ADAPTATIONS OF THE ENVIRONMENT: A SELF MANAGEMENT SYSTEM OF RESTORATION

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Abstract

Environmental stresses come in many forms, yet the most prevalent stresses have in common their effect on plant water status. The availability of water for its biological roles as solvent and transport medium, as electron donor in the Hill reaction, and as evaporative coolant is often impaired by environmental conditions. Although plant species vary in their sensitivity and response to the decrease in water potential caused by drought, low temperature, or high salinity.

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The biochemical studies have revealed similarities in processes induced by stress that lead to accumulated metabolites in vascular and nonvascular plants, algae, fungi, and bacteria. These metabolites include nitrogen-containing compounds (proline, other amino acids, quaternary amino compounds, and polyamines) and hydroxyl compounds (sucrose, polyols, and oligosaccharides) (McCue and Hanson, 1990). Accumulation of any single metabolite is not restricted to taxonomic groupings, indicating that these are evolutionarily old traits. Third, molecular studies have revealed that a wide variety of species express a common set of genes and similar proteins (for example, Rab-related proteins and dehydrins) when stressed (Skriver and Mundy, 1990; Vilardell et al., 1994). Although functions for many of these genes have not yet been unequivocally assigned, it is likely, based on their characteristics, that these proteins play active roles in the response to stress.

Learning about the biochemical and molecular mechanisms by which plants tolerate environmentat stresses is necessary for genetic engineering approaches to improving crop performance under stress. By investigating plants under stress, we can learn about the plasticity of metabolic pathways and the limits to their functioning. Also, questions of an ecological and evolutionary nature need investigation. Are the genes that confer salt tolerance on halophytes and/or drought tolerance on xerophytes evolutionarily ancient genes that have been selected against in salt and drought-sensitive plants (glycophytes) for the sake of productivity? Or have some species obtained novel genes in their evolutionary history that have enabled them to occupy stressful environments?

Pathways involving more familiar compounds may also be exploited to produce stress-tolerant plants. Some of these may not require obtaining genes from tolerant species: over expressing or altering regulatory features of an endogenous gene ora gene from a different, but stress-intolerant, species might be sufficient. Relevant examples are the engineered over expression of genes for enzymes that increase putative osmoprotectant compounds such as proline, polyols, or fructans (Delauney and Verma, 1993; Tarczynski et al., 1993; Pilon-Smits et al., 1995). Some of these metabolites, which 1100, The Plant Cell are produced through ubiquitous

pathways, have already been demonstrated to be efficient in conferring tolerance on bacteria (Dandekar and Uratsu, 1988; Potts, 1994; Nomura et al., 1995). Similarly, spinach and other chenopods, which are only moderately water stress tolerant, accumulate glycine-betaine and related compounds (Weretilnyk and Hanson, 1990; Summers and Weretilnyk, 1993; Hanson et al., 1994; Ishitani et al., 1995), and genes responsible for this accumulation could be utilized for transfer. Finally, manipulation of enzymes in the proline metabolic pathway might also be an effective approach, to judge from the positive correlation between proline accumulation and water stress tolerance (McCue and Hanson, 1990; Delauney and Verma, 1993).

Application of New Methods to Old Problems

In the past, many studies of abiotic stress tolerance have monitored the physiological status of a stressed plant compared with unstressed controls. Mechanisms have been deduced from such descriptions, but in general these studies have notincluded molecular and genetic analysis of stress tolerance principles. Most important, knowledge from physiological studies has led to only a few studies on the biochemical mechanisms underlying tolerance and sensitivity to abiotic stress factors. The challenge now is to utilize this vast store of accumulated information involving molecular and biochemical analyses and modeling of the emerging mechanisms in transgenic plants.

One promising genetic avenue is the mapping of quantitative trait loci that relate performance and yield to drought, low temperature, or salinity tolerance. Thus, regions of chromosomes can be identified that carry genes that improve stress tolerance. A lucid example is the work on such loci in crosses of Chinese spring wheat and cultivated wheat, which differ in their degree of salinity tolerance (Dvorak and Zhang, 1992; Dubcovsky et al., 1994). The means to clone and identify mapped genes rapidly are straightforward. Certainly, for the major crop species-rice, corn, wheat, potato, and barleyand for some model species, all genetic material will be available soon in a cloned, accessible form (Hofte et al., 1993; Newman et al., 1994; Sasaki et al., 1994).

