THE EFFECT OF DEPTH OF ROOTING ON CITRUS ROOT STRUCTURE AND WATER ABSORPTION

By

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No man is an island, entire of itself;
every man is a piece of the continent,
a part of the main; if a clod be
washed away by the sea, Europe is the less,
as well as if a promontory were, as well
as if a manor of thy friends or of thine
own were; any man's death diminishes me,
because I am involved in mankind; and
therefore never send to know for whom the
bell tolls; it tolls for thee.

John Donne

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Co-Chairman: Dr. R.C.J. Koo
Major Department: Fruit Crops

The effect of rootstock root distribution on water absorption and citrus root morphology and anatomy was investigated. Experimental units were trees on 4 rootstocks, rough lemon, sweet orange, sour orange and 'Rusk' citrange in an 'Orlando' tangelo rootstock trial located among a commercial tangelo orchard in Lake County, Florida. Soil samples were taken from the experimental site for chemical and physical analysis. Soil water depletion was studied by the neutron moderation method. Selected water extraction data were compared to root distribution data obtained from the same trees in a previous study.

The results indicated that soil water loss was directly proportional to root quantity as measured by the dry weight of feeder roots. The general pattern of moisture depletion for trees on all stocks showed that significant losses in soil moisture occurred near the surface first, followed by gradual increases in the contribution of deeper roots as the surface moisture was depleted.

Meaningful differences were found in root efficiency among depths and rootstocks when soil water depletion was compared to root distribution. The magnitude of the ratios of these 2 factors emphasized the significance of deep roots especially when surface moisture was rapidly lost as a result of a high root density. It appeared that differences in rootstock adaptation to the soil environment could be explained on the basis of inherent differences in the root distribution of trees on the 4 rootstocks and on an interaction of these differences with the physical characteristics of the soil environment. This interaction seemed to have been the source of differences in root effectiveness in water uptake.

The morphology and anatomy of field-sampled roots of each rootstock and from several soil depths were remarkably similar on the basis of observations made both with the scanning electron microscope and with a light microscope. Several features were observed which had possible significance to citrus root function. Root hairs were found on roots from every rootstock and depth; radial elongation of groups of hypodermal cells and bark cracks were frequently noted; and the epidermis generally deteriorated and was shed at a short distance from the root apex.

The chemical environment of soil from the experimental site changed considerably in pH, organic matter content, cation exchange capacity and mineral ion content with depth. A subsoil clay horizon differed in physical and chemical characteristics from the sandy soil. The soil environment at all depths appeared to be able to sustain considerable root growth. Soil physical data demonstrated the low water-retention characteristic of sandy soil.

INTRODUCTION

The existence of meaningful differences among root systems of agricultural plants has long been recognized. Many laborious excavations have revealed the rooting characteristics of both agronomic crops and fruit trees including citrus. Nevertheless, many years of research effort regarding the water and nutritional relationships between roots and their environment have yielded little direct information on the functional significance of root distribution. Most knowledge of the physiology of root systems has been obtained from studies on individual excised roots or small greenhouse plants in sand or solution culture. The few field studies have been largely limited to field crops which have relatively shallow roots and lend themselves more readily to study of their entire root system.

Root systems of fruit trees are diverse, often deep, and inherently difficult to investigate. Attempts to determine if any relationships existed between fruit tree root systems and certain scion characteristics have led to some gross observations and scientific evidence indicating that the size and density of a root system was related to tree size and fruit yield (31,217). In the past, it has generally been accepted that an increase in tree size was accompanied by a proportional increase in fruit yield and the size of the root system; however, size of root system may refer to lateral and vertical spread or quantity of roots. In the latter case, a positive relationship of citrus yield to feeder root quantity was demonstrated but a point was reached beyond which other factors began to limit yield (34).

A similar role for depth of rooting in plant growth and yield has also been supported by field observations and limited experimental data. Surveys of soils in deciduous fruit production indicated that both tree size and yield are favorably influenced by greater rooting depths. Studies of citrus trees also imply that deep, well-distributed root systems are essential for optimum growth and productivity. In Florida, the largest trees on well-drained sands, were associated with deep root systems (38). Moreover, the vertical development of root systems was not always associated with an increase in root quantity indicating some significance to depth alone. Trees that develop in the shallower soils of Florida are smaller and less productive where root growth is restricted.

It is not clearly understood whether differences in root systems are related to plant growth and yield; however, it is apparent that current economic and production requirements dictate the need to improve the efficiency of plant functions. Therefore, it is essential that the physiological significance of root distribtuion be investigated.

The objectives of this research were to study the water absorption pattern of 4 citrus rootstocks as it varies with depth of rooting and soil moisture stress and characterize the root environment of the same rootstocks as it varies with depth and relate this information to root anatomy and morphology.

LITERATURE REVIEW

The Citrus Root System

Control of Root Development

There are basically 3 forms of root systems among vascular plants, but only the tap root type is common in woody plants such as fruit trees (66). Root development is however strongly modified by environment (127). It is often difficult to ascertain the relative influence of heredity or environment, although one factor appears to predominate over the other in some instances.

Heredity seems to exert its greatest influence upon root development during the early stages of tree growth (127) For example, substantial inherent differences were evident in the root systems of young citrus trees budded to several rootstocks (188). Genetically stable characteristics of the root system are maintained as seedlings or young, budded or grafted trees grow older but other characteristics are increasingly modified by environmental factors (127).

Citrus Root Distribution

The physical difficulties inherent in studying the entire, often deep root system of a tree have hindered the accumulation of knowledge about such root systems. One of the traditional methods for examining root distribution until recently was the trench method (2,4,15,17,22,104, 164,165,215). This procedure required a considerable amount of laborious excavation that discouraged broad sampling. Newer methods such as the use of radioisotopes (85,151,152,153,185,186) and measuring soil moisture depletion (4,30,46,121,207) have eased the task of measuring root distribution.

General information on citrus root distribution has been reported from most areas of the United States where citrus is grown (2,30,32,33, 34,50,75), yet there are very few detailed descriptions of citrus root systems. Nevertheless, it was apparent from early root studies that *Citrus* and related species had a tap root system with the potential to root very deeply and extensively (50,75,145,171,215) and whose extent was strongly modified by the soil environment (2,76,77,78,149,172).

The most detailed and comprehensive descriptions of citrus root distribution have come from studies conducted in Florida. An early study reported the vertical and lateral spread of 4 to 6 year old nursery trees of sweet orange budded on several rootstocks (188). Striking differences were found in the character of the root systems; however, the results were representative of young, closely spaced trees. It was not known whether the root distribution of older trees was similar.

Ford was the first to quantitatively examine citrus root systems in detail (72,73,74,75,76,77). Comparisons were made on the basis of the dry weight of small roots collected from cores of soil taken at selected depths. Root systems of several common Florida rootstocks, rough lemon (*C. jambhiri* Lush.), Celopatra mandarin (*C. reshni* Hort. ex Tan.), sour orange (*C. aurantium* L.) and sweet orange [*C. sinensis* L. (Osbeck)] in the deep sandy soils typical of the central "Ridge" area of Florida were examined (75). Rough lemon rooted as deeply as 5.5 m in contrast to 3 m reported earlier (72) Trees on rough lemon were found to have as many as 50 percent of their feeder roots below 75 cm in the soil with 15 percent below 3 m. Ford consistently found in repeated sampling that trees on rough lemon in deep sandy soil were deep rooted with numerous well-distributed fibrous roots (72,73,74,75,77) Lateral roots were equally extensive, often reaching out to 8 m from the trunk. Ford later showed that lateral roots might extend a distance of 18 m (81). A report from California confirmed the general nature of the rough lemon root system but strong development of the tap root was not observed (217).

Sour orange roots occasionally penetrated as deeply as those of rough lemon but differed in root distribution. There were fewer roots below 75 cm in the soil and more above, especially in the 0 to 25 cm zone. Sweet orange roots were found to a depth of 3.5 m. Trees on this rootstock had the highest total weight of feeder roots for any rootstock studied. Cleopatra mandarin compared favorably to rough lemon in depth of rooting and total feeder root weight. Both sweet orange and Cleopatra mandarin had a larger proportion of their feeder roots near the surface than did rough lemon (75).

Ford's studies revealed that citrus trees are capable of extensive root development in a favorable environment. These results were confirmed and expanded in a recent study where root distribution was sampled twice over a 2-year period (38). This study included the 4 rootstocks examined by Ford plus Palestine sweet lime (C. limettioides Tan.), several citrange (C. paradisi x C. recticulata) cultivars, and 2 selections of trifoliate orange (Poncirus trifoliata Raf.). Trees in this experiment had a common scion and were planted in a site with fairly uniform sandy soil underlain by clay at 210 to 240 cm. General characteristics of the root systems were similar but trees on sweet and sour orange and Cleopatra mandarin rootstocks were not as deep rooted as reported by Ford. Total feeder root weights reported by Ford were generally smaller for all rootstocks.

The root system of trees on sweet lime was similar to that of trees on rough lemon. Other studies supported this observation (150,162,188). Trees on the trifoliate rootstocks were shallow rooted, 3 m, but they had a large number of feeder roots with the majority at less than 75 cm deep. Total feeder root weights were comparable to those of rough lemon. Trees on 'Rusk' citrange were consistently the shallowest rooted, 2 5 m, and had the smallest total feeder root weights. Those on 'Troyer' citrange were intermediate in depth of rooting and number of feeder roots, while those on 'Carrizo' citrange were similar to rough lemon. The lateral extent of rooting could not be accurately determined because the root systems overlapped in some areas (38).

Drastic modifications in the root systems described above can occur as a result of changes in root environment. Root growth in the Indian River area of Florida is severely limited by a high water table. The depth to the water table in this area necessitates bedding the land to provide an adequate volume of soil for root development. Depth of rooting is often limited to 0.7 to 1 m and 75 percent of the roots are found in the top foot of soil (76,81,172). Nevertheless, these root systems have a larger number of feeder roots per unit volume of soil as compared to the root systems of trees growing in deep sands (172).

It can be concluded that citrus trees even under moderate environmental restrictions have characteristic root systems which can be defined quantitatively. These characteristics are probably lost in environments where root development is severely limited.

Citrus Root Anatomy and Morphology[1]

Citrus trees form a tap root system. The primary root emerges from the seed coat and continues to grow and enlarge forming the tap root from which the main lateral roots arise. Secondary laterals along with the other main roots eventually form the framework as the root system expands. The smallest laterals branch and rebranch to support and form a network of "bunch-like" groups of fine fibrous or feeder roots.

Gross anatomy of an individual citrus root is similar to that depicted in textbooks (66) as typical of a woody dicotyledenous plant. The primary body of elongating roots consists of several distinct tissues and regions or zones of functional significance, including the root apex (root cap and meristematic area), zone of elongation and zone of differentiation and maturation.

A typical citrus root apex has 3 histogens. The basipetal root initial, or plerome, gives rise to the stele or vascular cylinder. The histogen adjacent to the plerome is the periblem which gives rise to the cortex. A common initial, the dermatogen-calyptrogen, gives rise to the epidermis and root cap, respectively at the root apex. The root cap is almost always present and easily recognized but is most prominent in rapidly growing roots.

The 3 root initials are not easily discerned in the root apex of the primary root but they can be identified in fibrous roots. The tissues arising from each initial are distinct at a small distance from the histogens. The meristematic organization in the root apex of Citrus is different from that of the pear, apple and peach (65,154,174,191).

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[1] This discussion is taken primarily from the work of Hayward and Long (109), Schneider (189) and Cossman (48). Contributions from researchers other than those mentioned are cited in the discussion.

The epidermis can be identified in the proximal portion of the meristematic region. It is generally 1, and occasionally 2, cells thick. Several different cell types appear in groups randomly distributed around the root as the epidermis matures. The outer tangential wall becomes thickened in 1 type while there is only secondary thickening and the wall remains very thin in another one. The epidermis is eventually sloughed off or ruptured by secondary growth and replaced by a periderm.

The tissue adjacent to the epidermis is the cortex. The outer layer of the cortex forms a hypodermis (exodermis) in the zone of elongation. The hypodermis is usually 1 cell thick and composed of cells considerably larger in volume than those of the epidermis. The outer periclinal walls become impregnated with some material of which there is disagreement as to its nature. It is agreed, however, that the inner walls become strongly suberized. The remainder of the cortex consists of thin-walled parenchyma tissue with an occasional sclerid or crystal. Peripheral cortical cells are generally smaller and thinner-walled with a denser cytoplasm.

The inner most single-cell layer of the cortex matures further behind the root apex in the zone of elongation and in the zone of differentiation into a specialized tissue called the endodermis. Conspicuous casparian strips, which are a continuous band of suberin in the transverse and radial walls of individual cells, appear in the mature region of the root. Unsuberized endodermal cells, called passage cells may occur opposite protoxylem strands.

The plerome gives rise to the stele which contains the provascular strands. The pericycle forms from the outer one or 2 layers of stelar cells and lies adjacent to the endodermis. Alternating strands of protoxylem and protophloem can be seen interior to the pericycle. The protoxylem strands are arranged in the shape of a multipointed star with the protophloem lying between the xylem strands adjacent to the pericycle. Primary roots typically have 6 to 8 protoxylem strands. The larger lateral or framework roots commonly have 3 to 5 strands while smaller laterals and fibrous roots have only 2 or 3 strands. The relationship of root size to the number of xylem strands has been observed in other fruit species (65,66,154,174).

The central tissue of fibrous roots is composed of metaxylem. The center of the stele in larger roots with polyarch xylem contains a parenchymatous pith interspersed with metaxylem particularly near the periphery.

Differentiation of the provascular elements begins at different levels in the stele. Young protopholem elements can be observed in the zone of cell division and more clearly in the zone of elongation near the root tip but protoxylem elements do not appear before the zone of differentiation. This pattern of vascular maturation is common in woody plants (66,182,223).

Secondary development of the citrus root closely resembles that of woody dicotyledons (66). Lateral roots frequently have extensive growth with little or no secondary enlargement occurring in the small fibrous roots. All tissues external to the pericycle are sloughed off in roots where considerable secondary growth has taken place. A transverse section of an older, large root will thus show a periderm, secondary phloem, cambium, secondary xylem, and pith. The xylem is diffuse porous. Vestiges of the cortex may remain in roots with less or no secondary growth although one or more periderms may be formed.

Secondary growth can result in the formation of longitudinal growth cracks. Tissues exterior to the new cambium are stretched beyond their elastic limit when the vascular cylinder enlarges and a cambium forms. The hypodermis proliferates locally by reverting to a meristematic state and forms "hypodermal absorbing areas" in some areas.

The most controversial facet of citrus root morphology has been the development of root hairs. Early general studies on citriculture indicated that citrus roots do not produce root hairs (116); however, this view has subsequently been disproven (48). Root hairs are finger-like projections from individual epidermal, and rarely hypodermal cells, which arise in the region of elongation. Their formation is apparently an adaptive response in that they may occur at different distances from the root apex in response to factors such as light, soil pH, temperature, and moisture and rate of root growth (93,126). Evidence proving the existence of root hairs has been largely obtained under laboratory or greenhouse conditions. There is little information available regarding their formation and response under field conditions.

Another relatively uninvestigated aspect of citrus root morphology is the mycorrhizal relationship of roots with different Endogone species of fungi. The fungal hyphae penetrate the root cortex, but this relationship has not been shown to alter the anatomy or morphology of citrus roots (120,147).

There is a paucity of information regarding the comparative anatomy and morphology of citrus roots collected from different rootstocks and from several depths in the soil. Differences were noted in the one instance where shallow roots of several rootstocks were compared as to cell size, mode of lignification of the pith, suberization in the endodermis, thickening of epidermal cell walls, and the shape of protoxylem strands (48).

Root Physiology

Several comprehensive reviews in the field of root physiology have been published in recent years (20,28,29,137,203). These reviews have encompassed the many facets of the subject, which have been studied in great detail, generating a large amount of literature and making it difficult to survey root physiology in its entirety. The present review, therefore, will be focused on the physiology and anatomy of water and ion uptake, preceded by a few remarks regarding procedures and new terminology which have arisen from these studies.

Preliminary Remarks

Most knowledge pertaining to root physiology has been obtained from investigations of excised herbaceous plant roots. Very few studies have employed roots of woody plants. Thus, it is commonly assumed that the information obtained from, for example corn roots, is applicable to woody plant species.

The object of many absorption studies has been to determine answers to questions such as how ions and water move to the plant root, by what mechanisms and pathways do ions and water move radially to the xylem, how are root function and anatomy related, and what factors influence them.

It is generally agreed that the first step in the absorption of mineral ions is the free diffusion of ions into the "apparent free space" (A.F.S.) (63,126). The A.F.S. is composed of 2 parts, "outer" and "Donnan" free space (63,126). Both represent extracellular space within the root that is in direct contact with the soil solution. A continuum is formed in fact by which ions are able to freely diffuse from the soil solution into the root, primarily the cortex region. The "Donnan" free space is that part of the A.F.S. where ions are adsorbed onto the negative exchange sites present in cell walls.

There are several unresolved questions regarding the A.F.S. It is not agreed how far it extends into the root; however recent evidence indicates that the endodermis is probably the inner boundary (137). Secondly, there is a question as to the boundary of the A.F.S. on a cellular level. The plasmalemma is often considered the first barrier of a cell (63,126), while others consider the tonoplast as the primary boundary (135).

The "Donnan" free space has been implicated in ion uptake. It has been suggested that it qualitatively affects ion absorption as a result of the cation exchange (C.E.C.) sites in the cell walls (196,197,210, 211). Roots with a high C.E.C. favor the uptake of divalent cations over monovalent ones (197,224). Nevertheless, the importance of the root C.E.C. has been challenged. It is uncertain how reliable C.E.C. measurements are and the supposed influence of C.E.C. on the selectivity of ion absorption is not well established (63). The "Donnan" free space may be important, though, at extremely low ion concentrations (63).

Theories of Ion and Water Absorption

An important function of roots is to supply the aboveground parts of the plant with water and mineral nutrients. Ions and water must move through the soil to the root to perform this function. Ions then move from the root surface into the A.F.S. of the cortex where they are accumulated. These ions, and water, then move laterally into the xylem where translocation takes place (63,126).

Events occurring prior to ion movement into the stele, and their subsequent absorption by the xylem, are reasonably well defined and agreed upon. Two processes, first, ion absorption by the cortical cells, which requires crossing the plasmalemma, and, second, radial transfer of absorbed ions to the xylem, are occurring simultaneously in that region of the cortex where the A.F.S. exists (63,126). The first event takes place independent of water movement. The second process is affected, however, by the rate of water uptake.

The first activity presents 2 pathways for radial movement of ions. Ions may travel from vacuole to vacuole or through the cytoplasm of adjacent cells or the ions may move through the A.F.S. if they are not absorbed. Free diffusion beyond the endodermis is usually considered to be prevented by the deposition of suberin (43,63,126).

The first pathway, within the cell, is not too important because the vacuole is considered an ion "sink" where ions are deposited (126,137). It has been shown that ions do not leave the vacuole rapidly (28). The second pathway is considered the primary route. Ions move from cell to cell through the plasmodesmata. This pathway is called the symplasm as opposed to the apoplast or the A.F.S. (29). Each pathway, including free diffusion to the endodermis, has some significance, but the symplastic path is thought to be the most important.

Ions are carried to the vascular cylinder via the symplasm where they are transferred to the conducting xylem elements and translocated to the shoot. It is not known how the ions gain entrance into the xylem.

This problem was recently reviewed by Brouwer (28). It is apparent that some form of metabolic activity is involved (63). Earlier, it was thought that the endodermis actively secreted ions into the stele (63,126). Ultrastructural studies have not shown the endodermis to be particularly suited for secretion (18). Nevertheless, the endodermis is considered an effective physiological sheath, which in the suberized state, prevents free diffusion of both water and ions into and out of the stele (43,48).

There are essentially 4 hypotheses which attempt to explain ion absorption and translocation. They are generally in harmony, as mentioned previously, with the major divergence involving the processes occurring in the vascular cylinder.

The oldest and most frequently cited theory is that of Crafts and Broyer (49) which proposes that ions are actively accumulated by cells in the well-aerated cortex, move symplastically into the stele and "leak" out. Oxygen-deficient stelar cells are less able to retain ions and therefore they escape and accumulate in xylem cells. This theory has been subjected to criticism on several grounds. One of the strongest arguments raised against it has been the demonstration by electron microprobe analysis that stelar cells often contain a higher ion concentration than cortical cells (137).

Laties and Budd (136) modified the Crafts-Broyer theory by suggesting that an inhibitor prevented the stelar cells from retaining ions. This hypothesis is similar to Crafts-Broyer and has been criticized on the same grounds.

Hylmo (117) proposed that xylem cells with living protoplasts accumulate ions that are released upon the death of the protoplast. There is little experimental evidence to support this hypothesis. However, it was found in corn roots that ion uptake was associated with the number of living xylem cells in the stele. Both uptake and the number of living cells decreased basipetally from the root apex (6).

These 3 theories presume that some form of active or metabolic, energy-requiring process is responsible for the absorption of ions across the plasmalemma in the cortex. This process is the basis for the fourth theory, the carrier theory of Epstein (63,64). Evidence such as the effect of temperature, oxygen and metabolic inhibitors all indicate that some form of active process is occurring (63). Salient features of this hypothesis include:

(1) A carrier molecule located in the plasmalemma unites with an ion exterior to the cell and carries it across the membrane where it is released into the cytoplasm.
(2) Michaelis-Menton kinetics are applicable.
(3) The kinetics of the mechanism imply an enzyme-like situation and ion selectivity.
(4) Two mechanisms are involved, one operating at low ion concentration and the other at high ion concentration.
(5) The mechanism requires Ca in order to maintain the semipermeable state of the plasmalemma.

This hypothesis proposes that ions are accumulated in the cortex, move through the symplasm into the stele, and then are transferred out of stelar cells by carrier molecules into adjacent xylem cells. This view has not been completely accepted. Sites of the high and low concentration mechanisms have been vigorously debated (63,135). Also, the carrier molecule has not as yet been physically or chemically identified (64).

The physiology of water uptake has not been as difficult to elucidate as the uptake of ions. Water moves through the soil and plants largely in response to decreasing gradients of water potential (205). The gradient within the plant is dependent upon the rate of water loss due to transpiration. Therefore, water absorption is primarily a dependent and passive process. Water follows the path of least resistance within the root and moves by mass flow through the A.F.S. Water does not, however, flow unhindered as evidenced by the frequently observed lag of absorption behind transpiration. Water movement is resisted in the root, chiefly due to the need for water at some time to pass through living cells (126). A primary point of resistance is the endodermis (43,48).

Ion uptake has been reported as being directly proportional to the rate of water uptake; however, the considerable amount of evidence regarding the validity of this effect is conflicting (28,29).

Relationship of Root Anatomy and Morphology to Ion and Water Absorption

Absorption of water and mineral nutrients by a root is related, in part, to its anatomy and morphology. Evidence for this relationship has been obtained primarily by examining the uptake of various radioisotopes and water by isolated segments along intact roots. This information is then correlated with changes in anatomy at the respective sites along the root.

Numerous studies have shown that many roots have a region characterized by a large accumulation of ions, a second region where a large number of ions are absorbed and translocated and a third region where the activity of the region is not firmly established and varies considerably with the plant species (126,184,219). The first region corresponds to the meristematic root tip. Meristematic cells are small, filled with cytoplasm, and closely spaced, with little intercellular space. Movement of water and ions is therefore strongly impeded. Moreover, it has been suggested that slow movement of water and nutrients in this region restricts activity of the root tip and is, thus, the primary factor limiting root growth (126). It is commonly noted in uptake experiments, despite the apparent impermeability of the root apex, that this region is the site of maximum ion accumulation (184,219). Earlier investigations led to the false conclusion that this region was paramount in the supply of nutrients to the plant (126). It is now thought that accumulation in this region occurs as a response to high metabolic needs of the root apex (126).

The second uptake site corresponds to the location in the root where elongation has essentially been completed and differentiation is beginning. The cortex is well formed with large vacuolate cells here. The endodermis has casparian strips and suberization has begun. Mature xylem elements are present. The root is most active in simultaneous absorption and translocation at this level (219).

