Potassium in viticulture and enology

Russell Moss (Graduate Research Assistant, Virginia Tech)

May 2016

Introduction

Potassium (K+) is of interest to Virginia vintners, as many of the soils upon which vineyards have been planted have high exchangeable K+ levels and while excessive K+ does not cause "toxicity", high soil concentrations can interfere with uptake of certain other nutrients. Furthermore, high K+ concentrations in grapes has potentially negative implications for wine acid profiles, pH and color stability. In a warm climate, such as Virginia, titratable acidity is known to degrade rapidly from véraison until harvest. This leads to wines which can be out of balance and considered "flabby" (i.e. lacking acidity), and such wines may also have significantly elevated pH. Tartaric acid can be added to the must to reduce pH; however, high concentrations of K+ in the juice can reduce the effectiveness of the acid addition. Therefore, it is to the advantage of the vintner to minimize the negative effects of K+ in the juice. This review will discuss:

1. The forms in which K+ is found in the soil
2. Mode of uptake and transport of K+ in the plant
3. Function of K+ in the plant
4. Environmental factors effecting uptake and transport of K+
5. Viticultural practices which influence K+ uptake and transport
6. Enological consequences of high K+ in the juice

K+ in the soil

Potassium is generally the most abundant cation found in mineral soils (Reitemeier 1951). However, much of the K+ found in soils isn't easily exchangeable and is held in primary minerals which only release the K+ gradually over considerable periods of time (Brady and Weil 1996). K+ concentration in soil ranges from 0.04 to 3% by weight (Sparks 1987). In fact, about 98% of the K+ found in soil is fixed in its mineral form and a mere 2% is found in soil solution or in potentially exchangeable forms (Schroeder 1978).

There are four forms of K+ in the soil (Brady and Weil 1996):

1. K which forms mineral structures (not available)
2. K in secondary minerals (not readily available)
3. Exchangeable K+ (readily available)
4. K+ in soil solution (readily available)

The K+ found in primary mineral structures accounts for roughly 90-98% of the soils total K+ content and is unavailable to the plant. This K+ is mostly found within the crystalline structures of micas and feldspars. This K+ is released over many years through weathering, but its release is extraordinarily slow (Brady and Weil 1996).

Nonexchangeable K+ in secondary minerals accounts for roughly 1-10% of soil K+ concentration, and is slowly available. This nonexchangeable form occurs in 2:1 minerals such as vermiculites, smectites and montmorillonites. The structure of 2:1 clay minerals can be seen in Figure 1.

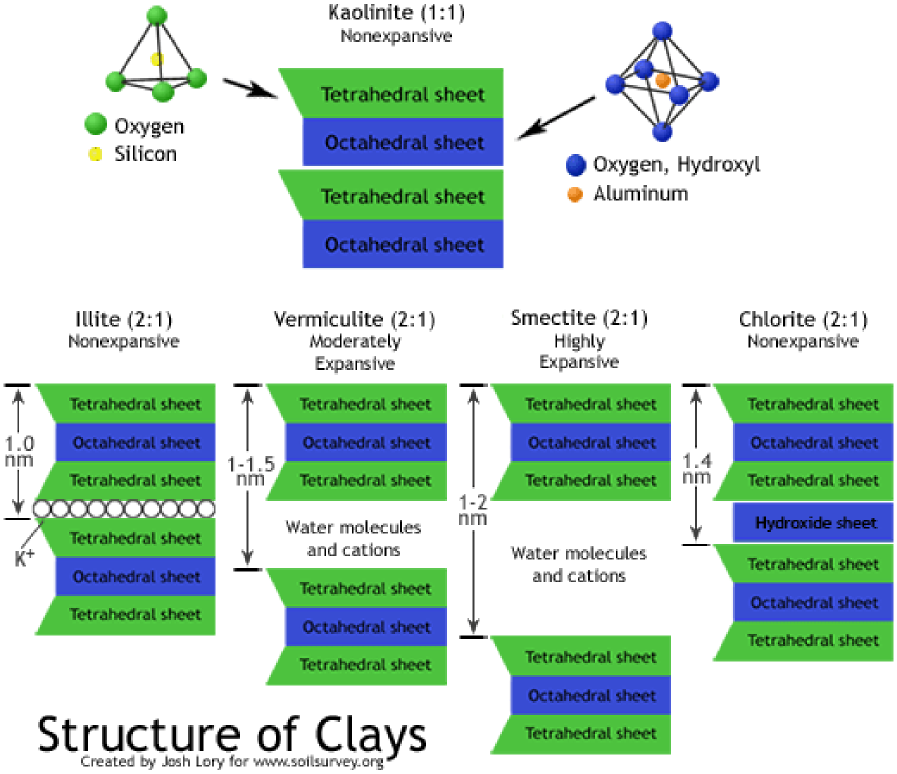

Figure 1: Structure of clay (From: http://learnbioremediation.weebly.com/uploads/9/0/6/9/9069787/9875180_orig.png)

The K+ ion has a hydrated radius such that it is small enough to fit tightly between the crystalline layers of these 2:1 clays, thus fixing the K+ in a nonexchangeable form. As such, when K+ fertilizer is added to soils with these clays, it can be quite well buffered against the fertilizer, as the added K+ may be tied up within these crystalline layers. This nonexchangeable K+ can be released over time through normal weathering processes (Brady and Weil 1996). Nonexchangeable K+ is also released as the soil solution K+ and exchangeable K+ are decreased by cropping and leaching (Sparks 1987). The most readily available forms of K+ are found as exchangeable K+ on the soil colloid and as K+ dissolved in soil solution. These readily available forms of K+ account for a mere 1-2% of total K+ in the soil, and are subject to leaching, depending on the depth and other features of the soil.

Soil pH is known to have a significant impact upon K+ availability. Generally, lower soil pH (e.g., 4.5 to 6.0) increases K+ availability and decreases Ca^{2+} and Mg^{2+} availability (Brady and Weil 1996). Conversely, high soil pH (e.g., > 7.0) is often associated with reduced uptake of K+ and increased uptake of Ca^{2+} and Mg^{2+}. In fact, very heavy applications of limestone can induce K+ deficiency on certain soils. This is due in part to the increased soil pH, but also to the increased antagonism with Ca and Mg ions for CEC sites, as discussed next.