In addition, our growing understanding of biochemical mechanisms involved in stress tolerance makes it possible to search for specific genes, a strategy made feasible by the development of the polymerase chain reaction. Another technique, differential display polymerase chain reaction (Liang and Pardee, 1993), may make finding stress-induced transcripts even more feasible, but the technique has potential pitfalls and is yet largely untested in plant research. Finally, many mutated lines of Arabidopsis are available in which genes are tagged by insertion (Feldmann, 1991). Having characterized a DNA or transcript sequence with a putative significance in conferring stress tolerance is, however, no longer sufficient, and in the future, emphasis must be placed on functional characterizations and biochemical integration of molecular and genetic data.

A Model Halophyte, Mesembryanthemum Crystalinum

Mesembryanthemum crystallinum (ice plant) (Aizoaceae, Caryophyllales) is native to the Namibian Desert of southern Africa and is adapted to growth in high sodium and under drought and low-temperature conditions. Its genome is approximately twice the size of that of Arabidopsis (DeRocher et al., 1990; Meyer et al., 1990). The ice plant shows developmentally regulated cell-specific polyploidy, up to 128N, which is also influenced by stress. Its development is characterized by pronounced phase changes separating seedling establishment, juvenile and adult growth, flowering, and seed formation. Each phase exhibits easily scorable morphological, physiological, and biochemical markers (Bohnert et al., 1994; Cushman and Bohnert, 1995). Growth and phase changes are plastic and may be influenced by external conditions, light, temperature, COn, and stresses that limit water availability. The ice plant's development and phase changes are reflected in the expression of a number of marker genes (Meyer et al., 1990; Cushman and Bohnert, 1995; Yamada et al., 1995). Finally,

the ice plant has been used in many stress physiology studies. Although our knowledge about the magnitude of changes in gene expression is still limited, it appears that transcriptional regulation is the source of developmental changes in gene expression, whereas both transcriptional and post-transcriptional controls are important during stress.

One example of the interplay between transcriptional and post-transcriptional controls is the induction of the CAM pathway, which increases water use efficiency. The CAM pathway is characterized by closed stomata during the daytime and by malate fluctuations during day-night cycles. Opening stomata only at night reduces transpiratory water loss, the essential advantage of plants with CAM over those with C, photosynthesis (for a review of C, and C, photosynthesis, see Furbank and Taylor, 1995, this issue). Reducing water loss is also essential for the ice plant's tolerance to prolonged salinity stress. COn that is taken up at night is assimilated into oxaloacetate by the CAM characteristic enzyme, phosphoenolpyruvate carboxylase (PPC), and finally into malate.

The malate is stored in the vacuole, from where it is mobilized during daytime, providing CO, for the action of ribulose- 1,5 bisphosphate carboxylasebxygenase. A housekeeping PPC (encoded by the gene, which is constitutively expressed at a low level) provides C, intermediates to the citric acid cycle. The CAM specific isoform of PPC (encoded by fpcl) shows low basal expression in young plants, and little mRNA can be detected unless the plants are stressed. Water stresses lead to fivefold transcriptional activation of fpcl, followed by a more than 100-fold accumulation of its mRNA and the resulting accumulation of the CAM-specific PPC. CAM induction is, however, more complex than a simple and other geneslenzymes of the pathway. High salinity in plants less than -4 weeks old does not lead to full fpcl induction; induction remains incomplete (Cushman et al., 1990; Vernon et al., 1993a; Bohnert et al., 1994). Productive CAM switching is correlated with a phase change that commences when plants are ~5 weeks old, depending on growth conditions. That is, the onset of CAM photosynthesis is controlled by a developmental program accelerated by stress. These results illustrate an important point, namely, that plant stress responses must be seen in a developmental context.

Even though CAM induction in young ice plants is incomplete, such plants survive severe stress, which indicates that there must be additional mechanisms that act in the short term to confer stress tolerance on the ice plant. Three such mechanisms have been identified: induced polyol biosynthesis, regulation of ion uptake and compartmentation, and facilitated water uptake.