The endodermis continues to suberize and the cell walls thicken beyond the site of maximum uptake and translocation. The epidermis, and hypodermis if present, suberize. The endodermis, epidermis and hypodermis represent possible barriers to water and ion movement. Tissues external to the pericycle are shed when secondary growth occurs and a periderm forms. Suberized cells formed from the periderm and vascular cambium may then function as barriers at this stage. Little or no absorption is thought to occur at this point; however, it has been shown that some absorption does occur in this region in trees (1,125,128). The volume of soil occupied by unsuberized roots is too small to supply the water needs for an entire tree. Therefore, it is significant that some tree roots, for example, citrus, can absorb water through lenticels and growth cracks in the surface of older root tissue (52,110).

The relative positions of the regions described above are thought to be similar for most roots. Actual distances from the root apex are not known for most plants for these regions and appear to be dependent upon plant species and the rate of root growth (126).

A recent report (43) exemplifies the present manner in which the relationship of root function to anatomy has been approached. In this study, the experimental units were the intact roots of barley plants. Root segments were isolated in a solution of radioisotopes and their absorption pattern recorded. Cereal and other agronomic crops are commonly used in this type of experiment. The root system of barley, like those of other monocotyledonous plants, consists of 2 types of roots; seminal roots or those of embryonic origin and nodal (adventitious) roots that arise from the growing shoot. Laterals arise from the seminal and nodal axes. They differ in anatomy, the seminal axes containing only 1 long vessel in the stele. Nodal axes have several vessels in which the individual elements are shorter (101).

The results of the investigation, which are listed below, confirm earlier findings (19,183,184,185) and add some new information.

(1) Ion uptake was related to root volume more so than to any other physical dimension.

(2) Seminal axes absorbed the most PO_4 per unit volume with the absorption peak for all roots located 2 to 5 cm behind the root tip.

(3) The point of maximum absorption corresponded to the point where cell elongation was complete and mature vascular tissue was present.

(4) Uptake for some ions, viz. Ca, was dependent upon root anatomy.

(5) The symplasm, by way of plasmodesmata, extended through the endodermis.

(6) Sites of maximum ion and water uptake were essentially identical.

(7) Removal of the cortex (stele stripping) eliminated some barrier to ion and water uptake thought to be the endodermis.

Many experiments of this nature point out the need to study water and nutrient uptake on the basis of an individual root. Survey of the literature shows that there is a virtual absence of any comparable research involving species of fruit trees. However, the relative location and anatomy of the site of active uptake and translocation for some tree roots is similar to that reported for common experimental plants such as barley (48,65,109,154,174,189,191). Consideration must then be given, assuming that all roots have a zone of active absorption and translocation of minerals and water, to: (1) anatomical features of this region that seem to have some functional significance and (2) how these features may differ between plants, thus affecting the functioning of their roots.

Nearly every aspect of the root anatomy in the active absorption zone has some meaning in terms of root function. The epidermis in the suberized state has been proposed as an important ion barrier (28,48); however, the endodermis is considered to be the primary barrier regardless of its actual role. The importance of the epidermis in explaining absorption differences between plants must consider factors other than its physical presence. Most plant roots have an epidermis but each epidermis does not have the same dimensions nor does each one exhibit the same degree or rate of impregnation with suberin or lignin (48,126). Quantitative and qualitative differences in suberization of the epidermis have been observed between several species of citrus (48). Moreover, citrus has a hypodermis which suberizes and thus may enhance the barrier effect of the epidermis.

The cortex is the primary accumulation site for ions. Thickness of the cortex and the proportion of individual cell contents may be important factors. An increase in the thickness of the cortex provides a larger absorption surface area. Then, an ion may follow 1 of 2 pathways once it is absorbed, either through the symplasm or into the vacuole. Cells with large vacuoles may be more competitive for ions thus reducing the radial flux to the xylem (28).

The endodermis is generally agreed to serve as a passive barrier to water and ion movement due to casparian strips (43,126). Two features of the endodermis are, therefore, significant. First, the time and rate of formation of casparian strips and subsequent suberization may be important. Second, unthickened endodermal cells (passage cells) are frequently found adjacent to xylem arches. These cells represent permeable sites in the endodermis. They have been observed in Citrus (48).

The significance of anatomy in the root vascular cylinder at the level of active uptake is more controversial than any other zone in the radial pathway of ion and water transfer (137). The stele in this zone is composed of parenchyma cells and mature xylem and phloem elements. Several hypotheses have been proposed which attempt to explain the function of these tissues. Briefly, it is thought that ions are released either passively or are actively secreted into the xylem. Active secretion is considered a reversal of the ion absorption that occurs in the cortex. Therefore, the ions must cross a membrane, either the plasmalemma of parenchyma cells adjacent to metaxylem elements (137) or the same membrane of the xylem elements themselves (137). Xylem parenchyma cells have been implicated because they have a known large capacity to accumulate ions (137). The xylem elements have been implicated on the basis of a recent report which showed a positive relationship between the amount of ion absorption along a root and the number of xylem elements that had retained their cytoplasm (6). The actual mechanism of ion transfer to the xylem is unknown, but it is not unreasonable to assume that the certain stelar cells are involved. Quantitative differences in these cells within the stele may be responsible for differences in physiological behavior (137).

An area of the root which has not been as fully investigated as the regions closer to the root apex lies above the root hair zone and the site of active water and ion uptake. Suberization and lignification of primary tissues or periderm and cambium formation during secondary growth supposedly prevent the easy movement of water and minerals in this region (126).

The physiological significance of this supposed impermeable area has not been determined. It is known that water and minerals may enter through this region in some plants (1,110,125,128). Entrance of these materials into this area is probably due to pathways opened by emerging lateral roots, growth cracks, and lenticels (126). Also, the observation that high rates of water flux increase the width of the absorbing zone significantly is indicative of the complexity of uptake. Thus, it seems probable that the contribution to absorption by this zone may be considerable, especially by the suberized roots of trees (1,125,128).

Considerable attention has been given to root hairs and root volume because of their possible relationship to water and ion uptake. Root hairs are found in many woody plants although rarely in large numbers under field conditions (16,47,111,179,180). It is difficult to obtain field samples for study because of the fragile nature of root hairs. Development of root hairs is influenced by root environment and their presence can add to the root surface in contact with the soil. There is, however, no consistent evidence indicating that root hairs are important for either water or mineral ion absorption (47,126,157). Root volume has been the physical dimension of a root most consistently related to uptake in controlled environments (19,43,183,184,185). One cannot assume that the same relationship would be equally applicable in a field environment where many variables could influence root volume.

The Soil Environment and Its Effects on Root Structure, Function and Distribution

The edaphic environment of a root system is complex and highly variable and has a profound but meaningful influence on the development of root systems and root growth. The task of identifying the components of this environment and studying their relationship to plant roots has been difficult. The numerous physical, chemical and biological aspects do not function independently but are strongly interrelated. The plant root is continuously responding to and "integrating" changes in its surroundings. Thus, researchers have often been restricted to studying only 1 or 2 factors under artificial conditions. The real cause of a noted response is not always known with certainty in these circumstances, as in the field. Nevertheless, there is ample evidence to support some general observations regarding specific soil factors.

Soil Texture

The physical entity which supports plant root systems is the soil. Texture is an important soil characteristic based on the percentage particle-size distribution of the solid mineral matter. Pore size and distribution, another significant physical characteristic of soil, results from the spatial arrangement of the particulate matter. The texture of a soil is intimately related to soil moisture and aeration. Mineralogical attributes of the various particle fractions greatly influence soil chemistry. Thus, soil texture exerts a rather broad influence over the soil environment in addition to influences that result directly from its own physical nature. Indirect effects of texture upon roots are discussed where appropriate in later sections. This discussion is devoted primarily to the direct physical interaction of soil texture and root growth.

Field observations have shown that certain soils or soil layers limit root growth. Tobacco and corn roots were restricted by tillage pans (56,71,119). Citrus roots were prevented from further extension by a subsoil clay layer (37,75). The direct cause of this restriction is not always known, but it is generally agreed that "soil strength" has a significant role. Root growth here is mechanically impeded.

The ability of soil to limit root extension is approximated by determining "soil strength" with a penetrometer (60,96,98). A thin probe constructed to be physically similar to a root is driven into the soil and the resistance measured. The force required to penetrate the soil is related to texture and bulk density. Root extension ceases if the soil offers a greater resistance than the maximum pressure a root can exert.

Soils containing a large percentage of fine particles such as clays, have higher bulk densities and are more resistant to root penetration than sandy soils. Clay soils are less susceptible to compression and have a greater number of small pores. Controlled experiments that employed materials with known pore sizes showed that roots did not penetrate pores with diameters smaller than those of young roots (220).

Soil density is related to texture and may impede root growth as described above. Studies of bulk density showed that this factor was negatively correlated to root extension (205). In one case (208), an attempt was made to establish a "threshold bulk density." Increases in bulk density in the form of tillage pans and other compactions due to cultural operations restricted root penetration (56,71,119).

Mechanical impedance affects root structure and distribution. When growing roots encounter strong resistance in the soil, they ramify and individual roots become shortened, stubby and often expand radially in the region behind the meristem (11,12,60,71). The number of root hairs may increase and act as miniature anchors as the root exerts pressure on the soil (60). Lateral and tap root development may be severely reduced (98,113).

Changes in root structure resulting from mechanical impedance reduce the rate of water and mineral absorption because root growth is restricted (126).

Soil Moisture

Water is essential for all stages of plant growth and development and is normally obtained from the soil through the root system. Root growth is affected as well as the growth and yield of the whole plant when there is insufficient moisture in the soil profile. Plant roots are also unable to function when soil pore spaces are filled with water. Plants are subjected to a "physiological drought" under these circumstances, where water absorption is inhibited indirectly as a result of reduced aeration (126). This phenomenon is not completely understood, but it is apparent that roots are able to survive when inundated by water as evidenced by their growth in aerated solution culture.

Plants vary in their ability to withstand wet or dry habitats and also differ in the anatomy of their roots (67). Roots of plants from wet environments frequently have a larger cortex with a greater percentage of intercellular space (126). Some differences in cortical porosity have been demonstrated for several species of citrus (143). Furthermore, the soil moisture status affected quantity and length of root hairs (48).

Roots develop a characteristic anatomy which reflects the moisture status of their environment, but other changes occur in response to daily and seasonal moisture fluctuations. The primary response is the cessation of root elongation as has been reported during seasonal dry periods when root growth stops despite an otherwise favorable environment (48,162,171,176,179). Failure of roots to continue elongating is thought to result from the inability of a plant to maintain the necessary water potential gradient to cause water movement into the root (205).

There are few reports regarding the quantitative effects of soil moisture stress on such factors as plant growth or yield. Nevertheless, some evidence is available implying basic differences between plants in their response to soil water deficits. Such differences may be anatomical or physiological. Studies with citrus trees have repeatedly demonstrated the greater ability of trees budded to rough lemon and sweet lime rootstocks to extract water from the soil (42,161,162,163). Roots of these rootstocks have an inherently high osmotic value and are therefore able to maintain water movement during greater stresses compared to other rootstocks (48); however they also have larger root systems.

Soil moisture stress modifies root distribution. Irrigation water is used to supplement rainfall to prevent water deficits in most areas where cultivated plants are raised. It has long been debated whether depth of rooting and root proliferation are controlled by irrigation. Rooting depth was not increased, in one case (115), in contrast to more recent reports (33,35) showing that less frequently watered trees rooted deeper. Studies with citrus trees showed that frequency of irrigation can significantly alter root distribution (33,35). Those trees which were subjected to frequent additions of water had a large percentage of roots near the surface. Those less frequently irrigated had more evenly distributed root systems. Roots growing in soil with a continuous supply of water tend to branch and ramify throughout the available volume of soil, while roots growing in drier soil are prone to extension of individual roots rather than the formation of laterals (53).

Soil Aeration

An adequate supply of O_2 is an essential prerequisite for good root growth. Poor soil aeration limits the metabolic activities of roots, eventually reducing plant growth. Soil O_2 concentration is usually lowered while the CO_2 level increases during root and microbial respiration. Thus, the O_2 and CO_2 composition of the soil atmosphere commonly changes reciprocally and the sum of the 2 gases parallels that of the aerial atmosphere (21,205). Soil O_2 and CO_2 also show seasonal fluctuations due to changes in soil temperature and water content (21,24). Moreover, CO_2 content generally increases with depth (21,24).

Oxygen consumed by root respiration must be replaced and CO_2 released must be removed in order to avoid permanent damage to the root system. Many plant roots are not affected by high O_2 content. They are capable of functioning within a wide range of O_2 concentrations (23). The critical O_2 concentration may vary, however, according to the phase of root activity (25,140). It has been suggested that the rate of O_2 supply and CO_2 removal are more significant than their content in the soil (95).

Gas exchange occurs by diffusion and mass flow (95). The effectiveness of these processes is related chiefly to soil texture. Soils with a loose texture and structure readily permit gas movement (21,205). This is evidenced by the analysis of air samples collected at different depths from these types of soils (21). The gas composition of the samples was very similar to that of the above ground atmosphere (21). Finer textured soils have a larger number of small pores that restrict gas movement and consequently, allow CO_2 to accumulate to high levels.

Soil water content is an important factor in gas exchange. Oxygen diffuses considerably faster through air than water. There is very little gas exchange when the total pore space of a soil becomes filled with water. Roots must rely on their inherent capacity to tolerate flooded or essentially anaerobic conditions. Thus, it has been suggested that deeply rooting trees possess in their deep roots an ability to tolerate low soil O_2 (126,201,202,221,222). Research with small citrus plants demonstrated some rootstock differences during controlled flooding tests (79). Rough lemon, 'Rangpur' lime, and 'Carrizo' citrange had satisfactory tolerance. Sour orange, sweet orange, and trifoliate orange were damaged by flooding. Cleopatra mandarin was the least tolerant of all rootstocks tested. Root damage has also been shown to result from the microbial production of toxic substances, such as H_2S, under anaerobic conditions caused by flooding (79,80).

Some plants, such as those growing in bogs, are adapted to wet environments and have a well-developed internal transport mechanism for supplying O_2 to their roots. This has been verified with radioactive tracer studies (10,97). Circumstantial evidence indicates that a similar system is present in some mesophytic plants (97). Differences in root anatomy, especially gas space as has been found in some citrus rootstock seedlings, may be significant (143).

Root function is impaired during periods of deficient aeration (105). Moreover, root efficiency also falters during periods of unusual O_2 demand. For example, root O_2 requirement is greatly increased as a result of the stress encountered upon growth into a mechanically stronger soil layer. Roots also require additional O_2 as soil water potential decreases. Water uptake is reduced if this need is not met.

Experiments with citrus and avocado seedlings illustrate the effect of deficient aeration on ion uptake. Absorption of all ions was reduced except for N. This nutrient was supplied in the NO_3 form. Liberation of O_2 during its reduction was thought to enhance its uptake (130,131, 132,133,141).

The O_2 status of the soil indirectly influences the absorption of certain micronutrients. Iron chlorosis in sweet orange was associated with O_2 deficiency and limed soils (212,214). There is considerable uncertainty as to whether an O_2 deficit per se or CO_2 was responsible for the observed effects (213,214).

The morphogenetic effect of O_2 is manifested primarily through the activity of apical and lateral root meristems. Low soil O_2 stimulates branch root formation and depresses root elongation (90). Root hair formation requires adequate aeration (47,48,93).

Soil Nutrients

The primary source of mineral nutrients for plants growing in soil, is the solution bathing the roots (9). The quantitative and qualitative composition of this solution is constantly changing as nutrients are absorbed and replaced by natural processes and fertilization. Those changes resulting from normal root activity, do not generally have any unfavorable effects upon the roots. Undesirable consequences on root growth and function are usually due to the accumulation of excess salts in the soil, and specific ion effects.

Root growth is reduced and root maturation hastened when the total salt concentration of the soil solution reaches an inordinate level. The high osmotic potential of the external solution prevents water absorption and seems to reduce root permeability. Plant root permeability, nevertheless, is apparently affected only temporarily and roots recover after a short period of time. Rate of water uptake, however, is then less than the original rate (126). Ability of a plant to tolerate high salt levels is a function, in part, of the species. Considerable research has shown that Cleopatra mandarin and Rangpur lime have high salt tolerance, while rough lemon, many mandarins, tangelos, sweet oranges and sour orange have moderate tolerance. Sweet limes, trifoliate orange and citrange cultivars generally are intolerant to salt (39).

There are several well-established specific ion effects. Excessive quantities of either Cu, P, N, Cl or B are known to damage citrus roots (35,39,84,193,198,199). Roots from high Cu soils differ in color from healthy ones (26,69). They are shriveled, corked and lack an active meristem. Lateral roots were reduced to stubby outgrowths. Copper accumulates in the hypodermis, endodermis and pericycle. These accumulations were thought to "plug" the root and interfere with root function. The number of feeder roots was decreased and their distribution modified by excess P and N in the soil (35,84,192,198,199). Similar responses were noted in Fe deficient soils (83). Root hair formation was reportedly depressed by high Ca (47).

Ca and B are recognized as being essential for root growth (41,126). Roots have failed to penetrate soil in which Ca is absent (88,114). Neither nutrient is apparently readily translocated within the root system. Therefore, they must be available in the root environment. Roots become short and stubby and eventually die when either Ca or B is absent (41). Other nutrients, however, such as K, are translocated via the root system from soil areas adequate in K to roots growing in soil containing no K (27,55).

The overall fertility level in a soil affects root quantity and distribution. Trees growing in infertile soils often have a greater root:shoot ratio as compared to those growing in fertile soils. Differences in this ratio have been interpreted to indicate that less root growth or permeation of the soil is needed to supply the required nutrients in the latter case (175,176,177,178,181).

Changes in nutrient concentration and balance indirectly influence roots through changes in soil pH, structure and modifications of the microbial population and their activities, in addition to direct effects.

Soil Temperature

Most plants are adapted to a wide range of temperatures. They are able to function satisfactorily within this range but optimum growth is generally restricted to only a small part of the spectrum. Moreover, the temperature response of a plant varies with species, stage of development and O_2 supply (126). It is also possible that the temperature range, and that part of it optimum for growth, are different for the roots and the aerial parts of a plant. The soil temperature reportedly most favorable for root growth of deciduous fruit trees is 25°C (126). Citrus trees have maximum root growth rates at slightly higher temperatures, which are species dependent (155,156,159,160,171).

Root growth and function are not greatly impaired by soil temperature fluctuations until very high or low temperatures are reached. Cool or cold soils halt or severely reduce root extension and maturation (218). Roots of herbaceous annual plants generally deteriorate and die when growth stops. Woody plant roots, however, often only become quiescent and resume growth when the environment is again favorable (103). Roots of many deciduous tree fruits cease growth at soil temperatures ranging from 4 to 10^{o}C; however, death does not occur until much lower temperatures are reached.

The reported "vital" temperature for citrus is 13^{o}C (155,216). At this temperature, most physiological activities appear to cease, including root extension. It is not known whether this temperature can be equally applied to both roots and shoots or to all species of citrus. Nevertheless, in California, soil temperatures below 13^{o}C apparently caused root growth to be periodic (171). Root growth is not normally limited by low soil temperatures in other areas, such as Florida (59).

Soil temperatures well above the optimum also prevent root growth (44). Only a small quantity of active roots was found in the top 30 cm of soil in some deciduous fruit orchards during July and August because of high soil temperature and rapid loss of moisture (168). A scarcity of citrus feeder roots near the surface has also frequently been observed in Florida (37,75) where the surface soil temperature may reach 33^{o}C during summer months (59).

Changes in root activity are not entirely associated with soil temperature (112). For example, some citrus root growth was observed in California during the winter months (51). Soil temperatures and some internal factors apparently interact in controlling the growth of individual roots, but water stress and temperature often override the intrinsic controls (104,107,171,227). Further evidence obtained from observations of roots grown in uniform environments supported this hypothesis (227).

Temperature extremes that do not cause root death normally affect only the rate of root activity in water and ion uptake (36,94,100,124, 134,148). Thus the transpiration rates of young, budded citrus trees were reduced at root temperatures above and below the optimum (139,161). Citrus and apple trees continued to absorb N at temperatures as low as 0 to 5°C but at reduced rates (3,14,40,209). Greenhouse studies with citrus have shown marked effects of variations in soil temperature and rootstock on the scion leaf mineral content. Significant differences in absorption and translocation were noted for most nutrients (159).

Root structure is affected by temperature changes primarily as a result of modifications in differentiation. Peach and apple roots grown at temperatures above their optimum, 20°C, had tips containing fewer primary cells, were smaller in diameter and vascular tissue had differentiated closer to the apex (153). Cortical cells were suberized and many appeared dead. Roots grown below optimum temperatures were white and succulent. Differentiation occurred at a greater distance from the root tip. Other plants have an opposite reaction: root extension proceeds at a faster rate than maturation at higher temperatures compared to lower temperatures where maturation follows root growth closely (126).

Temperature indirectly influences root morphology particularly the occurrence of root hairs. The zone of elongation, where root hairs emerge, is lengthened and persists longer when root maturation is slowed by either high or low temperature (153).

Soil pH

Solution culture studies have shown that many plants are capable of satisfactory growth over a wide range of pH values (7,8). The pH range for adequate root growth in soil is more limited, however, and the primary effect of pH changes is indirect. Generally, a soil pH near 6.0 is considered optimum for most plants because large departures from this value render essential nutrients unavailable. Also, at very low pH values other elements such as aluminum and manganese become soluble in toxic amounts.

A change in pH is by definition a change in H^+ concentration. Thus fluctuations in soil pH do not preclude a direct effect on roots due to H^+ toxicity. Smith (169,194) has been a particularly active proponent of this hypothesis. He contended that most pH experiments were poorly designed and were unable to separate direct from indirect effects of pH. Smith (194) studied the ion uptake pattern of citrus seedlings growing in solution culture with a pH of 4.5 or 6.0 and ample available nutrients. Fewer ions were absorbed at the lower pH and root growth ceased. Other researchers have conceded a possible toxic effect of H^+ at very low pH values but there is less agreement about its direct effect at pH values near neutrality (7,8,99,170).

Citrus root growth and morphology were modified by pH in the experiments of Smith (194). Root elongation was severely reduced or stopped below pH 4.0 to 4.5. Roots became thickened and turned brown but were not killed. Roots were white, smooth and elongated freely at pH 5.0. Root hairs were most prevalent at pH 6.0, which allowed rapid root growth. Root growth was proportionately reduced without any apparent deviation in morphology above pH 6.0.

Soil Microorganisms

The micro-environment immediately adjacent to roots, or rhizosphere, is the habitat for a large and diverse population of microbes, primarily bacteria, fungi, and actinomycetes. These organisms are involved in a large number of activities which include important mineral transformations, various types of associations and specific pathogenic infections of roots. Recent emphasis in rhizosphere investigations has been to determine how these microbes affect the supply of nutrients to roots and the characteristics of roots that are related to water and nutrient absorption.

The microbial composition of the rhizosphere has been used to gather information regarding the root microenvironment and root physiology. For example, isolating anaerobic bacteria from well-aerated soil indicated a localized O_2 deficiency (20). Furthermore, many plant roots seem to exude a mucilagenous material, called mucigel, that is often cited as a dominant factor affecting the qualitative nature of the microflora (20,102,118). The mucigel may be colonized by specific microbes depending upon its chemical nature. Mucigel has been observed on citrus roots (26,69,189,190).

Many essential elements are mineralized or rendered unavailable by microbial activity, especially that of bacteria. They are particularly significant in N transformations. Certain species which form nodules modify root morphology and function but bacteria with the exception of the N-fixing species do not generally affect roots other than by intercepting nutrients which might otherwise normally be absorbed by the root.

Fungi are virtually ubiquitous in the rhizosphere and are responsible for many pathogenic infections. Some form mycorrhizae which greatly alter certain roots of Pinus and related gymnosperms (20,106). This ectomycorrhizal association causes pine roots to form an apparent dichotomy. Root hairs are absent. Fungal mycelia form an external sheath and penetrate the cortex up to the endodermis. The function of this fungal association remains moot but considerable evidence supports a role in the uptake of immobile ions such as P when the native fertility is low. This suggested role is manifested, in view of the absence of root hairs, through the increased effective absorption volume and surface area resulting from infection (20,123,126,127).