Antagonism of K^+ with Ca^{2+} and Mg^{2+}

Liming will also supply the soil with Ca^{2+} and Mg^{2+} (depending upon the liming agent used). Mg^{2+} and Ca^{2+} can have an antagonistic effect upon K+ uptake (Hannan 2011; Jakobsen 1993; Kabu and Toop 1970; Pathak and Kalra 1971). The divalent cations can easily displace the monovalent K+, as CEC binding sites will be preferentially adsorbed by Mg^{2+} and Ca^{2+}. Therefore, if soil magnesium or calcium concentrations are high, these cations can outcompete K+ (Hannan 2011; Marschner 2011). In a study conducted by Hannan (2011) it was found that magnesium could induce a K+ deficiency in the grapevine if the soil has a concentration of available K/Mg of less than 0.30. Conversely, high K+ concentrations in the soil has been found to lead to a reduction in Mg^{2+} uptake by the grapevine (Conradie and Saayman 1989b). If K+ is in high concentration in the soil, as is the case in some vineyards in Virginia, the plant can take up far more K+ than is needed to support normal growth and metabolism (Conradie and Saayman 1989a). Therefore, the displacement of K+ with Mg^{2+} and Ca^{2+} may be one method which vintners can use to *intentionally* limit K+ uptake by the grapevine. While this sounds good in theory, the results of field studies to attempt this goal have not been consistently positive. Depending on the soil conditions and site climate, one may also risk inducing a Ca^{2+} or Mg^{2+} induced K+ deficiency by taking this approach.

K+ in Virginia soils

There are over 600 soils series which have been mapped in VA. However, VA can be broken up into 5 geologic regions (figure 2) (Sherwood et al. 2010):

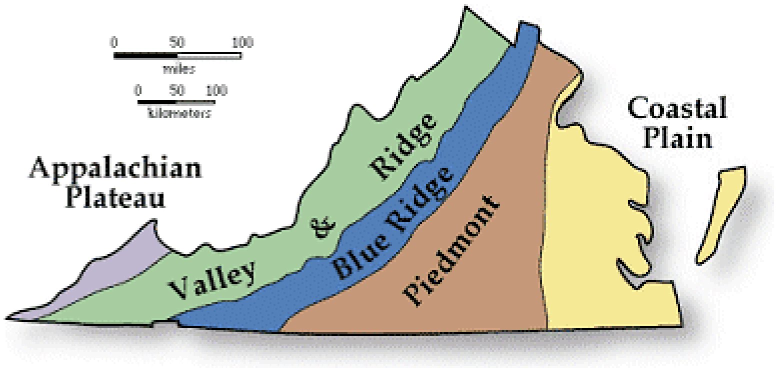

Figure 2: Virginia's five major geologic regions
(from: https://notnecessarilygeology.files.wordpress.com/2011/04/picture-81.png)

Of these five regions, most of Virginia's 3,500+ acres of grapes are planted within the Piedmont, with most of the remainder planted within the Blue Ridge region. The chemical fertility of a soil will be site specific and we cannot make gross generalizations about all of the soils in the 5 geological provinces that will hold true for every site.

Much of the soil in the Piedmont was formed from igneous and metamorphic parent materials with a high base content. Also, much of the vermiculite (a 2:1 clay) in Virginia is found in the Piedmont province. It should be noted that soils which are dominated by montmorillonite are likely to have greater K+ availability than most soils, as the interlayer space is less tightly held together by hydrogen bonds, therefore montmorillonite is able to swell more with hydration than vermiculites, thereby allowing for rapid exchange of ions (Sparks 1987). Exchangeable K+ can increase over time in montmorillonite soils, even in the absence of K+ fertilization. The phenomenon gave rise to the expression "the potassium paradox" (Khan et al. 2014) which arguably casts a question on the value of soil tests for exchangeable K+ and as a basis for fertilizer K+ recommendations. This phenomenon occurs due to the release of fixed K+ from the interlayer spaces between the octahedral and tetrahedral sheets.

The Eastern slopes of the Blue Ridge geological region are also mostly derived from base cation rich crystalline rocks coming from igneous and metamorphosed material, some of which are rich in feldspars (Brann et al. 2009). As much of the soils in Virginia vineyards are derived from igneous and metamorphosed parent material, it is not surprising that vintners are finding their soils to have high K+ concentrations. The soils in VA which will have the highest concentrations of readily available K+ will be those which are derived from primary minerals such as feldspars and micas and those soils with shrink-swell 2:1 clays, especially montmorillonite (Sparks 1987). Soils comprised of kaolinite and other 1:1 clays will contain the lower concentrations of K+ (Brady and Weil 1996). However, kaolinitic clays are not as well buffered against K+ additions, so it is easier to over apply K+ fertilizer to vineyards in which these types of 1:1 clays dominate, as the vine can luxuriously consume K+. There are some kaolinite dominated soils in the

Piedmont, due to the presence saprolite, which has weathered from the underlying bedrock. It is most likely that one will find the soils with the highest K+ concentrations in the soils of the Eastern slopes of the Blue Ridge, as these soils are less weathered than the Piedmont lowlands, due to their steep slopes, thin soil profiles, and propensity for surface run-off.

One might be able to ameliorate the issue of high soil K+ concentration through the application of antagonistic cations to the soil. Divalent cations such as Ca^{2+} and Mg^{2+} are preferentially adsorbed to the soil particle, thereby displacing the monovalent K+, suppressing its exchange (Mitra and Prakash 1957). Interlayer K+ can be displaced by the addition of sodium, however this will also collapse the clay structure and can lead to an increase in soil bulk density (Scott and Smith 2013). Interlayer K+ can also be displaced by the addition of NH4^{+}, as the hydrated radii is similar to that of K+ (Acquaye and MacLean 1966; Bartlett and Simpson 1967; Mitra and Prakash 1957). However, the addition of an ammonium fertilizer will cause soil acidification. It's possible that the addition of an ammonium based fertilizer, coupled with a liming will not only displace the fixed K+ in between the clay interlayers with NH4^{+}, but will also displace the readily exchangeable K+ on the surface exchange sites of the colloid with Ca^{2+} or Mg^{2+} (depending upon the material used). This will then lead to higher soil solution K+ which can then be easily leached from the soil profile.

K+ uptake and translocation

More than 90% of the K+ in soil reaches the root via diffusion (Chatterjee and ani Ghosh 2014; Oliveira et al. 2004). Therefore, anything which can affect diffusion such as root surface area, soil moisture and soil temperature play a large role in the availability of K+ to the plant. If soil moisture is low, K+ will not readily diffuse to the root (Kuchenbuch et al. 1986; Zeng and Brown 2000). Not surprisingly, greater root surface area correlates highly positively with greater K+ uptake, as the vine can simply exploit more of the soil (Brouder and Cassman 1990; Kodur et al. 2009). As soil temperature increases, this can increase the rate of diffusion of K+ in the soil. A study conducted in Bozeman silt loam found that increasing the soil temperature from 5 – 30^{o}C increased the rate of K+ diffusion by about 1.6 times (Figure 3) (Schaff and Skogley 1982).