Induced Polyol Biosynthesis

Accumulation of polyols, either straight-chain metabolites such as mannitol and sorbitol (Bieleski, 1982) or cyclic polyols such as myo-inositol and its methylated derivatives (Loewus and Dickinson, 1982), is correlated with tolerance to drought and/or salinity, based on polyol distribution in many species, including bacteria, yeasts, marine algae, higher plants, and animals. Polyols seem to function in two ways that are difficult to separate mechanistically: osmotic adjustment and osmoprotection.

In osmotic adjustment, they act as osmolytes, facilitating the retention of water in the cytoplasm and allowing sodium sequestration to the vacuole or apoplast. Alternatively, protection of cellular structures (possibly by scavenging active oxygen) might be accomplished through interactions of such osmolytes, often termed compatible solutes (see following discussion), with membranes, protein complexes, or enzymes. Proline, quaternary ammonium, and tertiary sulfonium osmolytes are zwitterions at physiological pH. Although they are ionic, they have no net charge. Their osmoprotective function in the cytosol may be related to their unique chemistry. Those polyols that are nonreducing sugars may also store excess carbon under environmental stress

conditions (Bieleski, 1982; Ford, 1984; Paul and Cockburn, 1989; Smirnoff and Cumbes, 1989; Vernon et al., 1993b).

The importance of altered metabolism under abiotic stress, for example, the diversion of carbon to polyol biosynthesis, is exemplified, as shown in Figure 1, by the metabolic reactions originating from the glucose-6-phosphate pool. Outlines the inositol biosynthetic pathway catalyzed by inositoll-phosphate synthase (IN01) and inositol monophosphatase as well as pathways that originate from inositol and inositol-lphosphate. There are several interesting aspects of the inositol biosynthetic pathway. First, it is essential for membrane biosynthesis and signaling functions in all organisms, because IN01 is the sole enzyme catalyzing entry into the pathway.

Connected to this pathway in the ice plant (and in other species with different evolutionary histories) is a pathway that leads to accumulation of methylated inositols, catalyzed by inositol O methyltransferase (IMT1). Inositol and inositol-1-phosphate also fuel the production of other compounds that have been correlated with stress tolerance, for example, gums, cell walllocated carbohydrates, carbohydrates in glycoproteins, and mucilages. Plants use inositol to synthesize vegetative storage carbohydrates such as slachyose and verbascose, which are stress induced in some species. Yet another product of this pathway is phytate, inositol-hexakisphosphate, which serves as phosphate storage for seed.

Regulated lon Uptake and Compartmentation

A second mechanism that protects the young ice plant against water stress is the regulation of ion uptake and compartmentation (Adams et al., 1992). The ice plant takes up sodium when it is available and deposits it in a gradient along its axis, with the highest amounts in the youngest tissues. This gradient parallels the increase ino-pinitol. Particularly high accumulations of sodium and pinitol have been observed in a morphological specialization of the ice plant, the epidermal bladder cells, which are developmentally preformed but increase in size dramatically when plants are salt stressed. Sodium concentrations exceeding 1 M have been measured in these cells (Adams et al., 1992). The ability of the ice plant to use sodium as an osmoticum confined to vacuoles in growing parts of the plant (compensated by D-pinitol accumulation in the cytoplasm) is in stark contrast to glycophytic plants, which attempt to limit sodium uptake or partition sodium into older tissues that serve as storage compartments that are eventually sacrificed.

Facilitated Water Permeability

A third mechanism for stress protection appears to be regulation of facilitated water permeability. Transcripts of Mip (major intrinsic protein) genes whose abundance changes under salt stress have been isolated from root cDNA libraries of ice plants (Yamada et al., 1995). The encoded MIPs are homologous to plant and animal aquaporins, or water channels, as well as to glycerol facilitator proteins from bacteria (Chrispeels and Agre, 1994). Expression of different Mip mRNAs after injection into Xenopus oocytes and determination of water permeability demonstrate that the encoded proteins function as water channels. Two classes of plant aquaporins, located in the plasma membrane and tonoplast, respectively, have been identified.

Transcripts of two ice plant Mip genes are found predominantly in cells presumably involved in water' flux, that is, the root epidermis, the root tip before a functional central cylinder is formed, the endodermis, and regions surrounding strands of xylem cells in roots after secondary growth (Yamada et al., 1995).

