

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

Abbreviations: ABA, abscisic acid; CWI, cell wall invertase; DMDP, 2,5-dideoxy-2,5-imino-D-mannitol; GA, gibberellic acid; JA, jasmonic acid; MAMP, microbe associated molecular patterns; MAPKs, mitogen activated protein kinases; NO, nitric oxide; OGs, oligogalacturonides; PAMP, pathogen associated molecular patterns; Phy, phytochrome; PR, pathogenesis-related; SA, salicylic acid; SAR, systemic acquired resistance; WAK, wall-associated kinase.

© The Author [2012]. Published by Oxford University Press [on behalf of the Society for Experimental Biology]. All rights reserved.
For Permissions, please e-mail: journals.permissions@oup.com

(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* (AtVII 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 myoinositol 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 *NtACSI*, 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 (Wingler *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) (Wingler *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

Sugars and sugar-like compounds	Function	Reference
Sucrose	Anthocyanin accumulation, activation of PR genes	Solfanelli <i>et al.</i> , 2006; Thibaud <i>et al.</i> , 2004; Gómez-Ariza <i>et al.</i> , 2007
Galactinol	Activation of defence genes <i>PR1a</i> , <i>PR1b</i> , and <i>NtACSI</i>	Kim <i>et al.</i> , 2008
Raffinose-family oligosaccharides	Induction of resistance against nematode infection?	Hofmann <i>et al.</i> , 2010
Trehalose	Induction of resistance against powdery mildew and aphid infestation	Reignault <i>et al.</i> , 2001; Muchembled <i>et al.</i> , 2006; Singh <i>et al.</i> , 2011
Oligogalacturonides	Response to fungal invasion	Ridley <i>et al.</i> , 2001; Denoux <i>et al.</i> , 2008
Palatinose, fluoro-sucrose, and turanose	Activation of MAPKs	Sinha <i>et al.</i> , 2002
Psicose	Induction of resistance to bacterial blight	Kano <i>et al.</i> , 2011
Allose and DMDP	Activation of defence-related genes	Birch <i>et al.</i> , 1993; Derridj <i>et al.</i> , 2009; Kano <i>et al.</i> , 2011

acid (SA), wounding, and bacterial infection (He *et al.*, 1998; Wagner and Kohorn, 2001). 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 gibberellic acid (GA)-mediated signalling in a hexokinase-dependent way (Fukumoto *et al.*, 2011). In rice, it has also been documented that psicose induces resistance to bacterial blight (Kano *et al.*, 2011). Furthermore, exogenous application of the sucrose isomers palatinose and turanose and fluorosucrose (a sucrose analogue) can act as elicitors to activate MAPKs (Sinha *et al.*, 2002). 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 isoflavanoids.

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).

It has been known for a long time that virus infection leads to increased sugar levels in plant tissues (Watson and Watson, 1951; Shalitin and Wolf, 2000). This suggests that plants have the ability to modulate their sugar pools to act either as a source of carbon and energy or to use as signals and perhaps as putative priming agents to intensify immune reactions (Gómez-Ariza *et al.*, 2007).

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 Chrispeels, 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 (Garcarrubio *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 *VvmybA1* 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 signalling (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 *PR1* 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 *PR1* 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

- Asselbergh B, De Vleeschauwer D, Hofte M. 2008. Global switches and fine-tuning: ABA modulates plant pathogen defence. *Molecular Plant-Microbe Interaction* **21**, 709–719.
- Audenaert K, De Meyer GB, Höfte MM. 2002. Abscisic acid determines basal susceptibility of tomato to *Botrytis cinerea* and

suppresses salicylic acid-dependent signaling mechanisms. *Plant Physiology* **128**, 491–501.

Balibrea Lara ME, Gonzalez Garcia MC, Fatima T, Ehness R, Lee TK, Proels R, Tanner W, Roitsch T. 2004. Extracellular invertase is an essential component of cytokinin-mediated delay of senescence. *Plant Cell* **16**, 1276–1287.

Ban T, Ishimaru M, Kobayashi S, Shiozaki S, Goto-Yamamoto N, Horiuchi S. 2003. Abscisic acid and 2,4-dichlorophenoxyacetic acid affect the expression of anthocyanin biosynthetic pathway genes in 'Kyoho' grape berries. *Journal of Horticultural Science and Biotechnology* **78**, 586–589.

