

# PLANT STRESS-INDUCED MORPHOGENIC RESPONSE (SIMR): A STRATEGY OF ACCLIMATION TO ENVIRONMENTAL STRESSES.

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## Abstract

*Plants can acclimate to various environmental stresses by inducing a common physiological response called “stress-induced morphogenic response” (SIMR). This SIMR was observed when plants were exposed to soil pollutions such as metallic trace elements, pesticides or salts, or when soils present an excess of water or a deficiency in several minerals. Moreover, UV-B, ozone or mechanical stress can generate a similar response on plants. SIMR is characterized by a reduction of principal roots and a proliferation of lateral roots and hairy roots. This phenotype is considered as a strategy to avoid stress by increasing root surface in different directions. It was also observed on aerial organs (but less frequently) with a reduction of the main stem and a more branching. This re-orientation of growth is first caused by reactive oxygen species (ROS) which accumulate in root and stem apical meristems and cause lipid peroxidation and lignification. At root level, the consequence is a reduction of mineral absorption and thus a lower growth. Moreover, ROS accumulated in root apical meristem inhibit directly several auxin transporters (or indirectly by modifying pH) and stimulate auxin oxidase, leading to a decrease of auxin concentration in meristem and a subsequent inhibition of cell division. Auxin produced by the aerial organs and transported to roots accumulates then above root meristem and promotes lateral root formation.*

**Keywords:** auxin, meristem, reactive oxygen species, salinity

## Résumé

*Face à divers stress environnementaux, les plantes peuvent adopter un mécanisme d'acclimation commun appelé réponse morphogénique induite par le stress (RMIS). Ces contraintes externes peuvent être d'origine aérienne (UV-B, stress mécanique) mais concernent principalement la qualité du sol (pollution par des métaux lourds ou des pesticides, salinité importante, hydromorphie excessive, ou des carences en certains minéraux essentiels comme le phosphore ou le soufre). La réponse commune des plantes est caractérisée par un arrêt de croissance des racines principales, un développement de nombreuses nouvelles racines et une production accrue de poils absorbants. Ces modifications sont interprétées comme une tentative d'échapper aux conditions défavorables en développant des racines dans diverses directions. Ce phénomène est aussi observé au niveau des parties aériennes avec un arrêt de croissance de la tige principale et une surproduction de ramifications feuillées. La réorientation de la morphogénèse est principalement due à une perturbation du métabolisme de l'auxine qui se manifeste par une diminution de sa synthèse, une accentuation de sa dégradation et une modification de son transport. L'auxine ne s'accumule plus au niveau des méristèmes apicaux, ce qui stoppe la croissance. Elle est distribuée alors de manière moins précise dans les racines et les tiges et déclenche la formation de nouveaux organes latéraux. Les espèces réactives de l'oxygène (ERO) générées par un stress oxydant jouent un rôle important dans la régulation de l'auxine, par une répression de gènes impliqués dans la synthèse et le transport de cette dernière. Les ERO altèrent aussi directement le fonctionnement de plusieurs transporteurs d'auxine (ou indirectement par une modification du pH) et/ou oxydent l'auxine via des peroxydases. De plus, les ERO peuvent aussi stimuler la production de certains composés phénoliques qui agissent comme inhibiteurs de transport de l'auxine.*

**Mots clés :** auxine, méristème, espèce réactive de l'oxygène, salinité

## MANY STRESSES GENERATE A SIMR

The SIMR was often recorded when soils were contaminated with metallic trace elements or metalloids such as cadmium, copper, aluminum, cobalt, iron, or arsenic [1-5]. Pesticides are another source of pollution that drives the development of a SIMR by plants. Indeed, Pasternack *et al.* [6] observed this plant modification when plants were exposed to the herbicide paraquat. Soil salinity generates a similar plant response but all experiments were performed with NaCl and literature doesn't mention the potential effect of other salts ( $MgCl_2$ ,  $MgSO_4$ ...) on the induction of a SIMR [7,8]. Furthermore, one study highlighted a SIMR when plants were submitted

to soil hypoxia [9]. Moreover, an artificial stress such as application of  $H_2O_2$  in culture medium can cause similar reactions than those registered with previous stresses [6].

