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# ASR1 transcription factor and its role in metabolism

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***Asr1** (ABA, stress, ripening) is a plant gene widely distributed in many species which was discovered by differential induction levels in tomato plants subjected to drought stress conditions. ASR1 also regulates the expression of a hexose transporter in grape and is involved in sugar and amino acid accumulation in some species like maize and potato. The control that ASR1 exerts on hexose transport is interesting from a biotechnological perspective because both sugar partitioning and content in specific organs affect the yield and the quality of many agronomically important crops. ASR1 affect plant metabolism by its dual activity as a transcription factor and as a chaperone-like protein. In this paper, we review possible mechanisms by which ASR1 affects metabolism, the differences observed among tissues and species, and the possible physiological implications of its role in metabolism.*

**Keywords:** amino acids, *Asr1*, hexose transporter, sugar, sugar-hormone crosstalk, stress

**Abbreviations:** ABA, abscisic acid; WDS, water deficit stress; LEA, late embryogenesis abundant; BCAAs, branched-chain amino acids; ROS, reactive oxygen species.

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Plant primary metabolism includes those pathways that are essential for plant growth and development, in opposition to secondary metabolism that provides adaptive advantages.[1] The importance of primary metabolism lies on the control of all the basic processes in the life of plants: photosynthesis, respiration, solute transport, protein synthesis, etc. The primary metabolic pathways are ubiquitous, unlike the secondary ones which are specific to certain species. Additionally, primary metabolism regulation has significant consequences for agronomically important species through their effect on the physiology of the plants. In this context, transcription factors provide an attractive solution to control complex traits, although in certain cases undesired pleiotropic effects are manifested.[2]

Genes of the *Asr* (ABA, stress, ripening) family were initially characterized by their strong induction under stress conditions and during tomato fruit ripening.[3,4] Their members harbor the ABA/WDS (abscisic acid/water deficit stress) domain (Pfam entry PF02496) as a common denominator. This protein family is widely distributed in the *Plantae* kingdom, both in angiosperms and in gymnosperms, but not in all species. Members of the ASR family are present in *Solanaceae*, grape, maize and conifers, but surprisingly the model plant *Arabidopsis thaliana* lacks structural homologs.[5] The organization of the family varies among the species: 5 paralogs have been described in tomato,[6,7] 9 in maize,[8] 3 in potato,[9] 6 in rice,[10] 4 in banana[11] and one in melon.[12] In general, the ASR proteins are small (molecular mass of tomato ASR1 is 13 kDa) and, specifically, tomato ASR1 is intrinsically unstructured.[13] Some authors propose that ASR proteins belong to the LEA (late embryogenesis abundant) protein group because of their small size, their physicochemical properties and participation in stress pathways.[14]

## Functional Roles of *Asr1*

Functional analyses on this family have been historically centered on the first described member, *Asr1*. The *Asr1* orthologs have been extensively described as functionally involved in stress responses. In a wide variety of species, including strawberry,[15] tomato,[3,16] grape,[17] rice[18] and lily,[19] the expression of *Asr1* can be induced by ABA. In addition, *Asr1* expression levels increase under different stress conditions in a wide range of species. Among others, this increase occurs in tobacco and tomato by osmotic and drought stress;[4,16,20-22] in rice by drought, saline and osmotic stress;[10,23,24,25] and in plantain and banana by osmotic and biotic stress.[11,26,27] Only a few physiological studies with transgenic tomato,[28] tobacco,[22] maize,[29] and rice[18] plants have proved the involvement of ASR1 in stress tolerance.

It has been proposed that the stress tolerance observed in plants over-expressing ASR1 is conferred by at least 2 mechanisms, which presumably operate simultaneously. On one hand, ASR1 acts as a chaperone-like protein in the cytoplasm. Indeed, in vitro assays showed that tomato, plantain and lily ASR1 proteins can prevent enzyme denaturation after heating or freezing-thaw cycles.[26,30,31] On the other hand, ASR1 acts as a transcription factor. This proposed dual function is supported by ASR1 localization both in the nucleus and in the cytosol,[4,17,32,33] as well as by its role as a DNA-binding protein.[17,33-35] Moreover, ASR1 was recently found to interact physically with regulatory regions of genes related to cell wall synthesis and remodeling as well as with channels implicated in water and solute flux, such as aquaporins.[36] These findings support 2 physicochemical studies that suggest that the tomato ASR1 acts as a chaperone-like protein in the cytosol while being unstructured and as a transcription factor in the nucleus after acquiring its quaternary structure.[13,31]

