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Review

Fine regulation of leaf iron use efficiency and iron root uptake under limited iron bioavailability

José M. García-Mina [a,b,*], Eva Bacaicoa [a], Marta Fuentes [a], Esther Casanova [a]

[a] R&D Department (CIPAV-Roullier Group) Timac Agro, Polígono Arazuri-Orcoyen c/C, 31160 Orcoyen (Navarra), Spain
[b] Chemistry and Soil Chemistry Department, Faculty of Sciences, University of Navarra, Spain

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ABSTRACT

Numerous studies have investigated the molecular and physiological–morphological mechanisms induced in plant roots in response to specific nutrient deficiencies. Both transcriptional and post-transcriptional mechanisms are involved that increase root uptake under nutrient deficiency. Root nutrient deficiency-stress root responses are mainly regulated by the nutrient status in the shoot. The signals involved in shoot to root cross-talk regulation processes for the activation of nutrient-deficiency induced root responses are not clearly elucidated. The physiological-molecular events in the leaf linked to the nutrient availability for metabolic use, are also poorly known.

In this context, we focus our attention on iron plant nutrition. Some experimental evidence suggests the existence of a regulatory system concerned with the optimization of the metabolic use of iron, mainly under conditions of iron starvation. This system seems to be activated by the deficiency in iron-availability for metabolic processes in the leaf and regulates the activation of some iron-stress root responses. This regulation seems to be probably expressed by affecting the production and/or translocation of the activating signal sent from the shoot to the root under conditions of iron deficiency in the shoot.

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Contents

1. Introduction

In general, crop physiologists define nutrient-use efficiency combining two factors that are considered as independent to each other: (i) nutrient-uptake efficiency (NupE) that is defined as the ratio between nutrient-uptake by plants and nutrient-available in soil; and (ii) nutrient-utilization efficiency (NutE) that is the ratio between crop harvested and nutrient-uptake by plant. Nutrient-use efficiency (NUE) is obtained by multiplying nutrient-uptake efficiency and nutrient-utilization efficiency, thus giving the ratio between grain yield (or fruit, aerial part ...) and nutrient available in soil [1]:

$$\mathrm{NUE} = \mathrm{NupE} \times \mathrm{NutE} = \mathrm{Yield} : \mathrm{NavS}\,(\text{nutrient available in soil})$$

These parameters can be applied to all mineral nutrients included in plant nutrition and fertilization [1]. This approach, both involving plant and fertilizer, may be called *standard model* (Fig. 1A). However this model, although useful, has some conceptual problems.

* Corresponding author at: Timac Agro, R&D Department (CIPAV-Roullier Group), Polígono Arazuri-Orcoyen c/C, 31160 Orcoyen (Navarra), Spain.
E-mail address: jgmina@timacagro.es (J.M. García-Mina).

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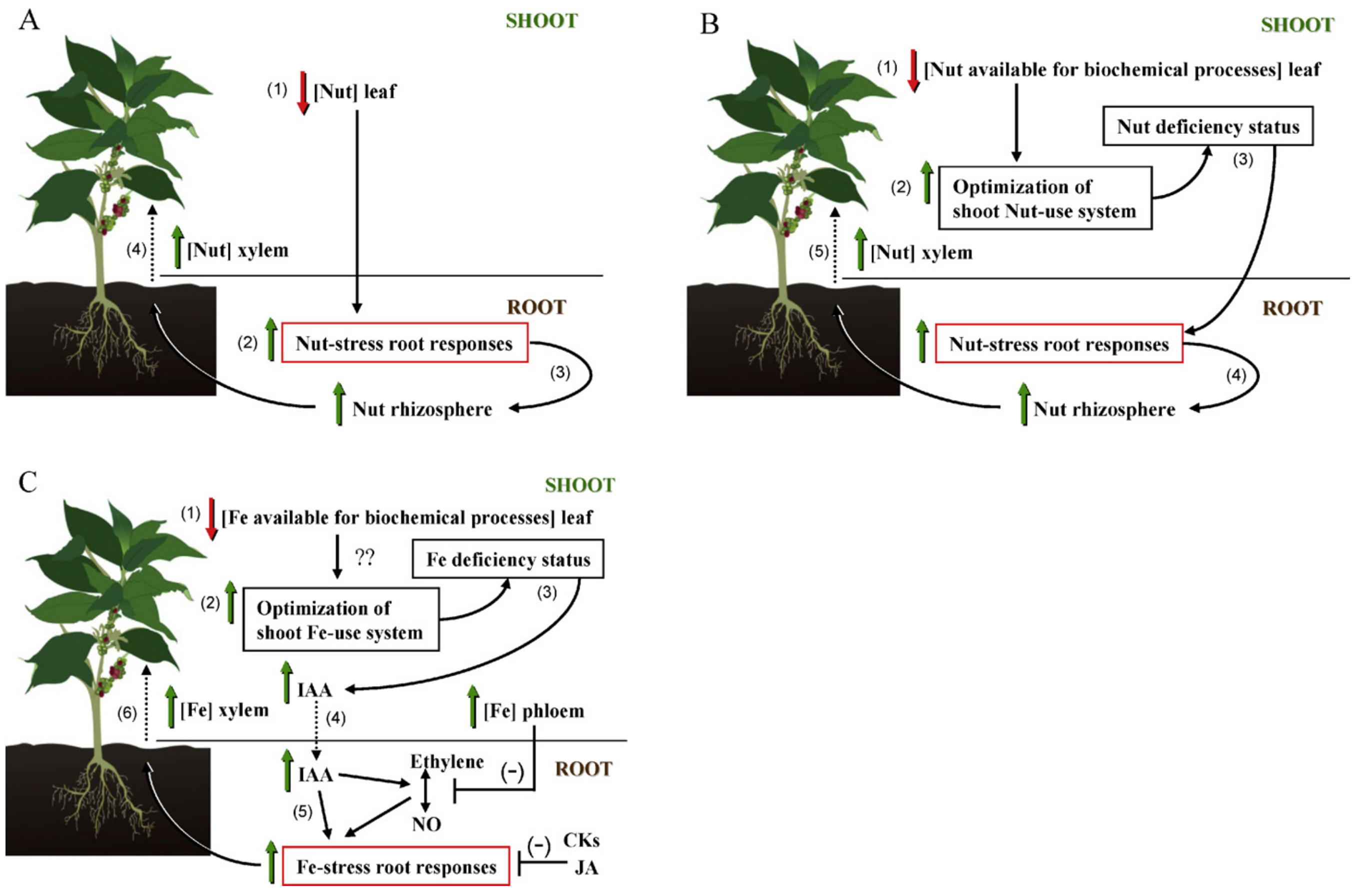

