Seasonal Distribution of Micronutrients in Mature ‘Concord’ Grape: Boron, Iron, Manganese, Copper, and Zinc

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ABSTRACT. This study investigated the distribution of the micronutrients boron (B), iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn) in 42-year-old ‘Concord’ grapevines (*Vitis labruscana* Bailey) grown in a calcareous soil to understand seasonal partitioning and distribution of micronutrients throughout various grapevine tissues. In 2006 and 2007, four vines each were excavated at winter pruning, budbreak, the three- to four-leaf stage, bloom, veraison, harvest, and postharvest. Separated plant organs were measured for biomass and analyzed for B, Fe, Mn, Cu, and Zn. The results showed that seasonal patterns of micronutrient concentrations varied considerably with respect to organ and growth stage. Leaf blades, shoot tips, and petioles had the highest concentration of B at bloom and Mn at harvest, whereas Fe, Cu, and Zn concentrations were highest in fine roots but values varied over time each year. Whereas seasonal patterns of Fe, Cu, and Zn contents differed year by year, B and Mn contents had a similar pattern over both years. Translocation of B and Mn from woody tissue to actively growing organs occurred at the beginning of the season. The majority of B uptake occurred between bloom and veraison, whereas that of Mn occurred between bloom and harvest. There were similar B concentrations in shoot tips and leaf blades. Boron remobilization to woody tissues from the leaves occurred between veraison and harvest, suggesting moderate, late-season, phloem mobility of B in ‘Concord’ grapevines. Microsite differences in soil pH likely contribute to variable nutrient availability around the root system, demonstrated by high variability of Fe, Cu, and Zn contents in different vine organs.

‘Concord’ grapevine is a cold climate juice grape originating in the New England region of the United States in naturally acidic soils (Brady and Weil, 1999). Currently, the majority of U.S. ‘Concord’ production is in Washington State (U.S. Department of Agriculture, 2008), where the predominantly calcareous and/or high pH soils could limit the availability of micronutrients, because they tend to precipitate out of soil solution in a carbonate-dominated environment (Epstein and Bloom, 2005). Micronutrient deficiencies have been shown to result in chronic chlorosis and subsequent yield loss in ‘Concord’ grape grown in calcareous soils when cold, wet soil conditions before bloom impede root growth and/or function (Davenport and Steven, 2006).

Although macronutrients are either involved structurally (proteins and nucleic acids) or electrochemically (key cations involved in charge stabilization), micronutrients tend to function as catalysts in enzyme systems (Marschner, 2002). Nutrients are transported in the soil solution by either diffusion or mass flow (Brady and Weil, 1999). Mass flow generally satisfies B requirements of plants growing in most soils (Tinker and Nye, 2000), whereas transfer of Zn from the soil solution to the root surface occurs mainly by diffusion and is likely to occur very close to root hairs. Previous research reported that the diffusion

coefficient of Zn in a calcareous loam was ≈ 50 -fold lower than that of an acidic soil (Melton et al., 1973). Meeting plant demand for Cu, Fe, Mn, and Zn is challenging because they typically are found in low concentrations in the soil solution (Cass, 2005). Concentrations of Mn, Fe, Zn, and Cu in the soil solution depend largely on the soil pH, redox potential, and soil organic matter content, all of which will fluctuate throughout the season in temperate climates (Chesworth, 1991; Sinclair et al., 1990). In addition, Fe, Cu, Zn, and Mn transport is often complicated by the chemical nature of these cations, which tend to form metal–organic complexes of varying stability, size, and charge (Tiffin, 1972).

Micronutrient availability generally decreased as the soil pH increased with the exception of molybdenum (Anderson and Christensen, 1988; Shuman, 1998). Increasing soil pH decreased the exchangeable fractions and increased the more tightly bound fractions of Zn (Iyengar et al., 1981), Cu (Sims, 1986) Fe (Daniels and Haering, 2006), and Mn (Loganathan et al., 1977). Bates et al. (2002) studied the effects of soil pH on young ‘Concord’ grapevines and reported no difference in vegetative growth of the ‘Concord’ vines grown in soil of pH ranging from 5.0 to 7.5. However, they reported a trend toward decreased shoot growth with an increased root:shoot ratio above a soil of pH above 7.0.

