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Trick and Treat: A Review on the Function and Regulation of Plant Invertases in the Abiotic Stress Response

By

Alfonso ALBACETE*), Dominik K. GROSSKINSKY*) and Thomas ROITSCH*)

With 1 Figure

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Summary

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The disaccharide sucrose and the cleavage products glucose and fructose are the central molecules for carbohydrate translocation, metabolism and sugar sensing in higher plants. Invertases mediate the hydrolytic cleavage of sucrose into the hexose monomers. Abiotic stresses modify source-sink relations and thus influence adaptation and responses that alter plant growth and development and ultimately crop productivity. It has become evident that invertases play an important role in the response of the plant to environmental stimuli because their substrates and reaction products are both nutrients and signal molecules. Thus, the induction of sink strength through invertases is a general response to sustain the signaling cascade under abiotic stress conditions. However, plants undergo continuous exposure to various biotic and abiotic stresses in their natural environment. With their influence on phytohormone and MAP-Kinase signaling networks, invertases seem to be also involved in the crosstalk between biotic and abiotic stress responses. Invertases thus work as pivotal enzymes at the integration point of metabolic, hormonal, and stress signals. This review explores the function and regulation of plant invertases under abiotic stress conditions and the possible role of these key enzymes as a convergence point between biotic and abiotic stress signaling pathways.

*) Dr. A. ALBACETE (corresponding author), Dipl. Biol. D. K. GROSSKINSKY, Prof. Dr. T. ROITSCH, Institut für Pflanzenwissenschaften, Karl-Franzens-Universität Graz, Schubertstraße 51, 8010 Graz, Austria, Europe; e-mail: alfmoreno@cebas.csic.es

Zusammenfassung

ALBACETE A., GROSSKINSKY D. K. & ROITSCH T. 2011. Trick and Treat: A review on the function and regulation of plant invertases in the abiotic stress response. [Trick and Treat: Ein Review über Funktion und Regulation von pflanzlichen Invertasen in der abiotischen Stressabwehr]. – *Phyton* (Horn, Austria) 50 (2): 181–204, 1 Abbildung.

Das Disaccharid Saccharose und dessen Spaltungsprodukte sind die zentralen Moleküle von Kohlenhydrat-Translokation, Kohlenhydrat-Metabolismus und Zucker-Signalling in Höheren Pflanzen. Invertasen katalysieren die hydrolytische Spaltung von Saccharose zu Hexose-Monomeren. Abiotische Stressfaktoren verändern in der Pflanze die Source-Sink-Verhältnisse. Sie beeinflussen somit Wachstum und Entwicklung, und letztlich auch die Produktivität von Nutzpflanzen. Es konnte gezeigt werden, dass Invertasen eine bedeutsame Rolle bei der Reaktion von Pflanzen auf diverse Umweltreize spielen, denn ihre Substrate und Reaktionsprodukte sind Nährstoffe und Signalmoleküle zugleich. Dementsprechend ist die Induktion der Sink-Stärke durch Invertasen eine allgemeine Reaktion, die die Aufrechterhaltung von Signalkaskaden unter abiotischen Stressbedingungen gewährleistet. Pflanzen sind in ihrem natürlichen Lebensraum permanent verschiedensten biotischen und abiotischen Stressfaktoren ausgesetzt. Der Einfluss von Invertasen auf Phytohormon- und MAP-Kinase-Netzwerke deutet darauf hin, dass Invertasen auch in die Wechselwirkungen zwischen biotischer und abiotischer Stressantwort involviert sind. Invertasen wirken als Schlüsselenzyme an jenem Punkt, an dem die Integration von hormonellen und stressbedingten Signalen stattfindet. Dieser Review-Artikel behandelt Funktion und Regulation von Invertasen unter abiotischen Stressbedingungen und die mögliche Rolle dieser Schlüsselenzyme am Konvergenzpunkt zwischen abiotischen und biotischen Signalwegen.

Abbreviations: cytInv, cytoplasmic invertase; cwInv, cell wall invertase; vacInv, vacuolar invertase; SUS, sucrose synthase.

1. Introduction

In most plants the disaccharide sucrose is the major end product of photosynthesis. Sucrose is synthesized in source leaves and translocated to sink tissues via the phloem to sustain heterotrophic metabolism and growth, or to be stored as sucrose or starch. Growth and development of plants is accompanied by changes in source-sink relations (ROITSCH & GONZÁLEZ 2004). Sucrose and its cleavage products glucose and fructose are the central molecules for carbohydrate translocation, metabolism and sensing in higher plants (KOCH 2004, ROITSCH & GONZÁLEZ 2004, TROUVERIE & al. 2004). Sucrose catabolism in plants is one of the largest metabolic fluxes on the planet, second only to fluxes in primary carbon assimilation. Only two types of enzymes can catalyze sucrose under physiological conditions: invertases and sucrose synthase (KOCH 2004, ROITSCH & GONZÁLEZ 2004, TROUVERIE & al. 2004, BARRATT & al. 2009).

