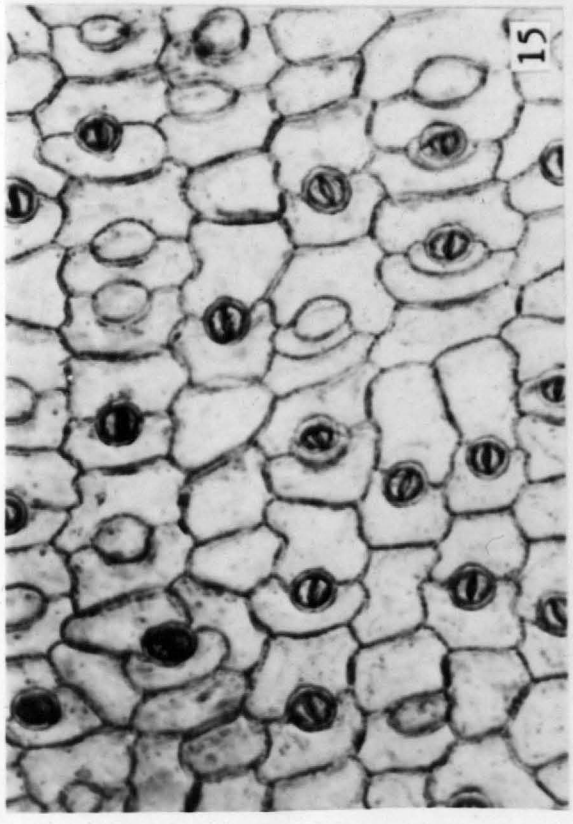
Figure 16: Enlargement of Figure 15. X636.

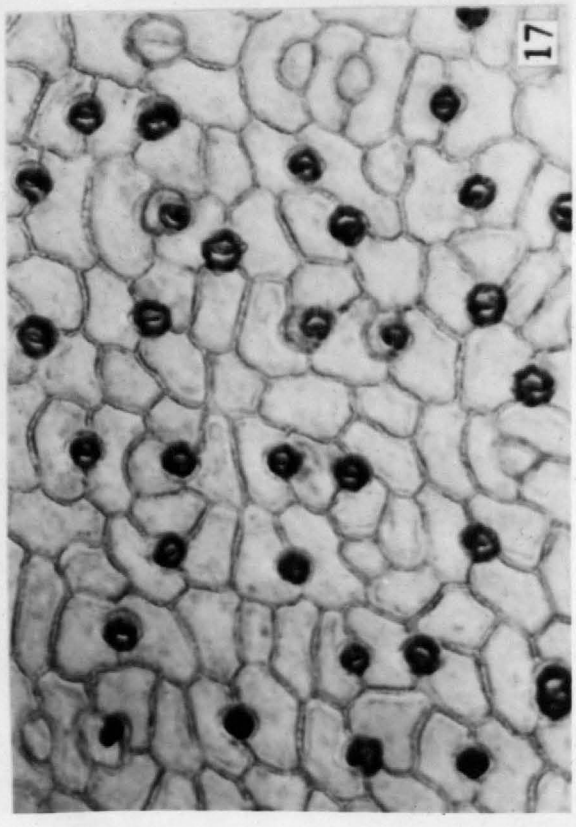
Figure 17: Upper epidermis of carnation leaf from a plant grown in soil A-4". X145.

Figure 18: Enlargement of Figure 17. X636.


16


18


15


17

larger epidermal cells and fewer stomata per unit area (Table 6).

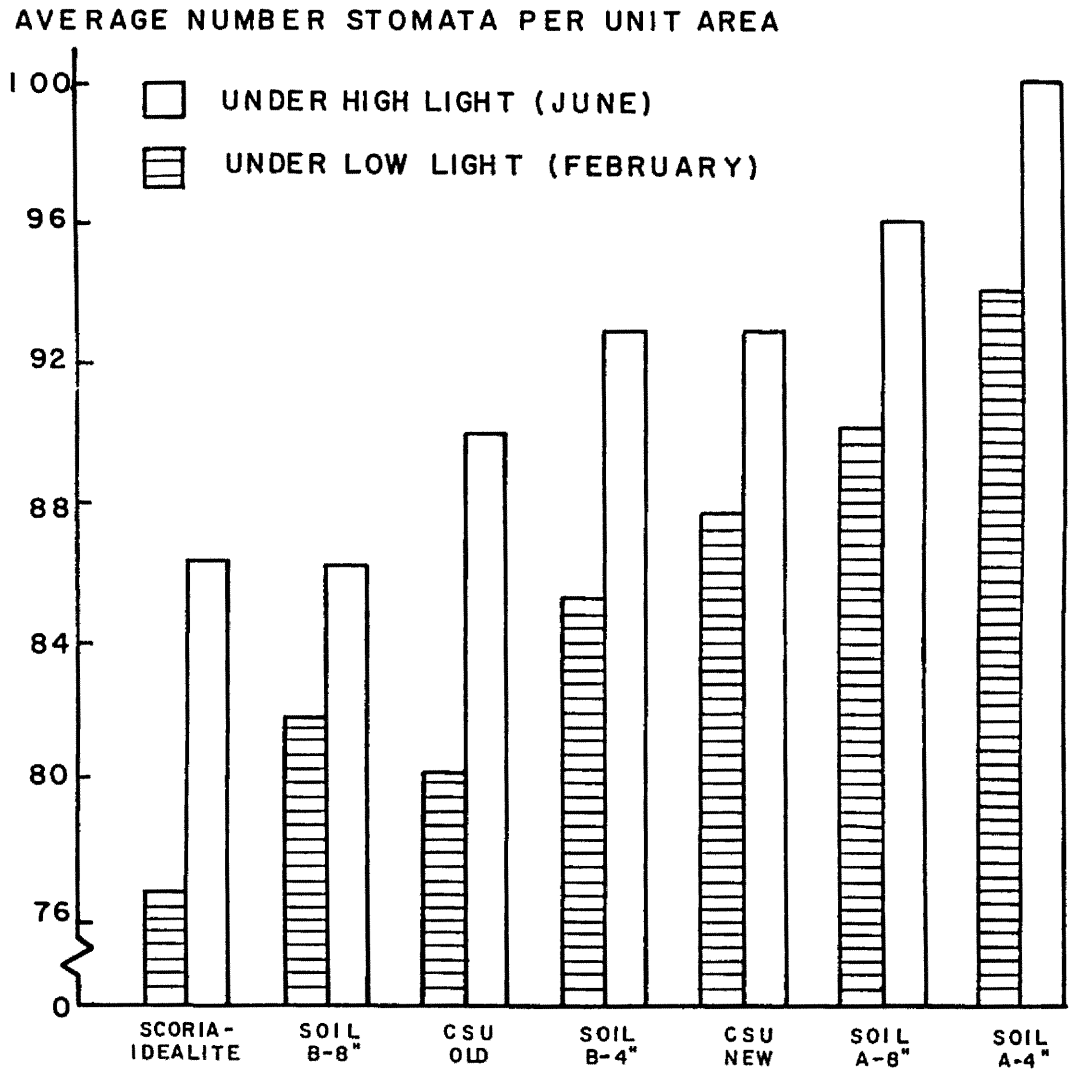
Table 6. Summary of stomatal and epidermal cell frequency per mm^2, stomatal index and number of stomata per leaf area sampled by the hygrometer leaf cup on all soil plots and Scoria-Idealite.

Soil type	Number of stomata per mm^2	Number of epidermal cells per mm^2	Stomatal index (I)*	Mean number of stomata in area covered by leaf cup
Scoria-Idealite	77.8	227.0	23.9	13,226
Soil B-8"	82.0	230.3	26.3	13,932
CSU Old	82.4	236.8	25.8	14,008
CSU New	85.8	248.0	25.7	14,578
Soil A-4"	87.1	252.7	25.6	14,199
Soil A-8"	87.6	248.2	26.1	14,892
Soil B-4"	87.7	253.4	25.7	14,909
LSD 5% level	1.5	3.3		

$$*I = \frac{\#\text{ stomata per mm}^2}{\#\text{ stomata} + \#\text{ epidermal cells per mm}^2}$$

Plants grown in 4-inch plots had the opposite relationship. The differences between treatments as to number of stomata and epidermal cells on the upper leaf surfaces of carnation plants were statistically significant. Cover also effected the stomatal-epidermal cell relationship (Table 7); as did solar radiation (Fig. 19). Plants grown under high solar energy conditions, eventually produced leaves having more stomata and epidermal cells per unit area than those produced under low light. Leaves from plants grown in Scoria-Idealite and CSU Old soil showed the largest increase in number of

Figure 19: Effect of substrate and light on the number of stomata per mm^2 in compartment D.


