SEASONAL VINE NUTRIENT DYNAMICS AND DISTRIBUTION OF SHIRAZ GRAPEVINES

Authors:Bruno HOLZAPFEL[1,2*], Jason SMITH[1] and Stewart FIELD[3]

[1]National Wine and Grape Industry Centre, Wagga Wagga, New South Wales 2678, Australia
[2]NSW Department of Primary Industries, Wagga Wagga, New South Wales 2678, Australia
[3]Nelson Marlborough Institute of Technology, Blenheim 7240, New Zealand

*Corresponding author: *bruno.holzapfel@dpi.nsw.gov.au*

Abstract:

Context and purpose of the study - The nutrient reserves in the grapevine perennial structure perform a critical role in supplying the grapevine with nutrients when demand cannot be meet by root uptake. The seasonal changes in these reserves largely depend on the developmental stage and the associated growth requirements of grapevines. These stored reserves are influenced by environmental conditions and vineyard management practices, such as production levels and water availability.The aim was to assess the nutrient dynamics of a major wine grape variety grown in Australia, for determining the key nutrient uptake periods and to understand the mobilisation patterns in a season.

Material and methods - The own-rooted 10 year old Shiraz vines utilised for the trial were located in the Riverina, being a warm grape growing region. Uniformly sized vines were selected for 11 excavation dates with four replicates from bud-burst to leaf-fall. The above ground section of the vines were separated into different parts, with the number of tissues varying with the destructive harvest dates. The below ground section of the vines were obtained in an allocated area (6 m^2/vine) and were excavated to a depth of 1 m, the roots were separated into rootstock and three root sizes. The sub-samples of each tissue were freeze dried and the remaining tissues were oven dried at 70 ^{o}C, for both procedures the dry weight (DW) was recorded. For the nutrient analysis the tissue samples were ground, and nutrients were determined with an N analyser and an ICP-OES.

Results - The annual organs showed the highest N concentrations in spring, with the leaves 2.5 % and inflorescences with 3 %, but shoot N concentration increased again at the end of the season to 0.7 % DW. Root N concentrations are at least double the other perennial sections, these reserves decline early in the season and were replenished by leaf-fall. The changes in concentrations for perennial sections are similar for the other macro nutrients, while they differ for Ca and S in the annual tissues. The N content of the perennial structure declined considerably until flowering, with a sharp increase after harvest. The majority of the N uptake occurred four weeks before flowering and four weeks before veraison, more than half the N of the vinewas allocated to the annual organs at harvest. Other macro nutrients show a pattern of decline and replenishment in the roots and wood and most nutrients were taken up predominantly four weeks prior to flowering. The amounts of nutrients allocated to the perennial structure and annual parts varied between the nutrients, the understanding of the nutrient dynamics will led to an optimisation of nutrient status and supply for grapevines.

Keywords: Macro nutrients, annual organs, perennial reserves, concentrations, content, dynamics

1. Introduction

The nutrient reserves in the grapevine perennial structure perform a critical role in supplying the annual growth with nutrients under conditions of insufficient nutrient uptake by the roots. The seasonal changes in these reserves largely depend on the developmental stage and the associated growth requirements of grapevines. These stored reserves are influenced by environmental conditions and certain vineyard management practices, such as production levels, water supply and canopy status. Thus, these stored resources likely contribute to the grapevine capacity within and between seasons.

The grapevine stores a substantial amount of nutrients in the perennial structure after leaf fall. For N, the amounts can vary between 10 and 75 g per vine (Löhnertz *et al*., 1989; Treeby & Weatley, 2006), being influenced by environmental and management factors. Where reported, K and Ca are present in similar concentration ranges to N at 30 to 65 g and 30 to 75 g per vine respectively, with P and Mg

present in smaller amounts ranging from 4 to 10 g for P and 10 to 13 g for Mg (Schreiner et al.; 2006, Pradubsuk & Davenport, 2010). In the warmer climates, a substantial amount of N is acquired after harvest and provides 60 % of the stored N for the following season (Conradie, 1992). Other nutrients are taken also up in the post-harvest period, but accumulated Mg and Ca is mostly lost with leaves prior to dormancy (Conradie, 1980, 1981). However, the majority of nutrient uptake occurs from bloom to veraison, except P where uptake is predominantly prior to bloom (Schreiner *et al.*, 2006). While the importance of stored N, together with carbohydrate reserves, are known to be required to support shoot growth in the following spring as demand in spring cannot be guaranteed by root uptake (Bates *et al.*, 2002; Conradie, 1992, 2005; Zapata *et al.*, 2004; Cheng *et al.*, 2004). Other nutrients could be equally important for the next season's growth (Sánchez-Alonso & Lachica 1987; Tromp, 1983), although the different mobility of each nutrient determines the accumulation and mobilization from the perennial structure. Root growth that is generally most pronounced between bloom and veraison and after harvest (Van Zyl 1984) when carbohydrates are more available for the process (Candolfi-Vasconcelos *et al.*, 1994), affects these nutrient dynamics of vines within a season.