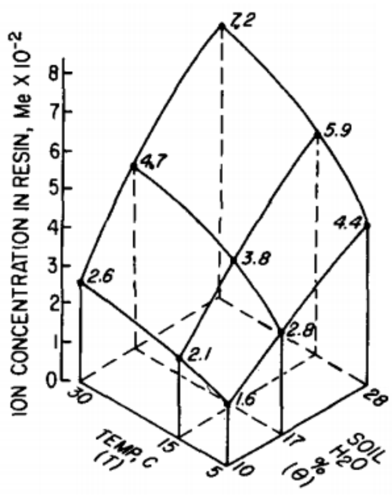

Figure 3. Potassium diffusion as affected by soil temperature and moisture (From Schaff and Skogley, 1982).

As K+ is a highly mobile nutrient within the plant, there are many membrane proteins which facilitate its movement throughout the plant. There are two main K+ transport systems in the grapevine (Figure 4). High affinity proteins are active when the external (soil solution) supply of K+ is low. These high affinity proteins symport protons (H+) along with K+ (Maathuis and Sanders 1994). The other K+ transport mechanism includes low affinity proteins which create voltage gated channels (i.e. K+ moves down the electrochemical gradient) (Maathuis and Sanders 1996).

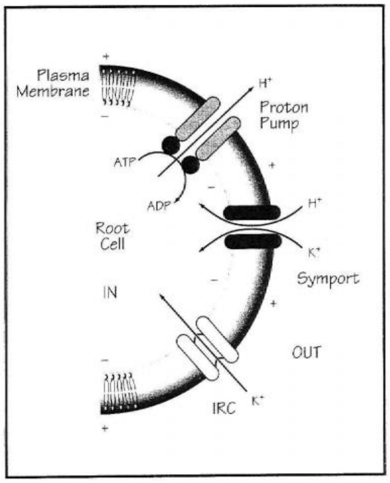

Figure 4. High affinity and low affinity K+ membrane proteins. Low affinity uptake is through the inward rectifying channels (IRC). Both forces are regulated by the activity of the H+/ATP-ase pump.

Once in the plant, K+ is highly mobile and can move easily throughout the xylem and phloem. K+ is not metabolized and has the highest concentration of any cation in the cytosol, the aqueous fluid of the cytoplasm (Marschner 2011). Perhaps the most critical role of K+ in the cell is to counterbalance the charge of soluble organic acid anions (such as malate and tartrate), other anionic species and the movement of protons (H+), thereby maintaining cytosolic pH between 7 to 8 (Marschner 2011). K+ also plays a role in cellular expansion, enzyme activation, osmoregulation and photosynthesis (Keller 2010; Marschner 2011). As K+ is associated with cellular expansion, it is in high demand during periods of rapid growth. The vine mostly depends upon its internal K+ reserves from budbreak until flowering, at which point soil uptake proceeds until just a few weeks prior to leaf senescence (Pradubsuk and Davenport 2010). In a study on Concord, it was found that the vine uptake of K+ was approximately 6 times greater from bloom to veraison than from budbreak to bloom (Pradubsuk and Davenport 2010) (Figure 5).

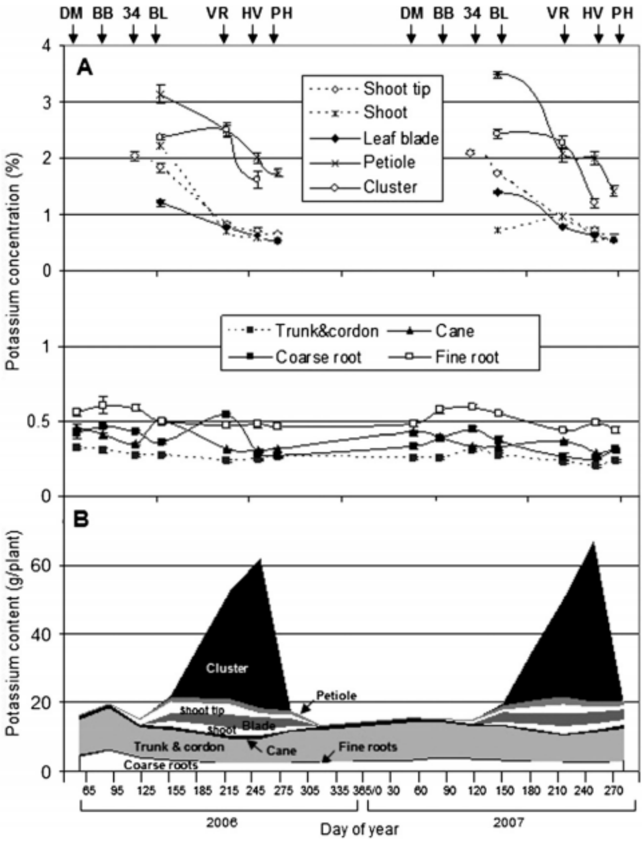

Figure 5. Seasonal dynamics of potassium in the grapevine. Arrows indicate phenological times such as dormancy (DM), budbreak (BB), 3-4 leaf stage (34), bloom (BL), veraison (VR), harvest (HV) and postharvest (PH) (From: Pradubsuk and Davenport, 2010).

K+ in the berry, juice and wine

Berry K+: Pulp and skin have been found to be the greatest sinks for K+ in the grape berry (Rogiers et al. 2015). This is likely due to the role that K+ plays in cellular expansion. In general, the highest proportion of K+ is located in the skins, but this can be dependent upon grape variety, as Walker et al. (1998) found that Muscat grafted upon Ramsey contained 60% of its K+ in the pulp (Iland and Coombe 1988; Walker et al. 1998). In a study which evaluated the mineral sinks in ripening berries, Rogiers et al. (2006) found that although K+ accumulation in the berry was positively related to berry fresh weight, K+ continues to accumulate in the berry after veraison. This is likely due to the role K+ plays in the loading of sucrose into phloem sap, as phloem is the vascular tissue by which most K+ enters the grape berry. Influx of solutes into the berry via the xylem is unlikely to be important due to the low rate of transpiration of a berry relative to other plant tissues (i.e. leaves) (Blanke and Leyhe 1987; Palliotti and Cartechini 2001). Recent research has found that phloem water influx may even be so great that it can exceed berry water needs and can use the berry xylem for outflow (Keller et al. 2015; Tilbrook and Tyerman 2009).