Barna B, Smigocki AC, Baker JC. 2008. Transgenic production of cytokinin suppresses bacterially induced hypersensitive response symptoms and increases antioxidative enzyme levels in *Nicotiana* spp. *Phytopathology* **98**, 1242–47.

Bechtold U, Karpinski S, Mullineaux PM. 2005. The influence of the light environment and photosynthesis on oxidative signaling responses in plant–biotrophic pathogen interactions. *Plant Cell and Environment* **28**, 1046–1055.

Berger S, Papadopoulos M, Schreiber U, Kaiser W, Roitsch T. 2004. Complex regulation of gene expression, photosynthesis and sugar levels by pathogen infection in tomato. *Physiologia Plantarum* **122**, 419–428.

Birch ANE, Roberson WM, Geoghegan IE, MC-Gavin WJ, Alpheyt JW, Porter EA. 1993. DMDP – a plant-derived sugar analogue with systemic activity against plant parasitic nematodes. *Nematologica* **39**, 521–535.

Birch ANE, Shepherd T, Hancock R, Goszcz K. 2009. Understanding sugar sensing in induced plant defences and stress tolerance. In: *Proceedings of the 25th meeting of the International Society of Chemical Ecology*, 23–27 August 2009, Neuchatel, Switzerland, 230.

Bolouri-Moghaddam MR, Le Roy K, Xiang L, Rolland F, Van den Ende W. 2010. Sugar signalling and antioxidant network connections in plant cells. *FEBS Journal* **277**, 2022–2037.

Bonfig KB, Gabler A, Simon UK, Luschin-Ebengreuth N, Hatz M, Berger S, Muhammad N, Zeier J, Sinha AK, Roitsch T. 2010. Post-translational derepression of invertase activity in source leaves via down-regulation of invertase inhibitor expression is part of the plant defence response. *Molecular Plant* **3**, 1037–1048.

Bonfig KB, Schreiber U, Gabler A, Roitsch T, Berger S. 2006. Infection with virulent and avirulent *P. syringae* strains differentially affects photosynthesis and sink metabolism in *Arabidopsis* leaves. *Planta* **225**, 1–12.

Brutus A, Sicilia F, Macone A, Cervone F, De Lorenzo G. 2010. A domain swap approach reveals a role of the plant wall-associated kinase 1 (WAK1) as a receptor of oligogalacturonides. *Proceedings of the National Academy of Sciences, USA* **107**, 9452–9457.

Chisholm ST, Coaker G, Day B, Staskawicz BJ. 2006. Host-microbe interactions: shaping the evolution of the plant immune response. *Cell* **124**, 803–814.

Cho YH, Yoo SD. 2011. Signaling role of fructose mediated by FINS1/FBP in *Arabidopsis thaliana*. *PLOS Genetics* **7**, 1–10.

Clément M, Leonhardt N, Droillard MJ, Reiter I, Montillet JL, Genty B, Laurière C, Nussaume L, Noël LD. 2011. The cytosolic/nuclear Hsc70 and Hsp90 molecular chaperones are important for stomatal closure and modulate abscisic acid-dependent physiological responses in *Arabidopsis*. *Plant Physiology* **156**, 1481–1492.

Cutler SR, Rodriguez PL, Finkelstein RR, Abrams SR. 2010. Abscisic acid: emergence of a core signaling network. *Annual Review of Plant Biology* **61**, 651–679.

Conrath U. 2011. Molecular aspects of defence priming. *Trends in Plant Science* **16**, 524–531.

De Coninck B, Le Roy K, Francis I, Clerens S, Vergauwen R, Halliday AM, Smith SM, Van Laere A, Van den Ende W. 2005. *Arabidopsis* AtcwINV3 and 6 are not invertases but are fructan exohydrolases (FEHs) with different substrate specificities. *Plant Cell and Environment* **28**, 432–443.

Deikman J, Hammer PE. 1995. Induction of anthocyanin accumulation by cytokinins in *Arabidopsis thaliana*. *Plant Physiology* **108**, 47–57.

Dekkers BJ, Schuurmans JA, Smeekens SC. 2008. Interaction between sugar and abscisic acid signalling during early seedling development in *Arabidopsis*. *Plant Molecular Biology* **67**, 151–167.