AVERAGE NUMBER STOMATA PER UNIT AREA
100
96
92
88
84
80
76
0
UNDER HIGH LIGHT (JUNE)
UNDER LOW LIGHT (FEBRUARY)
SCORIA-IDEALITE
SOIL B-8"
CSU OLD
SOIL B-4"
CSU NEW
SOIL A-8"
SOIL A-4"

stomata from February to June. Soil B-8" had the least increase during the same period. An interaction was found to exist between cover and root substrate on stomatal and epidermal cell distribution but was low in comparison to the individual effects of cover and medium.

Table 7. Summary of stomatal and epidermal cell frequency per mm^2, stomatal index, and number of stomata per leaf area sampled by the hygrometer leaf cup per compartment.

Compartment	Number of stomata per mm^2	Number of epidermal cells per mm^2	Stomatal index (I)*	Mean number of stomata in area covered by leaf cup
A	77.5	233.8	24.9	13,177
B	84.0	242.9	25.7	14,280
C	83.7	247.5	25.3	14,231
D	92.1	256.4	26.4	15,649
LSD 5% level	2.0	4.4		

$$*I = \frac{\text{\# stomata per } mm^2}{\text{\# stomata + \# epidermal cells per } mm^2}$$

The difference between the values of stomatal index (I) (Table 6) for all soil plots was only 0.7, while there was a difference of 1.7 between Scoria-Idealite and the lowest soil plot. Although Scoria-Idealite had fewer stomata and epidermal cells than any soil plot, there was a greater decrease in the number of stomata than epidermal cells resulting in a lower I. No consistent relationship between I and growth could be found.

Part 4. Transpiration Measurements

Measurement of both Δt (time required for a standard relative humidity change in an electric hygrometer cell) and stomatal aperture were used to indicate transpiration rate during a drying period, September 27 to October 5 in compartment D. Data was taken daily at 10:00 a.m. MST. Computing the average opening of stomatal apertures from silicon rubber impressions was time consuming and tedious. In contrast, the electric hygrometer was a simple and more practical technique.

As seen in Fig. 20, Δt decreased as aperture and solar radiation increased. However, variations are evident from the different Δt values with the same stomatal aperture. Thus, the variations shown in Fig. 20 cannot be attributed solely to changes in stomatal apertures. A linear regression of Δt on stomatal aperture and solar radiation was computed. Figs. 21 and 22 show that Δt was positively correlated to both stomatal aperture and solar radiation.

There was a sharp decrease in Δt on the seventh day from watering in Fig. 20. The decrease coincided with a corresponding sharp decrease in solar radiation. On the eighth day after watering, the plants in the 4-inch soils showed visible signs of water stress, but Δt values in all plots were higher than those of the previous day.

Measurements of Δt were taken at 9:00 a.m. and 1:00 p.m. MST in compartment D over a drying period from March 21 to March 26. The results of morning and afternoon measurements on all plots are shown in Figs. 23-25. The afternoon readings in Fig. 23 showed consistent variations, in that Δt was consistently greater for plants in 4-inch

Figure 20: Relationship of stomatal aperture and transpiration rate (Δt) to solar radiation during the drying period from September 27 to October 5, 1966. Data were taken at 10:00 a.m. MST in compartment D.

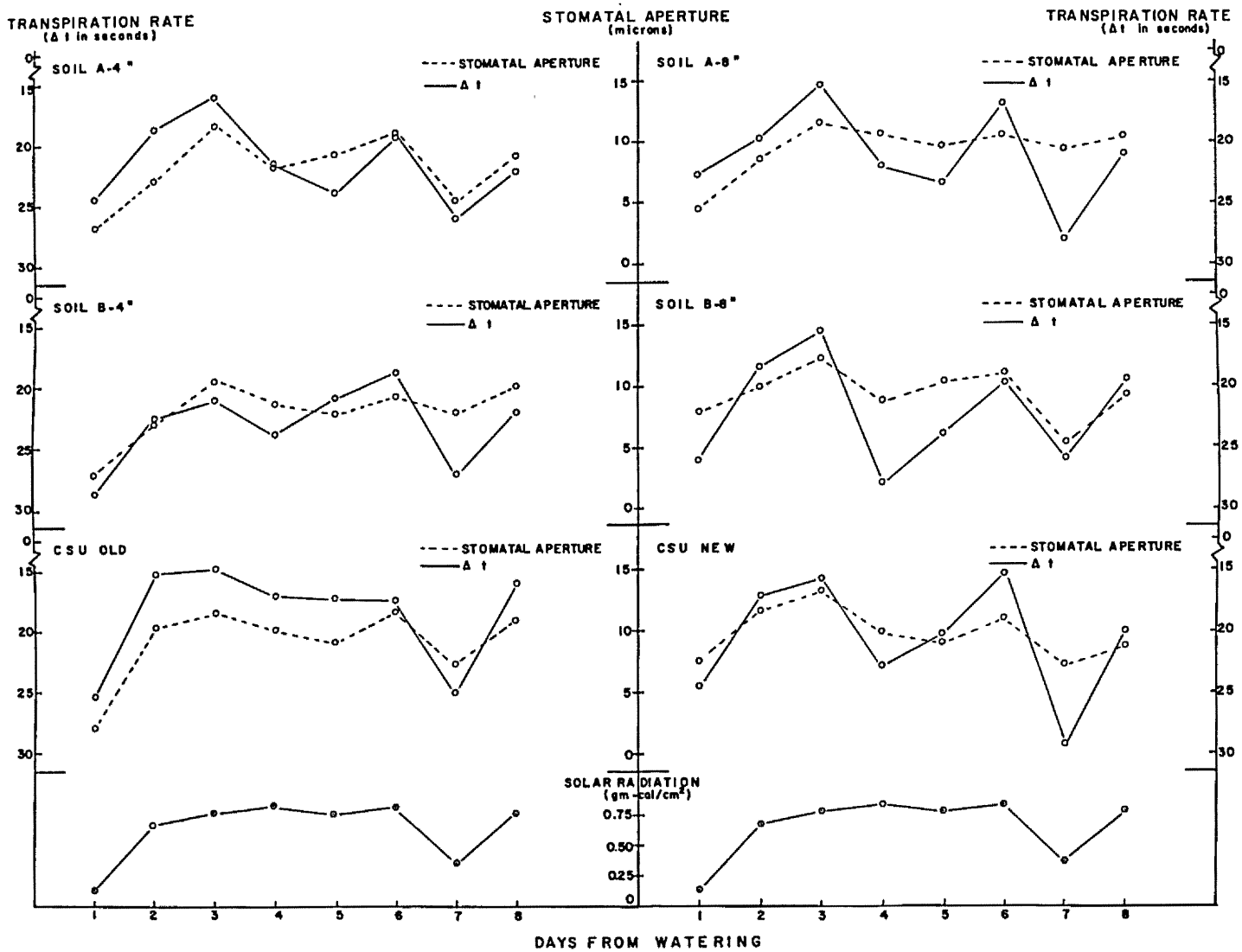

TRANSPIRATION RATE
(Δ t in seconds)
STOMATAL APERTURE
(microns)
TRANSPIRATION RATE
(Δ t in seconds)
SOIL A-4"
SOIL A-8"
SOIL B-4"
SOIL B-8"
CSU OLD
CSU NEW
STOMATAL APERTURE
Δ t
SOLAR RADIATION
(gm-cal/cm²)
0.75
0.50
0.25
DAYS FROM WATERING

Figure 21: Regression line showing the positive correlation between stomatal aperture and transpiration rate.

