

ROOT PHYSIOLOGY AND WALNUT ROOTSTOCK CHARACTERISTICS

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Tree roots reside in an environment that is totally different and more complex physically, chemically, and biologically than that of the shoot. Roots and root systems are accessible for study only with difficulty and methods of examination usually make profound alterations in the system being studied. Thus, the extent and quality of information about roots is subject to more uncertainty than for shoots. This is particularly true for walnut. The extent, bulk, and perennial nature of the walnut root system adds complexity with carry-over effects from one season to another. There are also changes during development from a young tree to a mature or bearing one. Fortunately, research with other deciduous trees has revealed a general similarity in behavior among them so that reasonable interpretations and projections are possible.

Until some problem affecting roots or a rootstock becomes severe enough to limit production the below-ground portion of the tree often is taken for granted. If roots remain free of pathogens and are reasonably well supplied with water and nutrients adequate, though not necessarily optimal, performance results. Obviously, the above- and below-ground parts of the tree are intimately dependent upon each other. Recent information suggests that less than ideal performance by roots may have a greater impact on the top than vice versa. Thus, an appreciation of what is, or should be occurring in the roots is fundamental to understanding the tree as a complete unit.

Before discussing the functions provided by roots and root systems it is necessary to describe the system and its components. Figure 1 shows the form expected for a root system of a mature

walnut tree. A framework, only generally similar to that of the top, consists of relatively few large diameter roots extending both laterally and vertically. A taproot may or may not exist. From the framework roots there is branching and re-branching of laterals of decreasing diameter. This branched network terminates with the tips of recently formed fine roots. Root systems are shorter vertically and more spreading than the tops. Walnut roots have been reported at depths of 12 feet in light textured, well-drained soil but are frequently restricted to much shallower depths of 5 to 6 feet and sometimes even less than this. Lateral extension of roots has been observed in excess of 30 feet.

Branching or lateral root formation does not fit a regular pattern and roots are not uniformly distributed in the soil. Root systems remain in balance with the top but this balance changes with age and can be altered by cultural management. Root systems of woody perennial trees are considerably smaller than above-ground portions on either a weight or length basis.

Root systems are comprised of at least two different types of roots. The form and tissues of recently formed roots including the root tip is shown in Figure 2. Growing new roots may become highly branched with laterals arising from cell division and differentiation originating in the pericycle. Elongating and recently matured new roots may persist for varying lengths of time but are usually short lived.

In some new roots a vascular cambium forms and secondary development or enlargement occurs. Cell division in the cambium produces new xylem ("wood") toward the inside and new phloem

("bark") toward the outside (Fig. 3A). As this occurs tissues external to the pericycle collapse, are sloughed off, and decay. Other important changes are the formation of periderm and suberization. Periderm (Fig. 3B) is analagous to the corky outer bark of stems. Suberin, a complex mixture of fatty substances, resins, and tannins, is deposited in association with cell walls of the outer periderm. Death of outer periderm cells and suberin account for the dark external color of older roots. The large framework roots have the structure indicated in Figure 3B. With increasing diameter there is a greater proportion of xylem in relation to exterior tissues which are gradually sloughed off.

There is increasing evidence with woody perennials for the presence of variants to the fine roots described above. With one type, surfaces turn brown, the cortex and associated tissues are lost (Fig. 3A) but little if any secondary thickening occurs. In other instances roots become brown but the cortex is retained. Both types persist as fine brown roots for one to several seasons. Outer cells appear to be suberized.

ROOT FUNCTIONS

There are five primary functions provided by roots. The degree of success with which these are realized can have much to do with growth and production by the top or scion. Root function can depend upon the type of rootstock, the scion variety, the soil environment, and especially cultural management practices.

Anchorage. One obvious function of the root system is to provide anchorage in the soil. Good anchorage results when root

systems are deep and spreading. Such systems are more likely to occur when the scion is vigorous. Deep, spreading root systems are difficult to realize in shallow soils or in ones with restrictions to root growth such as sand layers, clay pans, high or fluctuating water tables, or very fine textured soils. Anchorage characteristics can differ with rootstock type and method of propagation with other species, but problems with walnut in this regard are rare.

