



Challenging the potassium deficiency hypothesis for induction of the ripening disorder berry shrivel in grapevine



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ABSTRACT

Berry shrivel (BS) is a ripening dysfunction resulting in grapes with low sugar content, high acidity, reduced anthocyanins and flaccid berries. In this study we challenge the K⁺-deficiency hypothesis as underlying cause for BS in grapevine. The hypothesis is based on empirical vineyard studies and proposes that K⁺-deficiency or a disbalance of K⁺/Mg²⁺ in plant content cause of BS. Recent studies on more grapevine varieties and further geographical locations lack supporting evidence for the K⁺ hypothesis. Here we review existing evidence from the field and apply physiological analyses to study processes involved in K⁺ and nutrients transport in BS and non-symptomatic clusters. For the first time the molecular background of K⁺ transportation is being studied over the course of BS disorder.

Our objectives were (1) to determine the distribution of nutrients in BS vines and clusters and (2) to evaluate the role of selected potassium transport proteins and channels during grape berry development and BS induction in pedicels and berries. Our results with ICP-MS show a strong and significant reduction of K⁺ concentration in rachis and pedicels of BS grapes, whereas boron, zinc, copper and aluminum were increased. Concentration of nutrients in BS berries were either not changed or increased compared to non-symptomatic clusters. Expression analyses with qPCR in pedicels revealed no pre-symptomatic differences of genes involved in potassium transport (VviKUP1, VviKUP2 and VviK1.2), but later during ripening reduced expression was observed. In BS berries the expression of VviK1.2 was reduced before veraison. We show significant K⁺ deficiency in BS rachis and pedicels along with partial reduced expression of K⁺ transporter genes. Consequently K⁺ phloem transport is involved in BS induction, however our study did not provide conclusive evidence to support the K⁺ deficiency hypothesis as a single factor for BS induction. Instead the idea that a combination of further stress factors influences K⁺ and assimilates translocation towards sink organs before veraison is proposed.

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1. Introduction

Grape berry ripening is characterized by a first growth phase with rapid cell division, followed by a lag period corresponding with the onset of ripening called veraison. Major physiological and biochemical changes occur during this phase, preparing grape berries

for the ripening process with sugar accumulation and organic acid depletion (Coombe, 1992). Especially the phloem unloading process is changed dramatically with a shift from symplast to apoplast, characterized by the activity of transport proteins and invertases (Zhang et al., 2006). Sometimes this complex ripening process is disturbed leading to physiological ripening disorders as berry shrivel (BS). BS is also named sugar accumulation disorder (SAD) (Krasnow et al., 2009a) and suppression of uniform ripening (SOUR) (Bondada, 2014). Several *Vitis vinifera* cultivars such as Cabernet Sauvignon (Bondada and Keller, 2012; Krasnow et al., 2009b), Sauvignon blanc (Raifer et al., 2014) and Zweigelt (Bachteler et al., 2013; Griesser et al., 2012; Knoll et al., 2010) have been described being BS susceptible and subject to major economic losses. BS

Abbreviations: BS, berry shrivel; ICP-MS, inductively coupled plasma mass spectrometry; qPCR, quantitative polymerase chain reaction; SAD, sugar accumulation disorder; SOUR, suppression of uniform ripening; NRQ, normalized relative quantities; DAA, days after anthesis; V, veraison.

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symptoms are well described with loss of turgor, high acidity, low pH, low anthocyanin and sugar contents and mesocarp cell death in the berry and the rachis (Bondada, 2014; Bondada and Keller, 2012; Griesser et al., 2012; Hall et al., 2011; Krasnow et al., 2009b). Visible symptoms of BS appear shortly after the beginning of ripening implying BS induction around veraison. Study shows that berry development from flowering to veraison is not affected including complete seed development (Bondada and Keller, 2012; Hall et al., 2011). Causes for BS remain hypothetical and functional studies are difficult to perform since BS cannot be artificially induced in controlled studies so far. Seen as a physiological disorder, an attributed cause of BS may be deficiency or imbalance of nutrients. The K⁺ deficiency hypothesis claims that BS is induced by K⁺ shortage or a surplus of magnesium in the subsoil leading to an imbalanced K⁺:Mg²⁺ ratio in the soil and subsequently also inside the plant (Fardossi, 2000; Mehofer and Regner, 2010). Significant lower amounts of K⁺ in BS affected berries of Cabernet Sauvignon as compared to healthy berries have been observed (Bondada, 2014; Bondada and Keller, 2012). Whereas effects on berry K⁺ content were only observed in one out of three years with Gewürztraminer, Pinot blanc and Pinot gris (Raifer et al., 2014). Similar results were obtained with Zweigelt (Griesser et al., 2012) and with Pinot blanc and Zweigelt, where no significant difference in K⁺ content in berry juice was determined in two years (Bachteler et al., 2013). Experiments with different K⁺ and Mg²⁺ fertilizers have been conducted in Germany and no influence on BS and BSN incidence on different varieties could be observed (Bachteler et al., 2015; Bachteler et al., 2013). Regarding other nutrients, recently strong reduction of nutrients (K, P, Ca, Mg, S, B, Fe, Cu, Zn, Al) in SOUR berries of Cabernet Sauvignon was determined (Bondada, 2016). The current knowledge on K⁺ distribution in BS grapes provides contradicting results and no functional studies have been published so far.