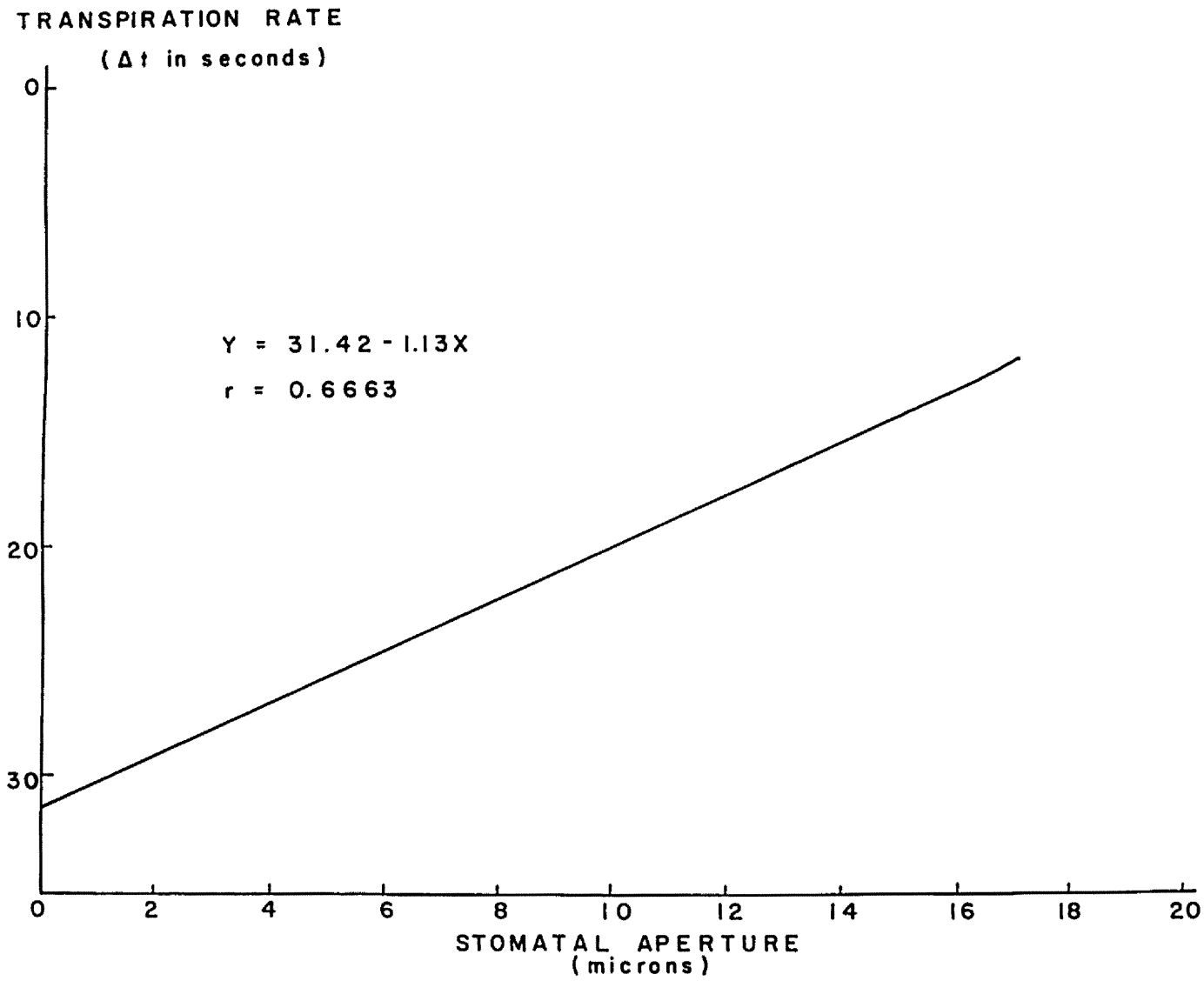

TRANSPIRATION RATE
(Δt in seconds)
0
10
20
30
Y = 31.42 - 1.13X
r = 0.6663
0
2
4
6
8
10
12
14
16
18
20
STOMATAL APERTURE
(microns)

Figure 22: Regression line showing the positive correlation between solar radiation and transpiration rate.

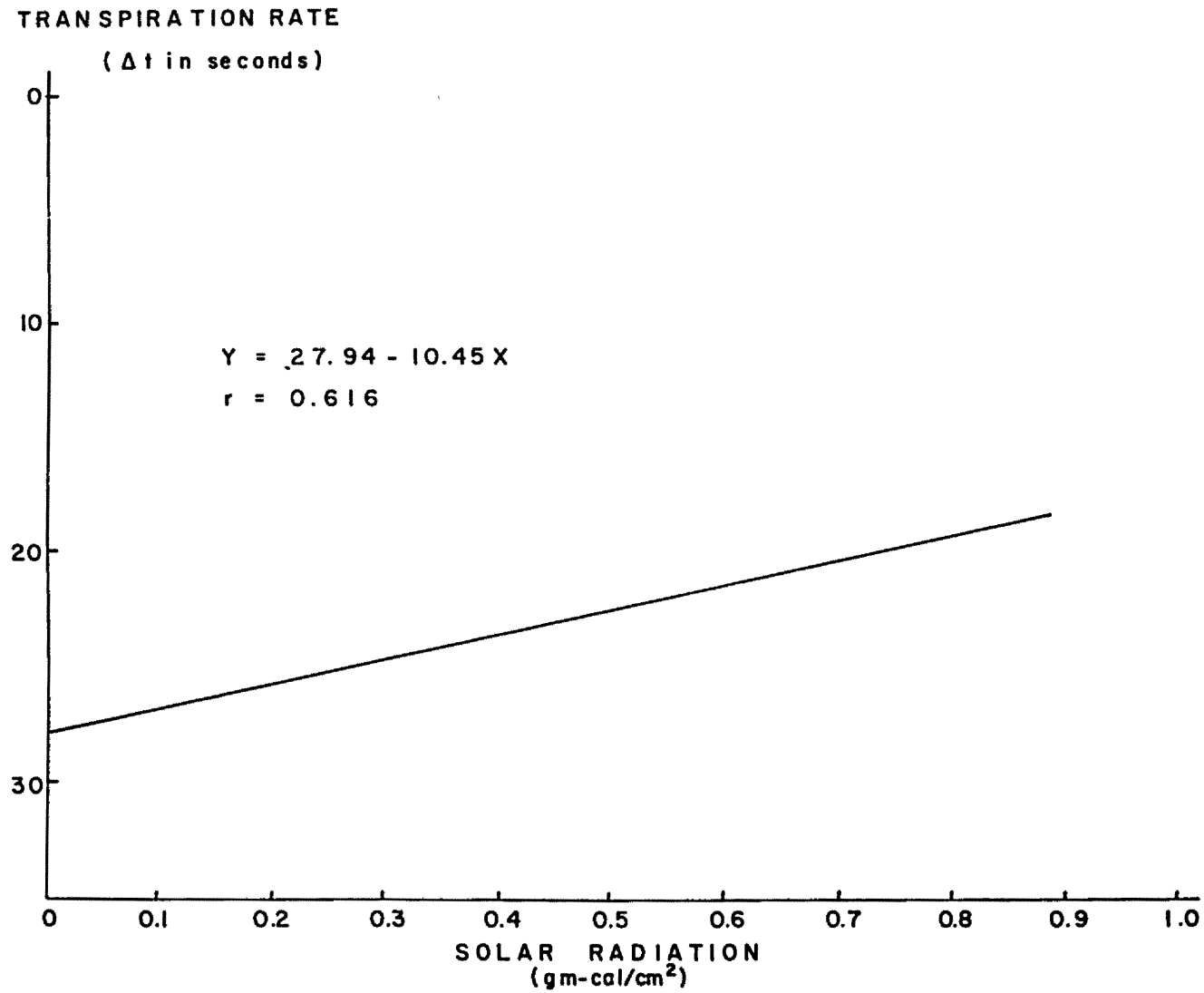

TRANSPIRATION RATE
(Δ t in seconds)
0
10
20
30
Y = 27.94 - 10.45 X
r = 0.616
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
SOLAR RADIATION
(gm-cal/cm²)

Figure 23: Transpiration rate of carnations in soil A and Scoria-Idealite during one drying period. Data taken at 9:00 a.m. and 1:00 p.m. MST in compartment D from March 21 to March 26, 1967.

