UPTAKE AND PARTITIONING OF MINERAL NUTRIENTS
IN CONCORD GRAPE

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To the faculty of Washington State University:

The members of the committee appointed to examine the dissertation of SUPHASUK PRADUBSUUK find it satisfactory and recommend that it be accepted.

__________________________
Chair
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Finally, I want to thank Washington State Concord Grape Research Council for providing the financial support for this research.
The objectives of this research were to develop methodology for root and tissue sampling to monitor the nutrient status of Concord grapes (Vitis labruscana Bailey), investigate seasonal distribution pattern of Concord grape roots, investigate seasonal pattern of macronutrients and micronutrient uptake and redistribution in Concord grapes, and identify the tissue type and the best time to sample grapevines for routine nutritional evaluation.

The study was conducted in a 42 year-old Concord vineyard. The site was furrow irrigated fine sandy loam. In 2005, six vines were excavated at 650°C degree days. The results showed a higher density of fine roots when sample spacing was closer to the vine trunk at 20, 60, 120 cm from the vine trunk.

In 2006, four vines were excavated at winter pruning, budbreak, 3-4 leaves, bloom, veraison, harvest, and post-harvest. Different tissue fractions were measured for biomass and analyzed for C, N, P, K, Ca, Mg, B, Fe, Mn, Cu and Zn. Similar nutrient concentrations between fruiting shoots and vegetative shoots as well as between trunk and cordon throughout the growing season suggests that the most efficient way to sample the whole plant tissues for 2007 was to collect 9 tissue types (woody tissues, canes, coarse roots, fine roots, shoots, leaf blades, petioles, shoot tips and clusters) in parallel growth stages to 2006.

The result showed that the seasonal dynamics of nutrient contents, except Fe, Cu and Zn, which highly fluctuated between years, shared a practical pattern: translocation of
nutrients from woody tissues to active growing organs at the beginning of season, majority uptake of N, Ca and Mn from soil occurred from bloom to harvest while P, K, Mg and B occurred from bloom to veraison, and restoration of N, P, K, Ca, Mg, B and Mn back to woody tissues occurred after veraison until before leaf fall with no further nutrient uptake. Leaf blade analysis at bloom seems to best to represent vine’s nutrient status for fertilizer recommendation since substantial nutrient uptake from the soil occurred after bloom and leaf blades indicate overall status of nutrients.
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Grape (*Vitis sp.*) is a perennial crop in which mineral nutrient concentration changes over time throughout the growing season. Some of the mineral nutrients are newly taken up from the soil each year and some are redistributed throughout the plant from woody and root tissues that function as storage organs. Mineral uptake can occur throughout the year, although the majority occurs during the growing season. Concord grape (*Vitis labruscana* Bailey) has emerged as the dominant cold climate American variety. Washington is the leading state in Concord grape production, and accounts for approximately 50 percent of the U.S. production (USDA NASS, 2008). Concord grape does not reach full production until about the fifth year after planting (Aegerter and Folwell, 1996). Size and seasonal duration of vegetative, reproductive and storage sinks might vary with vine age (Borchert, 1976), cultivars (Colugnati et al., 1997), and variable weather conditions (Robinson, 2005). Direct comparison of winegrape (*Vitis vinifera* L.) and Concord nutrient uptake and portioning may not be possible due to differences in management strategies (e.g., pruning, thinning) as well as desired crop yield levels (typically less than 8 Mg/ha for wine grape and over 20 Mg/ha for Concord).

Petiole analysis is a useful tool that commercial grape growers use to determine nutrient status of a vine during the growing season for fertilizer recommendations. However, concentrations in this plant part do not provide information on nutrient uptake or allocation of nutrients in various organs. With the economic pressures for high yields and production efficiency of juice grapes in the US, growers are encouraged to use other information regarding plant growth and fruit quality, specific to their site, to support the interpretation of leaf or petiole nutrient data. Changes in whole-vine nutrient content (concentration x biomass) is exceptionally important to understand mineral nutrient
uptake in grapes, since grapevines have the capacity to store and re-allocate potentially large quantities of carbon and mineral nutrient reserves (Roubelakis-Angelakis and Kliewer, 1992). To understand the relationship between vine performance (i.e., yield, quality) and the concentration of mineral nutrients in specified parts of grape plants, there is limited quantitative knowledge of nutrient uptake patterns in mature grapevines, presumably because of the difficulties in experimentation presented by large biomass.

Nitrogen has been the primary nutrient examined in whole-vines studies. Most studies report that grapevine takes up the most N between bloom and veraison (Williams, 1987; Lohnertz, 1991; Williams and Biscay, 1991; Hanson and Howell, 1995; Bates et al., 2002). However, Conradie (1980, 1981) reported substantial N uptake after harvest in potted Chenin Blanc grown in the South Africa. He reported N uptake during the postharvest period comprised 27% and 37% of the total annual N uptake (Conradie, 1980, 1986) and provided 60% of the stored N for the next season (Conradie, 1992).

Cheng and Xia (2004) experimented in one year old Concord grape and found that fall foliar urea application increased the proportion of vine N content mobilized for the growth of shoots, leaves and fruits. They reported that both vegetative growth and fruiting of young Concord vines are largely determined by reserve N, not by reserve carbohydrates, and that current-season N supply plays a very important role in sustaining vine growth and development, especially fruit growth. However this significant effect might be seen only in young grape plants as a larger proportion of the N taken up during active vine growth is used for structural growth and less is available for storage.

While research focusing on N uptake in whole vines has been conducted in several different growing regions, little has been done on other nutrients. Potassium uptake in whole vines was examined in several studies (Conradie, 1981; Williams and Biscay, 1991; and Schreiner et al., 2006). These studies showed that the bulk of K uptake
occurred between bloom and veraison. Of the three studies, only Conradie (1981) in South Africa and Schreiner et al. (2006) in Oregon examined P, Ca, and Mg uptake in their whole vine studies. Their results agreed that the time of maximum Ca and Mg uptake was between bloom and veraison. However, the Oregon study on 23-year-old Pinot Noir showed that P uptake occurred predominantly before bloom while the South African study on 2-year-old Chenin Blanc showed peak uptake between bloom and veraison. This is probably because differences in subtle factors such as vine age, soil texture, temperature, water management, root density and nutrient availability contribute to differences in grapevine performance and nutrient uptake. Schreiner et al. (2006) also reported that uptake for most macro elements was very closely related to canopy demand, whereas concentrations of micronutrients Fe, Mn, B, Zn, and Cu in whole vine varied highly from vine to vine.

The root system serves important physiological and biological functions, and it has been shown that both grape yield and quality are dependent on root health (Morlat and Jaquet, 1993). Nutrient uptake is a key for vine growth and fruit production. While nutrient uptake depends on the quality of root environment, there are difficulties in properly calibrating tissue tests in woody perennials because precise experiments are not easy to conduct with large, long-lived plants that explore a variable root zone (Robinson, 2005). Root spatial distribution is mainly related to local soil environment, bulk density, and water content. The ratio of fine to coarse roots increased in soil with high water potential (Van Zyl, 1988). Grapevine root density increases with the age of the plant to reach a constant value after 5 to 10 years (Smart and Coombe, 1983). Depending on age, variation in root diameters is usually between 6-100 mm. Small permanent roots (diam. 1-2 mm) arise from the main framework and grow horizontally and vertically. These roots extend and branch in a few main extension root that are generally thin (diam. 1-2 mm).
These fine roots grow rapidly and die within weeks after emergence but are replaced continuously (Richards, 1983).

Grapevine roots show a very distinctive growth pattern with two main growing phases, one at flowering and the other near harvest (Van Zyl, 1988). This differs from woody tree species where the main root growth phase occurs before budburst (Deans and Ford, 1986). Grapevines do not form terminal buds at the end of shoots, which continue to grow late into the season, with individual flower parts forming soon after budbreak (Smart and Coombe, 1983). This probably results from the temperature requirement and the sink demand related to the growth of shoots and roots. In early spring, soil temperature is lower than air temperature, which favors bud growth. Shoots are active sinks for assimilates and root growth is apparently delayed until the set of leaves emerge which allow a net positive photosynthesis balance. Later, berry growth competes with roots for assimilates until harvest (Delrot et al., 2001).

Changes in root physiology with root age can strongly influence nutrient acquisition and competition. Bouma et al. (2001) measured the effect of root age on respiration and P uptake in fine roots of apple (Malus domestica Borkh) and orange (Citrus aurantium L.) and found both declined rapidly with age. The decline in P absorptive capacity with root age is consistent with several studies showing a decline in hydraulic conductivity. Van Rees and Comerford (1990) reported that pigmented roots had diminished Ca and K uptake compared to young white roots. Volder et al. (2005) reported that both nitrate uptake and root respiration declined rapidly with increasing root age. They found that the decline in both N uptake and root respiration corresponded with a strong decline in root N concentration, suggesting N translocation out of the roots. However, they found no correlation between root age and specific root length or
diameter, nor a relationship between root age and C concentration, which suggest that the
decline in N concentration was due to N moving out of roots, rather than a dilution effect.

Plant nutrient demand changes with different stages of vine physiological
development, resulting in different nutrient concentration throughout the plant
(Christensen, 1969). When nutrient deficiency occurs, mobile nutrients are moved from older leaves to the growing tip and symptoms appears in the older tissue, whereas immobile nutrients show deficiency symptoms in actively growing shoot tips or in the younger leaves (Robinson, 2005). Several investigations have compared two methods of tissue analysis, total N in leaf blades or petioles vs. NO$_3^-$ in petioles, to assess N status in grapevines. The main disadvantage of using total N as an indicator of the N status of grapevines in the relatively narrow range often found between deficient and adequately supplied vineyard with N (Kliewer, 1971). Bertoni and Morard (1982) found that the level of total N in blade and petioles was not closely correlated and suggested that both tissue should be analyzed separately. Christensen (1984) reported that leaf blade total N was not as useful as petiole NO$_3^-$ to determine N needs of vineyards. Although blades contain more N than petioles, much of it is in organic forms, such as proteins which tend not to vary as much as NO$_3^-$ and NH$_4^+$ in grape leaf tissues.

Petiole nutrient results may not always reflect the nutrient status in other parts of the vine. Davenport et al. (2003) studied Concord grape response to variable rate fertilizer application by using soil and tissue samples to evaluate crop nutrient status. The research found that analysis of leaf blades was more related to yield than petiole analysis.

Different leaf sampling times have been studied for the nutritional diagnosis of vineyards. Choice of sampling time should be made according to the diagnostic purpose. For example, a four year study by Porro et al. (1995) on leaf sampling time to diagnose nutrient status of Chardonnay in Italy found that lowest variability in leaf nutrient levels
was at fruit set for P, K and Mg, and at veraison for N, Ca and B. They concluded that fruit set is the most suitable time to evaluate P, K, Ca and Mg status and veraison sampling better for N.

In cold climate regions, the rapid drop of temperature and short time period between harvest and leaf fall may significantly affect mobilization of nutrients from leaves back to storage organs, and may limit nutrient uptake from soil as well. Understanding nutrient movement throughout various plant tissues and plant nutrient uptake, as well as the limitation of reserve nutrients, on growth and fruiting of grapevine is important for optimizing viticultural practices to improve growth and yield in cool climate regions.

Whole plant sampling can be used to look at nutrient partitioning and distribution/redistribution. With the extensive root system of Concord grape, fine roots are mainly involved in nutrient and water uptake. It is also important to develop techniques for fine root sampling to determine the extent that represents its highest production. This will make possible of resample the same plant for mass gain, which will pave the way for long term study in this perennial plant.