Compared with other crops, grapevines appear to have low root densities (Schreiner and Linderman, 2005; Smart and Coombe, 1983) but extensive lateral and vertical spread (Smart et al., 2005). Grape yield and quality are both dependent on root health (Morlat and Jacquet, 1993) with fine roots largely 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 having a well-distributed and functioning root system, which is, in turn, influenced by access through the soil solution to the plant nutrients required for growth.

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Nutrient recycling is key to grapevine nutrient supply. Within the vineyard, when no supplements are provided, nutrients are largely derived from leaf senescence and shredded debris that becomes available after decomposition (Mullins et al., 1992; Winkler et al., 1974). Harvested fruit represent a net nutrient loss as do nutrient losses resulting from leaching and runoff (Mullins et al., 1992; Winkler et al., 1974). Perennial tissues or woody structures are sources of nutrients at the beginning of the season and thus exhibit a demand for late-season nutrient storage for the next season. Conversely, annual tissues (leaves, fruit, new roots) are the greatest determinant of vine nutrient demand. Nutrients contained in the annual tissues come from soil uptake and reserves translocated from permanent structures (Conradie, 1980, 2005).

Although research in grapevine nutrition has been conducted in several different growing regions, previous studies have focused on the uptake of nitrogen and other macronutrients in whole vines. Little research has been done on micronutrient distribution and uptake in grapevines. Schreiner et al. (2006) found that uptake for most macronutrients was very closely related to canopy demand, whereas concentrations of micronutrients Fe, Mn, B, Zn, and Cu in the whole vine varied considerably from vine to vine in Oregon 'Pinot Noir' wine

grape (*Vitis vinifera* L.) and did not show clear seasonal trends. Colugnati et al. (1995) studied vine Fe, Mn, and B content in four different grape cultivars and found total B absorption increased continuously throughout the growing period, whereas total Fe and Mn content increased during the vegetative cycle, then remained steady before veraison, and then progressively increased from veraison to fruit maturity. However, direct comparison of wine grape and 'Concord' nutrient uptake and partitioning may not be possible as a result of differences in management strategies (e.g., pruning, thinning) as well as desired crop yield levels (typically less than 8 Mg·ha⁻¹ for wine grape and greater than 20 Mg·ha⁻¹ for 'Concord'). In addition, size and seasonal duration of vegetative, reproductive, and storage sinks might vary with vine age (Borchert, 1976), cultivars (Colugnati et al., 1995), and variable weather conditions (Robinson, 2005).

The goal of 'Concord' production is to produce the highest yielding 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 of plant growth and development on juice quality. This study was undertaken to investigate seasonal patterns of above-ground and below-ground biomass as well as micronutrient

Table 1. Weather condition and sampling date according to phenological development of 'Concord' grapes in a Yakima Valley, WA, vineyard in 2006 and 2007.

Growth stage	Sampling date		GDD greater than 10 °C ^z		Mean temp (°C) ^z		
	2006	2007	2006	2007	2006	2007	
Dormant	7 Mar.	5 Mar.	—	—	6.63	8.21	March
Budbreak	3 Apr.	2 Apr.	52	41	10.79	10.08	April
Three- to four-leaf stage	8 May	7 May	172	177	15.21	14.99	May
Bloom	6 June	6 June	278	246	18.79	17.43	June
			430	466	23.27	23.54	July
Veraison	26 Aug.	10 Aug.	336	318	20.84	20.30	August
Harvest	18 Sept.	17 Sept.	197	186	16.52	15.86	September
Postharvest	9 Oct.	8 Oct.	34	27	10.25	8.27	October
Cumulative GDD ^y			1503	1414			

^zGrowing degree days {GDD = [(high temperature + low temperature)/2] - 10} and temperature were monitored from a nearby weather station using data loggers (CR-1000; Campbell Scientific, Logan, UT).

^yCumulative GDD between budbreak and harvest for each year.

Table 2. Relationships among dry weight, nutrient content and concentration, and grapevine growth stage, organs, and the interactive factor growth stage (GS) and organ (O) of 'Concord' grape in 2006 and 2007.