Absorption. Trees with deep and spreading root systems are the best suited for performing the two most commonly recognized functions; the absorption of water and mineral nutrients. Such root systems possess the best potential for exploration of the soil profile. The absorption of water and nutrients are different processes physiologically. Selective and active absorption of nutrients requires the expenditure of respiratory energy and the existence of cells and tissues characteristic of the root tip region. Uptake of water depends on physical forces in the soil and within the plant. Absorption has been considered to occur mainly, or even exclusively in the root tip region. The efficiency and rate of absorption does appear greatest near the root tip but there is increasing evidence for participation of other portions of roots in total uptake. Uptake has been demonstrated by both secondarily thickened and fine, but "browned" roots. With either of these, selective absorption of nutrients would not occur and increased resistance to water movement would be expected because of suberization. The presence of very small diameter brown roots appears capable of making significant contributions to total absorption because of their extensive length and surface.

Synthesis. The fourth function provided by roots, one that is frequently overlooked, is that of conversion or synthesis. Each year a considerable amount of nitrogen is lost from the tree in the crop, leaves, and prunings. This nitrogen must be replenished each year. Nitrogen absorbed from the soil as nitrate is reduced enzymatically to the ammonium form in roots. Carbohydrate from the top is converted to organic acids which are combined with ammonium to form amino acids and amides. The latter two types of compounds are the basic units of protein and are the forms in which nitrogen is transported to the shoot. Walnut may be a partial exception in that some nitrate appears to be transported to the top and accumulates in leaves.

Two types of hormones, gibberellins and cytokinins, are formed in the apical portions of roots. Supplies of these substances to the scion are involved in control of vegetative and reproductive growth. Small leaves and lack of vigor accompanying root problems of various sorts are expressions of reduced hormonal supply from roots. Experimental restriction of roots preventing new root formation has been shown to reduce shoot growth.

The occurrence of damage or stress in roots can cause ethylene to be formed. Transport of ethylene or its precursor to the shoot can cause senescence and abscission of leaves.

Storage. The fifth function of roots is to provide storage. Carbon is stored as starch and soluble carbohydrate which provides metabolic intermediates, respirable substrate for energy production, and the basic structural units for root growth. Nitrogen is stored mainly as amino acids and protein. Part of the nitrogen

absorbed, especially in late summer and autumn, is retained in the roots for later use. The accumulation of suitable reserves at this time is particularly important for resumption of growth the following spring.

Storage, as well as other root functions, depends on the supply of photosynthetic products from leaves. Any condition or cultural practice that adversely affects photosynthesis is of potential harm to root performance. Downward translocation of sucrose from leaves in the phloem cannot be unduly restricted or all root processes will be affected. Decline and death of trees from blackline is an extreme example of interrupted translocation to roots. The production of rootstock suckers by blackline-affected trees is likely an attempt to supply needed carbohydrate to the roots. Restricted transport to roots is also a main contributor to decline of trees with crown rot. Graft union incompatibility reactions and their effects on translocation are a continual concern with development of new rootstock-scion combinations.

ROOT GROWTH AND ACTIVITY

Root growth is essential for optimal performance of roots. Walnut trees would probably remain alive with very limited root growth. However, tree size and production would be severely limited. Smaller trees on very heavy or shallow soils are examples of this.

Increases in diameter of large roots and laterals provides the framework, anchorage, and storage capacity. Enlargement by secondary thickening has been described above and in Figure 3.

Enlargement of major laterals is regular and rapid in young trees. In mature trees secondary thickening of individual roots may stop for periods of several years but then resume.

The formation, extension, and branching of small diameter laterals is of major importance since this includes the root tip region (Fig. 2). Recently formed fine roots are white in color and are often referred to as new roots, white roots or feeder roots. As noted above, absorption and synthesis are major activities with these. With many plants root hairs--lateral extensions of epidermal cells--exist just behind the root apex. Root hairs greatly increase the absorbing surface. Walnut roots have been said to be without root hairs but they have been observed in some instances. Soil environmental conditions may be important in the formation of root hairs.

The length of new white roots can vary from a fraction of an inch to over two feet and they are usually 1/8-inch or less in diameter. Most are short lived, one to several weeks, later being replaced by newer ones provided soil or plant conditions are not limiting. Before dying new roots become brown in color with this change progressing from base to tip. Browning which progresses from the tip toward basal portions is indicative of damage from soil environmental or pathogenic causes.