Denoux C, Galletti R, Mammarella N, Gopalan S, Werck D, De Lorenzo G, Ferrari S, Ausubel FM, Dewdney J. 2008. Activation of defence response pathways by OGs and fig22 elicitors in *Arabidopsis* seedlings. *Molecular Plant* **1**, 423–445.

Derridj S, Elad Y, Birch ANE. 2009. Sugar signaling and a new way for vegetable and fruit induced resistance against insects, pathogens and nematodes. IOBC/WPRS Working Group “Induced resistance in plants against insects and diseases”, Granada, Spain, 12–16 May 2009. <http://www.fvccce.uji.es/abstractbook.pdf>.

Dong X. 2004. NPR1, all things considered. *Current Opinion in Plant Biology* **7**, 547–552.

Ehneß R, Roitsch T. 1997. Coordinated induction of extracellular invertase and glucose transporters in *Chenopodium rubrum* by cytokinins. *Plant Journal* **11**, 539–548.

Essmann J, Schmitz-Thom I, Schon H, Sonnewald S, Weis E, Scharte J. 2008. RNA interference-mediated repression of cell wall invertase impairs defence in source leaves of tobacco. *Plant Physiology* **147**, 1288–1299.

Fotopoulos V, Gilbert MJ, Pittman JK, Marvier AC, Buchanan AJ, Sauer N, Hall JL, Williams LE. 2003. The monosaccharide transporter gene, *AtSTP4*, and the cell-wall invertase, *Atβfruct1*, are induced in *Arabidopsis* during infection with the fungal biotroph *Erysiphe cichoracearum*. *Plant Physiology* **132**, 821–829.

Fukumoto T, Kano A, Ohtani K, et al. 2011. Rare sugar D-allose suppresses gibberellin signaling through hexokinase-dependent pathway in *Oryza sativa* L. *Planta* **234**, 1083–1095.

Gao JJ, Shen XF, Zhang Z, Peng RH, Xiong AS, Xu J, Zhu B, Zheng JL, Yao QH. 2011. The *myb* transcription factor *MdMYB6* suppresses anthocyanin biosynthesis in transgenic *Arabidopsis*. *Plant Cell Tissue and Organ Culture* **106**, 235–242.

Garcarrubio A, Legaria JP, Covarrubias AA. 1997. Abscisic acid inhibits germination of mature *Arabidopsis* seeds by limiting the availability of energy and nutrients. *Planta* **203**, 182–187.