The objectives of this research were to (i) develop methodology for root and tissue sampling to monitor the nutrient status of Concord grapes, (ii) investigate seasonal distribution pattern of Concord grape fine roots, (iii) investigate seasonal pattern of macronutrients and micronutrient uptake and redistribution in Concord grapes, and (iv) identify the choice of tissue type (petiole or leaf blade) and the best time to sample grapevines for routine nutritional evaluation.
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CHAPTER TWO

ESTABLISHMENT OF METHODOLOGY

FOR PLANT TISSUE AND ROOT SAMPLING

INTRODUCTION

While nutrient uptake is key for vine growth and fruit production, there is limited understanding of seasonal patterns of nutrient accumulation and uptake in mature, field grown grapevines largely due to the difficulties of experimentation presented by large woody biomass and variable root zones. Size and seasonal duration of vegetative, reproductive and storage sinks can vary with vine age (Borchert, 1976). Research conducted on the plant nutrient content of potted vines with a continuous nutrient supply or of field grown young vines, where the roots and permanent tissues are still not fully developed, may not represent an extensive pattern of nutrient accumulation and uptake associated with older vines grown in the field. Whereas nutrition experiments on mature vine have been focused on leaf blade and petiole analysis, they lack data from permanent structures involved in nutrient storage and the extensive root system involved in water and nutrient uptake (Chang and Kliewer, 1991; Colugnati et al., 1995; Robinson, 2005). Hence, these studies only provide a partial picture of nutrient uptake for the whole vine and may not fully calibrate tissue tests.

Balance of nutrients should be a high priority for vineyard management because there is a direct impact on how well the plants grow and on juice quality. Concord grape (*Vitis labruscana* Bailey) is a cold climate juice grape variety that evolved in the New England region in predominantly acid soils derived from granite rocks. Approximately 50 percent of the U.S. Concord grape is now grown in Washington State (USDA-NASS, 2008). The neutral to alkaline soils of central and eastern Washington result in a different
chemical environment for Concord roots which may limit the availability of many micronutrients, including Fe, B, Cu, and Zn (Shuman, 1991). Iron deficiency can result in yield loss because it is one of the most common nutrients associated with chlorosis in Concord grape growing in calcareous soils where a cold, wet soil environment prior to bloom impedes the root growth and/or function and triggers plant chlorosis (Davenport and Stevens, 2006).

Cheng et al. (2004) found that fall foliar urea application increased the proportion of vine N content mobilized for the growth of shoots, leaves and fruits in one year old Concord vines. They reported that both vegetative growth and fruiting of young Concord vines are largely determined by reserve N, not by reserve carbohydrates, and that current-season N supply plays a very important role in sustaining vine growth and development. Bates et al. (2002) studied the effects of soil pH on Concord grapevines and reported that liming soil resulted in higher Mg and lower K concentration in leaf and petiole tissues. However, excessive K fertilization of grapevines may cause potential loss of juice acidity, which is deleterious to the quality of grape juice product (Morris et al., 1980). There is a strong relationship between vine size and nutrient uptake. Schreiner et al. (2006) reported that uptake for most macronutrients was very closely related to canopy demand, whereas concentrations of micronutrients Fe, Mn, B, Zn, and Cu in whole vine varied highly from vine to vine.

Whole plant sampling can be used to look at nutrient partitioning and distribution/redistribution. We hypothesize that vine destructive harvest, biomass determination, and nutrient analysis of whole, field-grown Concord grape in association with soil analysis will provide a full picture of their nutrient partitioning. The objective of the study was to develop methodology for root and tissue sampling of Concord grape. The aim was to use
the acquired methodology in studying nutrient partitioning and uptake at main physiological stages of Concord grape in the next growing season.

MATERIALS AND METHODS

The study was conducted in a 42 year-old own-rooted Concord single-curtain vineyard (lat 46°15’59” N, long 119°44’4” W) at the Irrigated Agriculture Research and Extension Center (IAREC) in Prosser, WA. The site is furrow irrigated and has been managed with uniform fertilization, water and pest management practices. Due to the great diversity in plant sizes of this very old vineyard, all grape plants in the 1.5 acre vineyard were measured to determine uniform sized vines for excavation, which included 12.8-15.0 cm trunk circumference at 30 cm above the soil surface, 87-99 cm trunk length from soil surface to cordon split, and 25-36 cm cordon length prior to attachment to the cordon wire.

In 2005, at 650° C degree-days, two different root sample interval spacings (20, 60, 120 cm and 50, 100, 150 cm in a radial pattern around the vine trunk) were compared on three vines to determine the extent that represented the highest density of fine roots (Fig. 2. 1). Soil cores (6.25 cm diam.) were collected from 0-30 cm and 30-75 cm to represent the surface and subsurface soil depths. Soil core samples were composited across each single radius. Fine roots (< 4 mm diam.) were separated from the soil by washing through a 2 mm wet sieve and were expressed on a per liter soil basis for comparison purposes.

In 2006, four whole Concord grape plants were excavated at winter pruning, bud break, 3-4 leaves, bloom, veraison, harvest, and post-harvest. Separated plant tissues were dried, weighed, ground and analyzed for nutrient elements. Total N and C were analyzed using dry combustion (Yeomans and Bremner, 1991) with a LECO CNS 2000 (St.
Joseph, MN. Tissue analysis for P, K, Ca, Mg, Na, Cu, Fe, Mn, Zn and B was determined by commercial lab (Brookside Laboratories, Inc, OH) using Inductively Coupled Plasma Spectroscopy (Soltanpour et al., 1996). The samples digested with nitric acid and hydrogen peroxide in a CEM microwave were analyzed on a Thermo Jarrell Ash 1100 ICP (Franklin, MA).

RESULTS AND DISCUSSION

Fine root sampling

As shown in Table 2.1, density of fine roots was higher with spacing closer to the vine (20, 60, 120 cm) than with more distant spacing (50, 100, 150 cm). The high root densities are consistent with findings of Bassoi et al. (2003) who studied grapevines cv. Italia grafted on the rootstock IAC-313 and found grape root concentration decreased with distance from the trunk within 1 m soil depth and 1 m away from the trunk. Although Concord grapevine roots on a loess soil were found to reach 4 m in depth and over 7 m in horizontal spread (Doll, 1955), a vineyard environment with closer vine spacing resulted in a smaller and denser root system (Morano, 1995).

In subsequent collections, based on 2.4 m vine spacing and 2.7 m row distance, fine root sampling will be conducted by using the radial pattern at 20, 60, and 120 cm from the trunk to achieve highest root density without overlapping of roots among neighboring vines. In addition, each soil core sample (48 samples/plant) will be washed individually to better illustrate fine root distribution patterns around grape trunk.

Plant tissue sampling: Nutrient composition in different tissues

Concentrations of mineral nutrients in different tissues were significantly different, except between trunk and cordon (Fig. 2.2) as well as similar tissues - shoots,
leaf blades, petioles, and shoot tips separated from fruiting shoots and vegetative shoots (Fig. 2.3). Concentrations of all nutrients from trunk and cordon were very similar throughout the growing season and significantly lower than coarse root in every growth stage for the nutrients N, P, Ca, and Fe. Apparently, nutrient distribution was unrelated to differentiation among above ground woody tissues as well as among similar tissues from fruiting shoots and vegetative shoots. Consequently, plant destructive harvest for the 2007 growing season combined woody tissues from cordon and trunk as well as similar tissues of shoots, leaves, petioles, and shoot tips from vegetative shoots and fruiting shoots.

Petioles showed higher concentrations of K, P, Mg, B and Zn than leaf blades. This is probably because analysis of petioles indicates the current movement of nutrient toward the leaf blade and therefore is sensitive to the status of mobile nutrients such as K, P and Mg. In contrast, concentrations of N, Ca, Mn, Cu and Fe in blades were higher than in petioles (Fig. 2.3). This is probably because the portion of some nutrients like N (Christensen, 1984) and Fe (Smith and Cheng, 2006) were in forms that were not available for assimilation by plants, and immobile nutrients tend not to move around in the plant phloem (Robinson, 2005). In addition, when compared with petioles, there was less fluctuation of P, Mg, and Zn concentrations in the blade throughout the growing season. Thus, blades seem to better indicate overall status of nutrients, including mobile nutrients.

Blades and shoot tips appeared to have very close nutrient concentrations, except for Ca, Zn, Mn and B, which had higher concentrations in leaf blades than in shoot tips at bloom (Fig. 2.3). These are immobile nutrients which do not move freely in the plant phloem (Marschner, 2002), which means that they cannot be translocated from mature leaves to the shoot tip. In later growth stages, however, Ca, Zn, Mn and B concentrations in shoot tips increased to become very close to those in blades. Highest concentrations of
Ca and Mn occurred in leaf blades at harvest, probably because with low mobility in plant phloem; they became immobile once deposited in individual leaves and continuously increased in concentration throughout the season.

Plant tissue sampling: Seasonal pattern of nutrient concentrations

Based on the same nutrient concentrations found between fruiting shoots and vegetative shoots, as well as between trunk and cordon, sampling for seasonal patterns of nutrient concentrations was reduced from 14 to 9 tissue types (Fig. 2.4) to give a clear and concise seasonal pattern of nutrient concentration of Concord grape.

After the shoots showed 3-4 leaves, the large increase in all macronutrients in the shoot tips correlated to a decrease in the woody tissues, coarse roots and canes (Fig. 2.4). At bloom, N concentrations in leaf blades shoot tips, and clusters, and P concentrations of these organs plus petioles were similar, whereas there was a wider range of K concentration in these organs. In the following stages, N concentration in cluster considerably decreased whereas concentrations of P and K in the clusters remained consistently high through harvest. Ca and Mg showed highest concentrations at harvest in leaf blades, shoot tips and petioles. The annual tissues, including leaf blades, shoot tips, petioles and clusters, showed very high concentration of N, P, K and Mg in comparison to woody tissues and coarse roots. Remarkably, these high concentrations in the actively growing tissues are consistent with their known high mobility in the plant phloem (Epstein and Bloom, 2005).

Seasonal pattern of micronutrient concentrations varied considerably as to which organ and growth stage they attained the highest concentration. Fine roots at budbreak appeared to have highest concentrations of Fe, Cu and Zn. Leaf blades, shoot tips and
petioles showed highest concentration of B at bloom, and showed highest concentration of Mn at harvest.

CONCLUSION

Density of fine roots was higher when sample spacing was closer to the vine trunk; therefore, a fine root sampling pattern at 20, 60, 120 cm from trunk was chosen for the study in 2006 and 2007. Each soil core in subsequent collections were washed and weighted individually to better illustrate root distribution patterns.

The same nutrient concentrations between fruiting shoots and vegetative shoots as well as between trunk and cordon suggested the most efficient way to sample whole plant tissues is to sample woody tissues, canes, coarse roots, fine roots, shoots, leaf blades, petioles, shoot tips and clusters.

The results of nutrient analysis reflected the mobility of nutrients. Nitrogen, P, K and Mg, known to be high mobility in the plant phloem (Epstein and Bloom, 2005), where there were very high concentrations in annual organs including leaf blades, shoot tips, petioles and clusters. Conversely, large fractions of low mobility nutrient elements in the plant phloem, like Ca, B, Fe, Mn and Zn, were found in fine roots and permanent structure including woody tissues and coarse roots.
LITERATURE CITED


Table 2.1. Density (g/L soil) of fine roots collected by soil core method at 2 distance tracking at 650°C degree days in 2005.