Other types of fungi form endomycorrhizas (92,146). The fungus invades the cortex and does not form a sheath. There is little or no change in root form. The nature and extent of this association has been largely overlooked and is not well understood. Citrus forms this type of association without any apparent change in root anatomy (120,147). Root hairs are reportedly absent in endotrophic roots as with the ectomycorrhizas (48,123).

Two soil-borne organisms, burrowing nematode (Rhadopholus similus Cobb) and citrus nematode (Tylenchulus semipenetrans Cobb), are serious pests of citrus.

Burrowing nematode occurs to considerable depths in deep sandy soils in Florida where it is of cardinal interest; however, high soil temperatures and rapid loss of moisture prevent a large population from developing in the surface 2 to 3 feet (62,82). Burrowing nematode attacks young feeder roots causing a quantitative decrease in the number of these roots as compared to healthy trees (58,74). Nematodes enter a root in the zone of elongation or at the root tip. Growth ceases if the root apex is damaged. The primary tissue damaged is the cortex. Other tissues are invaded but not suberized or lignified cells (58). Certain apparent morphological changes have been noted, one of the most interesting being the induction of local proliferation of the pericycle when penetrated by a nematode (58).

Citrus nematode is a serious pest in California and is common in Florida. It poses a more serious threat because it can form cysts. Also, it occurs throughout a soil profile. A study conducted in California showed some basic differences in entry sites and damage caused by this nematode compared to burrowing nematode (190). The citrus nematode penetrates older fibrous root tissue and does not normally feed deeper than the outer layers of cortical cells. This nematode does not appear to have any profound physiological or morphological influence because invaded roots are able to initiate new roots in the vicinity of infection. Invaded areas are readily isolated by wound periderm.

The Influence of Depth of Rooting on Root Structure and Function

Anatomy

Most roots used for anatomical studies have been obtained from young plants grown in a controlled environment. Those roots collected from more mature plants growing in the field have been taken from shallow depths in the soil. No reports describing the anatomy of roots collected from below the soil surface were found in the literature.

Water Absorption

A deep and extensive root system is generally believed to be a drought survival mechanism for trees (89,123,166,226). Many deep-rooted plants appear to remove water in proportion to the quantity and activity of their feeder roots when soil moisture stress is absent and the soil profile is uniformly moist (4,5,46,142,207). Deep-rooted plants often have a large percentage of their roots located at shallow depths (4,57, 108,144,225). Therefore, soil moisture is depleted first at this level. Reduced availability of water in this region is then compensated for by increased absorption at successively greater depths in the soil. It is only under these circumstances that deep roots have been shown to markedly increase their rate of water uptake and substantially contribute to the total water needs of a plant (205).

There are conflicting statements in the literature concerning the response of roots growing in soils of different water potential to total plant water requirement (86). Nevertheless, data from irrigation (87) and "split-root" (27,138) studies have generally supported the contention that when roots in one area are stressed, water uptake increases in other root zones where the water potential is higher. The water uptake of deep roots in frequently watered plants is usually smaller than that of less frequently irrigated ones in irrigation experiments. The root system of a small plant is divided in half with each part placed in an environment (soil or solution) that differs in water potential in "split-root" studies. Root response to water stress can be observed in this manner.

The moisture depletion pattern of citrus root systems is reportedly similar to the typical case described above; however, these studies have not always been supplemented by a study of root distribution (40,91,121, 122,187). Thus, it is not known if water absorption occurred in proportion to root quantity. A deviation from this relationship was apparent in one study where moisture depletion and root distribution were compared (30). Deep roots were found to be more efficient, i.e., they absorbed more water per unit weight of root compared to surface roots. Moreover, the water absorption pattern for the same rootstock varied with soil texture.

Nutrient Absorption

Available information regarding the relative extent to which nutrients are absorbed from different depths in the soil is meager. Early investigations were limited to those of Weaver (54) who placed fertilizers in different zones in the soil, separated the zones with wax seals permeable to roots, and then recorded plant mineral content and yield. These investigations were conducted with relatively shallow-rooted plants but Weaver showed that moderate quantities of nutrients were absorbed by deep roots.

The method of Weaver has been criticized because it was subject to limitations imposed by changes in root structure and function due to localized high nutrient concentrations (152). The development of radioactive tracer techniques has greatly enhanced the investigation of nutrient uptake with depth, but research by the method was again with grain crops whose root systems are rather shallow, fibrous, and otherwise dissimilar in many respects to those of tree crops (13). Uptake of nutrients with depth, as determined through the use of tracers, follows somewhat the same pattern as water but appears to be considerably more complex (61,151,152,153,158). Uptake of ^{32}P and ^{45}Ca generally decreased with root concentration and depth; however, it was clearly evident that the selective absorption or perhaps translocation abilities of roots from different depths, were dissimilar. The uptake pattern of the tracers was attributed to inherent factors rather than external ones. Further study revealed the difficulty of interpreting tracer uptake data due to the strong influence of soil water content and the lack of root distribution data. Radioactive isotopes have been used with tree crops but largely limited to studies with young plants.

MATERIALS AND METHODS

Description of the Experimental Site

Samples for this study were collected from an experimental planting of 'Orlando' tangelo trees located in Lake County, Florida. The planting consists of an approximately equal number of trees on each of 11 rootstocks, spaced at a distance of 4.5 x 9.0 m. The trees were set out in 1961 as part of a commercial tangelo orchard using a completely randomized design. The orchard and the experimental trees have received standard commercial care to maintain fruit production.

The soil of the experimental site, Astatula (formerly Lakeland) fine sand, is a typical soil of Florida's ridge area that is planted to citrus. It is classified according to Great Soil Group as an Entisol. It is well-drained and has low water and mineral nutrient retaining properties. The soil is underlain at depths of 2.5 to 3.5 m by a finer textured horizon of undetermined thickness. The clay content of this horizon varies from 10 to 38 percent (37).

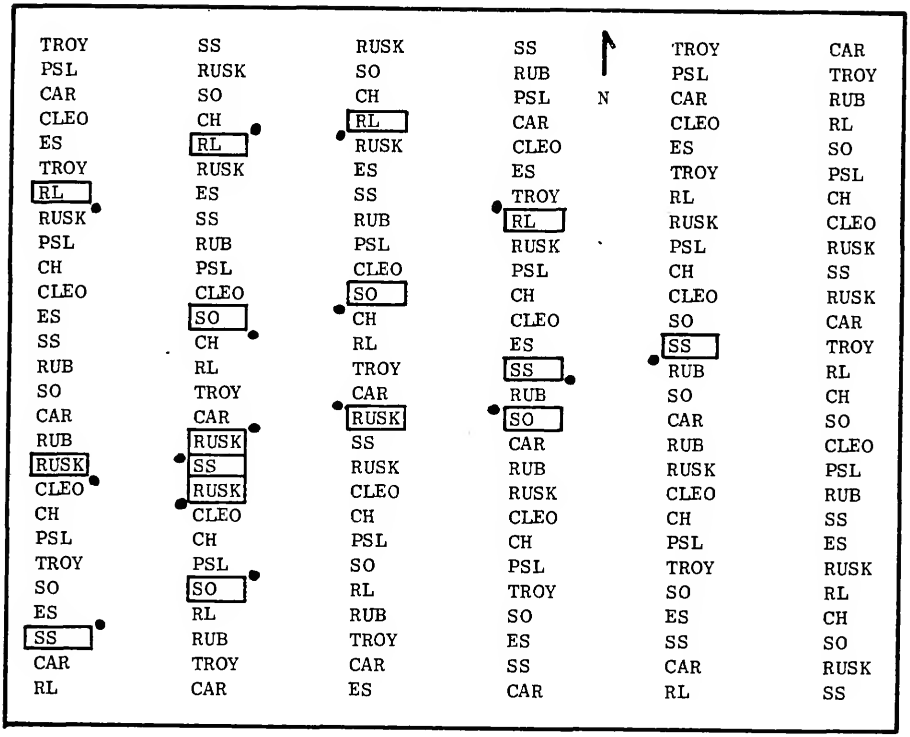
Experimental Units

Trees in the experimental planting differ considerably in their adaptation to the environment of the site. Therefore, 4 rootstocks were chosen for study on the basis of known differences in tree size, fruit production and root system characteristics. These were rough lemon, sour orange, sweet orange, and 'Rusk' citrange, representing the 2 major rootstocks of Florida, and 2 of lesser importance, respectively. These trees were used for investigation of soil water depletion and root anatomy and morphology. In addition, soil samples from the root environment of each rootstock were taken for certain physical and chemical analyses.

Field Sampling Procedure

Soil Moisture Depletion

Moisture changes in the soil profile of each rootstock were measured with a Troxler neutron probe, Model 1603, and scaler, for 1 year beginning in April, 1973. Aluminum access tubes were installed just inside the drip line of 16 trees, 4 trees of each rootstock (Fig. 1). One tube was installed per tree at either a NE, SE, SW or NW location. Readings were taken at 30 cm depth intervals, beginning at 30 cm, to a depth of 3.6 m. Trees on rough lemon were measured to a depth of 3.9 m because they were generally deeper rooted as compared to those on other rootstocks. Also, there was a gradual increase in the depth to the clay horizon from the south to the north end of the planting where the trees on rough lemon were located. The neutron probe measures the water content by volume of a sphere of soil approximately 30 cm in diameter. Therefore, it could not be used to measure the surface 15 cm of soil without serious error. Water content of the 0 to 15 cm zone was determined gravimetrically. Combined samples of 3, 2.5 x 15 cm cores of soil were collected around each access tube.



TROY	SS	RUSK	SS	TROY	CAR
PSL	RUSK	SO	RUB	PSL	TROY
CAR	SO	CH	PSL	CAR	RUB
CLEO	CH ●	RL	CAR	CLEO	RL
ES	RL	● RUSK	CLEO	ES	SO
TROY	RUSK	ES	ES	TROY	PSL
RL ●	ES	SS	● TROY	RL	CH
RUSK	SS	RUB	RL	RUSK	CLEO
PSL	RUB	PSL	RUSK	PSL	RUSK
CH	PSL	CLEO	PSL	CH	SS
CLEO	CLEO	SO	CH	CLEO	RUSK
ES	SO	● CH	CLEO	SO	CAR
SS	CH ●	RL	ES	SS	TROY
RUB	RL	TROY	SS ●	● RUB	RL
SO	TROY	CAR	RUB	SO	CH
CAR	CAR ●	● RUSK	● SO	CAR	SO
RUB	RUSK	SS	CAR	RUB	CLEO
RUSK	● SS	RUSK	RUB	RUSK	PSL
CLEO ●	RUSK	CLEO	RUSK	CLEO	RUB
CH	● CLEO	CH	CLEO	CH	SS
PSL	CH	PSL	CH	PSL	ES
TROY	PSL ●	SO	PSL	TROY	RUSK
SO	SO	RL	TROY	SO	RL
ES	RL	RUB	SO	ES	CH
SS ●	RUB	TROY	ES	SS	SO
CAR	TROY	CAR	SS	CAR	RUSK
RL	CAR	ES	CAR	RL	SS

Fig. 1. Planting plan of the experimental site showing the location of various rootstocks for 'Orlando' tangelos. Trees used in this study (▭) and access tube locations (●) are indicated.

Key to Rootstock Symbols:

RL - rough lemon
PSL - Palestine sweet lime
SO - sour orange
SS - sweet orange
CLEO - Cleopatra mandarin
CAR - 'Carrizo citrange

TROY - 'Troyer' citrange
RUSK - 'Rusk' citrange
CH - 'Christian' trifoliate orange
RUB - 'Rubideaux' trifoliate orange
ES - 'English Small' trifoliate orange

Soil moisture content was determined twice weekly from 1-minute readings taken at each depth. A value as percent soil water by volume was obtained from the instrument calibration curve using a ratio of these readings to the mean of 3 standard readings, i.e., readings taken with the neutron probe above ground and in its shield.

A calibration curve for this instrument was prepared at another location prior to its use in this study. Extensive recalibration at the experimental site for this study did not indicate any change in the curve.

Soil Samples for Chemical and Physical Analyses

Access tubes used for measuring soil water content were installed by boring holes of slightly smaller diameter before the tubes were inserted. Soil obtained from these borings was collected in 30 cm intervals and retained for chemical and particle-size analysis. In addition, undisturbed cores in 6 cm brass cylinders, 3 cm deep, were collected at depths of 7.5, 20.0, 45.0, 60.0, 120.0, 150.0, 210.0, 240.0 and 270.0 cm from several locations to determine the soil moisture characteristic curve for the experimental site.

Root Samples

Roots of the selected rootstocks were obtained by excavation near the tree drip line in April 1973, for anatomical study and observation under the scanning electron microscope (SEM). Relatively undisturbed soil samples containing roots were taken from 2 trees on each rootstock from the surface, the subsoil clay horizon, and at an intermediate depth. The same trees were not used for root sampling and the soil water study.

Sample Preparation and Analysis

Soil Chemical Analyses

All field samples were prepared for analysis by air drying for 48 hours and sieving through a 2 mm screen. An outline of the various determinations made on these samples is shown in Table 1.

Soil Physical Analyses

Particle-size analysis. The soil of the experimental site is essentially pure sand as determined by a previous study (37). Therefore, only the texture of subsoil clay samples was determined using the hydrometer method.

Moisture characteristic curve. The moisture characteristic curve of the field samples was determined through the use of a special porous-plate pressure cell and a procedure developed by van Bavel and Reginato (206). This required collecting field samples in special brass cylinders as previously described, to accomodate data collection by the pressure-cell method. Briefly, the procedure involved placing the soil cores with retaining cylinder, in the pressure cell (commercially known as a Tempe cell), saturating the soil, then closing the cell and connecting it to a regulated source of compressed air. The moisture characteristic curve, i.e., a plot of volumetric soil water content versus soil matric potential, was obtained by adjusting the air pressure to a preselected value, allowing the soil core to come to equilibrium, then weighing the cell. Appropriate data were obtained by repeating this procedure at a number of preselected air pressure values. Air pressure was gauged as cm of water by bubbling air through a column of water the required height.

Table 1. Outline of soil chemical analyses.

Analysis	Method	Procedure	Remarks
pH	combination electrode	2:1 solution to soil ratio using 10 g soil and either H_2O, 0.01 *M* $CaCl_2$ or 1.0 *M* KCl.	
Organic Matter	Walkley-Black wet combustion	2.0 g oven-dried soil.	Calculation: $\text{O.M.} = 0.69 \times \frac{\text{ml } 1.0\ \underline{N}\ K_2Cr_2O_7 \text{ reduced}}{\text{sample wt.}}$
Cation Exchange Capacity	a. Saturation by neutral 1.0 *N* NH_4OAc (sand)	a. 25 g sample leached with NH_4OAc; leachate retained.	
	b. Na saturation (clay)	b. 5 g samples saturated with 1.0 *N* NaOAc, centrifuged and displaced with NH_4OAc. Na determined by atomic absorption.	
NO_3	Orion model 92-07 electrode	50 g sample extracted with 100 ml H_2O.	
NH_4	Orion model 95-10 electrode	10 g sample extracted with 50 ml 1.0 *M* KCl.	
P	Bray P_2 Test	5 g sample extracted with 0.03 *N* NH_4F in 0.1 *N* HCl; color development by the ascorbic acid-molybdate method.	

Table 1 - continued.

Analysis	Method	Procedure	Remarks
K, Ca, Mg	Extraction with neutral 1.0 N NH_4OAc.	10 g sample extracted with 50 ml NH_4OAc by shaking for 30 minutes; mineral content was determined by atomic absorption.	
Cu, Fe, Zn, Mo, and Mn	HCl extraction	10 g sample extracted with 50 ml 1.0 N HCl by shaking for 30 minutes; mineral content was determined by atomic absorption.	
Al		Analysis done by atomic absorption on the samples used for NH_4 determination.	

Subsamples of the soil cores were used to determine the 15-bar water content by the pressure-plate method when the pressure-cell phase was terminated (206).

Root Samples

Anatomy. Roots were washed in water to free them of adhering soil particles. Approximately 20 root tips, 20 mm long from each rootstock and depth, were selected, divided into 5 mm segments, fixed in 50 percent formalin-acetic acid-alcohol (5-5-90), embedded in paraffin, sectioned at 10µ and stained with safranin-fast green by standard procedures.

Scanning electron microscopy. Roots were washed and selected as described above then fixed in a solution of 6 percent glutaraldehyde in 0.1 M phosphate buffer, pH 6.8, for 2 hours. This was followed by rinsing in several changes of buffer, and post-fixing in 2 percent OsO_4 in buffer for 2 hours. Segments were dehydrated in a graded water-acetone series, infiltrated with a freon solvent and critically point dried with Freon 13. Selected segments were mounted on viewing stubs and coated with a gold-palladium alloy. A set of roots collected from seedlings grown on filter paper was similarly prepared. Roots were examined with a Cambridge Mark II SEM at 20 KV.

Statistical Analysis

Certain soil moisture data were submitted to analysis of variance. Total soil profile water losses for selected periods during the year of study were analyzed as a randomized complete-block design using time as a block. Soil water content data for the period October 10 to 20, 1973, were analyzed as a 4^2 x 12 factorial experiment using rootstock and depth as the variables. The analysis was repeated using rootstock replicates, which represented access tube locations, as blocks. A 4 x 13 factorial analysis was performed on feeder root weights of the same trees. Significant differences between treatments were determined using Duncan's Multiple-Range test at the 5 percent level. Correlations were made between feeder root weight and water use.

RESULTS

Characterization of the Soil Environment

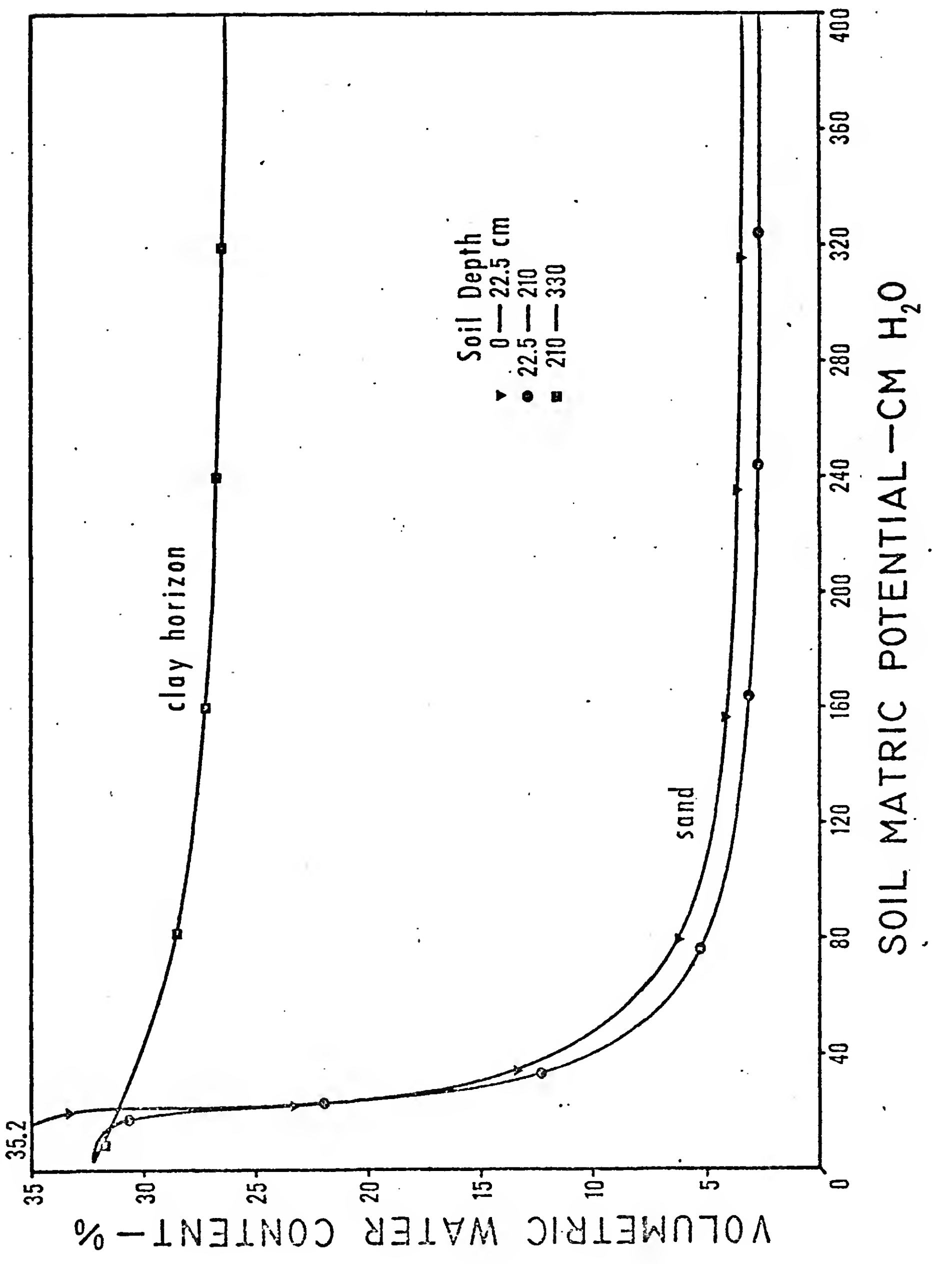
Physical

Moisture relationships of a soil are controlled largely by soil texture. A particle-size analysis performed earlier (37) showed the soil of the experimental site, Astatula fine sand, is a sand with small amounts, 1 to 2 percent, of silt and clay size particles. A clay horizon which lies under this sandy soil beginning at a depth of approximately 210 cm contained 21 to 34 percent clay, generally increasing in clay content with depth. This horizon is part of the Citronelle Formation and kaolinite is the dominant clay mineral (68).

The moisture release curve for soil from the experimental site (Fig. 2) shows the water retention capacity for the Astatula sand is very low. The water content at only 80 cm of pressure potential was reduced from its maximum value to only 5 percent by volume. A small amount of organic matter in the surface 23 cm (Table 5) affected the saturation moisture value without influencing the remainder of the moisture release curve to a significant extent.

Release of moisture in the clay horizon (Fig. 2) is more gradual, although the initial water content was similar to that for the sand. The release curve for both the sand and clay horizon shows that a small change in water content is associated with a much larger change in soil matric potential after an initial quantity of water is removed.

Fig. 2. Soil moisture release curve for Astatula fine sand and the subsoil clay horizon from the experimental site.


VOLUMETRIC WATER CONTENT — %
35
30
25
20
15
10
5
0
35.2
SOIL MATRIC POTENTIAL — CM H_2O
40
80
120
160
200
240
280
320
360
400
clay horizon
sand
Soil Depth
▼ 0 — 22.5 cm
● 22.5 — 210
■ 210 — 330

Values from the moisture release curve (Fig. 2) were used to determine the amount of water commonly referred to as "readily available" (RAW). Field capacity moisture content was obtained from the appropriate curve (Fig. 2) at a matric potential of 60 cm. Resulting values indicated 10 cm of water was available in the soil profile to a depth of 210 cm (Table 2). The clay horizon from 210 to 330 cm contained an additional 11 cm of available water.

Ability of water to move through a soil is largely a function of water content and pore size. Hydraulic conductivity for the sand and clay horizon (Fig. 3) is shown to parallel their respective release curves with regard to changes in volumetric water content. Water moves at a rate 100 times faster in the sand than in the clay at water content values near saturation. Conductivity changed rapidly in the sand as water content decreased.

The sandy soil has an average bulk density of 1.56 g/cm^3 and thus has approximately 41 percent pore space (Table 3). Mean bulk density of the clay horizon was 1.73 g/cm^3, corresponding to a porosity value of 33.7 percent. Size and distribution of the pores in the sand and clay horizon is presented in Table 4 and Fig. 4, respectively. Pores in the sandy soil showed an unbalanced distribution with the majority of the pores having the larger diameters. These pores retained the major portion of the soil water but also drained under relatively low tension (Fig. 2). Soil obtained from the clay horizon had few large pores. Pore sizes were more evenly distributed (Table 4) and therefore the soil released water at a more gradual rate (Fig. 2).

Table 2. Selected soil moisture values for the experimental site.