By contrast, SIMR can be generated when soils were deficient in several compounds, more precisely minerals required for plant growth and development. All minerals were not tested but a deficiency in macroelements such as phosphorus or sulfur as well as microelements such as boron can enhance a SIMR [10-12].

Furthermore, SIMR can be induced by a stress occurring at the aerial level such as an excess of UV-B or ozone or a mechanical stress applied on plants [13,14].

## WHAT PHENOTYPICAL MODIFICATIONS ARE CHARACTERISTIC OF SIMR?

The most frequently observed modifications are at root level. The general response is an arrest of principal root growth which is due to an inhibition of cell division in root apical meristem (RAM) (Figure 1). As a consequence, the elongation zone is reduced and thus hairy roots are localized closer to the RAM. Moreover, more cells of pericycle are re-differentiated and initiate more lateral roots and more hairy roots.

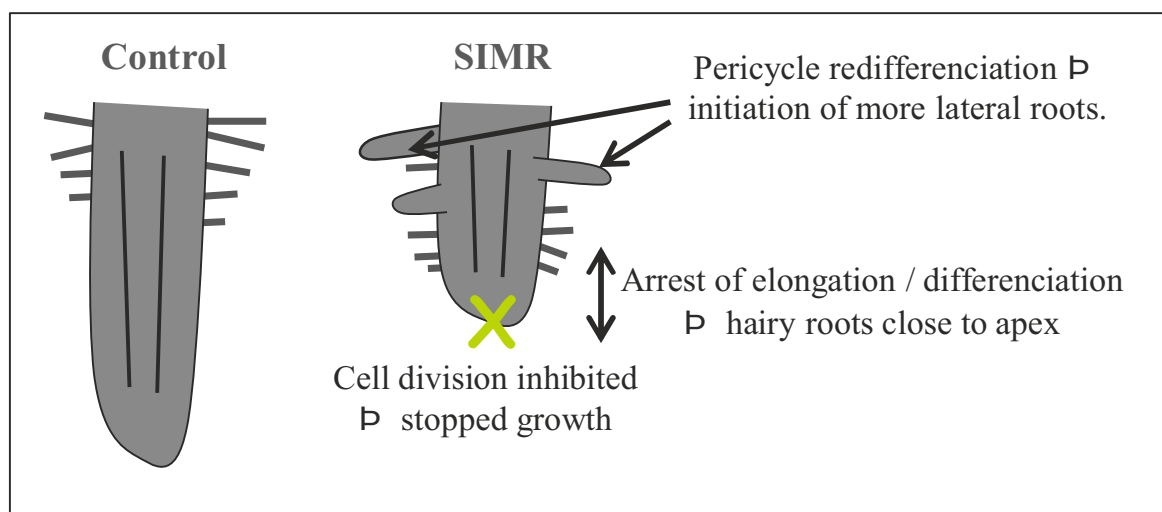


**Figure 1.** Phenotype of control roots and root developing a SIMR.

Several metallic trace elements tested on various plants shows similar RMIS: corn exposed to iron [2], rice exposed to cobalt [4], the fern *Pteris vittata* exposed to arsenic [15], barley treated with cadmium [16] or *Arabidopsis thaliana* as a response to copper [6]

or cadmium (Saladin, personal data) (figure 2). Salinity often results in developing a SIMR in various species including *Arabidopsis thaliana* [7] and crops such as pea, broad bean or wheat (Saladin, personal data) (figure 3). As previously indicated, a deficiency

of minerals in soils can cause a SIMR but few works are related to this aspect. Indeed, *Arabidopsis thaliana* is the only model cited as developing a SIMR when exposed to low concentrations of phosphorus [11,17], sulfur [10] or boron [12].