<table>
<thead>
<tr>
<th>Plant</th>
<th>Soil depth</th>
<th>Distance from trunk</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>20 cm</td>
<td>60 cm</td>
</tr>
<tr>
<td>1</td>
<td>0-30 cm</td>
<td>0.78</td>
<td>1.48</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.77</td>
<td>0.70</td>
</tr>
<tr>
<td>2</td>
<td>0-30 cm</td>
<td>1.34</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.45</td>
<td>0.65</td>
</tr>
<tr>
<td>3</td>
<td>0-30 cm</td>
<td>1.22</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.29</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50 cm</td>
<td>100 cm</td>
</tr>
<tr>
<td>4</td>
<td>0-30 cm</td>
<td>0.67</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.59</td>
<td>0.25</td>
</tr>
<tr>
<td>5</td>
<td>0-30 cm</td>
<td>0.48</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.39</td>
<td>0.18</td>
</tr>
<tr>
<td>6</td>
<td>0-30 cm</td>
<td>0.30</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.61</td>
<td>0.06</td>
</tr>
</tbody>
</table>
Figure 2.1. Radial pattern of soil core sampling used in the study.
Figure 2.2. Concentration of nutrients in cordons, trunks, and coarse roots at different growth stages in 2006.
Figure 2.3. Concentration of nutrients in shoots, leaf blades (LB), petioles, and shoot tips (ST) separated from vegetative shoots and fruiting shoots at different growth stages in 2006.
Figure 2.4. Nutrient concentration in different tissues of Concord grapevines destructive harvested in 2006.
CHAPTER THREE
DISTRIBUTION OF CONCORD ROOTS

INTRODUCTION

Compared to other crops, grapevines appear to have low root densities in soil (Smart and Coombe, 1983) but extensive lateral and vertical spread of root systems (Smart et al., 2005). It has been shown that both grape yield and quality are dependent on the health status of the roots (Morlat and Jaquet, 1993) and fine roots are mostly involved in water and nutrient uptake. The rate of nutrient uptake by the plant depends not only on the mobility of the nutrients in the soil but also on a well distributed and functioning root system, which is influenced by access to the plant nutrients required for growth.

Nutrients are transported in soil by either diffusion through the soil solution or mass flow of the soil solution through soil pores. Diffusion is the main mechanism for movement of P and K to the root surface (Marschner, 2002) while mass flow generally satisfies N, S, Ca, Na, Mg and B requirement of plants growing in most soils (Tinker and Nye, 2000). However, meeting plant demand for K, P, Cu, Fe, Mn, and Zn is challenging due to their generally low concentrations in the soil solution (Cass, 2005). Concentrations of K and P are much lower at root surface than in bulk soil, whereas concentrations of Mn, Fe, Zn, and Cu in the soil solution mainly depend on the soil pH, redox potential, and soil organic matter content, and may fluctuate throughout the season in temperate climates (Sinclair et al., 1990).

In addition to mass flow and diffusion, a small portion of plant nutrient requirements is met by root interception. The degree of contact between perennial plant roots and soils varies with root types, age, and the surrounding environment. Root-soil contact can be good if the root deformed the soils during its growth rather than using an
existing channel (Atkinson and Wilson, 1979), whereas root-soil contact can be reduced by diurnal changes in root diameter due to water stress (Huck et al., 1970), and has been shown to be poor after browning and decay of the root cortex, as the loss of cortex can cause a 50% reduction in root diameter (Rogers, 1968).

Grapevine root size and density increases with the age of the plant, reaching a consistent value after 5 to 10 years (Smart and Coombe, 1983). The majority of the grapevine root system is usually within the top 1 m of the soil (Hellman, 2003), however, individual roots can grow much deeper under favorable soil conditions. Different grape varieties showed no clear differences in root distribution patterns; however, studies on rooting patterns generally reported highest root densities within 1.5 m of grapevine trunk (Saayman and Van Huyssteen, 1980; Mckenry, 1984; Nagarajah, 1987).

Grapevines have a complicated branching root system. Small permanent roots arise from the main framework and grow either horizontally or vertically. Fine roots grow rapidly and die within weeks after emergence but are continuously replaced (Richards, 1983). Two flushes of new root growth are believed to occur around bloom and after harvest (Mullins et al., 1992). New root production begins very slowly after budbreak, and significantly accelerates during the rapid shoot growth period. A second root growth period has been shown after harvest in warm climate regions where the postharvest growth period may be long (Van Zyl and Van Hayssteen, 1987).

Generally, root distribution studies include root biomass or root length as a function of soil depth, distance from the plant stem, and position of neighboring plants (Bassoi et al., 2003). Root distribution is mainly related to the local soil environment, specifically temperature, bulk density, texture, water and nutrient availability. Many management factors such as mechanical resistance, aeration, frequency and depth of tillage, mulching and organic matter content may also affect root distribution patterns.
(Kirchhof et al., 1991; Morlat and Jaquet, 1993; Richards, 1983). Types of irrigation system have been shown to affect root distribution (Morano and Kliewer, 1994). Stevens and Douglas (1994) reported that in the horizontal direction, roots of drip-irrigated plants were concentrated under the vine row, and 50% of the root length was within 45 cm distance from the plant row, in comparison with 35% of the root length in the same distances when grapes were irrigated by microsprinkler. Araugo et al. (1995) reported that furrow irrigated vines had a deep and widespread root system, suggesting that the water alleyway in this system could have a directional effect on root distribution.

There are several methods to study grape root distribution, and the choice of method depends on specific site conditions, the accuracy required, availability of data about the expected root distribution, soil depth, and soil texture. For nondestructive observation techniques, root distribution analysis by the monolith method requires cutting a monolith of the soil, from which the roots are separated by washing. Bassoi et al. (2003) used this method to study grapevine root distribution under drip and microsprinkler irrigation. Eissenstat et al. (2001) and Comas et al. (2005) used the minirhizontron tube installation and video imaging to study environmental effects on root production in Concord grape. Nagarajah (1987) and Stevens and Douglas (1994) used the soil core method to study rooting patterns of grapevine under different soil textures and different irrigation systems, respectively. For destructive observation techniques, Schreiner (2003) used the destructive harvest method to study mineral allocation in Pinot Noir vines, and the profile method by Bohm (1979), Jackson (1996), and Padgett-Johnson (1999) provided information of root-wall intercepts recorded from a wall of the trench excavated parallel to the vine row.

In the present study, distribution of Concord grape roots was studied by using soil core sampling and destructive harvest methods. The objectives of this study were (i) to
investigate seasonal distribution pattern of Concord grape fine roots, (ii) to determine
distribution of the fine roots as affected by soil depth, distance from the trunk, and
azimuth direction, and (iii) to provide a broad distribution pattern of Concord grape
coarse roots.

MATERIALS AND METHODS

The sampling site location was a 42 year-old own-rooted Concord vineyard (lat
46° 15' 59" N, long 119° 44' 4" W) at the Irrigated Agriculture Research and Extension
Center (IAREC) in Prosser, WA. The vineyard was on a Warden fine sandy loam (coarse-
silty, mixed, superactive, mesic Xeric Haplocambid). The site is furrow irrigated and has
been managed with uniform fertilization, water and pest management practices.

In 2006 and 2007 at winter pruning, bud break, 3-4 leaves, bloom, veraison,
harvest, and post-harvest, soil cores were collected at 20, 60, and 120 cm distance from
the trunk in a radial pattern (Fig. 3.1), and were separated into surface (0-30 cm) and
subsurface (30-75 cm) soil depths. Each core was washed individually to remove fine
roots (< 4 mm diam.). Four vines with uniform size were sampled at each growth stage
and then destructively harvested at the comparable dimensions (2.4 x 2.7 x 1 m) of the
soil volume. Coarse roots and fine roots were separated from the excavated vines after
length measurement of coarse roots (Fig. 3.2).

The root mass data from soil core sampling was extrapolated across the area of
collection by using Inverse Distance Weighting (IDW) method in ArcGIS 9 (ESRI,
Redland, CA) with power = 2 and number of neighbor samples = 24. Density (grams of
dry roots per liter of soil) of fine roots separated from the soil core sampling method was
analyzed in relation to growth stage, soil depth, distance from the trunk, and direction
around the trunk. Distribution of fine roots from soil cores and destructive harvests were
then determined by quantifying root density, whereas those of coarse roots were
determined by root density and length density (meter length per cubic meter of soil), all of
which were compared based on plant basis and growth stages. The SPSS 15.0 (SPSS,
Chicago, IL) was used to perform all the statistical analysis.

RESULTS AND DISCUSSION

Distribution of fine roots sampled by soil cores

Fine root distribution of Concord grape was strongly influenced by growth stage.
In the 2006 growing season, fine root density at the plant growth stages winter, budbreak,
and 3-4 leaves were not significantly different. The fine root density was lowest at bloom
and almost doubled by veraison, then declined again at later growth stages (Table 3.1). In
2007, fine root density was not significantly different at winter and budbreak, then
dropped at 3-4 leaves and bloom. The density increased at veraison and remained close to
that level until the end of growing season (Table 3.2).

The data in 2006 and 2007 showed the general occurrence that root densities at
surface soil (0-30 cm) were significantly higher than subsurface soil (30-75 cm) root
density at every growth stage. The average root densities of surface soil were
approximately two times of those of the subsurface soil. This is probably because the fine
sandy loam texture of the furrow irrigated vineyard soil has a rather high water holding
capacity and a relatively slow water infiltration rate, encouraging root growth to be more
dense and widely distributed in the surface rather than subsurface soil. This is consistent
with other findings in grape. Eissenstat et al. (2001) found that most of the roots of
Concord grapevines grown in gravelly loam were confined in the top 40 cm soil depth.
Nagarajah (1987) studied rooting patterns of own rooted Thompson seedless (*Vitis
vinifera* L.) and Thompson seedless on Ramsay (*V. champinii*; hybrid of *V. candicans x
V. rupestris) rootstocks in coarse soil and found that roots were concentrated in the surface layers and sharply reduced in growth in the deeper layers of the moderately coarse and fine soils. Padgett-Johnson (1999) reported over 95% of Ramsay roots in the upper 60 cm of soil in a 1 m square area within the berm of the vine row and trenched perpendicular to the vine row. Smart et al. (2005) took a thorough look at over 200 root studies and found that on average, 63% of roots were found in the top 60 cm of soil.

Non-significant differences in root density with direction around the trunk found at surface soil implies that fine root density within 120 cm of the trunk had the highest density in the surface soil. The subsurface soil depth had very low fine root densities, which made it difficult to notice significant effects of distance and direction around the trunk. However, it could be implied from the lowest values of root densities found at 120 cm from trunk in the subsurface soil that the further away from the trunk, the lower the concentration of fine roots.

Seasonal maps of fine root distribution in 2006 (Fig. 3.3) and 2007 (Fig. 3.4) showed that grapevine roots were not uniformly distributed throughout plant growth stage and the soil profile, which was consistent with the results from statistical analysis of field data. Since the root distribution appeared to have large changes in the surface soil within a short distance, the edge effects of the root maps derived from the interpolation method suggest that grapevine roots have low densities in soil across an extensive lateral and vertical spread.

Distribution of fine roots sampled by destructive harvest

In 2006, two peaks of root density were found in 3-4 leaves and veraison periods, whereas in 2007 there were only small changes in root density during the growing season (Fig. 3.5a and 3.5b). Apart from the very small amount of young white fine roots found
during the growing season between 3-4 leaves and veraison, there was no other clear
evidence to confirm that a fall flush of root is common. The similarity between patterns of
fine root distribution in 2006 and 2007 was that the root density decreased after harvest,
which implies that roots typically do not grow during the dormant season. The fine roots
collected by soil cores showed a 10 x greater density than the root density found with the
destructive harvest method (Fig. 3.4), which suggests that the amounts of fine roots
collected by soil core method were sufficient to represent the whole plant fine roots for
further nutrient analysis even in the growth stage that the grapevine had lowest
production of fine roots.