- Golem S, Culver J.** 2003. Tobacco mosaic virus induced alterations in the gene expression profile of *Arabidopsis thaliana*. *Molecular Plant–Microbe Interactions* **16**, 681–688.
- Gómez-Ariza J, Campo S, Rufat M, Estopà M, Messeguer J, San Segundo B, Coca M.** 2007. Sucrose-mediated priming of plant defence responses and broad-spectrum disease resistance by overexpression of the maize pathogenesis-related PRms protein in rice plants. *Molecular Plant–Microbe Interactions* **20**, 832–842.
- Griebel T, Zeier J.** 2008. Light regulation and daytime dependency of inducible plant defences in *Arabidopsis*: phytochrome signaling controls systemic acquired resistance rather than local defence. *Plant Physiology* **147**, 790–801.
- Großkinsky DK, Naseem M, Abdelmohsen UR, et al.** 2011. Cytokinins mediate resistance against *Pseudomonas syringae* in tobacco through increased antimicrobial phytoalexin synthesis independent of salicylic acid signalling. *Plant Physiology* **157**, 815–830.
- Harborne JB, Williams CA.** 2000. Advances in flavonoid research since 1992. *Phytochemistry* **55**, 481–504.
- 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.
- He ZH, He DZ, Kohorn BD.** 1998. Requirement for the induced expression of a cell wall associated receptor kinase for survival during the pathogen response. *Plant Journal* **14**, 55–63.
- Herbers K, Meuwly P, Frommer W, Métraux JP, Sonnewald U.** 1996a. Systemic acquired resistance mediated by the ectopic expression of invertase: possible hexose sensing in the secretory pathway. *Plant Cell* **8**, 793–803.
- Herbers K, Meuwly P, Métraux JP, Sonnewald U.** 1996b. Salicylic acid independent induction of pathogenesis-related protein transcripts by sugars is dependent on leaf developmental stage. *FEBS Letter* **397**, 239–244.
- Hofmann J, El Ashry A, Anwar S, Erban A, Kopka J, Grundler F.** 2010. Metabolic profiling reveals local and systemic responses of host plants to nematode parasitism. *The Plant Journal* **62**, 1058–1071.
- Hothorn M, Van den Ende W, Lammens W, Rybin V, Scheffzek K.** 2010. Structural insights into the pH-controlled targeting of plant cell-wall invertase by a specific inhibitor protein. *Proceedings of the National Academy of Sciences, USA* **107**, 17427–17432.
- Hyun TK, Hoffmann A, Sinha AK, Roitsch T.** 2009. Tomato mitogen activated protein kinases regulate the expression of extracellular invertase Lin6 in response to stress related stimuli. *Functional Plant Biology* **36**, 1088–1097.
- 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. *OsC1-MYB*. *Plant Science* **166**, 1505–1513.
- Jeong ST, Goto-Yamamoto N, Kobayashi S, Esaka M.** 2004. Effects of plant hormones and shading on the accumulation of anthocyanins and the expression of anthocyanin biosynthetic genes in grape berry skins. *Plant Science* **167**, 247–252.
- Ji X, Dong B, Shiran B, Talbot MJ, Edlington JE, Hughes T, White RG, Gubler F, Dolferus R.** 2011. Control of abscisic acid catabolism and abscisic acid homeostasis is important for reproductive stage stress tolerance in cereals. *Plant Physiology* **156**, 647–662.
- Johnson R, Ryan CA.** 1990. Wound-inducible potato inhibitor II genes: enhancement of expression by sucrose. *Plant Molecular Biology* **14**, 527–536.
- Jones JD, Dangl JL.** 2006. The plant immune system. *Nature* **444**, 323–329.
- Kano A, Hosotani K, Gomi K, et al.** 2011. D-Psicose induces upregulation of defence-related genes and resistance in rice against bacterial blight. *Journal of Plant Physiology* **168**, 1852–1857.
- Karpinski S, Gabrys H, Mateo A, Karpinska B, Mullineaux PM.** 2003. Light perception in plant disease defence signalling. *Current Opinion in Plant Biology* **6**, 390–396.
- Keller F, Pharr DM.** 1996. Metabolism of carbohydrates in sinks and sources: galactosyl-sucrose oligosaccharides. In: Zamski E, Schaffer AA, eds. *Photoassimilate distribution in plants and crops: source–sink relationships*. New York: Marcel Dekker, 157–183.
- Kim JY, Mahé A, Brangeon J, Prioul JL.** 2000. A maize vacuolar invertase, IVR2, is induced by water stress, organ/tissue specificity and diurnal modulation of expression. *Plant Physiology* **124**, 71–84.
- Kim MS, Cho SM, Kang EY, Im YJ, Hwangbo H, Kim YC, Ryu CM, Yang KY, Chung GC, Cho BH.** 2008. Galactinol is a signaling component of the induced systemic resistance caused by *Pseudomonas chlororaphis* O6 root colonization. *Molecular Plant–Microbe Interactions* **21**, 1643–1653.
- Kocal N, Sonnewald U, Sonnewald S.** 2008. Cell wall-bound invertase limits sucrose export and is involved in symptom development and inhibition of photosynthesis during compatible interaction between tomato and *Xanthomonas campestris* pv. *vesicatoria*. *Plant Physiology* **148**, 1523–1536.
- Koch K.** 2004. Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. *Current Opinion in Plant Biology* **7**, 235–246.
- Koh EJ, Lee SJ, Hong SW, Lee HS, Lee H.** 2008. The ABA effect on the accumulation of an invertase inhibitor transcript that is driven by the CAMV35S promoter in *Arabidopsis*. *Molecules and Cells* **26**, 236–242.
- Kohorn BD, Kobayashi M, Johansen S, Riese J, Huang LF, Koch K, Fu S, Dotson A, Byers N.** 2006. An *Arabidopsis* cell wall-associated kinase required for invertase activity and cell growth. *The Plant Journal* **46**, 307–316.
- Kohorn BD, Kohorn SL, Todorova T, Baptiste G, Stansky K, McCullough M.** 2011. A dominant allele of *Arabidopsis* pectin-binding wall-associated kinase induces a stress response suppressed by MPK6 but not MPK3 mutations. *Molecular Plant* doi: 10.1093/mp/ssr096 (Epub ahead of print).
- Kwon YR, Oh JE, Noh HN, Hong SW, Bhoo SH, Lee HJ.** 2011. The ethylene signaling pathway has a negative impact on sucrose-induced anthocyanin accumulation in *Arabidopsis*. *Journal of Plant Research* **124**, 193–200.