The glycosyltransferase sucrose synthase (SUS, EC 2.4.1.13) catalyzes the reversible cleavage of sucrose to UDP-glucose and fructose conserving the energy of the sucrose α 1- β 2-glycosidic bond. In contrast, invertases (EC 3.2.1.26, β -fructosidase, β -fructofuranosidase) catalyze the irreversible hydrolysis to glucose and fructose. Based on their solubility, subcellular localization, pH-optima and isoelectric point, three different types of invertase isoenzymes can be distinguished: cell wall bound (cwInv), cytoplasmic (cytInv), and vacuolar (vacInv) invertases, which are located in the apoplast, the cytoplasm and the vacuole, respectively (STURM 1999, KOCH 2004, ROITSCH & GONZÁLEZ 2004). VacInvs and cwInvs are glycoproteins that share several biochemical properties, e.g. they cleave sucrose most efficiently between pH 4.5 and 5.0 and attack the disaccharide from the fructose residue. Thus, these so-called acid invertases are β -fructofuranosidases and also hydrolyze other β -fructose-containing oligosaccharides such as raffinose and stachyose. The cytInvs are less well characterized, they are not glycosylated and because of their neutral or slightly alkaline optimum pH range are also known as neutral/alkaline invertases. In contrast to the acid invertases, the cytInvs appear to be sucrose specific (ROITSCH & GONZÁLEZ 2004, HUANG & al. 2007).

It has become evident that invertases are key metabolic enzymes that are involved in various aspects of the plant life cycle and the response of the plant to environmental stimuli because their substrates and reaction products are both nutrients and signaling molecules (ROITSCH & GONZÁLEZ 2004, VARGAS & al. 2007). Abiotic stresses, such as salinity and drought, modify source-sink relations which influence plant growth as well as adaptation to the stress and consequently affect crop productivity. Although little is known about the mechanisms responsible for growth reduction under drought or salinity, tolerance towards abiotic stresses (eg. ionic regulation) and crop productivity will depend on the capacity of the plant not only to provide resources to the actively growing sink tissues (new vegetative and harvestable biomass), but also on the maintenance of assimilate production in mature leaves (by delaying senescence) (ROITSCH 1999, BALIBREA & al. 2000, BALIBREA & al. 2003, ROITSCH & GONZÁLEZ 2004). Metabolic regulation of leaf senescence is thus an important developmental process in response to plant stresses. Stress can affect senescence through altered sugar metabolism, e.g. by breakdown of starch or altered sucrose metabolism, and/or altered sugar sensitivity, e.g. by interaction with phytohormones (WINGLER & ROITSCH 2008).

Invertases attracted a lot of attention and to date a growing number of studies have revealed that invertases play a crucial role in various aspects of plant growth and development. However, the physiological role of invertases during abiotic stress conditions is not yet fully understood. The current knowledge about this isoenzyme family, with special focus on key

findings of recent years on the function of invertases in the regulation of different abiotic stresses as well as the crosstalk with biotic stress is reviewed here.

2. Major Types of Abiotic Stress

2.1. Salinity

Salinity is a major factor reducing crop productivity in agriculture as well as a key determinant for land use for growing crop plants. To reduce such losses caused by salinity, insight about the limiting effects on plant growth and development is required. The water deficit induced by salinity results in osmotic stress, while an excess of sodium ions has harmful effects on numerous key biochemical processes (MUNNS 1993, MUNNS & TESTER 2008). Furthermore, salinity inhibits growth in both vegetative (MUNNS 1993, BALIBREA & al. 2000, ALBACETE & al. 2009) and reproductive tissues (BALIBREA & al. 1999, BALIBREA & al. 2003, LU & al. 2010). The decreasing sink demand provokes accumulation of assimilates in source leaves that subsequently restricts photosynthesis by the so-called feedback limitation (STITT 1991). Photoassimilates produced under salt stress are used to support crucial, mutually exclusive processes such as growth, maintenance and osmotic adjustment (YEO 2007). Hence, the competition of different physiological processes and sink organs for the limited carbon supplies under salinity significantly affects overall plant growth, dry matter distribution and crop yield (MUNNS & TERMAAT 1986, DAIE 1996). Pérez-Alfocea and coworkers (BALIBREA & al. 2000) suggested that the regulation of carbon allocation and partitioning and its use in the sink organs is important to maintain plant growth under salinity. Invertases seem to be involved in this process by coordinating sink-source relations and by maintaining sink demand, sucrose synthesis and transport (ROITSCH 1999). Although these parameters are not directly involved in salt tolerance, they could have an indirect effect on the overall plant performance under a salinization regime by alleviating the osmotic stress and/or delaying the toxic effect of salinity (MUNNS & TESTER 2008). However, little is known about the effect of salt stress on invertases and consequently on sink strength. The first studies addressing this topic date from the early 1980s. It was suggested that regulation of ion homeostasis in combination with carbohydrate metabolism contributes to salt tolerance of cotton varieties (RATHERT 1983). However, only in the 1990s, when the important function of invertases was recognized, an increasing number of studies investigated the role of invertases in the regulation of saline stress. In particular the work of Pérez-Alfocea and coworkers (BALIBREA & al. 1996) addressed the effect of moderate and high salinity on sucrose metabolism in relation to tomato fruit growth. They observed that *cytInv* and *SUS* controlled sink strength and fruit growth in tomato plants subjected to salinity during the