K+ plays a major role in osmoregulation within the plant, it has been theorized that K+ may establish an osmotic potential gradient between the leaves and the fruit (Rogiers et al. 2006). At about 80 days after flowering, Rogiers et al. (2006) found that K+ accumulation in the berry declined. This decline in K+ accumulation was associated with a decline in sugar accumulation, which the authors suggested was due to a decrease in flow of phloem sap to the berry (McCarthy and Coombe 1999). In an earlier study conducted by Rogiers et al. (2000) it was found that K+ concentrations in Shiraz berries increased even after phloem sap flow is thought to slow and K+ concentration increased steadily until harvest (Rogiers et al. 2000). This is either because phloem-berry connectivity is not completely severed or K+ is able to translocate through non-vascular connections, such as plasmodesmata.

Pradubsuk and Davenport (2010) found that the clusters of Concord grapes were the most important sinks for K+ and that they accounted for 40-60% of the total K+ concentration in the vine at harvest (Figure 5). These researchers found that K+ mobilizes rapidly into the grape from fruit set until veraison, at which point it is remobilized to the woody tissues.

Many researchers have reported a significant positive correlation between juice/wine pH and potassium concentration (Boulton 1980a; Hale 1977; Hepner and Bravdo 1985; Iland and Coombe 1988; Morris and Cawthon 1982; Schmidt et al. 2011; Walker and Blackmore 2012). Schmidt et al. (2011) found a significant positive linear relationship ($p<0.01$) between juice pH and K+ concentration (Figure 6). High juice K+ concentrations do not, however, *always* result in high juice pH. In a study evaluating the relationship between K+ and pH, Boulton (1980) found that a juice may have a pH less than 3.25, yet the potassium concentration of the juice may be quite high (Boulton 1980a). This can occur due to K+ exchange with protons from organic acids.

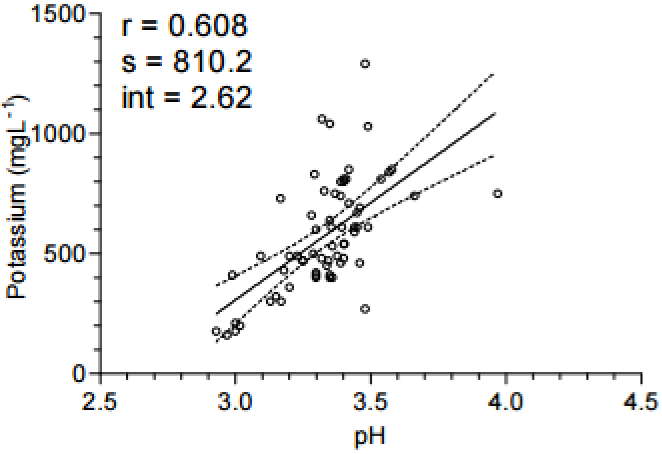

Figure 6. Correlation between Chardonnay juice potassium concentration and pH (From: Schmidt et al. 2011)

Potassium plays a major role in pH regulation of the cell. As H+ protons are loaded into the cell's cytoplasm, pH would decrease, thereby acidifying the cell and hindering normal function. To account for this, cell membranes have several types of cation pumps that help regulate the electrochemical proton gradient that drives the transport of organic acids, sugars, and inorganic ions into the vacuole of the cell. One such pump or membrane transport protein is known by the acronym NHX (Gout et al. 1992; Rodríguez-Rosales et al. 2009). This transporter can exchange K+ (and Na+) for H+ in the vacuole, thereby maintaining not only electrochemical charge balance, but pH (Hanana et al. 2007; Rodríguez-Rosales et al. 2009). Organic acids (i.e. malic and tartaric acid) and sugar are stored primarily in the vacuoles of the mesocarp cells (Lund and Bohlmann 2006). The pH of the vacuole is more acidic than that of the cytosol, normally ranging between 2.2 – 3.5. Tartaric acid has a Pka_1 of 2.89 and malic acid had a Pka_1 of 3.4. Therefore, at vacuolar pH, most tartaric acid is in the deprotonated bitartrate form ($C_4H_6O_6 \rightarrow H+_{(aq)} + C_4H_5O_6-_{(aq)}$). K+ can satisfy the negative charge of bitartrate to form the sensorially inactive K+ salt, potassium bitartrate. At vacuolar pH, this will result in the liberation of an H+ proton and a lowering of the pH. Protons (H+) can diffuse across the tonoplast (vacuole membrane) into the cytoplasm. The NHX antiporter can compensate for this by importing more K+ cations into the vacuole. Therefore, K+ does not directly influence pH, but rather, by forming K+ salts with tartaric acid, K+ can raise juice/wine pH.

Juice and wine K+: Not only does K+ play a role in pH, but it can also influence titratable acidity and modify the tartaric acid:malic acid ratio, through the formation of potassium salts with the anionic organic acid, tartrate (Philip and Kuykendall 1973). As K+ concentrations increase in the grape, so does the formation of potassium bitartaric acid, leading to the subsequent decrease in free tartaric acid. Further, high K+ concentration in the fruit can inhibit the degradation of malic acid (Hale 1977; Lobit et al. 2006). Tartaric acid is associated with the pleasant "crisp" acidity that is desired in high quality wines, whereas malic acid is associated with "sourness" (Amerine et al. 1965). Therefore, as higher K+ concentrations in the berry can result in less free tartaric acid and a greater retention of malic acid, this will shift the tartaric:malic acid ratio towards malic acid, thereby creating an unpleasantly sour acid profile in the resulting wine.

Titratable acidity and pH are mostly adjusted for through the addition of tartaric acid in the juice prior to fermentation. Upon addition to juice, protons dissociate from tartaric acid, thereby lowering the pH of the juice. However, it's effect upon titratable acidity may be mitigated by the K+ concentration in the juice, as the potassium salt may form, thereby resulting in crystallization and precipitation. Potassium bitartrate is far more soluble in an aqueous solution than an alcoholic one. Therefore, as fermentation progresses, more potassium bitartrate is likely to precipitate out of solution, thereby lowering the titratable acidity of the wine. It is for this reason that high K+ concentrations in the juice leads to difficulty juice acidification.

The effect of K+ upon wine pH has significant implications for wine microbial stability and quality. Anthocyanins, the principal pigments found in red grapes and wine, are in a dynamic pH dependent equilibrium between 5 forms. The red pigment, the flavylium cation, accounts for less than 30% of the anthocyanin species above pH 3.0 and declines as pH increases (Keller 2010). Not only will higher pH result in less red color, but the color that does exist will be less stable. Sims and Morris (1985) found that wines made from higher pH juices resulted in wines which browned over time. Anthocyanin-tannin polymerization, which stabilizes color, is hampered by increasing pH (Sims and Morris 1985). The browning of wine at higher pH is due to the oxidation by superoxide radicals of phenols which then form quinones that can undergo further transformations to form brown pigments (Li et al. 2008).

