ROOTS AND ROOT FUNCTION

Brian Freeman, N.S.W. Department of Agriculture
Viticultural Research Station, Griffith, N.S.W. 2680, AUSTRALIA

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INTRODUCTION:

Roots are vital to overall grapevine growth and production but relatively little is known about their activity because it is hard to study them directly. The adage "out of sight, out of mind" has always plagued our understanding of root systems.

It is best to study fruiting grape vines because the growth of roots, shoots and fruits is intimately related. Grapevines are hard to study in a laboratory because of the difficulty of growing small fruiting grapevines. Digging a trench to study root growth also has its limitations because cutting roots, just as occurs by cutting shoots, will stimulate new growth.

The problems of studying root systems should not belittle the importance of roots. To survive in a non-aqueous environment plants became bipolar by developing a root system to supply water and nutrients to the aerial part of the plant. The only way plants could evolve on land was to develop a root system which unavoidably anchored the plants and prevented mobility. The bipolar development resulted in two-way transport, the transport of energy substrate from the leaves to the roots and the supply of water and nutrients from the roots to the leaves.

ROOT DISTRIBUTION:

1) Physical Obstruction:

The distribution of grapevine roots is limited by the soil profile. Dense layers or other physical barriers limit root growth. Roots proliferate in zones that are favorable for growth, but some roots will penetrate unfavorable areas. The majority of roots are concentrated in the top meter of soil directly under the vine and fewer roots grow into the interrow space mainly due to soil compaction by machinery wheels. Compaction of the soil reduces the holes or pores which both mechanically restricts root growth and reduces oxygen which is required for root growth.

Roots can either enter small pores and expand or become thinner to grow into compacted soil. The growth of roots into a soil depends on the pore size and soil strength. The soil strength depends mainly on the water content, a wet soil is easier to deform than a dry soil. Roots can exert pressures of between 120 and 180 psi. But more important than the maximum pressures roots can exert are the pressures that reduce the rate of root growth.

Root growth is halved by a pressure of 3 psi and reduced to one fifth by pressure of 7 psi. Thus low pressure will greatly reduce root growth rate.

Soil physical properties also effect the form of the root system. If the pore size is intermediate between the size of lateral and structural roots and the soil incompressible few structural roots would develop and the root system would consist of a shallow, densely branched root system. Such a situation could occur in sand which has large pores but is relatively incompressible and grapevines grown in sand culture develop densely branched but fine roots.

ROOT DISTRIBUTION:

2) Soil Oxygen and Water:

Oxygen is required for the respiratory processes of roots, bacteria and fungi in the soil. The requirement depends on temperature. At low temperatures (10°C) the requirement is low but at higher temperatures the requirement is increased and the oxygen stored in the soil can be depleted in 2 days. Oxygen enters at the soil surface and diffuses through gas filled pores. Soil types most favorable for oxygen supply would be ones with uniform large pores that drain easily, e.g. a coarse sand. But a soil with large pores would not store adequate water. An ideal soil with regard to water supply would be one with small pores, such as occurs in clay soils. Thus the ideal soil for root growth is one with a mixture of large and small pores. The large ones would drain quickly and ensure an adequate supply of oxygen, but the small pores would retain water for the vines. Well structured loams or clay loam without sudden changes in texture would be examples of soils favorable for promoting root growth. The best viticultural soils in France are on slopes, partially because they are free draining and hence favorable for vine growth.

Waterlogging leads to an oxygen deficiency which can be tolerated for a long time in winter when the oxygen requirement is low.

In summer waterlogging rapidly produces symptoms of water deficiency in the leaves, the leaves become a pale yellow colour due to nitrogen deficiency and in some cases the leaves turn red.

In the roots glucose is broken down to CO_2 and H_2O to provide energy. The oxygen is required for this reaction and if inadequate oxygen is available then ethanol, ethylene and other toxic substances are produced by roots and microorganisms in the soil.

$$C_6\,H_{12}\,O_6 \xrightarrow{+\,O_2} 6\ H_2O + 6\ CO_2 + 300{,}000 \text{ calories}$$

$$C_6\,H_{12}\,O_6 \xrightarrow{-\,O_2} 2\ C_2\,H_5\,OH + 2\ CO_2 + 16{,}000 \text{ Calories}$$

ethanol
ethylene
organic acids

The production of these toxic substances kills roots more quickly than if lack of oxygen was the only problem.