- Lecourieux F, Lecourieux D, Vignault C, Delrot S.** 2010. A sugar inducible protein kinase, VvSK1, regulates hexose transport and sugar accumulation in grapevine cells. *Plant Physiology* **152**, 1096–1106.
- Leng NGS.** 2008. Physiological effects of BA and ABA on caixin seedlings. Masters thesis, National University of Singapore, Singapore.
- Leon J, Lawton MA, Raskin L.** 1995. Hydrogen peroxide stimulates salicylic acid biosynthesis in tobacco. *Plant Physiology* **108**, 1673–1678.
- Leon P, Sheen J.** 2003. Sugar and hormone connections. *Trends in Plant Science* **8**, 110–111.
- Levitz SM.** 2004. Interactions of Toll-like receptors with fungi. *Microbes and Infection* **6**, 1351–1355.
- Li P, Wind JJ, Shi X, Zhang H, Hanson J, Smeekens SC, Teng S.** 2011. Fructose sensitivity is suppressed in *Arabidopsis* by the transcription factor NAC089 lacking the membrane-bound domain. *Proceedings of the National Academy of Sciences, USA* **108**, 3436–3441.
- Li Y, Smith C, Corke F, Zheng L, Merali Z, Ryden P, Derbyshire P, Waldron K, Bevan MW.** 2007. Signaling from an altered cell wall to the nucleus mediates sugar-responsive growth and development in *Arabidopsis thaliana*. *Plant Cell* **19**, 2500–2515.
- Loreti E, Povero G, Novi G, Solfanelli C, Alpi A, Perat P.** 2008. Gibberellins, jasmonate and abscisic acid modulate the sucrose-induced expression of anthocyanin biosynthetic genes in *Arabidopsis*. *New Phytologist* **179**, 1004–1016.
- Melotto M, Underwood W, He SY.** 2008. Role of stomata in plant innate immunity and foliar bacterial diseases. *Annual Review of Phytopathology* **46**, 101–122.
- Melotto M, Underwood W, Koczan J, Nomura K, He SY.** 2006. Plant stomata function in innate immunity against bacterial invasion. *Cell* **126**, 969–980.
- Miller G, Schlauch K, Tam R, Cortes D, Torres MA, Shulaev V, Dangl JL, Mittler R.** 2009. The plant NADPH oxidase RBOHD mediates rapid systemic signaling in response to diverse stimuli. *Science Signal* **2**, ra45.
- Moore B, Zhou L, Rolland F, Hall Q, Cheng WH, Liu YX, Hwang I, Jones T, Sheen J.** 2003. Role of the *Arabidopsis* glucose sensor HXK1 in nutrient, light, and hormonal signaling. *Science* **300**, 332–336.
- Morker KH, Roberts MR.** 2011. Light exerts multiple levels of influence on the *Arabidopsis* wound response. *Plant, Cell and Environment* **34**, 717–728.
- Morkunas I, Marczak Q, Stachowiak J, Stobiecki M.** 2005. Sucrose-stimulated accumulation of isoflavonoids as a defence response of lupine to *Fusarium oxysporum*. *Plant Physiology and Biochemistry* **43**, 363–73.
- Moxon ER, Kroll JS.** 1990. The role of bacterial polysaccharide capsules as virulence factors. *Current Topics in Microbiology and Immunology* **150**, 65–85.
- Muchembled J, Loune's-Hadj Sahraoui A, Grandmougin-Ferjani A, Sancholle M.** 2006. Changes in lipid composition of *Blumeria graminis* f. sp. *tritici* conidia produced on wheat leaves treated with heptanoyl salicylic acid. *Phytochemistry* **67**, 1104–1109.
- Müller J, Aeschbacher R, Sprenger N, Boller T, Wiemken A.** 2000. Disaccharide-mediated regulation of sucrose: fructan-6-fructosyltransferase (6-SFT), a key enzyme of fructan synthesis in barley leaves. *Plant Physiology* **123**, 265–273.
- Núñez-Pastrana R, Arcos-Ortega GF, Souza-Perera RA, Sanchez-Borges CA, Nakazawa-Ueji YE, Garcia-Villalobos FJ, Guzman-Antonio AA, Zuniga-Aguilar JJ.** 2011. Ethylene, but not salicylic acid or methyl jasmonate, induces a resistance response against *Phytophthora capsici* in Habanero pepper. *European Journal of Plant Pathology* **131**, 699–683.
- Pattanagul W.** 2011. Exogenous abscisic acid enhances sugar accumulation in rice (*Oryza sativa* L.) under drought stress. *Asian Journal of Plant Sciences* **10**, 212–219.
- Pieterse CMJ, Leon-Reyes A, Van der Ent S, Van Wees SCM.** 2009. Networking by small-molecule hormones in plant immunity. *Nature Chemical Biology* **5**, 308–316.
- Piskurewicz U, Tureckova V, Lacombe E, Lopez-Molina L.** 2009. Far-red light inhibits germination through DELLA-dependent stimulation of ABA synthesis and ABI3 activity. *EMBO Journal* **28**, 2259–2271.
- Pogany M, Koehl J, Heiser I, Elstner E, Barna B.** 2004. Juvenility of tobacco induced by cytokinin gene introduction decreases susceptibility to Tobacco necrosis virus and confers tolerance to oxidative stress. *Physiology and Molecular Plant Pathology* **65**, 39–47.
- Proels RK, Roitsch T.** 2009. Extracellular invertase LIN6 of tomato: a pivotal enzyme for integration of metabolic, hormonal, and stress signals is regulated by a diurnal rhythm. *Journal of Experimental Botany* **60**, 1555–1567.
- Qi T, Song S, Ren Q, Wu D, Huang H, Chen Y, Fan M, Peng W, Ren C, Xie D.** 2011. The jasmonate-ZIM-domain proteins interact with the WD-repeat/bHLH/MYB complexes to regulate jasmonate-mediated anthocyanin accumulation and trichome initiation in *Arabidopsis thaliana*. *The Plant Cell* **23**, 1795–1814.
- 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.
- Rahnamaeian M.** 2011. Antimicrobial peptides: modes of mechanism, modulation of defence responses. *Plant Signaling and Behavior* **6**, 1325–1332.
- Rasul S, Dubreuil-Maurizi C, Lamotte O, Koen E, Poinssot B, Alcaraz G, Wendehenne D, Jeandroz S.** 2012. Nitric oxide production mediates oligogalacturonides-triggered immunity and resistance to *Botrytis cinerea* in *Arabidopsis thaliana*. *Plant, Cell and Environment* doi: 10.1111/j.1365-3040.2012.02505.x (Epub ahead of print).
- Reignault P, Cojan A, Muchembled J, Sahouri AL, Durand R, Sancholle M.** 2001. Trehalose induces resistance to powdery mildew in wheat. *New Phytologist* **149**, 519–529.
- Ridley BL, O'Neill MA, Mohnen D.** 2001. Pectins: Structure, biosynthesis, and oligogalacturonide-related signaling. *Phytochemistry* **57**, 929–967.