Parameter	2006					2007				
	Growth stage		Organ		GS × O	Growth stage		Organ		GS × O
	P	LSD	P	LSD	P	P	LSD	P	LSD	P
Dry wt	0.0001	102.73	0.0001	111.4	0.0001	0.0001	100.57	0.0001	100.56	0.0001
Calcium concn	0.0001	0.05	0.0001	0.05	0.0001	0.0001	0.06	0.0001	0.07	0.0001
Magnesium concn	0.0001	0.016	0.0001	0.02	0.0001	0.0001	0.01	0.0001	0.01	0.0001
Boron content	0.0001	1.32	0.0001	1.44	0.0001	0.0001	1.49	0.0001	1.62	0.0001
Iron content	0.0001	19.32	0.0001	20.92	0.0001	0.0230	65.72	0.0001	48.80	0.1075
Manganese content	0.0001	1.33	0.0001	1.46	0.0001	0.0001	1.50	0.0001	1.64	0.0001
Copper content	0.0001	0.61	0.0001	0.68	0.0001	0.0001	0.78	0.0001	0.84	0.0001
Zinc content	0.0001	5.24	0.0001	5.49	0.0001	0.0001	4.51	0.0001	4.39	0.0001
Boron concn	0.0001	1.03	0.0001	1.13	0.0001	0.0001	1.59	0.0001	1.72	0.0001
Iron concn	0.0001	63.62	0.0001	69.27	0.0001	0.0001	93.79	0.0001	97.74	0.0001
Manganese concn	0.0001	1.64	0.0001	1.81	0.0001	0.0001	2.43	0.0001	2.55	0.0001
Copper concn	0.0001	1.32	0.0001	1.46	0.0001	0.0001	1.61	0.0001	1.75	0.0001
Zinc concn	0.0001	3.37	0.0001	3.56	0.0001	0.0001	4.32	0.0001	4.66	0.0001

LSD = least significant difference.

uptake and redistribution in mature 'Concord' grapevines grown in a calcareous soil.

Materials and Methods

The study was conducted in an own-rooted 'Concord' single-curtain vineyard (lat. 46°15'59" N, long. 119°44'4" W) at the Irrigated Agriculture Research and Extension Center in Prosser, WA. Vines were planted in 1965 spaced with 1.83 m between plants and 3.05 m between rows. The site was furrow-irrigated and had been managed with uniform fertilization, water, and pest management practices for 40 years. The vineyard soil was a Warden fine sandy loam (coarse-silty, mixed, superactive, mesic Xeric Haplocambid). As a result of the great diversity in plant sizes in the vineyard, all grape plants in the 1.5-acre vineyard were measured to determine uniform-sized vines for excavation. These criteria were 12.8- to 15.0-cm trunk circumference at 30 cm above the soil surface, 87- to 99-cm trunk length from soil surface to cordon split, and 25- to 36-cm cordon length before attachment to the cordon wire.

In 2006 and 2007 at winter pruning, budbreak, three- to four-leaf stage, bloom, veraison, harvest, and postharvest (Table 1), all above-ground portions and a comparable below-ground portion (2.4 × 2.7 × 1 m) of four uniformly sized vines were destructively harvested. Each vine was separated into trunk and cordon, coarse roots (diameter greater than 4 mm), fine roots (diameter less than 4 mm), canes, shoot, leaf blades, petioles, shoot tips, and clusters (including rachis and seeds). Coarse roots and fine roots were washed through a 2-mm wet sieve to completely remove soil and were thoroughly rinsed twice with deionized water to remove any physical contaminants.

Separated plant tissues were dried (70 °C, 48 h), weighed, and finely ground to pass through a 40-mesh screen, except for the large woody pieces. For the large woody pieces such as the trunk, two small sections were collected. One was weighed and dried to determine dry weight, whereas the other was pre-ground moist in a coffee mill (Krupps, Millville, NJ), then dried, and finely ground. Samples were digested with nitric acid and hydrogen peroxide in a microwave oven (CEM, Matthews, NC) and analyzed using an inductively coupled plasma spectrometer [ICP (Thermo Jarrell Ash, Franklin, MA)] (Soltanpour et al., 1996) for B, Fe, Mn, Cu, and Zn by a commercial laboratory. Surface (0 to 30 cm) and subsurface (30 to 75 cm) soil samples were collected at each harvest point and analyzed for the availability of the

Fig. 1. Seasonal changes in dry mass of 'Concord' grape plant parts in a vineyard in the Yakima Valley, WA, in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SE at each sampling date (n = 4).