**Figure 2.** SIMR in *Arabidopsis thaliana* as a response to cadmium treatment (Saladin, personal data). One-week-old *in vitro* grown plantlets of the ecotypes Col and Ws were transferred for one week on medium containing no Cd (C for Control) or 100  $\mu\text{M}$  Cd. Treated roots showed a proliferation of root hairs close to the apex and initiation of lateral roots very close to another.

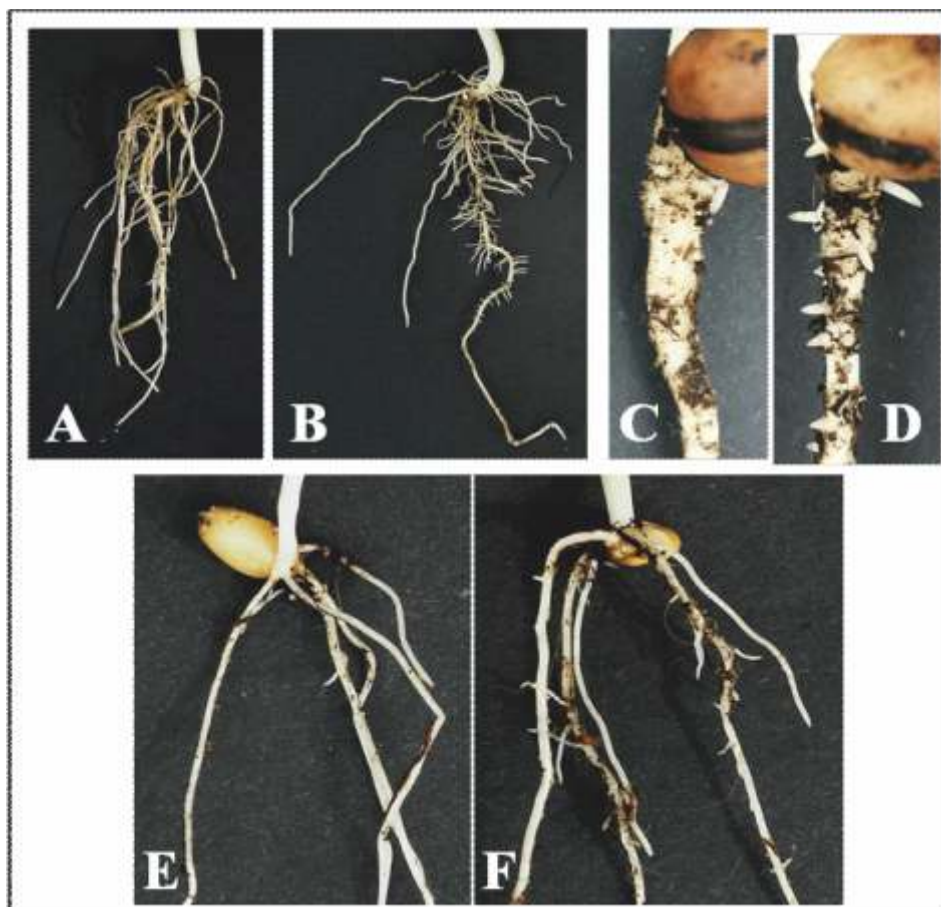


**Figure 3.** SIMR in crops as a response to salinity (Saladin, personal data). A, C and E: one-week old pea, broad and wheat control plantlets. B, D and F: pea, broad bean and wheat plantlets germinated for one week in 100 mM NaCl.

At aerial level, several works mentioned the development of SIMR as a response to abiotic stresses (figure 4). This phenomenon is less frequent than for root system and phenotypes are

not always the same. For example, several authors recorded an increase in leaf thickness during SIMR [18] whereas others observed the opposite effect, i.e. a decrease [13,19]. Moreover, the increase in

lateral stem number is not always detected: Hopff *et al.* [2], Arduini *et al.* [20] and Potters *et al.* [21] mentioned this phenotype as an aerial SIMR but Kakani *et al* [13] did not observe it.