critical growing period from 30 to 40 days after anthesis. This response was also observed in the fruits of two interspecific tomato hybrids. The early reduction in sink activity was related with sucrose accumulation and a decrease in the total sucrolytic activity, especially that of SUS and cytInv (BALIBREA & al. 2003). SUS was also shown to play an important role on N_2 fixation in nodules of soybean plants subjected to salt stress (GORDON & al. 1997). In this regard, more recently it has been reported that the increased N_2 fixation of a moderate salt tolerant *Medicago ciliaris* line was related to significantly higher SUS and cytInv activities and therefore a better use of photoassimilates in the nodules of the tolerant line compared to the salt sensitive line (BEN SALAH & al. 2009). VacInvs are also involved in the regulation of salt stress responses. The growth capacity of tomato plants under salinity has been related to the increased sink activity of young leaves and roots by the induction of vacInv activity (BALIBREA & al. 2000). Recently, it has been reported that vacInvs might function coordinately with an abiotic stress-inducible transporter for monosaccharides from *Arabidopsis thaliana* to regulate osmotic pressure through the accumulation of sugars in plant cells (YAMADA & al. 2010). Despite the involvement of cytInvs and vacInvs in tolerance towards salinity, the cwInvs are the most widely investigated in relation to salt stress (ROITSCH & al. 2003). Experiments with transgenic tobacco plants expressing a yeast invertase in the apoplast showed that these plants were able to maintain photosynthetic activities under saline conditions (FUKUSHIMA & al. 2001). Thus, cwInvs seem essential in maintaining sucrose import to sink tissues (ROITSCH & EHNESS 2000, ROITSCH & al. 2003) during pollen development and fruit set (ROITSCH & GONZÁLEZ 2004). Furthermore, a recovery in the sink strength of hybrid tomato fruits subjected to moderate salinity was observed, that was related to the maintenance of cwInv activity (BALIBREA & al. 2003). More recently, it was shown that flower abortion under salinity was apparently correlated to decreased carbohydrate availability in inflorescence and pollen-producing tissues due to a dramatic reduction in cwInv activity, in spite of increased carbohydrate concentrations within source leaves (GHANEM & al. 2009).

The physiological mechanisms involved in altered assimilate partitioning and tolerance towards salt stress by invertases remain unclear (PÉREZ-ALFOCEA & al. 2010). Invertase activity seems to be tightly regulated by phytohormones as part of an integrated and coordinated mechanism to control growth and development. Thus, changes in phytohormone concentrations may be responsible for decreased sucrolytic activities under salinity (ROITSCH & al. 2003, ALBACETE & al. 2008, ALBACETE & al. 2010) or *vice versa*. Decreased root cytokinin concentrations and an increased basipetal transport of auxins from the shoot to the root, with a concomitant change in the activity of the sink-related enzyme cwInv, have been implicated (SACHS 2005, ALBACETE & al. 2008).

2.2. Drought Stress

Drought stress is one of the most serious factors limiting crop yield. The prospect of feeding an increasing global population in a world with increasingly erratic rain, temperature and drought patterns presents a serious challenge to plant scientists (MARRIS 2008). Water deficit in plants leads to physiological modifications such as reduced photosynthesis, transcriptional and post-transcriptional regulation of various genes, protein turnover and osmolyte biosynthesis (SEKI & al. 2007, SHINOZAKI & YAMAGUCHI-SHINOZAKI 2007). Drought stress, like salinity, induces large changes in source-sink relations with source limitations resulting in a reduced export of assimilates and therefore a decreased crop yield (PELLESCHI & al. 2006, LUQUET & al. 2008). For example, it was reported that moderate water stress modifies the fluxes around the sucrose cycle in growing potato tubers, leading to an activation of sucrose phosphate synthase and sucrose synthesis, and an inhibition of sucrose cleavage by invertases (GEIGENBERGER & al. 1997). Several studies on the effect of abiotic stresses on invertases address the effect of water stress on reproductive development (ROITSCH & GONZALEZ 2004). Since invertase gene expression can be modulated by sugar concentration, it is possible that decreased sugar delivery to reproductive tissue upon inhibition of photosynthesis by stress is the signal that triggers metabolic lesions leading to failure of male gametophyte development (SAINI 1997, SAINI & al. 1999). It has been reported that water deficits during pollination disrupt carbohydrate metabolism in maize ovaries and both *cwInv* and *vacInv* are important for establishing and maintaining reproductive sink strength during pollination and early kernel development (ZINSELMEIER & al. 1995). In *Papaver duvium*, the capacity for germination and desiccation tolerance of pollen were associated with a decrease in starch and an activation of the sucrose metabolism (HOEKSTRA & VAN ROEKEL 1988). KOONJUL & al. 2005 reported that transitory water deficit in wheat during male meiosis selectively down-regulates the transcription of two genes encoding a vacuolar (*Ivr5*) and a cell-wall (*Ivr1*) invertase isoforms in the anthers. Interestingly, it has been suggested that pollen sterility, or the concomitant inhibition of starch accumulation in water-stressed rice plants is unlikely to be caused by carbohydrate starvation *per se*. Instead, an impairment of enzymes of sugar metabolism and starch synthesis may be among the potential causes of this failure (SHEORAN & SAINI 1996). It was also shown that induction of male sterility in wheat at the meiotic stage caused by water deficit is preceded by a decline in *vacInv* activity, supporting a crucial role of *vacInv* and thus of the carbohydrate supply for this stress response (DORION & al. 1996). A reduced *vacInv* activity has also been reported for drought-stressed young maize ovaries (NEUMANN ANDERSEN & al. 2002). The correlation between low *vacInv* activity and reduced seed yield suggests that soluble