This project aimed to assess the nutrient uptake and partitioning of nutrition in a major red wine variety grown in Australia. For this purpose whole vines were excavated monthly over the growing season to determine the key uptake periods of the nutrients and to understand some of the mobilization patterns during a season. Such a study has previously not being undertaken on wine grapes in Australia and similar work in warm grape growing regions was mostly limited to N or not undertaken under field conditions. The work intended to provide further information for the optimization of fertilizer application for vine productivity and grape composition.

2. Materials and Methods

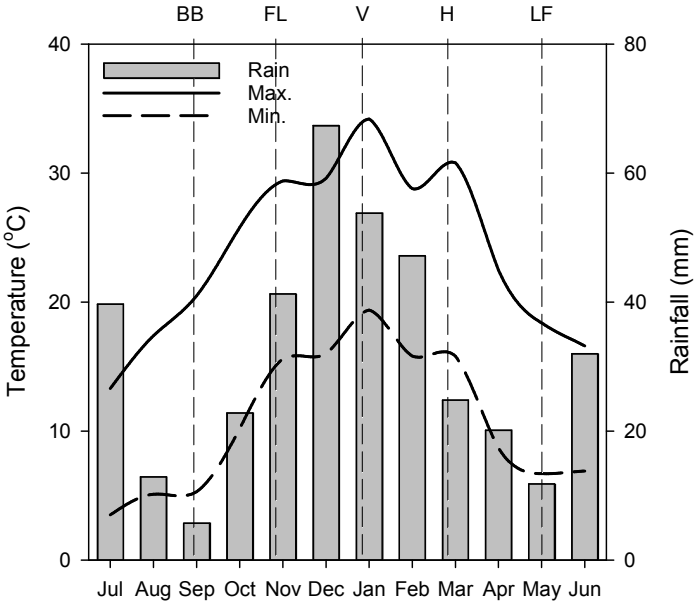
1. Site details

The own-rooted Shiraz grapevines (clone PT23, South Australia) utilized for the trial were located at the Charles Sturt University vineyard (35°03'38"S, 147°21'50"E). Wagga Wagga is a hot and semi-arid area with a mean January temperature (MJT) of 24 °C and average annual rainfall of 572 mm. The vineyard was located within the Riverina wine region, which is classified as hot climate with a mean growing season temperature of 21.5°C (Hall & Jones, 2010).The vineyard soil was a red Kandosol; with an A horizon of dark reddish brown sandy clay loam overlying, at ca 40 cm a porous B horizon of massive granitic saprolite. The growing season 2007/08 was warmer and drier than the average, with 378 mm of rain and a MJT of 26 °C (Figure 1), the data were obtained from a weather station nearby (Wagga Wagga Agriculture Institute). The vines were planted in 1997 and trained to a single bilateral cordon 1.2 m from ground level to an approximately total length of 2 m. The vines were first mechanically trimmed and then hand pruned to about 80 to 90 buds per vine. The grapes were harvested mechanically. Vine and row spacing was 2 and 3 m respectively, with a planting density of 1,667 vines/ha. The vineyard was drip irrigated, and in the 2007/2008 season received approximately 3.5 ML/ha of irrigation, the vineyard was harvested at 24.1° Brix and carried an average yield of 14.6 t/ha with a pruning weight of 2.2 t/ha.

2. Vine excavations

The trunk circumference of all vines in the 1.1 ha trial area were measured during winter in 2007, and 44 uniformly sized vines were selected to allow for 11 excavation dates with four replicates. These were selected by assessing the trunk circumference of each Shiraz vine at 30 cm above ground, with circumference ranging from 12.3 to 14.5 cm. Vines were grouped into four sized based replicates of 5 mm intervals (12.3-12.8, 12.9-13.4, 13.5-14.0 and 14.1-14.5). The excavation began prior to bud-burst on August 21, 2007 and the last one was undertaken after leaf-fall on May 29, 2008.The nine dates in between were on September 20, October 17, November 14, December 13, January 9, February 6, March 3, April 2 and April 30 in the 2007/2008 growing season. The timing of excavation dates and key E-L developmental stages (Coombe, 1995) are indicated in Figure 1. The procedure at each excavation was as follows: the above ground section of the vine was cut off and separated into different parts, with the number of tissues varying with the destructive harvest dates. Prior to bud-burst this was trunk, cordon, spurs sites, while during the season stems, leaves (including petioles) and inflorescences/bunches were also separated. March 3 was the excavation date a few days before the commercial harvest on March 7. The grapes from the vines for the last three excavation dates after March 3 (post-harvest period) were harvested before the commercial harvest on March 7 (Figure 1). All of the individual tissues were cut

into smaller pieces, and representative sub-samples collected, washed in phosphate-free detergent (Deconex, Borer Chemie AG, Zuchwil, Switzerland) and triple rinsed with deionized water. The sub-samples were then freeze dried for later analysis, and the dry weight recorded. The remaining wood and annual tissue was oven dried at 70 °C, and the dry weight also recorded.