Not all new roots die. A few undergo secondary thickening and become a part of the perennial root framework. Others which persist as fine brown roots have been described above. Although these fine brown roots provide considerable length and surface and

some absorptive capacity, it is doubtful that they fulfill storage or synthetic functions.

Growth of new roots is not continuous throughout a season but occurs in cycles under non-limiting conditions. Root growth is controlled mainly by temperature, available moisture, and activities of the scion. An idealized diagram of the cyclic growth that would be expected with walnut is shown in Figure 4. In the California climate relatively little new root growth would occur in mid-winter (December, January, early February). As soil temperatures begin to rise in February, growth increases. Both the number of new roots formed and their rate of elongation increase from 3 to 4 weeks before leafing out until shoot growth becomes rapid. Decreased new root growth during accelerated growth in the top appears to be a competitive effect from retention of photosynthate for shoot and fruit growth. After shoot growth stops and fruit development slows a renewed cycle of new root formation occurs. This second cycle reaches a minimal level at about the time of leaf fall.

Root growth studies with mature walnut are currently being conducted by Dr. John Duniway. First years' results indicate general agreement with the pattern indicated in Figure 4 for shallow soil depths which contained the most roots. Below 4 feet there was only a single peak of root growth which occurred in late summer. A relatively small peak also was evident after leaf senescence in early December.

Pruning, if sufficiently severe to stimulate vigorous shoot growth, will tend to suppress root growth in spring. Except where

drastic pruning occurs, as with "de-horning", stimulated root growth later in the season would be expected.

The term "root activity" is often used in discussing the performance of roots. In a limited sense activity means uptake of water and nutrients. Here, root activity is considered in addition to include synthesis, storage, and root growth. This is because these are interrelated and deficiencies in one or more will affect others, and ultimately the performance of the top. Probably the most important component is root growth since this provides the potential for realization of other functions.

SOIL ENVIRONMENTAL EFFECTS ON ROOTS

Nematodes, bacteria, and fungal pathogens are important components of the root-soil environment. These are not considered here because they are dealt with in other chapters. Water relations and irrigation are also subjects of more detailed treatment elsewhere. Because of the importance of soil moisture--both too little or too much--this subject is treated here from the standpoint of its effects on roots. It is also a soil environmental variable which can be controlled.

Readily available moisture is necessary for optimum root activity. Roots will not grow through dry soil and exploration of available resources would be limited under these conditions. The uptake of water and nutrients becomes more difficult with reduced available moisture. Movement of nutrients to roots is slower with low soil moisture. For example, potassium deficiency can sometimes be corrected by improving irrigation practices. Insufficient

moisture or an incompletely filled soil profile before leafing out can suppress root activity and delay or reduce vegetative and reproductive growth in spring. Synthetic functions of roots and thus the supplies to the scion are reduced with restricted root growth. Early spring mineral nutrient deficiencies can occur under these conditions. Examples of these responses were observed during the recent drought years.

Late summer or postharvest water deficits will inhibit the second cycle of root growth (Fig. 4). Nitrogen fertilizers are frequently applied to coincide with late season root growth. Inadequate root growth at this time will inhibit establishment of nitrogen reserves needed for resumption of growth the following spring.

Under certain conditions excessive water in the soil can be more damaging than insufficient amounts. Air is displaced from the poor spaces of the soil when they become filled with water and the supply of oxygen to roots is removed. This can occur with flooding, seepage, perched or fluctuating water tables, or even irrigation. Excessive soil moisture is also important in soil-pathogen effects (root and crown rots) but discussion here is restricted to direct effects on oxygen requirements of roots.

The terminal portions of new roots of walnut can be killed within one to four days in a saturated soil. Such short periods of waterlogging may cause inhibition of growth in the top. Damage to roots becomes greater as saturation is prolonged and can lead to chlorosis, abscission, and wilting of leaves. Entire root systems can be killed in extreme cases. The effects of waterlogging

proceed faster as soil temperatures increase. Survival of walnut trees in saturated soils during winter results from a combination of low soil temperature and the paucity of active roots.