invertases could play a role in providing hexoses to support cell division during the pre-storage phase. The decrease in vacInv activity could also affect the post-phloem transfer of sucrose in maternal tissues and the generation of a hexose-based turgor pressure for cell expansion during growth and development (NEUMANN ANDERSEN & al. 2002). The predominant role of a vacInv in early stages of maize kernel development was further substantiated by the finding that reduced *Ivr2* (vacInv) expression localized in the perianth and adhering to the kernels as a consequence of drought stress could result in decreased assimilate import into the grain (QIN & al. 2004). Moreover, a tissuespecific expression analysis of cwInv genes (*OsCIN1-9*) in rice plants showed a rapid response to water deficit in anthers and peduncles and through a reduction in sink strength help to coordinate a delay in anthesis and heading (JI & al. 2005). Recently, it has been reported that differences in storage carbohydrate accumulation in drought-sensitive and drought-tolerant wheat are correlated with differences in sugar profiles, *cwInv* expression and levels of fructan biosynthesis in anther and ovary (JI & al. 2010). The resulting increased level of sugars might potentially be a natural response in providing protection against oxidant damage by strengthening the antioxidant system in anthers (NGUYEN & al. 2010). An analysis of leaf and grain responses in maize plants to drought stress suggested the existence of a compensatory mechanism at both phloem source and sink end, which tends to increase export and import efficiency. The differential regulation of vacInvs in both source and sink tissues may be understood as a component of this compensation process (TROUVERIE & PRIOUL 2006). It was shown that water shortage resulted in an early and strong stimulation of vacInv activity in adult maize leaves, whereas cwInv activity remained constant. This response was closely related to the mRNA level for only one invertase gene (*Ivr2*), encoding a vacuolar isoform (PELLESCI & al. 1997, PELLESCI & al. 1999). In this regard, the organ-specific induction of vacInv activity in vegetative sink and source organs of water stressed maize plants was correlated with an increase in *Ivr2* expression and in the vacInv protein amount (KIM & al. 2000). ABA appeared to be a powerful enhancer of the vacInv activity and *Ivr2* expression (TROUVERIE & al. 2003). A recent study in rice characterizing the dynamics of transpiration, development, growth and carbon metabolism in response to drought stress showed that the expression of cwInv and vacInv genes (*OsCIN* and *OsVIN*) under stress increased in sink leaves, which was interpreted as a mechanism to maintain sink activity (cell wall) and osmotic adjustment (vacuolar) (Luquet & al. 2008). Interestingly, an adequate balance between acid invertases and SUS activities was associated with higher dehydration tolerance of wheat seedlings (BOGDAN & ZAGDANSKA 2009), therefore also SUS seems to play a role in the regulation of water stress.

Invertases thus play a key role during water deficit. The analyses of invertase activity and expression indicate that these enzymes respond to carbohydrates and various plant hormones (KIM & al. 2000, TROUVERIE & al. 2003, TROUVERIE & al. 2004, WERNER & al. 2008). However, a detailed understanding of the mechanisms regulating invertase activity under drought stress in different plant tissues is still lacking (TROUVERIE & al. 2004). The up-regulation of cwInvs and other sucrose cleaving enzymes by cytokinins could provide the molecular basis for a localized induction of sink metabolism and, as a consequence, the adaptation to drought and other abiotic stresses by maintaining growth and delaying leaf senescence (ROITSCH & EHNESS 2000, GUIVARC'H & al. 2002, LARA & al. 2004). ABA seems to be another key factor regarding the regulation of invertase activity under water deficit (YANG & al. 2004). In maize leaves and roots subjected to both control and drought stress conditions, a strong concentration-dependent induction of invertase gene expression and activity was observed upon ABA treatment, while other factors such as glucose were rather ineffective in triggering the response (TROUVERIE & al. 2003, TROUVERIE & al. 2004).

