REVIEW PAPER

Sugars and plant innate immunity

Mohammad Reza Bolouri Moghaddam and Wim Van den Ende*

KU Leuven, Laboratory of Molecular Plant Biology, Kasteelpark Arenberg 31, B-3001 Leuven, Belgium

* To whom correspondence should be addressed. E-mail: wim.vandenende@bio.kuleuven.be

Received 27 January 2012; Revised 25 March 2012; Accepted 30 March 2012

Abstract

Sugars are involved in many metabolic and signalling pathways in plants. Sugar signals may also contribute to immune responses against pathogens and probably function as priming molecules leading to pathogen-associated molecular patterns (PAMP)-triggered immunity and effector-triggered immunity in plants. These putative roles also depend greatly on coordinated relationships with hormones and the light status in an intricate network. Although evidence in favour of sugar-mediated plant immunity is accumulating, more in-depth fundamental research is required to unravel the sugar signalling pathways involved. This might pave the way for the use of biodegradable sugar-(like) compounds to counteract plant diseases as cheaper and safer alternatives for toxic agrochemicals.

Key words: immunity, pathogen, priming, signal, sugar.

Introduction

Sugars such as glucose, fructose, and sucrose are recognized as signalling molecules in plants (Rolland et al., 2006; Bolouri-Moghaddam et al., 2010), in addition to their typical roles as carbon and energy sources (Koch, 2004). Invertases play crucial roles in the regulation of sucrose levels, sink strength, and sucrose:hexose ratios linked to sugar signalling. Vacuolar, cell wall, and neutral/alkaline invertases can be discerned (Koch, 2004; Xiang et al., 2011). Sugar signalling might also be of great importance in plant (defence) responses under biotic and abiotic stresses. Therefore, sugars from microbial (Moxon and Kroll, 1990; Smith, 1990; Levitz, 2004; Zaragoza et al., 2009) or plant (Herbers et al., 1996a) origin might play critical roles in host–pathogen interactions (Morkunas et al., 2005) and determine the outcome of such reactions. Plant innate immunity involves two kinds of responses: a response to slowly emerging pathogen/microbe-associated molecular patterns (PAMP or MAMP, respectively) such as flagellin through transmembrane pattern recognition receptors leading to PAMP-triggered immunity and a response inside the cell via the activation of most resistance genes, known as effector-triggered immunity (Jones and Dangl, 2006; Chisholm et al., 2006). Sugars are well known to activate various pattern recognition genes (Herbers et al., 1996a,b; Johnson and Ryan, 1990). Among these, cell wall invertases (CWIs), extracellular enzymes that split sucrose into glucose and fructose, are also considered PR proteins (Roitsch et al., 2003). Among sugars, sucrose is emerging as a candidate signalling molecule in plant innate immunity (Gómez-Ariza et al., 2007; Birch et al., 2009). Whether or not sucrose can be considered a true ‘priming’ agent remains unclear. Defined in a narrow sense, priming is a process that prepares a plant for a faster and/or stronger defence response without actually starting those defence responses prior to the respective stress condition (Conrath, 2011). The important benefit of priming is that the plant does not suffer from a cost benefit (reduced fitness/yield) accompanied by the actual defence response.

It is likely that a coordinated interaction of sugar and hormonal pathways in plants leads to effective immune responses. It can be speculated that shifts in apoplastic sugar levels are sensed, and these signals might be integrated with those derived from the sensing of PAMP and further activation through systemic acquired resistance.
(SAR). In plants, these mechanisms are probably affected by light and photoperiod.

The aim of this paper is to review current evidence on the roles of sugars in plant innate immunity. The functions of sugars (or sugar-like compounds) as metabolites and as signal molecules and their interaction with hormones and light during pathogen attacks are discussed.