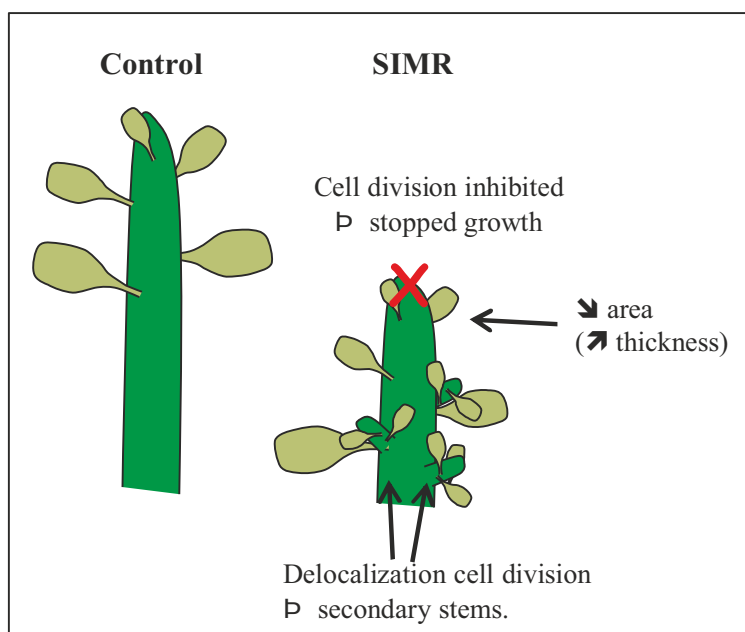


**Figure 4.** Phenotype of control shoots and shoots developing a SIMR.

However, several modifications are always recorded such as a reduction of leaf surface [6,22-23] (figure 5) and a shorter principal stem caused by an inhibition of cell division in stem apical meristem [18].



**Figure 5.** Phenotype of one-week old *Arabidopsis thaliana* plantlets exposed for one week to 100  $\mu$ M Cd (Saladin, personal data).

## WHAT IS THE INTEREST OF SIMR AND HOW DOES IT TAKE PLACE?

### 1. Role of SIMR

The main characteristic of SIMR is an increase of surface in several directions, not only for root system (with more lateral roots and more root hairs), but also for aerial organs with the production of more leafy stems. This response is interpreted as an attempt to

counteract unfavorable conditions of environment and to find a more optimal medium (less pollutant, salts or UV-B or more essential minerals for example).

However, SIMR is dependent of stress intensity and / or duration. Indeed, an important pollution is toxic for plants which are no more able to defend (and thus to produce SIMR) and the consequences are similar for

mineral deficiency. For example, it was shown that corn plantlets can induce a SIMR when exposed to 100  $\mu\text{M}$  iron but not to 500  $\mu\text{M}$  [2]. Zolla *et al.* [7] showed that *Arabidopsis thaliana* was able to develop a SMIR until 50 mM NaCl but when treated with 100 mM, the number of lateral roots was close to zero. Similar results were obtained with broad bean (figure 6).