3. Other Abiotic Stresses

3.1. Cold Stress

Ambient temperature is perhaps one of the major stress factors that determine geographic distribution of plants and their productivity. Plant damage caused by low temperature results in severe losses in agriculture, thus reducing yield and quality of products. During recent decades, various biochemical and molecular aspects of the plant adaptation to cold stress have been studied. Among numerous protective processes, an important role belongs to the accumulation of sugars in the cells caused by the changes in carbohydrate metabolism, in particular the activity of invertases (SIN'KEVICH & al. 2008). It has been reported that cold-induced stalk elongation in tulip (*Tulipa gesneriana*) is mediated by the induction of invertase expression, but not by SUS (BALK & DE BOER 1999). It was also shown that poor sprouting of stubble buds at low temperatures appears to be due to a reduced availability of reducing sugars concomitant with a lower acid invertase activity (JAIN & al. 2007). In contrast, SUS activity, but not acid invertase, is regulated by cold acclimation and deacclimation, which plays important roles in sugar accumulation and acquisition of freezing tolerance in the leaves of cabbage seedlings (SASAKI & al. 2001). Moreover, it has been suggested that low temperatures hinder pollen functioning in pepper, by interfering with starch accumulation, thereby decreasing the concentrations of soluble sugars in the mature pollen grains (SHAKED & al. 2004). Similarly, OLIVER & al. 2005 reported that the down-regulation of a cwInv gene (*OSINV4*) in the tapetum of a rice cultivar

caused a disruption in hexose production and starch formation in the pollen grains. However, in a cold-tolerant cultivar *OSINV4* expression was not reduced by cold, sucrose did not accumulate in the anthers, and starch formation in the pollen grains was not affected. A study with transgenic potato plants transformed with a yeast *cwInv* showed that transformed plants were more cold resistant than the control plants as suggested by the lack of disturbance of ion permeability of their membranes. It was concluded that owing to accumulation of low-molecular carbohydrates in the course of cold acclimation caused by activation of acid invertase, cold resistant plants adapt better to the drop in temperature (SIN'KEVICH & al. 2008). In cold stored potato tubers, the accumulation of reducing sugars (cold-induced sweetening) was described and associated with invertase activity (DAVIES & al. 1989). Two potato invertases have been shown to be specifically regulated during cold treatment (e.g. not by wounding) by alternative splicing leading to a shorter mRNA due to a skipped exon (BOURNAY & al. 1996). It seems that low temperatures possibly interfere with the metabolism/translocation of certain metabolites under cold stress conditions. The mechanisms that lead to sucrose accumulation due to cold acclimation and sucrose reduction by deacclimation remain unclear. Probably, because of the accumulation of low-molecular carbohydrates (sucrose and glucose) in the course of cold acclimation through the activation of acid invertases, cold resistant plants better adapt to lower temperatures occurring in nature (SIN'KEVICH & al. 2008). On the other hand, higher activities of antioxidant enzymes, such as catalase and peroxidase may protect plants from oxidative damage (JAIN & al. 2007), while the implication of plant hormones cannot be ruled out (OLIVER & al. 2007).

3.2. Heat Stress

Heat stress adversely affects the activity of invertases but it is still unclear whether this stress influences gene expression or the kinetic properties of invertases (ASTHIR & BHATIA 2010). In this regard, it has been reported that the genetic diversity in kinetic properties and thermal stability of soluble invertases in wheat may enable the grain carbon metabolism to adapt to high temperatures experienced during the reproductive phase of grain development (ASTHIR & al. 1998). It was also shown that soluble invertase activity was inhibited by both short-term and long-term heat stress in maize kernels, whereas the activity of insoluble invertase was affected only by long-term heat stress. These results support the hypothesis that the disruption of kernel growth in response to heat stress is mainly associated with changes in carbon utilization and partitioning (CHEIKH & JONES 1995). In this regard, high temperatures have been shown to decrease hexose content in the anthers (PRESSMAN & al. 2002) due to a reduction in *cwInv* activity (PRESSMAN & al. 2006), and the heat tolerance

of two tomato cultivars has been related to increased carbohydrate content in developing and mature pollen grains (FIRON & al. 2006). Similarly, it was reported that heat stress affects pollen germination in pepper by affecting sucrose metabolism (KARNI & ALONI 2002). A study in developing microspores of grain sorghum revealed that impairment of cwInv-mediated sucrose hydrolysis and subsequent lack of sucrose biosynthesis may be the most upstream molecular dysfunction leading to altered carbohydrate metabolism and starch deficiency under elevated growth temperature conditions (JAIN & al. 2007). Recently, it has been reported that heat stress-induced reduction in the cwInv gene *SbIncw1* during microspore meiosis was irreversible despite return of optimal growth temperature conditions through further reproductive development (JAIN & al. 2010). The inhibition of invertases leads to an accumulation of carbohydrates in the leaves generating a short-term feedback inhibition of photosynthesis and some long-term modifications in gene expression (JEANNETTE & al. 2000).

3.3. Low Oxygen Stress

Higher plants require oxygen to maintain growth and metabolism, but frequently they experience limited oxygen availability, mainly due to soil flooding. The utilization of carbohydrates under conditions of oxygen deficiency remains a matter of debate. Using maize double mutants (*sh1sus1*) the crucial role of SUS in supplying glycolysis in oxygen-deprived maize root tips was shown (RICARD & al. 1998). Similarly, by in situ activity staining of wheat roots, an increased SUS activity was observed in the tip region and stele of root axes, whereas invertase activity decreased (ALBRECHT & MUSTROPH 2003). Invertases increase ATP costs relative to sucrose cleavage by SUS, since invertases generate 2-fold more hexoses, each requiring ATP for phosphorylation. In maize root tips low oxygen stress reduced invertase expression (*Ivr1* and *Ivr2*) but did not affect SUS activity, decreasing the INV/SUS ratio (ZENG & al. 1999). These responses have an important implication in acclimation to low oxygen stress by the conservation of sucrose and ATP and reducing the hexose-based sugar-signaling system. The shift from hydrolytic sucrose cleavage by invertases to the sucrolytic cleavage by SUS as an adaptation to hypoxic conditions is also supported by data from Biemelt and coworkers (BIEMELT & al. 1999).