However, ASR1 is also expressed under many other physiological conditions, such as tomato and strawberry fruit ripening.[3,4,15] This indicates that ASR1 may have other functions beyond its role in stress. More than a decade ago, Çakir et al.[17] proved that a grape ASR1 ortholog called MSA recognizes specific sites in the regulatory region of the hexose transporter 1 gene (Ht1 is described in Hayes et al.[37] Vignault et al.[38] and Fillion et al.).[39] In that study, it was also shown that *Asr1* expression is regulated by ABA and sugar in grape fruits. However, the physiological relationship between ASR1 and hexose content was first demonstrated in potato *Asr1* transgenic plants. These plants showed altered glucose levels correlating with the levels of a hexose transporter mRNA in tubers.[40] Later studies revealed that *Asr1*-silenced tobacco plants showed increased glucose levels and lower *Ht1* mRNA levels in source leaves[41] and that the heterologous over-expression of plantain ASR1 in Arabidopsis increased total soluble sugar levels in leaves.[26] In addition, *Asr1* overexpression in maize plants increased yield and reduced sugar and amino acid levels; which suggests that ASR1 also participates in plant growth through the regulation of this kind of metabolites.[29]

## The Role of *Asr1* in Sugar Metabolism Differs Among Species

ASR1 functional analyses through the use of transgenic plants have shown that the metabolic effects depend not only on the species but also on the tissue under study. ASR1 levels are inversely related to glucose levels in tobacco and maize leaves of *Asr1* transgenic plants.[29,41] Moreover, *Ht1* mRNA levels are reduced in the *Asr1*-silenced tobacco leaves.[41] HT1 is a plasma membrane transporter with high affinity for glucose, and is involved in the retrieval of hexoses from the apoplast in the phloem region of vascular bundles of grape leaves, petioles and fruits.[38,42,43] These findings suggest that ASR1 induces the expression of *Ht1* in tobacco leaves and that in this way it regulates the glucose uptake from the apoplast into the phloem companion cells. However, sugar levels of *Asr1* transgenic potato plants remained almost unaltered in leaves.[40] Differences among species could be due to variations in gene regulation. Indeed, although the coding region of *Asr1* is highly conserved among the different species of *Solanum*, their response to drought stress is different; which suggests that their regulatory regions and/or regulatory proteins are not conserved.[44] This could also be true for the role of *Asr1* in leaf metabolism. In spite of the results reported for potato leaves, *Asr1*-silenced potato tubers showed increased glucose and fructose levels as well as increased levels of *Ht1* mRNA. Accordingly, over-expressing potato lines showed reduced glucose and fructose levels and reduced *Ht2* (an *Ht1* homolog) mRNA levels in tubers. These results suggest that ASR1 suppresses the expression of hexose transporters in tubers, in opposition to the observed function of ASR1 in leaves. In other words, ASR1 could have antagonistic effects on source and sink tissues in sugar metabolism. This duality in the effect of ASR1 could be caused by the interaction of ASR1 with different factors that regulate gene expression.

## ASR1 is Involved in Sugar-hormone Crosstalk and in Sugar Signaling

As mentioned before, grape ASR regulates a hexose transporter and its expression is controlled by ABA and sugar;[17] which pinpoint this transcription factor to be involved in sugar trafficking whose signals are sugar and ABA. This is particularly interesting because the signaling mechanisms of sugar-hormone interaction are not completely known.[45] Evidence of the involvement of *Asr1* in sugar-hormone crosstalk has been also found in other species. For instance, Joo et al.[18] demonstrated that *Asr1* mRNA levels in rice leaves increased significantly after sucrose and ABA treatment, whereas *Asr3* (an *Asr1* paralog) mRNA levels in roots increased after sucrose, glucose and gibberellic acid treatment. The characteristics of the *cis*-acting elements present in the regulatory regions of *OsAsr1* and *OsAsr3* suggest that stress, sugar and hormones are the key regulators of the expression of these rice paralogs.[18] In the same line, Pérez-Díaz et al.[46] found that *OsAsr1, OsAsr2* and *OsAsr3* regulatory regions have a motif of sugar repression, whereas all rice ASR paralogs (*Asr1* to *Asr6*) have an element of sugar induction and gibberellin repression in their regulatory regions. These data suggest that other paralogs of ASR1 could be involved in sugar-hormone crosstalk as well. In some species and under certain physiological conditions, sugar-hormone cross-talk has been described as being linked by 2 of the most relevant proteins in sugar signaling, hexokinase 1 and SnRK1 (Snf1-related kinase).[45,47,48] Moreover, Saumonneau et al.[49] have found evidence of the regulation of the expression of grape *Asr1* by ABA, glucose, hexokinase1 and SnRK1. In that study, a model was proposed where MSA (grape ASR) expression is inhibited by hexokinase 1 and stimulated by ABA at high glucose levels, whereas the inhibition by hexokinase 1 is released at low glucose levels in grape protoplasts. On the other hand, *Asr1*-silenced tobacco plants not only showed high glucose levels in leaves but also showed altered ABA and gibberellin levels.[41] These plants also had high hexokinase 1 and low SnRK1 mRNA levels. The high glucose and hexokinase1 levels of these plants suggest that ABA and gibberellin catabolism is enhanced, although other sugar signaling pathways might be involved.