Date	E-L Number	Key stage
August 21	1	
September 16*	4	Bud-burst
September 20	5	
October 17	16	
November 5*	23	Flowering
November 14	26	
December 13	32	
January 9	35	Veraison
Februrary 6	36	
March 4	38	Harvest
April 2	41	
April 30	43	
May 15*	47	Leaf Fall
May 29		

Figure 1. Climate data from the 2007/08 growing season (left), monthly rainfall and average temperatures. Excavation dates with E-L numbers and key stages (right).
The key developmental stages are indicated for bud-break (BB), flowering (F), veraison (V), harvest (H) and leaf-fall (LF). Excavation of Shiraz vines at the first sampling date in winter (right). The star after date indicates key development stage only.

The below-ground section of the vines were obtained on the same day wood samples were collected. The area allocated to each vine (6 m^2) was marked out and then excavated with a backhoe to a depth of 80 to 100 cm (Figure 2). Deeper excavation was prevented due to high density sub-soils and the size of machinery, meaning that deeper structural roots occasionally observed cut off at the base of the excavation pit could not be followed. After each excavation a large majority of the root system was immediately collected. This was separated into the rootstock and three root size categories (described below), and were sub-sampled and dried as described for the wood.
Over the next three days the soil from the four vine excavation sites was manually sieved through 10 x 10 mm mesh to remove all remaining roots. All the roots from each vine were separated into three size classes which corresponded approximately to the diameter range of the main structural roots (large > 7 mm), secondary roots (medium 3 to 7 mm), and tertiary roots (small < 3 mm) and washed. On the basis of random measurements made after the roots from each vine were separated, the average diameter in each class was 10.7, 4.0 and 1.1 mm respectively. The method of excavation did not allow the inclusion of any of the new seasons fine root growth, as these were either too fine to be caught in the sieve, or too delicate to survive the excavation process. The tissues were then oven dried as described for the wood.

Figure 2. Excavation of Shiraz vines at dormancy (left) and shortly after veraison (right).

3. Nutrient analysis

For the nutrient analysis the sub-sampled tissue samples were ground to 0.12 mm using a heavy duty cutting mill (Retsch ZM2000, Haan, Germany), and then an ultra-centrifugal mill (Retsch ZM100). Total N was determined on a 50 mg subsample with a VarioMAX combustion analyser (Elementar, Hanau, Germany), and other nutrients (P, K, Mg, S and Ca) with an inductively coupled plasma-optical emission spectrometer (ICP-OES) (ARL 3580B, Applied Research Laboratories, Ecublens, Switzerland) on a 300-400 mg sub-sample.

4. Data analysis

Data were compiled using Microsoft Excel 2016 (Microsoft Corporation 2016) and further manipulated and analyzed using SigmaPlot 14.0 (Systat Software Inc., San Jose, USA). The concentrations reported are on the medium size roots and cordon, while the amounts included are all combined root fractions (all root sizes and rootstock), cordon and spurs sites were also combined. Individual data values and points in the tables and graphs are shown with standard errors of the mean (n=4).

3. Results and Discussion

The nutrient dynamics of Shiraz grapevines, which during this study were in full production, showed considerable changes over the season in both annual and perennial organs. Similarly, the dry matter changed through the season, with some decline in the perennial structure in early spring and significant annual accumulation due to shoot growth and berry development. This study was undertaken on an irrigated major wine grape variety in a region with a long post-harvest period, providing a contrasting situation to earlier work undertaken on grapevines that were considerably older and were either rain fed or furrow irrigated and had either much lower or higher yield levels (Pradubsuk & Davenport, 2010; Schreiner *et al.*, 2006).

The seasonal concentration and content changes of the six macronutrients were more pronounced in the annual parts of vine than in perennial tissues (Figure 3 and 4). The inflorescences/bunches showed a decline in all nutrient concentrations, while the amounts per vine increased towards harvest. However, leaf concentrations declined during the season for four nutrients, with Mg and Ca increasing until leaf-fall. Therefore the concentrations of these nutrients were highest after harvest, while for the other nutrients occurring pre-harvest. All nutrient concentrations in stems declined rapidly until flowering or veraison, but with Ca only minor changes occurred in the stems. The concentration changes of the perennial structure were relatively small, with decline in spring and replenishment during the season. However, the total content of macronutrients varied substantially during the growing season, with 50 %

or more allocated to the below ground reserve sections of the vine early and late in the season. These results indicate the buffer capacity of the perennial structure, providing the annual organs with sufficient nutrients when the supply is limited. The vines total nutrient content reached a seasonal maximum prior to harvest, being highest for N with 60 g/vine and lowest for S with about 4 g/vine that corresponds to 100 kg N and 6.5 kg S per hectare respectively. For most nutrients more than half is located in the annual organs, with the majority in the leaves. However, the majority of K was present in the bunches, therefore the removal of this nutrient is the highest from the vineyard system.