Distribution of coarse roots

In this study, root density and root length density were determined from root
biomass and root length (Fig. 3.2) within a certain soil volume unit to characterize the
presence of coarse roots as a function of soil depth and distance from the trunk. Concord
coarse roots appeared to have density between 0.11-0.19 g/L soil and length density range
between 1.5 and 2.3 m/m³ (Table 3.3). In this regard, the root density seems to correspond
well with the root length density based on medium-high positive correlation, especially in
2006 when both density and length density at budbreak were higher than other growth
stages. During the growing season in 2007, root length density did not significantly differ
by growth stage whereas the density of coarse roots did. Root length density and root
density were correlated in both years (Fig. 3.6a and Fig. 3.6b), with R² 0.53 and 0.62 for
2006 and 2007, respectively, suggesting an intermediate relationship between root length
density and root density. More root parameters, for instance root diameter, might be
required for investigation to understand dynamics of the coarse root system.
Concord root distribution in relationship to irrigation furrow

The result of the fine root distribution analysis showed root response to long-term furrow irrigation with non-uniform distribution patterns that could extensively spread beyond the distance between plants (2.4 m) and rows (2.7 m) as well as toward 1 m soil depth. The widespread root system that develops under furrow irrigation may less depend on fertilizer management than a root system that is area confined due to irrigation (Atkinson, 1980) and the furrow irrigated vineyards may lead to inefficient control of plant growth with fertilizer and water use. Concord grape has high water demand compared to wine grapes (Reynolds et al., 2005). Hence, to ensure yield and quality of Concord grape growing in arid area like central Washington with furrow irrigation, it is important to supply adequate irrigation water to the root system.

CONCLUSION

Fine root distribution of Concord grape was strongly influenced by growth stage and soil depth but was not affected by distance from or direction around the trunk. Root densities at surface soil were higher than subsurface soil at every growth stage and surface soil within 120 cm of the trunk represented the area that had the highest root distribution. This suggested a basic pattern of fine roots where most of these roots were concentrated in the top 30 cm of soil and the root density was sharply reduced with depth and distance from the vine trunk. Understanding the fine root distribution in the subsurface soil is needed to show area of root contacts which can relate to the different mobilities of soil nutrients. Distribution of Concord fine roots and coarse roots varied slightly from one year to the next. Reasonable correlation between root length density and root density of coarse roots was found to support the fine root distribution pattern.
LITERATURE CITED


Table 3.1. Density (g/L soil) of Concord fine roots as affected by growth stage, soil depth, distance and direction around the trunk in 2006.

1 No significant differences by direction or distance at $P < 0.05$.

| Growth stage | Depth  |  | Direction
degree |  | Distance
cm |  | Average |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0°</td>
<td>45°</td>
<td>90°</td>
<td>135°</td>
<td>180°</td>
<td>225°</td>
</tr>
<tr>
<td>Winter</td>
<td>0-30 cm</td>
<td>0.25</td>
<td>0.23</td>
<td>0.24</td>
<td>0.35</td>
<td>0.28</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.13</td>
<td>0.17</td>
<td>0.12</td>
<td>0.15</td>
<td>0.12</td>
<td>0.22</td>
</tr>
<tr>
<td>Budbreak</td>
<td>0-30 cm</td>
<td>0.22</td>
<td>0.18</td>
<td>0.24</td>
<td>0.21</td>
<td>0.17</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.13</td>
<td>0.16</td>
<td>0.15</td>
<td>0.07</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>3-4 Leaves</td>
<td>0-30 cm</td>
<td>0.26</td>
<td>0.16</td>
<td>0.39</td>
<td>0.29</td>
<td>0.35</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.10</td>
<td>0.24</td>
<td>0.10</td>
<td>0.17</td>
<td>0.03</td>
<td>0.06</td>
</tr>
<tr>
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<td>0.12</td>
<td>0.16</td>
<td>0.27</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
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<td>0.06</td>
<td>0.04</td>
<td>0.16</td>
<td>0.08</td>
<td>0.06</td>
</tr>
<tr>
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<td>0.60</td>
<td>0.41</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.16</td>
<td>0.22</td>
<td>0.11</td>
<td>0.22</td>
<td>0.08</td>
<td>0.15</td>
</tr>
<tr>
<td>Harvest</td>
<td>0-30 cm</td>
<td>0.29</td>
<td>0.20</td>
<td>0.46</td>
<td>0.31</td>
<td>0.34</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.14</td>
<td>0.16</td>
<td>0.13</td>
<td>0.06</td>
<td>0.15</td>
<td>0.20</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>0-30 cm</td>
<td>0.22</td>
<td>0.27</td>
<td>0.22</td>
<td>0.26</td>
<td>0.19</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.10</td>
<td>0.14</td>
<td>0.09</td>
<td>0.07</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>$P$-value</td>
<td>&lt; 0.001</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>
Table 3.2. Density (g/L soil) of Concord fine roots as affected by growth stage, soil depth, distance and direction around the trunk in 2007.

1 No significant differences by direction or distance at $P < 0.05$.

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Depth</th>
<th>Direction$^1$</th>
<th>Distance$^1$</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$0^\circ$</td>
<td>$45^\circ$</td>
<td>$90^\circ$</td>
</tr>
<tr>
<td>Winter</td>
<td>0-30 cm</td>
<td>0.25</td>
<td>0.23</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.12</td>
<td>0.14</td>
<td>0.13</td>
</tr>
<tr>
<td>Budbreak</td>
<td>0-30 cm</td>
<td>0.23</td>
<td>0.18</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.11</td>
<td>0.12</td>
<td>0.08</td>
</tr>
<tr>
<td>3-4 Leaves</td>
<td>0-30 cm</td>
<td>0.18</td>
<td>0.15</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.09</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>Bloom</td>
<td>0-30 cm</td>
<td>0.18</td>
<td>0.17</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.11</td>
<td>0.25</td>
<td>0.11</td>
</tr>
<tr>
<td>Veraison</td>
<td>0-30 cm</td>
<td>0.26</td>
<td>0.18</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.13</td>
<td>0.11</td>
<td>0.13</td>
</tr>
<tr>
<td>Harvest</td>
<td>0-30 cm</td>
<td>0.25</td>
<td>0.26</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.12</td>
<td>0.08</td>
<td>0.10</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>0-30 cm</td>
<td>0.27</td>
<td>0.19</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>30-75 cm</td>
<td>0.16</td>
<td>0.15</td>
<td>0.17</td>
</tr>
</tbody>
</table>

$P$-value $< 0.001$
Table 3.3. Density (g/L soil) and length density (m/m\(^3\)) of Concord grape coarse roots at different growth stages in 2006 and 2007. The coefficient is for correlations between root density and length density.

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>2006</th>
<th></th>
<th>2007</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Density (g/L soil)</td>
<td>Length density (m/m(^3))</td>
<td>Density (g/L soil)</td>
<td>Length density (m/m(^3))</td>
</tr>
<tr>
<td>Winter</td>
<td>0.15 b</td>
<td>1.82 b</td>
<td>0.14 a</td>
<td>2.07</td>
</tr>
<tr>
<td>Budbreak</td>
<td>0.19 a</td>
<td>2.29 a</td>
<td>0.15 a</td>
<td>2.08</td>
</tr>
<tr>
<td>3-4 Leaves</td>
<td>0.13 b</td>
<td>1.76 b</td>
<td>0.11 b</td>
<td>1.64</td>
</tr>
<tr>
<td>Bloom</td>
<td>0.13 b</td>
<td>1.77 b</td>
<td>0.12 ab</td>
<td>1.71</td>
</tr>
<tr>
<td>Veraison</td>
<td>0.13 b</td>
<td>1.87 b</td>
<td>0.14 a</td>
<td>1.80</td>
</tr>
<tr>
<td>Harvest</td>
<td>0.11 b</td>
<td>1.55 b</td>
<td>0.13 ab</td>
<td>1.65</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>0.14 b</td>
<td>1.76 b</td>
<td>0.14 a</td>
<td>1.77</td>
</tr>
<tr>
<td>(P)-value</td>
<td>0.06</td>
<td>0.03</td>
<td>0.34</td>
<td>0.89</td>
</tr>
<tr>
<td>Correlation</td>
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<td></td>
<td>0.788</td>
<td></td>
</tr>
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</table>
Figure 3.1. Radial pattern of soil core sampling used in the study.
Figure 3.2. Concord horizontal root distribution in different growth stages: a) budbreak in 2006 and b) post-harvest in 2007. Each grid equal to 0.04 square meters.
Figure 3.3. Distribution of Concord grape fine roots in surface and subsurface soil depth collected at key growth stages in 2006. Analysis performed by using Inverse Distance Weighting (IDW) technique.
Figure 3.4. Distribution of Concord grape fine roots in surface and subsurface soil depth collected at key growth stages in 2007. Analysis performed by using Inverse Distance Weighting (IDW) technique.
Figure 3.5. Density (g/L soil) of Concord grape fine roots collected by a) soil core and b) destructive harvest methods at different key growth stages in 2006 and 2007.
Figure 3.6. Relationship between length density (m/m\(^3\)) and density (g/L soil) of Concord grape coarse roots in a) 2006 and b) 2007. \(P = 0.05\)

\[\text{Root}_{\text{length}}_{\text{density}}2006 = 0.89 + 6.73 \times \text{Root}_{\text{density}}2006\]
R-Square = 0.53

\[\text{Root}_{\text{length}}_{\text{density}}2007 = 0.20 + 12.08 \times \text{Root}_{\text{density}}2007\]
R-Square = 0.62
CHAPTER FOUR
MINERAL NUTRIENT PARTITIONING AND UPTAKE IN CONCORD GRAPE

INTRODUCTION

Concord grape (Vitis labruscana Bailey) is a cold climate juice grape bred in the New England region in predominantly acid soils derived from granite rocks. Current Concord production has been shifted to Washington State, where the predominantly calcareous or high pH soils could limit the availability of micronutrients, including Fe, Mn, Cu and Zn, since they tend to precipitate in soil solution in a carbonate-dominated environment (Epstein and Bloom, 2005). The goal of the Concord production is to produce the largest crop of mature fruit while maintaining vine performance. Balance of nutrients should be a high priority for vineyard management to accomplish this goal because there is a direct impact on how well the plants grow and juice quality.

Most studies report that grapevines take up the most N between bloom and veraison (Araujo and Williams, 1988; Lohnertz, 1991; Williams and Biscay, 1991; Mullins et al., 1992; Hanson and Howell, 1995; Bates et al., 2002). However, Conradie (1980, 1981, 1986) reported substantial N uptake after harvest in potted Chenin Blanc grown in the South Africa. He reported that N uptake during the postharvest period comprised 27% and 37% of the total annual N uptake (Conradie, 1980, 1986) and provided 60% of the stored N for the next season (Conradie, 1992).

Potassium uptake in whole vines was examined in several studies (Conradie, 1981; Williams and Biscay, 1991; Schreiner et al., 2006). These studies showed that the bulk of K uptake occurred between bloom and veraison. Of the three studies, only Conradie (1981) in South Africa and Schreiner et al. (2006) in Oregon examined P, Ca and Mg uptake in their whole vine studies. Their results agreed that the time of maximum Ca and
Mg uptake was between bloom and veraison. Schreiner et al. (2006) also reported that uptake for most macro elements were very closely related to canopy demand, whereas concentrations of micronutrients Fe, Mn, B, Zn, and Cu in whole vine varied highly from vine to vine.

Different nutrients have different mobilities in phloem and considerable variability in nutrient mobility exists among genotypes, nutritional status of plants and environmental influences (Welch, 1986; Marschner, 2002). N, P, K, Mg, S, Cl, Na can be classified as having high phloem mobility whereas Ca and B are known to be immobile in plant phloem. Heavy metals like Fe, Mn, Zn and Cu are immobile in phloem due to precipitation as oxides or hydroxides, or as carbonates when phloem sap is slightly alkaline (Epstein and Bloom, 2005). Phloem transport is important in nutrient cycling since uptake of phloem-mobile nutrients is driven by the nutrient requirement of plant organs. Nutrients with low mobility in the phloem can be transported through the xylem, where solute flow is driven by root pressure and water potential gradient.