Waterlogging also causes a loss of nitrogen from the soil. The nitrate form of nitrogen is converted to nitrogen and up to 40% of applied nitrogen or 30 lbs. per acre can be lost by this process.

3) Soil Temperature:

Maximum root growth occurs between 20 and 30°C and higher temperatures restrict growth. Roots are rarely found in the top 10 cm of soil in exposed

3) Soil Temperature (Cont.):
areas due to the high temperature. Surface soil temperatures in some grape growing areas may exceed 60°C, which are fatal for roots. High temperatures (35°C) reduce root growth more than shoot growth. This is believed to be associated with a decrease in cytokinin and potassium levels in roots at high temperatures.

4) Root Density:
Root density is important for absorption of water and mineral nutrients and can be expressed relative to the soil surface, LA(Cm Cm^{-2}) or soil volume, Lv(Cm Cm^{-3}).

TABLE 1: Root Density for different crops grown under field conditions.

	LA(Cm Cm^{-2})	Lv(Cm Cm^{-3})
grapevines	.9 - 4	.002 - .03
apple trees	.8 - 23.8	.01 - .2
pear trees	7 - 69	.12 - .56
prunes	15 - 68	.13 - .56
conifers	5 - 126	.5 - .69
cereals	100 - 4,000	-- ---

Grapevines have a low root density (Table 1). As water is used adjacent to the roots it has to be replenished from the bulk soil. If removal is faster than the rate of replenishment then localised drying will occur and thus a gradient in water potential occurs adjacent to the root. The gradient will be steep for grapevines with low root densities and in soils with low water conductance capacities. This causes waterstress to occur and reduces the uptake of nutrients that move in the soil by mass flow (calcium) and by diffusion (potassium and nitrate).

ROOT ANATOMY:

Young grapevine roots are white but become brown after about 2 weeks in summer. This browning, due to suberisation of the cortex is followed by decay and disintegration of the outer cells of the root. Secondary thickening becomes apparent in some roots which become part of the permanent root structure. Other roots remain unthickened for several years or disappear completely.

The root tip contains the meristem or center of cell division where new tissue is established. New roots are white and have typical root cross section as in Fig. 1.

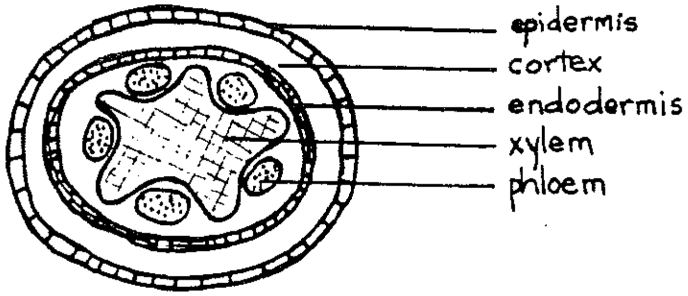


Figure 1: Cross section of a young root tip.

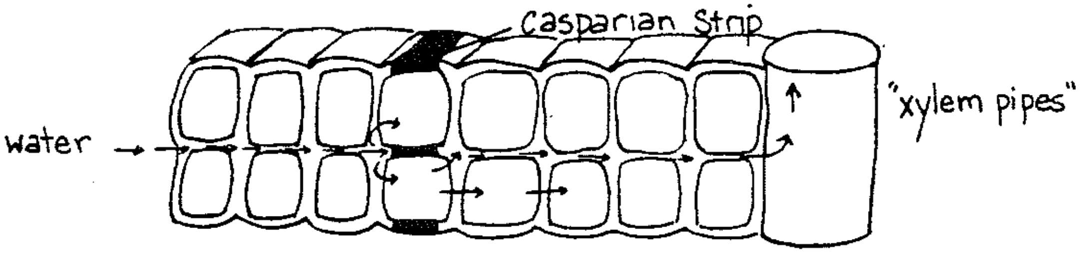
ROOT ANATOMY (Cont.):

The zone immediatly behind the root tip has been termed the zone of absorption because of the apparent easy access for iron and water. This term is misleading as will be discussed in the section on root functions.