- Roberts MR, Paul ND.** 2006. Seduced by the dark side: integrating molecular and ecological perspectives on the influence of light on plant defence against pests and pathogens. *New Phytologist* **170**, 677–699.
- Robert-Seilaniantz A, Navarro L, Bari R, Jones JDG.** 2007. Pathological hormone imbalances. *Current Opinion in Plant Biology* **10**, 372–379.
- Robson F, Okamoto H, Patrick E, Harris SR, Wasternack C, Brearley C, Turner JG.** 2010. Jasmonate and phytochrome A signaling in *Arabidopsis* wound and shade responses are integrated through JAZ1 stability. *The Plant Cell* **22**, 1143–1160.
- Roden LC, Ingle RA.** 2009. Lights, rhythms, infection: the role of light and the circadian clock in determining the outcome of plant–pathogen interactions. *The Plant Cell* **21**, 2546–2552.
- Roitsch T, Balibrea ME, Hofmann M, Proels R, Sinha AK.** 2003. Extracellular invertase: key metabolic enzyme and PR protein. *Journal of Experimental Botany* **54**, 513–524.
- Rolland F, Baena-Gonzalez E, Sheen J.** 2006. Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annual Review of Plant Biology* **57**, 675–709.
- Sano H, Seo S, Koizumi N, Niki T, Iwamura H, Ohashi Y.** 1996. Regulation by cytokinins of endogenous levels of jasmonic and salicylic acids in mechanically wounded tobacco plants. *Plant and Cell Physiology* **37**, 762–769.
- Schaarschmidt S, Roitsch T, Hause B.** 2006. Arbuscular mycorrhiza induces gene expression of the apoplastic invertase LIN6 in tomato (*Lycopersicon esculentum*) roots. *Journal of Experimental Botany* **57**, 4015–4023.
- Schwachtje J, Karojet S, Thormählen I, Bernholz C, Kunz S, Brouwer S, Schwochow M, Köhl K, van Dongen JT.** 2011. A naturally associated rhizobacterium of *Arabidopsis thaliana* induces a starvation-like transcriptional response while promoting growth. *PLoS ONE* doi:10.1371/journal.pone.0029382.
- Serrano M, Kanehara K, Torres M, Yamada K, Tintor N, Kombrink E, Schulze-Lefert P, Saijo Y.** 2012. Repression of sucrose/ultraviolet B light-induced flavonoid accumulation in microbe-associated molecular pattern-triggered immunity in *Arabidopsis*. *Plant Physiology* **158**, 408–422.
- Shalitin D, Wolf S.** 2000. Cucumber mosaic virus infection affects sugar transport in melon plants. *Plant Physiology* **123**, 597–604.
- Shan X, Zhang Y, Peng W, Wang Z, Xie D.** 2009. Molecular mechanism for jasmonate-induction of anthocyanin accumulation in *Arabidopsis*. *Journal of Experimental Botany* **60**, 3849–3860.
- Shirasu K.** 2009. The HSP90–SGT1 chaperone complex for NLR immune sensors. *Annual Review of Plant Biology* **60**, 139–164.
- Singh V, Louis J, Ayre BG, Reese JC, Shah J.** 2011. TREHALOSE PHOSPHATE SYNTHASE11-dependent trehalose metabolism promotes *Arabidopsis thaliana* defence against the phloem feeding insect *Myzus persicae*. *The Plant Journal* **67**, 94–104.
- Sinha AK, Hofmann MG, Romer U, Kockenberger W, Elling L, Roitsch T.** 2002. Metabolizable and non-metabolizable sugars activate different signal transduction pathways in tomato. *Plant Physiology* **128**, 1480–1489.
