Citrus Root Systems: Their Structure, Function, Growth and Relationship to Tree Performance

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William S. Castle
University of Florida
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CITRUS ROOT SYSTEMS: THEIR STRUCTURE, FUNCTION, GROWTH, AND RELATIONSHIP TO TREE PERFORMANCE[1]

WILLIAM S. CASTLE
University of Florida, IFAS,
Agricultural Research and Education Center,
P. O. Box 1088, Lake Alfred, FL 33850, USA

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Abstract. **Reports concerning citrus roots and root systems are reviewed and examined for practical implications. Those aspects considered include: (1) root anatomy and morphology with emphasis on the relationship of root structure to function; (2) distribution of fibrous and framework roots, their variation with rootstock and soil environment, and the expected distribution for trees allowed maximum expression of inherent potential; (3) root growth—those areas, e.g., periodicity of growth, in which there is conflicting evidence are identified and discussed; (4) the water and nutrient uptake activities of individual roots and the entire root system, the significance of mycorrhizae and a summary of root hormone physiology; and (5) a study of the root:shoot ratio in citrus, practical means of its manipulation and the relationship of root density and distribution to tree performance.**

Today, it is becoming increasingly apparent that the root system interacts with the shoot system in significant ways not heretofore understood. As a result, considerable effort has been expended to review certain aspects of root systems (63, 65, 69, 98) as well as to summarize the state of knowledge related to roots (20, 99, 110).

Much of our knowledge about roots has been obtained from monocotyledonous plants which are characterized by relatively short life cycles, rapid growth and shallow root systems. Such plants are readily adapted to short-term studies in controlled environments. Moreover, many of these investigations have been directed toward a fundamental understanding of root growth and function. A considerably smaller body of information is available pertaining to horticultural tree crops. In general, greater attention has been focused on forest trees.

The subject of this discussion is the evergreen *Citrus* in which, as with nearly all fruit and nut tree crops, the root system is provided by a rootstock thereby adding an extra dimension not present in most agricultural plants. The citrus root system is a separate biological entity the effect of which can be modified simply through rootstock selection. Thus, it is important to understand not only what conditions favor optimum root growth and function and how they might differ with rootstock, but also to examine the relationship of the root system in achieving desired scion performance.

The objective of this paper is to summarize the existing knowledge concerning citrus root systems and identify areas where additional research may be helpful in solving practical problems; and to examine the root-shoot relationship in citrus and its potential manipulation, especially toward the control of tree size needed for higher density plantings.

In this review, several root characteristics are not mentioned or discussed in detail largely because citrus roots *per se* have not been used for fundamental studies of plant roots. Readers are referred to other reviews (20, 65, 69, 98, 99, 110) for a more comprehensive treatment of certain basic aspects of root growth and function. They present knowledge and identify problem areas which are probably inclusive of citrus.

The Citrus Root System

Root Anatomy and Morphology

Studies of plant anatomy and structure are generally considered to be within the domain of botany and descriptive in nature. Such studies often do not consider function and therein lies the critical subject area in the study of citrus root structure.

The structure of citrus roots is similar to that depicted in standard textbooks (33) for woody, dicotyledonous plants. The most comprehensive studies of citrus root anatomy are those of Schneider (93), Cossman (27), and Hayward and Long (57). Briefly, their collective work has shown that the primary root tissues are derived from 3 histogens in the apex which give rise to the vascular cylinder, cortex, and rootcap-epidermis respectively. The organization and differentiation of the root tissues appear to be generally similar to that of a woody vascular plant root. Citrus forms a distinctive hypodermis from the outer layer of the cortex. The vascular cylinder contains alternating strands of protoxylem and protophloem, the number varying according to root size. The primary root may contain 6 to 8 protoxylem strands but only 2 or 3 are found in the small, highly branched fibrous roots and 3 or more in the main fibrous, and in the lateral roots. Certain roots differentiate a cambium and may begin secondary growth. As growth proceeds, longitudinal cracks may appear in the epidermis and hypodermis (57, 93).