Many plants have extensions of epidermal cells called root hairs but root hairs are generally absent from grapevine roots.

The xylem conducts water and nutrients up to the leaves and the phloem conducts products from the leaves to the roots. In newly formed roots the phloem doesn't entirely surrond the xylem but nutrients can't leak out of the xylem due to an impermeable layer of suberin in cell walls of the endodermis. This layer is called Casparian strip and it forces nutrients and water which can move freely in the cell walls to enter the cells.

Figure 2. Path of water into root



Water stress causes roots to shrink and root diameter to flucuate diurnally. Shrinkage reduces contact with soil particles. Rapid development of the casparian strip near the root tip may increase the resistance to water and nutrient movement. If water flow is more restricted at the casparian strip than in the cortex it may reduce diurnal shrinkage and improve contact with soil.

A restriction to waterflow in the xylem may also reduce diurnal shrinkage. Plants with small xylem vessels are more productive when water is limiting. St. George, 99R and 3306 have large xylem vessels and low vigor whereas 1202 and Salt Creek with smaller xylem vessels are more vigorous. In roots with secondary thickening the phloem completely surrounds the xylem as shown in Fig. 3

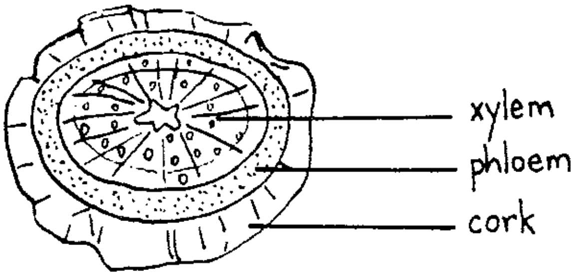


Figure 3: Cross section of a woody root.

Thus roots become more complex as they age. Different varieties of grapevines have anatomically different roots and this may be related to the adaption of varieties to specific conditions.

ROOT FUNCTION:

Roots developed to supply nutrients to the aerial parts of plants. This led to immobility, as the plants were anchored to the soil but has also developed into a site for the production of hormones which control growth and development.

1) Anchor:

Grapevine root systems are like an uncontrolled, wild grapevine without leaves. There are main structural and branching roots, and new roots are produced each year. One of the functions of the root system is to anchor grapevines and so effective are grapevine roots in this respect that the weak part in the system is the trunk above ground.

2) Absorption of nutrients:

Grapevine roots are very sparse compared to other plants (see root density section) but can still accumulate nutrients efficently. The nutrient concentration in leaves can be 1,000 times higher than in the soil solution. Nutrient accumulation depends on the rate of movement in the soil to the root, rate of uptake into the root and movement within the grapevine.

Nutrients absorbed adjacent to the root must be replaced by nutrients in the bulk soil. Calcium and sulphate can move freely in the soil and reach the root surface by mass flow with the water used by grapevines. The slow diffusion of potassium and phosphate can cause them to become depleted in the soil near the roots.

So the availability depends not only on the soil concentrations of the nutrient but also it's mobility.

Uptake into the root depends on temperature, external concentration and variety.

The optimum temperature is about 25-30°C but uptake can occur at very low temperature as shown in the following diagram.