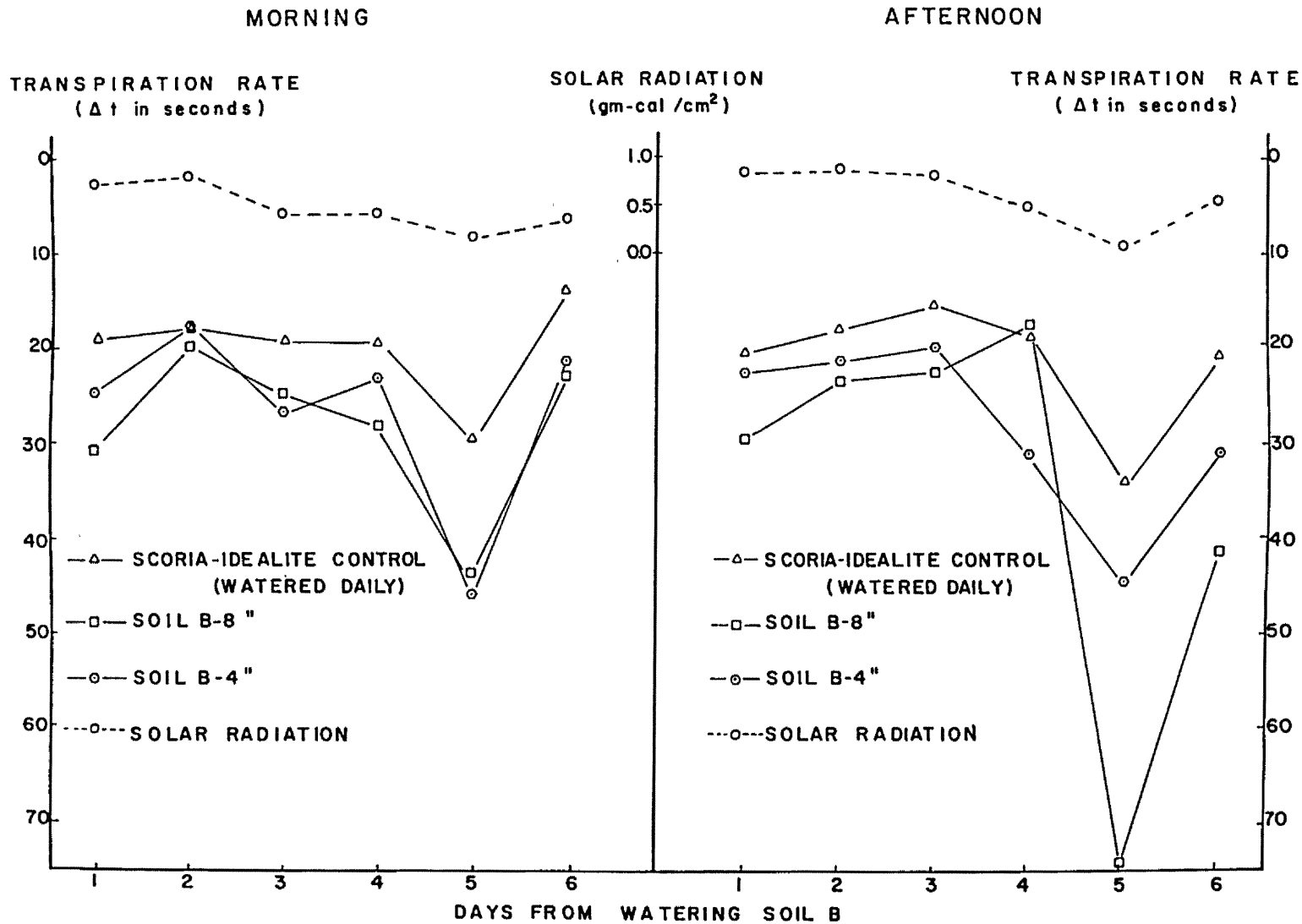

MORNING
AFTERNOON
TRANSPIRATION RATE
(Δ t in seconds)
SOLAR RADIATION
(gm-cal /cm²)
TRANSPIRATION RATE
(Δ t in seconds)
0
10
20
30
40
50
60
70
1.0
0.5
0.0
SCORIA-IDEALITE CONTROL
(WATERED DAILY)
SOIL B-8 "
SOIL B-4"
SOLAR RADIATION
1
2
3
4
5
6
DAYS FROM WATERING SOIL B

Figure 24: Transpiration rate of carnations in soil B and Scoria-Idealite during one drying period. Data taken at 9:00 a.m. and 1:00 p.m. MST in compartment D from March 21 to March 26, 1967.

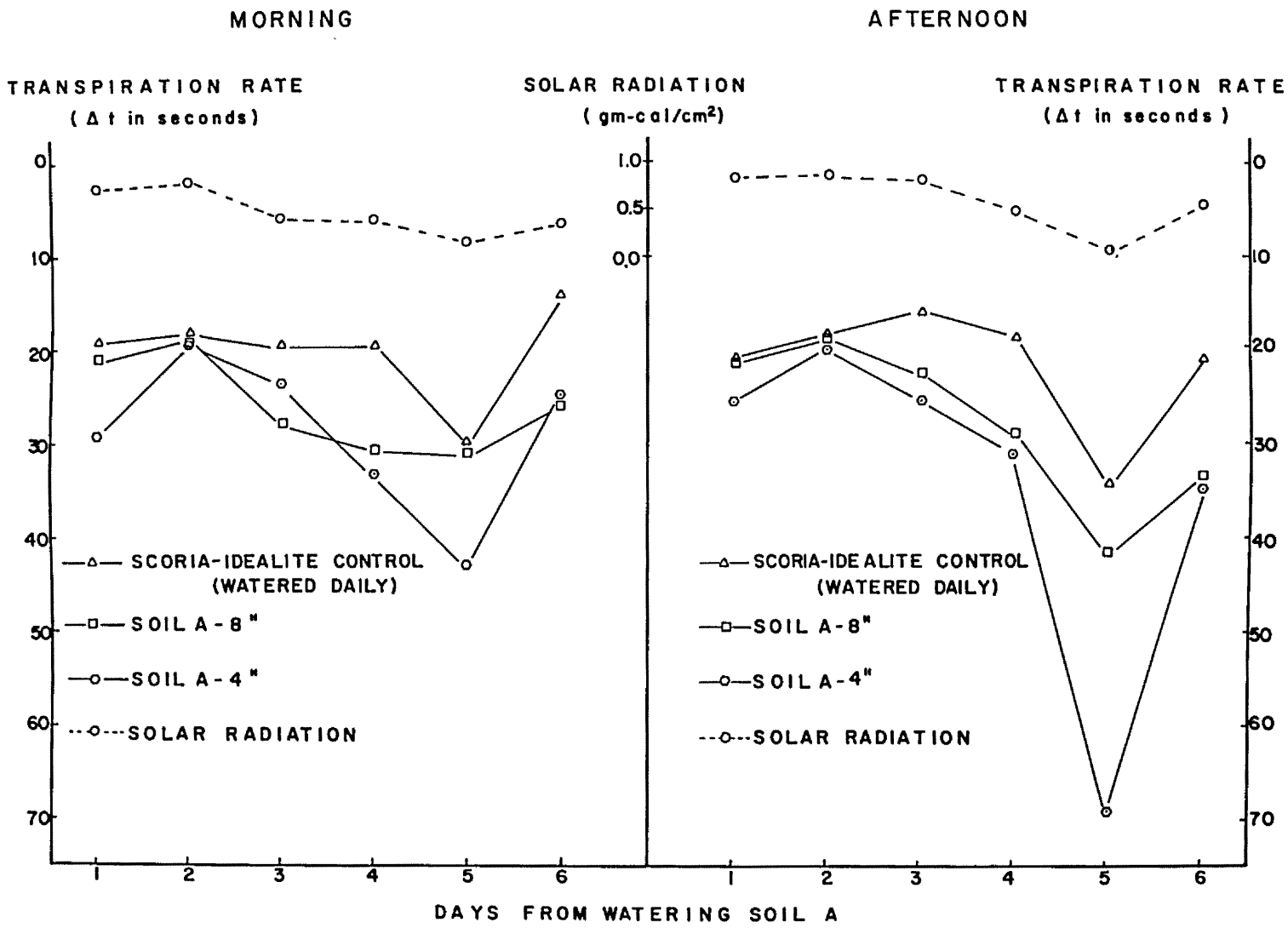
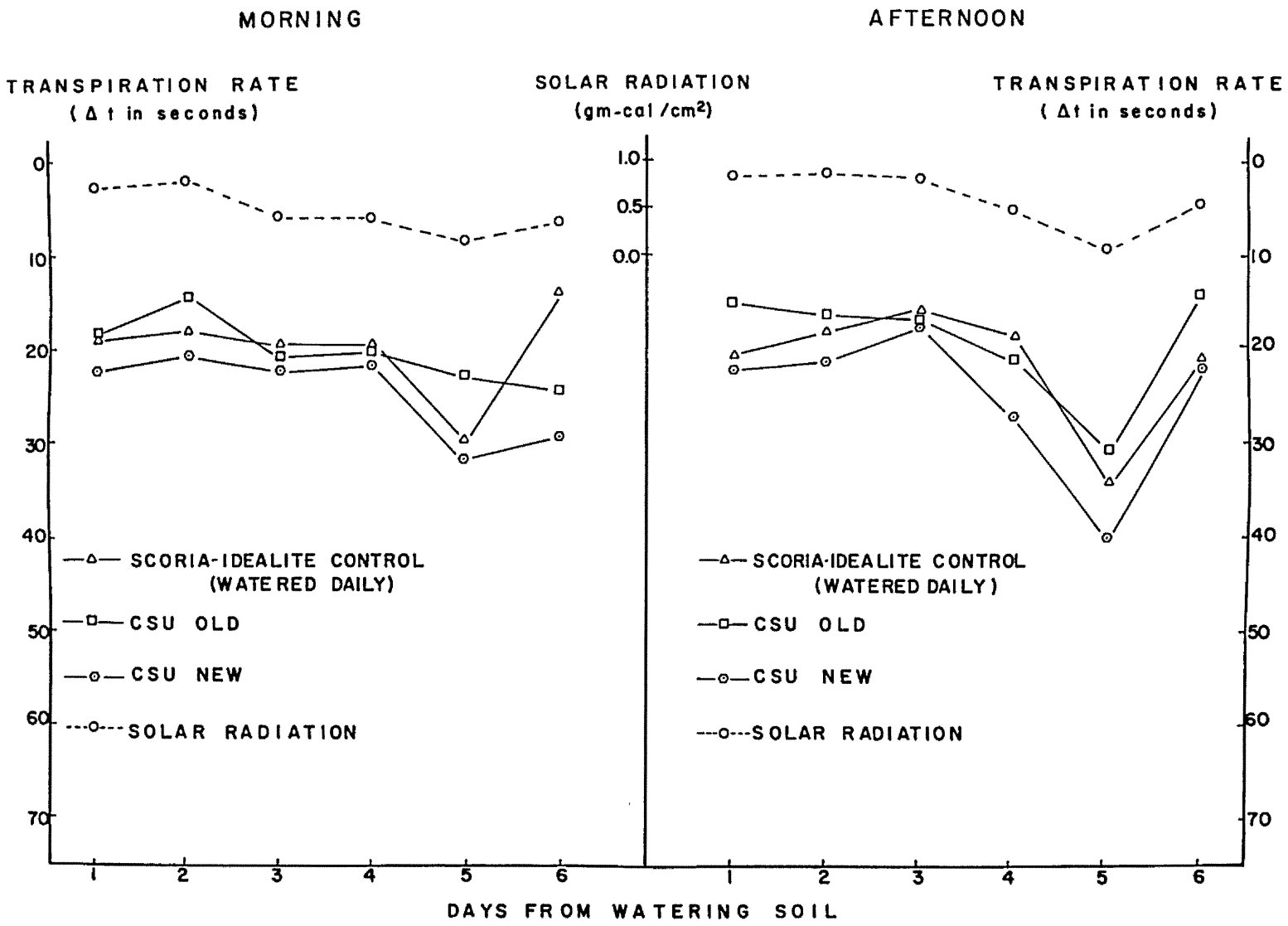