It should not be assumed that citrus root structure is a stable characteristic, unchanged even in subtle ways by such factors as species, soil depth, soil physical or chemical differences or soil organisms (68). Differences in 4 anatomical root characteristics were reported by Cossman (27) in his study of 9 citrus species. Root hair characteristics also differed with rootstock (27). Further studies are necessary to determine what effect these and other factors may have on structure and how these changes may be related to modification of root function.

The most controversial feature of citrus root structure has been the formation of root hairs which appear on citrus perhaps as an adaptive response to changes in soil aeration, temperature, water content, or pH (21, 27, 51, 57, 94). They can often be observed on the primary root soon after it emerges from the seed (Fig. 1). Less is known about their occurrence under field conditions where they have been observed but vary in size, shape, and relative abundance (Fig. 2) (21, 27). Earlier claims which stated that citrus does not form root hairs are now clearly refuted (27). The central unresolved issue is now a matter of understanding the interaction of the soil environment and root hair formation. For example, it is not known whether the *Endogone* fungi which invade citrus roots and form *endo*mycorrhizae affect root hair formation. This association does not appear to affect root anatomy (72).

Another anatomical feature of potential functional significance was reported by Hayward and Long (57). They noted that the primary root of sweet orange contained groups of radially elongated hypodermal cells which they described as functionally active 'hypodermal absorbing areas.'

The usefulness of anatomical study is well exemplified in a report relating the unusual resistance of a citrus relative, *Citropsis gilletiana* Swing. and M. Kell, to the burrowing nematode, *Radopholus similis* Cobb. The relative has an 'abnormally' thickened epidermis which may prevent nematode penetration (38). Also, recent investigations of a disorder characterized by an interruption of water flow have revealed the previously unreported presence of plugs
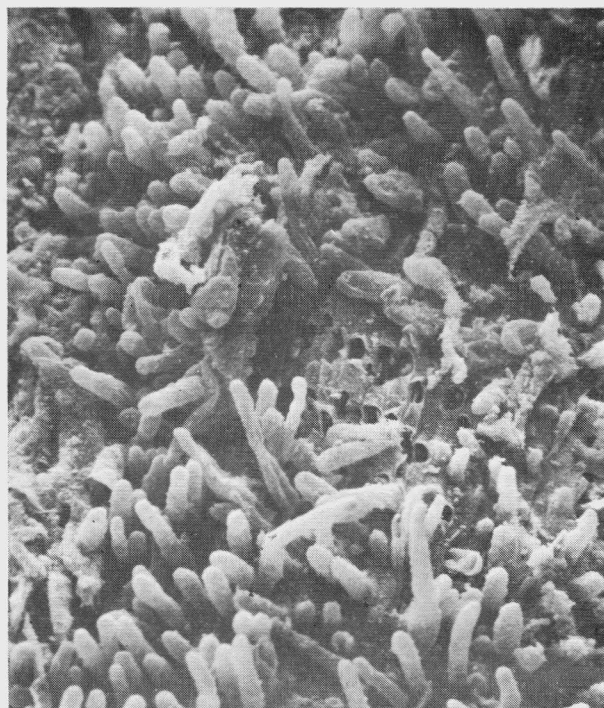

Fig. 1. Scanning electron micrograph of the root hair zone of a rough lemon primary root. The root was obtained from seed germinating in perlite.
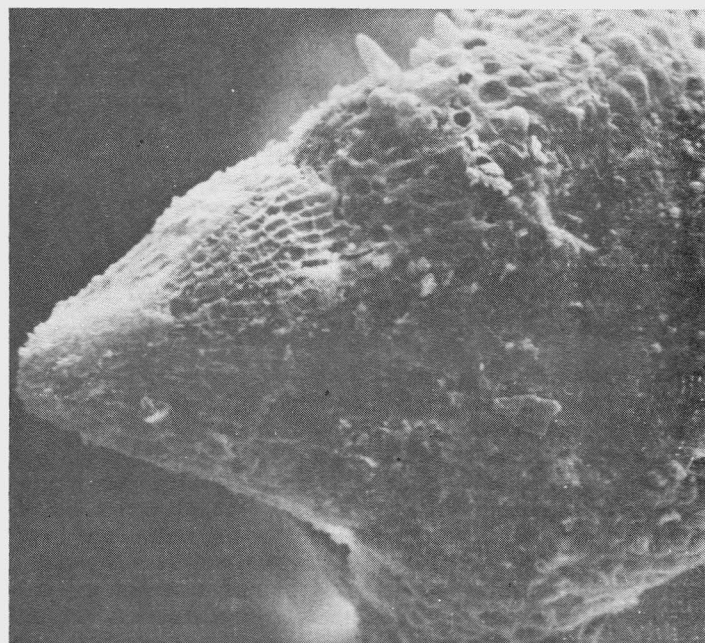