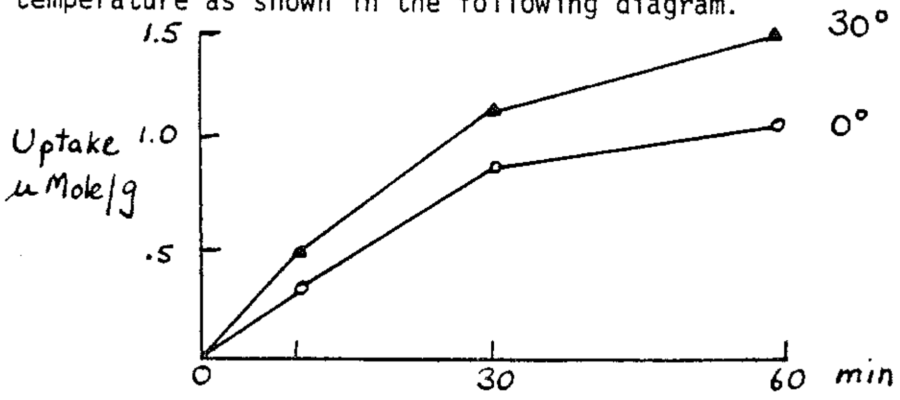


Figure 4: Uptake of potassium at 0 and 30°C. (Maggioni, A. 1979 Riv. Viticolt. Enol)

ROOT FUNCTION (Cont.):

Nutrient uptake increases with increasing external concentration but reaches a maximum rate as shown in the following diagram of iron uptake.

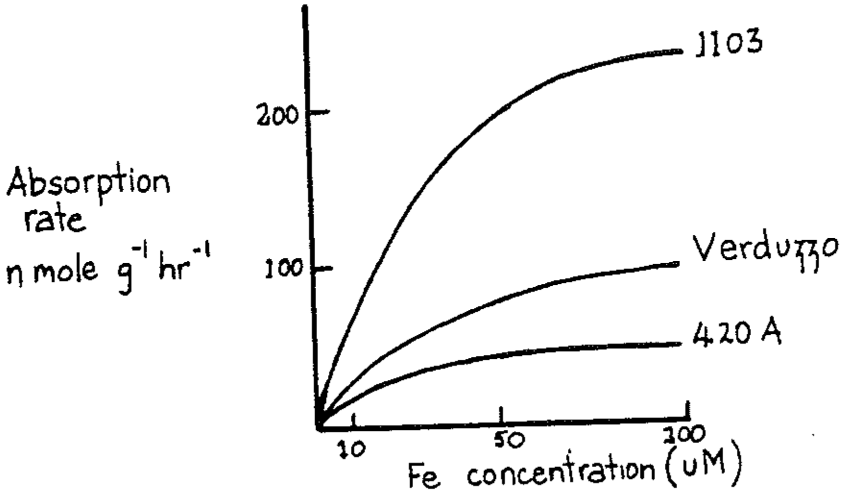


Figure 5: Iron uptake by root sections of 3 rootstocks (Maggioni, A. 1980. Vitis 19).

This diagram shows that rootstock 1103 can accumulate iron faster than 420A and the rate of uptake for 420A reaches a maximum rate at a low external concentration.

An increase in iron concentration, greater than 50 uM in the soil would not increase the rate of uptake for 420A and this variety would apparently not respond to fertilization. It appears that at high iron concentrations 1103 vines would have a higher iron concentration than 420A. But these are the maximum uptake rates for excised roots and the levels of iron in the roots and leaves also control uptake. The control of uptake by internal concentration is not well understood.

To summarise, nutrient uptake depends on the concentration in the soil, rate of movement in the soil, uptake rate and level present in the grapevine.

3) Water Movement:

Evaporation of water at the leaf surface draws water through grapevines, as if a suction pump is drawing the water up. The xylem vessels or "pipes" and other restrictions to flow regulate the amount of water movement. Root density and distribution are important regulators of water movement. The sparse root system of a grapevine helps conserve water and distribute it over the growing season, and is an adaption for survival rather than supplying large quantities of water for peak demand.

As water is drawn up, the roots shrink and break contact with the soil. This gap between the root and the soil restricts water movement into the root. Roots of maize plants shrink considerably due to midday water stress but roots of cherry trees only shrink slightly. This resistance to shrinkage is an adaption to dought, and is thought to be due to a restriction to water movement within the root.

effect of shrinkage is very important for plants with low root densities A less than 10 Cm Cm^{-2}). Grapevines are below this critical root density and sistance to root shrinkage would be very important for grapevines.