1. Dry matter accumulation

A decline of perennial structure biomass was observed in roots, trunk and cordon in spring, starts to increase again around flowering, but only significantly to recover during berry maturation, with further gains after harvest (Table 1). The roots made up about 50 % of the perennial structure and, even at harvest, roots and wood had more than half of the total biomass. The dry mass of the shoots (stems and leaves) particularly increased from a month after bud-burst to a week after flowering, while the bunches had the largest increase from pea size to veraison. These periods have considerable nutrient requirements (Schreiner *et al.*, 2006), which need to be matched firstly from the perennial reserves and then from accessing more nutrients from the soil, with further requirements after harvest for replenishing reserves. The dry matter declined during the post-harvest period for the stems and leaves, as parts of shoots would have broken off (non-mature wood) and leaf fall occurred.

Table 1. Biomass accumulation (g DW/vine) in Shiraz grapevines during the growing season in the Riverina.

Standard errors of the mean are indicated in small type (n = 4).

Date	Roots		Trunk		Cordon		Stems		Leaves		Bunch	
21/08/2007	2615	247.6	871	49.9	1433	84.0	0	0.0	0	0.0	0	0.0
20/09/2007	2702	181.4	947	41.7	1433	98.2	1	0.3	0	0.0	0	0.0
17/10/2007	1935	204.1	763	101.6	1137	163.6	101	8.0	156	14.7	11	1.6
14/11/2007	2004	122.7	929	74.0	1394	76.9	594	31.4	708	22.8	55	5.7
13/12/2007	2098	249.1	906	107.2	1208	135.5	605	79.6	706	68.2	497	78.8
9/01/2008	2188	161.0	1100	32.8	1498	138.2	791	67.6	890	53.3	1578	170.3
6/02/2008	2492	187.5	1142	66.0	1397	94.8	743	30.2	882	28.2	2165	111.2
4/03/2008	2644	439.9	1018	112.2	1491	142.5	826	123.7	809	45.4	1737	306.2
2/04/2008	2691	160.0	1133	80.2	1601	107.9	1009	138.7	606	58.8	0	0.0
30/04/2008	2937	370.1	1206	120.6	1755	221.2	970	25.5	400	39.5	0	0.0
29/05/2008	2909	99.5	1162	88.1	1578	197.6	785	78.2	0	0.0	0	0.0

2. Nutrient concentrations

The concentrations of N are generally the highest compared to the other nutrients. The annual organs started with high concentrations in spring, with the leaves 3 % and inflorescences with 2.5 %, only the emerging buds are higher with nearly 4 % DW (Figure 3). Bunches at harvest and leaves prior to leaf-fall declined to about 1 % DW, stems regain N concentration at the end of the season and finish with an N concentration of 0.7 % DW. Both below and above ground parts declined during the season until the post-harvest period when concentrations increase. The concentrations were at least double in the roots than in the other sections of the perennial structure. At the end of the season the concentration largely regained the levels observed prior to but-burst. The changes for both perennial and annual sections were similar for P and K. However only the reserve tissues for K, Ca and Mg was similar. The concentrations varied with K and Ca slightly below 0.5 % DW; Mg concentrations were below 0.1% and S

below 0.5 % DW. The K concentrations were highest shortly after bloom for both bunches and leaves, with 2.2 % and 1.5 % respectively. At harvest the concentrations declined to 1 % in bunches and just over 0.5 % in the leaves prior to leaf-fall. The concentration changes of P and S declined from early spring towards the end of the season similar to N, but at much lower levels. In contrast the nutrients Ca and Mg increased substantially in the leaves, Ca from 1 to 3.7 % and Mg from 0.18 to 0.46 %. While the Ca concentration was highest in the inflorescence with 1 %, Mg had the concentration peak of 0.25 % in bunches after flowering. The decline in spring of nutrient concentration in the perennial structure indicates the mobilization from theses tissues for the support of annual growth and development, while the accumulation of Ca and Mg in the leaves indicates the poor redistribution of the nutrients into the perennial structure during senescence (Conradie, 1981). Both observations are demonstrated in the dynamics by nutrient content on a whole vine basis.