Fig. 2. Scanning electron micrograph of a Rusk citrange fibrous root tip collected from a depth of approx 2 m in a sandy soil.

in the roots of apparently healthy and diseased trees (82, 100).

Root Distribution

Among horticulturists, the study of tree root distribution has been of common and frequent interest. In this section, an attempt is made to explore the genetic potential of root system development.

Basic morphology. Citrus trees are taprooted. During germination, the radicle generally appears first and rapidly grows downward forming a well-defined taproot if left undisturbed. It is common practice however, to sever the tap-

root during the digging of nursery trees and it may lose the strong identity evident in the seedling stage.

The citrus tree root system has the potential for extensive development although the range is influenced by rootstock (22, 34, 36, 37, 74, 92, 108). The natural tendency of citrus seems to be the formation of a bimorphic distribution (63) characterized by a network of numerous, relatively shallow lateral roots which provide the supporting framework for a dense mat of fibrous roots (Fig. 3) and by a second layer of fibrous roots and smaller laterals. This second grouping is more or less vertically oriented and associated with roots which have emerged from the crown (Fig. 4). These roots can partially account for the substantial number of fibrous roots collected at depths greater than 0.5 to 1 m in the deep sands of central Florida (22, 34, 36, 37).

Fig. 3. A portion of the surface mat of fibrous and lateral roots of a 15-year-old Valencia/rough lemon tree excavated from a deep, sandy Florida soil.
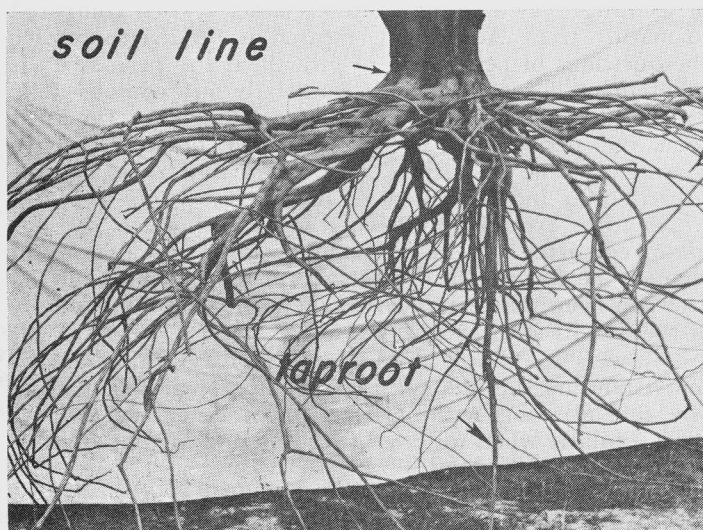

Fig. 4. Framework roots of a 15-year-old Valencia/rough lemon tree excavated from a deep, sandy Florida soil.

Lateral roots do not have a specific or consistent order of branching. A regular division is not apparent. The roots are most easily categorized by size. Small laterals may branch from larger ones or arise at the base of the tree. Laterals may develop to lengths 2 or 3 times the canopy diameter (43) while remaining uniform in thickness throughout their length. The smallest roots have been labeled feeder or fibrous roots and rootlets. Subdivision of

the larger lateral roots establishes a framework of pioneer roots (93) from which arise smaller ones capable of vigorous terminal growth. Small clusters of fine or fibrous roots occur along these roots. In some instances, the main root of the cluster does not branch or branches weakly and may continue growth as essentially a single root (see Fig. 4 ref. 24).