Roles of various saccharides in the plant defence system

The role of soluble sugars in resistance responses to pathogens has been recognized (Table 1), as they can stimulate isoﬂavone accumulation in plants as part of a defence mechanism (Morkunas et al., 2005). Among them, small oligosaccharides like 1-kestose (a fructosyl oligosaccharide) and rafﬁnose (a galactosyl oligosaccharide), as well as the disaccharide trehalose and galactinol (galactosyl-myoinositol) were found to accumulate to a high extent in syncytia during nematode infection (Hofmann et al., 2010). Moreover, some of these metabolites, especially 1-kestose and rafﬁnose, were accumulating in a systemic way in non-infected plant parts, suggesting that these non-reducing oligosaccharides can be used as transportable stress signals. Indeed, these oligosaccharides are known to be phloem mobile. Some plant families even use rafﬁnose-family oligosaccharides as their main transport sugars (Keller and Pharr, 1996) and small fructans have also been reported as phloem-transportable sugars (Wang and Nobel, 1998; Zuther et al., 2004). The origin of these oligosaccharides during nematode infection is unknown, but it can be assumed that they cannot originate from the nematodes themselves (Hofmann et al., 2010). It can be speculated that 1-kestose is produced by the activity of vacuolar invertases. Two forms occur in Arabidopsis (AtVI1 and AtVI2), and both enzymes produce signiﬁcant amounts of 1-kestose when the enzymes are challenged with very high sucrose concentrations (De Coninck et al., 2005). Source-sink disturbances and local increases in sucrose and myo-inositol concentrations are often observed under (a)biotic stresses (Valluru and Van den Ende, 2011). Such mechanisms stimulate the production of galactinol (mediated by galactinol synthase) as a precursor for the synthesis of rafﬁnose (catalysed by rafﬁnose synthase). Evidence has been generated that galactinol and probably also rafﬁnose are involved as signals to stimulate plant immunity under pathogen attack (Kim et al., 2008). Indeed, external application of galactinol resulted in the activation of PR1a, PR1b, and MtACS1, which are well-known defence-related genes in tobacco (Kim et al., 2008).

Trehalose is another well-known non-reducing sugar that has been shown to partially induce resistance against powdery mildew (Blumeria graminis f. sp. tritici) in wheat by activation of phenylalanine ammonia-lyase and peroxidase genes (Reignault et al., 2001; Muchembled et al., 2006). The expression of a putative trehalose 6-phosphate synthase/phosphatase 11 (TPS11) gene increased in Arabidopsis plants infected with tobacco mosaic virus (Golem and Culver, 2003). In contrast to wild-type plants, no trehalose accumulation and proper resistance against green peach aphid were observed in tps11 knockout plants. Resistance could be restored by external trehalose application, suggesting that trehalose is an essential signal in the defence process (Singh et al., 2011). It should be noted that a phosphorylated form of this sugar, trehalose 6-phosphate, is emerging as an important regulator of plant growth, development, and senescence processes (Wingerl et al., 2012), linked to important alterations in carbohydrate metabolism (e.g. altered sucrose-to-starch ratios). Similar alterations are observed during aphid infestation (Singh et al., 2011). It is likely that trehalose 6-phosphate functions as an inhibitor of SnRK1 (KIN10/KIN11) (Wingerl et al., 2012). In Arabidopsis, TPS11 mediates resistance against the green peach aphid through the expression of the phytoalexin deficient 4 (PDA 4) gene (Singh et al., 2011).

It is well known that some plant defence genes are induced by cell-wall-derived oligogalacturonides (OGs) in response to fungal invasion. These compounds are released from the plant cell wall and act as elicitors of the immune system (Ridley et al., 2001; Denoux et al., 2008). It is probable that wall-associated kinase 1 (WAK1) and WAK2 are the actual receptors of these molecules (Brutus et al., 2010), transferring the signal across the plasma membrane. Furthermore, these WAK genes are upregulated by salicylic

Table 1. Roles of various sugars and sugar-like compounds in plant innate immunity

<table>
<thead>
<tr>
<th>Sugars and sugar-like compounds</th>
<th>Function</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sucrose</td>
<td>Anthocyanin accumulation, activation of PR genes</td>
<td>Sofianelli et al., 2006; Thibaud et al., 2004; Gómez-Ariza et al., 2007</td>
</tr>
<tr>
<td>Galactinol</td>
<td>Activation of defence genes PR1a, PR1b, and MtACS1</td>
<td>Kim et al., 2008</td>
</tr>
<tr>
<td>Raffinose-family oligosaccharides</td>
<td>Induction of resistance against nematode infection</td>
<td>Hofmann et al., 2010</td>
</tr>
<tr>
<td>Trehalose</td>
<td>Induction of resistance against powdery mildew and aphid infestation</td>
<td>Reignault et al., 2001; Muchembled et al., 2006; Singh et al., 2011</td>
</tr>
<tr>
<td>Oligogalacturonides</td>
<td>Response to fungal invasion</td>
<td>Ridley et al., 2001; Denoux et al., 2008</td>
</tr>
<tr>
<td>Palatinose, fluoro-sucrose, and turanose</td>
<td>Activation of MAPKs</td>
<td>Sinha et al., 2002</td>
</tr>
<tr>
<td>Psicose</td>
<td>Induction of resistance to bacterial blight</td>
<td>Kano et al., 2011</td>
</tr>
<tr>
<td>Allose and DMDP</td>
<td>Activation of defence-related genes</td>
<td>Birch et al., 1993; Derridj et al., 2009; Kano et al., 2011</td>
</tr>
</tbody>
</table>
Sucrose:hexose ratio might influence defence responses. The link between WAKs and transcriptional/enzyme regulation is established by mitogen-activated protein kinases (MAPKs) such as MPK3 and MPK6 (Kohorn et al., 2011). Intriguingly, loss-of-function wak2 mutants need external sugars for normal growth and also show reduced vacuolar invertase activities (Kohorn et al., 2006). Taken together, the WAK signalling pathway controls the expression of many defence genes and alters cellular sugar metabolism through sensing of extra-cellular OGs.