Depth cm	Moisture Values, percent by Volume		Available Soil Moisture
	F.C.^{z}	15-bar	cm
7.5	7.39	2.28	
	6.85	2.17	
	6.63	2.06	
20.0	6.62	1.40	
	10.53	2.82	
MEAN (0-23 cm)	7.60	2.15	1.23
30.0	7.01	1.83	
45.0	7.61	2.63	
	6.62	1.42	
60.0	6.46	1.49	
	5.65	1.22	
120.0	6.60	1.20	
	5.24	0.95	
150.0	4.86	1.11	
	5.10	1.10	
210.0	5.32	0.86	
MEAN (23-210.0 cm)	6.05	1.38	8.76
210.0	22.35	13.92	
240.0	30.11	20.91	

Table 2 - continued.

Depth cm	Moisture Values, percent by Volume F.C.[z]	15-bar	Available Soil Moisture cm
270.0	29.23	21.30	
330.0	35.65	25.24	
MEAN (210.0-330.0)	29.35	20.34	10.81

---

[z] "Field Capacity" value was the moisture content at 60 cm pressure from Fig. 2.

Fig. 3. Hydraulic conductivity-water content relationship for Astatula fine sand and the subsoil clay horizon from the experimental site.

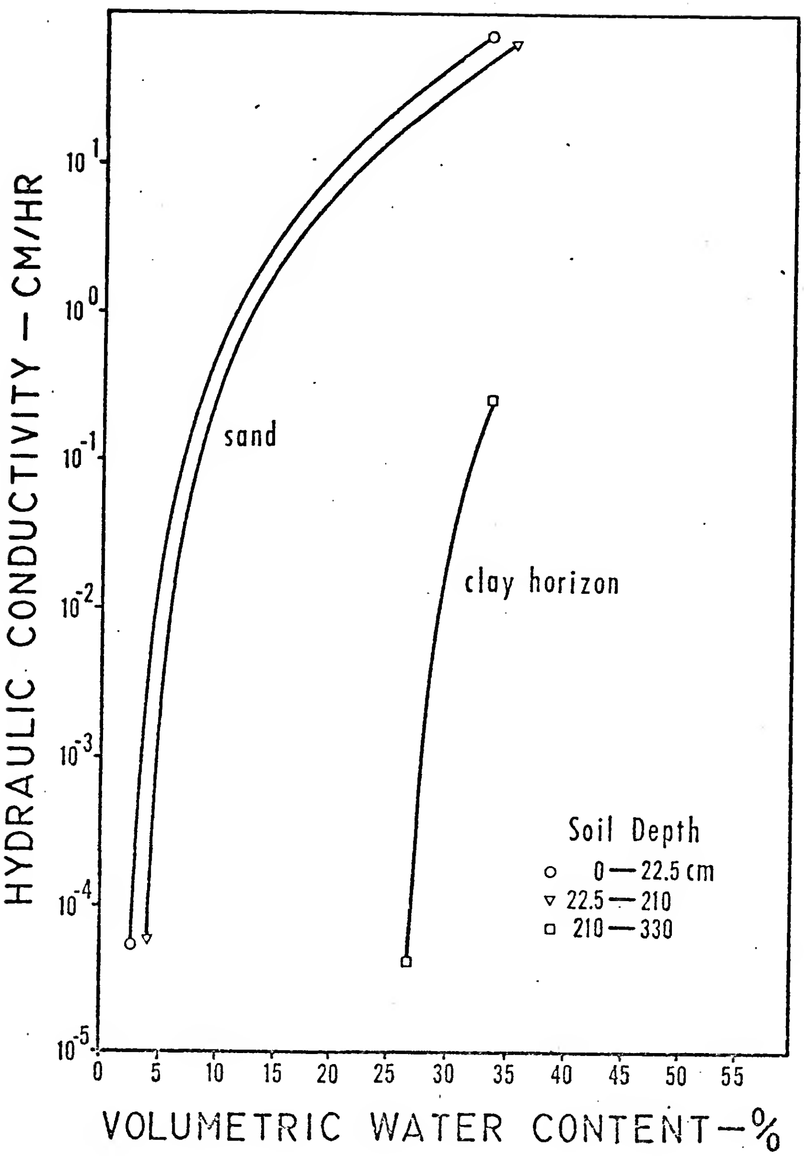

HYDRAULIC CONDUCTIVITY — CM/HR
10^1
10^0
10^-1
10^-2
10^-3
10^-4
10^-5
0
5
10
15
20
25
30
35
40
45
50
55
VOLUMETRIC WATER CONTENT—%
sand
clay horizon
Soil Depth
○ 0—22.5 cm
▽ 22.5—210
□ 210—330

Table 3. Soil bulk density and porosity for the experimental site.

Depth, cm		
0-23	23-210	210-330
	Bulk Density[z], g/cm^3	
1.55	1.58	1.73
	Soil Porosity, percent	
41.5	40.4	33.7

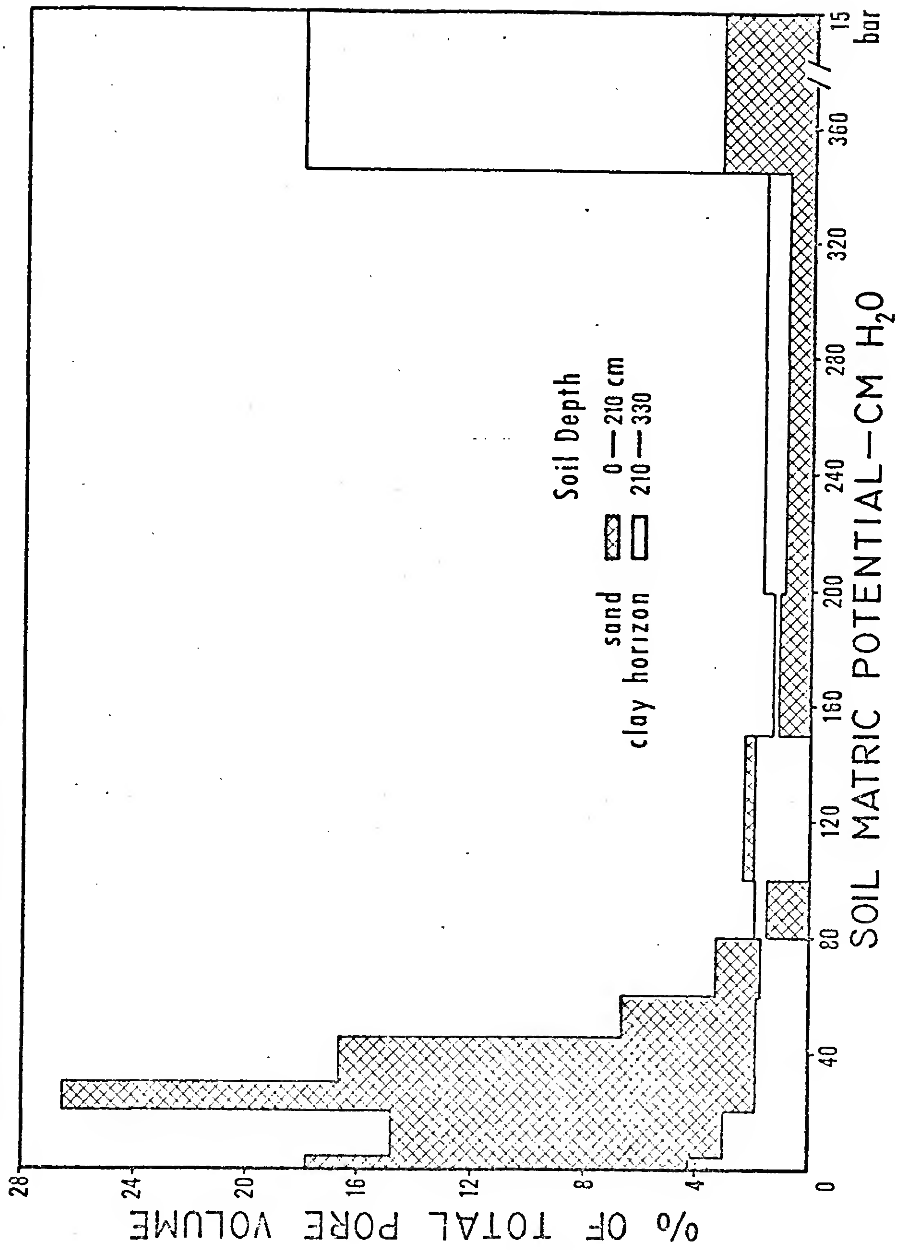
[z] Assumed particle density of 2.65

Table 4. Soil porosity characteristics for the experimental site.

Soil Matric Potential, cm H_2O											
0	3.5	20	30	45	60	80	100	150	200	345	15-bar
Pore Size, mm[z]											
	.4210	.0737	.0491	.0327	.0246	.0184	.0147	.0098	.0074	.0043	.0001
Volumetric water content change, in percent per cm H_2O for each soil matric potential interval											
Soil Depth, 0-210 cm											
2.08	0.37	1.13	0.45	0.18	0.07	0.03	0.02	0.01	<0.01	<0.01	
Soil Depth, 210-330 cm											
0.41	0.06	0.06	0.04	0.04	0.03	0.03	0.01	0.01	<0.01	<0.01	

[z] Pore size at each matric potential represents the effective pore diameter just retaining water. All larger sized pores will have drained.

Fig. 4. Pore space distribution according to pore size for Astatula fine sand and the subsoil clay horizon from the experimental site. Pore sizes are based on the moisture release curve (Fig. 2) and are given in Table 4.


% OF TOTAL PORE VOLUME
0
4
8
12
16
20
24
28
SOIL MATRIC POTENTIAL—CM H_2O
40
80
120
160
200
240
280
320
360
15
bar
Soil Depth
sand ▨ 0—210 cm
clay horizon ☐ 210—330

Chemical

Organic matter content of the soil profile was highest at the surface, 0.77 percent, and decreased sharply with depth (Table 5). Little or no organic matter was detected at depths greater than 180 cm. Cation exchange capacity of the soil was very low and reflected primarily the presence of either organic matter or clay minerals. Exchange capacity of organic matter is approximately 200 meq/100 g. The surface 30 cm of soil had an exchange capacity of 1.49 meq which corresponds to the 0.77 percent organic matter content found. This indicates that the cation exchange capacity of the sand is primarily due to organic matter present. The 3 to 4 meq of exchange capacity in the subsoil layer results from the presence of kaolinite.

Soil pH was measured in water, 0.01 $\underline{M}$ $CaCl_2$ and 1.0 $\underline{N}$ KCl. Mean pH in water ranged from 6.49 at the surface to 5.45 near the clay horizon where the pH continued to decrease another unit with depth (Table 6). The range in pH included values as low as 3.85. Measurement of soil reaction in $CaCl_2$ theoretically represents the true field pH value because a 0.01 $\underline{M}$ salt solution approximates the concentration of the soil solution in the field. Mean pH values in $CaCl_2$ as compared to H_2O values were consistently reduced but the general trend with depth was not altered. Measurement in 1.0 $\underline{N}$ KCl reduced the pH values even further, but again, without affecting the general depth trend. Measurement in KCl theoretically eliminates fluctuations in pH in the field due to changes in soluble salt concentration because of the high ionic strength of the KCl solution. These values represent maximum pH development because all exchangable ions are replaced particularly Al.

Table 5. Soil organic matter content and cation exchange capacity values for experimental site.

Depth^z cm	Organic Matter percent	Range	Cation Exchange Capacity meq/100 g	Range
15	0.77	0.47-1.05	1.49	0.95-2.25
45	0.38	0.19-0.75		
75	0.20	0.11-0.36	0.52	0.25-1.50
105	0.14	0.08-0.18		
135	0.11	0.08-0.14	0.24	0.10-0.33
165	0.10	0.07-0.14		
195	0.08	0.04-0.10	4.00	4.10-5.52
225	<0.05		3.76	3.56-3.96
225			3.88	3.31-4.93
285			3.36	2.28-4.48

^{z}Each depth value represents the center of a 30 cm interval.

Table 6. Soil pH values for experimental site.

Depth[z]	Mean Values			Range		
cm	H_2O	$CaCl_2$	KCl	H_2O	$CaCl_2$	KCl
15	6.49	5.95	5.79	6.25-6.83	5.58-6.10	5.38-6.20
45	6.11	5.57	5.28	5.70-6.45	4.95-5.93	5.00-5.50
75	6.01	5.46	5.27	5.70-6.28	5.08-5.73	5.08-5.73
105	5.91	5.36	5.22	5.43-6.30	5.05-5.60	4.85-5.55
135	6.01	5.26	5.05	5.40-6.58	5.03-5.48	4.73-5.35
165	5.94	5.29	5.15	5.13-6.38	4.65-5.73	4.63-5.50
195	5.45	5.19	4.86	4.68-5.78	4.80-5.75	4.30-5.40
225	5.11	4.58	4.55	4.25-5.80	3.98-5.20	3.85-5.15
255	4.82	4.36	4.32	4.08-5.53	3.90-5.00	3.55-5.15
285	4.62	4.29	4.23	4.05-5.75	3.90-5.30	3.75-5.05
315	4.70	4.22	4.17	4.15-5.85	3.73-5.28	3.65-5.08
345	4.49	4.10	4.20	3.85-5.78	3.48-5.40	3.58-5.20

[z] Each depth value represents the center of a 30 cm interval.

Soil Mineral Nutrient Content

Soil nutrient analyses were conducted primarily to characterize the soil environment and not to study the influence of rootstock on nutrient absorption. However, samples were selected for analysis by rootstock, in such a manner that the mean value for all samples could be considered as representative for the levels of the soil nutrients in the entire area the experimental trees were located. Results are given by rootstock and a mean for all samples, shown as a dashed line, is also given.

Macronutrients

The soil levels of NH_4 and NO_3 ions are shown in Figs. 5 and 6 respectively. All NH_4 values were less than 10 ppm. The mean value was approximately 5 ppm and this concentration was uniform with depth. NO_3 ion is mobile, moves primarily in the soil solution and was relatively uninfluenced by exchange phenomena. Highest NO_3 levels were found at the surface where they ranged from 8 to 30 ppm. NO_3 level decreased rapidly with depth to less than 4 ppm with little variation between rootstocks. Downward rate of water movement was hindered by the subsoil clay horizon, hence a bulge appeared in the NO_3 level at a depth which varied according to the location of the clay horizon.

The level of $Bray_2$ extractable P is shown in Fig. 7. The largest variation in soil P occurred at the surface with the content ranging from 40 to 85 ppm. P content decreased below the surface to 10 ppm, and continued to decrease slightly with depth except in the soil samples from the trees on rough lemon where P increased below 190 cm. It is

Fig. 5. The relationship of rootstock and soil depth to the level of 1.0 N KCl extractable NH_4 in Astatula fine sand and the subsoil clay horizon from the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow.

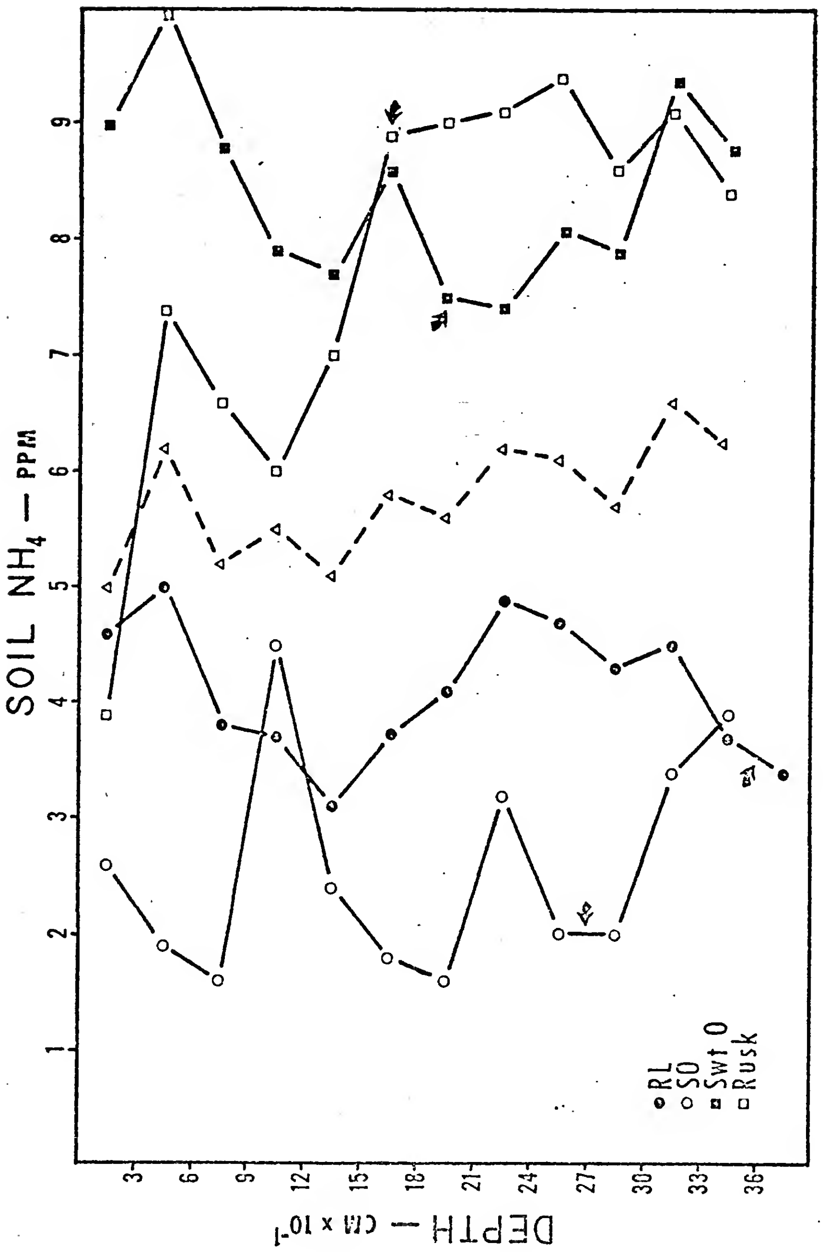

SOIL NH$_4$ — PPM
1
2
3
4
5
6
7
8
9
DEPTH — CM x 10^{-1}
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
■ Swt O
□ Rusk

Fig. 6. The relationship of rootstock and soil depth to the NO_3 level of a water extract from Astatula fine sand and the subsoil clay horizon of the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow.

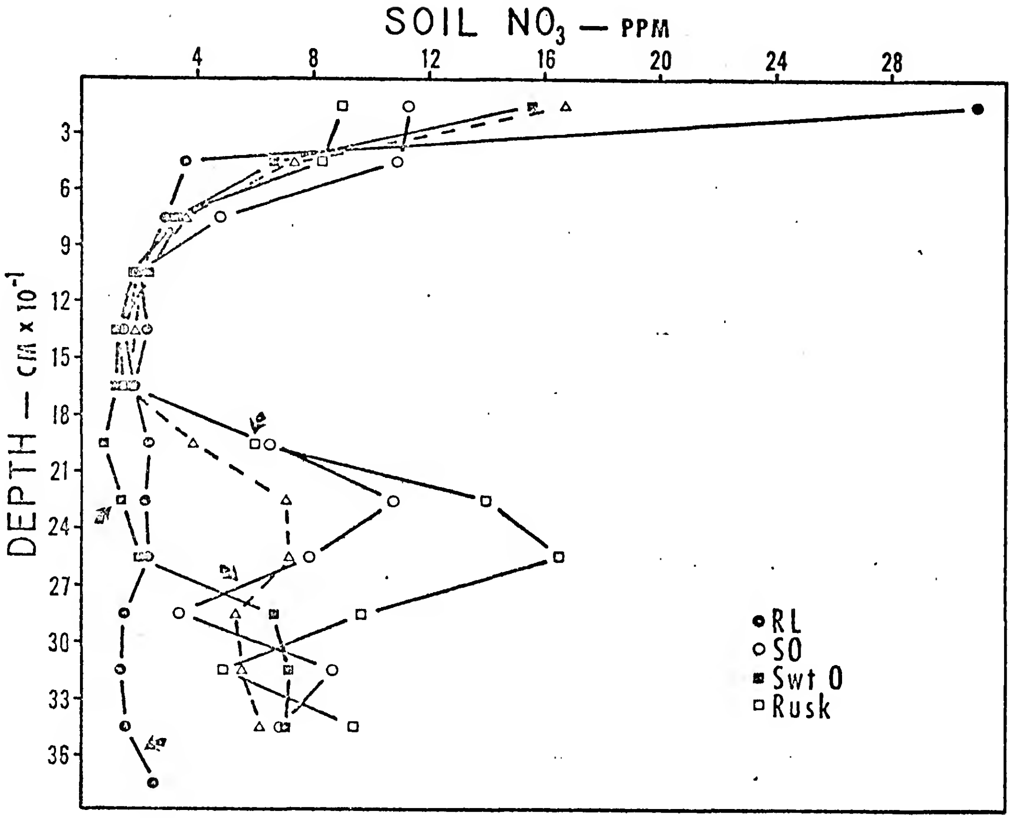
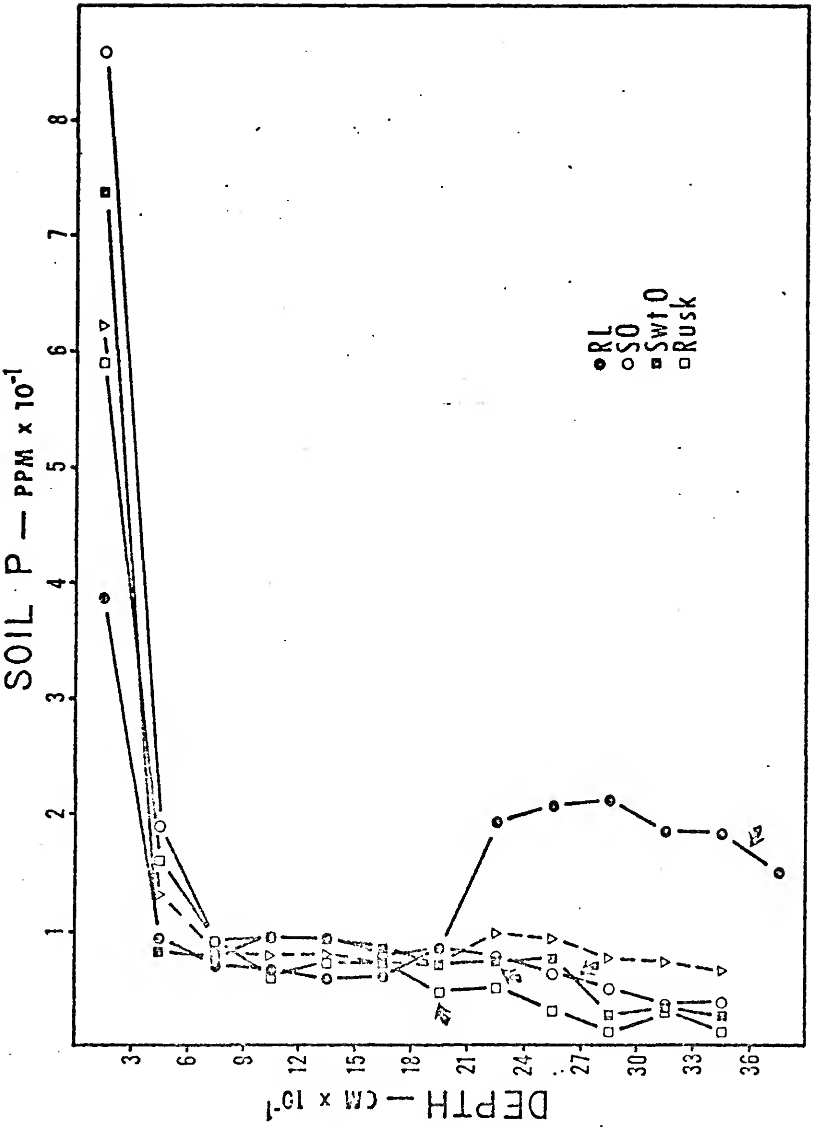

SOIL NO_3 — PPM
4
8
12
16
20
24
28
DEPTH — CM x 10^{-1}
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
▪ Swt O
□ Rusk

Fig. 7. The relationship of rootstock and soil depth to the level of Bray_2 P in Astatula fine sand and the subsoil clay horizon from the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow.