MORNING
AFTERNOON
TRANSPIRATION RATE
(Δ t in seconds)
SOLAR RADIATION
(gm-cal/cm²)
TRANSPIRATION RATE
(Δ t in seconds)
0
10
20
30
40
50
60
70
1.0
0.5
0.0
SCORIA-IDEALITE CONTROL
(WATERED DAILY)
SOIL A - 8"
SOIL A - 4"
SOLAR RADIATION
1
2
3
4
5
6
DAYS FROM WATERING SOIL A

Figure 25: Transpiration rate of carnations in CSU Old, CSU New, and Scoria-Idealite during one drying period. Data taken at 9:00 a.m. and 1:00 p.m. MST in compartment D from March 21 to March 26, 1967.


MORNING
AFTERNOON
TRANSPIRATION RATE
(Δ t in seconds)
SOLAR RADIATION
(gm-cal /cm²)
TRANSPIRATION RATE
(Δt in seconds)
0
10
20
30
40
50
60
70
1.0
0.5
0.0
SCORIA-IDEALITE CONTROL
(WATERED DAILY)
CSU OLD
CSU NEW
SOLAR RADIATION
1
2
3
4
5
6
DAYS FROM WATERING SOIL

soil depths than for plants in 8-inch soil depths. That is, transpiration in most circumstances was greater for those plants subjected to lower soil moisture stress, provided other factors were equal. However, Figs. 24 and 25 are typical examples of inconsistent relationships that were found between $\triangle t$ values on different media. In Figs. 23 and 24, there was a general trend for the difference in $\triangle t$ values between Scoria-Idealite and soil plots to increase as the days from watering increased. However, there were some exceptions as can be seen from the afternoon values in Fig. 25.

Statistical analysis indicated many factors, such as days from watering, type of media, and the hour readings were taken, as well as their interactions, were highly significant. Statistically, $\triangle t$ was affected most by days from watering. Plants grown in Scoria-Idealite generally had the lowest $\triangle t$ rate or greatest transpiration rate.

As a general rule, transpiration decreased as the substrate dried out, or as radiant energy decreased. Plants in 4-inch soils also had slower transpiration rates. Changes in solar radiation masked any definite increase in $\triangle t$ at the end of the drying cycle. However, as days from watering increased, $\triangle t$ values were higher (less transpiration) with decreased solar radiation.

Changes in solar radiation were also found to affect $\triangle t$ measurements taken at hourly intervals from 7:00 a.m. to 4:00 p.m. Figs. 26 and 27 indicate the effects of solar radiation on $\triangle t$ of plants in various root substrates. As indicated in Figs. 23 and 24, the lowest $\triangle t$ values were obtained from plants grown on Scoria-Idealite which

Figure 26: Transpiration rate of carnations in soils A and B and Scoria-Idealite. Data taken April 3, 1967, in compartment D.