Furthermore, evidence is accumulating that some rare sugars such as psicose and D-allose and the sugar-like 2,5-dideoxy-2,5-imino-D-mannitol (DMDP, a fructose analogue) can stimulate the plant immune system and upregulate defence-related genes. It has been suggested that these compounds act as signals through hexokinase-dependent or -independent pathways (Birch et al., 1993; Derridj et al., 2009; Kano et al., 2011). However, DMDP also acts as a strong invertase inhibitor by binding in the heart of the active site of CWIs and vacuolar invertases (Verhaest et al., 2007). DMDP can also enter the cell (Müller et al., 2000) and, as such, it can increase the cellular sucrose:hexose ratio, differentially influencing glucose- (Moore et al., 2003), fructose- (Li et al., 2011), and sucrose-specific signalling pathways (Smeekens et al., 2010). Such an altered sucrose:hexose ratio might influence defence responses. In Arabidopsis, D-allose interferes with gibberellin acid (GA)-mediated signalling in a hexokinase-dependent way (Fotopoulos et al., 2003; Kocal et al., 2010). Therefore, exogenous application of rare sugars as non-metabolized compounds might be recognized as pathogen-derived elicitors triggering the plant defence signalling cascade.

Sucrose, invertase, and plant immunity

Sucrose is the major product of photosynthesis and the major transport carbohydrate in plants (Koch, 2004). It has been recognized as contributing to various regulatory mechanisms in plants including growth and development, differential gene expression and stress-related responses (Wind et al., 2010). Interestingly, it has been proposed that sucrose can act as an endogenous signal to induce defence responses against pathogens in rice. Indeed, exogenous sucrose application 1 day before infection effectively increased plant resistance (Gómez-Ariza et al., 2007). Accordingly, exogenous sucrose application, UVB irradiation and MAMPs activate PR1 and PR2 genes (Thibaud et al., 2004). It has also been documented that defence-related genes such as OsPR1a, OsPR1b, PBZ1, and PR5 were upregulated systemically in rice leaves when sucrose was fed to the roots (Gómez-Ariza et al., 2007). Sucrose applications also lead to increased defence responses against Fusarium in lupin (Morkunas et al., 2005), probably (at least partly) mediated by the accumulation of isoflavonoids.

Anthocyanins as a type of flavonoid, in addition to their function as pigments with UV-protecting properties, can also act as antimicrobial agents as part of the plant defence system against pathogen invasion (Harborne and Williams, 2000; Winkel-Shirley, 2001). However, the precise mechanisms remain unclear.

Sucrose specifically stimulates the accumulation of anthocyanins (Solfanelli et al., 2006), while, in contrast, pathogen-derived flg22 can selectively inhibit this sucrose-mediated anthocyanin accumulation (Serrano et al., 2012). The specificity of sucrose as a signalling molecule was demonstrated by the fact that equimolar applications of glucose and fructose did not lead to extensive anthocyanin accumulation (Solfanelli et al., 2006). It has been reported that anthocyanin biosynthesis by sucrose-specific induction needs the MYB75/PAP1 gene (Teng et al., 2005). In conclusion, high sucrose:hexose ratios can probably trigger a sucrose-specific signal for inducing genes needed to produce an array of protective agents such as anthocyanins and other secondary metabolites (Kwon et al., 2011).