3.4. Starvation

Availability of various nutrients is important for plant growth and development. Lack of these nutrients leads to starvation symptoms which results especially in yield losses in crop species. Plants grown under phosphate deficiency react with dramatic changes in sugar accumulation and metabolism reflected by changes in activities of invertases and other enzymes of the carbohydrate metabolism. In phosphate starved bean plants,

cytInv and cwInv showed increased activity in leaves and roots and accumulated more glucose, sucrose and starch (CIERESZKO & BARBACHOWSKA 2000). Furthermore, *Arabidopsis* plants with altered phosphate status (*pho* mutants) and wild-type plants grown under phosphate deficiency conditions showed an increase in invertase transcripts, whereas *Sus1* was downregulated in phosphate deficient mutants (CIERESZKO & KLECZKOWSKI 2005). This suggests that invertases (together with other sugar metabolic enzymes) are transcriptionally regulated by phosphate deficiency and may by this contribute to adaption of the plant to the stress via homeostatic mechanisms. By the increased activity of invertases, also a signaling effect of sucrose and/or its cleavage products could be involved in acclimation to phosphate stress (HAMMOND & WHITE 2008).

3.5. Stress by Heavy Metals

Environmental pollution due to heavy metals is a growing problem. They can be released into air, water and soil through human, agricultural, industrial or urban activities. Notably, the high levels of heavy metals observed in many agricultural fields are due to long-term uses of phosphate fertilizers, sewage sludge applications and waste water irrigation. Although most heavy metals are not essential for plant growth, their mobility in soil-plant system allows an easy entry into vegetables, where it may cause toxic effects on animals and human health through food chain (SFAXI-BOUSBIH & al. 2010). Only little information is available on the effect of heavy metals on invertases. In bean seeds, the application of cadmium during the germination stage caused a reduction of vacInv, cytInv and cwInv activities, resulting in a defective fructose provision (SFAXI-BOUSBIH & al. 2010). There are almost no studies on key enzymes of sucrose cleavage in metallophyte plants so far, which may be crucial for maintaining root growth and heavy metal tolerance. In *Kummerowia stipulacea* plants subjected to copper treatment a positive correlation was shown between the activity of acid invertases, the root growth and root/shoot ratio (XIONG & al. 2008). The results of this study suggested that the higher acid invertases activities in mine population plants might at least partly associate with Cu tolerance by supplying carbon and energy for tolerance mechanisms.

3.6. Mechanical Wounding

Wounding effects are caused by various factors like herbivore attack, weather impact (e.g. wind, rain) and, especially important for crop species, during harvesting and post-harvest processing. Wounding of tomato roots resulted in enhanced transcription of *LIN6* (cwInv) (SCHAARSCHMIDT & al. 2006) and in wounded tomato leaves, the time dependent induction of *LIN6*, *TIV1* (vacInv) and *SUS* was also shown (GODT & ROITSCH 1997). Ad-

ditionally, increased transcript levels of *Wiv-1* (cwInv, sequence similarities to *LIN6*) and *Aiv-1* (vacInv) were detected after wounding of tomato leaves (OHYAMA & al. 1998, OHYAMA & al. 2006). Also these two genes were shown to be regulated differently by time, as *Wiv-1* had a high maximum of transcripts 96 h after wounding, whereas *Aiv-1* transcripts showed a lower maximum 48 h past wounding (OHYAMA & al. 1998). As JA is known to be accumulated after wounding in plants (SCHILMILLER & HOWE 2005) and induction of invertases by JA, e.g. *LIN6* by methyl jasmonate (THOMA & al. 2003), JA is suggested to mediate increased invertase accumulation after wounding (AHKAMI & al. 2009).

4. Signaling and Regulation

Invertases are strongly involved in responses to abiotic stress situations. For acclimation to different stress conditions described, they are differently regulated at transcriptional and post-translational levels by many different factors including sugars, phytohormones, and proteinaceous inhibitors. Therewith, other methods of control have also been identified such as protein trafficking and transcript turnover (reviewed by HUANG & al. 2007). Together, these mechanisms allow a fine tuned regulation of invertase activities and sugar accumulation, compilation and distribution.