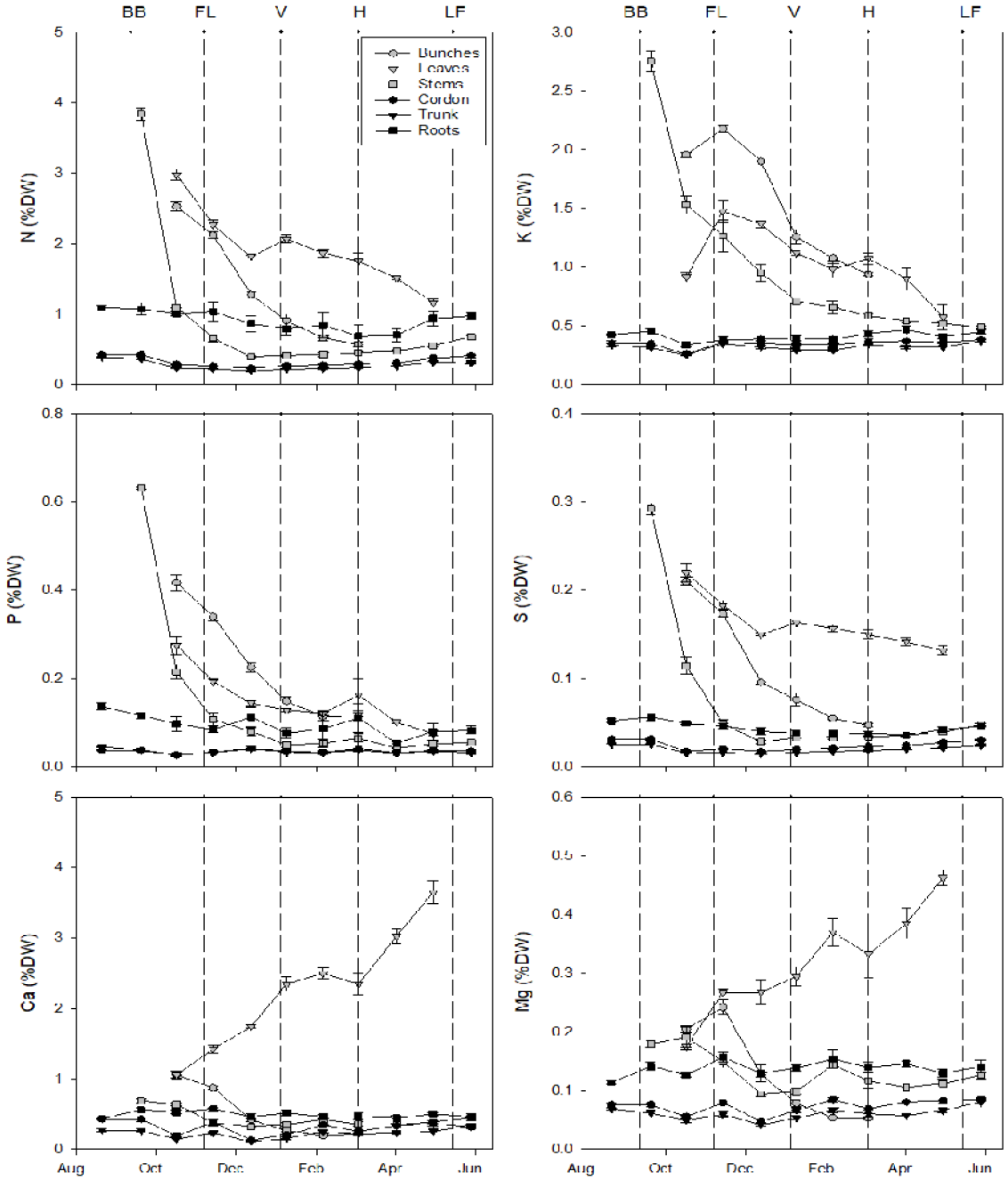


Figure 3. Seasonal changes of macronutrient concentrations in the different parts of Shiraz grapevines.

The key developmental stages are indicated for bud-break (BB), flowering (F), veraison (V), harvest (H) and leaf-fall (LF). Standard errors are indicated as bars below and above the mean (n = 4).

3. Nutrient accumulation

During the growing season the grapevine accumulates considerable nutrients in the annual growth, which is supplied mostly from new nutrient acquisition, but also from reserves located in the roots and the wood (Figure 4). The values presented here are additive contributions of each organ, for instance the perennial reserves at bud burst consist of 27 g root, 3 g trunk and 6 g cordon N. The N reserves in this study were 36 g/vine prior to bud burst, which is about half that of other work reported from Australia for Sultana (Wheatly & Treeby, 2006) but similar to research undertaken on Pinot Noir in Oregon (Schreiner *et al.*, 2006) or on Concord in Washington (Pradubsuk & Devonport, 2010). The N content of the perennial structure **declined considerably until around flowering, where accumulation was only seen after veraison with a sharp increase after harvest. In this study the decline of whole vine N one month after bud-break indicates that the N in the root and wood tissues appears to have been at least half** mobilized for growing new fine root growth. Sifting soil through 10 x 10 mm mesh did not allow new fine growth to be accounted for during the destructive harvests. Fine roots are known to be the vines major nutrient absorbing structures (Keller, 2015) and considerable fine root growth occurs prior flowering (Comas *et al.*, 2005). With the majority of N uptake occurring four weeks before flowering in this study, it supports the view that a significant amount of N had been used for fine root growth during the period after bud-break. Other nutrients analyzed showed this same trend of decline after bud-break indicating the use of all perennial nutrient reserves for an early root growth flush to support nutrient uptake prior to flowering.

Four weeks before veraison, and then four weeks after harvest, were two additional uptake periods for N. The decline in N directly after harvest could again be due to a fine root growth flush that we could not account for with the recovered root biomass (Comas *et al.*, 2010). At harvest the annual growth contains more than half the N of the vine, with grapes being 10 g/vine. Most of the annual N is in the leaves and the least was in the stems, however, this will not be lost from the system with both amounts being available to the vine after decomposition after leaf-fall and pruning. However, the findings indicate that some of the N in the leaves has already been moved into the shoots and the perennial structure as reported in earlier studies (Conradie, 1981). The N in the crop is usually removed from the vineyard system and needs to be replaced by fertilizer or appropriate cover crops.