SOIL P — PPM x 10-1
1
2
3
4
5
6
7
8
DEPTH — CM x 10-1
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
▣ Swt O
□ Rusk

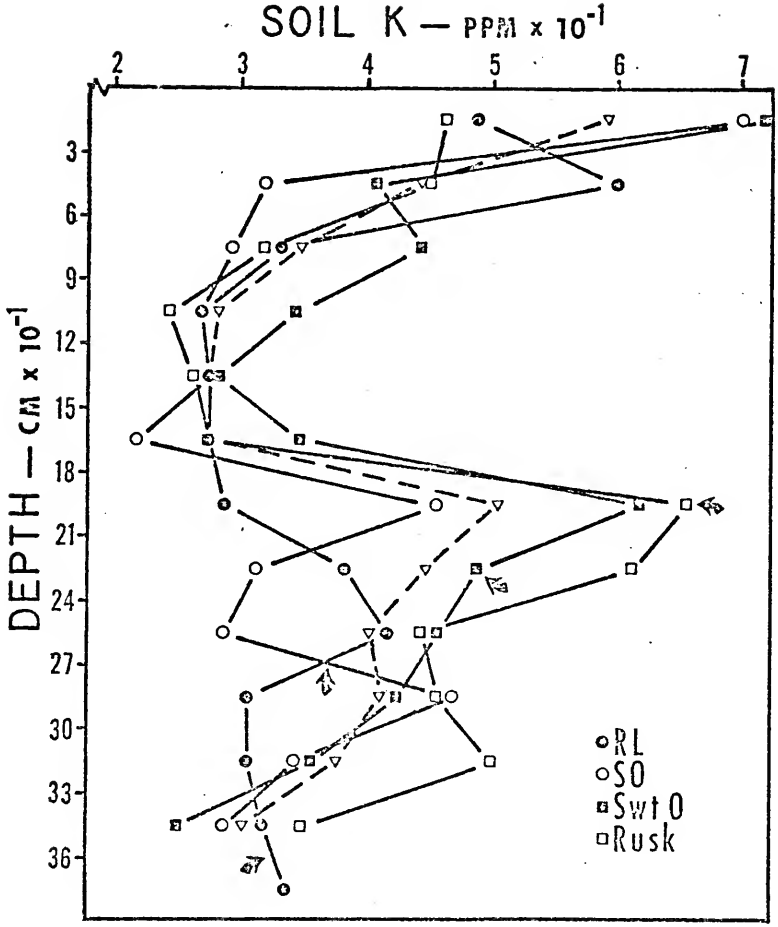


Fig. 8. The relationship of rootstock and soil depth to the level of extractable K in Astatula fine sand and the subsoil clay horizon from the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow.

Fig. 9. The relationship of rootstock and soil depth to the level of extractable Mg in Astatula fine sand and the subsoil clay horizon from the experimental site Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow

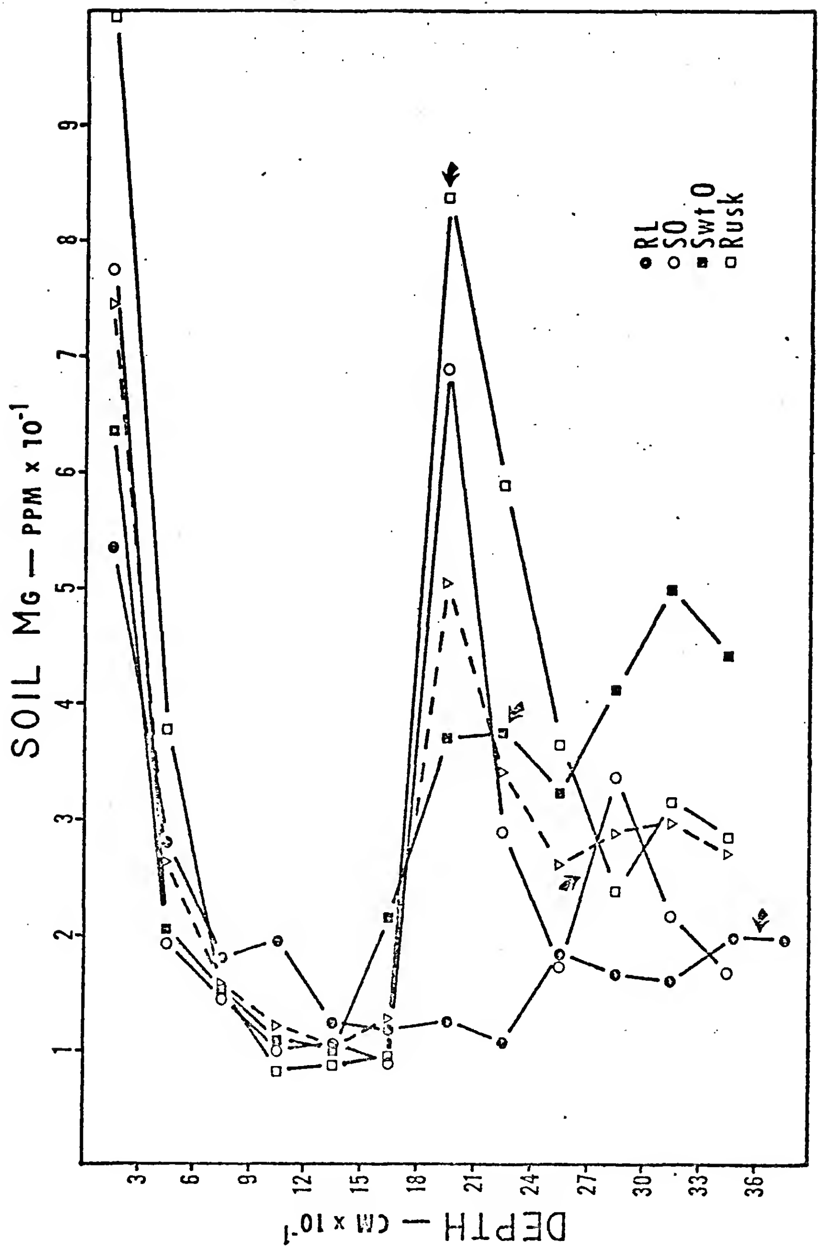
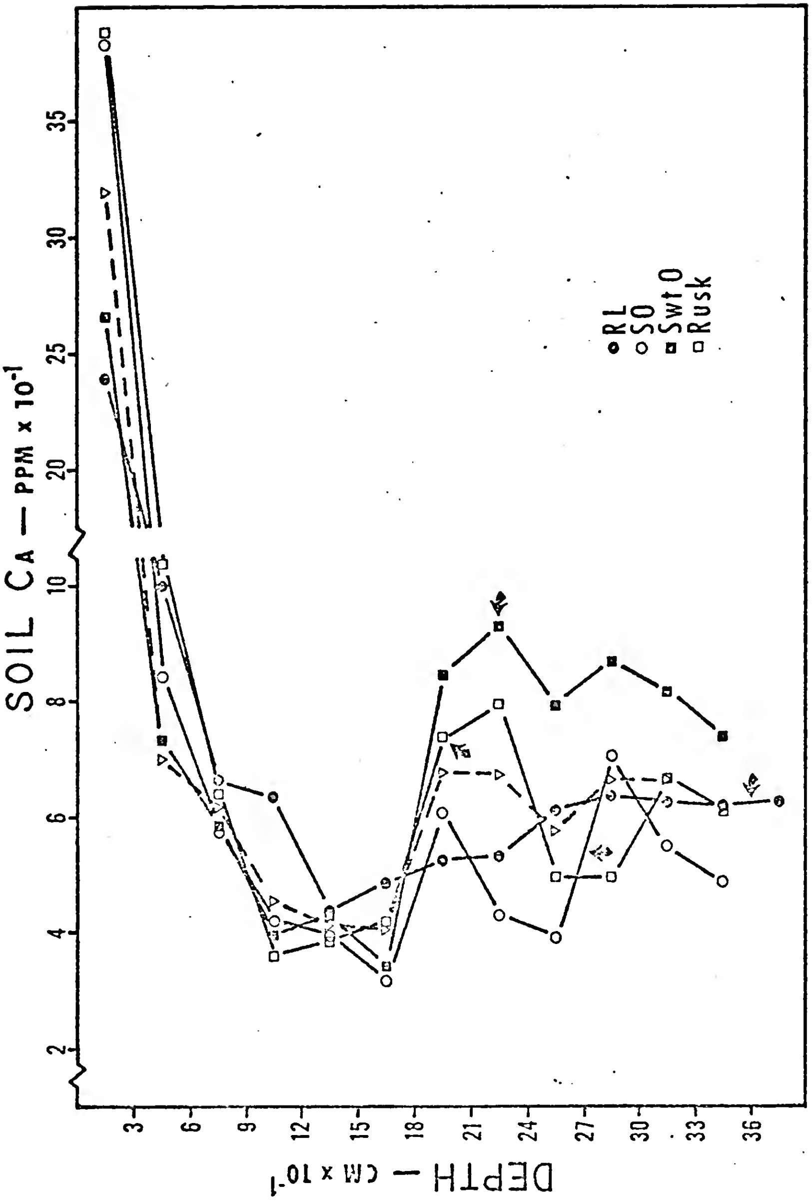

SOIL MG — PPM x 10-1
1
2
3
4
5
6
7
8
9
DEPTH — CM x 10-1
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
■ Swt O
□ Rusk

Fig. 10. The relationship of rootstock and soil depth to the level of extractable Ca in Astatula fine sand and the subsoil clay horizon of the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow


SOIL CA — PPM x 10^{-1}
DEPTH — CM x 10^{-1}
2
4
6
8
10
20
25
30
35
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
■ Swt O
□ Rusk

possible that some lenses of native phosphatic material were present at the north end of the planting where the trees on rough lemon were located.

The extractable bases, K, Ca and Mg, showed a similar distribution with depth (Figs. 8, 9 and 10 respectively). The mean surface values were 320, 75 and 60 ppm for Ca, Mg and K, respectively. All 3 nutrients showed a second peak value at a point near the sand-clay horizon interface.

Micronutrients

The extractable Fe content of the soil (Fig. 11), unlike that of the macronutrients, decreased gradually from 90 ppm at the surface to approximately 25 ppm at 165 cm and then increased in the clay horizon. Values for Zn, Mn and Cu varied so little between samples that only means were plotted (Fig. 12). These nutrients appeared to be relatively immobile, with high values at the surface. The concentration of each nutrient was less than 2 ppm for every depth below 30 cm.

The solution containing the extracted nutrients was also analyzed for Mo. If Mo was present, it was not detectable by the procedures used.

Aluminum

The level of exchangable Al, extracted with 1.0 *N* KCl, was very small in the sandy soil (Fig. 13). Appreciable quantities of Al were not detected until samples from the clay horizon were analyzed. The level of Al rose sharply with depth from 2 to 28 ppm in the clay horizon. The values shown in Fig. 13 are means for all rootstocks but do not include those values for rough lemon samples for the depths 180 to 300 cm. Thus, the sharp increase in Al content at 180 cm can be considered to represent the change that occurs when the clay horizon is encountered.

Fig. 11. The relationship of rootstock and soil depth to the level of 1.0 N HCl extractable Fe in Astatula fine sand and the subsoil clay horizon of the experimental site. Mean values are shown as a dashed line. Depth to the clay horizon for each rootstock is indicated by an arrow.

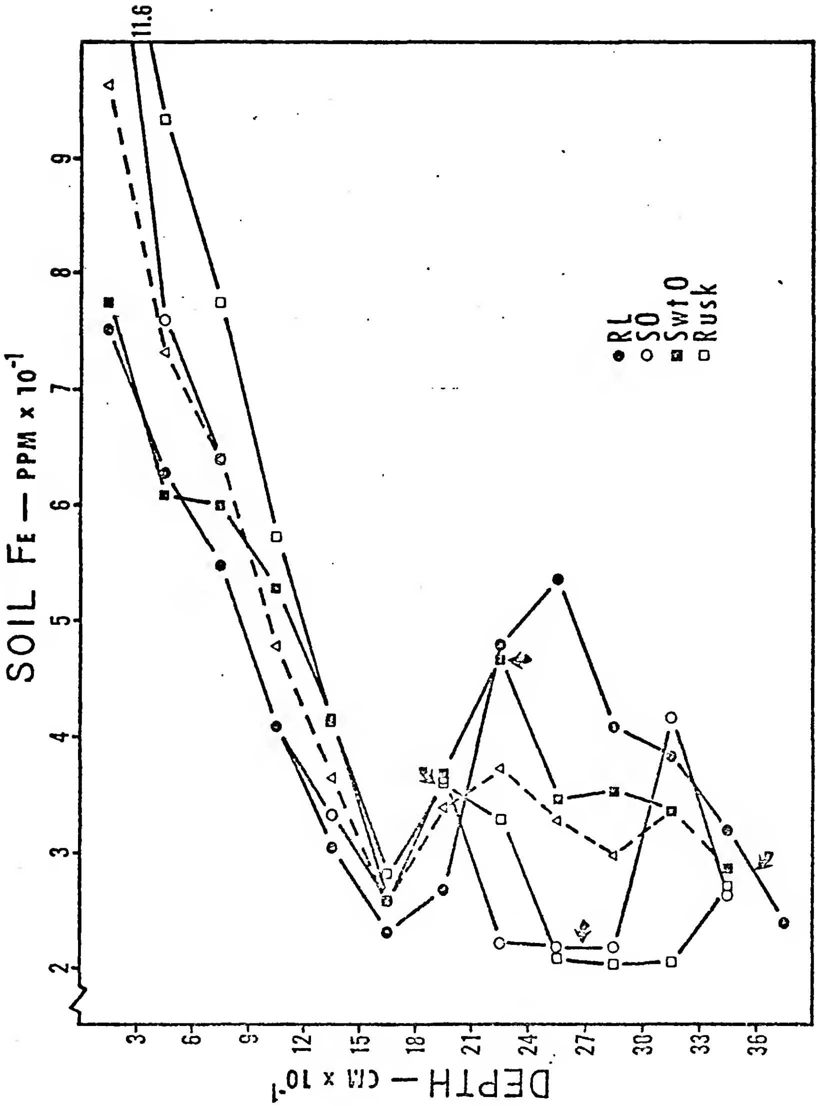

SOIL FE — PPM x 10-1
2
3
4
5
6
7
8
9
11.6
DEPTH — CM x 10-1
3
6
9
12
15
18
21
24
27
30
33
36
● RL
○ SO
▣ SwtO
□ Rusk

Fig. 12. The influence of depth on the mean Zn, Mn and Cu content of Astatula fine sand and the subsoil clay horizon of the experimental site. Samples were extracted with 1.0 N HCl.

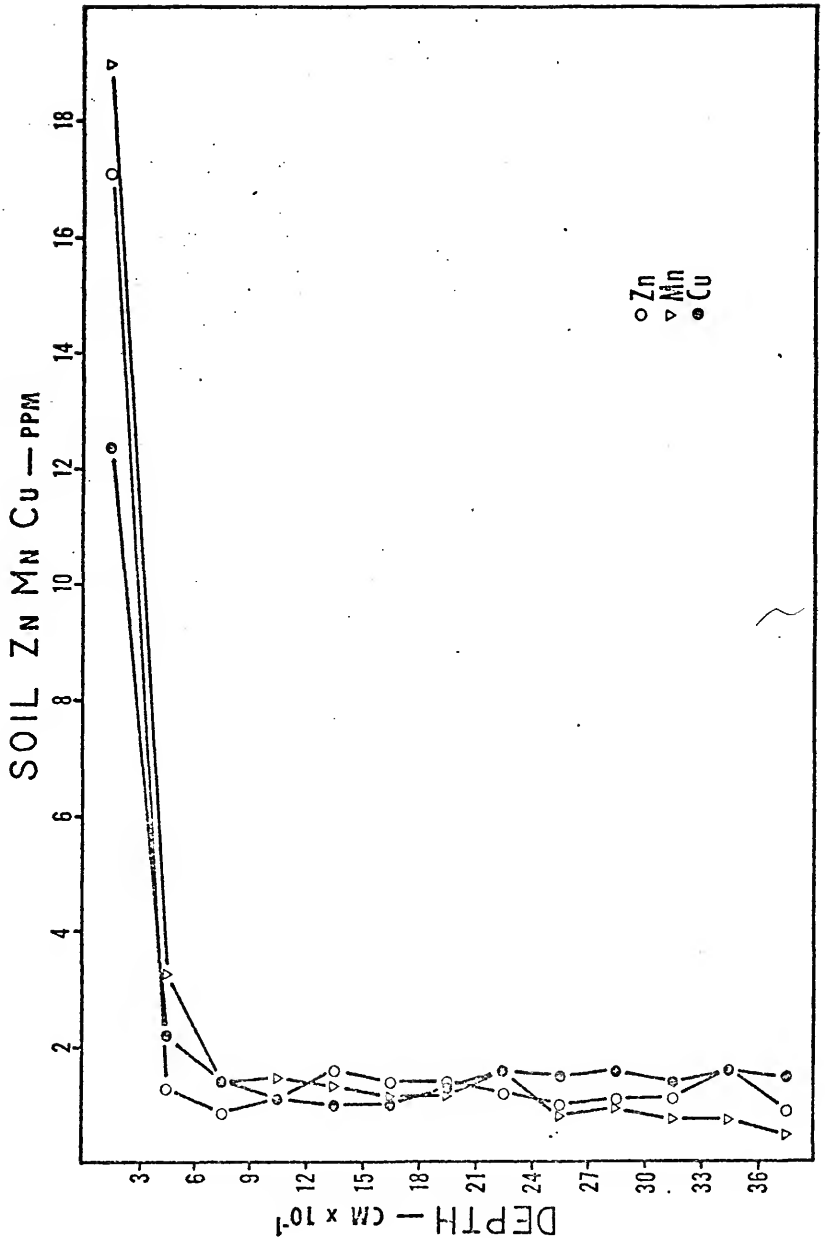
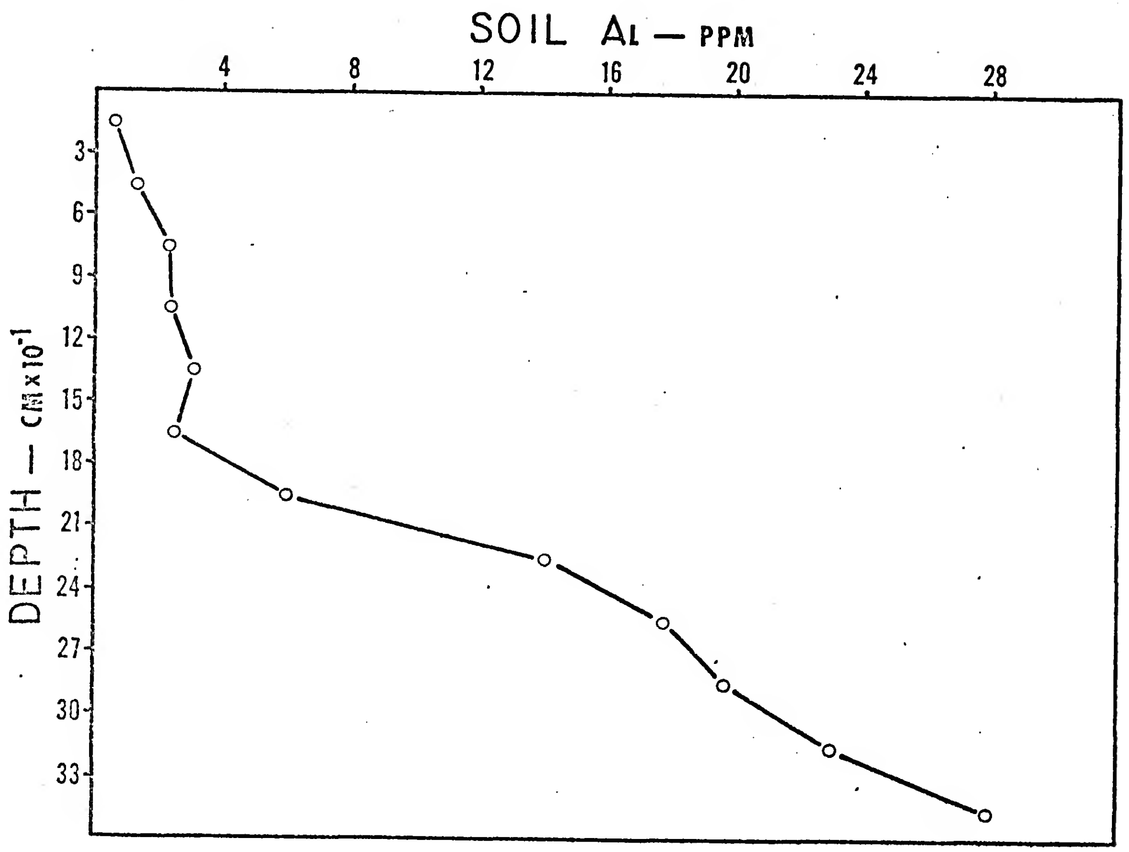

SOIL ZN MN CU — PPM
2
4
6
8
10
12
14
16
18
DEPTH — CM x 10⁻¹
3
6
9
12
15
18
21
24
27
30
33
36
○ Zn
▽ Mn
● Cu

Fig. 13. The mean exchangable Al content with depth of Astatula fine sand and the subsoil clay horizon from the experimental site.


SOIL AL — PPM
4
8
12
16
20
24
28
DEPTH — CM x 10^{-1}
3
6
9
12
15
18
21
24
27
30
33

Milliequivalent values for the nutrients presented are given in Table 7.

Rootstock Water Use

Fluctuations in Soil Moisture Content

Two months during the year of study, August and December, were selected to illustrate the general trend of soil water content with depth and with the seasonal variation in rainfall. Table 8 shows the general decrease in water content with depth except for a small peak at 60 cm. The highest water content for the sandy soil was usually in the surface 15 cm. The water content of this depth interval also showed the greatest fluctuation.

Water content increased at the bottom of the profile due to the increase in clay content of the soil. A noticeable increase often occurred 30 to 40 cm above the clay horizon. It was apparent in this case that the water from a preceding rain of 2.5 cm or more had caused the water content to increase in the soil profile to the clay horizon where further rapid drainage was impeded. Lighter rains of approximately .50 to .75 cm or less, appeared to increase the water content only to 60 to 90 cm. Depth of penetration in every case was dependent on the profile water content at the time of the rainfall.

December was a month of moderate rainfall, 12.19 cm (Table 9); however there was very little rain in the preceding 2 months. The lowest soil water contents for the year were reached as a result, on December 5, 1973. These values correspond to the low end of the range shown in Table 8. The majority of the rain for the month fell after that date. Nevertheless,

Table 7. Mean soil level of selected nutrients in milliequivalents.

Depth[z] cm	Nutrient level, meq/100 g[y]									
	P	K	Mg	Ca	Cu	Fe	Zn	Mn	Al	Total
15	1.01	0.15	0.61	1.60	0.04[x]	0.52	0.05[x]	0.14[x]	0.01	4.13
45	0.21	0.11	0.22	0.35		0.39			0.01	1.32
75	0.13	0.09	0.13	0.31		0.34			0.03	1.06
105	0.13	0.07	0.10	0.23		0.26			0.03	0.85
135	0.13	0.07	0.09	0.21		0.20			0.03	0.76
165	0.12	0.07	0.11	0.20		0.14			0.03	0.70
195	0.11	0.13	0.42	0.34		0.18			0.17	1.28
225	0.16	0.11	0.28	0.34		0.20			0.16	1.28
255	0.15	0.10	0.21	0.29		0.18			0.20	1.16
285	0.12	0.11	0.24	0.33		0.16			0.22	1.21
315	0.11	0.10	0.25	0.33		0.18			0.26	1.26
345	0.11	0.08	0.22	0.31		0.15			0.31	1.21

[z] Each depth value represents the center of a 30 cm interval.

[y] See Table 1 for methods of analysis.

[x] All remaining values are approximately 0.01 meq.

Table 8. Range in soil profile water content for the months of August and December, 1973.