In plants soluble sugars provide the energy and carbon currencies, but also act as signaling molecules to regulate gene expression. The term “metabolic regulation” was introduced by KARRER & RODRIGUEZ 1992. In general, hexoses favor cell division and expansion, whereas sucrose favors differentiation and maturation. The importance of the exact source, nature and location of the sugar signals and the role of invertases as modulators of the sucrose/glucose ratio it has been stated (WESCHKE & al. 2003, BOLOURI-MOGHADDAM & al. 2010). Many sugar-regulated genes that cover different physiological pathways, including invertases, are known from plants (KOCH 1996, ROITSCH 1999, SHEEN & al. 1999, BOLOURI-MOGHADDAM & al. 2010). Notably, different cwInvs are metabolically induced by glucose, which provides a positive feed-forward mechanism that is also relevant for regulation by other stimuli (including stress stimuli): the up-regulation of a cwInv by any kind of stimulus can be maintained or amplified via the sugar signal generated by the elevated invertase activity to further enhance the flow of assimilates (ROITSCH & al. 2003, ROITSCH & GONZÁLEZ 2004). Therefore, sucrose metabolism lies at the heart of a sensitive, self-regulatory developmental system in plants. Moreover, the fact that both metabolizable sugars and stress stimuli studied in different systems regulate invertases, makes them important candidates to be used as marker genes for the analysis of converging signaling pathways (ROITSCH & al. 2003).

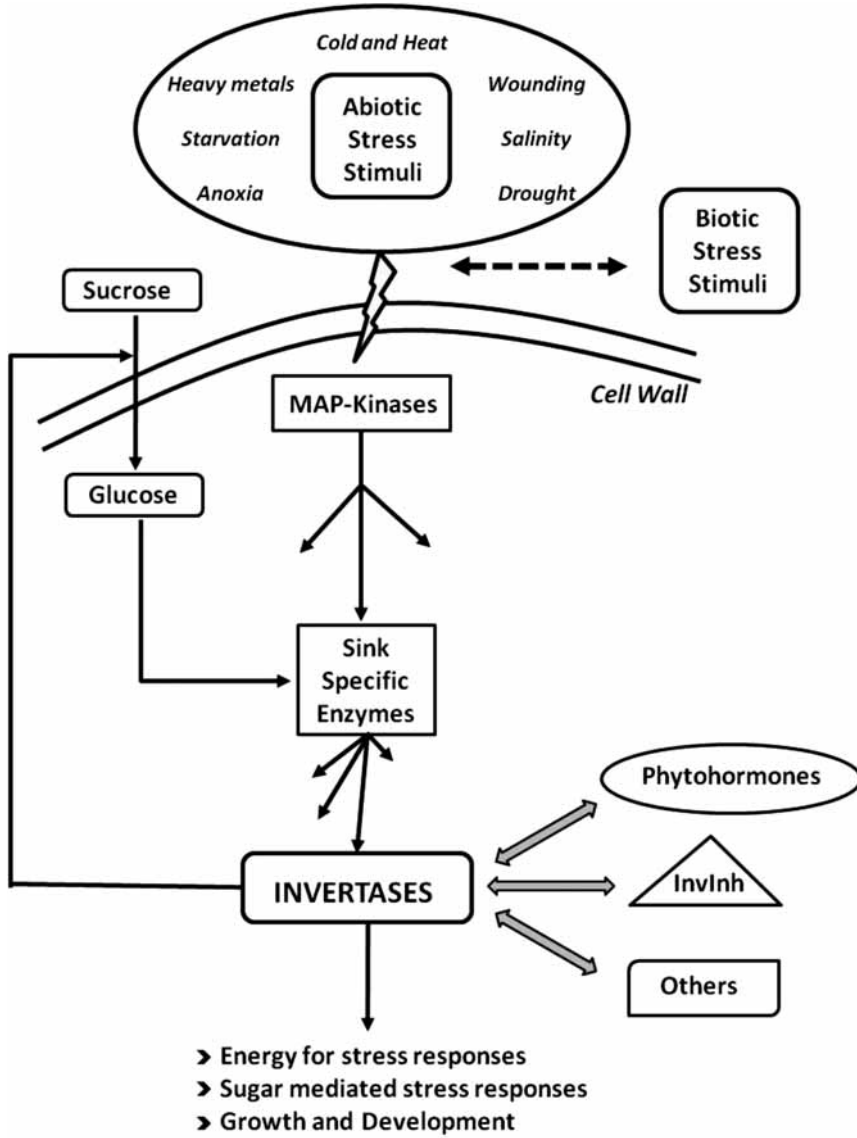


Fig. 1. Model for the regulation of sink metabolism/stress responses by abiotic stress-related stimuli. Abiotic stresses alone or in combination with biotic stresses (cross-talk) activate different signal transduction pathways that are ultimately integrated to coordinately regulate gene expression. The induction of invertases by sugars provides a feedback mechanism to amplify or maintain the initial stress-related signal. Invertases thus act as pivotal enzymes at the integration point of metabolic, hormonal and stress signals.