All nutrients showed a pattern of decline and replenishment in the roots and wood tissues and most nutrients were taken up in the four weeks prior to flowering and bloom and then again during the four weeks prior to veraison. Mg is also strongly accumulated four weeks after veraison, while P is predominantly taken up and accumulated four weeks before and after flowering. Both of these nutrients were further accumulated in the post-harvest period, Mg in the first weeks after harvest and P in the later part, both following a decline prior to this accumulation. The amounts of nutrients allocated to the perennial structure and annual parts varied between the nutrients, but most important is the removal by the crop being highest for K with 16 g vine, followed by Ca with 4 g, P with 2 g, S and Mg with about one gram each. Re-mobilization from the leaves to the perennial structure and shoots does not appear to be taking place for Ca and Mg. Both have been described as taken up after harvest, but the accumulated nutrients are lost to the vine by leaf fall (Conradie, 1981). As for N, the nutrients remaining in the leaves and shoots will most likely be recycled in the vineyard system over time after leaf-fall and pruning.

Overall there was a decline in all nutrients in the perennial structure from bud burst to flowering, when an increase in the annual organs takes place (Table 2), from flowering to veraison there were only small changes in the perennial sections. A considerable accumulation in annual organs was present in this period, indicating that a considerable uptake of macro nutrients in this period occurred. During the rest of the season more macronutrients were accumulated in the roots and wood, being particularly elevated for N in the post-harvest period, seen as an important time to store N for the following season (Conradie, 1992). There is a decline of nutrients during grape maturation and from harvest to leaf-fall in the annual organs, even without including the removal of nutrients due to grape harvest. During maturation leaf loss had been observed likely due to high temperatures frequently present, after harvest and close to leaf fall most nutrients are commonly re-mobilized from the leaves to the perennial structure. However, Ca and Mg accumulated in the leaves is most likely being lost due to the poor mobility of these nutrients (Conradie, 1981). At the end of the season the grapevine perennial structure nutrient reserves had increased from the previous dormancy, due to the growth of this structure. The nutrient requirements for the development of the wood and the roots has to be considered, as the perennial structure growth in every season. In addition, the removal of nutrient by fruit and the varying seasonal demands has to be included in these wants to ensure a vineyards productivity level.