There is greater danger of damage from excessive moisture with heavy or compacted soils because of slower re-entry of oxygen after saturation. Deficient aeration is in part responsible for shallower root systems and small trees in fine-textured soils even without excessive water. A fluctuating water table can have more serious effects than a static one because of periodic encroachment on active roots.

Rootstocks used for walnut are among the most sensitive of any deciduous tree to inadequate oxygen. Small differences among types have been demonstrated with Paradox being less sensitive than Black walnut and English walnut the least tolerant. Differences also exist among individual seedlings of each type.

Excessive salt is potentially a problem wherever irrigated agriculture is practiced and is of increasing concern in California. High levels of sodium, chloride, and boron are of most importance with walnuts. Grower concern is mainly whether or not leaf toxicity symptoms are present. If these are absent the potential for adverse effects on the tree is often ignored. Salinity can influence the tree in two ways and accumulation of high levels of salts (specific ion toxicity) is only one of these. Effects on water relations (osmotic effects) can also have a major influence on tree performance.

Because water is absorbed by the tree more rapidly than are salts, their concentrations in the soil increase as moisture is

depleted. Increased salt concentrations decrease water availability in addition to that which occurs from water depletion alone. Water stress is more likely to occur with saline conditions and trees need more frequent irrigation. Reduction in growth is a major effect of the osmotic effects of salinity. Osmotic influences do not cause leaf toxicity symptoms though these can ultimately develop after prolonged exposure to saline conditions.

The effect of individual salts are of great importance with walnut as with other woody perennial plants. High levels of sodium, chloride or boron can have toxic or "specific ion" effects. As any one or more of these ions accumulate within the plant they have increasingly inhibitory effects on normal cellular processes. Ultimately, toxicity symptoms develop on leaves---necrosis of tips and margins which later expands toward the midrib. Such symptoms are more prevalent late in a season. On a dry weight basis amounts are considered toxic when greater than 0.3% chloride, 0.1% sodium or 300 ppm boron. The resultant loss of photosynthetic capacity further reduces tree performance. Monitoring toxicity symptoms on leaves does not take into account the deleterious effects which occur before symptoms become evident. Damage to new roots of young walnuts in advance of leaf symptoms has been observed experimentally.

Rootstocks differ in their capacities to absorb and transport salts to the scion. This is true of both individual plants and type of rootstock. Among walnut rootstocks, Black walnut is more tolerant than English. Paradox may be quite variable but is generally less tolerant than Black walnut. Walnut rootstocks

absorb more chloride than sodium. In one trial there was no difference in boron accumulation with rootstock type.

Interest has developed recently regarding mycorrhizae--an association between roots and beneficial fungi. Some mycorrhizal fungi penetrate the root whereas others are mainly on the surface. This association can provide increased surface as well as specific absorptive capacities, especially for phosphorus or zinc.

Plant species differ considerably in their dependence on mycorrhizal fungi and positive responses usually have been associated with conditions of low fertility. In fact, regimes of regular, high fertilization have been shown to suppress mycorrhizae. Mycorrhizal fungi occur naturally in most soils, have been reported to exist with walnut roots, but these may be of questionable importance with intensive cultural practices employed in fertile soils in California. Beneficial effects of mycorrhizal inoculations have sometimes been realized in nursery or replant situations following fumigation.

Opinion differs as to whether a specific replant problem exists with walnut apart from the many factors influencing establishment of newly planted trees. Paradox roots have been reported to perform better in replant situations. Whether this is an effect in addition to the potentially greater vigor of this stock is not known. Nematodes and soil pathogens may play important roles. As noted, the presence or absence of mycorrhizae may be important considerations if soil has been fumigated. Shading from existing trees can severely limit photosynthesis and in turn inhibit both shoot and root growth.

The presence of toxic compounds in the soil originating from decaying walnut roots has sometimes been suggested as a cause of replant problems. Substances from walnut tissues have been shown to inhibit growth of certain other plants. Components of walnut leaves, hulls, prunings, and roots can be toxic to new roots of walnut if they occur in sufficiently high concentrations. These effects are separate from the release of toxic gases such as hydrogen sulfide and methane during anaerobic decay of plant material.