Within sugar pools, the cellular sucrose:hexose ratio is emerging as an important parameter determining cellular responses (bolouri-Moghaddam et al., 2010; Xiang et al., 2011). Invertases, as sucrose-splitting enzymes, are involved in carbohydrate partitioning and the regulation of sucrose:hexose ratios. As such, some invertase forms may take a central position (Proels and Roitsch, 2009) as key regulators linked to the different (sugar) signalling pathways in plants. Invertase-related sugar signals seem to be very important during plant defence reactions (Fotopoulos et al., 2003; Kocal et al., 2008), as well as during symbiosis (Schaarschmidt et al., 2006). During plant–pathogen interactions, CWI genes are induced by elicitors in different plant species (Sturm and Chrisspeels, 1990; Roitsch et al., 2003; Berger et al., 2004). MAPKs are involved in this process (Hyun et al., 2009). However, there are contradictory reports on the role of CWIs and their inhibitors in pathogen responses (Bonfig et al., 2006, 2010; Essmann et al., 2008; Kocal et al., 2008). The exact functions of invertase/invertase inhibitor complexes in source and sink tissues remain unclear and require further investigations (Hothorn et al., 2010). Furthermore, the precise roles of so-called fructan exohydrolases in non-fructan plants (De Coninck et al., 2005), now considered to be defective CWIs, remain puzzling (Van den Ende et al., 2009).

High CWI activities were reported to be required to generate hydrogen peroxide (H2O2), a reactive oxygen species and signalling molecule in defence responses (Essmann et al., 2008). H2O2 was shown to be a key signal...
independent of SA and jasmonic acid (JA) pathways in plant immune responses (Miller et al., 2009). Abscisic acid (ABA) might play a role in such processes by increasing the expression of CWIs and hexose importers (Hayes et al., 2010). It was also shown that H₂O₂ stimulates biosynthesis of glutathione S-transferase, contributing to the SA pathway (Leon et al., 1995; Dong, 2004).

Taken together, the evidence described in the two paragraphs suggests the importance of sucrose and other soluble saccharides in mediating plant defence responses. However, the precise mechanism of saccharide-induced immunity and the related signalling mechanisms remain unclear. The putative roles of invertases and reactive oxygen or nitrogen species in these processes also require further investigation. Moreover, microbial invertases and sugar importers can also greatly determine the outcome of plant–microbial interactions (Wahl et al., 2010; Schwachtje et al., 2011), adding an extra layer of complexity.

Sugar–hormone interactions, light, and immunity

Cross-talk between sugar and hormone signalling pathways in defence reactions of plants has been demonstrated (Leon and Sheen, 2003). When plants face pathogen invasion, some phytohormones function as signalling molecules for stimulation of plant innate immunity to activate defence responses (Pieterse et al., 2009).

A fine-tuned cross-talk among ABA, SA, and PAMP-triggered signals culminates in stomatal closure and affects the defence responses together with other signalling pathways (Melotto et al., 2008; Ton et al., 2009; Cutler et al., 2010). As susceptibility to foliar pathogens has been observed in many mutants with open stomata (Melotto et al., 2006), stomatal closure is probably the first layer of defence against PAMPs with a recognized stimulatory role for ABA (Ton et al., 2009). Recently, HSP90 and HSC70, important players in plant (Ting et al., 2008) and animal (Shirasu, 2009) innate immunity, have been reported to fulfil a critical role in stomatal closure and modulation of physiological responses to ABA (Clément et al., 2011). The transcription of HSP90 is increased by ABA (Leng, 2008). ABA-dependent stomatal closure is mediated by elevated H₂O₂ as a signal and usually occurs in response to drought stress, leading to carbohydrate accumulation (Pattanagul, 2011). ABA-induced H₂O₂ can activate MAPK and related antioxidant pathways (Zhang et al., 2006). In addition, it has been demonstrated that ABA can positively affect and control a sugar-inducible protein kinase in grape (Lecourieux et al., 2010). However, these pathways need to be dissected further.