Petiole analysis at bloom time is a useful tool that commercial grape growers use to determine nutrient status of a vine during the growing season for fertilizer management; however, wide year-to-year fluctuation has been reported for some nutrients, such as NO$_3^-$ and K (Christensen, 1984). Petiole nutrient results may not always reflect the nutrient status in other parts of the vine. Davenport et al. (2003) studied Concord grape response to variable rate fertilizer application by using soil and tissue samples to evaluate crop nutrient status. The research found that leaf blade nutrient concentration was more closely related to yield than petiole.

Grapevines have the capacity to store and re-allocate potentially large quantities of carbon and mineral nutrient reserves (Roubelakis-Angelakis and Kliwer, 1992), and there is a strong relationship between canopy demand and nutrient uptake (Schreiner et
al., 2006). Size and seasonal duration of vegetative, reproductive and storage sinks might vary with vine age (Borchert, 1976), but most of the studies on the partitioning of nutrient have been conducted in highly fertilized young vines (Conradie, 1980, 1986, 1991; Bates et al., 2002), making it impractical to predict nutrient requirements by mature vines. More quantitative information in mature grapevines is needed to produce a balance between vegetative and reproductive growth to ensure nutrient requirements are met for optimal production. This study investigates the uptake and redistribution of mineral nutrients in whole Concord grapes grown in a calcareous soil in Washington to understand nutrient movement between various plant tissues and plant nutrient uptake on growth and fruiting of grapevines. The objectives of this research were to (i) investigate seasonal patterns of macronutrients and micronutrient uptake and redistribution in Concord grapes, and (ii) identify the choice of tissue type (petiole or leaf blade) and the best time to sample grapevines for routine nutritional evaluation.

MATERIALS AND METHODS

The study was conducted in a 42 year-old own-rooted Concord single-curtain vineyard (lat 46° 15’ 59” N, long 119° 44’ 4” W) at the Irrigated Agriculture Research and Extension Center (IAREC) in Prosser, WA. The site is furrow irrigated and has been managed with uniform fertilization, water and pest management practices. The vineyard soil is Warden fine sandy loam (coarse-silty, mixed, superactive, mesic Xeric Haplocambid).

In 2006 and 2007 at winter pruning, bud break, 3-4 leaves, bloom, veraison, harvest, and post-harvest, four vines of uniform size were sampled at each growth stage and then destructively harvested at the comparable dimensions (2.4 x 2.7 x 1 m) of the
soil volume. Each vine was separated into trunk and cordon, coarse roots, fine roots, canes, shoot, leaf blades, petioles, shoot tips, and clusters.

Plant organs and tissues were dried, weighed, ground and analyzed for nutrient elements. Total N and C were analyzed using dry combustion (Yeomans and Bremner, 1991) with a LECO CNS 2000 (St. Joseph, MI). Analysis for P, K, Ca, Mg, Na, Cu, Fe, Mn, Zn and B was done by a commercial lab (Brookside Laboratories, Inc, OH) using ICP (Soltanpour et al., 1996). The samples were digested with nitric acid and hydrogen peroxide in a CEM microwave and analyzed on a Thermo Jarrell Ash 1100 ICP (Franklin, MA). Surface and subsurface soil samples were collected at each harvest point and analyzed to determine the availabilities of each element listed above using standard soil tests for Washington. Modeling nutrient movement throughout various plant tissue compartments and whole plant nutrient uptake were accomplished by calculating the content of each mineral element within each tissue (dry mass x concentration) at each destructive harvest.

RESULTS AND DISCUSSION

Dry matter and carbon

Dry weights of the whole vines ranged from 4,229 to 9,068 grams (Fig. 4.1). The highest biomass of the whole plants occurred at harvest, which was approximately double of that in winter, budbreak, 3-4 leaves, and bloom. Carbon concentration appeared to be significantly different among petioles (41-42% of dry weight), clusters (44-46%), and the other plant organs (46-48%; Fig. 4.2). This reflects the fact that the bulk of dry weight is cell wall, which consists mainly of cellulose, a carbohydrate polymer. Due to small variation of carbon concentrations in plant organs compared to other nutrients, seasonal pattern of carbon content (Fig. 4.2) was nearly analogous to the seasonal pattern of plant
dry weight. There was a significant decrease in total plant dry weight from budbreak (5,353 grams) to the 3-4 leaf stage (4,229 grams). The loss occurred mostly in trunk, cordons and coarse roots. This is probably because reserve C in the woody tissues was utilized to support the new growth of grapevines when the photosynthesis is still limited.

Nutrient uptake and partitioning

N, P and K

The total contents of N, P and K remained constant at the beginning of the season and a large drop in these nutrient contents in woody tissues occurred when the vines developed 3-4 leaves, suggesting that the new growth of grapevines depends on reserve nutrients in permanent structure (Fig. 4.2). Nitrogen concentrations in shoot tips decreased steadily after 3-4 leaves until the end of the season, whereas P and K contents showed a strong decrease at bloom and continued the decrease in later growth stages at a much slower rate. Such a dilution effect of N, P and K concentration in shoot tips might result from rapid leaf expansion and translocation of nutrients from shoot tips to leaf blades and clusters.

The whole vine N content gradually increased from 3-4 leaves to veraison before rapidly increased from veraison to harvest, while P and K contents showed a rapid increase from 3-4 leaves to harvest. At veraison, clusters contained about 40% of their total N demand and about 65% of their total P and K demand (Fig. 4.2). Nitrogen concentration in clusters rapidly decreased after bloom while P concentration slightly decreases and K concentration remained unchanged until the end of the season. After reaching the maximum in leaf blades at bloom, N concentration declined more slowly than P and K. The slow decrease in N concentration in shoot tips and leaf blades
compared with P and K concentration reveals that clusters were a strong sink for P and K whereas leaves and clusters are both important N sinks.

Potassium supply seems to have a dominant influence on fruit production whereas N supply dominated leaf development. Total N content per vine was significantly higher than K at every growth stage, except at harvest where total content of N and K were nearly equal at 55.1 g/vine and 64.6 g/vine, respectively (Table 4.1). This resulted from a high concentration of K (1.42 %) in the clusters, which was approximately two and a half times that of N (0.60 %; Fig 4.2).

Remobilization of N, P and K back to the woody tissues was observed after veraison. After reaching the lowest content in the trunk, cordon and coarse roots at veraison, woody tissue N, P and K content increased again until the end of season (Fig 4.2). In addition, there was a large drop in N, P and K concentrations in leaf blades and petioles post-harvest, indicating their remobilization back into the woody tissues. Nitrogen, P and K content in trunk, cordons and coarse roots post-harvest were lower than at the beginning of season. This suggests that movement of nutrient from annual tissues back to woody tissues continued after the post-harvest sample collection until the grapevines entered dormancy. The finding is consistent with Lohnertz (1991), who found that accumulation of N in permanent structures occurred from veraison to harvest, Alexander (1958), who found translocation of N back from leaves to woody tissues, and Schreiner et al. (2006), who found N losses between harvest and leaf fall. The result, however, contradicts Conradie (1980, 1981, 1986), who found substantial uptake of N, P and K at postharvest in young vines in South Africa.

Throughout the growing season, average total uptake per plant of N, P and K were 26.9 g, 6.3 g, and 41.8 g, respectively (Table 4.2). These 42 years old Concord grape took up twice as much N than 3 years old Concord grapes studies by Bates et al. (2002), who
reported 13 g N uptake during the growing season. The mature Concord grapevines appeared to have considerably higher N, P and K uptake when compared with 8 g N, 1.5 g P, and 19 g K uptake from budbreak through leaf fall in 23 years old Pinot Noir vines (Schreiner et al., 2006) and 18 g N and 25 g K uptake in 20 years old Cabernet Sauvignon vines during the same time frame (Williams and Biscay, 1991). Hence, the differences in vine age, size, and species (vinifera vs labruscana) seem to have major impacts on nutrient uptake since these 42 years old Concord grapevines were about 3 times larger than the juvenile Concords reported by Bates et al. (2002) and at least 2 times larger in vine size and 3 times larger in crop level compared with the 20 year old Cabernet Sauvignon (Williams and Biscay, 1991).

Differences in timing of nutrient uptake between studies were observed. Approximately 95% of the N uptake in mature Concord grape occurred between bloom and harvest (Table 4.2), which differs from the other reported findings. Conradie (2005) found remarkably consistent N uptake (10-35%) by 2 years old Chenin Blanc vines occurred in each growth stage throughout the growing season. Schreiner et al. (2006) found 87% N uptake by 23 years old Pinot Noir occurred between budbreak to veraison, Williams and Biscay (1991) found 86% N uptake by 18 years old Cabernet Sauvignon occurred between bloom and veraison, and Hanson and Howell (1995) found 60% N uptake by 10 years old Concord grapevines occurred between bloom and veraison. On the other hand, the highest uptake of P and K occurred between bloom and veraison, which agrees with previous studies (Conradie, 1981; Williams and Biscay, 1991; Schreiner et al., 2006).

Others have found that peak N uptake occurred before veraison but in this study significant N uptake occurred both before and after veraison. The differences in timing of majority N uptake are probably because with higher proportion of vine mass in woody
tissues, the mature vines can rely more on nutrients reserves during the early part of the season. In addition, bigger canopy and higher crop yield of Concord grapes (typically less than 8 Mg/ha for wine grape and over 20 Mg/ha for Concord) might intensify the grapevine mechanism to have prolonged N uptake period during active vine growth. Heavy N uptake between veraison and harvest resulted from the newly absorbed N that was not only partitioned into leaves and clusters but also restored to woody tissues. To this end, N appeared to be mainly partitioned among woody tissues (33%), leaves and shoot tips (27%) and clusters (34%) at harvest (Fig. 4.2).

It can be implied from the path of nutrient movement that fertilizers, if needed, should be applied before bloom, but not before bud break since the grape vine has no need at this stage and excessive rainfall may cause unwanted leaching of soluble nutrients. Split-application of fertilizers could enhance efficiency of nutrient use in growth and production. In addition, fertilization is not required at postharvest for this crop in cool climate regions, as uptake does not occur after harvest.

**Mg and Ca**

Throughout the growing season, average total uptake per plant of Ca and Mg were 31.3 g and 5.7 g, respectively (Table 4.2). Although Mg is classified as a phloem mobile nutrient, in Concord grape the accumulation pattern of Mg almost paralleled Ca. After highest uptake occurred from bloom to veraison (Table 4.2), the whole vine Ca and Mg contents still progressively increased until reaching the highest content at harvest. In particular, Ca and Mg concentrations in the cluster decreased after bloom while Ca concentration in leaf blades, petioles, and shoot tips increased from bloom to post-harvest. Magnesium increased only in petiole and remained constant in leaf blades and shoot tips. Calcium and Mg concentrations in leaf blades, shoot tips and petioles did not
decline after harvest as occurred with N, P and K. This indicates that neither Mg nor Ca migrated back from leaves into woody tissues. Although the trends of nutrient uptake and accumulation are alike, major changes of Ca or Mg content occurred in different vine tissues. Apart from the greatest quantity found in trunk and cordon, the major change of Mg was located in leaves and clusters whereas for Ca major changes occurred in the coarse roots. Mg content in trunk, cordons and coarse roots at post-harvest was lower than at the beginning of season while the change in Ca content was not significant. This is probably because Mg remobilized back to woody tissues after harvest until the grapevines entered dormancy while this movement did not occur in Ca due to its very low phloem mobility.

This mature Concord grapevine had a similar Mg uptake, but three times higher Ca uptake, than the 23 years old Pinot Noir vines reported by Schreiner et al. (2006), who reported approximately 10 g Ca and 4.5 g Mg uptake per vine during the growing season. Likely reasons for this considerable difference in the amount of Ca uptake is not only the age of the Concord grapevines but also higher Ca available in soil since the Concord grapevines were grown in fine sandy loam, pH 7.8-8.4, with average 309 meq.kg⁻¹ Ca whereas the Pinot Noir vines were grown in silty clay loam, pH 5.3-5.6, with average 28.2 meq.kg⁻¹ Ca.