WALNUT ROOTSTOCK CHARACTERISTICS

Rootstock selection can make the difference between success and failure to achieve long-term high productivity. Losses or failure to realize returns of many millions of dollars annually has been attributed to root or rootstock related problems. Many biological and physical factors must be considered in rootstock selection.

There are three rootstocks commercially available. These are English walnut, Northern California black walnut, and Paradox hybrid. All are seedlings and within a type each plant differs slightly from every other one. There are distinct advantages and disadvantages which must be considered for the intended planting site. There is no ideal rootstock for walnut. Characteristics and responses of the tree rootstocks are listed in Table 1. Responses to soils saturated with water and to salinity have been described under Soil Environmental Effects on Roots. Only the major features and comparative aspects are discussed below.

English walnut. English or Persian walnuts (Juglans regia) were originally grown as self-rooted seedlings in California. In the late 1800's the propagation of more desirable English walnut varieties onto seedlings of the species became common. Vigor and resultant tree size and productivity were quite variable. Because of high susceptibility to oak root fungus of English seedlings, the tolerant Northern California black walnut became the rootstock of choice beginning about 1910.

During the 1970's renewed interest in English seedlings developed as substitutes for black walnut and Paradox in areas where blackline occurred. Seedlings of Eureka, and to some extent Serr, have been commercially available. English walnut is not immune to blackline although the characteristic girdling symptom at the graft union is not common. Recent research has indicated a wide range of response among English walnut seedlings inoculated with blackline virus. Use of this species to escape blackline is not presently recommended.

English walnut rootstocks are inferior in most respects in comparison with black walnut and Paradox (Table 1). Especially important are sensitivity to root and crown rot, excessive soil moisture, salinity, and oak root fungus where this is a problem. There is also some indication of greater incidence of autumn frost damage or "winter kill" with cultivars on English walnut roots.

Black walnut. After early trials with the Southern California black walnut (J. californica), the Eastern black walnut (J. nigra), and a number of presumed hybrids, seedlings of the Northern California black walnut (J. hindsii) became the predominant rootstock

after about 1915. Reasons for this were superior vigor and resistance to oak root fungus. J. hindsii is still a preferred rootstock where this soil pathogen is a problem. Other comparative advantages are low susceptibility to crown gall, intermediate tolerance to deficient aeration and greater tolerance to salinity than other stocks.

The most serious problem with black walnut is its hypersensitivity to blackline virus when present in the English walnut scion. Girdling at the graft union results in loss of vigor, decline, and ultimately death of the scion. A second major disadvantage of black walnut is its great sensitivity to crown and root rots.

Black walnut possesses desirable wood grain characteristics. Thus, rootstock stumps may be of value when large trees are removed.

Paradox. Paradox hybrids are seedlings resulting from fertilization of Northern California black walnut flowers with pollen of the English walnut. Because each is a seedling the same variation among individuals exists as within species populations. Increased use of Paradox rootstocks began in the early 1950's. Demand for this stock is expected to become even greater in the future.

Trees on Paradox roots tend to be the most vigorous, especially as soil characteristics depart from the ideal. With highly vigorous, large trees, the more extensive root systems are more able to supply zinc and iron. Thus, zinc deficiency and line-induced chlorosis may be less prevalent. With superior soils and management there may be little if any difference in vigor compared

to black walnut. The potential for greater vigor is also an advantage for replants or interplanting in existing orchards.

Probably the most noteworthy attribute of Paradox is its generally greater tolerance to Phytophthora root and crown rots. Resistance is not to be implied. Response differs with the species of Phytophthora present in a given orchard and water must be very carefully managed to realize this advantage. Paradox is also the most tolerant of heavy or poorly-drained soils.

The most serious limitation to the use of Paradox rootstock is its hypersensitivity to blackline virus. No advantage over black walnut exists. In fact, more rapid decline and death of trees on Paradox roots may occur in some instances.

Other rootstocks. Several other types of seedling rootstocks have been tested over the years. These have been mostly other species of black walnut and no advantages have been revealed. A few plantings on wingnut (Pterocarya stenoptera), a relative of walnut, exist in California. Although sensitive to blackline, superior responses to Phytophthora, lesion nematodes, and inadequate aeration exist with this species. Graft union incompatibility with many producing cultivars is also a serious limitation.