Fig. 2. Seasonal change in concentrations (A) and contents (B) of boron in various organs of 'Concord' grape in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SE at each sampling date (n = 4).

elements listed by using a Mehlich III extraction (Mehlich, 1984) and ICP analysis.

Initial data analysis was conducted using Proc GLM of PC SAS (Version 9.2 for Windows; SAS Institute, Cary, NC) to evaluate the influence of the main and interactive effects on both tissue nutrient concentration (ICP values) and content [dry mass $\times$ concentration (Table 2)]. Additionally, nutrient content was analyzed relative to nutrient concentration, plant dry weight, and the interaction between concentration and dry weight. Although B and Zn were significantly correlated ($P < 0.01$), Cu, Fe, and Mn were not ($P > 0.05$).

Data were subsequently analyzed using analysis of variance with SPSS (Version 15.0; SPSS, Chicago, IL) to examine changes in dry weight and nutrient concentrations of each micronutrient in all plant parts over time. Because dry weight was significantly different by year, data were analyzed separately for each year. Mean separation used least significant difference at $P < 0.05$ level. Seasonal whole vine micronutrient contents were calculated (dry mass $\times$ concentration) and graphed. Net nutrient movement between various plant parts was demonstrated by dividing the calculated content of each micronutrient within each plant part by the number of days between sampling dates (Pradubsuk and Davenport, 2010).

Results and Discussion

The overall patterns of 'Concord' dry weight accumulation are reported in Pradubsuk and Davenport (2010). The patterns were similar over 2 years with the whole plant biomass at harvest approximately double that in winter, budbreak, three- to four-leaf stage, and bloom (Fig. 1). However, there were differences between 2006 and 2007 in woody tissue (trunk and cordon) dry weight between budbreak and the three- to four-leaf stage as well as cluster dry weight at harvest. The change in tissue dry weight was consistent with losses and gains in carbon (C) content, notwithstanding small variation of C concentrations (46% to 48% of dry weight) of various vine parts (Pradubsuk and Davenport, 2010). In addition, concentrations of B, Fe, Mn, Cu, and Zn in the clusters did not vary between years (Figs. 2–6).

MICRONUTRIENT CONCENTRATIONS IN VINE ORGANS. Changes in B concentrations of various vine parts were similar in 2006 and 2007, except that shoot tip B concentrations increased significantly between bloom and veraison in 2006 but decreased during the same period in 2007 (Fig. 2). In both years, leaf blade and petiole B concentration decreased significantly between bloom and veraison, whereas fine root, coarse root, and cane B concentration increased after harvest, and trunk and cordon B concentration remained constant throughout the season. In this regard, lower B concentrations were found in petioles and clusters at bloom and in shoots at veraison in 2006 as compared with 2007.

Iron concentrations were highest and most dynamic in fine roots, petioles, leaf blades, and shoot tips (Fig. 3). However, there were no clear seasonal patterns of concentration changes in fine roots and petioles, whereas leaf blade and shoot tip Fe concentrations were the highest between veraison and harvest. Throughout the two growing seasons, Fe concentrations in trunk, cordon, coarse roots, canes, shoots, and clusters remained constant and were approximately two to four times lower than leaf blade and shoot tip concentrations and ≈ 10 times lower than fine roots.

Manganese concentrations in permanent structures (trunk, cordons, and coarse roots) did not change over time, whereas cane Mn concentrations were high at the beginning of the season and gradually decreased at or after budbreak, reaching the lowest values between bloom and veraison with a slight increase at harvest (Fig. 4). In both years, shoot tip Mn concentrations significantly decreased from the three- to four-leaf stage to bloom and then significantly increased until the end of the season, which mirrored changes observed in leaf petioles and blades during the same period. Conversely, cluster Mn concentrations significantly declined after bloom, reaching the lowest values at veraison or harvest. With the exception of the fine roots, Mn concentration changes in the other organs were similar in both years with highest concentration found in leaf blade.