Role of K+ in fermentation

Potassium is an essential mineral nutrient for a successful fermentation. In yeast, just as in plants, potassium exchanges for H^+ in the cytosol in order to modify cytosolic pH (Martínez-Muñoz and Kane 2008). Potassium nutrition is also known to stimulate fermentative rates, by enhancing glucose metabolism by yeast (Rothstein and Demis 1953; Schmidt et al. 2011). There seems to be a relationship between glucose metabolism, pH and K+ during fermentation. Kudo et al. (1998) found that K+ should be at a concentration of 25:1 relative to H+ in order for a fermentation to successfully complete. If the K+:H+ ratio was below 25:1, it was found that fermentation would arrest soon after inoculation (Kudo et al. 1998). Arrested fermentation as caused by K+ deficiency seems to be more of an issue in musts with a pH less than 3.5 (Kudo et al. 1998; Schmidt et al. 2011). If K+ nutrition is limiting in the grape must, it must be ameliorated in the juice prior to inoculation, as yeast viability will be negatively affected and may not recover if K+ concentrations are ameliorated once fermentation has started (Kudo et al. 1998). Potassium amelioration of must is generally unnecessary though, as there are yeast strains available which can withstand a low pH/low K+ fermentative environment (Schmidt et al. 2011).

Rootstock effects upon K+ uptake and translocation

Rootstock choice has been found to have a significant impact upon the uptake and translocation of K+. As K+ reaches the root through diffusion, it might be assumed that those rootstocks known to confer high vigor might also prove efficient at K+ uptake and translocation due to their extensive root systems. However, the relationship between rootstock and K+ may not be that simple.

Rootstocks with *V. berlandieri* parentage do not take up and/or translocate K+ as readily as those stocks coming from a *V. champinii* parentage (Ruhl 1989, 1991; Wolpert et al. 2005). However, there is even significant differences between cultivars of rootstocks coming from the same *Vitis* parentage. In a study conducted upon 6 common rootstocks, it was found that 1103 Paulsen (*V. berlandieri* X *V. rupestris*) had a significantly higher uptake of K+ than 110 Richter (*V. berlandieri* X *V. rupestris*) ($p<0.05$). In the same study, it was found that the translocation efficiency of K+ within 1103 P was significantly greater than that of 140 Ruggeri (*V. berlandieri* X *V. rupestris*)(Kodur et al. 2009). Interestingly, 140Ru is known to confer high vigor to the scion, however it is less efficient at translocating K+ than 110 R or 1103 P (Bettiga 2003; Kodur et al. 2009). 420A (*V. berlandieri* X *V. riparia*) has been shown to confer low vigor to the scion and translocates significantly less K+ than many other rootstocks (Bettiga 2003; Ruhl 1989; Wolpert et al. 2005). As such, 420A may prove useful in Virginia vineyards, should the vineyard be planted on a site with excess K+ concentrations in the soil. In the literature, the most consistently restrictive rootstock with regard to K+ uptake, is 140Ru, however this roostock may not be appropriate for Virginia conditions, as it is known to confer high vigor to the scion (Jones et al. 2009; Kodur 2015).

However, to further complicate matters, it has been found that the rootstock/scion combination also has a significant effect upon berry K+ accumulation. In a study which evaluated potassium accumulation in the berry among 5 varieties either own rooted or grafted to Ramsey, it was found that own rooted vines generally contained lesser K+ in their berries than the grafted vines. The researchers also found that the fruit coming from the Muscat grafted upon Ramsey contained significantly less K+ per berry than Shiraz grafted upon the same rootstock ($p=0.05$) (Walker et al. 1998).

Ruhl (1989) found that rootstock not only affected the K+ uptake and translocation in the vine, but that petiole K+ was highly positively correlated with grape juice pH (figure 7).

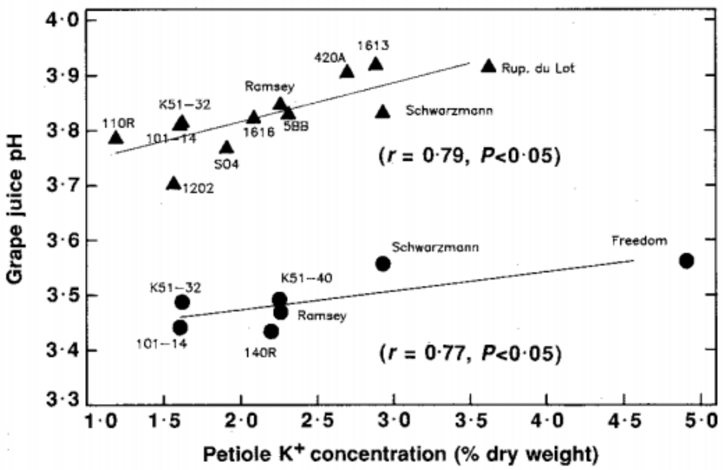

Figure 7. Relationship between petiole K+ concentration and grape juice pH of Chardonnay (▲) and Ruby Cabernet (●) (From: Ruhl, 1989)

Choice of rootstock to limit K+ translocation might partially improve wine pH in vineyards with high soil K+ concentrations.

K+ and irrigation

Studies evaluating the effect of irrigation upon K+ uptake have found that irrigation increases K+ uptake by the vine, thereby increasing berry, must and wine K+ concentrations (Freeman and Kliewer 1983; Hepner and Bravdo 1985; Klein et al. 2000). This is not due to an increase in transpiration, as transpirational rate was not found to be correlated to uptake and translocation of K+ in the grapevine (Kodur et al. 2009). As soil water increases, this facilitates the dissolution of K+ into soil solution, thereby increasing K+ supply to the roots, which can in turn lead to higher K+ uptake. Increased soil water content can also increase vine growth, which in turn can lead to greater demand, uptake and translocation of K+ by the grapevine (Kodur et al. 2009; Matthews et al. 1987). The increased growth associated with higher water status can also increase canopy density, this increase in canopy density will result in leaf shading, which in turn can result in greater K+ accumulation in the fruit (Dokoozlian and Kliewer 1995; dos Santos et al. 2007; Morrison and Noble 1990; Rojas-Lara and Morrison 1989; Smart et al. 1985). The effect of irrigation upon vine and berry K+ uptake/accumulation has not been decoupled from the effect of the increase in vegetative growth.

Because irrigation is less commonly used in Virginia, it is unlikely that the Virginia vintner would be able to utilize a deficit irrigation scheme to limit K+ uptake by the vine. However, root restriction through the use of permeable rootbags may limit root exploration, restricting the root system’s access to water and the amount of K+ able to diffuse to the root in soil. Root restriction has been found to limit K+ uptake/accumulation in tomato (Bar-Tal and Pressman 1996).