The gross morphology as described above is illustrated in Fig. 4. The root system displayed is that of a 15-year-old 'Valencia' tree on rough lemon grown under good management in a typical deep, central Florida sand. This example is considered to be a reasonable representation of root development in an environment allowing the maximum expression of genetic potential.

Modifying factors. Substantial differences among rootstocks in vertical and horizontal root distribution have been demonstrated (22, 36). In deep sandy soils, the most vigorous rootstocks were characterized by extensive root systems with an abundance of fibrous roots. Other less vigorous rootstocks had shallower root systems with the major portion of their fibrous roots concentrated near the surface (22). These differences among rootstocks may not be constant, however, and will vary with changes in soil type (1, 108).

Changes in the physical, chemical, or biological characteristics of the rooting medium affect not only root distribution, but also growth and function. Texture probably determines root distribution more so than any other soil property. Root growth is vigorous in sands (22, 34, 36, 37) except when impeded by layers of high organic (40, 42) or clay content (37). In soils with a high water table, the root system tends to 'pancake' with nearly 75% of the fibrous roots located near the surface (15, 16, 35, 42, 45, 46, 88, 112). In other soil types such as loams, fewer roots are required to support a tree of comparable size growing in sand. Roots of trees in the former soils tend to be shallower and have a less prominent bimorphic distribution (1, 9, 11, 108).

Root distribution can be affected by fertilizer applications (47, 48, 97). High N rates, especially of sodium nitrate, are reportedly detrimental to root growth (48, 54, 97). The extent of response and rapidity at which changes occur may be dependent on soil type (12, 13, 48).

For deep-rooted crops where irrigation is practiced, there has always been a question as to what effect the frequency and duration of application has upon the root system. In a long-term California experiment, citrus trees under 2 furrow-irrigation regimes were compared. The infrequently watered trees had significantly more roots between 30 to 90 cm deep (11, 13). The initial treatments resulted in different root distributions. When treatments were reversed, change occurred very slowly. Irrigation effects are not likely to be drastic except possibly with young trees or in areas where rainfall is limited and water is supplied by low volume, under-the-tree systems (5, 91).

Observations on the effects of spacing showed that closely-spaced trees had higher root densities at surface and deep locations as compared to widely-spaced trees (58). The distribution suggested a compensatory adjustment but probably represents the rapid development of roots in smaller soil volumes. Similar root distributions might be achieved with time by the widely-spaced trees. Nevertheless, tree root system response to spacing is essential information in the management of higher density plantings (7) and also helps to reveal the maximum root density a given soil may support. Fibrous root concentration expressed in dry weight, was observed to be 0.5 gm to 1.2 gm/dm^3 in sandy loam (58), 1.9 gm/dm^3 in deep sand (W. S. C., unpublished data) and 9.3 gm/dm^3 in poorly drained sands with a high water table (16).

The scion can influence root distribution. Ford compared grapefruit and orange trees on rough lemon. The grapefruit trees had a higher percent of fibrous roots in the surface 25 cm (34). Also, tree root systems are not static but may slowly change in distribution with age (36), tillage treatment (59), or perhaps fluctuate seasonally.

Knowing where tree roots are located and in what concentration serves several practical purposes. The efficiency of cultural practices such as irrigation and fertilization can be increased, and any adverse responses could be detected. Information on root distribution is needed to make sound rootstock decisions.

Root Growth

Root growth is a complex physiological process whereby the direct effects of environmental factors and endogenous mechanisms of the plant are combined. The periodicity of citrus root growth (elongation) particularly in relation to shoot growth, and the effects of soil temperature and water content have received considerable attention. Equally important questions concerning the magnitude and uniformity of growth, role of phytohormones and life cycles have been overlooked.

Observations and data from citrus root studies have not been consistent. It is possible though, that the differences are valid and reflect to some extent, the variety of experimental conditions. The following points summarize certain disparities in citrus root growth literature. There are documented reports to the contrary for each **observation** listed except as noted.