Compared with other organs, fine root Cu concentrations were highest and the most variable, especially at the beginning

Fig. 3. Seasonal change in concentrations (A) and contents (B) of iron in various organs of 'Concord' grape in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SE at each sampling date ($n = 4$).

Fig. 4. Seasonal change in concentrations (A) and contents (B) of manganese in various organs of 'Concord' grape in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SE at each sampling date ($n = 4$).

of the season when the concentrations were very high at budbreak in 2006 and at dormancy in 2007 (Fig. 5). In both years, trunk, cordon, coarse root, cane, and shoot Cu concentrations were lowest at the three- to four-leaf stage, whereas the highest Cu concentration was found in shoot tips at the three- to four-leaf stage as well as in leaf blades, petioles, and clusters at bloom. Copper concentrations in annual tissues significantly decreased from bloom to veraison and showed little change through the remainder of the season.

Zinc concentrations were highest and varied the most in fine roots, whereas Zn concentration in other organs was much lower throughout both growing seasons (Fig. 6). Although there was no clear fine root seasonal pattern, highest Zn concentrations were found at budbreak in 2006 and at bloom in 2007. In both years, Zn concentrations in the trunk, cordon, coarse roots, and canes at budbreak were slightly higher than at later growth stages through harvest. Zinc concentrations in shoot tips were highest at the three- to four-leaf stage and Zn in leaf blades and clusters were highest at bloom and then significantly decreased until the end of the season. However, shoot tip Zn concentrations in 2007 were significantly higher than in 2006, especially during the three- to four-leaf and bloom stages. In contrast to the other micronutrients, petiole Zn concentrations significantly in-

creased from the three- to four-leaf stage to harvest before gradually decreasing after harvest.

SEASONAL PARTITIONING OF MICRONUTRIENTS. From 1 year to the next, tissues in which the majority of changes in nutrient content occurred differed between nutrients. Almost half of the total B, Fe, Mn, and Cu content was in leaf blades and clusters from veraison to harvest (Figs. 2–5, respectively), whereas up to 77% of the Zn was located in the trunk and cordon (Fig. 6), and $\approx 15\%$ of Fe and Cu was found in fine roots throughout the growing season. The largest Zn content (80 to 110 mg) was found in trunks, consistent with Schreiner et al. (2006), who found that most of the Zn (≈ 99 mg) was located in vine trunks.

Schreiner et al. (2006) reported that the greatest content of Fe in 'Pinot Noir' wine grape was found in coarse and fine roots, whereas the highest Mn content was located in leaf blades and those of B and Zn were in the trunk. In our study, the total micronutrient content of the whole plant was consistent with whole plant total micronutrient content reported for 'Pinot Noir'. However, we found that the 'Concord' micronutrients were distributed differently throughout the vine when compared with 'Pinot Noir' (Schreiner et al., 2006). In 'Concord', the greatest Cu and Mn content were found in the trunk, whereas the highest B and Fe content were in both the leaf blade and trunk. These differences could be the result of differences in vine age and cultivar and/or site conditions such as soil characteristics and water availability, which impact both nutrient demand and storage reserves. Plants in both studies were own-rooted.

Examining whole vine total micronutrient content, seasonal changes in B and Mn were similar between 2006 and 2007 in terms of highest nutrient accumulation in the leaf blades and clusters during active vine growth (Figs. 2 and 4, respectively). Boron uptake (53% to 90% of total) was highest from bloom to veraison, whereas the highest uptake of Mn (76% to 95% of total) occurred from bloom to harvest. Increased B content during this period is consistent with findings in which total B content of the entire plant increased throughout the season (Colugnati et al., 1995). Throughout the growing season, average total uptake per plant of B and Mn were 59 and 64 mg, respectively, in 2006 and in 2007 73 and 92 mg, respectively, were taken up. The greater uptake of both B and Mn in 2007 compared with 2006 corresponds to a higher cluster biomass in the 2007 (Fig. 1). Clusters at the time of harvest constituted 45% of the dry matter and up to 63% B was located in the soft (annual) tissues.