- Smeekens S, Ma J, Hanson J, Rolland F.** 2010. Sugar signals and molecular networks controlling plant growth. *Current Opinion in Plant Biology* **13**, 274–279.
- Smith H.** 1990. Pathogenicity and the microbe *in vivo*. The 1989 Fred Griffith Review Lecture. *Journal of General Microbiology* **136**, 377–393.
- Solfanelli C, Poggi A, Loreti E, Alpi A, Perata P.** 2006. Sucrose-specific induction of the anthocyanin biosynthetic pathway in *Arabidopsis*. *Plant Physiology* **140**, 637–646.
- Sturm A, Chrispeels MJ.** 1990. cDNA cloning of carrot extracellular β -fructosidase and its expression in response to wounding and bacterial infection. *Plant Cell* **2**, 1107–1119.
- Teng S, Keurentjes J, Bentsink L, Koornneef M, Smeekens S.** 2005. Sucrose-specific induction of anthocyanin biosynthesis in *Arabidopsis* requires the MYB75/PAP1 gene. *Plant Physiology* **139**, 1840–1852.
- Thibaud MC, Gineste S, Nussaume L, Robaglia C.** 2004. Sucrose increases pathogenesis-related PR-2 gene expression in *Arabidopsis thaliana* through an SA-dependent but NPR1-independent signaling pathway. *Plant Physiology and Biochemistry* **42**, 81–88.
- Ting JP, Willingham SB, Bergstralh DT.** 2008. NLRs at the intersection of cell death and immunity. *Nature Reviews Immunology* **8**, 372–379.
- Ton J, Flors V, Mauch-Mani B.** 2009. The multifaceted role of ABA in disease resistance. *Trends in Plant Science* **14**, 310–317.
- Trouverie J, Chateau-Joubert S, Thévenot C, Jacquemot MP, Prioul JL.** 2004. Regulation of vacuolar invertase by abscisic acid or glucose in leaves and roots from maize plantlets. *Planta* **219**, 894–905.
- Valluru R, Van den Ende W.** 2011. Myo-inositol and beyond – emerging networks under stress. *Plant Science* **181**, 387–400.
- Van den Ende W, Lammens W, Van Laere A, Schroeven L, Le Roy K.** 2009. Donor and acceptor substrate selectivity among plant glycoside hydrolase family 32 enzymes. *FEBS Journal* **276**, 5788–5798.
- Verhaest M, Lammens W, Le Roy K, De Ranter CJ, Van Laere A, Rabijns A, Van den Ende W.** 2007. Insights into the fine architecture of the active site of chicory fructan 1-exohydrolase: 1-kestose as substrate vs sucrose as inhibitor. *New Phytologist* **174**, 90–100.
- Wagner TA, Kohorn BD.** 2001. Wall-associated kinases are expressed throughout plant development and are required for cell expansion. *Plant Cell* **13**, 303–318.
- Wahl R, Wippel K, Goos S, Kämper J, Sauer N.** 2010. A novel high-affinity sucrose transporter is required for virulence of the plant pathogen *Ustilago maydis*. *PLoS Biology* **8**, e1000303.
- Wang N, Nobel PS.** 1998. Phloem transport of fructans in the crassulacean acid metabolism species *Agave deserti*. *Plant Physiology* **116**, 709–714.
- Warnasooriya SN, Porter KJ, Montgomery BL.** 2011. Tissue- and isoform-specific phytochrome regulation of light-dependent anthocyanin accumulation in *Arabidopsis thaliana*. *Plant Signaling and Behavior* **6**, 624–631.
- Watson MA, Watson DJ.** 1951. The effect of infection with beet mosaic viruses on the carbohydrate content of sugar-beet leaves, and on translocation. *Annals of Applied Biology* **38**, 276–289.