In addition to its emerging role in plant defence responses, ABA probably also fulfils an important regulatory role in sugar supply and/or osmoregulation under (a)biotic stress. However, at low sugar concentrations, antagonistic effects of ABA have been observed during Arabidopsis seed germination (Garcia-Ruiz et al., 1997). ABA increases the expression of some cell wall and vacuolar invertase genes (Trouverie et al., 2004; Hayes et al., 2010) and increases invertase activities under drought stress (Kim et al., 2000). It has also been suggested that ABA activates invertase by downregulating its inhibitor (Koh et al., 2008). In contrast, an inhibitory role for ABA in invertase expression has been reported in wheat anthers (Ji et al., 2011). It seems that responses to drought stress and pathogens might partially overlap, with ABA as a positive stimulator. Nevertheless, it has been documented that ABA also negatively affects immune responses (Hayes et al., 2010), depending on pathogen type, plant tissues, and developmental stages (Robert-Seilaniantz et al., 2007; Asselbergh et al., 2008; Ton et al., 2009). Therefore, it is becoming clear that ABA shows a complex and dual role in pathogen resistance.

A positive interaction of ABA and fructose signalling through hormone biosynthesis has been reported (Cho and Yoo, 2011). It was also demonstrated that ABA provokes the expression of anthocyanin biosynthesis-related genes such as CHS, CHI, DFR, and UFGT, as well as the regulatory factor VmPyb1A1 in grape skin (Jeong et al., 2004; Ban et al., 2003). In addition, exogenous application of ABA results in anthocyanin accumulation in grape with no effect on fruit quality and yield (Quiroga et al., 2009). However, ABA-induced anthocyanin accumulation might be affected by the genotype (Ithal and Reddy, 2004).

Cytokinins are another class of plant hormones regulating various processes including plant immunity. Recently, it has been shown that cytokinins have a beneficial effect on pathogen resistance by strongly increasing the levels of antibacterial activities against Pseudomonas syringae pv. tabaci and by upregulating the production of two antimicrobial phytoalexins in tobacco, independent of SA signaling (Großkinsky et al., 2011). Cytokinins also induce resistance against various viruses (Sano et al., 1996; Pogany et al., 2004), induce SA in wounding responses (Sano et al., 1996), and suppress the hypersensitive response (Barna et al., 2008).

Cytokinins can induce CWI and hexose transporter expression in Chenopodium rubrum (Ehneß and Roitsch, 1997). They cannot delay leaf senescence in the absence of CWI activity (Balibrea et al., 2004). Recently, the association between cytokinin and nitric oxide (NO) has been demonstrated. NO is a multi-functional messenger molecule. It contributes to many physiological processes such as flavonoid production and antioxidant activation by stimulating plant defence genes (Xie et al., 2008). NO mediates OG-triggered immunity and contributes to resistance responses against Botrytis cinerea in Arabidopsis (Rasul et al., 2012). Therefore, although cytokinins show antagonism with ABA in stomatal closure, their interaction with invertase and NO points to a signalling network operating in the next layers of defence.

There is a strong correlation between sucrose and either JA or cytokinin in the induction of the anthocyanin biosynthesis-related genes. This not only indicates the capacity of sucrose to modulate some common anthocyanin regulatory factors (Shan et al., 2009) but also substantiates the significance of both sugars and hormones as joined
modulators of pathways leading to anthocyanin accumulation (Deikman and Hammer, 1995; Weiss, 2000; Solfanelli et al., 2006).

These findings suggest that ABA and sucrose exhibit similar effects on anthocyanin accumulation in plants. Several lines of evidence illustrate the intimate cross-talk of ABA and sugar signalling pathways. Involvement of ABI3 and two other loci in glucose-insensitive signalling demonstrates that glucose signalling shares high similarities with ABA signalling (Dekkers et al., 2008). Interestingly, a similar cross-talk has also been observed between ethylene and sugar signalling (Li et al., 2007). Ethylene-insensitive mutants of Arabidopsis (ein2-1) showed increased levels of anthocyanin accumulation in response to sucrose treatment, indicating a negative role of ethylene in the sucrose and fructose signalling pathways (Kwon et al., 2011). However, exogenous application of ethylene, but not methyl jasmonate or SA, conferred resistance against Phytophthora blight in Habanero pepper through an NPR1-independent, SAR-like response (Núñez-Pastrana et al., 2011).

In tobacco, the expression levels of PR-Q and PRI seem to be increased in response to sucrose, glucose, and fructose treatments in an SA-independent manner. Equimolar application of sorbitol was insignificant, suggesting that osmotic effects were not involved in the process (Herbers et al., 1996b). Therefore, Herbers et al. (1996b) hypothesized that such an SA-independent, sugar-mediated route in defence against pathogen attacks might play a significant role in the early stages of plant–pathogen interactions, before the onset of SA-mediated SAR (Herbers et al., 1996b).