Table 1. Comparison of walnut rootstock characteristics and responses.

ROOTSTOCK	Response to Biological Factors								Response to Soil and Physical Factors				
	OAK ROOT FUNGUS	CROWN GALL	CROWN AND ROOT ROTS	BLACK- LINE DISEASE	DEEP BARK CANKER	ROOT LESION NEMA- TODE	RING NEMA- TODE	ROOT KNOT NEMA- TODE	DEFI- CIENT AERA- TION ¹	SALIN- ITY ²	TREE VIGOR	ZINC DEF.	LIME INDUCED IRON CHLOROSIS
No. Calif. bl.walnut <u>J. hindsii</u>	Very resis- tant	Least suscep- tible	Very suscep- tible	Hyper- sensi- tive	Immune	Very suscep- tible	Suscep- tible	Resis- tant	Inter- mediate sensi- tivity	Most toler- ant	Mod. vigor- ous	Suscep- tible	Suscep- tible
Eng.walnut <u>J. regia</u> ~~Eureka~~ variety	Suscep- tible	Suscep- tible	Very suscep- tible	Vari- able effects	Unknown	Very suscep- tible	Suscep- tible	Suscep- tible	Most sensi- tive	Least toler- ant	Vari- able, low vigor	Suscep- tible	Suscep- tible
Paradox hybrid bl.walnut <u>J. regia</u>	Inter- medi- variable suscep- tibility	Suscep- tible	Gener- ally more toler- ant ³	Hyper- sensi- tive	Immune	Vari- able ⁴	Unknown	Unknown	Least sensi- tive	Inter- medi- ate toler- ance, vari- able	Vigor- ous	Mod. toler- ant	Mod. toler- ant

¹ Saturated soils, water tables, fine textured soils. All rootstocks sensitive.

² All rootstocks sensitive, especially to chloride.

³ Variability with species of Phytophthora present.

⁴ Selections with some tolerance may exist.



Fig. 1. Form of the root system expected for a mature walnut tree.

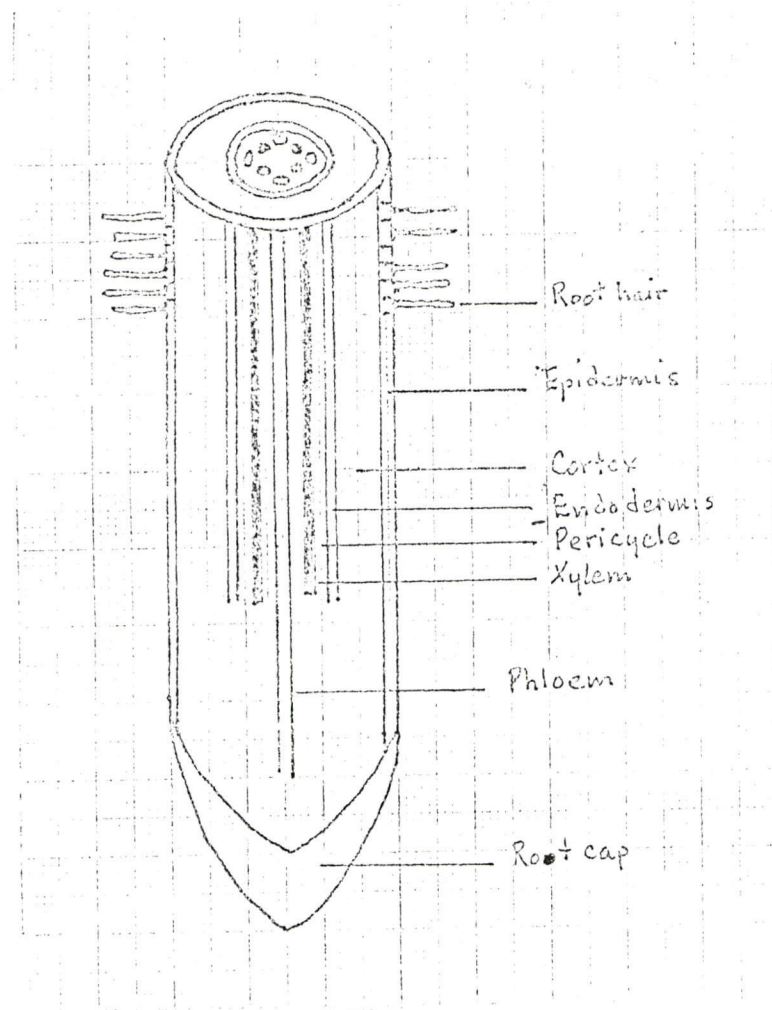


Fig. 2. Diagram of a recently formed, growing root including the tip and internal tissues.