In both years, at the three- to four-leaf stage, there was a large reduction in B content in the coarse roots versus a slight decrease in the trunk and cordons, suggesting that more reserve B for new growth was translocated from coarse roots than from the trunk and cordon (Fig. 2). The combination of B concentration and the plant dry weight contributing to vine B content

Fig. 5. Seasonal change in concentrations (A) and contents (B) of copper in various organs of 'Concord' grape in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SE at each sampling date ($n = 4$).

supports the finding that B movement between woody and annual tissues at the beginning of the season was consistent with what happened at the end of season when B was withdrawn from annual to woody tissues. Potentially, the degree of B translocated out of mature leaves back to woody tissues would depend on the proportion of the B fraction that is readily mobile versus how much B is incorporated into the cell wall and thus unavailable (Hu and Brown, 1994).

The lack of a strong correlation between Mn concentration and content (Table 2) was probably the result of high variability in fine root Mn concentration at the beginning of the season in both years as well as leaf blade and petiole Mn concentration postharvest in 2007 (Fig. 4) despite consistent dry weight accumulation over both years (Fig. 1). However, Mn content was significantly different by organ and growth stage each year, suggesting that seasonal changes of Mn content reflected greater mobilization of Mn from the canopy in 2006 in comparison with 2007. Specifically, the continuous decrease in Mn content in the trunk, cordons, and coarse roots from the beginning of the 2007 season until reaching the lowest point at veraison was consistent with continuous increase of Mn content in leaf blades and petioles. The increase in vine Mn content could be attributed to leaf blades with a high Mn content at harvest (25 to 30 mg/vine). This is consistent with the findings of Schreiner et al. (2006) on 23-year-old 'Pinot Noir', who reported that leaf blades contain the greatest quantity of Mn at

fruit maturity (85 to 93 mg/vine), although there was no consistent pattern of Mn accumulation in vine roots.

During active vine growth, B and Mn concentrations changed in the annual tissues with different stages of vine physiological development. The highest B concentration in leaves and clusters occurred at bloom followed by a sharp decrease in cluster B concentration, whereas that of leaf blades, petioles, and shoot tips decreased slightly in later growth stages (Fig. 2). In contrast, Mn concentrations in leaves and cluster drastically increased from the three- to four-leaf stage to harvest (Fig. 4). Hence, during active vine growth, Mn seems to have had a higher accumulation rate in leaves than B, whereas a higher proportion of B was translocated to clusters. However, after harvest, B and Mn content of leaf blades, petioles, and shoot tips remained unchanged until the end of the season, suggesting that they did not migrate from leaves into woody tissues.

Boron is generally recognized as being immobile in the phloem tissues of plants (Marschner, 2002; Zimmermann, 1960). However, in our study, B had moderate phloem mobility in 'Concord' grapevines as evidenced by similar B concentrations in shoot tips and leaf blades with the exception of lower shoot tip B concentration at budbreak in 2006. Furthermore, high B accumulation in clusters suggested that fruit was a strong sink for B. The finding is consistent with Brown and Hu (1996) who studied B mobility in various plant species. They reported that B is phloem-mobile in grape as a result of higher B concentrations found in apical (younger) than basal (older) leaves and that younger leaves transpired less water than older leaves. Gupta (1979) found that the supply of B needed for reproductive growth in many crops was in excess of the need for vegetative growth found and this is probably because B is an essential micronutrient for pollen germination and pollen tube growth (O'Kelley, 1957).

In addition, Brown and Hu (1996) and Brown and Shelp (1997) reported much higher B concentrations in almond (*Prunus dulcis* Mill.) and apple (*Malus ×domestica* Borkh.) fruit organs (hull, kernel, and shell) than fruit organs of pistachio (*Pistacia vera* L.) and walnut (*Juglans regia* L.) grown under similar condition of B availability. Brown and Shelp (1997), Hanson (1991), and Picchioni et al. (1995) demonstrated that foliar-applied B readily translocated out of the mature leaves of sorbitol-rich species within the genera *Prunus* L., *Pyrus* L., and *Malus* Mill. Hence, there is an obvious need to study B mobility in economically important perennial fruit to improve the most effective B fertilization methods to correct B deficiency and to optimize crop yield. For example, foliar application of B has not been widely used as a result of the belief that B immobility would limit the effectiveness of the foliar applications (Brown and Shelp, 1997).