JA- and SA-dependent defence responses have been found to function antagonistically (reviewed by Robert-Seilaniantz et al., 2007). ABA antagonizes SA (Audenaert et al., 2002) but synergizes with JA (Asselbergh et al., 2008), suggesting a pivotal role for ABA between these two pathways.

Although JA and a number of transcription factors are potential regulators of the anthocyanin pathway in Arabidopsis (Gao et al., 2011; Qi et al., 2011), it has been shown that the cross-talk among GA, JA, ABA, and sucrose in a complex signalling network can modulate anthocyanin accumulation and, notably, sucrose signalling seems to be a primary and essential component in this network (Loreti et al., 2008).

Defence responses of plants to pathogens and herbivores have been recognized to be highly affected by light (Karpinski et al., 2003; Bechtold et al., 2005; Roberts and Paul, 2006; Roden and Ingle, 2009). Arabidopsis transcriptomic data showed that the plant transcriptional response to the light/dark transition strongly resembles responses associated with carbon depletion (Morker and Roberts, 2011). Next to sucrose (Solfanelli et al., 2006), light is an essential factor for anthocyanin accumulation (Morker and Roberts, 2011). The regulatory role for phytochromes in light- and sucrose-induced biosynthesis, accumulation of anthocyanins, and SAR has been revealed in many plants (Griebel and Zeier, 2008). Although it has been shown that all members of the phytochrome (Phy) family enhance the accumulation of sucrose-dependent anthocyanins in continuous red light, Phy A has a distinct regulatory role in response to sucrose. Unlike other isoforms, Phy E can suppress anthocyanin biosynthesis/accumulation in continuous red light (Warnasooriya et al., 2011). Interestingly, sucrose, light, and hormonal balances (probably the GA:ABA ratio) seem to affect seedling growth differentially in the light and in the dark in Arabidopsis (Zhang et al., 2010). Notably, there is a central role for DELLA proteins in similar processes during seed germination (Piskurewicz et al., 2009).

In rice, it has been demonstrated that JA and SA signalling pathways are regulated by phytochromes, inducing PRI and conferring resistance to the blast fungus Magnaporthe grisea. Phy A and JA have been proposed to act synergistically against herbivores and after wounding (Robson et al., 2010). All the above data suggest that activation of various defence-related mechanisms, including a putative sugar-signalling pathway, may depend greatly on the applied photoperiod and light intensity.

Conclusions and perspectives

Plant innate immunity does not involve straightforward pathways but arises as a highly complicated network including many signalling molecules and various cross-talks. In this intricate network, sugar signals may contribute to immune responses and probably function as priming molecules. It is likely that these putative roles also depend greatly on coordinated relationships with hormones and light status. Today, plant protection against a vast range of invasive pathogens and pests needs promising strategies to produce various agrochemicals to confer crop resistance (Rahnamaeian, 2011). However, producing agrochemicals with no environmental risks is almost impossible. Moreover, plant resistance breeding programmes are time-consuming, and conferred resistance may be lost in a relatively short time. Therefore, there is a strong need to find biodegradable and cheap alternatives. More fundamental research is needed towards sugar-mediated plant immunity in order to explore further the possibilities of using biodegradable sugar-(like) compounds as alternatives to toxic agrochemicals.

Acknowledgements

W.V.d.E. is supported by funds from FWO-Vlaanderen.

References


Audenaert K, De Meyer GB, Høfte MM. 2002. Abscisic acid determines basal susceptibility of tomato to Botrytis cinerea and


Hayes MA, Feechan A, Dry IB. 2010. Involvement of abscisic acid in the coordinated regulation of a stress-inducible hexose transporter (VvHT5) and a cell wall invertase in grapevine in response to biotrophic fungal infection. Plant Physiology 153, 211–221.


Ithal N, Reddy AR. 2004. Rice flavonoid pathway genes, OsDfr and OsAns, are induced by dehydration, high salt and ABA, and contain stress responsive promoter elements that interact with the transcription activator. OsCT1-MYB. Plant Science 166, 1505–1513.


Quiroga AM, Berli FJ, Moreno D, Cavagnaro JB, Bottini R. 2009. Abscisic acid sprays significantly increase yield per plant in vineyard-grown wine grape (*Vitis vinifera* L.) cv. *Cabernet Sauvignon* through increased berry set with no negative effects on anthocyanin content and total polyphenol index of both juice and wine. *Journal of Plant Growth Regulation* 28, 28–35.


Physiology