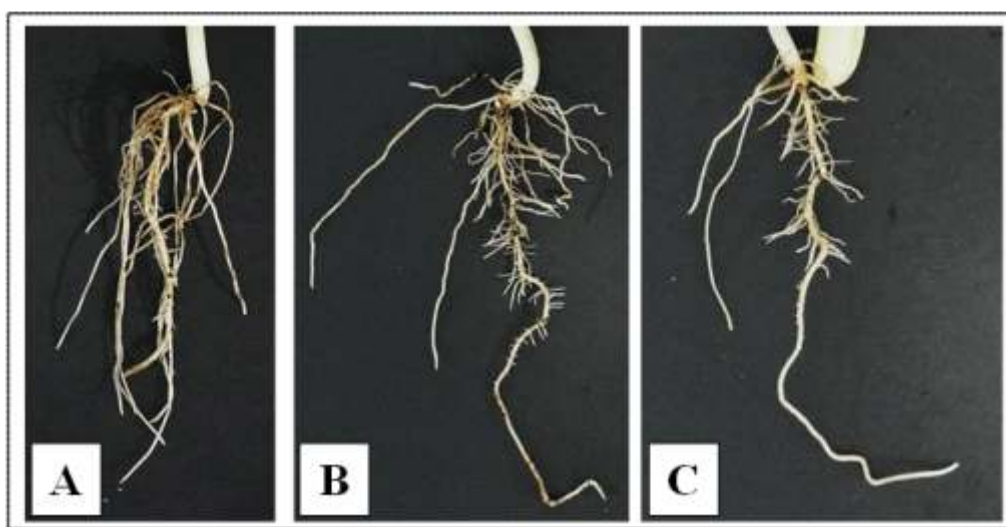


**Figure 6.** Phenotype of broad bean roots exposed to NaCl (Saladin, personal data). Seeds were germinated on horticultural compost and sand for 7 days on 0 (A), 100 mM (B) and 200 mM (C) NaCl. With 100 mM NaCl, more lateral shoots were initiated compared to control but this is not the case with 200 mM NaCl.

### 2. ROS induce the first steps of SIMR

Many stresses generate an oxidative stress and the production of ROS. When stress is not lethal for plant, a specific accumulation of ROS is registered at the root and shoots apex. For example, *Brassica* sp. exposed to Cu and incubated with several fluorescent markers (specific of different ROS), exhibited an accumulation of nitric oxide, superoxide ions and  $\text{H}_2\text{O}_2$  at

the root apex [3]. Moreover, lipid peroxidation increased at the apical level because of ROS accumulation. Furthermore, the authors showed an increase in lignification which reduces absorption of water and minerals and thus causes an arrest of growth for the main root (one of the characteristic of the SIMR indicated in figure 1).

The second consequence of ROS accumulation is a disturbing of 3-

indol-acetic acid (IAA) metabolism. Indeed, IAA is transported by several families of transporters and it was shown that  $\text{H}_2\text{O}_2$  can inhibit some of them [21]. In parallel, ROS can stimulate the activity of IAA oxidase which is involved in IAA catabolism [5]. As a consequence, root apex, which is enriched in ROS as a response to stress, has a lower IAA content.

## THE CENTRAL ROLE OF IAA

IAA is synthesized in shoot apical meristem as well as in young leaves, terminal buds and, in a lower concentration, in root apical meristem (RAM) [24-25]. IAA transport is polarized from aerial to underground organs, more precisely to RAM. Cell wall pH being more acid, IAA is protonated and can

cross cell wall and diffuse across plasma membrane (Figure 7). In cytoplasm, pH is less acid and IAA is deprotonated. Protons are exported to the cell wall through ATPase pumps and deprotonated IAA required specific transporters (localized in the plasma membrane) to be delivered to the next cell [26]. The accumulation of protons in cell wall stimulates the activity of

enzymes such as expansins, yieldins, xyloglucan endotransglycosylase and several endoglucanases [27]. These enzymes are involved in cell wall loosening and extension and thus contribute to cell elongation. In parallel, IAA accumulated in RAM induces the expression of genes related to cell cycle and promotes cell division.