1. Root growth occurs in flushes, and precedes the shoot (27, 28, 79, 87, 107, 112).
2. Roots have distinct growth and rest periods and become dormant (28, 70, 87, 112).
3. Root growth is generally limited by an adverse soil temperature or water content (55, 70, 79, 87).
4. Root growth and shoot growth do not overlap (56, 107).
5. Root elongation does not proceed at a uniform rate. The rate is increased at night (general agreement).

In attempting to unify these apparently conflicting observations, several qualifications must be taken into consideration.

Root growth is an ambiguous term unless defined. It embodies root elongation and increase in diameter. It has generally been used, however, to describe the elongation of fibrous roots which often do not undergo secondary growth. Root studies are limited by being able to examine directly only a small part of the root system at any one time. Often there is some uncertainty as to the root being studied— with citrus, is it a pioneer root, the main root in a cluster, or one of the branch roots in the cluster? Specific information about the activity of each of these *per se* and in concert is needed.

Despite the aforementioned limitations, a general picture of citrus root growth can be constructed. Beginning with the seed, the primary root emerges well before the shoot, rapidly elongates and starts to branch, forming the rudimentary root system. In the young seedling, root growth probably slows after budding until growth of the new shoot ceases. When the nursery tree is transplanted, root growth may resume in advance of shoot growth (70). Virtually no data regarding growth rates are available except for those of Waynick and Walker (107) who reported fibrous roots grew approx 0.5 to 1.3 cm/day and Crider (28) who reported an elongation rate of 4.32 mm/day for a spring flush.

The root system for established field trees is reported to exhibit alternating growth flushes with the shoot (56). The issue of which organ initiates growth first is unsettled. The growth periods may overlap particularly in flushes which occur after the spring cycle (56) since the growth of one component does not necessarily eliminate simultaneous growth by the other. Some roots are probably elongating at any given time. A cyclic growth pattern is not unreasonable since each major organ is basically heterotrophic and competes for the available food supply. The normal distribution of plant assimilates becomes temporarily unbalanced to support the growing, more competitive organ.

Vigorous root growth in young trees is likely to proceed until one of 2 critical events happen in the tree life cycle. When the tree begins to fruit or the soil vol available becomes permeated, the growth pattern may then change, with emphasis being shifted to the fibrous roots. In the former event, the fruit are an additional carbohydrate sink; in the latter, the root system is physically restricted and has fewer opportunities for expansion.

Environmental factors can inhibit root elongation and branching. Growth reportedly ceases below soil temperatures of approx 13°C or above 36°C with the optimum near 26°C (51, 67, 83, 84). The optimum value varies with rootstock (51). Soil water excesses and deficits affect root elongation. Reduced growth has not been associated with a specific soil water stress, but the response of citrus to flooding has been studied and is related to rootstock (41, 42, 44). Soil water stress tends to promote the growth of long, single roots with restricted branching. The role of internal factors is poorly understood and deserves further attention. Hormones may be responsible for the observation that no root growth may take place even when soil conditions are optimum (69).

The interaction of both external and internal factors as manifested in root growth is not clearly understood. Often the various factors, once identified, must necessarily be studied independently. The use of young, budded plants or seedlings may account for discrepancies when compared to mature trees. Additional research is needed to resolve the questions of periodicity of growth, if the periodicity is inherent or if root growth is essentially autonomous (69). Furthermore, little is known about root longevity. Do citrus roots die periodically or do they just become inactive (dormant)? Many observers have noted that roots become suberized to include the formally active, white root tip which turns a yellowish-brown color as it loses its meristematic character (27, 57). Cossman noted an anatomical change, the formation of a metaderm which sealed off the root cap from the remainder of the root (27). The activity of these roots is unknown.

Answers to all of these questions may contribute to understanding the one consistent root growth observation, viz., that all roots within a given root system do not behave similarly when followed over a period of time even in a uniform environment.

Root Function

Root function like root growth is a physiological activity which has been the object of numerous investigations. Most studies have been concerned with water and nutrient uptake and more recently, hormone synthesis. Few such studies have involved citrus roots. It is assumed in this discussion that citrus does not differ greatly from other similar plants in its physiology.