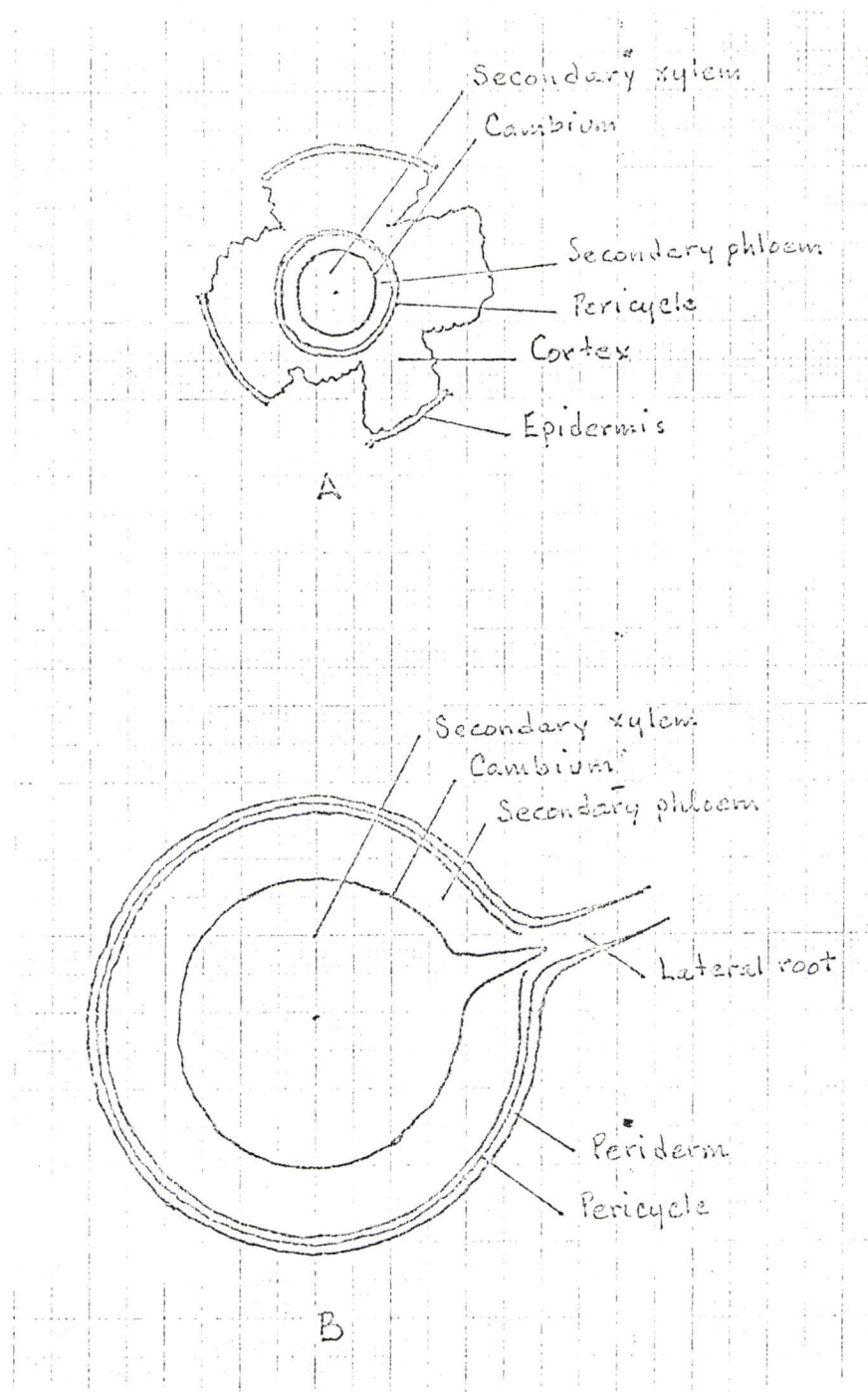


Fig. 3. Cross section diagrams of roots with secondary development: (A) early stage; (B) advanced.