Initial experimental results (from Hill et al. 2015 [unpublished]) indicate that grapevine root restriction through the use of porous rootbags can significantly lower concentrations of berry K+ (Table 1).

Table 1: Mean berry K+ concentrations of root-restricted and non-root manipulated vines

Treatment	**Berry K+ concentration (mg/L)***
Rootbag	701.3 b
Non-Root manipulated	930.3 a

*****Significant difference between treatments ($P<0.001$) as determined by Student’s T test. Means followed by different letters are significantly different.

Results from the same study indicate that cover cropping had no significant effect upon K+ concentration in the berry (unpublished data).

Impact of canopy management upon K+

Fruit zone light environment has also been shown to be highly correlated with K+ accumulation in the berry, with fruit shading promoting the accumulation of K+ and subsequent increase in pH (Dokoozlian and Kliewer 1995; Jogaiah et al. 2013; Kliewer and Bledsoe 1986; Morrison and Noble 1990; Rojas-Lara and Morrison 1989). Several studies have found that fruit which is shaded by leaves accumulate significantly fewer soluble solids than fruit which is exposed to more light (Jogaiah et al. 2013; Morrison and Noble 1990; Rojas-Lara and Morrison 1989). Through shading cloth experiments, it was found that K+ accumulation as a result of shading was due to shading of the foliage, rather than the fruit itself (Morrison and Noble 1990). Mpelasoka et al. (2003) suggest that K^+ may be transported to grape berries under shaded conditions in order to compensate for the lack of sugar accumulation, which in turn effects the osmotic potential. By importing more K+ to the berry, the vine is able to maintain cellular turgor and avoid a reduction in berry growth (Mpelasoka et al. 2003). Therefore, any activity which can affect the grapevine canopy light environment (specifically leaf layer number) can influence the K+ concentration in the grape berry (i.e. shoot positioning, leaf removal, trellis type, hedging, pruning, cover cropping, plant material selection).

Conclusions

One of the major challenges faced by Eastern wine growers is that of elevated juice pH at harvest. This is likely not only a function of heat during ripening which is associated with the metabolization of malic acid through respiration, but also high potassium concentrations in fruit. High juice/wine K+ can lead to:

1. Formation of K+ acid salts
2. Less solubility of tartaric acid additions
3. Higher juice/wine pH
4. Reduced microbial stability of wines
5. Less oxidative buffering
6. Less color intensity and stability
7. Lower tartaric:malic acid ratio (increased perception of sourness)

To limit K+ accumulation in the grape one might proceed as follows:

1. Lime the soil with calcitic and/or dolomitic lime if pH is less than 6.8
2. Use rootstocks with *V. berlandieri* parentage
3. Employ root restriction at planting by using porous rootbags (experimental only)
4. Avoid premature leaf senescence by avoiding shading through canopy management
5. Avoid K+ fertilizer applications unless absolutely necessary, and they only with foliar K fertilizer

6. Avoid *unnecessary* irrigation of vines, recognizing that irrigation might be needed under drought conditions or with young vines (small root systems)

Obviously, K+ performs many critical biological functions within the plant. Care must therefore be taken when attempting to manage K+ uptake, as a deficiency in K+ can be equally harmful to not only wine quality, but also vine function, including crop yield. As such, further research and optimization of management strategies relating to K+ should be undertaken in Virginia in order to provide the Virginia vintner with specific, proven and relevant management strategies.

References

Acquaye, D., and A. MacLean. 1966. Influence of form and mode of nitrogen fertilizer application on the availability of soil and fertilizer potassium. Canadian Journal of Soil Science 46:23-28.

Amerine, M., E. Roessler, and C. Ough. 1965. Acids and the acid taste. I. The effect of pH and titratable acidity. American Journal of Enology and Viticulture 16:29-37.

Bar-Tal, A., and E. Pressman. 1996. Root restriction and potassium and calcium solution concentrations affect dry-matter production, cation uptake, and blossom-end rot in greenhouse tomato. Journal of the American Society for Horticultural Science 121:649-655.

Bartlett, R., and T. Simpson. 1967. Interaction of ammonium and potassium in a potassium-fixing soil. Soil Science Society of America Journal 31:219-222.

Bettiga, L.J. 2003. *Wine grape varieties in California*. UCANR Publications.

Blanke, M.M., and A. Leyhe. 1987. Stomatal activity of the grape berry cv. Riesling, Müller-Thurgau and Ehrenfelser. Journal of plant physiology 127:451-460.

Boulton, R. 1980a. The general relationship between potassium, sodium and pH in grape juice and wine. American Journal of Enology and Viticulture 31:182-186.

———. 1980b. A hypothesis for the presence, activity, and role of potassium/hydrogen, adenosine triphosphatases in grapevines. American Journal of Enology and Viticulture 31:283-287.

Brady, N.C., and R.R. Weil. 1996. *The nature and properties of soils*. Prentice-Hall Inc.

Brann, D.E., A. Abaye, P. Peterson, D.R. Chalmers, D.L. Whitt, G.F. Chappell, D.A. Herbert, S. McNeill, J. Baker, and S.J. Donohue. 2009. Agronomy handbook.

Brouder, S., and K. Cassman. 1990. Root development of two cotton cultivars in relation to potassium uptake and plant growth in a vermiculitic soil. Field Crops Research 23:187-203.

Chatterjee, S., and D. ani Ghosh. 2014. Effect of Different Factors on Diffusion Characteristics of Potassium in Alluvial Soils of Eastern Inclo Gangetic Plain. International Journal of Soil Science 9:75.

Conradie, W., and D. Saayman. 1989a. Effects of long-term nitrogen, phosphorus, and potassium fertilization on Chenin blanc vines. I. Nutrient demand and vine performance. American journal of enology and viticulture 40:85-90.

———. 1989b. Effects of long-term nitrogen, phosphorus, and potassium fertilization on Chenin blanc vines. II. Leaf analyses and grape composition. American journal of enology and viticulture 40:91-98.

Cuéllar, T., F. Azeem, M. Andrianteranagna, F. Pascaud, J.L. Verdeil, H. Sentenac, S. Zimmermann, and I. Gaillard. 2013. Potassium transport in developing fleshy fruits: the grapevine inward K+ channel VvK1. 2 is activated by CIPK–CBL complexes and induced in ripening berry flesh cells. The Plant Journal 73:1006-1018.

Davies, J.M., R.J. Poole, P.A. Rea, and D. Sanders. 1992. Potassium transport into plant vacuoles energized directly by a proton-pumping inorganic pyrophosphatase. Proceedings of the National Academy of Sciences 89:11701-11705.