Phytohormones that play an integral role in controlling growth, differentiation, and development of plants turned out to be potent compounds of invertase regulation (TYMOWSKA-LALANNE & KREIS 1998, ROITSCH & GONZÁLEZ 2004) thereby indicating that invertases are involved in mediating the corresponding hormone responses as described above for the different abiotic stress situations. Apart from the mentioned effect of cytokinins, ABA, auxins and jasmonates, gibberellins (PROELS & al. 2006, RANWALA & MILLER 2008), brassinosteroids (GOETZ & al. 2000) and ethylene (LINDEN & al. 1996) have also been shown to affect invertases. The metabolic regulation by sugars may represent a short-term regulatory mechanism to adjust the carbohydrate import to actual demand, whereas hormone regulation may constitute a developmental program to adjust sink-source relations (PÉREZ-ALFOCEA & al. 2010). The interaction of invertases with phytohormones strengthens their central position in signaling networks. The influence of sucrose cleavage products on hormone systems combined with the regulation of sucrose metabolism by those hormone systems together comprise a means of integrating individual cellular responses into those of the multicellular organism (KOCH 2004).

Another control mechanism of invertase activity is the presence of endogenous inhibitor proteins. Although this post-translational regulation of invertases has been known for a long time, the physiological role is still not fully understood, especially under stress conditions (RAUSCH & GREINER 2004, BONFIG & al. 2010). It has been shown in *Arabidopsis* that invertase inhibitors show specific expression patterns in response to a number of stresses or during certain stages of plant development (RAUSCH & GREINER 2004). In a recent study, BONFIG & al. 2010 encountered that, upon pathogen infection, invertase activity was released by repression of invertase inhibitor expression, thus linking the local induction of sink strength to the plant defence response. In transgenic *Arabidopsis* plants harboring a putative invertase inhibitor gene (*At3g17225*), application of ABA had an impact on the stability of the invertase inhibitor transcripts, which suggests that phytohormones also play a role in the regulation of invertase inhibitors and therefore in the final invertase activity (KOH & al. 2008).

The observed coordinated regulation of source/sink relations and defence reactions in response to sugars and various stress-related stimuli (ENHNESS & ROITSCH 1997, ROITSCH & al. 2003) raises the question about the mechanisms whereby diverse signals may be integrated to result in coordinated responses while simultaneously maintaining the possibility for unique signal-specific downstream effects. Mitogen-activated protein kinases (MAPKs) have been shown to play a major role in the initiation and coordination of a plant's defence response to various biotic and abiotic stimuli. Using a non-biased biochemical approach it has been shown that a

particular stress-related stimulus results in the simultaneous activation of several MAPKs in photoautotrophic tomato cell cultures (LINK & al. 2002). The finding that different stress-related stimuli result in the differential activation of available MAPKs indicates that MAPKs may be involved in the integration of stress-related stimuli to coordinate direct defence responses with the regulation of primary carbon metabolism. In this regard, the role of MAPKs in the coordinated regulation of defence reactions and sucrose metabolism by stress-related stimuli has been analysed in tomato (HYUN & al. 2009). In this work, the authors demonstrated that LpMPK2 or LpMPK3 are required for the induction of the cwInv *Lin6* promoter following different stress treatments, suggesting that sucrose metabolism is a target of MAPK signaling during the stress response in plants. The interaction of sucrose metabolism with stress signal transduction pathway should be complemented by future research on the regulation of source/sink-relations via MAPK cascades.

5. General Conclusions and Future Prospects

Despite the dramatic effect of abiotic stresses on yield in agriculture, only a limited number of studies have focused so far on the regulation of invertases in response to the impact of environmental factors. It is well documented that the reduction of the sink demand under stress conditions leads to a feedback inhibition of the photosynthesis. Therefore, modulation of the processes involved in carbon metabolism and energy production seems to be crucial in the plant adaptability to abiotic stress situations. Invertases might thus work as pivotal enzymes at the integration point of metabolic, hormonal, and stress signals (PROELS & ROITSCH 2009).

In addition to their function in responses to abiotic stresses, invertases are known to directly interact with defence against pathogens. The availability of soluble sugars can be important as nutrient for pathogens as well as energy supply for plant's defence, known as high-sugar resistance phenomenon (HORSFALL & DIMOND 1957). In many plant-pathogen interactions, essential roles of invertases and modulated sugar levels have been described (reviewed by ROITSCH & al. 2003). For this reason, cwInv was suggested to be also assigned as PR protein (ROITSCH & al. 2003). However, plants in general and food crops in the field usually encounter a combination of different biotic and abiotic stresses. There is still a great gap of knowledge with respect to the mechanisms involved in the response of plants to the impact of simultaneous action of different types of stresses. However, for the successful development of crops with enhanced tolerance to various stress conditions, it is necessary to fill this gap of knowledge and to take into account the differences in plant acclimation mechanisms to a combination of stresses. With their influence on various signaling networks, invertases are key regulators for biotic and abiotic interactions.

Especially the connection to MAPK signaling (FUJITA & al. 2006) and ABA (ABUQAMAR & al. 2009), which are involved in the crosstalk between biotic and abiotic stress responses, indicates that invertases are important aims to develop plants more tolerant to abiotic stress conditions, pathogen attack and particularly to multi-stress scenarios. Invertases are thus key enzymes in the regulation of plant stress. However, there are still many open questions that should be answered with multidisciplinary approaches including physiological, biochemical and molecular techniques. The knowledge gained will fill the gaps in our understanding of invertase function under stress conditions.

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Autor(en)/Author(s): Albacete Alfonso, Grosskinsky Dominik K., Roitsch Thomas

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