## *Asr1* is Involved in Amino Acid Metabolism in Different Species and Tissues

As mentioned previously, the alterations in *Asr1* expression lead to changes in amino acid metabolism. In potato tubers, for instance, both *Asr1*-overexpressing and silenced plants showed reduced levels of amino acids.[40] Indeed, glutamine, phenylalanine, threonine, proline and valine were reduced in *Asr1*-silenced tubers, whereas phenylalanine, GABA and threonine were reduced in *Asr1*-overexpressing lines. Furthermore, the main metabolic changes observed in tomato fruits from *Asr1*-overexpressing and silenced plants correspond to amino acids (Dominguez et al., unpublished data); which suggests that the amino acid metabolism is directly affected by ASR1 rather than being a secondary effect related to alterations in sugar content. Similarly, leaves from *Asr1*-overexpressing maize plants showed reductions in amino acid levels including branched-chain amino acids (BCAAs: isoleucine, leucine, valine), aromatic amino acids (phenylalanine, tryptophan) and the glutamate family amino acids (asparagine, glutamine, proline).[29] Interestingly, in the same study, the protein levels of some enzymes belonging to different metabolic pathways were altered in the maize leaves, whereas their mRNA levels remained unaltered. In agreement with these results, the authors suggest that the mechanism of action of ASR1 on certain enzymes is through its chaperone-like activity. However, in the case of the BCAAs, the data support the idea that ASR1 acts both as a transcriptional regulator and as a chaperone-like protein. Actually, alterations in BCAA content were accompanied by alterations in the transcriptional levels of BCAA biosynthetic genes and in the protein levels of other enzymes involved in this pathway.

## Metabolic Pathways Involved in ASR1 Stress Responses

In spite of the clear participation of *Asr1* in the stress response, the metabolic pathways that are involved remain unclear. However, there is evidence suggesting that ASR1 has a role in the antioxidant activity of the cell. For instance, the overexpression of wheat ASR1 in tobacco enhances the expression of ROS-related (reactive oxygen species-related) and stress-responsive genes under osmotic stress.[20] In addition, these transgenic lines exhibit improved tolerance to oxidative stress by activating the antioxidant system. Moreover, rice ASR1 can scavenge ROS,[50] whereas soybean ASR1 buffers metal ions and thus provides antioxidant protection.[51] Therefore, ASR1 is probably involved in ROS depuration through several different mechanisms. Regarding other stress-related pathways, significant reductions in proline contents have been described in *Asr1*-overexpressing tobacco leaves under salt stress.[22] Also, as mentioned before, important alterations in amino acid contents occurred in *Asr1*-overexpressing maize leaves[29] as well as in *Asr1*-silenced and overexpressing potato tubers.[40] Many amino acids, including proline and BCAAs, participate in the response to several types of stresses.[52] Although these metabolites usually accumulate under stress conditions, their final accumulation depends on the sort of stress and the combination of different types of stresses. However, the alteration in amino acid contents suggests that ASR1 may also participate in the metabolic response to stress by regulating the amino acid concentrations. On the other hand, glucose is associated to certain types of stresses (like K deficiency and freezing tolerance) and sucrose is usually increased under most stress conditions.[52] Although sucrose was not altered in *Asr1* transgenic tobacco and potato plants,[41,40] its level was reduced in maize leaves;[29] which suggests that its regulation might take part in the *Asr1* response to stress in this species.

## Conclusions and Perspectives

The role of *Asr1* on metabolism is increasingly being studied. Evidence shows that *Asr1* controls the expression of a hexose transporter and glucose levels in different species, although this control seems to be exerted differently on source and sink tissues. This is particularly interesting from a biotechnological perspective because sugar contents affect the quality of many agronomically important crops. Moreover, *Asr1* expression is regulated by sugars and hormones, and it can be proposed that it represents a point of convergence in the sugar-hormone crosstalk. On the other hand, *Asr1* controls amino acid levels, which have a role in growth and stress. Although metabolomics studies on transgenic plants have broadened our knowledge of the role of *Asr1* in metabolic pathways, there is still a need of a deeper study on a higher number of species and tissues.

As for *Asr1* control of metabolism during stress, some evidence indicates that it has an effect on the amino acid metabolism and reactive oxygen species depuration. Nevertheless, broader physiological studies on metabolism under stress conditions are still lacking.

Altogether, it is tempting to speculate that ASR1 mechanism of action on metabolism is a combination of its activity as a transcription factor and as a chaperone-like protein. However, further experimental studies are needed to completely elucidate the mechanisms.

### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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