Dokoozlian, N., and W. Kliewer. 1995. The light environment within grapevine canopies. II. Influence of leaf area density on fruit zone light environment and some canopy assessment parameters. American Journal of Enology and Viticulture 46:219-226.

dos Santos, T.P., C.M. Lopes, M.L. Rodrigues, C.R. de Souza, J.M. Ricardo-da-Silva, J.P. Maroco, J.S. Pereira, and M.M. Chaves. 2007. Effects of deficit irrigation strategies on cluster microclimate for improving fruit composition of Moscatel field-grown grapevines. Scientia Horticulturae 112:321-330.

Freeman, B.M., and W.M. Kliewer. 1983. Effect of irrigation, crop level and potassium fertilization on Carignane vines. II. Grape and wine quality. American Journal of Enology and Viticulture 34:197-207.

Gout, E., R. Bligny, and R. Douce. 1992. Regulation of intracellular pH values in higher plant cells. Carbon-13 and phosphorus-31 nuclear magnetic resonance studies. Journal of Biological Chemistry 267:13903-13909.

Hale, C. 1977. Relation between potassium and the malate and tartrate contents of grape berries. Vitis-Berichte ueber Rebenforschung mit Dokumentation der Weinbauforschung (Germany, FR).

Hanana, M., O. Cagnac, T. Yamaguchi, S. Hamdi, A. Ghorbel, and E. Blumwald. 2007. A grape berry (Vitis vinifera L.) cation/proton antiporter is associated with berry ripening. Plant and cell physiology 48:804-811.

Hannan, J.M. 2011. Potassium-magnesium antagonism in high magnesium vineyard soils. Masters thesis, Iowa State University.

Hepner, Y., and B. Bravdo. 1985. Effect of crop level and drip irrigation scheduling on the potassium status of Cabernet Sauvignon and Carignane vines and its influence on must and wine composition and quality. American journal of enology and viticulture 36:140-147.

Iland, P., and B. Coombe. 1988. Malate, tartrate, potassium, and sodium in flesh and skin of Shiraz grapes during ripening: concentration and compartmentation. American Journal of Enology and Viticulture 39:71-76.

Jakobsen, S.T. 1993. Interaction between plant Nutrients: III. Antagonism between potassium, magnesium and calcium. Acta Agriculturae Scandinavica B-Plant Soil Sciences 43:1-5.

Jogaiah, S., K.R. Striegler, E. Bergmeier, and J. Harris. 2013. Influence of Canopy Management Practices on Canopy Characteristics, Yield, and Fruit Composition of ‘Norton’Grapes (Vitis aestivalis Michx). International Journal of Fruit Science 13:441-458.

Jones, T., B.R. Cullis, P.R. Clingeleffer, and E. Rühl. 2009. Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines. Australian Journal of Grape and Wine Research 15:284-292.

Kabu, K., and E. Toop. 1970. Influence of potassium-magnesium antagonism on tomato plant growth. Canadian Journal of Plant Science 50:711-715.

Keller, M. 2010. *The science of grapevines: anatomy and physiology*. Academic Press/Elsevier, Amsterdam; Boston.

Keller, M., Y. Zhang, P.M. Shrestha, M. Biondi, and B.R. Bondada. 2015. Sugar demand of ripening grape berries leads to recycling of surplus phloem water via the xylem. Plant, cell & environment 38:1048-1059.

Khan, S., R. Mulvaney, and T. Ellsworth. 2014. The potassium paradox: Implications for soil fertility, crop production and human health. Renewable Agriculture and Food Systems 29:3-27.

Klein, I., M. Strime, L. Fanberstein, and Y. Mani. 2000. Irrigation and fertigation effects on phosphorus and potassium nutrition of wine grapes. VITIS-GEILWEILERHOF- 39:55-62.

Kliewer, M., and A. Bledsoe. Influence of hedging and leaf removal on canopy microclimate, grape composition, and wine quality under California conditions. *In* Proceedings of the Symposium on Grapevine Canopy and Vigor Management, XXII IHC 206. pp. 157-168.

Kodur, S. 2015. Effects of juice pH and potassium on juice and wine quality, and regulation of potassium in grapevines through rootstocks (Vitis): a short review. Vitis-Journal of Grapevine Research 50:1.

Kodur, S., J. Tisdall, C. Tang, and R. Walker. 2009. Accumulation of potassium in grapevine rootstocks (Vitis) as affected by dry matter partitioning, root traits and transpiration. Australian Journal of Grape and Wine Research 16:273-282.

Kuchenbuch, R., N. Claassen, and A. Jungk. 1986. Potassium availability in relation to soil moisture. Plant and Soil 95:233-243.

Kudo, M., P. Vagnoli, and L.F. Bisson. 1998. Imbalance of pH and potassium concentration as a cause of stuck fermentations. American journal of enology and viticulture 49:295-301.

Li, H., A. Guo, and H. Wang. 2008. Mechanisms of oxidative browning of wine. Food chemistry 108:1-13.

Lobit, P., M. Genard, P. Soing, and R. Habib. 2006. Modelling malic acid accumulation in fruits: relationships with organic acids, potassium, and temperature. Journal of Experimental Botany 57:1471-1483.

Lund, S.T., and J. Bohlmann. 2006. The molecular basis for wine grape quality-A volatile subject. Science 311:804-805.

Maathuis, F., and D. Sanders. 1994. Mechanism of high-affinity potassium uptake in roots of Arabidopsis thaliana. Proceedings of the National Academy of Sciences 91:9272-9276.

Maathuis, F.J., and D. Sanders. 1996. Mechanisms of potassium absorption by higher plant roots. Physiologia Plantarum 96:158-168.

Marschner, H. 2011. *Marschner's mineral nutrition of higher plants*. Academic press.

Martínez-Muñoz, G.A., and P. Kane. 2008. Vacuolar and plasma membrane proton pumps collaborate to achieve cytosolic pH homeostasis in yeast. Journal of Biological Chemistry 283:20309-20319.

Matthews, M., M. Anderson, and H. Schultz. 1987. Phenologic and growth responses to early and late season water deficits in Cabernet franc. Vitis 26:147-160.

McCarthy, M.G., and B. Coombe. 1999. Is weight loss in ripening grape berries cv. Shiraz caused by impeded phloem transport? Australian Journal of Grape and Wine Research 5:17-21.

Mitra, S., and D. Prakash. 1957. Some Studies on Ionic Competition in Base Exchange Reactions of Homo-Ionic Montmorillonites. Proceedings of the Japan Academy 33:341-345.

Morris, J., and D. Cawthon. 1982. Effect of irrigation, fruit load, and potassium fertilization on yield, quality, and petiole analysis of Concord (Vitis labrusca L.) grapes. American Journal of Enology and Viticulture 33:145-148.