It is not always the case that N is always the most abundant mineral nutrient in the plant. These 42 years old grapevines were found to have a higher total Ca content than N content throughout growing season (Table 4.1). Woody tissues such as trunk, cordons, and coarse roots had higher content of Ca than N at every growth stage, whereas annual tissues such as shoot tips, leaf blades, and clusters showed higher content of N than Ca at bloom. However, N content in the annual tissues were very close to that of Ca from veraison to harvest, and were only half of Ca at post-harvest since N clearly migrated
back to the woody tissues before leaf fall. The amount of N and Ca in woody tissues (13 g N and 20 g Ca) and leaf blade (10 g N and 11 g Ca) at veraison in this study was consistent with the finding of Schreiner et al. (2006), who reported approximately 14 g N and 19 g Ca in woody tissues and approximately 10 g N and 8 Ca in leaf blades of Pinot Noir vines at veraison.

The reason for high Ca accumulation over time in the plant is that higher plants appear to regulate differences between the natural abundance of Ca and the very low Ca requirement by controlling the distribution of Ca within the cell (Marschner, 1995). Calcium oxalate (CaOx) crystal deposition can occur within the vacuoles of cells (Kinzel, 1989) or associated with the cell wall (Demarty et al., 1984), which is the main component of plant dry weight. In other words, the annual increase in permanent tissue biomass resulted in increased vine Ca content.

Micronutrients

From one year to the next, seasonal patterns of micronutrient concentrations varied considerably as to which organ and growth stage they attained the highest concentration. Leaf blades, shoot tips and petioles showed highest concentration of B at bloom and showed highest concentration of Mn at harvest, whereas Fe, Cu and Zn showed highest concentration in fine roots where values fluctuated over time each year (Fig. 4.3). The result is consistent in general with the finding of Schreiner et al. (2006) who reported that micronutrient concentrations in various organs of the whole vine varied highly over time.

Considering the total content of micronutrients in the whole vine (Fig. 4.4), the trend of seasonal changes of B and Mn content in 2006 were similar to those in 2007. Apparently, the highest uptake of B (90%) occurred from bloom to veraison whereas the
highest uptake of Mn (95 %) occurred from bloom to harvest (Table 4.2). In both years at 3-4 leaves, a large drop of B content occurred in coarse roots whereas a slight decrease occurred in the trunk and cordons, suggesting that reserve B for the new growth of grapevines was translocated from coarse roots more than from the trunk and cordons. Conversely, Mn content in the trunk, cordons and coarse roots continuously decreased from the beginning of season until reaching the lowest at veraison, and increased again in the next growth stage. This reveals that Mn was remobilized from permanent structures to support the new growth of grapevine annual tissues such as leaves. Movement of B and Mn between woody tissues and annual tissues at the beginning of the season was consistent with what happened at the end of season when Mn was restored to the trunk, cordons and coarse roots at harvest while B seems to move only into the coarse roots post-harvest (Fig. 4.4).

Concentrations of B and Mn in the annual tissues changed with different stages of vine physiological development. After the highest concentration of B in leaves and clusters occurred at bloom (Fig. 4.3), the concentration of B in clusters sharply decreased while that of leaf blades, petioles, and shoot tips slightly decreased in later growth stages. In contrast, Mn concentrations in leaves and cluster drastically increased from 3-4 leaves to harvest. Hence, during the active vine growth, Mn seems to have a higher accumulation rate in leaves than B, whereas a higher proportion of B was translocated to clusters compared to Mn (Fig. 4.4). However, after harvest concentrations of B and Mn in leaf blades, petioles and shoot tips remained unchanged until the end of the season, indicating that neither of them migrated back from leaves into woody tissues. Boron is recognized as being immobile in the phloem of many plant species, however, these result showed that B had moderate phloem mobility in Concord grapevines, which agrees with the other reported findings. Brown and Hu (1998) found that B in fruit, stone fruit, and
nut tree crops was highly phloem mobile, Hanson (1991) found that the supply of B needed for reproductive growth in fruit tree crops was more than that needed for vegetative growth, and O'Kelley (1957) found that B is required to support carbohydrate metabolism, sugar translocation, and pollen tube germination.

Fe, Cu, and Zn content appeared to have an obvious year-to-year difference in seasonal change due to their fluctuating contents in various organs (Fig. 4.4), especially fine roots that showed their highest concentrations at every growth stage (Fig. 4.3). Total Fe content in the whole vines was highest at veraison in both years but the Fe content in 2007 appeared to be higher in woody tissues and clusters and lower in leaf blades and shoot tips when compared to 2006. This resulted from different tissue concentrations rather than changes in vine biomass. Iron concentrations were highest and most dynamic in fine roots, leaf blade and shoot tips.

In 2006, both Cu and Zn showed the first peak content at budbreak (Fig. 4.4) resulting from high concentrations in trunk, cordons and fine roots (Fig. 4.3). Total content of Cu and Zn was lowest between 3-4 leaves and bloom because of decreased concentration in trunk and cordons. The second peak content of Cu occurred at harvest, with a considerable amount of Cu accumulated in clusters whereas that of Zn occurred at veraison with elevated concentrations in the trunk and cordons. Seasonal change of Cu and Zn content in 2007 showed only one peak at harvest. The amount of Cu and Zn in the trunk and cordon at each growth stage was more consistent than in 2006, and accumulated Cu and Zn in clusters became pronounced by harvest. In 2007, highest uptake of Cu and Zn likely occurred from veraison to harvest, which were approximately 20 mg and 30 mg per vine, respectively (Fig. 4.4).

Different nutrients appeared to have different tissues where the majority of changes in content occurred. Almost half of B, Fe, Mn, and Cu contents were in leaf
blades and clusters from veraison to harvest, whereas up to 77% of Zn content was located in the trunk and cordon, and about 15% of Fe and Cu were found in fine roots throughout the growing season. While the changes in Fe, Mn and Zn concentrations in various parts were similar between years, higher concentrations were found in the clusters in 2007 as compared to 2006. All micronutrients except Cu that showed dissimilar results between years, seeming to have lower contents in trunk, cordons and coarse roots at post-harvest than what was measured at winter. This suggests that their remobilization back to woody tissues might occur after harvest until the grapevines enter dormancy.

Difference between canopy and root development

Apart from a very small amount of young white fine roots found during the growing season between 3-4 leaves and veraison, there was no other clear evidence of a change in fine root biomass to confirm that a fall flush of root growth is common. However, a significant decrease in fine root biomass was found after harvest, which implies that roots typically do not grow during the dormant season. Hence, root growth, as well as root nutrient acquisition and competency in the study, was inferred from nutrient contents in fine roots and coarse roots, according to Volder et al. (2005), who found that the decline in both N uptake and root respiration corresponded with a strong decline in root N concentration.

Highest contents of N, P, and K in shoot tips occurred from bloom to veraison, and those in shoots, leaf blades, petioles and clusters occurred from veraison to harvest (Fig. 4.5). Nitrogen, P and K contents in coarse roots were lowest from veraison to harvest. In fine roots, N and K contents were very similar from winter to bloom and sharply declined at veraison and later growth stages, whereas P content showed non-significant difference throughout the season. Hence, the nutrient decline in roots suggests...
nutrient translocation out of the roots and competition for nutrients between roots developing canopy and fruit production.

Similar activities were found in other nutrients during the active vine growth. Highest contents of Ca and Mg in shoots, shoot tips and leaf blades occurred from veraison to post-harvest, which corresponds to the period of lowest contents in coarse and fine roots. On the other hand, B and Mn content in coarse and fine roots significantly decreased at the 3-4 leaf stage and gradually increased at later growth stages, while B and Mn contents in shoot tips sharply increased at 3-4 leaves and reached the highest at veraison, while shoots, leaf blades and cluster reached the highest B and Mn content at harvest.

Total contents of nutrients and their correlations

Total content of all nutrients tended to increase from winter to budbreak and again from 3-4 leaves to veraison or harvest (Table 4.1), which implies a high nutrient requirement to support growth at budburst and production during fruit ripening.

Strong correlations were found between total content of the individual nutrients, except for Fe and Zn where the $R^2$ values were $< 0.50$ (Table 4.3). This emphasizes the seasonal pattern of the total content in the whole vine that most nutrients shared: the total nutrient contents remained constant at the beginning of the season indicating the importance of stored nutrient reserves in permanent structure, the total nutrient content significantly increased after bloom, indicating nutrient uptake from the soil commenced; a progressive increase until reaching a peak at harvest, followed by a significant decrease post-harvest due to nutrient losses through fruit harvested and preparation for dormancy. In contrast, the lack of strong correlations between Fe and the other nutrients as well as
Zn and the other nutrients reflect the variation in total Fe and Zn content in the whole vines throughout the growing season.

Leaf blade and petiole analysis

Concentration of N, P, K, B, Cu and Zn in leaf blades and petiole were highest at bloom and sharply reduced by veraison, then slowly decreased until the end of season (Table 4.4). Such a dilution effect of nutrient concentration in leaf blades might result from rapid leaf expansion and translocation of nutrients from leaves to clusters. In contrast, concentrations of Ca and Mn in leaf blades and petioles were highest post-harvest, probably because with low mobilities in plant phloem they became immobile once deposited in individual leaves and continuously increased in concentration throughout the season.

Relationships between leaf blade and petiole concentrations appeared to be strong for N, K, Ca, Mn and Cu, and intermediate for P and B (Table 4.5). Weak relationship found in correlation between leaf blades and petioles of Fe (R² = 0.043), Mg (R² = 0.127) and Zn (R² = 0.030) suggests antagonistic phenomena, previously demonstrated by Smith and Cheng (2006) who reported higher blade than petiole Fe concentration, and Atalay (1978) and Christensen (2005) who reported higher petiole than blade Zn concentrations from bloom to veraison, whereas higher petiole than blade Mg concentration are not reported else where.

Leaf blades showed higher concentrations of N, Ca, Mn, Cu and Fe than petioles, whereas those of K, P, Mg, B and Zn were higher in petioles than leaf blades (Table 4.4). This is probably because analysis of petioles indicates the current movement of nutrient toward the leaf blade and therefore was sensitive to the status of mobile nutrients such as K, P and Mg. In addition, when compared with petiole, there was less fluctuation of P,
Mg, and Zn concentrations in the blade throughout the growing season. Thus, blades seem to better indicate overall status of nutrients, including mobile nutrients. Hence, when consider a convenient and economical way for sampling only one plant part for nutrient analysis, the whole leaf seems to be the best to represent nutrient status.

It would be most accurate to sample leaves at both bloom and veraison to evaluate the nutrient status. Leaf analysis at bloom reflects nutrient remobilized from storage reserves which allow fertilizer decision to be made within the current season and to correct nutritional problems for the current crop. Leaf analysis at veraison reflects nutrient supply for the most of season in which change of the mineral nutrients compared with bloom is useful for estimating fertilizer required for split application and for planning the next season’s fertilization. In this regard, good understanding of vine physiological development is important for leaf sample timing. Leaf samples taken between late bloom and early veraison may lead to data variation that is not because of excessive nutrients or nutrient deficiencies but because of rapid nutrient change in leaf tissues and substantial nutrient uptake from the soil.

Soil nutrients

Nutrient availabilities in soil did not show clear seasonal trend, however, apart from nitrate which is very soluble, significant differences were found between availability of all nutrients at surface and subsurface soils (Table 4.6). Most nutrient concentrations in surface soil were higher than subsurface soil, except Ca and Mg. In this regard, highly accumulated Ca in permanent structure of the Concord grape reflects the high CaCO$_3$ in this vineyard soil (Warden fine sandy loam). The reason why high contents of Ca and Mg found in subsurface soil is probably due to calcification process and weathering of basalt contained in the vineyard soil. In addition, difference between surface and subsurface soil
pH might resulted in greatly varies of nutrient availability around surface area of the root system. This could be a reason for high fluctuations of Fe Cu and Zn contents in fine roots.