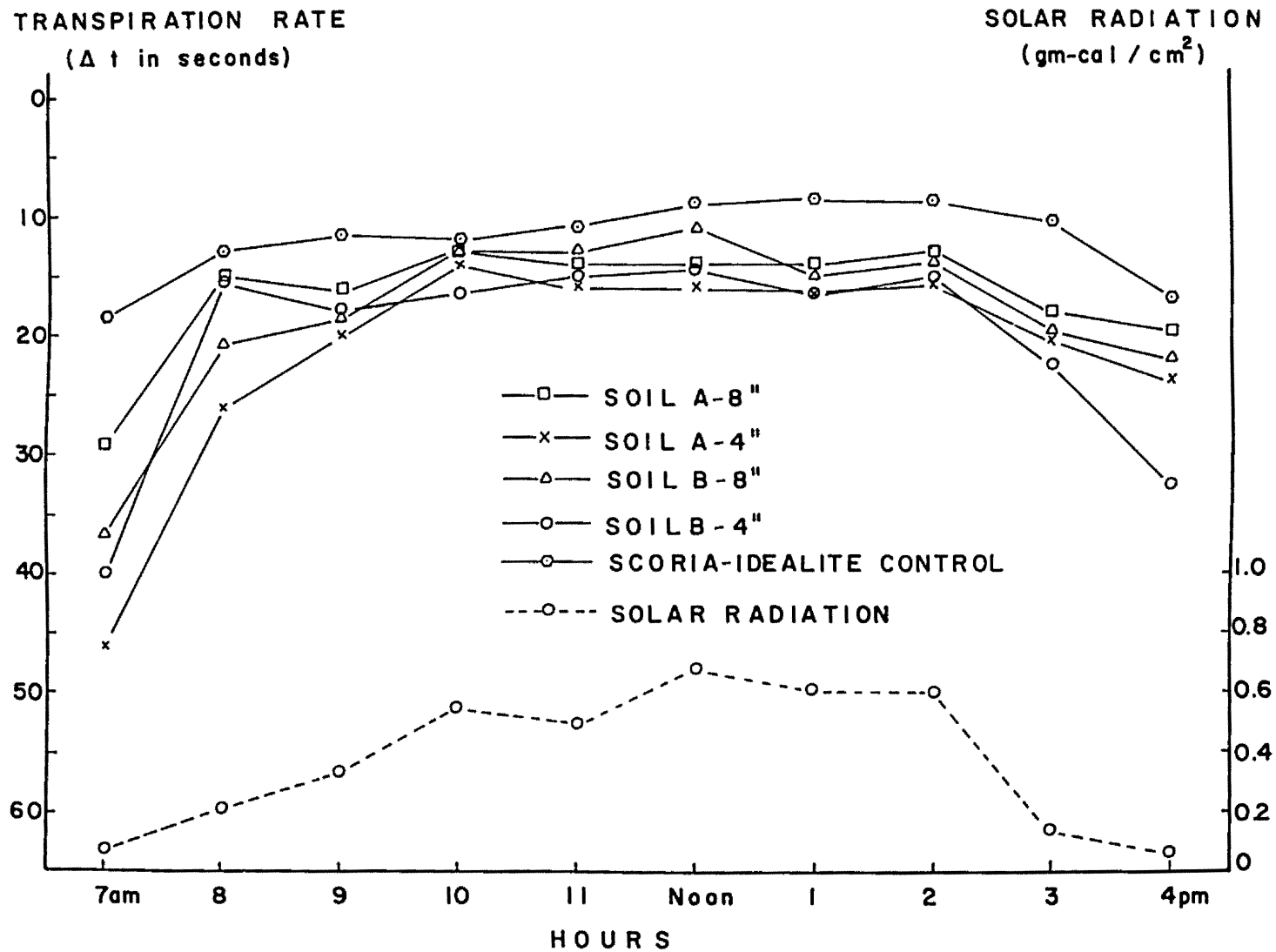
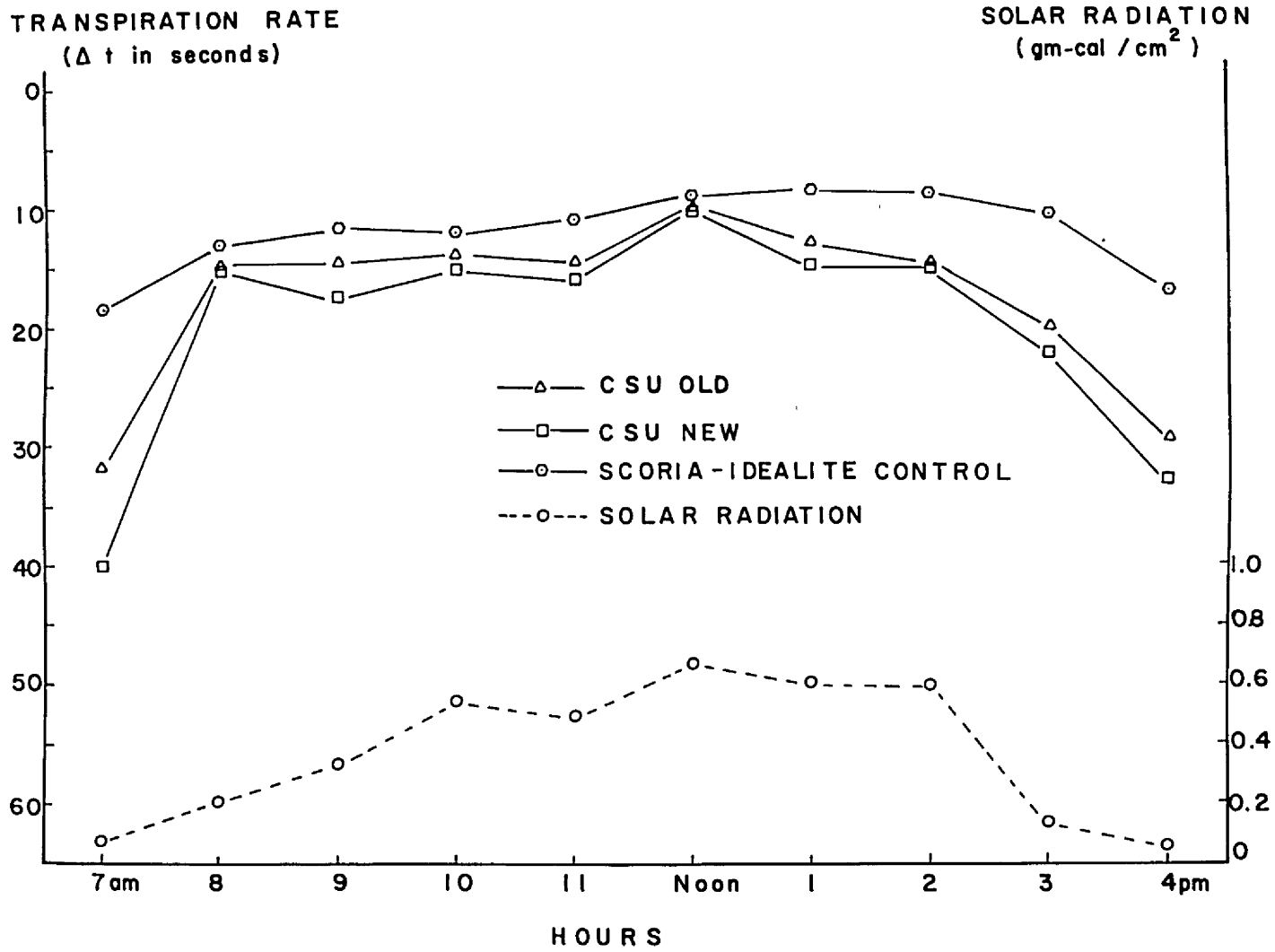

TRANSPIRATION RATE
(Δ t in seconds)
SOLAR RADIATION
(gm-cal / cm²)
0
10
20
30
40
50
60
1.0
0.8
0.6
0.4
0.2
0
SOIL A-8"
SOIL A-4"
SOIL B-8"
SOILB-4"
SCORIA-IDEALITE CONTROL
SOLAR RADIATION
7am
8
9
10
11
Noon
1
2
3
4pm
HOURS

Figure 27: Transpiration rate of carnations in CSU Old, CSU New, and Scoria-Idealite. Data taken April 3, 1967, in compartment D.

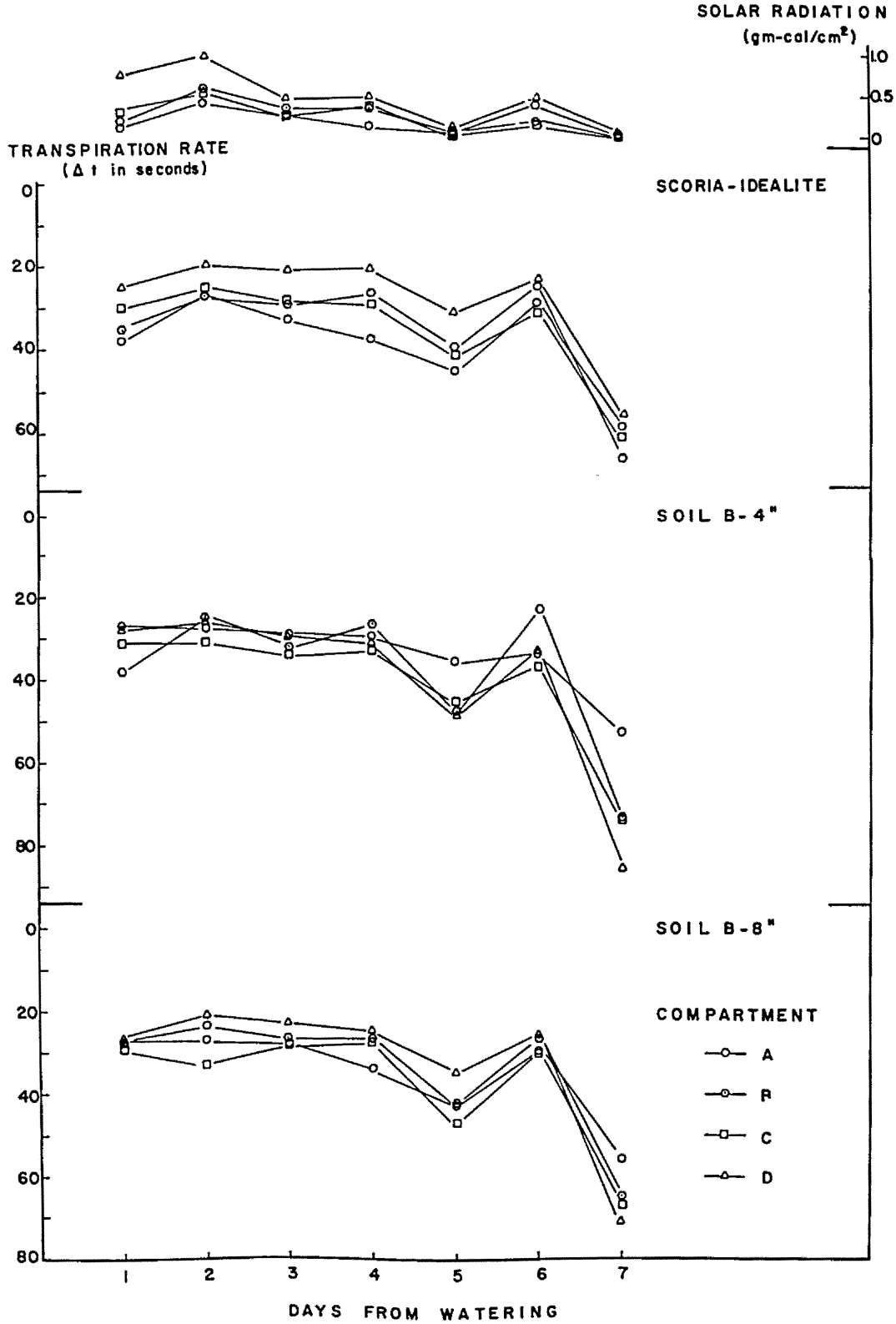

TRANSPIRATION RATE
(Δ t in seconds)
SOLAR RADIATION
(gm-cal / cm²)
0
10
20
30
40
50
60
1.0
0.8
0.6
0.4
0.2
0
CSU OLD
CSU NEW
SCORIA-IDEALITE CONTROL
SOLAR RADIATION
7am
8
9
10
11
Noon
1
2
3
4pm
HOURS

were also least affected by low solar radiation in both the morning and afternoon.