Depth[z]	August				December			
cm	RL	SO	Swt O	RK	RL	SO	Swt O	RK
0	3.4-9.0[y]	4.2-8.1	4.1-7.7	4.3-7.7	2.4-5.6	2.6-4.8	2.8-5.2	2.4-4.3
30	2.6-5.4	3.9-6.2	3.4-5.6	3.0-5.5	1.4-5.0	2.4-5.9	1.9-5.2	1.8-4.6
60	4.6-6.4	4.9-6.1	7.0-7.2	5.5-6.8	2.0-5.6	2.7-6.1	3.9-7.4	3.9-7.1
90	4.3-5.9	4.6-5.9	5.1-6.7	4.4-6.0	2.0-5.6	1.7-5.5	3.6-6.8	2.8-6.2
120	3.9-5.6	4.4-5.7	4.7-6.5	4.3-5.9	1.2-5.5	1.5-5.5	3.4-6.4	2.5-5.8
150	3.3-4.8	4.4-5.6	4.9-6.7	4.4-6.1	0.7-4.7	2.1-5.0	3.8-6.7	2.8-6.1
180	3.4-6.5	6.3-7.7	3.7-6.4	6.5-8.0	0.9-4.3	3.7-6.6	3.9-6.7	4.4-8.2
210	5.0-7.4	7.9-9.7	4.4-8.3	11.3-13.8	2.4-5.0	6.6-8.5	5.1-8.3	9.0-12.4
240	4.2-6.2	12.0-13.0	10.0-15.8	19.8-21.3	3.7-5.5	10.8-12.1	11.1-14.1	19.0-19.8
270	4.3-6.2	19.4-20.3	18.3-22.0	19.1-20.3	3.5-4.7	18.5-19.2	18.5-20.1	18.5-19.0
300	4.7-5.7	18.6-19.7	20.4-22.9	17.1-19.1	3.7-4.2	18.3-18.5	20.3-21.2	17.5-17.7
330	5.1-6.0	18.0-18.7	19.0-23.0	17.8-19.0	3.7-3.8	17.6-17.8	20.7-21.0	17.6-17.9
360	5.2-7.0	17.5-18.2	18.0-22.8	18.0-19.1	4.1-4.2	17.0-17.3	21.1-21.4	17.9-18.1

[z] Each depth represents the center of a 30 cm interval; depth 0 equals the 0-15 cm interval.

[y] Water content in percent by volume.

Table 9. Precipitation or irrigation water additions to the soil profile during the year of study.

Time Period			Water Addition cm
May 12	-	June 2, 1973	11.20
June 2	-	June 30	11.48
June 30	-	July 14	(rain gauges inoperative)
July 14	-	August 4	10.74
August 4	-	September 8	20.35
September 8	-	October 3	11.10
October 3	-	November 3	3.00
November 3	-	December 5	5.33
December 5	-	January 12	12.19
January 12	-	February 8	0.58
February 8	-	March 8	5.08
March 8	-	April 26	4.22

these low initial soil water contents at the beginning of the month precluded any changes of more than 1 percent by volume from occurring at depths below about 270 cm. Heavy rains in August, the wettest month (Table 9), caused the soil water content to increase at all depths.

The months of August and December were also chosen because the lowest moisture values of the year occurred in December and the highest values in August. Applying these values to the moisture release curve (Fig. 2) gives an indication of soil water availability assuming that water becomes less available as the matric potential increases. Soil moisture content had been depleted to its lowest point, less than 1 percent, in December by trees on rough lemon rootstock at depths of 150 and 180 cm.

Analysis of Rootstock Water Use

Soil water loss as influenced by rootstock and depth of rooting was determined by selecting periods from the year of study in which the confounding effects of rainfall and percolation were either absent or minimal. This was accomplished by selecting approximately 16 periods in which no rainfall had occurred but which had been preceded by sufficient precipitation so that the soil profile contained a reasonable amount of available water. These 16 time periods were well distributed over the year of study and the same periods were used for each rootstock; however, there were 2 time periods in which the data for 1 rootstock were not used. An increase in water content occurred at 1 depth, apparently due to some peculiarity in the drainage of that profile, which precluded using the data for that rootstock. The mean values for these time periods are a measure of water use under a variety of conditions due primarily to seasonal fluctuations in profile water content.

Results of the analysis described above are given in Table 10. Water use for all rootstocks decreased consistently with depth with few exceptions. Differences between rootstocks existed at nearly all depths. Total water depletion from the profile ranged from 3.68 to 4.29 mm day^{-1} and rootstock differences were statistically significant. Approximately 50 percent of the total water losses occurred from the surface 90 cm of soil.

The time period, October 10 to 20, 1973, one of the preselected periods, was chosen for more detailed analysis. Water content was measured 4 times during this period. Mean change in water content between each measurement was used for statistical analysis. Data were analyzed as a 4 x 12 factorial experiment. Moisture changes in the 0 to 15 cm depth were not included because the 0 to 15 cm interval is subject to considerable water loss by evaporation making it difficult to accurately estimate the portion of water loss that resulted from transpiration.

Two sources of variation, rootstock and depth, were statistically significant but their interaction was not (Table 11). Replicates, which were represented as access tube locations, were included in the initial analysis as blocks. They were not significant as a source of variation.

Mean change in water content was used for the analysis. The actual change in percentage volumetric water content between measurements is shown in Fig. 14. Each bar of the histogram for the time periods represents a 30 cm depth interval beginning at 15 cm. The general trend was similar for each rootstock. A large portion of the water loss took place at the

Table 10. Mean water loss from the soil profile for selected periods during the year April, 1973 to April, 1974.

Rootstock	Depth, cm													
	0[z]	30	60	90	120	150	180	210	240	270	300	330	360	Total[y]
	Water loss, mm day^{-1}													
RL	.635	.660	.432	.356	.356	.356	.330	.279	.229	.203	.152	.152	.152	4.292 a
SO	.660	.559	.406	.406	.356	.305	.330	.229	.254	.178	.178	.102	.102	4.065 b
Swt O	.684	.533	.406	.356	.305	.254	.203	.229	.305	.254	.229	.178	.152	4.088 b
Rusk	.584	.508	.406	.330	.305	.254	.254	.330	.178	.178	.127	.127	.102	3.683 c
	Water loss, percent by depth													
RL	14.0	15.4	10.4	8.3	8.3	8.3	7.4	6.5	5.3	5.1	3.5	3.5	3.5	
SO	16.0	13.5	10.5	10.5	9.2	7.5	8.1	5.6	6.2	4.4	4.4	2.5	2.5	
Swt O	15.7	12.5	9.9	9.5	8.1	6.8	5.4	6.6	8.5	6.2	5.0	4.4	3.7	
Rusk	15.7	13.6	11.0	9.4	9.0	7.5	7.5	9.7	4.8	4.8	3.4	3.4	2.8	

[z] Each depth value represents the center of a 30 cm interval; depth 0 equals the interval 0 to 15 cm. The underlined value in each row represents the depth from which approximately 2.5 mm of water was removed. The contribution from depth 0 was taken as one-half the indicated value.

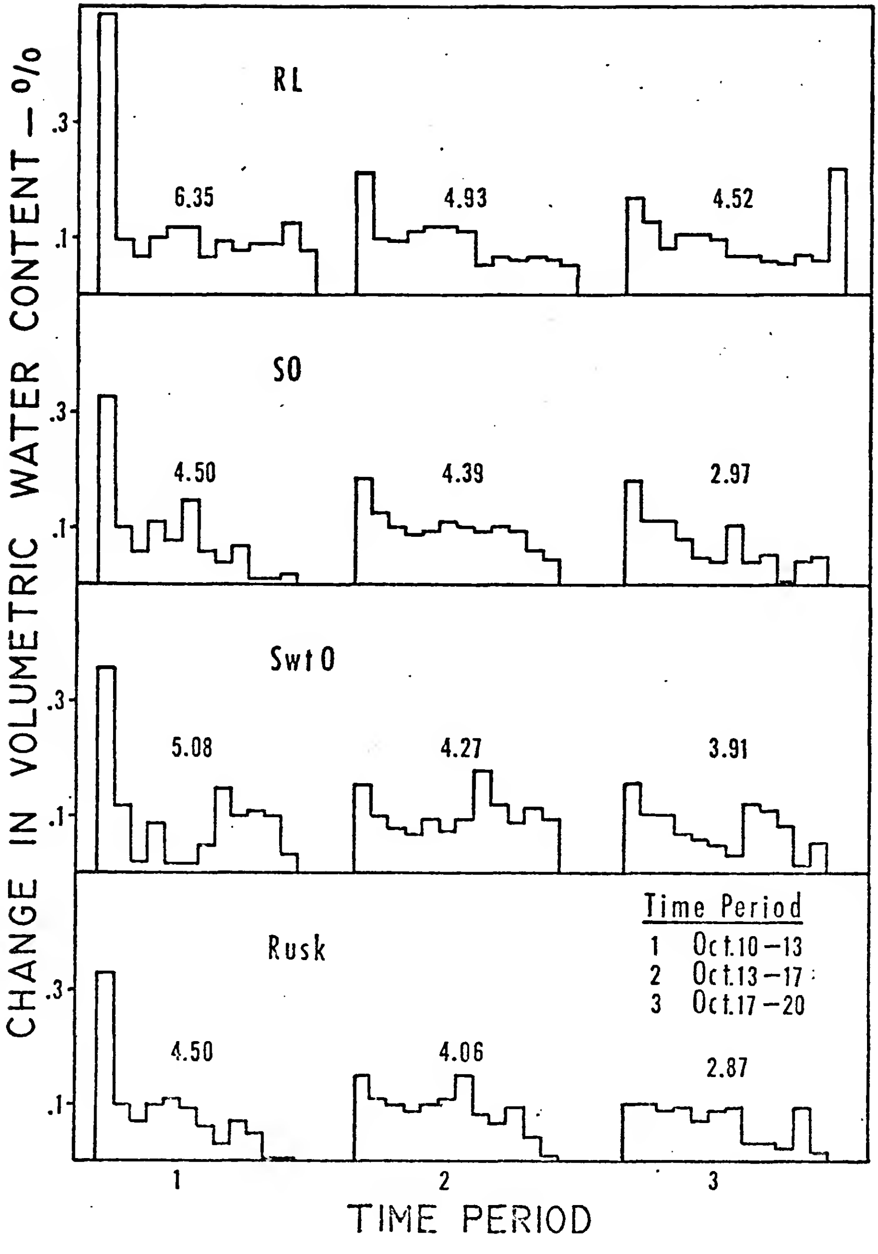
[y] Significant at the 5 percent level.

Table 11. Analysis of variance for mean change in water content, October 10 to 20, 1973.

Source of Variation	Degrees of Freedom	Mean[z] Square
Rootstock	3	217.24 *
Depth	11	1753.82**
Depth x Stock	33	112.16 n.s.
Error	528	84.19

[z] Significant at * 5 percent level.
** 1 percent level.

Fig. 14. A profile of rootstock effect on soil water depletion for the period October 10 to 20; 1973. No water was added to the profile during this period. Each bar in the histograms represents a 30 cm depth interval beginning at 15 cm. The number above each histogram is the daily water loss in mm for that time period.


CHANGE IN VOLUMETRIC WATER CONTENT — %
RL
6.35
4.93
4.52
SO
4.50
4.39
2.97
Swt O
5.08
4.27
3.91
Rusk
4.50
4.06
2.87
.3
.1
Time Period
1 Oct.10–13
2 Oct.13–17
3 Oct.17–20
1
2
3
TIME PERIOD

surface initially. There was a gradual increase in the contribution of deeper roots during the second period. Overall profile losses were reduced from October 17 to 20, as indicated by the entries on Fig. 14 for mean daily water loss. The water absorption pattern indicated a continued reduction in the contribution of the top and lower portions of the profile.

Statistical separation of means (Table 12) showed that the highest values which occurred at depth 30 cm were significantly different from the remaining depths within each rootstock. There were few other differences within rootstocks. Significant differences between rootstocks appeared at only 2 depths, 30 and 240 cm. The underlined values in Table 12 indicate the depth from which approximately 2.5 mm of water per day was lost. A similar value for daily water loss was obtained in previous studies of citrus trees in Florida (91,121).

The Relationship of Root Distribution to Soil Water Depletion

A 4 x 12 factorial analysis of feeder root weights obtained in an earlier study (37,38) was performed in order to evaluate and compare the effectiveness of roots from the 4 rootstocks in water absorption at different depths. The same trees were used for the feeder root analysis and the water depletion study. Rootstock was significant at the 5.17 percent level, while depth and the depth by rootstock interaction were highly significant (Table 13).

Root weights and the results of the test for differences between and within rootstocks are listed in Table 14. Feeder root weights for every rootstock were generally largest in the surface 45 cm and decreased with depth. Trees on rough lemon, however, had an increase in feeder

Table 12. Mean soil water loss for October 10 to 20, 1973.

Depth[z] cm	Water Loss, mm day^{-1}			
	RL	SO	Swt O	Rusk
0[y]	0.991	0.787	0.940	0.864
30	0.889 a/a[x]	0.711 a/b	0.787 a/b	0.660 a/b
60	0.330 b/n.s.	0.356 b	0.330 bc	0.305 b
90	0.254 b/n.s.	0.279 bc	0.203 c	0.254 bc
120	0.330 b/n.s.	0.279 bc	0.254 c	0.279 b
150	0.356 b/n.s.	0.229 bc	0.178 c	0.279 b
180	0.356 b/n.s.	0.305 bc	0.152 c	0.279 b
210	0.254 b/n.s.	0.254 bc	0.178 c	0.305 b
240	0.229 b/b	0.178 bc/b	0.457 b/a	0.154 bc/b
270	0.203 b/n.s.	0.229 bc	0.330 bc	0.178 bc
300	0.203 b/n.s.	0.127 bc	0.279 bc	0.152 bc
330	0.229 b/n.s.	0.102 bc	0.229 bc	0.203 bc
360	0.254 b/n.s.	0.102 c	0.178 c	0.051 c

[z] Each depth value represents the center of a 30 cm interval; depth 0 represents the interval 0-15 cm and was not included in the statistical analysis (see text). The underlined value in each column represents the depth from which approximately 2.5 mm of water was removed. The contribution from depth 0 was taken as one-half the indicated value.

[x] Significant at the 5 percent level. Letters to the left of the slash correspond to comparisons within rootstocks and letters to the right to comparisons between rootstocks.

Table 13. Analysis of variance of root weight.

Source of Variation	Degrees of Freedom	Mean Square[z]
Rootstock	3	28312.12 *
Depth	12	1336081.06**
Stock x Depth	156	25403.44**
Error	207	16672.61

Note: Root weight equals the dry weight of feeder roots for a column of soil 30 cm square and the depth of the interval. Roots were obtained from borings at the drip-line of the same trees used for soil moisture measurement.

[z] Significant at * 5.17 percent level.
** 0.01 percent level.

Table 14. Duncan's Multiple-Range test for root weight.

Depth[z] cm	Root Weight, g[y]			
	RL	SO	Swt O	Rusk
0	13.92 a/a[x]	9.33 b/b	10.33 a/b	13.63 a/a
30	8.61 bc/b	13.85 a/a	11.84 a/ab	13.13 a/a
60	3.87 de/n.s.	5.52 cd	4.95 bc	6.38 b
90	6.89 cd/n.s.	5.81 cd	6.96 b	7.97 b
120	9.90 bc/a	6.10 bc/b	5.81 b/b	6.38 b/b
150	10.48 b/a	5.88 cd/b	4.88 bc/bc	1.86 c/c
180	8.47 bc/a	3.01 de/b	2.58 cd/b	0.43 c/b
210	4.66 de/a	1.93 e/ab	2.22 cd/ab	0.29 c/b
240	4.52 de/n.s.	1.50 e	1.21 d	
270	2.43 e/n.s.	1.07 e		
300	1.58 e/n.s.	0.07 e		
330	1.11 e/n.s.			
360	1.80 e/n.s.			

[z] Each depth value represents the center of a 30 cm interval; depth 0 represents the 0-15 cm interval.

[y] Root weight equals the dry weight of feeder roots for a column of soil 30 cm square and the depth of the interval. Roots were obtained from borings at the drip-line of the same trees used for soil moisture measurements.

[x] Significant at the 5 percent level. Letters to the left of the slash correspond to comparisons within rootstocks and letters to the right to comparisons between rootstocks.

root weight from the depths 90 to 150 cm. The weight of feeder roots from trees on 'Rusk' was greater at depth 0 compared to those on the other stocks. Statistical differences in feeder root weights existed among rootstocks at all depths except below 240 cm and at 60 and 90 cm.

The relationship of root weight to water use for each rootstock is illustrated in Figs. 15 to 18. The correlation of root weight with water use was highly significant with each rootstock. Correlation coefficients were between 0.74 and 0.88.

The ratio of water use to feeder root weight was employed as a measure of root efficiency. A ratio of 1 indicated unity, i.e., water was being taken up directly in proportion to the number of feeder roots as measured by their weight. Ratios larger than 1 implied that those roots are more efficient, i.e., they are able to absorb a proportionally larger amount of water per unit of feeder root weight.

Apparent effectiveness of surface roots in the 0 to 15 cm layer did not vary to any extent with rootstocks. Rough lemon roots were most effective from 30 to 90 cm. There was an increase in root weight below 60 cm but those roots were relatively ineffective. Sour orange roots also showed a peak in effectiveness at similar depths; however, water use ratios were larger than 1 at greater depths. The water use pattern and distribution of sweet orange roots indicated a small zone, at 60 cm, of relatively efficient roots. The high root efficiencies near the bottom of the profile, as with the other rootstocks, reflected the presence of a very small number of roots growing in a generally more favorable environment with regard to available moisture.

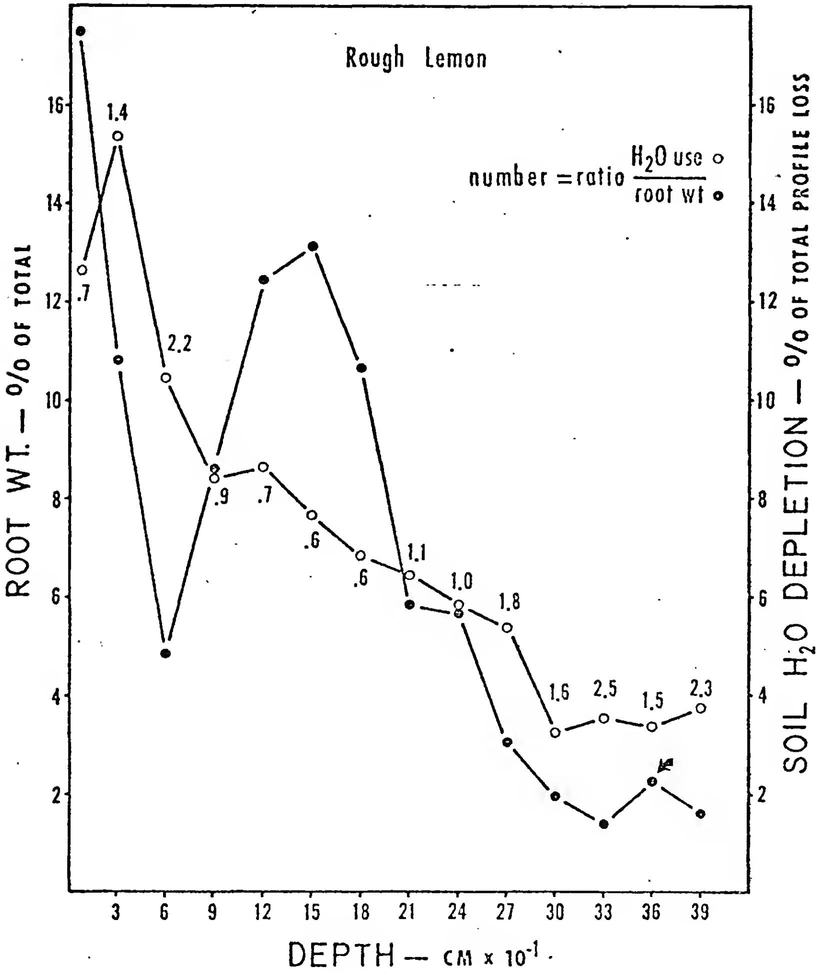


Fig. 15. Comparison of mean soil water use to root distribution of 'Orlando' tangelo trees on rough lemon rootstock, during selected periods from April, 1973 to April, 1974. Depth to the subsoil clay horizon is indicated by an arrow.

Fig. 16. Comparison of mean soil water use to root distribution of 'Orlando' tangelo trees on sour orange rootstock, during selected periods from April 1973 to April 1974 Depth to the subsoil clay horizon is indicated by an arrow.

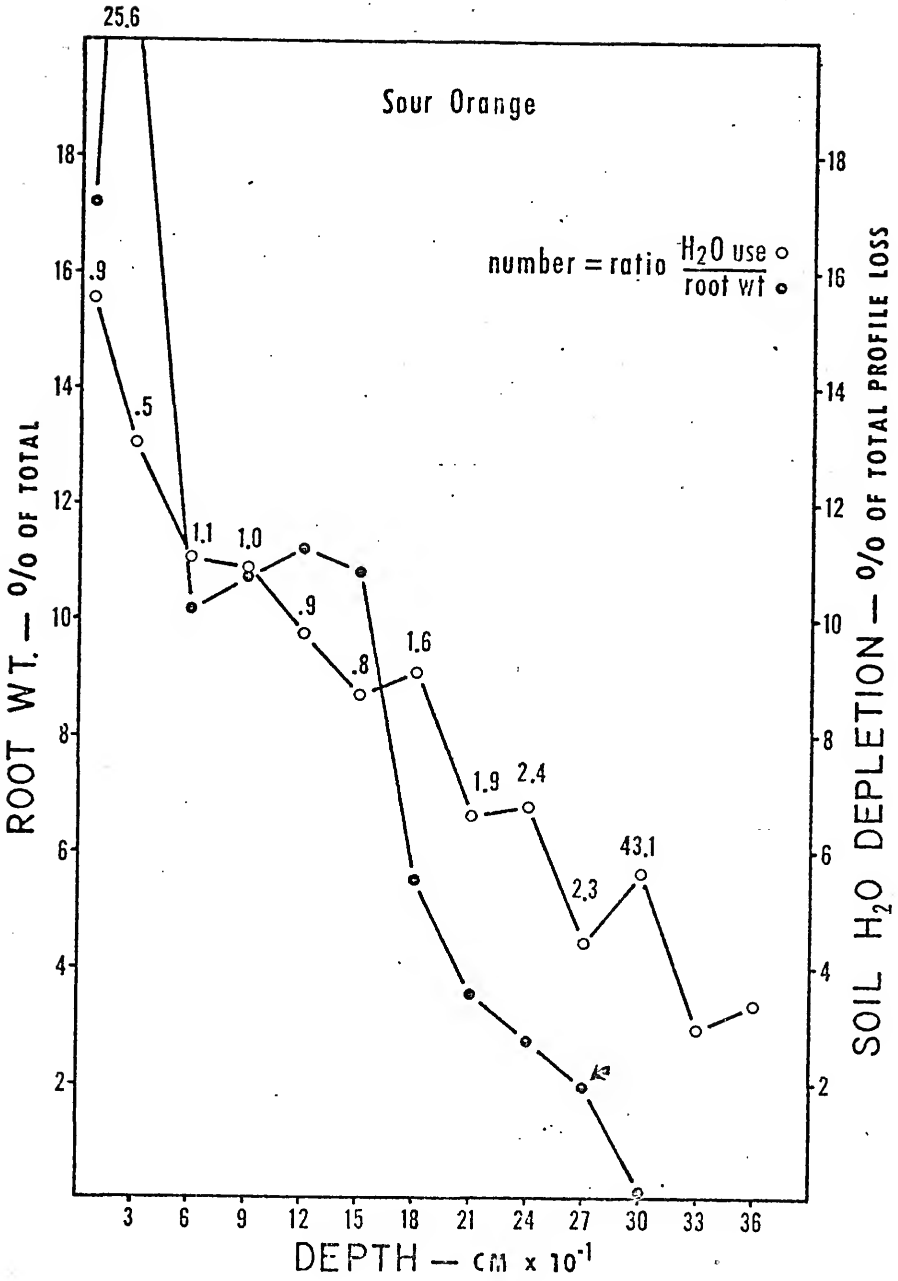
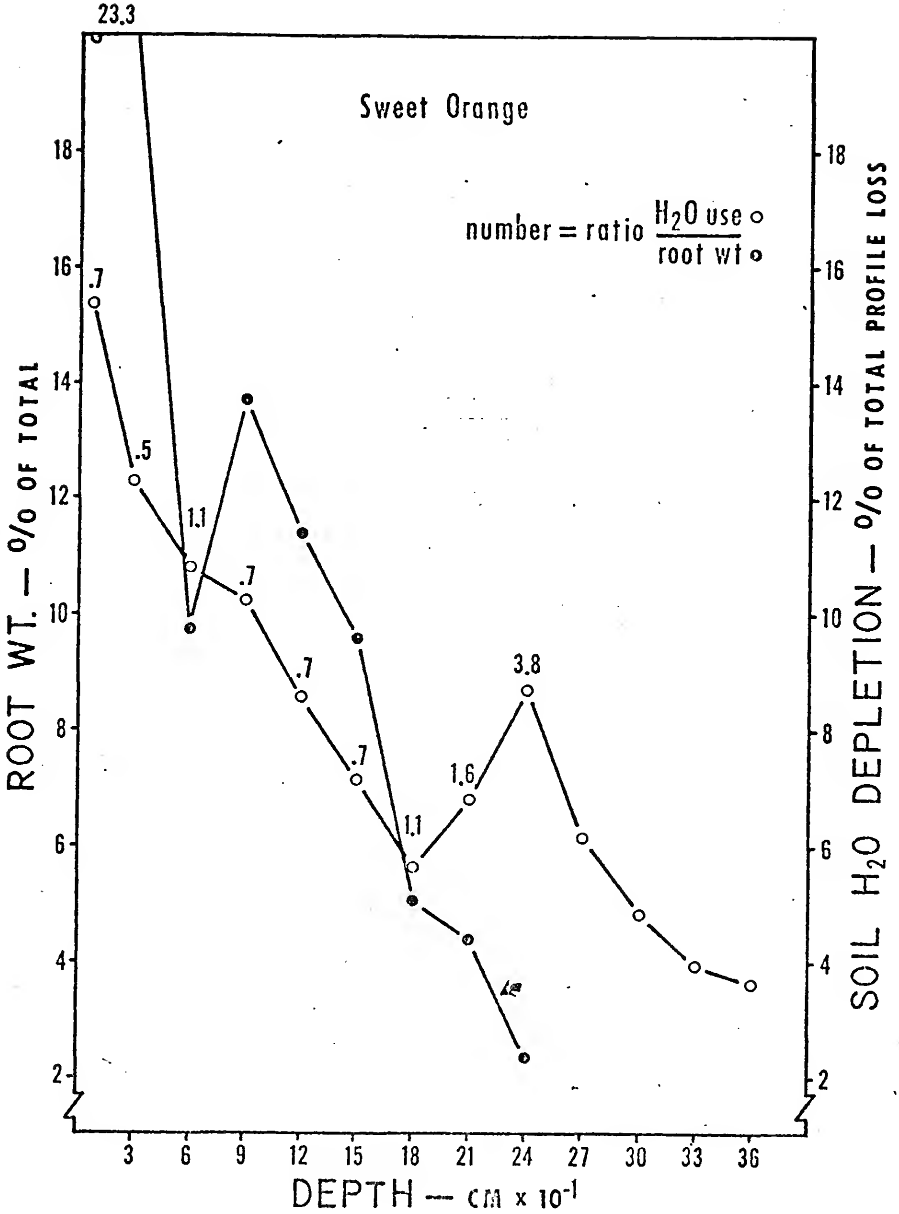