Information regarding citrus root function has generally come from studies directed toward a clearer understanding of rootstock differences since each rootstock essentially

represents a different genetic potential. This potential is evident in rootstock effects on leaf and root nutrient content (53, 95, 104), salt tolerance (61), and the toxicity to nematodes of expressed root sap (101).

In an effort to explore rootstock effects, it was determined that the root respiration rate, and catalase and peroxidase activity varied among mature sweet orange trees on several rootstocks (3). Wallace (102, 103) showed that root cation exchange capacity may also be involved in rootstock effects. These contributions were significant considering the nearly absolute absence of any data on the physiology of citrus roots. However, interest has shifted toward hormone physiology. It is becoming increasingly apparent that cytokinins or their precursors are manufactured in the root and transported to the shoot to exert morphological control (95). Auxins, gibberellins, and cytokinins have been extracted from citrus roots (2, 52, 81, 105, 106, 109) and one report (30) indicated the presence of an inhibitor. Continued study of these aspects of root physiology could have practical significance and lead to the manipulation of plant growth and fruiting.

The absorption of water and nutrients by roots is controlled genetically and influenced by external factors. Perhaps more studies have been conducted to evaluate the effects of environment on this root function than any other factor. Such studies show, e.g., that leaf nutrient content differs with soil temperature and oxygen content (66). In general, those soil factors that modify growth also affect function.

Another facet of individual root function receiving more attention lately concerns root microflora. Few attempts have been made to inventory the microorganisms that naturally inhabit the citrus rhizosphere (58, 71, 96). Most studies have involved isolations from soil samples rather than direct examination of roots. In citrus fibrous roots, a gelatinous substance (mucigel) apparently coats the epidermis of the immature root tip. Bacteria can be observed in the mucigel (8, 94). Fungi are also present in the vicinity of the root and may penetrate it. The most prominent species are members of the *Phytophthora* and *Endogone* genera. The latter form mycorrhizae which are purported to be ubiquitous in citrus and to improve plant nutrient uptake possibly through the exposure of a greater absorption surface area (72, 75, 76, 77). It has been suggested that mycorrhizae may compensate for differences in root density (69). Their presence and function may be dependent on rootstock, tree age, and soil conditions (77). In addition to their role in the mineral nutrition of plants, they may be involved in the normal hormone balance of the plant.

Root function, structure and growth can be considered separately but are not independent entities. Two questions related to their combined activities are pertinent. First, is root growth necessary for root function? Growth is typically thought to be evident when white root tips can be observed. If the citrus root system is cyclic and has quiescent periods of inactivity, then how are the water and nutrient requirements of evergreen trees sustained? An answer to this question is difficult to provide. It should be supplemented with an answer to the second question—how are root structure and function related? Kramer suggests that suberized roots are functional thus reducing the need for growing root tips (26, 64). Moreover, certain relatively unstudied features of citrus root anatomy, viz, growth cracks, lenticels, hypodermal absorbing areas and root hairs may be functionally significant.

Root function may take on a new meaning when the activity of all the roots in a complete root system are considered together. Recently, the effect of rootstock and soil depth on apparent root efficiency was reported (23). Deeper roots were generally more efficient in water uptake, but it was not conclusively shown that inherent root differences were responsible. Other studies, however, provide additional evidence that water uptake can vary with depth of rooting and support the conclusion that some differences among rootstocks may be genetic in origin (9, 17, 29, 32, 50, 62, 73, 78, 85). The relationship of soil depth to nutrient uptake is unknown.

The functional relationship of a portion of the citrus root system, such as a major root and its subordinate branches and fibrous roots, to the shoot has always been of practical concern. It is generally thought that such a root has direct connections with the shoot branches immediately above (31). This hypothesis was tested by Furr and Taylor (49) in their study of lemon trees irrigated on alternate sides at different times. They showed that such connections exist while also demonstrating that internal cross-transfer occurred in sufficient magnitude to preserve the water status of alternate-side-irrigated trees.