Iron, Cu, and Zn contents varied seasonally as evidenced by variable organ contents (Figs. 3, 5, and 6). The weak correlation

Fig. 6. Seasonal change in concentrations (A) and contents (B) of zinc in various organs of 'Concord' grape in 2006 and 2007. Arrows at the top of graph indicate the time of dormant (DM), budbreak (BB), three- to four-leaf stage (34), bloom (BL), veraison (VR), harvest (HV), and postharvest (PH). Data points represent means with SES at each sampling date ($n = 4$).

between Fe concentration and content (Table 2) was likely the result of the high concentrations occurring in fine roots and varying concentrations in petioles and shoot tips throughout the two growing seasons (Fig. 3). Compared with other micronutrients in which whole vine contents peaked at harvest, Fe content in the whole plant was highest at veraison in both years, but the content in 2007 appeared to be higher in woody tissues and clusters and lower in leaf blades and shoot tips than in 2006. In this regard, Fe concentration in clusters at veraison was higher in 2007, whereas the other tissues were consistent between years. In addition, lower Fe concentration, but higher plant biomass, was observed in clusters at harvest 2007, suggesting a combination effect of concentration and biomass at peak content.

Analysis of nutrient content relative to concentration, plant dry weight, and the interaction between concentration and dry weight showed that B and Zn were significantly correlated ($P < 0.01$), whereas Cu, Fe, and Mn were not ($P > 0.05$; Table 2). Copper content was not related to Cu concentration overall but Zn was. In 2006, both Cu and Zn content peaked at budbreak, which was associated with high concentrations in the trunk, cordon, and fine roots (Figs. 5 and 6, respectively). Decreased trunk and cordon Cu and Zn concentrations occurred when Cu and Zn contents were lowest at both the three- to four-leaf stage and bloom. In 2006, Cu content peaked a second time at harvest with a considerable amount of Cu accumulated in clusters (35%

of the total), whereas that of Zn peaked at veraison with highest contents in the trunk and cordon (80% of the total). In 2007, Cu and Zn content peaked at harvest. Their amounts in clusters increased continuously through to harvest, but those in the trunk and cordon at each growth stage were more consistent than in 2006. In 2007, Cu and Zn uptake occurred from veraison to harvest, being ≈ 20 and 30 mg/vine, respectively.

SOIL NUTRIENTS. In both growing seasons, soil nutrient availability did not show clear seasonal trends. However, with the exception of Ca, nutrient concentrations in the surface soil were significantly higher than in the subsurface soil (Table 3). This is consistent with the finding of Schreiner (2005) on Oregon 'Pinot Noir' study, who reported that the site subsoil contains significantly higher Mg concentrations than the topsoil.

Microsite differences in soil pH likely contribute to variable nutrient availability around the root system, which could explain the high variability of Fe, Cu, and Zn content in fine roots. Bulk soil sampling and extraction processes would not capture this variability. In addition, nutrient status of perennial tissues is a combination of remobilization and uptake. It is also possible that the soil extractions overestimated plant-available nutrients and therefore did not show a relationship with vine nutrient status.

Changes in the soil environment often have a greater effect on micronutrient rather than the macronutrient nutritional status of plants (Moraghan and Mascagni, 1991). Soil

climatic conditions such as high moisture and low temperature can greatly affect the productivity of 'Concord' grape grown in calcareous soil (Davenport and Steven, 2006). In particular, the development of grape chlorosis has been shown to be associated with high levels of available soil Ca and Mg as well as low levels of Fe and Mn (Davenport and Steven, 2006). Understanding of nutrient partitioning and balances in 'Concord' grape may be further elucidated by research into the relationship between soil and vine nutrient status, nutrient–nutrient interactions, pH adjustment in calcareous vineyard soils, and soil physical properties affecting mineral nutrient availability, movement, and uptake in grapevines (Cass, 2005).

Conclusions

Seasonal patterns of micronutrient concentrations varied considerably as to in which organ and growth stage that attained the highest concentration. Leaf blades, shoot tips, and petioles showed the highest concentrations of B at bloom and showed the highest concentration of Mn at harvest, whereas fine roots had the highest concentration of Fe, Cu, and Zn, although values varied with sampling time each year.