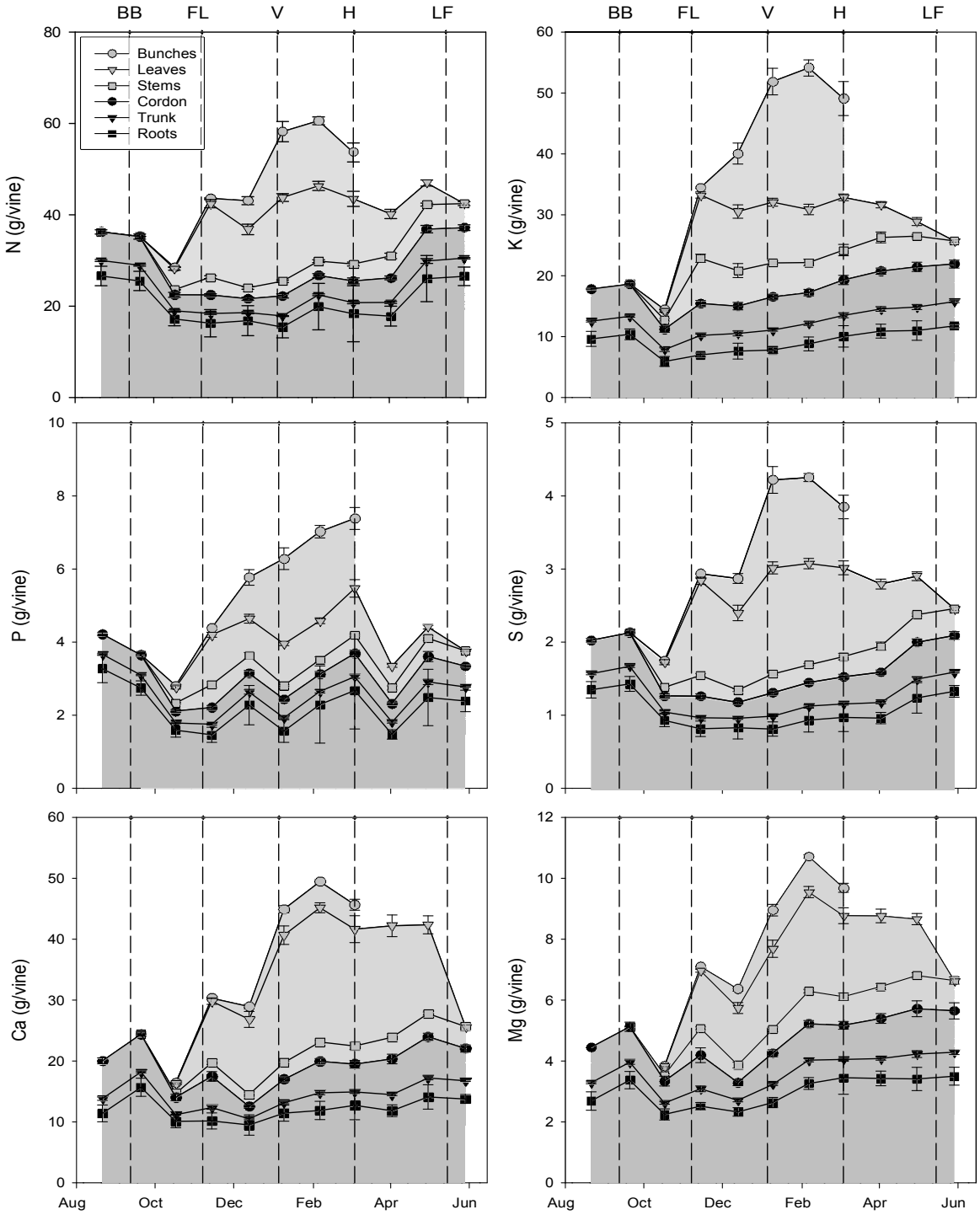


Figure 4. Seasonal accumulation of macronutrients in the different parts of Shiraz grapevines, showing the additive contribution of each organ to the total vine content at each date.

Perennial vine nutrient content indicated in dark grey and annual nutrient content in light grey.The key developmental stages are indicated for bud-break (BB), flowering (F), veraison (V), harvest (H) and leaf-fall (LF). Standard errors are indicated as bars below and above the mean (n = 4).

Table 2. Nutrient accumulation between major phenological stages in Shiraz 2007/08.

Budburst to flowering BB-FL, flowering to veraison (FL-V), veraison to harvest (V-H), harvest to leaf fall (H-LF). Standard errors of the mean are indicated in small type (n = 4).

Tissue	Period	N (g)		K (g)		P (g)		S (g)		Ca (g)		Mg (g)	
Perennial	BB-FL	-12.77	2.46	-3.19	1.06	-1.44	0.37	-0.87	0.09	-6.94	2.64	-0.94	0.33
	FL-V	-0.22	0.92	1.08	0.66	0.23	0.22	0.05	0.04	-0.52	1.19	0.07	0.19
	V-H	3.29	4.49	2.78	1.94	1.25	0.95	0.22	0.14	2.52	2.07	0.92	0.44
	H-LF	6.44	13.48	2.62	2.01	-0.35	1.33	0.57	0.24	2.58	2.92	0.47	0.17
Annual	BB-FL	19.93	0.78	18.99	0.98	2.17	0.08	1.67	0.05	12.82	0.51	2.91	0.05
	FL-V	14.82	3.20	16.35	3.68	1.67	0.41	1.24	0.30	15.14	2.61	1.79	0.58
	V-H	-7.86	6.04	-5.57	5.76	-0.15	0.41	-0.59	0.49	-1.78	4.34	-0.18	0.57
	H-LF	-22.85	3.59	-26.00	3.58	-3.28	0.19	-1.96	0.24	-22.58	2.70	-3.52	0.19

4. Conclusion

This research, undertaken on 10-year-old own rooted Shiraz grapevines excavated from an irrigated hot climate vineyard, shows the nutrient concentrations and content over a growing season for all macronutrients. The study demonstrates the decline of nutrients in the root and wood tissue, the utilization of these mobilized nutrients for the annual growth and development and their replenishment towards the end of the season. The observed decline of vine nutrients one month after bud-break indicates significant nutrient reserves are being used to support a root growth flush for nutrient uptake prior to flowering. The amount accumulated during the growing season in the annual parts at harvest is most pronounced for K, Ca and N with a range between 26 and 30 g per vine, while for the nutrients P, Mg and S the amount is between 2 and 5 g.However, further accumulation occurred after harvest in the perennial structure for essentially all macronutrients. This is a period to replenish the reserve tissue to the level of the start of the season, indicating that the total uptake is higher than just the amount accumulated at harvest. The main periods of nutrient uptake are four weeks before flowering and also before veraison, with P having uptake peaks four weeks before and after bloom, while Mg is significantly also taken up four weeks after veraison. The reason behind this difference in uptake is not clear at this point in time, but the increase in P accumulation after bloom is in the developing bunch, while for Mg this accumulation is predominantly in the roots. However, the accumulation pattern indicates that nutrient supply is important, generally prior to bloom and veraison for the annual parts, and after harvest to replenish the reserves if required.

5. Acknowledgements: The work was supported by the National Wine and Grape Industry Centre, and the Australian grape growers and winemakers through their investment body, Wine Australia, with matching funds from the Australian government. We are also grateful for the support and assistance from our technical staff during various stages of this project.