It might be surmised from the available data, that the root system characteristics of citrus are an adaptive strategy. The relatively shallow mat of fibrous roots will rapidly absorb applied nutrients and, water from light rains. The remaining deeper roots are a reserve that prevent extreme stress from drought and can take up nutrients not absorbed by fibrous roots above. The concept of root system strategy and tactics in plant establishment and growth is persuasively argued in a discussion of a forest tree root system (89).

Root-Shoot Relationships

The equilibrium established between the roots and the top of a plant is represented by the root:shoot ratio, determined by comparing either the fresh or dry weight of each component. The ratio is not an absolute constant. It can vary with plant chronological age, developmental stage and species; however, the ratio may be permanently altered by changes in the environment or only temporarily affected when the balance is disturbed by removal of part of one system, e.g., by pruning or freeze damage (4, 6, 39). The ratio is interpreted as being a measure of the root and shoot relationship and their mutual dependency. It is assumed that an equilibrium exists as the result of root and shoot competition for carbohydrates, water, and mineral nutrients. Those organs closest to the source of each material will be the most successful competitor for their respective requirements. When the balance is disturbed, the plant responds with reduced growth by the dependent component (the root, e.g., in shoot-pruned plants). The ratio is restored by increased growth of the supplying organ, it being a better competitor (4).

Interest in the ratio lies in its usefulness as a means of studying the functional equilibrium of the major organs and of ascertaining how environmental changes and other factors affect this balance. The nature of the relationship implies that it is fixed and cannot be permanently modified in order to improve plant performance after plant establishment. However, as mentioned previously, the use of rootstocks in citriculture adds a significant factor, which unlike the difficulties to be encountered with attempts to modify the soil or aerial environment, is easily managed.

Ratio data are rare for mature citrus. Cameron (18) and Cameron and Compton (19) undertook the excavation of 36 bearing trees, reporting the N content and weights of several fractions of the trees. Calculation of the root:shoot ratio (0.28) indicated that the roots were supporting a top approximately 4 times their weight. The ratio (0.45) for 2 trees similarly excavated in Florida (see Fig. 4) illustrates a possible soil effect. Trees growing in the less fertile sands of Florida apparently require a larger root

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system to support a top comparable in size to trees growing in a loam soil. Data from younger trees, although meaningful, are not likely to be representative of older trees. The proportional weight of the root system reportedly decreases with plant age (25, 80).

The functional balance expressed in the top:root ratio suggests several possibilities for its manipulation with practical application. Smaller trees for use in higher density citrus plantings might be achieved by physically restricting, or pruning, the root system. This prospect was the objective of 2 investigations with peach trees (25, 90). The data were interpreted as suggesting that dry-weight distribution was controlled by the root system; that the mechanisms involved may be hormonal or related to the physical size of the root systems through its supply of stored carbohydrates or other substances; and that root morphology (root volume, length and number) were important characteristics. Detailed information on citrus roots has not been obtained and the carbohydrate status of roots is vague.

The efficacy of root manipulation should be observed in a field study not only to determine the effects on tree growth but also fruiting. Control of tree-size by root pruning cannot be judged successful if there are undesirable effects on yield. Fruit productivity was related to root density in California (10) and Israel (86) where high yields were associated with large root quantities. In Florida, trees growing in shallow, poorly drained soils are smaller and less fruitful than those located on deep, better drained sands (14); however, this difference does not become apparent until later years when the root system of the latter trees has exploited the larger soil volume available. These observations do not necessarily exclude possibilities for controlling the root system. Plants raised in containers frequently have tops much larger than the root system because of the very favorable root environment. A similar system might exist in the field if root pruning or restriction is accompanied by greater control over the soil environment with e.g., drip irrigation.

Conclusions

Citrus root systems have not been intensively studied as have those of some other plants. Those areas of research which have potential for immediate practical application include root distribution related to rootstock and soil type, and modification of the root:shoot ratio via chemical or mechanical means or through the selection of rootstocks which may differ in their effect on dry-weight distribution. Understanding the citrus root system and its relationship with the scion cannot be overlooked if closely-spaced orchards of smaller trees are to be successfully developed.

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