Allocation of absorbed and stored nutrients takes place based on nutrient mobility and relative organ nutrient demand. During the two growing seasons, almost half of the vine B, Fe, Mn, and Cu content was found in leaf blades and clusters from

Table 3. Average soil available calcium, boron, iron, manganese, copper, and zinc in both surface and subsurface soil at different growth stages of 'Concord' grape in 2006 and 2007.

Yr	Growth stage	Soil depth (cm)	Soil pH	Calcium (cmol·kg ⁻¹)	Boron (mg·kg ⁻¹)	Iron (mg·kg ⁻¹)	Manganese (mg·kg ⁻¹)	Copper (mg·kg ⁻¹)	Zinc (mg·kg ⁻¹)
2006	Budbreak	0–30	7.8	22.33	0.78	36.50	34.75	2.72	6.91
		30–75	8.4	27.27	0.43	32.75	15.75	2.12	0.79
	Three- to four-leaf stage	0–30	7.7	21.15	0.83	34.00	38.25	2.77	4.49
		30–75	8.3	28.03	0.56	29.25	19.00	2.36	1.60
	Bloom	0–30	7.7	24.17	0.68	32.25	29.75	2.67	7.06
		30–75	8.2	26.42	0.46	33.50	21.00	2.51	3.04
	Veraison	0–30	7.8	21.85	0.83	32.50	35.00	3.55	6.98
		30–75	8.3	26.93	0.57	30.00	23.25	2.89	2.12
	Harvest	0–30	7.7	23.52	0.63	32.00	34.25	2.50	4.55
		30–75	8.3	26.71	0.48	29.00	22.25	2.09	1.70
	Postharvest	0–30	7.8	21.91	0.65	30.00	40.75	2.49	6.46
		30–75	8.2	25.22	0.58	29.25	21.00	2.06	3.10
<i>P</i> value by soil depth				<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
2007	Budbreak	0–30	7.8	29.41	0.72	42.50	58.00	2.85	10.77
		30–75	8.3	40.94	0.36	28.25	17.50	2.53	1.62
	Three- to four-leaf stage	0–30	7.7	35.87	0.69	37.00	40.75	2.87	5.76
		30–75	8.4	44.65	0.46	28.50	21.75	2.54	2.64
	Bloom	0–30	7.7	33.39	0.62	42.00	52.75	3.08	8.86
		30–75	8.1	39.31	0.56	34.50	32.75	2.58	4.90
	Veraison	0–30	7.6	30.54	0.70	43.50	56.75	2.77	6.20
		30–75	8.2	41.75	0.47	30.25	23.25	2.45	1.42
	Harvest	0–30	7.6	32.08	0.66	38.00	48.25	2.75	7.03
		30–75	8.2	39.60	0.34	32.00	19.25	1.87	0.95
	Postharvest	0–30	7.8	33.46	0.79	39.50	40.50	2.87	5.71
		30–75	8.4	45.63	0.41	27.50	15.00	2.36	1.05
<i>P</i> value by soil depth				<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

veraison to harvest, whereas up to 77% of Zn was in the trunk and cordon and ≈15% of Fe and Cu in fine roots throughout the growing seasons. Seasonal dynamics of B and Mn content shared a common pattern. There was a translocation of the nutrients from woody tissues to actively growing organs early in the season. However, the majority of B uptake (53% to 90% of total) occurred from bloom to veraison, whereas Mn uptake (76% to 95% of total) continued until harvest. Thus, annual tissue demand was clearly the driver for nutrient uptake for these two elements. This is nicely depicted by the total annual uptake, in which the average per plant in 2006 were 59 mg B and 64 mg Mn in 2006, yet there was an overall higher uptake in 2007 (73 mg B and 92 mg Mn), which corresponded to a higher cluster biomass in the 2007.

Translocation of B back to woody tissues began after veraison and ended by leaf senescence. In addition, B movement between woody and annual tissues at the beginning of the season was consistent with what happened at the end of season when B moved into the coarse roots postharvest. The presence of fruit as a strong sink of B and moderate phloem mobility of B in 'Concord' grapevines suggest further study of B mobility in perennial plants to improve B fertilization and deficiency diagnosis methods.

Seasonal changes in Fe, Cu, and Zn content were variable between years. Unlike B and Mn, these micronutrients were primarily in woody tissues, indicating an important structural role in 'Concord' grape.

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