CONCLUSION

Dry weights of the whole vines ranged from 4,229 to 9,068 grams. The highest biomass of the whole plants occurred at harvest, which was approximately double of that in winter, budbreak, 3-4 leaves, and bloom. These 42 years old grapevines were found to have Ca as the most abundant mineral nutrient, followed by N and K. Between veraison and harvest, different tissues in which the majority of changes in Ca, N and K contents became obvious. Half of the Ca was in woody tissues, up to 65% of N content was in annual tissues and up to 70% of K was in the clusters. In this regard, highly accumulated Ca in permanent structure of the Concord grape reflects the high CaCO₃ in the vineyard soils, and resulted in the whole vine highest content of Ca throughout growing season.

On the other hand, during the growing season, major changes of P content occurred in cluster whereas the major change of Mg occurred in leaves and clusters. For micronutrients, almost half of the B, Fe, Mn, and Cu contents were located in leaf blades and clusters from veraison to harvest, whereas up to 77% Zn was located in trunk and cordon, and about 15% of Fe and Cu were found in fine roots throughout the growing season.

Seasonal dynamics of nutrient contents, except those of Fe, Cu and Zn which highly fluctuated between years, shared a common pattern. Translocation of nutrients from woody tissues to actively growing organs was found at the beginning of the season. Majority uptake of N, Ca and Mn from soil occurred from bloom to harvest while those of P, K, Mg and B occurred from bloom to veraison. Restoration of N, P, K, Ca, Mg, B
and Mn back to woody tissues occurred after veraison until before leaf senescence with no more nutrient uptake, plus remobilization of N, P and K from leaves back into the woody tissues was observed before leaf senescence.

Likely reasons for the majority N uptake occurring at veraison and continuing through harvest is not only high proportion of woody tissues that the mature vines can rely on for nutrients reserves at the early season, but also big canopy and high crop level. In addition, the long period of fruit ripening and short post-harvest period in this cool climate seem to intensify grapevine mechanism of having both a prolonged uptake period and rapid nutrient remobilization back to woody tissues during active vine growth. In this regard, the whole leaf seems to be the best tissue to represent vine’s nutrient status. It would be most accurate when leaf samples are taken at both bloom and veraison because leaf analysis at bloom reflects nutrient remobilized from storage reserves which facilitate fertilizer decision for the current season whereas veraison reflects nutrient supply for the most of season and useful for estimating fertilizer, if required for split application, and for planning the next season’s fertilization.
LITERATURE CITED


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Table 4.1. Average total contents of macronutrients (g/whole plant) and micronutrients (mg/whole plant) of the whole Concord grape plant destructively harvested at different growth stages from 2006-2007 (n = 8). Total content means with different letters in the same nutrient are significantly different (α=0.01).

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Macronutrient (g/whole plant)</th>
<th>Micronutrient (mg/whole plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
<td>N</td>
</tr>
<tr>
<td>Winter</td>
<td>2510.02 c</td>
<td>28.76 cd</td>
</tr>
<tr>
<td>Budbreak</td>
<td>2503.01 c</td>
<td>31.58 c</td>
</tr>
<tr>
<td>3-4 Leaves</td>
<td>2005.12 d</td>
<td>24.22 d</td>
</tr>
<tr>
<td>Bloom</td>
<td>2351.35 cd</td>
<td>30.35 cd</td>
</tr>
<tr>
<td>Veraison</td>
<td>3110.32 b</td>
<td>41.69 b</td>
</tr>
<tr>
<td>Harvest</td>
<td>4245.65 a</td>
<td>55.12 a</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>2723.87 bc</td>
<td>32.03 c</td>
</tr>
</tbody>
</table>

Level of significance (P-value) by growth stage

|              | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

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Table 4.2. Seasonal uptake of nutrient in 2006 and 2007 calculated from the change in total vine content of each nutrient between growth stages (n = 8). nd: not determined due to high fluctuation throughout the growing season.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Average total uptake per plant</th>
<th>% of total vine uptake</th>
<th>Level of significance (P-value) by growth stage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>3-4 Leaves to bloom</td>
<td>Bloom to veraison</td>
</tr>
<tr>
<td>N</td>
<td>26.9 g</td>
<td>5 b</td>
<td>51 a</td>
</tr>
<tr>
<td>P</td>
<td>6.3 g</td>
<td>16 b</td>
<td>59 a</td>
</tr>
<tr>
<td>K</td>
<td>41.8 g</td>
<td>14 b</td>
<td>65 a</td>
</tr>
<tr>
<td>Ca</td>
<td>31.3 g</td>
<td>5 b</td>
<td>57 a</td>
</tr>
<tr>
<td>Mg</td>
<td>5.7 g</td>
<td>2 b</td>
<td>79 a</td>
</tr>
<tr>
<td>B</td>
<td>54.1 mg</td>
<td>3 b</td>
<td>90 a</td>
</tr>
<tr>
<td>Fe</td>
<td>316.8 mg</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Mn</td>
<td>69.9 mg</td>
<td>5 b</td>
<td>44 a</td>
</tr>
<tr>
<td>Cu</td>
<td>18.4 mg</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Zn</td>
<td>29.4 mg</td>
<td>nd</td>
<td>nd</td>
</tr>
</tbody>
</table>
Table 4.3. Coefficients of determination ($R^2$; $P < 0.001$) between average total contents of all nutrients of the whole Concord grape plant throughout the growing season of 2006 and 2007 ($n = 8$).

<table>
<thead>
<tr>
<th>Coefficient of determination ($R^2$)</th>
<th>N (g/vine)</th>
<th>P (g/vine)</th>
<th>K (g/vine)</th>
<th>Ca (g/vine)</th>
<th>Mg (g/vine)</th>
<th>B (mg/vine)</th>
<th>Fe (mg/vine)</th>
<th>Mn (mg/vine)</th>
<th>Cu (mg/vine)</th>
<th>Zn (mg/vine)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (g/vine)</td>
<td>-</td>
<td>0.852</td>
<td>0.839</td>
<td>0.750</td>
<td>0.839</td>
<td>0.841</td>
<td>0.359</td>
<td>0.723</td>
<td>0.743</td>
<td>0.240</td>
</tr>
<tr>
<td>P (g/vine)</td>
<td>0.852</td>
<td>-</td>
<td>0.901</td>
<td>0.691</td>
<td>0.824</td>
<td>0.882</td>
<td>0.389</td>
<td>0.645</td>
<td>0.658</td>
<td>0.265</td>
</tr>
<tr>
<td>K (g/vine)</td>
<td>0.839</td>
<td>0.901</td>
<td>-</td>
<td>0.686</td>
<td>0.799</td>
<td>0.904</td>
<td>0.378</td>
<td>0.706</td>
<td>0.610</td>
<td>0.207</td>
</tr>
<tr>
<td>Ca (g/vine)</td>
<td>0.750</td>
<td>0.691</td>
<td>0.686</td>
<td>-</td>
<td>0.920</td>
<td>0.767</td>
<td>0.311</td>
<td>0.876</td>
<td>0.746</td>
<td>0.212</td>
</tr>
<tr>
<td>Mg (g/vine)</td>
<td>0.839</td>
<td>0.824</td>
<td>0.799</td>
<td>0.920</td>
<td>-</td>
<td>0.834</td>
<td>0.358</td>
<td>0.830</td>
<td>0.762</td>
<td>0.277</td>
</tr>
<tr>
<td>B (mg/vine)</td>
<td>0.841</td>
<td>0.882</td>
<td>0.904</td>
<td>0.767</td>
<td>0.834</td>
<td>-</td>
<td>0.514</td>
<td>0.757</td>
<td>0.681</td>
<td>0.307</td>
</tr>
<tr>
<td>Fe (mg/vine)</td>
<td>0.359</td>
<td>0.389</td>
<td>0.378</td>
<td>0.311</td>
<td>0.358</td>
<td>0.514</td>
<td>-</td>
<td>0.360</td>
<td>0.402</td>
<td>0.191</td>
</tr>
<tr>
<td>Mn (mg/vine)</td>
<td>0.723</td>
<td>0.645</td>
<td>0.706</td>
<td>0.876</td>
<td>0.830</td>
<td>0.757</td>
<td>0.360</td>
<td>-</td>
<td>0.632</td>
<td>0.176</td>
</tr>
<tr>
<td>Cu (mg/vine)</td>
<td>0.743</td>
<td>0.658</td>
<td>0.610</td>
<td>0.746</td>
<td>0.762</td>
<td>0.681</td>
<td>0.402</td>
<td>0.632</td>
<td>-</td>
<td>0.359</td>
</tr>
<tr>
<td>Zn (mg/vine)</td>
<td>0.240</td>
<td>0.265</td>
<td>0.207</td>
<td>0.212</td>
<td>0.277</td>
<td>0.307</td>
<td>0.191</td>
<td>0.176</td>
<td>0.359</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 4.4. Average concentration of each nutrient in leaf blade and petiole collected from growth stages bloom to post-harvest in 2006 and 2007 (n = 8). Concentrations with different letters in the same plant organ are significantly different (α=0.01).

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Macronutrient (%)</th>
<th>Micronutrient (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>P</td>
</tr>
<tr>
<td>Leaf blade</td>
<td>Petiole</td>
<td>Leaf blade</td>
</tr>
<tr>
<td>Bloom</td>
<td>2.73 a</td>
<td>1.04 a</td>
</tr>
<tr>
<td>Veraison</td>
<td>2.14 b</td>
<td>0.55 bc</td>
</tr>
<tr>
<td>Harvest</td>
<td>1.95 c</td>
<td>0.62 b</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>1.50 c</td>
<td>0.50 c</td>
</tr>
</tbody>
</table>

Level of significance (P-value) by growth stage

| Bloom        | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 0.723 | <0.0001 |
| Veraison     | 0.004   | <0.0001 | <0.0001 | 0.122   | <0.0001 | <0.0001 | <0.0001 | 0.046 | 0.018   |
| Harvest      | 0.046   | 0.018   | 0.046   | 0.018   | 0.046   | 0.018   | 0.046   | 0.018 | 0.046   |
| Post-harvest | 0.046   | 0.018   | 0.046   | 0.018   | 0.046   | 0.018   | 0.046   | 0.018 | 0.046   |
Table 4.5. Coefficients of determination ($R^2$) between average nutrient concentrations in leaf blade and petiole collected from growth stages bloom to post-harvest in 2006 and 2007 ($n = 8$).

<table>
<thead>
<tr>
<th>Nutrient concentration in leaf blade vs petiole</th>
<th>Coefficient of determination ($R^2$)</th>
<th>Level of significance ($P$-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (%)</td>
<td>0.757</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P (%)</td>
<td>0.587</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>K (%)</td>
<td>0.910</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Ca (%)</td>
<td>0.817</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mg (%)</td>
<td>0.127</td>
<td>0.046</td>
</tr>
<tr>
<td>B (ppm)</td>
<td>0.444</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fe (ppm)</td>
<td>0.043</td>
<td>0.256</td>
</tr>
<tr>
<td>Mn (ppm)</td>
<td>0.716</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Cu (ppm)</td>
<td>0.799</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Zn (ppm)</td>
<td>0.030</td>
<td>0.346</td>
</tr>
</tbody>
</table>
Table 4.6. Average mineral nutrient availabilities in both surface and subsurface soils at different growth stages of Concord grape from 2006 to 2007 (n = 8).