4) Hormone Production:

The root tip produces the hormones cytokinin, gibberellin and abscisic id which regulate shoot growth, cluster and fruit development.

Cytokinins are produced in the root tip and promote cell division and elontion. The movement of cytokinins to the shoots is inhibited by flooding, drought, linity and high temperatures. Extremes of temperature in the root zone inrfer with the production of cytokinins and cause leaf senescence and yellowing.

Developing buds have a group of cells known as primordia, which can develop to clusters or tendrils. Recent information indicates that the fate of these imordia, i.e., whether they become clusters or tendrils depends to a large tent on root produced hormones, particularly cytokinins. Thus, cuttings rarely rry clusters because the level of cytokinin production is very low due to the ck of a root system. Because leaves are a greater sink for cytokinins than usters, leaf growth is stimulated at the expense of cluster growth. However usters can be developed on cuttings by removing the leaves below the cluster fore they develop.

A major source of gibberellins are root apices and gibberellins promote stem ongation.

site of production of abscisic acid (ABA) is the root tip. ABA promotes scission and bud dormancy and inhibits transpiration, stem and root elongation l nutrient transport. Production of ABA is increased by drought, flooding, rient deficiency and salinity.

Roots also produce hormones which apparently exert some control over seed duction. Restricting the root volume of tomatoes reduces the number of seeds duced in the fruit, which in turn reduces the strength of the fruit as a sink carbohydrate. For example a pot-bound tomato plant may be very vigorous, but y produce small tomatoes which do not size up. Whether a similar relationship urs in grapes is not known.

Thus hormones produced in the root, particularly the root tip influence wth and development of the shoots and clusters of grapevines. The production transport of these hormones depend on the environment of the root system.

T SYSTEM MANAGEMENT:

Cultural practices modify root systems but the direct response of the root tem is invisible. Changes in the root system indirectly change the visible ial parts of the grapevine. An understanding of what may occur when cultural ctices are changed would help vineyard management.

1) Seasonal periodicity of root growth:

In mature vines, root growth commences several weeks after budbreak and re is a peak of root growth after shoot growth begins to slow down (see

Figure 6). Thus, root growth and aerial growth alternate; when shoots are growing rapidly there is little root growth and vice versa. Generally, root growth is most active immediately following the "grand" period of shoot growth, and before rapid berry growth commences. During berry growth and fruit ripening, root growth is suppressed. After harvest a second smaller peak of root growth occurs (Figure6).