6. References

Bates, TR, Dunst, RM, & Joy, P. (2002). Seasonal dry matter, starch, and nutrient distribution in 'Concord' grapevine roots. *HortScience* 37, 313-316. https://doi.org/10.21273/HORTSCI.37.2.313

Candolfi-Vasconcelos, MC, Candolfi, MP, & Koblet, W. (1994). Retranslocation of carbon reserves from the woody storage tissues into the fruit as a response to defoliation stress during the ripening period in *Vitis vinifera* L.. *Planta* 192, 567-573. https://link.springer.com/article/10.1007/BF00203595

Cheng, L, Xia, G, & Bates, T. (2004). Growth and fruiting of young 'Concord' Grapevines in relation to reserve nitrogen and carbohydrates. *J. Amer. Soc. Hort. Sci.* 129, 660-666. https://doi.org/10.21273/JASHS.129.5.0660

Comas, LH, Bauerle, TL, & Eissenstat DM. (2010). Biological and environmental factors controlling root dynamics and function: effects of root ageing and soil moisture. *Aust. J. Grape Wine Res.* 16, 131-137. https://doi.org/10.1111/j.1755-0238.2009.00078.x

Comas, LH, Anderson, LJ, Dunst, RM, Lakso, AN, & Eissenstat, DM. (2005). Canopy and environmental control of root dynamics in a long-term study of Concord grape. *New Phytologist* 167, 829-840. https://doi.org/10.1111/j.1469-8137.2005.01456.x

Coombe, BG. (1995). Adoption of a system for identifying grapevine growth stages. *Aust. J. Grape Wine Res.* 1, 100-110.https://dx.doi.org/10.1111/j.1755-0238.1995.tb00086.x

Conradie, WJ. (1980). Seasonal uptake of nutrients by Chenin blanc in sand culture. I. Nitrogen. *S. Afr. J. Enol. Vitic.* 1, 59-65.https://doi.org/10.21548/1-1-2414

Conradie, WJ. (1981). Seasonal uptake of nutrients by Chenin blanc in sand culture: I. Phosphorus, potassium, calcium and magnesium. *S. Afr. J. Enol. Vitic.* 2, 7-13. https://doi.org/10.21548/2-1-2403

Conradie, WJ. (1992). Partitioning of nitrogen in grapevines during autumn and the utilisation of nitrogen reserves during the following growing season. *S. Afr. J. Enol. Vitic.* 13, 45-51. https://doi.org/10.21548/13-1-2198

Conradie, WJ. (2005). Partitioning of mineral nutrients and timing of fertilizer application for optimum efficiency. In Proceedings for the Soil Environment and Vine Mineral Nutrition Symposium, American Society for Enology and Viticulture. Christensen, JP, & Smart, DR. (Eds.), pp. 69-81. San Diego, CA.

Hall, A, & Jones, GV. (2010). Spatial analysis of climate in winegrape-growing regions in Australia. *Aust. J. Grape Wine Res.* 16, 389-404. https://doi.org/10.1111/j.1755-0238.2010.00100.x

Keller, M. (2015).The Science of Grapevines – Anatomy and Physiology. Elsevier: Academic Press, San Diego, CA.

Löhnertz, O, Schaller, K, & Mengel, K. (1989). Nährstoffdynamik in Reben III. Mitteilung: Stickstoffkonzentration und Verlauf der Aufnahme in der Vegetation. *Vitic. Enol. Sci.* 44, 192-204.

Pradubsuk, S, & Davenport, JR. (2010). Seasonal Uptake and Partitioning of Macronutrients in Mature 'Concord' Grape. *J. Amer. Soc. Hort. Sci.* 135, 474-483. https://doi.org/10.21273/JASHS.135.5.474

Sanchez-Alonso, F, & Lachia, M. (1987). Seasonal trends in the elemental content of sweet cherry leaves. *Commun. in Soil. Sci. Plant. Anal.* 18, 17-29. https://doi.org/10.1080/00103628709367800

Schreiner, RP, Scagel, CF, & Baham, J. (2006). Nutrient uptake and distribution in a mature 'Pinot Noir' vineyard. *HortScience* 41, 336-345. https://doi.org/10.21273/HORTSCI.41.2.336

Treeby, MT, & Wheatley, DM. (2006). Effect of nitrogen fertiliser on nitrogen partitioning and pool sizes in irrigated Sultana grapevines. *Aust. J. Exp. Agri.* 46, 1207-1215. https://doi.org/10.1071/EA05238.

Tromp, J. (1983). Nutrient reserves in fruit trees, in particular carbohydrates and nitrogen. *Plant & Soil* 71, 401-413.https://link.springer.com/article/10.1007/BF02182682

Van Zyl, JL. (1984). Response of Colombar grapevines to irrigation as regards quality aspects and growth. *S. Afr. J. Enol. Vitic.* 5, 19-28.https://doi.org/10.21548/5-1-2365

Zapata, C, Deléens, E, Chaillou, S, & Magné, C. (2004). Mobilisation and distribution of starch and total N in two grapevine cultivars differing in their susceptibility to shedding. *Functional Plant Biology* 31, 1127-1135. https://doi.org/10.1071/FP04028