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Soil depth (cm)</th>
<th>NO$_3^-$ (mg/kg)</th>
<th>NH$_4^+$ (mg/kg)</th>
<th>P (mg/kg)</th>
<th>K (meq/kg)</th>
<th>Ca (meq/kg)</th>
<th>Mg (meq/kg)</th>
<th>B (mg/kg)</th>
<th>Fe (mg/kg)</th>
<th>Mn (mg/kg)</th>
<th>Cu (mg/kg)</th>
<th>Zn (mg/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Budbreak</td>
<td>0-30</td>
<td>1.88</td>
<td>2.10</td>
<td>20.50</td>
<td>9.63</td>
<td>258.68</td>
<td>30.79</td>
<td>0.75</td>
<td>39.50</td>
<td>46.38</td>
<td>2.78</td>
<td>8.84</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>1.18</td>
<td>1.26</td>
<td>3.50</td>
<td>3.23</td>
<td>341.06</td>
<td>34.31</td>
<td>0.40</td>
<td>30.50</td>
<td>16.63</td>
<td>2.32</td>
<td>1.20</td>
</tr>
<tr>
<td>3-4 Leaves</td>
<td>0-30</td>
<td>2.20</td>
<td>1.66</td>
<td>13.25</td>
<td>9.05</td>
<td>285.11</td>
<td>31.18</td>
<td>0.76</td>
<td>35.50</td>
<td>39.50</td>
<td>2.82</td>
<td>5.13</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>1.91</td>
<td>1.20</td>
<td>8.75</td>
<td>4.69</td>
<td>363.43</td>
<td>34.74</td>
<td>0.51</td>
<td>28.88</td>
<td>20.38</td>
<td>2.45</td>
<td>2.12</td>
</tr>
<tr>
<td>Bloom</td>
<td>0-30</td>
<td>2.51</td>
<td>1.54</td>
<td>10.50</td>
<td>7.77</td>
<td>287.82</td>
<td>31.68</td>
<td>0.65</td>
<td>37.13</td>
<td>41.25</td>
<td>2.88</td>
<td>7.96</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>1.98</td>
<td>1.20</td>
<td>7.42</td>
<td>5.03</td>
<td>328.64</td>
<td>35.25</td>
<td>0.51</td>
<td>34.00</td>
<td>26.88</td>
<td>2.54</td>
<td>3.97</td>
</tr>
<tr>
<td>Veraison</td>
<td>0-30</td>
<td>5.20</td>
<td>3.28</td>
<td>16.38</td>
<td>8.95</td>
<td>261.96</td>
<td>30.44</td>
<td>0.76</td>
<td>38.00</td>
<td>45.88</td>
<td>3.16</td>
<td>6.59</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>3.39</td>
<td>3.18</td>
<td>8.13</td>
<td>4.04</td>
<td>343.44</td>
<td>35.76</td>
<td>0.52</td>
<td>30.13</td>
<td>23.25</td>
<td>2.67</td>
<td>1.77</td>
</tr>
<tr>
<td>Harvest</td>
<td>0-30</td>
<td>5.30</td>
<td>1.59</td>
<td>9.00</td>
<td>8.33</td>
<td>278.01</td>
<td>31.75</td>
<td>0.64</td>
<td>35.00</td>
<td>41.25</td>
<td>2.63</td>
<td>5.79</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>2.89</td>
<td>1.33</td>
<td>5.50</td>
<td>3.72</td>
<td>331.59</td>
<td>35.51</td>
<td>0.41</td>
<td>30.50</td>
<td>20.75</td>
<td>1.98</td>
<td>1.33</td>
</tr>
<tr>
<td>Post-harvest</td>
<td>0-30</td>
<td>4.63</td>
<td>2.66</td>
<td>22.25</td>
<td>10.01</td>
<td>274.87</td>
<td>32.26</td>
<td>0.72</td>
<td>35.75</td>
<td>40.63</td>
<td>2.68</td>
<td>6.08</td>
</tr>
<tr>
<td></td>
<td>30-75</td>
<td>2.75</td>
<td>2.18</td>
<td>7.13</td>
<td>4.21</td>
<td>354.26</td>
<td>36.18</td>
<td>0.50</td>
<td>28.38</td>
<td>18.00</td>
<td>2.21</td>
<td>2.07</td>
</tr>
</tbody>
</table>

Level of significance (P-value) by soil depth

|                | 0.019 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
Figure 4.1. Seasonal change in dry weight (grams) in various organs and in the whole Concord grape plants from 2006 to 2007 (n = 8). Different letters on the graph indicate statistically different dry weight of the whole plant by growth stage ($\alpha=0.05$).
Figure 4.2. Average seasonal change in concentrations and contents of carbon and macronutrients in various organs of Concord grape from 2006 to 2007 (n = 8). Different letters on the content graphs indicate significantly different nutrient content of the whole plant by growth stage (α=0.05).
Figure 4.3. Average seasonal change in micronutrient concentrations in various organs of Concord grape plant in 2006 and 2007 (n = 8).
Figure 4.4. Average seasonal change in micronutrient contents in various organs and the whole Concord grape plant in 2006 and 2007 (n = 8). Different letters on each graph indicate significantly different content of the whole plant by growth stage (α=0.05).
Figure 4.5. Average seasonal change in N, P, K, Ca, Mg, B and Mn content in coarse roots, fine roots, shoot tips, shoots, leaf blades and clusters in 2006 and 2007 (n = 8).
CHAPTER FIVE

SUMMARY AND CONCLUSIONS

The objectives of this research were to (i) develop methodology for root and tissue sampling to monitor the nutrient status of Concord grapes, (ii) investigate seasonal distribution pattern of Concord grape fine roots, (iii) investigate seasonal pattern of macronutrients and micronutrient uptake and redistribution in Concord grapes, and (iv) identify the choice of tissue type (petiole or leaf blade) and the best time to sample grapevines for routine nutritional evaluation. The research was conducted on a 42 year-old own-rooted Concord vineyard. The site is furrow irrigated fine sandy loam and has been managed with uniform fertilization, water and pest management practices.

To develop methodology for root sampling, in 2005 at 650° C degree days two different sample interval spacings (20, 60, 120 cm and 50, 100, 150 cm in a radial pattern around the vine trunk) were compared on three vines to determine the extent that represented the highest density of fine roots. The result showed that density of fine roots was higher when sample spacing was closer to the vine trunk, therefore, fine root sampling pattern at 20, 60, and 120 cm from trunk was chosen for the study in 2006 and 2007. Each soil core in subsequent collections were washed and weighed individually to better illustrate root distribution patterns.

To develop methodology for tissue sampling, in 2006 four vines of uniform size were destructively harvested at seven key growth stages: winter pruning, bud break, 3-4 leaves, bloom, veraison, harvest, and post-harvest. Separated plant tissues were dried, weighed, ground and analyzed for C, N, P, K, Ca, Mg, Cu, Fe, Mn, Zn and B. The result showed similar nutrient concentrations between fruiting shoots and vegetative shoots as well as between trunk and cordon throughout the growing season, suggesting that the
most efficient way to classify the whole plant tissues for 2007 was to scale down from 14 to 9 tissue types including woody tissues, canes, coarse roots, fine roots, shoots, leaf blades, petioles, shoot tips and clusters.

Nutrient uptake and redistribution in the whole vines was determined based on dry weight and nutrient analysis of four vines each destructively harvested at the seven key growth stages in 2006 and 2007, as well as soil samples collected at each harvest point. Modeling nutrient movement throughout various plant tissue compartments and whole plant nutrient uptake were accomplished by calculating the content of each mineral element within each tissue (dry mass x concentration) at each growth stage.

The whole vines had dry weights ranging from 4,229 to 9,068 grams. The highest biomass of the whole plants occurred at harvest, which was approximately double of that in winter, budbreak, 3-4 leaves, and bloom. Grapevine roots were not uniformly distributed throughout plant growth stages and the soil profile. Root density appeared to be concentrated in the top 30 cm of soil within 120 cm away from the trunk and the root density was sharply reduced in the subsurface soil and with distance away from the vine trunk. Fine root distribution of Concord grape was strongly influenced by growth stage and soil depth but was not affected by distance from or direction around the trunk. Distribution of Concord fine roots and coarse roots varied slightly from one year to the next. Apart from very small amount of young white fine roots found between 3-4 leaves and veraison, there was no other clear evidence to confirm that fall flush of root occurred.

These 42 years old grapevines were found to have Ca as the most abundant mineral nutrient, followed with N and K. Between veraison and harvest, different tissues were identified for where the majority of Ca, N and K were loaded: half of Ca was in woody tissues, up to 65% of N content was in annual tissues and up to 70% of K was in the clusters. In this regard, highly accumulated Ca in permanent structure of the Concord
grape reflects the high CaCO$_3$ in the vineyard soils, and resulted in the whole vine highest content of Ca throughout growing season.

On the other hand, 50% of P content was located in clusters between veraison and harvest indicates that the clusters were a strong sink for P and it is important to ensure that the grapevines grown in calcareous soils have it enough for fruit production since the availability of P might be limited in high soil pH. During the same time frame, almost half of Mg, B, Fe, Mn, and Cu contents were located in leaf blades and clusters from veraison to harvest, whereas up to 77% Zn was located in trunk and cordon, and about 15% of Fe and Cu were found in fine roots throughout the growing season.

Seasonal dynamics of nutrient contents, except those of Fe, Cu and Zn which highly fluctuated from year to year, shared a practical pattern: Translocation of nutrients from woody tissues to actively growing organs was found at the beginning of the season. The majority uptake of N, Ca and Mn from soil occurred from bloom to harvest while P, K, Mg and B uptake occurred from bloom to veraison. Mobilization of N, P, K, Ca, Mg, B and Mn back to woody tissues occurred after veraison until before leaf senescence with no more nutrient uptake, plus remobilization of N, P and K from leaves back into the woody tissues was observed before leaf senescence.

Likely reasons for the majority N uptake occurring at veraison and continuing through harvest is not only high proportion of woody tissues that the mature vines can rely on for nutrients reserves at the early season, but also the big canopy and high crop level of Concord grapes. In addition, long period of fruit ripening and short period of post-harvest in this cool climate region seemed to intensify grapevine mechanism to have both prolonged the uptake period and early nutrient remobilization during active vine growth. Hence, it can be implied from the path of nutrient movement that fertilizers, if needed, should be applied before bloom, but not before bud break since the grape vine
has no need at this stage and excessive rainfall may cause unwanted leaching of soluble nutrients. Split-application of fertilizers could enhance efficiency of nutrient use in growth and production. In addition, fertilization is not required postharvest for this crop in cool climate regions, as uptake does not occur after harvest.

Leaf blades showed higher concentrations of N, Ca, Mn, Cu and Fe than petioles, whereas those of K, P, Mg, B and Zn were higher in petioles than leaf blades. This likely reflects that petiole tissue indicates the current movement of nutrient toward the leaf blade and therefore is sensitive to the status of mobile nutrients such as K, P and Mg. In addition, when compared with petiole, there was less fluctuation of P, Mg, and Zn concentrations in the blade throughout the growing season. Thus, leaf blade analysis at bloom seems to be the best to represent vine’s nutrient status for fertilizer recommendation since substantial nutrient uptake from the soil occurred after bloom and leaf blades indicate overall status of nutrients, including mobile nutrients.

In this study, high pH of the soil has played a role in highly accumulated Ca in permanent structure of these mature Concord grapes without occurrence of any nutrient deficiency symptom. However, the result showed high fluctuation of Fe, Cu and Zn contents in various vine organs, especially fine roots. In addition to variation of nutrient levels within the root zone relate to the difference between surface and subsurface soil pH, a likely reason for this is that parts of the nutrients were not in the active form that available for plant assimilation and therefore did not reflect the actual nutrient status of the vines. Research involving the relationship between various forms of mineral nutrient and vine nutrient status, as well as pH adjustment in calcareous vineyard soils and effects of increased apoplast pH on nutrient availability in grapevines, may yield more concrete information regarding nutrient partitioning and nutrition balances in Concord grape.