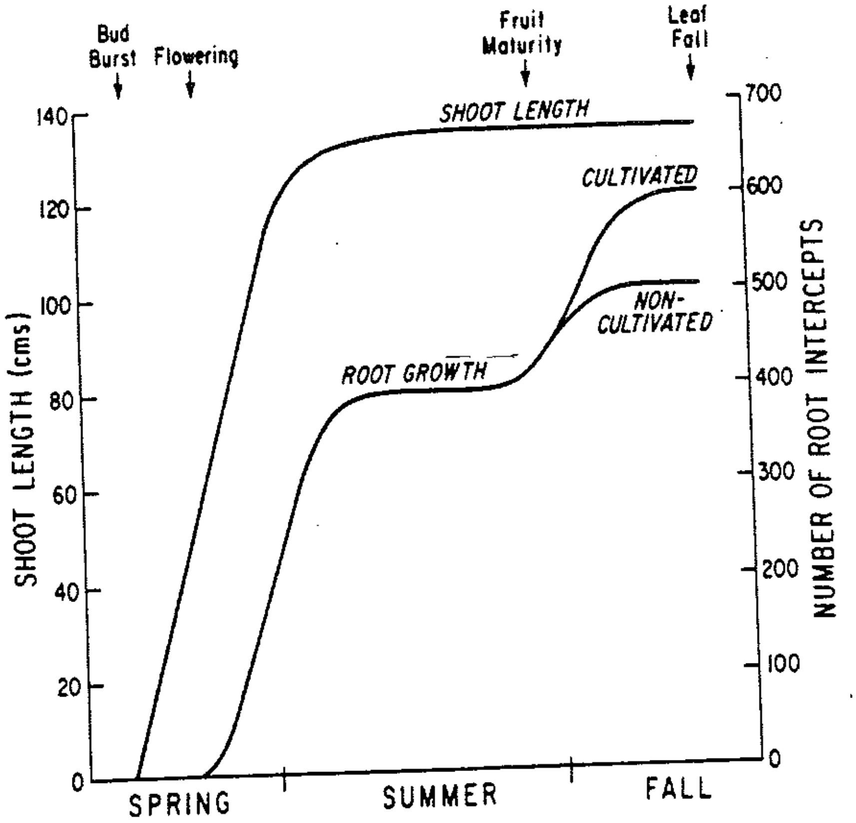


Figure 6. Periodicity of root gorwth for two cultivated and tow non-cultivated 15-year-old Shiraz vines located in the Root Observation Chamber at Griffith, Australia. The amount of root growth is indicated by the number of new roots crossing a grid of horzonal lines at one inch intervals on a glass panel.

In spring when shoots are growing rapidly, there are very few white, unsuberised roots but most of the roots are old woody or brown roots.

A flush of new growth will greatly increase the root length. Root length may be critical during some periods of the year and result in nutritional problems early in spring.

The absorption of water and nutrients is often assumed to occur exclusively in the younger white part of the root tip which is often described as the "absorbing zone". Studies with cereals, forest trees and apple trees show that most of the root system is capable of absorbing nutrients. The absorption of phosphate by apple roots was the same per unit of surface area for both woody and white roots. Calcium uptake was higher in woody roots but potassium uptake was higher in white roots. Both types of roots absorbed similar quantities of water.

Strong shoot growth reduced root growth in plum trees but I have not been able to modify grapevine root growth by severe pruning which increased vigour. Summer pruning or slashing may reduce root growth as summer pruning of apples, pears, currants and tea has delayed and reduced new root growth.

Most root growth occurs when the aerial parts of the grapevine are not growing rapidly. The relationship between root and shoot growth will be discussed in the next section.

2) Root shoot ratio:

The ratio of the amount of shoot growth to the amount of root growth tends to be constant for woody perennials. A restricted root volume will reduce root growth but shoot growth is also reduced so that the ratio of roots to shoots is constant. If part of the root system is removed, an equivalent root system will reestablish to maintain a constant ratio.

Environmental conditions can alter this ratio. Water stress and nutrient deficiency will increase the proportion of roots while high temperatures will reduce the proportion of roots compared to shoots.

The top to root ratio increased from 1 to 4 as peach trees matured. For young trees 20% of the growth goes into the roots compared to 1% for mature trees.

Thus there is a balance between root and shoot growth which can be altered by environmental conditions. Most of the root system is developed early as only a small proportion of growth goes into root development once production commences.

3) Cultivation:

Cutting a root stimulates production of new lateral roots and increases overall root production so that the effect of cultivation may not be as detrimental as it first seems. The practice of deep ripping or trenching, deep ploughing and burying prunings with fertilizer has been extensively practiced in many grape growing countries in the past. Through these practices, vines would produce more root growth due to the stimulative effect of root cutting, but also the improved aeration, water penetration and nutrients would favor root growth. This practice may be beneficial if soil compaction or other barriers within the root zone was restricting growth, however, the response would not be immediate, but would take time to re-establish the constant shoot-to-root ratio.

The root system is restricted by soil compaction by wheeled tractors and other implements. Ripping of this zone usually improved the soil environment for root growth by increasing aeriation and reducing physical obstructions. It is often difficult to rip where the wheel tracks are located because most large rippers are centrally mounted and there is not enough row space to maneuver the ripper. The benefits of such practices are difficult to assess because the soil is soon compacted again by wheeled traffic.

4) Fertilizer application:

The greatest concentration of roots occurs under the vine canopy and thus fertilizer should be applied under the vine canopy to maximize fertilizer uptake.