Fig. 27 indicates a lower hourly transpiration rate of plants in CSU New soil than those in CSU Old. This relationship also held true during drying cycles (see Fig. 25). Transpiration rates from plants in 4-inch soils were generally slower than those from the corresponding 8-inch plots. No definite mid-day stomatal closure was noted except for a slight decrease in $\triangle t$ values at 1:00 p.m., but there was also a lower level of solar radiation.

Fig. 28 indicates that there was a difference in $\triangle t$ values between compartments. Compartment D had the highest transpiration rate followed by B, A, and C. Compartment D had the highest solar radiation at the time the readings were taken. There appears to be a significant decrease in transpiration rate on the seventh day from watering. However, solar radiation on the seventh day was also the lowest during the entire drying period.

Figure 28: Comparison of effect of cover on transpiration rate of carnations during drying cycle. Data taken at 10:00 a.m. MST, June 17 to June 23, 1967.


SOLAR RADIATION
(gm-cal/cm²)
1.0
0.5
0
TRANSPIRATION RATE
(Δ t in seconds)
SCORIA-IDEALITE
SOIL B-4"
SOIL B-8"
COMPARTMENT
A
B
C
D
0
20
40
60
80
1
2
3
4
5
6
7
DAYS FROM WATERING

Chapter V

DISCUSSION

The observed plant response in this investigation showed several important effects of practical significance. Even though reducing soil depth resulted in a higher initial soil moisture content, the net effect was to increase soil moisture stress since less total water in the plot was available. The responses of the plants were those that would be expected from high soil moisture stress (45, 49). The effect of reducing soil A to a 4-inch depth was more severe on total yield than reducing soil B to 4 inches. The fact that soil B had a higher moisture content at all suction levels may be beneficial at reduced depths where the soil dries more rapidly. In essence, reducing soil depth to 4 inches increases problems that result from either too much or insufficient water.

Both Growers' Soils A and B at 8-inch depths produced similarly to CSU Old soil. However, soil B had a lower total yield than soil A even though soil B had a higher moisture content at all suctions. The soil moisture retention curve of soil A was more identical to CSU Old soil.

The approximate total pore space of the two problem soils was high and reflected their ability to retain more water at all suction values in comparison to CSU New soil which had a lower total pore space.

CSU New soil was observed to have a low organic matter content resulting in a greater bulk density value than the regular greenhouse soils. The extrapolation of the soil moisture retention curves on a logarathmic scale showed that the approximate total pore space of CSU New soil was lower than all others and resulted in the lowest percentage of available water to the plant at both high and low suction levels.

From the moisture retention curves (Fig. 3), it would not be expected that high water content would be a factor in the reduced plant response for CSU New soil (Figs. 7 and 8). However, the chlorotic condition of plants during initial growth stages, definitely indicated an aeration problem. At the time chlorosis was observed, the plants were small, and solar radiation levels were decreasing daily. These two factors resulted in a low rate of evapotranspiration. Consequently, the soil did not dry out very fast and chlorosis appeared as a result of poor aeration. Watering records showed that as solar radiation decreased, watering frequency also decreased even though plant size increased. This indicated that solar radiation affected the number of days between irrigations more than plant size. It is likely that poor aeration during initial growth, and insufficient water during later growth, both contributed to the decreased yield and grade.

The extrapolated soil moisture retention curves in Fig. 4 showed that CSU Old soil had neither the highest nor lowest moisture contents at all suction levels.

CSU New soil had the lowest moisture content and soil B the highest at all levels of suction, and both had a total yield and

grade lower than that for CSU Old soil. The amount of pore space in CSU Old soil provided good drainage and sufficient aeration for good plant growth since total yield and grade were highest from plants grown in CSU Old soil; this soil was the closest to what would be called an ideal soil. When handled similarly, all four soils produced acceptable cut flowers. There were no indications of marked problems from deficient aeration, extreme stress, or disease observed in the two growers' soils at either the 4- or 8-inch depths. When supposedly problem soils were handled properly, disease control and high production were attainable.

Plants grown under low moisture stress in Scoria-Idealite flowered earlier than those under high stress. This indicates that an adjustment must be made in scheduling, since the time required to produce a crop was shortened. The effect of stress was most noticeable in the flowering of the second crop. After the first crop was cut, plants grown in 4-inch plots responded by producing fewer breaks which developed slower than those on plants in 8-inch plots. The delayed growth resulted in a production peak 5 weeks later than the peak in the 8-inch plots.

The decreased grade and brittleness of flowers from plants grown in Scoria-Idealite may have been due to a lack of stress on plant growth. The beginning of the second crop was a period of low solar radiation and subsequent low evapotranspiration. Since the irrigation interval was the same as at high solar radiation, the plants had an optimum supply of water. Indications are that perhaps some stress is required by carnations for the best grade.

The effect of soil conditions early in the growth of carnations was not found to be directly related to total productivity (Table 4 and Fig. 11). However, general trends were indicated in that plants grown in both poorly aerated soil and shallow depths were shortest after 12 weeks of growth. The same plots also had the lowest total yield.

The different types of cover significantly affected transpiration rates, stomatal distribution, and plant height, but did not significantly affect yield and mean grade. From the data obtained, plants grown in compartment A should have shown the best response as to yield and mean grade. The taller plant growth and fewer number of stomata per mm^2 indicated that the plants were grown at lower levels of stress. However, this was not reflected in the response of the plants to yield and mean grade. Compartment D, which had the largest number of stomata per mm^2, had the highest total yield up to April 29.

The factor involved here was probably solar radiation. The higher solar radiation in compartment D provided more energy for photosynthesis and plant growth during the winter months. This resulted in a higher production for plants grown at higher values of stress. Fig. 28 showed that transpiration in the Scoria-Idealite media was lowest in compartment A and highest for compartment D. Soils B-4" and B-8" generally followed the same trend. This indicated that although plant growth was better at low values of stress, other environmental factors, especially solar radiation, were probably limiting. This opens up an area of future work that could be of practical importance to the grower. Since artificial media allows plant growth at lower levels of water stress, the additional solar

radiation under glass as compared to fiberglass might be better utilized for greater production as a result of a greater rate of photosynthesis.

Different levels of suction in the root substrate also had an effect on stomatal and epidermal cell distribution. A greater number per unit area was found on leaves from plants grown under high soil moisture stress. Fig. 15 showed the decreased density of stomata and increased size of epidermal cells on leaves from plants grown in Scoria-Idealite watered daily. The increased stomatal densities found in high stress treatments might not have been the result of continuous cell division, but rather decreased expansion of the cells during periods of low moisture availability (40). Denmead and Shaw (26) noticed that stress imposed while the plant was actively growing retarded cell enlargement.

Fig. 18 showed the effect of high water stress on the stomata in comparison to those under low stress in Fig. 16. The stomata from leaves on plants grown under high stress appeared to have adapted to their growth conditions. They were more cutinized and had thicker cell walls around the periphery of the guard cells. This might have been due to a lower amount of moisture available to maintain turgor during the growth of the cells which acted as a check against wide stomatal apertures and increased water loss. Another adaptation to high stress might have been the thicker cuticle over the epidermal cells. Since carnations have sunken stomata, the thickness of the cuticle layer would create a longer passageway for water vapor to travel from the interior of the leaf to the outside air.

The observation that leaves from plants grown at high stress had more stomata per unit area than those grown at low stress, would indicate a potentially greater transpiration rate. However, transpiration rates from plants grown under high stress were usually lower than those from plants grown under low stress. Waggoner (114) stated that although a greater stomatal density would seem to encourage a greater transpiration rate, it had nothing to do with decreased transpiration. The decreased transpiration rate at high stress might have been due to an increased resistance of the individual stomata to transpiration.