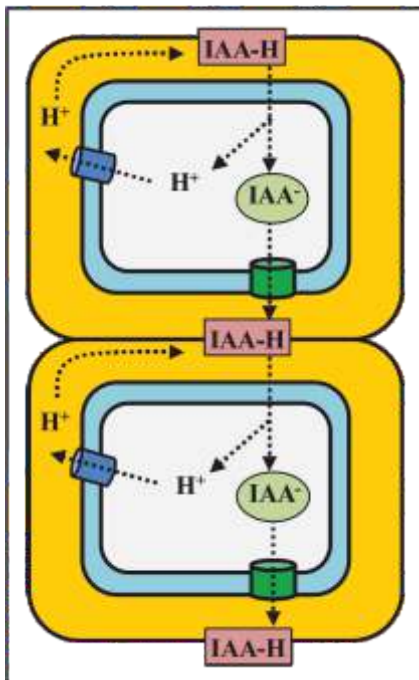


**Figure 7.** IAA polarized transport into two cells. IAA is protonated in the cell wall (IAA-H) and ionized in cytoplasm (IAA<sup>-</sup>). IAA transporters correspond to green cylinder and ATPase is represented by blue cylinder.

IAA is not continuously synthesized: it was reported that IAA production is light-dependent and that IAA pulses are recorded every 15 h [24]. Thus IAA promotes cell division (at the apex) and elongation at regular time lapses. In parallel, apical IAA is then partially exported from RAM to elongation zone by tissue-specific transporters such as PIN transporters [24,28-29] (figure 8). In the elongation zone, IAA increase activates pericycle cells which are adjacent to protoxylem poles and induces transcription

factors (such as PLT) which induce the expression of other IAA transporters (such as LAX) for a future lateral influx of IAA [24,30]. This lateral influx occurs during the following IAA pulse (meaning 15h later). At this moment, de-differentiated pericycle cells are located in the differentiation zone. Part of IAA which is transported to RAM is mobilized by these cells which can initiate lateral roots with meristems and thus with new zones of IAA accumulation for cell division [7,30].

The SIMR is characterized by a loss of apical IAA gradient [5,21]. Indeed, IAA did not accumulate in the RAM because of the inhibition of IAA transporters and the increase of IAA degradation by ROS as previously indicated. As a consequence, IAA accumulated before the apex, i.e. in the elongation zone and thus stimulates more cells of pericycle [21]. When IAA is still produced by aerial organs (apex, terminal buds, young leaves), the result is thus the regular initiation of more lateral roots.

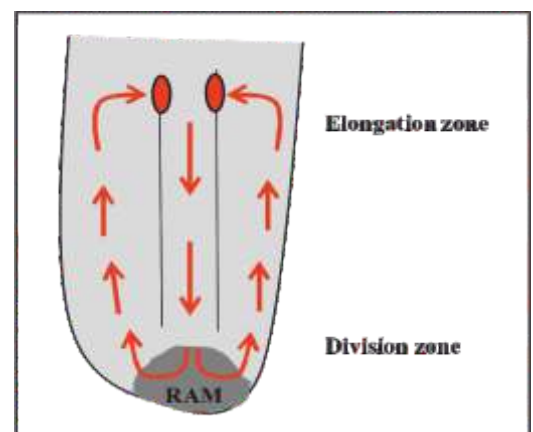


**Figure 8.** IAA flux in roots. IAA is translocated from aerial organs to RAM and is then partially redistributed to the elongation zone. This IAA efflux from RAM is controlled by specific transporters and can then induce the redifferentiation of pericycle cells (indicated by red spots on the figure) when IAA concentration is sufficient around these cells.

## CONCLUSIONS

SIMR is a common strategy to counteract several environmental stresses and could be used as a plant biomarker of stress and defense. However, SIMR regulation is not completely understood. For example, SIMR always induces

more lateral roots but it does not always stop growth of the main root [2 and personal observations]. Moreover, few studies indicated that Heme Oxidase (HO) is involved in the regulation of lateral root formation [4,8]. However, Hsu *et al.* [4] showed that neither nitric oxide nor  $H_2O_2$  is required for its

regulation and thus for lateral root development. It thus appears that a ROS-independent pathway could be involved in SIMR regulation. Furthermore, there is no information indicating if this pathway is species dependent or if it is a general regulation which has to be elucidated.

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