An interesting difference exists between the ice plant and Arabidopsis in the stress regulation of transcript levels for closely related aquaporins. Whereas increases in salinity lead to higher transcript levels for one of the plasma membrane aquaporins, RD28, in Arabidopsis (Yamaguchi-Shinozaki et al., 1992; Daniels et al.,

1994), the ice plant Mip transcripts decline transiently and recover as the leaves regain turgor in a time course that parallels the accumulation of pinitol (vernon and Bohnert, 1992; Yamada et al., 1995).

Although the changes in transcript levels in Arabidopsis are not reflected by a similar increase in aquaporin protein (Daniels et al., 1994), differences in gene activity between this glycophyte and the halophytic ice plant seem to indicate differences in how stress is perceived and/or how the signal is processed. This may be due to differences in growth regulator sensitivity, for example, different perception of abscisic acid (ABA), which is generally considered a stress hormone. Salt stress leads to ABA increases in both plants (Yamaguchi-Shinozaki et al., 1992; Thomas and Bohnert, 1993), but the ice plant seems to "interpret" changes in ABA in a way that is different from Arabidopsis.

Glycophyte Mechanism for Stress Tolerance

Mechanisms very similar to those that seem to function in stress protection in the halophytes have emerged from the analysis of glycophytic species, supporting the contention that stress tolerance mechanisms are ubiquitous. Because stress tolerante is a multigenic trait, the biochemical pathways leading to products or processes that improve tolerance are likely to act additively and, possibly, synergistically. Thus, the advantages of halophytes and xerophytes over glycophytes may result simply from the more efficient performance of a few basic biochemical tolerance mechanisms.

Induced Compatible Solute Biosynthesis

One wall organisms tolerate abiotic stress to some degree is way by accumulating solutes termed compatible because they do not interfere with normal biochemical reactions. We discuss here recent reports but also refer the reader to past reviews (Yancey et al., 1982; Csonka, 1989; Delauney and Verma, 1993; Galinski, 1993; Rhodes and Hanson, 1993; Bartels and Nelson, 1994). Comprehensive biochemical studies of the various compatible solutes effective as osmoprotectants are a necessary first step for engineering of plant metabolic pathways. A recent study exemplifies this point. A thorough examination of the Plumbaginaceae found that various members of this family accumulate not only glycine-betaine but also, or alternatively, other quaternary ammonium zwitterions, including choline-O-sulfate, palanine-betaine, prolinebetaine, and hydroxyproline-betaine (Hanson et al., 1994).

These compounds show similar efficacy as osmoprotectants in bacterial assays. In addition, a correlation has been observed between the particular compound accumulated and the natural environment of each species. For example, species growing in sulfate-containing soil synthesize choline-O-sulfate, balaninebetaine accumulates in species grown under saline conditions, and proline-derived betaines are accumulated by species growing in dry environments. It is not yet known why different abiotic conditions should favor the accumulation of different osmolytes in members of one family. Study of biochemical pathways leading to these individual compounds may provide insight into how to engineer plants to tolerate complex environments. Conversely, systematic studies of cereal crops for their lack of compatible solute accumulation under stress (Rathinasabapathi et al., 1993) have identified targets for introducing genes and their encoded pathways both to improve crops and to measure the efficacy of a given compatible solute. Focus by different investigators on a single model system, such as transgenic tobacco, for testing the various solutes and other mechanisms would be useful.

Facilitated Water Flux

The discovery of carrier proteins specific for water is an important step toward understanding the mechanisms by which plants adapt to water stress (for review, see Chrispeels and Maurel, 1994). Water channels facilitate

flux of water along an existing osmolarity gradient. Expression of tonoplast and plasma membrane aquaporin transcripts, some of which are water stress inducible, is correlated with cell elongation (Guerrero et al., 1990; Ludevid et al., 1992; Yamaguchi-Shinozaki et al., 1992; Daniels et al., 1994). Also, an Arabidopsis blue light-responsive transcript with homology with aquaporins is expressed primarily in expanding cells (Kaldenhoff et al., 1995). Whether water flux is the primary factor limiting cell expansion under either well-watered or stress conditions is not clear. Cell wall metabolism and relaxation are considered the major initiator and control point for cell enlargement (Cosgrove, 1993). Under stress conditions, especially in glycophytes, the inability to transport and compartmentalize inorganic solutes or to synthesize organic solutes may, however, be additional limiting factors.