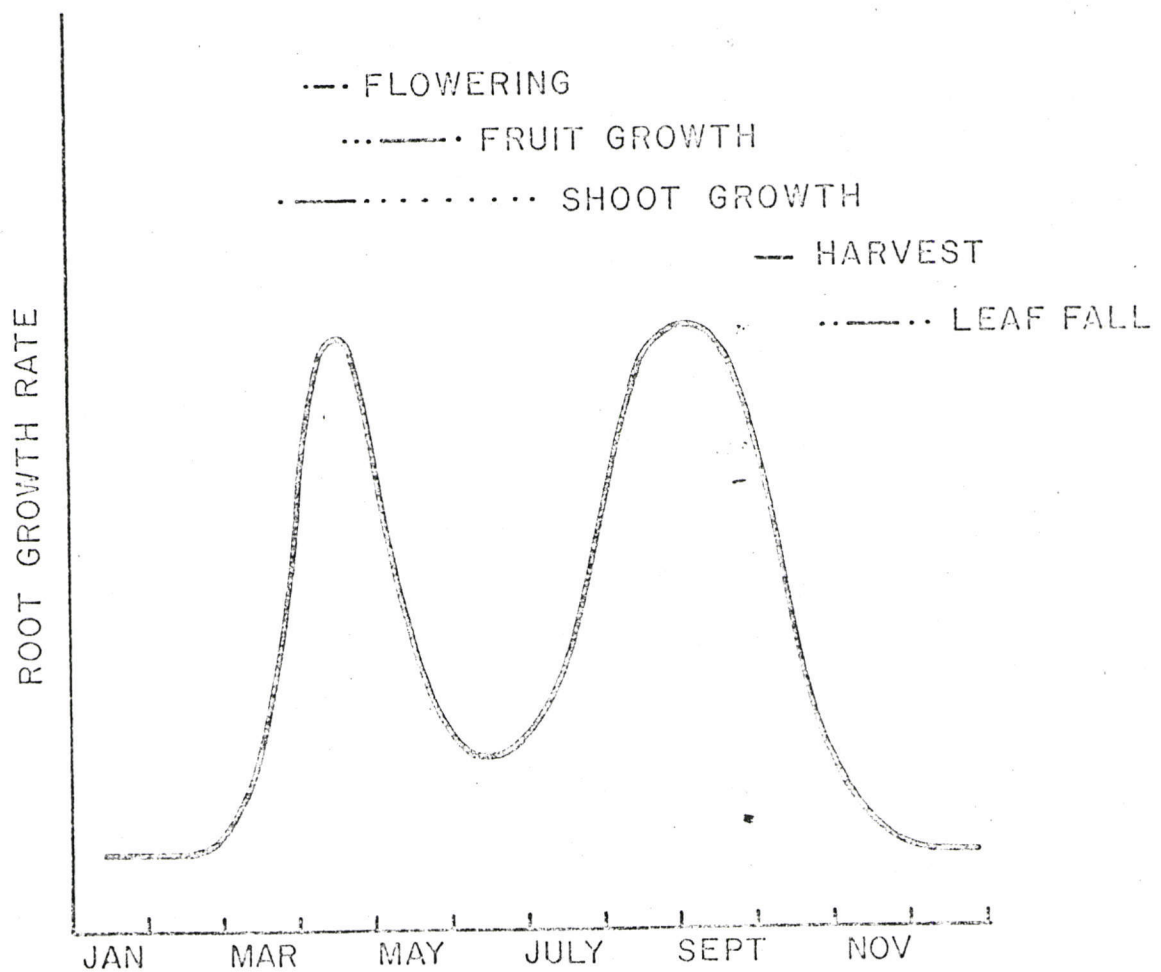


Fig. 4. Schematic relationship between rate of root growth and activities of the scion of walnut (shoot activities: ...slow, ---rapid).