Nitrogen fertilizers in California are generally applied in the fall or winter after buds have gone into a state of rest or dormancy. There is some information available that indicates that uptake of nitrogen is greater in the fall (November and December) while the soil is still relatively warm. At this time there is generally a new flush of root growth which should benefit mineral uptake. Care must be taken not to apply nitrogen too early in the fall since this may stimulate new shoot growth to occur. In California, generally by mi -November, most buds are in a state of rest or organic dormancy and nitrogen fertilization will not stimulate new growth. Nitrogen fertilization near flowering time may cause a stimulation of shoot growth and promote berry shatter. Therefore, fall or winter applications are generally recommended, the exact timing depending on the amount of winter rainfall that normally occurs in a given area.

5) Irrigation:

Both water stress and irrigation stimulate root growth. This paradox can be explained by examining the effects of water stress and irrigation.

Firstly as water stress develops in a grapevine, shoot growth stops first but photosynthesis continues till a higher level of stress is reached. After shoot growth has stopped surplus photosynthate can still be transported to the roots. The roots are closer to the supply of water and will not be as stressed as the shoots and hence continue to grow.

On the other hand irrigation reduces water stress and increases shoot growth. This produces a large grapevine and to maintain the same root to shoot ratio more roots are produced.

Trickle irrigation increases the amount of root growth in the wetted zone. This concentration of root growth creates a vine dependant on this reduced soil volume for nutrients and water. The grapevine would be more sensitive to drought and soon deplete the available water if trickle irrigation was stopped. Root growth outside the wetted zone has not been studied but may be supported by rainfall. The conversion of mature flood irrigated grapevines to trickle irrigation had an effect on root distribution after 3 years as shown in Figure 7.

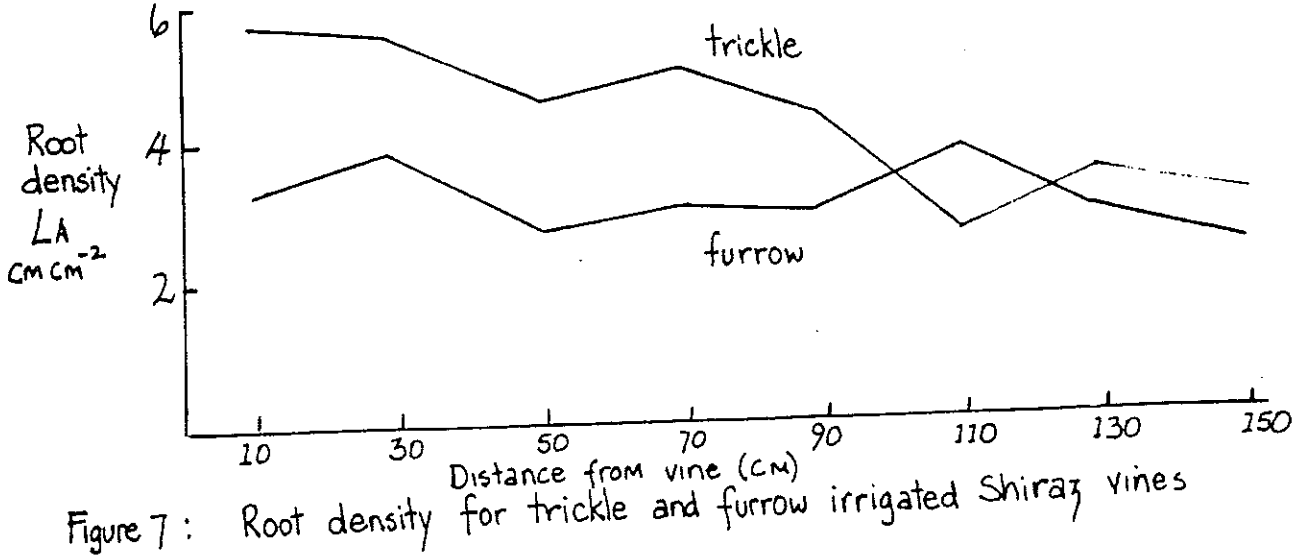


Figure 7 : Root density for trickle and furrow irrigated Shiraz vines

Thus management practices of pruning, cultivation, fertilization and irrigation can affect the root system. This in turn effect grapevine growth and production.