Water channels can be blocked or closed by phosphorylation (Chrispeels and Agre, 1994). Could this type of regulation be involved in root-to-shoot signaling under conditions of stress? A deviation of water flow from a value expected based on actual water potential might constitute a signal.

Alteration of gene expression is always involved in preparing plants for an existence under stress. The question is whether the regulatory elements are stress specific and, further, whether each is unique to a specific stress-tolerant species. Even more important, would engineering of plants for stress tolerance have to take into account a myriad of changes in signaling, gene activation, and protein modification? We do not think so. Mechanisms that control stress perception itself, and gene expression after stress perception, are most likely universal in the plant kingdom, considering the distribution of stress-adapted plants in many different families, the Occurrence of stress-tolerant relatives for many glycophytic species, and the genetic variability in stress tolerance of crop plants. After all, the machinery through which gene expression responses to a changing environment are mediated is present in guard cells in all plants (Assmann, 1993, 1994). Similarly, gene expression programs very much like those that operate during drought stress are also operative during seed desiccation (Bray, 1993; Delseny et al., 1994). However, differences may exist between naturally stress tolerant and sensitive plants that determine in which cell, in which tissue, or during which developmental stage a stress-mediating pathway is active. In addition, the ways in which gene expression responses to stress are inducible in a timely and spatially sensible fashion in tolerant plants may be different in stress-sensitive species.

Under severe stress, a plant adapts its metabolism and alters its development. Several of the necessary changes may be ordered on a scale of increasing complexity. Lowcomplexity mechanisms, similar to compatible solute production, ion uptake and partitioning, and possibly facilitated water uptake, would include the synthesis of other compounds, such as membrane lipids, LEA (late gnbryogenesis Bbundant) proteins, isoforms of chaperones, or proteins recruited from other functions.

Additionally, protection is likely provided by adjustments in amount andlor activity of proteins that assure membrane functioning in compartmentation and in ion and pH homeostasis, that is, various proton-translocating ATPases, ion channelsl transporters. In this context, comparative biochemical analyses of such proteins from glycophytes and halophytes should be done. It is important to discern whether, for example, plasma membrane ATPases from the halophyte Atriplex nummularia are structurally or functionally different from their homologs in Arabidopsis andlor whether their activity is differently regulated in glycophytes and halophytes (Niu et al., 1993). For protection of higher order processes, we believe that several low-complexity mechanisms must be induced coordinately. High-complexity mechanisms would be changes that protect major processes such as photosynthesis and respiration and those that preserve structures such as the cytoskeleton, the cell wall, or plasma membrane-cell wall interactions (Botella et al., 1994). Chromosome and

chromatin structure changes, for example, DNA methylation, polyploidization, amplification of specific sequences, or DNA elimination (Walbot and Cullis, 1985), would also be high