Sour Orange
number = ratio $\frac{H_2O\ use}{root\ wt}$ ○ ●
25.6
.9
.5
1.1
1.0
.9
.8
1.6
1.9
2.4
2.3
43.1
ROOT WT. — 0/0 OF TOTAL
SOIL H_2O DEPLETION — 0/0 OF TOTAL PROFILE LOSS
DEPTH — cm x 10^{-1}
2
4
6
8
10
12
14
16
18
3
6
9
12
15
18
21
24
27
30
33
36

Fig. 17. Comparison of mean soil water use to root distribution of 'Orlando' tangelo trees on sweet orange rootstock, during selected periods from April 1973 to April 1974. Depth to the subsoil clay horizon is indicated by an arrow.


Sweet Orange
number = ratio $\frac{H_2O \text{ use } \circ}{\text{root wt } \bullet}$
23.3
.7
.5
1.1
.7
.7
.7
1.1
1.6
3.8
18
16
14
12
10
8
6
4
2
ROOT WT. — o/o OF TOTAL
SOIL H_2O DEPLETION — o/o OF TOTAL PROFILE LOSS
3
6
9
12
15
18
21
24
27
30
33
36
DEPTH — cm x 10^{-1}

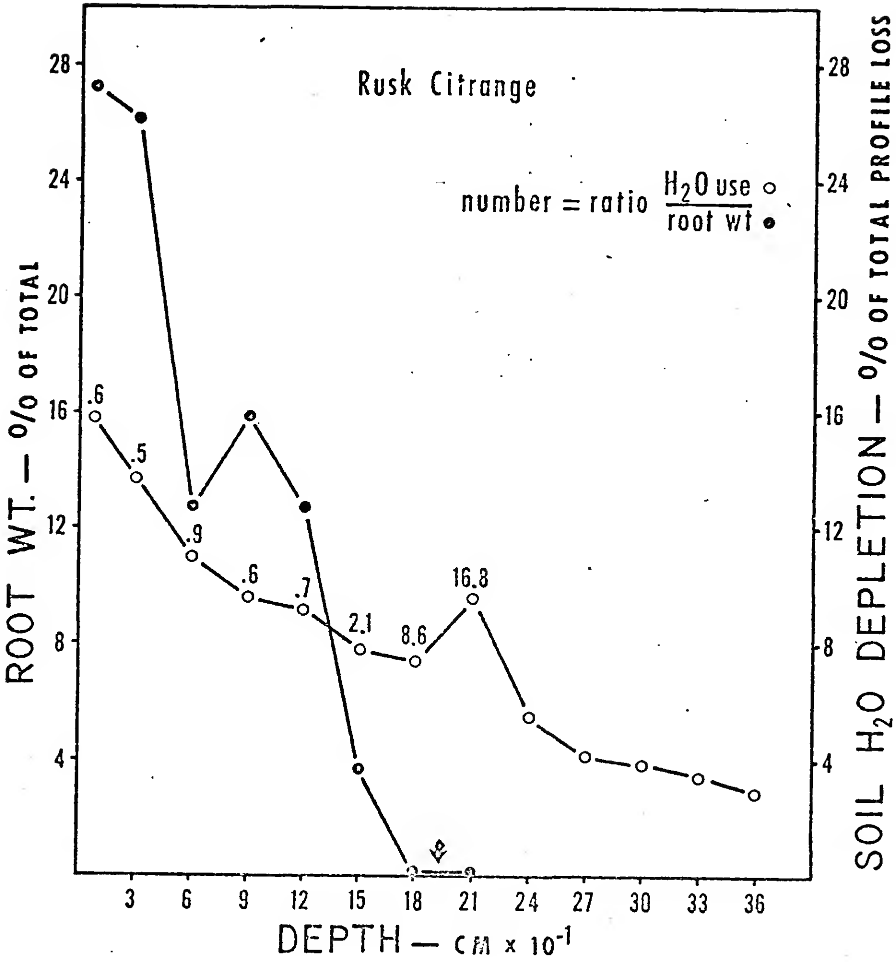


Fig. 18. Comparison of mean soil water use to root distribution of 'Orlando' tangelo trees on Rusk citrange rootstock, during selected periods from April 1973 to April 1974. Depth to the subsoil clay horizon is indicated by an arrow.

Trees on 'Rusk' citrange were shallow rooted with a large portion of their roots near the surface. Figure 18 shows the water use curve for 'Rusk' roots was below the root weight curve at all depths less than 120 cm.

Root Anatomy

Examination of root tips shown in Figs. 19 and 20 indicates that neither rootstock nor depth in the soil influenced root structure in any consistent manner. The basic anatomy of these field roots coincided with that established in previous studies (48,109,189). All of the roots possessed a root cap; however, it varied in thickness and prominence, the more elongated roots having a thinner cap. It was apparent that outer layers of the root caps deteriorated and were readily sloughed off.

The epidermis, hypodermis, cortex and vascular cylinder of most roots could be easily identified; however, the origin of these tissues could not be related to distinct apical initials. Maturation of the epidermis and hypodermis occurred very close to the root tip. Enlargement of epidermal cells and the impregnation of their walls generally preceded the same events in the hypodermis. The rapid development of the epidermis and hypodermis was soon followed by the disintegration of the epidermis. The outer periclinal wall usually deteriorated first. Loss of the epidermis was followed by the radial enlargement of groups of adjacent hypodermal cells in many areas. Hypodermal cell walls were impregnated, with an unidentified substance particularly the outer walls which appeared thicker (Fig. 21). The epidermis did not completely slough off.

Fig. 19A-I. Root tip anatomy of field citrus roots collected from different rootstocks and from 3 depths in a sandy soil including the subsoil clay horizon A,B) rough lemon roots, surface collected, AB-250X; C,D) surface roots from sweet orange rootstock, C-96X, D-93X;

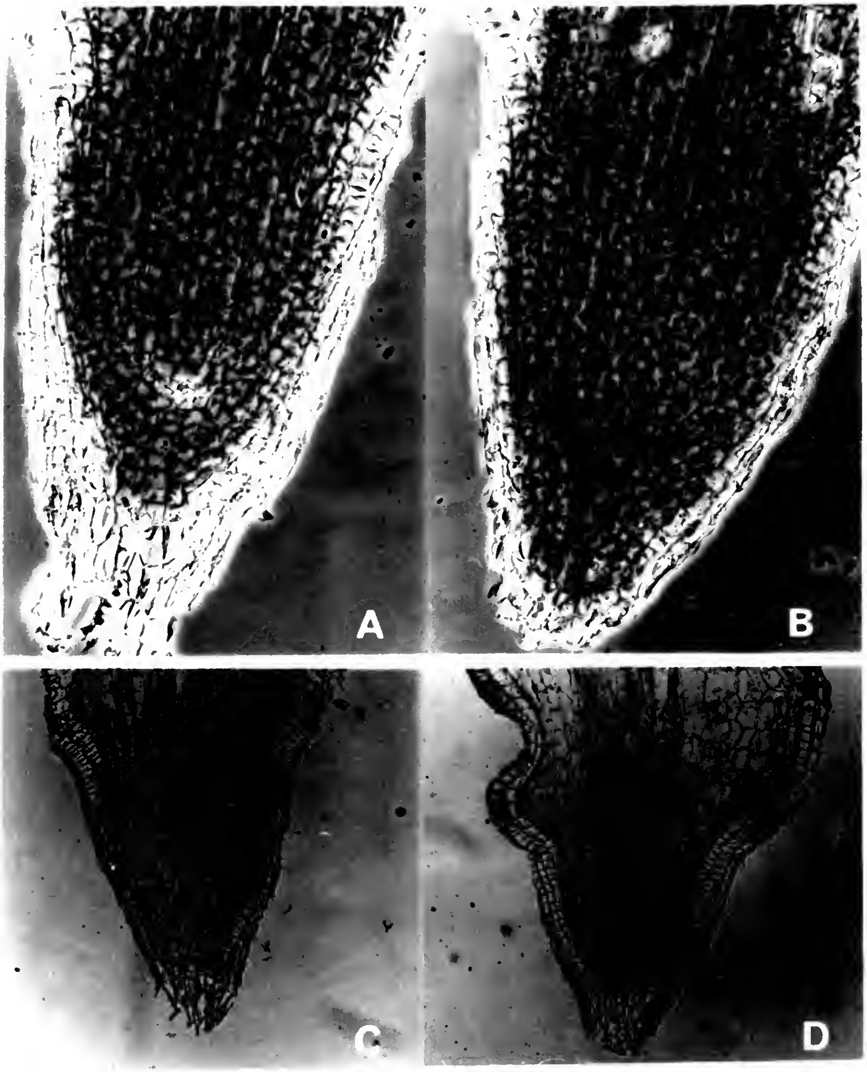

A
B
C
D

Fig. 19 - continued. E) surface roots from sweet orange rootstock, 205X; F) sour orange root tip from the sandy soil approximately 30 cm above the clay horizon, 325X; and G,H and I) roots of sour orange and 'Rusk' citrange respectively, obtained from the subsoil clay horizon, G-207X, H-333X, I-82X.

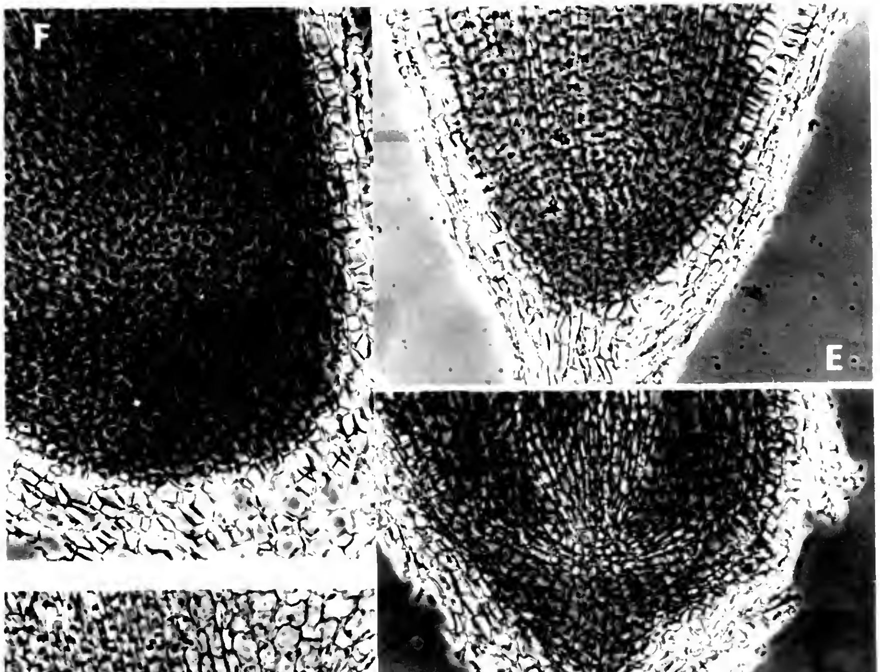

F
E
G

Fig. 20. Root tip from sour orange rootstock collected from a subsoil clay horizon (80X).

Fig. 21. Enlargement of groups of hypodermal cells after shedding of the epidermis (200X).

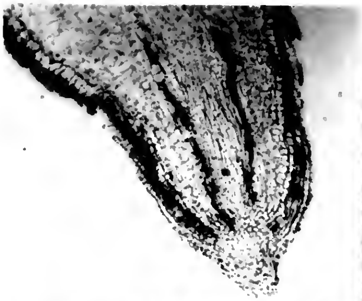
Fig. 22. Portion of a 'Rusk' citrange root showing small papillae-like root hairs appearing at approximately 7 mm from the root apex. The epidermis and hypodermis can be clearly distinguished. The epidermis has begun to deteriorate below the root hairs (196X).

Fig. 23. A small residual group of root hairs on a 'Rusk' citrange root growing in clay subsoil (197X).

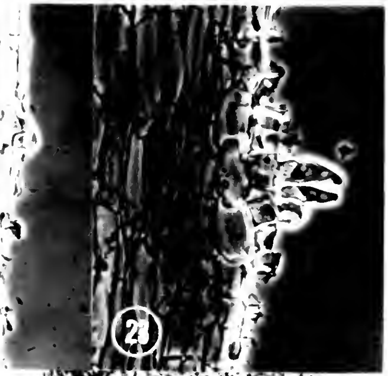
Fig. 24. Anatomy of a sour orange surface root at approximately 15 mm from the root apex. Growth of the metaxylem has nearly rounded out the pentarchal vascular cylinder and the endodermis is distinct. Small groups of hypodermal cells have elongated radially (80X).

Fig. 25. Anatomy of a 'Rusk' citrange root at a location similar to the preceding figure (192X).

Fig. 26. Close-up view of the vascular cylinder of a 'Rusk' citrange root showing tetrarchal xylem development. The endodermis with casparian strips can be seen (195X).

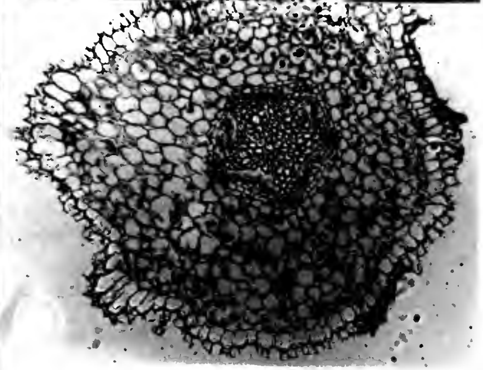


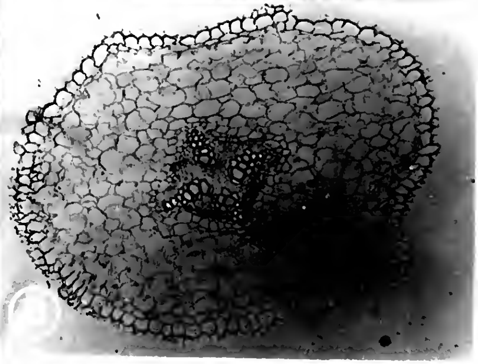
22



23

21





26

Root hairs were virtually absent because of the rapid shedding of the epidermis. Occasionally a small residual patch of root hairs, which ranged from small protuberances (Fig. 22) to more distinct forms (Fig. 23), was found.

Tissue maturation in essentially all roots occurred at a short distance closely behind the root apex. This consistent, marked characteristic was also observed in transection views which showed the formation of a distinct endodermis, with casparian strips, very near to the root tip.

Secondary growth did not occur in the length of root examined. A typical transection at 15 to 20 mm behind the root apex (Figs. 24,25) shows a large proportion of cortex, absence of epidermis (the function of which was apparently assumed by the hypodermis) and filling in of the stele with metaxylem cells. Xylem development was either tri-, tetra- (Figs. 25,26) or pentarch (Fig. 24).

A layer of mucilagenous-like material was present on the outer surface of most roots. Sand grains and bits of organic matter and other materials were observed adhering to the root. No fungus mycelia were found by visual inspection of the roots. There was evidence of internal fungal growth in only one instance.

Roots generally conformed to the environment in which they were growing. The largest pores in the soil were less than 0.5 mm in diameter (Table 4) while most roots were generally 1 mm or larger in size. Therefore, deformations could be seen in roots growing in either sand or the clay layer where the root partially enveloped an immobile particle. This was apparent on regions 15 to 20 mm basipetal to the apex (Fig. 27) and at the root tip (Fig. 19).

Fig. 27. Longitudinal section of a field root approximately 15 mm from the root tip showing the deformations formed by the root growing around immobile soil particles (370X).

Root Morphology

The scanning electron microscope (SEM) was used to examine both young seedling roots grown in a greenhouse and field roots of the rootstocks studied. The characteristic structure of the seedling roots is shown in Fig. 28. Fibrous roots of all rootstocks appeared similar. Root apices possessed orderly files of small, tightly-packed cells. Some roots had a pronounced root cap (Fig. 28A) while others did not (Fig. 28B). The root cap was generally several cell layers thick and distinct from the remainder of the root tip when it could be identified. Apparent absence of a root cap in some instances conflicted with the anatomical observations.

A zone of dense, uniform root hairs (Fig. 28C) was present on roots of each rootstock. The trichomes were tubular in shape and approximately 0.1 to 0.5 mm in length. It was readily evident that each appendage arose from the outer wall of a single epidermal cell when viewed close up (Fig. 28D). The epidermis began to crack and deteriorate (Fig. 28E) behind the root hair zone. The epidermis was shed eventually. Hypodermal cells developed in many areas after the epidermis had broken down, as shown in Fig. 21. Bark cracks (Fig. 28F) and lenticels were observed on older root tissues where secondary growth took place. A radial view of the epidermal and hypodermal layers and root hairs is shown in Fig. 29.

There were few observable differences in the general structure of the field roots (Fig. 30). Pronounced root caps were generally absent. A few residual root hairs often appeared close to the root tip (Fig. 30A), but frequently rapid maturation and loss of the epidermis (Fig. 30F)

Fig. 28A-F. Scanning electron micrographs of citrus roots from young seedlings grown in a greenhouse. A) root tip showing a distinct root cap, 213X; B) root tip without an apparent root cap, 672X; C) root hairs, 260X; D) close-up view of the root surface in the root hair zone showing that each root hair appears to arise from the outer wall of a single epidermal cell, 1242X; E) an area of the root surface basipetal to the root hair zone where the epidermis is deteriorating, 528X; F) bark crack in the root surface in area where secondary growth has occurred, 211X.

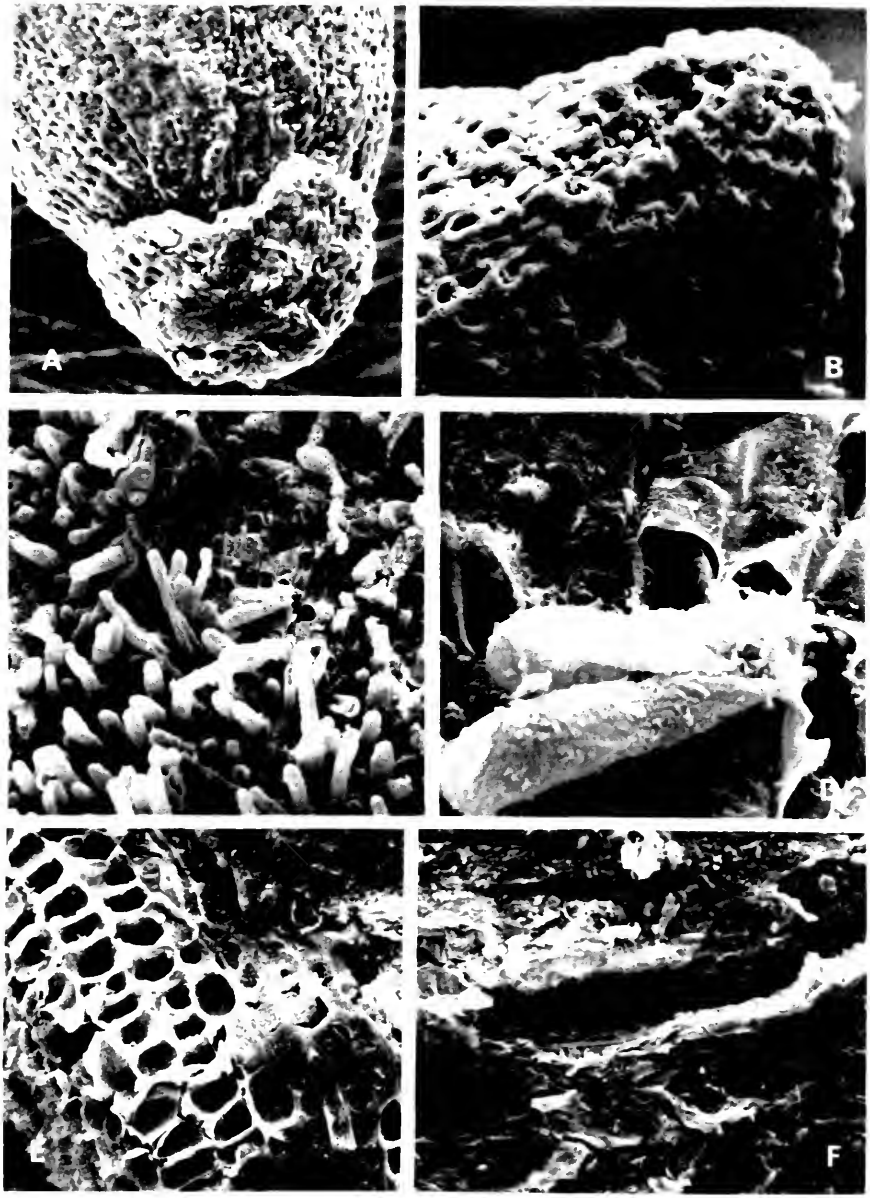
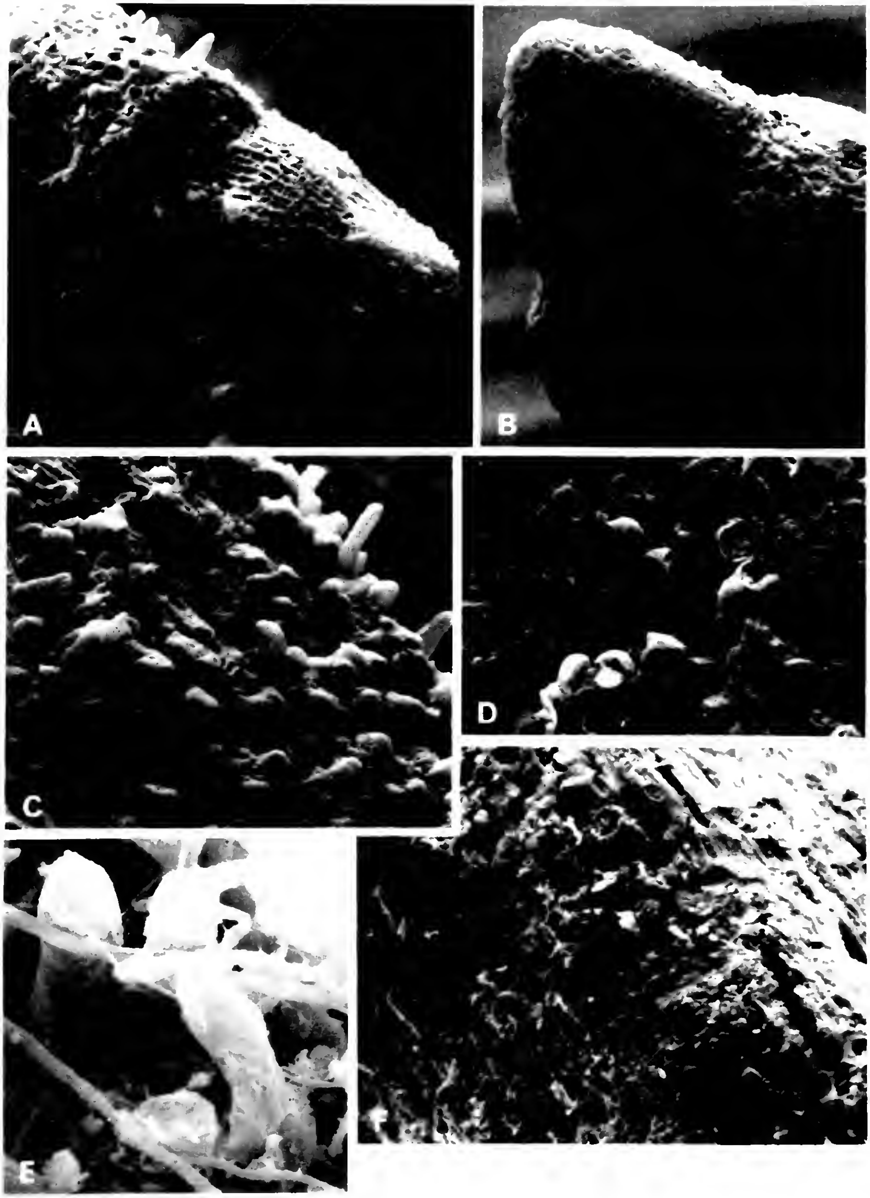

A
B
E
F

Fig. 29. Radial view in the root hair zone of a young, greenhouse-grown, seedling root showing the epidermis (E), hypodermis (H) and root hairs (650X).