- Weiss D.** 2000. Regulation of flower pigmentation and growth: multiple signalling pathways control anthocyanin synthesis in expanding petals. *Physiologia Plantarum* **110**, 152–157.
- Wind J, Smeekens S, Hanson J.** 2010. Sucrose: metabolite and signaling molecule. *Phytochemistry* **71**, 1610–1614.
- Wingler A, Delatte TL, O'Hara LE, Primavesi LF, Jhurrea D, Paul MJ, Schlupe H.** 2012. Trehalose 6-phosphate is required for the onset of leaf senescence associated with high carbon availability. *Plant Physiology* **158**, 1241–1251.
- Winkel-Shirley B.** 2001. Flavonoid biosynthesis: a colorful model for genetics, biochemistry, cell biology, and biotechnology. *Plant Physiology* **126**, 485–493.
- Xiang L, Le Roy K, Bolouri-Moghaddam MR, Vanhaecke M, Lammens W, Rolland F, Van den Ende W.** 2011. Exploring the neutral invertase-oxidative stress defence connection in *Arabidopsis thaliana*. *Journal of Experimental Botany* **62**, 3849–3862.
- Xie Y, Ling T, Han Y, et al.** 2008. Carbon monoxide enhances salt tolerance by nitric oxide mediated maintenance of ion homeostasis and up-regulation of antioxidant defence in wheat seedling roots. *Plant, Cell and Environment* **31**, 1864–1881.
- Zaragoza O, Rodrigues ML, De Jesus M, Frases S, Dadachova E, Casadevall A.** 2009. The capsule of the fungal pathogen *Cryptococcus neoformans*. *Advances in Applied Microbiology* **68**, 133–216.
- Zhang AY, Jiang MY, Zhang JH, Tan MP, Hu ZL.** 2006. Mitogen-activated protein kinase is involved in abscisic acid-induced antioxidant defence and acts downstream of reactive oxygen species production in leaves of maize plants. *Plant Physiology* **141**, 475–487.
- Zhang Y, Liu Z, Wang L, Zheng S, Xie J, Bi Y.** 2010. Sucrose-induced hypocotyl elongation of *Arabidopsis* seedlings in darkness depends on the presence of gibberellins. *Journal of Plant Physiology* **167**, 1130–1136.
- Zuther E, Kwart M, Willmitzer L, Heyer AG.** 2004. Expression of a yeast-derived invertase in companion cells results in long-distance transport of a trisaccharide in an apoplastic loader and influences sucrose transport. *Planta* **218**, 759–766.