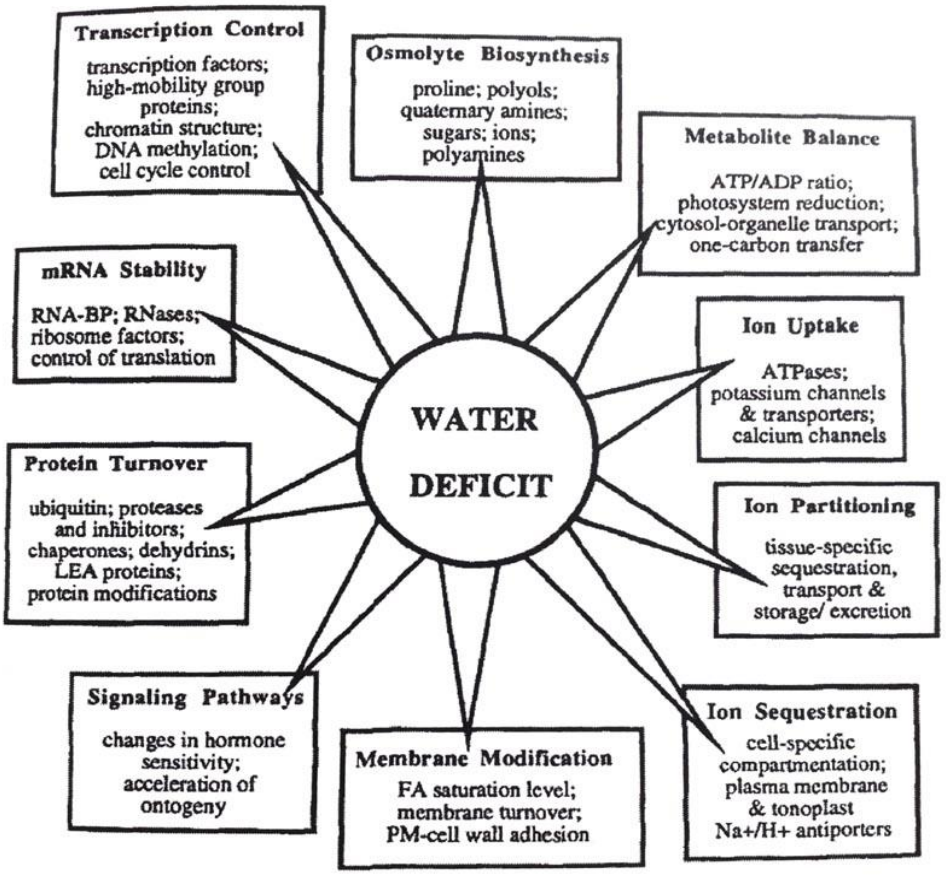

Fig. *Organismal Responses to Water Deficit.*

complexity and result in developmental changes. Higher complexity mechanisms, such as increased water-use efficiency, would be more difficult to engineer, considering the plethora of changes necessary in different biochemical pathways to cope with altered stomatal conductance and photosynthesis.

Testing Hypothesis in Transgenic Organisms

Mature fields in science work with a set of theories that allows predictions and serves as guidelines for applications. Rather than adding more phenomenological and anecdotal evidence to an already impressive body of observations concerning environmental stress tolerance, it seems appropriate to begin engineering traits associated with tolerance. There are several traits whose correlative association with tolerance can be tested.

One of these traits is radical scavenging during stress. That engineering of radical scavenging may improve tolerance is based on the observation of increased oxygen radical production in the light under water stress conditions (Foyer, 1994). Superoxide dismutases (SODs) are found in all aerobic organisms to detoxify active oxygen species. Different isoforms of SOD exist in the cytosol, chloroplasts, and mitochondria. The expression of some forms is dramatically induced during stress conditions in Nicofiene plumbaginifolie (Bowler et al., 1991; Tsang et al., 1991). Transgenic tobacco plants that overexpress SOD are more tolerant than untransformed controls to a superoxide- generating herbicide and to ozone (Herouart et al., 1993).

Low temperature and freezing, though distinct stressors, share a common factor: both may compromise membrane integrity (Guy, 1990; Thomashow, 1990). Changing membrane fluidity using plant and bacterial fatty acid desaturases has been tested in engineered plants (Murata et al., 1992; Wolter et al., 1992). By increasing the levels of desaturated lipids, decreased chilling sensitivity was observed; conversely, higher susceptibility to chilling was obtained by increasing the amounts of 16:0 fatty acids. These results have been challenged by the observation of a chilling-tolerant Arabidopsis mutant with a higher content of high-melting-point fatty acids than that found in most chilling-sensitive plants (Wu and Browse, 1995), probably indicating that there are multiple factors involved in chilling sensitivity.

Freezing stress also leads to oxygen radical production, because the light-harvesting reactions continue to function, while biochemical reactions are severely restricted. Overexpression of a SOD gene in alfalfa has been shown to ameliorate oxygen radical stress and protect against injury caused by freezing (McKersie et al., 1993).

Osmolyte production is yet another potential stress-protection mechanism in transgenic plants. We have chosen to test polyol functions by introducing the bacterial mflD gene into tobacco and Arabidopsis, neither of which normally synthesizes mannitol (Tarczynski et al., 1992; Thomas et al., 1995). Expression of the mflD gene led to mannitol accumulation in transformed plants. Further investigation of transgenic plants indicates that mannitol provides some protection when plants are exposed to high salinity, although not at all times during development (Tarczynski et al., 1993). Whereas young plants die when stressed by half seawater, plants that have developed source leaves for carbohydrate export survive such stress treatment.

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