In general, nutritional elements are essential for growth and development in plants, with roles as structural components, enzyme activators, charge carriers and osmoregulators (Marschner, 2012). K⁺ is the most abundant cation in plant cells and plants (Keller, 2010) and has four physiological-biochemical roles: enzyme activation, cellular membrane transport processes and translocation of assimilates, anion neutralization and osmotic potential regulation (Mpelasoka et al., 2003). Additionally K⁺ has multiple roles in biotic and abiotic stress resistance as has been reviewed recently (Wang et al., 2013). Drought conditions restrict root growth and nutrient diffusion in soils, limiting e.g. K⁺ acquisition. Keeping an adequate K⁺ level in plants is important, as a linkage between K⁺ nutritional status and plant drought resistance has been demonstrated. Affected processes cover cell elongation and cell membrane stability, aquaporin regulation, osmotic adjustment, stomatal regulation and detoxification of reactive oxygen species (Wang et al., 2013).

Within grapevine, grape berries become strong sinks for K⁺ and estimated K⁺ contents in grape berries at harvest reach approximately 60% of the total vine K⁺ content (Mpelasoka et al., 2003). Early in the season at exponential vegetative growth the majority of K⁺ is accumulated in leaves and redistributed towards berries after veraison (Mpelasoka et al., 2003). K⁺ may play distinct roles during berry development, first as osmoregulator before veraison, when berry cells divide and expand at high rates and second as co-factor of sugar accumulation after veraison (Conde et al., 2008). A positive correlation between vacuolar sugar and K⁺ concentrations was found, indicating a coupled sugar and potassium influx via the phloem (Keller and Shrestha, 2014). K⁺ deficiency is usually linked to a suppressed phloem loading which leads to excess sucrose in leaves triggering a feedback inhibition of photosynthesis (Tsay et al., 2011). Cell viability is also affected in K⁺ deficient plants, as plant organs low in K⁺ are likely to undergo induced programmed cell death (Demidchik et al., 2014).

The uptake of K⁺ into plant cells can be mediated by passive K⁺ channels and active K⁺ carriers, as for example in *Arabidopsis thaliana* more than 30 membrane proteins are proposed to be dedicated to K⁺ transport, which can be grouped in fine families (Shaker, TPK, Kir-like, HAK/KUP/KT, and KEA) (Sharma et al., 2013). The Shaker family encodes voltage-gated K⁺ channels, consisting of 6 transmembrane α -helices incorporating a pore loop and four subunits form a whole K⁺ channel complex (Wang and Wu, 2013). They are divided in three categories according to their voltage dependence: inward-rectifying activated by membrane hyperpolarization potential for mainly K⁺ uptake, outward-rectifying channels activated by membrane depolarization for mainly K⁺ efflux and weakly rectifying channels for both directions (Cherel et al., 2014; Lebaudy et al., 2007; Wang and Wu, 2013). Thereby they play roles in controlling the membrane potential, the sugar transport and maybe also the recirculation of K⁺ within the phloem as proposed for the Shaker channel AKT2 (Cherel et al., 2014). Plant HAK/KUP/KT (High-Affinity K⁺/K⁺ Uptake/K⁺ Transporter) transporter family have been identified in plants from their bacterial KUP and fungal KAK transporter homologues (Nieves-Cordones et al., 2016). Most of the functionally characterized HAK/KUP/KT transporters belong to cluster I (high-affinity K⁺ uptake) for K⁺ uptake at low external concentrations and cluster II (low-affinity K⁺ transport) complementing K⁺ channels (Grabov, 2007). They function as high affinity H⁺:K⁺ symport systems (Gierth and Maser, 2007). Two members of KUP/KT/HAK potassium transporter gene family, namely VviKUP1 and VviKUP2 were identified and characterized in grapevine and their function as K⁺ transporters was determined. The highest expression of both genes was observed in flowers, seeds and berry skins before veraison (Davies et al., 2006). The proposed function is either in K⁺ uptake into berries or in compartmentation into skin cells (Davies et al., 2006). Phylogenetic analyses of the plasma membrane potassium channel Shaker family revealed nine members, from which VviK1.2 has been characterized in more detail (Cuellar et al., 2013). The expression of VviK1.2 is strongly induced in grape berries after veraison and was localized in phloem tissues and perivascular cells surrounding vascular bundles feeding the pips (Cuellar et al., 2013). It was also observed that drought stress can dramatically increase the expression of VviK1.2 in berries (Cuellar et al., 2013). Two other channels have been characterized: VviSIRK with an expression in young berries, but not after veraison (Pratelli et al., 2002) and VviK1.1 with an expression in root peripheral cells and a low expression in seeds of young berries (Cuellar et al., 2013). There is evidence that VviK1.2 is controlled by the CBL-interacting Ser/Thr protein Kinase (CIPK)/calcineurin B-like Ca²⁺ sensor (CBL) complex VviCIPK04-VviCBL01 (Cuellar et al., 2013).

The K⁺ deficiency hypothesis for BS induction is both supported and contradicted by experimental evidence. The majority of data comprises K⁺ availability in soil (natural soils, fertilization studies) vs. K⁺ contents in BS vines and grapes. However, K⁺ contents and concentrations in BS berries are not consistent. Controlled experiments to prevent BS induction (environment and fertigation) (Bachteler et al., 2015; Bachteler et al., 2013; Raifer et al., 2014) were not successful so far, therefore we propose a molecular genetic perspective to study the K⁺ distribution within the grapevine cluster. Such gene expression studies focusing on K⁺ transport have not been conducted so far. In the presented work we therefore combined analytical analyses (leaves, rachis, pedicels, berries) with gene expression analyses in different tissues (pedicels and berries) of healthy and BS affected grape samples collected at six different dates representing developmental stages from BBCH79 (majority of berries touching) to BBCH89 (berries ripe for harvesting). Candidate gene of K⁺ transporter and channels, namely VviKUP1, VviKUP2, VviK1.2 and the CIPK-CBL control complex VviCIPK04-VviCBL01, were analyzed in our study. Their temporal expression profiles

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