Fig. 30A-F. Structure of citrus roots from the field. A) typical root tip showing the presence of a few residual root hairs very close to the root apex, 248X; B) root tip in which it appears root growth had ceased temporarily and then resumed, 215X; C,D) small patches of root hairs illustrating similar differences in their morphology as shown in Figs. 22 and 23, C-455X, D-620X; E) small group of root hairs with an apparent fungal mycelium crossing the root surface, 1154X; F) cracking and eventual shedding of the epidermis, 521X.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precluded their presence in meaningful amounts. The root tip had ceased growth then resumed activity (Fig. 30B) in some instances.

Root hairs were found on all stocks at all depths. They persisted in small irregular patches and differed in their morphology (Fig. 30C, D,E). Occasional strands of possible fungal origin were noted (Fig. 30E). Bark cracks, lenticels and radially elongated hypodermal cells were less frequently observed in field roots as compared to the roots of small seedlings grown in the laboratory. The characteristics of root structure established by the anatomical study were not contradicted by the SEM observations of gross morphology. The SEM study was complementary, adding a new perspective to the interpretation of root structure.

DISCUSSION

Rootstock Water Use

Relationship of Root Distribution to Water Absorption

Soil water depletion was significantly correlated with feeder root quantity; however, evidence was obtained showing that all roots were not equally effective in water uptake. The general pattern of moisture absorption coincided with that established in water extraction experiments with several other plants (167,204). Initial water depletion corresponded to root concentration followed by a progressively greater contribution from deep roots as the soil moisture content at shallow depths decreased. The depth at which roots showed an increase in water use generally paralleled the increase in depth of the drying front. This pattern of water use implied that the basic water needs of the citrus trees were met through adjustments within each root system, i.e., decrease of available water in one area was compensated for by increased absorption elsewhere. It is significant therefore, that citrus trees are potentially deep-rooting but also have 30 to 50 percent of their root system below 90 cm in the soil in many instances. Other fruit trees often have the majority of their roots within 90 cm of the surface and thus do not have a comparable "reserve" of deeper roots to support the tree when little soil moisture is available near the surface (144).

There were limits to the adjustments that occurred within a root system. Soil water became less available as it was depleted, as evidenced by the decrease in daily water loss from time period 1 to 3 shown in Fig. 14. Daily water loss is also a function, however, of water demand which fluctuates with a number of factors, including air temperature and the leaf area of the scion. Mean maximum daily temperature for period 3 was less than that for the first 2 periods. The influence of the size of the scion was evident in the mean daily soil water depletions shown in Table 10. There was a direct relationship of tree size and root quantity to water loss. Trees on rough lemon were large with extensive root systems (37,38) and had the corresponding largest water loss while the small, shallow-rooted trees on 'Rusk' depleted soil moisture the least. Trees on sweet and sour orange were intermediate in tree size, root quantity and water loss. Data in Fig. 14 generally support the relationship discussed above; however, the daily soil water depletion of trees on 'Rusk' was equal to that of trees on sour orange, which had a root system of intermediate size, for period 1. This was due to the slightly higher initial water content of the soil profile for trees on 'Rusk', which resulted in more available water, and because trees on 'Rusk' had a larger proportion and quantity of feeder roots in the surface zone than did those on sour orange.

Root Efficiency

Ratios of water use to root quantity (Figs. 15-18) showed that meaningful differences in the relative effectiveness of roots in water absorption existed with depth and rootstock respectively. Variation in these ratios indicates the limited usefulness of soil moisture extraction patterns for evaluating root distribution as has been done in the past. Spurious conclusions would have resulted if the results of this study were used as a measure of root distribution on the basis of the established relationship between water use and root quantity.

The known response of trees on the 4 rootstocks to the poor nutrient- and water-holding capacities of the soil of the experimental site can be explained on the basis of their relative root distributions and efficiencies. Trees on rough lemon are well adapted to deep, sandy soils. Their deep, well-distributed root systems occupy a large volume of soil and have access to a correspondingly greater amount of water. In addition, trees on rough lemon appeared to have a relatively effective root system for absorbing moisture. Rough lemon roots were the only ones to have ratios larger than 1 for the 30 to 90 cm rooting zone. This is significant because the soil water content is often increased to only shallow depths by the light rains that frequently occur during the summer rainy season in Florida. Rough lemon roots were comparatively inefficient in the 90 to 180 cm zone, probably due to the high root density and the failure of light rains to penetrate to that depth. Water use ratios for the deep roots were all close to, but greater than, unity. The absence of very large ratios for these roots may be interpreted to mean that: 1) the soil moisture environment in the 0 to approximately 120 cm depth of trees on rough lemon was such that the apparently efficient roots in this zone were able to adequately supply the tree's water requirements; thus, 2) a stress situation rarely developed which necessitated an increase in the rate of water uptake by the deep roots; however, the contribution of the deep roots was significant and essentially proportional to the concentration of roots present.

Trees on sweet and sour orange rootstocks are less well adapted to sandy soils as compared to those on rough lemon. Sour orange surface roots were relatively inefficient, as were those of all rootstocks. The poor absorption response of these roots was compensated for by the effectiveness of the remaining roots in the profile. Less than 15 percent of sour orange roots were located below 150 cm in the soil suggesting the deep roots were important in supplying water to the scion. The value of the deeper roots was also apparent for trees on sweet orange. Sweet orange roots were generally inefficient at all depths above 180 cm, which may explain why trees on this stock are notably drouthy on deep sands. The water use ratios of roots below 180 cm were all greater than 1; however, only 10 percent of the root system was present below that depth.

Trees on 'Rusk' had a limited root system, considering both depth of rooting and quantity of feeder roots. Furthermore, the 'Rusk' root system was relatively inefficient in extracting water from the soil in the surface 120 cm rooting zone. These 2 disadvantages were partially balanced by the comparatively high efficiency of roots below 120 cm. The large water use ratios of the deeper 'Rusk' roots clearly illustrates the important function of deep roots in circumstances where the activity of surface roots can not adequately supply the water needed by a tree.

The poor efficiency of the surface roots for all rootstocks was probably due more to environment than to inherent differences. A sandy soil is limited in the amount of water available for absorption. Moreover, as water content decreases, hydraulic conductivity also decreases rapidly (Fig. 3). A decrease in conductivity would not be significant, however, in a volume of soil well permeated with roots because the distance water would have to move would be short. Therefore, the limiting factor in sandy soils is water content in relation to root density. Theoretically, there is a maximum root density that would give a water use ratio of unity, given a limited amount of available water at the surface. An increase in root density beyond this maximum would decrease the ratio. This possibility is suggested when the surface ratios of the 4 rootstocks are compared. Trees on sour orange had the smallest feeder root weight at the surface (Table 14) and they had the correspondingly largest water use ratio. This root quantity-water use relationship has utility. For example, deep roots would be especially advantageous in high density plantings where the growth of surface roots rapidly surpasses the theoretical maximum density.

Validity of the Moisture Extraction Data

The results of this study represent 1 of only a few detailed examinations of moisture depletion patterns for citrus trees. A study of this type is usually subject to certain limitations which restrict the scope of interpretation. The results of this study, however, are considered to be accurate for the following reasons. Soil moisture content was determined using the neutron moderation method, a very reliable technique; mean values for soil water depletion were based on approximately 16 periods chosen from the year of study; these periods were well distributed throughout the year, thereby greatly reducing any time-of-year effect on the results due to changes in the environment or root activity; the periods were carefully selected to eliminate or minimize confounding due to rainfall or percolation within the profile; internal drainage was at a minimum because hydraulic conductivities were generally less than .24 mm day^{-1}; and the percolation characteristics of the soil normally assured a reasonably uniform vertical distribution of water contents in the soil profile. Root data were obtained during a 2-year period just prior to this research (38) and it was assumed that the quantity and depth of rooting may have increased slightly but the relative differences within and between rootstocks were unchanged. This assumption was supported by the small differences found in 2 consecutive samplings 16 months apart.

The validity of the results as discussed in the preceeding 2 sections was generally substantiated by the statistical analyses of the period October 10 to 20. For example, the large mean soil water loss at 30 cm for trees on rough lemon (Table 12) was statistically different from that of the other rootstocks. The large water loss by the smaller quantity of roots (Table 14) corresponds to the high water use ratio shown on Fig. 15, as compared to those of the other rootstocks in the 30 cm depth zone. Some comparisons were not statistically significant, particularly those between rootstocks. The magnitude of the changes in water content for the 10-day period were small. Thus, it was apparent the length of the period of analysis was not adequate to detect such small changes. Furthermore, the root weight data were obtained from a small number of replicates. The lack of statistical difference in a small scale comparison, however, does not negate the meaningfulness of the data given in Figs. 15 to 18.

Root Structure

The outstanding characteristic of the roots studied was their marked similarity with rootstock and depth despite being obtained from different locations within a diverse environment. This suggests that root structure was not a primary factor involved in differences in root function. Therefore, the results depicted in Figs. 19 to 30 provide information that assists in interpreting root function per se, not as it may vary with rootstock or depth in the soil.

Several consistent features were noted that could pertain to root function under field conditions. Root hairs were found on all stocks and at all depths. Their presence on field roots of citrus has frequently been debated. The evidence presented clearly shows the potential of root hairs to form on the roots of any rootstock at any depth when the environment is favorable. The functional significance of these trichomes is moot but it is generally recognized that they increase the absorbing area of a root. The differences in root hair morphology observed probably reflected variations in root micro-environment or density. The generally smaller size of root hairs on field roots as compared to seedling roots grown in the greenhouse, implied that optimum conditions for trichome development were not present in the soil. It was not an objective of this research to study root mycorrhizae but it is noteworthy that virtually no evidence was obtained indicating their presence.

Other features observed lent credence to Kramer's hypothesis that tree roots can absorb water through suberized tissue. It was proposed that this was necessary to supply water to trees like citrus which continue to transpire during periods unfavorable for root extension. Groups of radially elongated hypodermal cells, known as hypodermal absorbing areas (HAA), were frequently seen. It has been suggested that they are functional (109) but this has not been demonstrated. Another potential absorption site was the large surface area exposed by epidermal shedding. This event occurred at short distances behind the root apex as apparently did maturation. No secondary growth was observed in the length of root studied; thus, for at least 2 cm behind the root apex, the tissue underlying the shed epidermis consisted of cells associated with absorption, i.e., cortical and xylar cells.

Rootstock Adaptation

Information obtained in this and a previous study of the same trees (38) suggests the adaptation of trees on the 4 rootstocks to the soil environment of the experimental site was the result of inherent differences in their respective root systems.

The most obvious and apparently inherent difference among the root systems of each rootstock was the variation in their physical characteristics. Trees on rough lemon had deeper, more extensive, well-distributed root systems than trees on the other 3 rootstocks. Trees on 'Rusk' were the shallowest rooted and had the smallest quantity of feeder roots. Gross differences among these root systems were not primarily the result of the environment for several reasons. First, the results of other studies involving some of the same rootstocks, corroborated the basic physical characteristics of the root systems as they existed at the experimental site (2,162,217); second, rough lemon roots were found to depths as great as 6 m at the experimental site implying that soil environment, although perhaps not optimum, was adequate to support some root growth. Roots of the other rootstocks had not penetrated as deep as those of rough lemon at the time of measurement; third, the absence of any marked influence on the structure of roots collected from all depths also suggests that the soil environment was not so adverse as to prevent root growth; and finally, there were some differences, for example, in the distribution of roots with depth that were too large to have resulted strictly from an environmental influence.

The relative efficiency of water uptake at various depths and for the respective rootstocks, however, seemed to result from an interaction of root distribution with the physical characteristics of the soil. This interaction appears to be reasonable because: 1) the water use responses of all the root systems can be explained on the basis of this interpretation; 2) research with citrus and other plants has often indicated that individual roots do not differ significantly in their inherent capacity to absorb water; water uptake rate was generally a function of water availability (167,204). In the case of citrus, a study in California showed that trees, reasonably similar in all respects, but growing in soils of different texture, differed in the efficiency of roots with soil depths (30); and 3) if water absorption was assumed to be essentially a passive process, it would be affected primarily by the soil environment. Plant factors such as root surface area and the size and number of root hairs could affect water uptake but roots were found to be basically similar in structure in this study.

There is some evidence indicating that root efficiency in water absorption has a genetic basis. A study was conducted in California using small plants of navel orange on several rootstocks. The transpiration characteristics of these plants were investigated and showed that trees on rough lemon transpired a greater quantity of water as compared to those on other rootstocks when leaf area and root quantity were considered (161).

The differences in root systems as discussed above provided trees on rough lemon with an initial morphological advantage. The extensive root system of rough lemon permeated a larger volume of soil thereby making more water and mineral nutrients available to the trees on this rootstock as compared to those on the others. It is interesting, however, that trees on 'Rusk' despite the supposed disadvantages of a small root system, produced substantial yields of good quality fruit on a unit tree area basis in the same environment (129). One could speculate that the reason why these trees were so fruitful was due to the accompanying small size of the aerial portion of the tree which would reduce the transpiring leaf area and consequently the tree water requirement. The relationship of transpiring leaf area to functioning root surface in this case, may have represented a more efficient balance of these factors in terms of water use. Other factors not studied, however, may have been equally or more significant.

Trees on sweet and sour orange were larger in size than those on 'Rusk' but they were not as large or as productive as those on rough lemon. Trees on sweet and sour orange had a large proportion of their roots at depths less than 60 cm in the soil, a relatively small zone where moisture was ordinarily lost very rapidly, thereby imposing limitations on these trees. Reports have shown that trees on these stocks may be more productive in more favorable soil environments (34,35,217).

The Soil Environment

A major study of the soil environment was not an objective of this research but there were several aspects of the data obtained that merited discussion.

Chemical

The sandy nature of Astatula soil from the experimental site imposed certain chemical and physical limitations on the ability of the soil to support root growth. An important factor limiting the retention of applied mineral nutrients is the low cation exchange capacity (CEC) of the soil. Moreover, the values given in Table 5 are CEC values at pH 7.0 and do not represent the effective CEC that exists under field conditions. Soil components contributing to exchange capacity, i.e., organic matter and clay minerals, have a pH-dependent CEC. Kaolinite, the dominant clay mineral of the subsoil, has a pH-dependent component that is apparently due to a coating of Al or Fe hydrous oxide which may give a clay particle a net positive charge at a low pH (45). A study of some Florida soils showed the effective CEC of the clay horizon may be 50 to 75 percent less than that measured at pH 7.0 (70).

The low nutrient-retention capacity of the sandy soil allows fertilizer materials to readily leach through the soil. Ordinarily, nutrients not absorbed or taken up by plant roots would pass through the profile and enter the underground water system; however, the subsoil clay horizon impedes this rate of nutrient loss. The ions, K, Mg and Ca and NO_3 increased in concentration near the sand-clay interface forming a "zone of accumulation" of available nutrients. Root absorption of nutrients from this zone was not determined but the zone could serve as an important reservoir. The significance of this zone, however, varies with several obvious factors including the time-of-year and the timing and amount of fertilizer applied. The time-of-year effect is related to rainfall. The soil would be subject to considerable leaching of nutrients during periods of heavy rainfall. Therefore, it is important to recognize that the level of soil nutrients fluctuates greatly and the results of this study represent the soil nutrient status at 1 sampling date.

The data showing the distribution of mineral nutrients within a soil profile are useful for indicating the level of potentially available nutrients within the root zone. Furthermore, it can be assumed that the soil nutrient values at all depths are reasonably representative of levels that can sustain root growth since roots of some rootstocks were found at all depths within the area studied (38). It is possible however, that some ions may be absorbed at a site where they are plentiful and translocated to roots growing in environments deficient in the same nutrients.

The soil level of 2 elements, Al and Ca is particularly significant. The latter element is considered to be essential for root growth and must be present in the root environment because it is not readily translocated downward within a root system (63,126). The mean soil Ca content in the surface 15 cm was slightly less than the currently recommended value for Florida (173). Ca content, however, decreased rapidly with depth to approximately 40 ppm and increased again near the clay horizon. The presence of roots at the depths with the low Ca content implies that these levels were adequate to sustain root growth; however, the minimum soil Ca level is not known. Leaf Ca deficiency symptoms were reported for trees in Florida on a sandy soil in which the Ca content was 30 ppm in the surface 15 cm (200). Furthermore, the efficacy of Ca in a soil is often not related to a known quantity, but the total cation content and the percent base saturation.

Changes in soil pH indicated Al ions were present. Soil pH values were reduced when measured in KCl as compared to H_2O but the KCl values were all above 5.0 to a depth of 165 cm (Table 6). The pH values in KCl below this depth were all less than 5.0 indicating the presence of appreciable exchangeable Al (70). The CEC was not dominated by Al, however, because sufficient Ca had apparently leached to those depths to displace some Al and occupy a significant portion of the exchange capacity. This observation is supported by comparing the pH values in Table 6 and those from a virgin site of a similar soil (68). The latter values were lower.

Few roots were found in the clay layer (38) indicating that perhaps, despite the presence of Ca ions, the Al level was high enough to reduce root growth. The effect of Al could have resulted from a direct toxicity or its influence on pH. Smith has demonstrated a direct H ion effect on citrus root growth which manifests itself markedly at pH 4.0 (194,195). Little is known about Al toxicity to citrus roots under field conditions although 0.1 to 1.0 ppm are toxic in solution culture (39).

Physical

Low water-retention capacity and rapid drainage were the most striking features of the soil physical environment. These characteristics were due primarily to the high percentage of large pores that drained under low tension. The water content of the soil after the large pores have drained has been considered the "field capacity" value; however, this term has little utility and actually does not exist under field conditions since the soil water content continues to decrease due to evapotranspiration and percolation.

SUMMARY AND CONCLUSIONS

Trees of 'Orlando' tangelo on 4 rootstocks, rough lemon, sweet orange, sour orange and 'Rusk' citrange, were studied to determine the effect of rootstock root distribution on water absorption and root anatomy and morphology. Root samples were collected from near the surface, in a subsoil clay horizon and an intermediate depth to examine their anatomy and their morphology by scanning electron microscopy. Access tubes were installed at the drip-line of 4 replicates of each rootstock to investigate the pattern of water use by the neutron moderation method. Soil samples were also taken to characterize the chemical and physical environment of the plant roots.

Root distribution data from a previous study of the same trees were used to compare with the water extraction data.

1. A comparison of root distribution to water use showed that water extraction was directly proportional to root quantity, i.e., trees with the largest root systems decreased soil water content to the greatest extent.

2. The general pattern of moisture extraction for trees on all rootstocks was similar to that described for other plants. The greatest loss of soil water initially was in the top 30 cm. The use of available moisture from near the surface was followed by a gradual increase in the contribution of deeper roots. The total water loss from the profile, however, also gradually decreased with time as less water was available at all depths.

3. Ratios of water loss to root quantity indicated that roots at various depths of the respective rootstocks were not equally efficient in water absorption. Differences in these ratios appeared to be due to inherent variations in the physical characteristics of the root systems and the interaction of this factor with the soil physical environment. Trees on rough lemon had deep, well-distributed root systems that were relatively efficient in absorbing water. Root systems of trees on sweet and sour orange and 'Rusk', which had a larger proportion of roots near the surface, were less efficient. Therefore, the deeper roots of these trees had larger water use ratios as compared to those of rough lemon, illustrating the important role of deep roots in environments where the available water near the surface is rapidly depleted.

4. There were no apparent differences in anatomy or morphology of citrus roots with depth in the soil or rootstock. Root hairs were found on roots from all depths and rootstocks. This represents the first report demonstrating the presence of root hairs on field-grown Citrus, a controversial subject in the past.

5. Other structural features observed that are of possible functional significance were the radial elongation of groups of hypodermal cells and the deterioration and shedding of the epidermis soon after its apparent maturation.

6. Characterization of the soil environment showed that pH, organic matter content, cation exchange capacity and mineral ion content generally decreased with depth. The subsoil clay horizon apparently impeded water movement and mineral ion content often increased near this horizon. Cation exchange capacity also increased in this horizon because of its

native clay (kaolinite) content. The presence of roots throughout the soil profile implied the environment was adequate to sustain considerable root growth.

7. Soil physical data showed the low water-retaining capacity of soil from the experimental site was due to the high proportion of large pores which were drained under relatively low tension.

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BIOGRAPHICAL SKETCH

William Stanley Castle was born March 4, 1943, at Glen Ridge, New Jersey. He attended elementary and secondary school in Verona, New Jersey, graduating from high school in June, 1961. He received the degree of Bachelor of Science in Agriculture from Rutgers University in June, 1966. From April, 1967, until April, 1969, he served with the U. S. Army in Germany after obtaining a commission from the Army Artillery School, Fort Sill, Oklahoma, and completing parachute training at Fort Benning, Georgia. In June, 1969, he entered the Graduate School of the University of Florida. He was employed as a graduate assistant in the Department of Fruit Crops until August, 1971, when he received the degree of Master of Science in Agriculture. Continuing in this capacity, he received the degree of Doctor of Philosophy in December, 1974.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Fruit Crops

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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