Morrison, J., and A. Noble. 1990. The effects of leaf and cluster shading on the composition of cabernet sauvignon grapes and on fruit and wine sensory properties. American Journal of Enology and Viticulture 41:193-200.

Mpelasoka, B.S., D.P. Schachtman, M.T. Treeby, and M.R. Thomas. 2003. A review of potassium nutrition in grapevines with special emphasis on berry accumulation. Australian Journal of Grape and Wine Research 9:154-168.

Obermeyer, G., A. Sommer, and F.-W. Bentrup. 1996. Potassium and voltage dependence of the inorganic pyrophosphatase of intact vacuoles from Chenopodium rubrum. Biochimica et Biophysica Acta (BBA)-Biomembranes 1284:203-212.

Oliveira, R., C. Rosolem, and R. Trigueiro. 2004. Importance of mass flow and diffusion on the potassium supply to cotton plants as affected by soil water and potassium. Revista Brasileira De Ciencia Do Solo 28:439-445.

Ollat, N., and J. Gaudillère. 1995. Investigation of assimilate import mechanisms in berries of Vitis vinifera var.'Cabernet Sauvignon'. Strategies to Optimize Wine Grape Quality 427:141-150.

Palliotti, A., and A. Cartechini. 2001. Developmental changes in gas exchange activity in flowers, berries, and tendrils of field-grown Cabernet Sauvignon. American Journal of Enology and Viticulture 52:317-323.

Pathak, A., and Y. Kalra. 1971. Antagonism between potassium, calcium and magnesium in several varieties of hybrid corn. Zeitschrift für Pflanzenernährung und Bodenkunde 130:118-124.

Philip, T., and J. Kuykendall. 1973. Changes in titratable acidity, Brix, pH, potassium content, malate and tartrate during berry development of Thompson seedless grapes. Journal of Food Science 38:874-876.

Pradubsuk, S., and J.R. Davenport. 2010. Seasonal uptake and partitioning of macronutrients in mature 'Concord'grape. Journal of the American Society for Horticultural Science 135:474-483.

Reitemeier, R.F. 1951. The Chemistry of Soil Potassium. Advances in Agronomy 3:113.

Rodríguez-Rosales, M.P., F.J. Gálvez, R. Huertas, M.N. Aranda, M. Baghour, O. Cagnac, and K. Venema. 2009. Plant NHX cation/proton antiporters. Plant signaling & behavior 4:265-276.

ROGIERS, S., M. KELLER, B.P. HOLZAPFEL, and J.M. Virgona. 2000. Accumulation of potassium and calcium by ripening berries on field vines of Vitis vinifera (L) cv. Shiraz. Australian Journal of Grape and Wine Research 6:240-243.

Rogiers, S.Y., D. Greer, J. Hatfield, B. Orchard, and M. Keller. 2015. Mineral sinks within ripening grape berries (Vitis vinifera L.). VITIS-Journal of Grapevine Research 45:115.

Rogiers, S.Y., D.H. Greer, J.M. Hatfield, B.A. Orchard, and M. Keller. 2006. Solute transport into Shiraz berries during development and late-ripening shrinkage. American Journal of Enology and Viticulture 57:73-80.

Rojas-Lara, B., and J. Morrison. 1989. Differential effects of shading fruit or foliage on the development and composition of grape berries. Vitis 28:27-63.

Rothstein, A., and C. Demis. 1953. The relationship of the cell surface to metabolism. The stimulation of fermentation by extracellular potassium. Archives of biochemistry and biophysics 44:18-29.

Ruhl, E. 1989. Uptake and distribution of potassium by grapevine rootstocks and its implication for grape juice pH of scion varieties. Animal Production Science 29:707-712.

———. 1991. Effect of potassium supply on cation uptake and distribution in grafted Vitis champinii and Vitis berlandieri x Vitis rupestris rootstocks. Animal Production Science 31:687-691.

Schaff, B., and E. Skogley. 1982. Diffusion of potassium, calcium, and magnesium in Bozeman silt loam as influenced by temperature and moisture. Soil Science Society of America Journal 46:521-524.

Schmidt, S.A., S. Dillon, R. Kolouchova, P.A. Henschke, and P.J. Chambers. 2011. Impacts of variations in elemental nutrient concentration of Chardonnay musts on Saccharomyces cerevisiae fermentation kinetics and wine composition. Applied microbiology and biotechnology 91:365-375.

Schroeder, D. 1978. Structure and weathering of potassium containing minerals. I iunm:5.

Scott, A., and S. Smith. Susceptibility of interlayer potassium in micas to exchange with sodium. *In* Proceedings of the Clays and Clay Minerals: Proceedings of the Fourteenth National Conference, Berkeley, California. pp. 69. Elsevier.

Sherwood, W.C., A.S. Hartshorn, and L.S. Eaton. 2010. Soils, geomorphology, landscape evolution, and land use in the Virginia Piedmont and Blue Ridge. Field Guides 16:31-50.

Sims, C., and J. Morris. 1985. A comparison of the color components and color stability of red wine from Noble and Cabernet Sauvignon at various pH levels. American journal of enology and viticulture 36:181-184.

Smart, R., J. Robinson, G. Due, and C. Brien. 1985. Canopy microclimate modification for the cultivar Shiraz. II. Effects on must and wine composition. Vitis 24:119-128.

Sparks, D.L. 1987. Potassium dynamics in soils. *In* Advances in Soil Science. pp. 1-63. Springer.

Tilbrook, J., and S.D. Tyerman. 2009. Hydraulic connection of grape berries to the vine: varietal differences in water conductance into and out of berries, and potential for backflow. Functional Plant Biology 36:541-550.

Walker, R., and D. Blackmore. 2012. Potassium concentration and pH inter-relationships in grape juice and wine of Chardonnay and Shiraz from a range of rootstocks in different environments. Australian Journal of Grape and Wine Research 18:183-193.

Walker, R., P. Clingeleffer, G. Kerridge, E. Rühl, P. Nicholas, and D. Blackmore. 1998. Effects of the rootstock Ramsey (Vitis champini) on ion and organic acid composition of grapes and wine, and on wine spectral characteristics. Australian Journal of Grape and Wine Research 4:100-110.

Wolpert, J.A., D.R. Smart, and M. Anderson. 2005. Lower petiole potassium concentration at bloom in rootstocks with Vitis berlandieri genetic backgrounds. American journal of enology and viticulture 56:163-169.

Zeng, Q., and P.H. Brown. 2000. Soil potassium mobility and uptake by corn under differential soil moisture regimes. Plant and Soil 221:121-134.