Work in this area should be continued to determine if there are a greater number of stomata per plant when grown under high stress or whether this fact is compensated by a smaller total leaf area. Assuming the possibility that the total number of stomata per plant are equal under both high and low stress, the lower transpiration rates obtained at high stress would lead to the theory that the stomata increased their resistance to transpiration. Anatomical work on stomata might show what type of cellular changes occur that increase resistance to transpiration.

Cover also had a significant effect on the number of stomata per unit area. This might have been the direct result of different amounts of solar radiation and subsequent stress under the various covers. A definite effect of solar radiation was found when stomatal density was observed in February and again in June in compartment D as shown in Fig. 19. An increased stomatal density on corresponding soil plots was observed under high solar radiation in June, which might have been attributable to increasing stress.

Fig. 12 emphasized the variations that may be obtained in measuring stomatal numbers. The leaf midvein was also found by Hirano (53) to have fewer stomata. Large variations in the distribution of stomata over a leaf were observed and it was imperative that readings be made in a predetermined section of leaf surface for the best sampling technique.

The stomatal index (I) was found to be more constant than stomatal frequency as was reported by Salisbury (69). However, the decreased variation might have been due to the way I was computed; i.e. the total number of stomata were divided by the total number of stomata plus epidermal cells. This seemed to eliminate some of the variations that were found when looking at stomatal numbers alone. No relationships were found when stomatal index and total yield were compared. No importance could be attributed to the fact that I for Scoria-Idealite was different from the soil plots.

According to Ting (105), $\triangle t$ is a direct measure of transpiration. It should give an indirect measurement of stomatal aperture which indicates plant water balance through the effect of turgor pressure on aperture width. A general trend in $\triangle t$ measurements to stomatal apertures was noted. Larger apertures had a lower $\triangle t$ value which reflected a greater loss of water vapor from the stomata. The use of silicon rubber impressions was a laborious method of indicating transpiration rate because of the large number of observations per leaf and the time necessary for taking the readings. The lithium chloride hygrometer method was relatively easy to use and results were obtained quickly.

As seen from the measurements taken during the various drying periods, Δt values followed the general trend of transpiration, but did not give an indication for determining when the plant first came under water stress considered as the point where potential growth is reduced. Consequently, this technique would be adequate in controlled environment studies, but its practical application by a grower does not appear possible. The effect of other factors such as solar radiation, type of cover, days from watering, amount of water available to the plant in the particular plot being sampled, and the hour readings are taken, all entered into the final value of Δt.

Solar radiation appeared to be the most important factor affecting Δt values. During certain drying periods as in Figs. 23-25, Δt rates were higher on the day of watering due to higher levels of solar radiation than the day prior to watering. Measuring the transpiration rate by Δt values did not appear to be sensitive enough for commercial application. By the time definite decreases in transpiration rate occurred, the fact the plant was under stress could be observed visually.

The technique of measuring Δt with the lithium hygrometer may be excellent to show when the availability of water starts to decrease, when this is the only factor measured and all other environmental conditions are equal. The fact that plants grown on Scoria-Idealite were generally found to have the lowest Δt values demonstrated the technique to be reliable in showing the effects of differences in stress.

The increasing difference in Δt values between soil plots and Scoria-Idealite over a drying period suggested the possible use of the technique if a control plot of artificial media with plants grown at low stress is used. This would entail further study in determining what differences in absolute values must be obtained to indicate when the plant is under stress and the possibility of determining when to water.

Chapter VI

SUMMARY

The effect of differences in soil moisture stress, provided by the use of different soils and depths of soil, on yield and quality of carnations was investigated. A technique that would offer a better indication of when to water carnations under greenhouse conditions was also evaluated.

The best producing soils had neither the maximum nor minimum bulk density, moisture content at all suctions, or total pore space of all soils compared. The values of the best soils were usually an average of the extremes. These values could possibly be used as a guideline for determining a good greenhouse soil.

There were no indications of marked problems from deficient aeration, extreme stress, or disease in two soils, known to have problems, when treated alike. The reduction of soil depth from 8 to 4 inches increased problems that result from too much or insufficient water. Yield and grade were best on plants grown in 8-inch soil.

The raw field soil had an aeration problem when placed in a greenhouse bench resulting in decreased yield. The apparent low organic matter content might have been the cause of the low transpiration demand by small plants, aeration problem and resulting decreased yield.

Plants grown under low stress flowered one week earlier during the first crop, than those grown under high stress. The effect of stress was most noticeable in the flowering of the second crop which was delayed up to 5 weeks under high stress. Carnations grown under low stress conditions would require new planting schedules. There were indications that some stress may be required by carnations to produce higher grade flowers.

As either solar radiation or soil moisture stress increased, there was generally a corresponding increase in the number of stomatal and epidermal cells per mm^2. As stress decreased, there was an increase in size of epidermal cells and a decreased number of stomata. There was no relation between transpiration rate and the number of stomata per unit area. Stomata on leaves from plants grown under high stress adapted to the unfavorable growing conditions by having a greater resistance to transpiration. The resistance might have been due to a thicker cuticle layer which increased the diffusion path length for water vapor from the interior of the leaf to the outside air. Although stomatal index was found to vary less than stomatal frequency, it was not beneficial in understanding stomatal distribution.

Indications were that although plant height was greater at low values of stress, solar radiation should not be decreased as it probably became a limiting factor in photosynthesis and resulted in a lower total yield.

A higher correlation was found between transpiration rate and stomatal aperture than transpiration rate and solar radiation.

Although the lithium chloride hygrometer was easy to use, it was not sensitive enough to be used in a greenhouse as an indication of when to water. Many factors such as solar radiation, type of cover, days from watering, and hour readings are taken, all affected $\triangle t$ values. The measurements of stomatal apertures by the use of silicon rubber impressions was too laborious to be used as a practical field technique.

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APPENDIX

TABLE A. Analysis of variance of cover and root substrate on yield of "CSU Red" on soil plots and "Pink Coquette" on Scoria-Idealite.

Source of variance	df	MS	F
Weeks	29	580.80	29.4972**
Cover	3	40.16	2.0396
Error	87	19.69	
Root substrate	6	81.19	4.2799**
Cover X root substrate	18	13.33	.7027
Error	696	18.97	

TABLE B. Analysis of variance of cover and root substrate on mean grade of "CSU Red" on soil plots and "Pink Coquette" on Scoria-Idealite

Source of variance	df	MS	F
Weeks	29	36.38	37.8958**
Cover	3	.16	.1667
Error	87	.96	
Root substrate	6	5.78	7.6053**
Cover X root substrate	18	1.36	1.7895
Error	696	.76	

TABLE C. Analysis of variance of cover and soil plots on plant height after 3 months growth.

Source of variance	df	MS	F
Cover	3	473.33	8.1735**
Soil plots	5	47.76	.8247
Cover X soil plots	15	116.00	2.0031
Error	456	57.91	

TABLE D. Analysis of variance of soil depth and keeping life of "CSU Red" carnations.

Source of variance	df	SS	MS	F
Time	5	1.5	.300	2.5000
Depth soil plot	1	0.5	.500	4.1667
Error	5	0.6	.120	

TABLE E. Analysis of variance of root substrate and cover on stomatal density.

Source of variance	df	MS	F
Cover	3	856.86	30.1605**
Root substrate	6	192.02	6.7589**
Root substrate X cover	18	83.13	2.8372**
Error	364	28.41	

TABLE F. Analysis of variance of root substrate and cover on epidermal cell density.

Source of variance	df	MS	F
Cover	3	3,761.54	28.4728**
Root substrate	6	764.40	5.7861**
Root substrate X cover	18	301.32	2.2808**
Error	364	132.11	

TABLE G. Analysis of variance of $\triangle t$ data taken at 9:00 a.m. and 1:00 p.m. MST in compartment D from March 21 to March 26, 1967.

Source of variance	df	MS	F
Root substrate	6	1,659.35	123.7397**
Day	5	5,532.63	412.5749**
Day X root substrate	30	235.37	17.5518**
Hour	1	928.56	69.2438**
Hour X root substrate	6	141.11	10.5227**
Hour X day	5	815.98	60.8486**
Hour X day X root substrate	30	123.66	9.2215**
Error	420	13.41	

TABLE H. Analysis of variance of Δt data taken at 10:00 a.m. MST, June 17 to June 23, 1967, in compartment D.

Source of variance	df	MS	F
Cover	3	500.50	95.3333**
Root substrate	3	298.39	56.8362**
Root substrate X cover	9	484.19	92.2267**
Day	6	16,325.50	310.0962**
Day X cover	18	227.23	43.2819**
Day X root substrate	18	54.67	10.4133**
Day X root substrate X cover	54	38.27	7.2895**
Error	448	5.25	

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