Fig. 1. Different models to explain the shoot-root regulation of nutrient-stress root responses (A–B) and iron-stress root responses (C) in non-graminaceous plants.
(A) Standard model for the regulation of nutrient-stress root responses: (1) decrease in leaf-nutrient concentration; (2) promotion of nutrient-stress root responses; (3) increase in nutrient root uptake from the rhizosphere; (4) increase in nutrient concentration in the xylem and shoot.
(B) Coordinated model for the regulation of nutrient-stress root responses: (1) decrease in the concentration of nutrient available for metabolic processes in leaf; (2) activation of a regulatory network to optimize nutrient-metabolic use in the shoot; (3) if it is not enough, activation of nutrient-stress root responses; (4) increase in nutrient root uptake from the rhizosphere; (5) increase in nutrient concentration in the xylem and shoot.
(C) Main phytoregulators involved in the proposed mechanisms for the shoot to root regulation of Fe-stress root responses included in coordinated model: (1) decrease in the concentration of iron available for metabolic processes in leaf; (2) activation of a regulatory network to optimize iron-metabolic use in the shoot; (3–4) if it is not enough, increase of IAA content in shoot and roots; (5) activation of iron-stress root responses influenced by the phytoregulators studied; (6) increase in iron concentration in the xylem and shoot.
Abbreviations: Nut: nutrient; Fe: iron; IAA: indole-3-acetic acid; NO: nitric oxide; CKs: cytokinins; JA: jasmonic acid.
↑ Increase; ↓ Decrease; ► Translocation; ⟶ Activated process; ⊣ Blocked process.

From the definition of NUE it becomes clear that, in fact, this approach does not explicitly consider the possible importance of the concentration of nutrient taken up by the plant, and its relationships with a potential specific regulatory network oriented to optimize the metabolic use of the nutrient present within the plant. In fact, this approach considers that the concentration of nutrient in the shoot is directly related to the efficiency of mechanisms of nutrient uptake in the root. That means that the concept of nutrient-efficient plant variety is directly ascribed to the efficiency of root nutrient-uptake mechanisms of this variety (Fig. 1A). As a consequence, this definition of NUE becomes rather unspecific. Thus, a same value of NUE can correspond to different values of NupE and NutE.

These conceptual problems might be solved by considering the hypothesis that NupE and NutE are two processes closely related to each other and interacting during plant cycle. A plant that is very efficient in the optimization of the utilization of the nutrient and covers its metabolic needs would need to take up less nutrient amount than a less efficient plant, and produce the same yield. This suggests a hypothesis where by plants might have a specific system that is activated under limitation of nutrient availability in the shoot for metabolic processes that optimizes the metabolic use of this nutrient. This specific system would be expressed before the activation of the system present in the root that can increase both nutrient root uptake and nutrient availability in the rhizosphere. In this way, the two mechanisms would be co-regulated, and the mechanism in root will be activated when the mechanism in shoot, related to the optimization of nutrient metabolic efficiency, does not cover plant needs. The model derived from this hypothesis is named *coordinated model* (Fig. 1B).

It becomes clear that the key-step that differentiates *coordinated* and *standard models* is the presence of an intermediate system responsible for the optimization of nutrient efficiency in the shoot. This system would be functionally placed between the event triggered by the reduction of nutrient concentration in the shoot available for metabolic use, associated with a reduction in nutrient in the xylem and the leaf (leaf-nutrient), and the system of specific responses in the root that increases the fraction of available nutrient in the rhizosphere and nutrient root uptake (Fig. 1A and B).

The aim of this review is to study the hypothesis involved in the concept of the *coordinated model* by discussing the experimental evidence that supports this model in the regulation of iron (Fe) shoot deficiency and Fe root uptake under Fe limiting conditions in non-graminaceous plants.

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